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Solar heat gain in a desert rodent: unexpected increases with wind speed and implications for estimating the heat balance of free-living animals

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Abstract We quantified metabolic power consumption as a function of wind speed in the presence and absence of simulated solar radiation in rock squirrels, *Spermophilus variegatus*, a diurnal rodent inhabiting arid regions of Mexico and the western United States. In the absence of solar radiation, metabolic rate increased 2.2-fold as wind speed increased from 0.25 to 4.0 m·s⁻¹. Whole-body thermal resistance declined 56% as wind speed increased over this range, indicating that body insulation in this species is much more sensitive to wind disruption than in other mammals. In the presence of 950 W·m⁻² simulated solar radiation, metabolic rate increased 2.3-fold as wind speed was elevated from 0.25 to 4.0 m·s⁻¹. Solar heat gain, calculated as the reduction in metabolic heat production associated with the addition of solar radiation, increased with wind speed from 1.26 mW·g⁻¹ at 0.25 m·s⁻¹ to 2.92 mW·g⁻¹ at 4.0 m·s⁻¹. This increase is opposite to theoretical expectations. Both the unexpected increase in solar heat gain at elevated wind speeds and the large-scale reduction of coat insulation suggests that assumptions often used in heat-transfer analyses of animals can produce important errors.

Key words Convection · Metabolism · Solar heat gain · Rodent, *Spermophilus variegatus*

Abbreviations α absorptivity of coat to solar radiation · ν kinematic viscosity of air (mm²·s⁻¹) · ρ reflectivity of coat to solar radiation · a r_B expected at zero wind speed (s·m⁻¹) · A_P projected surface area of animal on plane perpendicular to solar beam (cm²) · A_{SKIN} skin surface area (cm²) ·

b Coefficient describing change in r_B with change in square-root of wind speed (s^{1.5}·m^{1.5}) ·
 d hair diameter (m) ·
 d characteristic dimension of animal (m) ·
 D_H thermal diffusivity of air (m²·s⁻¹) ·
 E evaporative heat loss (W·m⁻²) ·
 I probability per unit coat depth that photon will strike hair ·
 k constant equalling 1200 J·m⁻³·°C⁻¹ ·
 l_C coat depth (m) ·
 l_H hair length (m) ·
 M metabolic rate (W·m⁻²) ·
 n density of hairs of skin (m⁻²) ·
 Q_A solar heat gain to animal (W·m⁻²) ·
 Q_I solar irradiance intercepted by animal (W·m⁻²) ·
 RQ respiratory quotient ·
 r_A thermal resistance of boundary layer (s·m⁻¹) ·
 r_B whole-body thermal resistance (s·m⁻¹) ·
 r_E thermal resistance between animal surface and environment (s·m⁻¹) ·
 r_R radiative resistance (s·m⁻¹) ·
 r_S sum of r_B and r_E at 0.25 m·s⁻¹ (s·m⁻¹) ·
 r_T tissue thermal resistance (s·m⁻¹) ·
 T_{AIR} air temperature (°C) ·
 T_B body temperature (°C) ·
 T_E operative temperature of environment (°C) ·
 T_{ES} standard operative temperature of environment (°C) ·
 u wind speed (m·s⁻¹)

Introduction

Air temperature, solar radiation, and wind are among the most conspicuous factors affecting the energy budgets of animals in nature. Although the effects of air temperature are well-known, those of wind and solar radiation have received much less attention. In addition to their independent effects, both theory and empirical data suggest that effects of wind and irradiance

should importantly interact, e.g., increased convection is expected to reduce radiative heat gain (Porter and Gates 1969; Walsberg et al. 1978; Gebremedhin et al. 1983). For animals with coats of fibrous insulation, such as birds and mammals, such expectations are based largely upon biophysical theory. The limited set of empirical data describing interactions between convection and radiative heat gain are primarily based upon skin and coat preparations that have been removed from animals and mounted on heat flux transducers (Walsberg et al. 1978; Walsberg 1988a, 1990). Although the simplifications produced in such analyses greatly facilitate physical analyses of heat flow through animal coats, differences in heat-transfer properties between such preparations and interact animals are manifold. Even if microclimate selection is not considered, both convective and radiative heat transfer may be affected by changes in posture, orientation, piloerection, and vasomotor processes that alter skin temperature. The magnitude of such effects and the importance of rapid alterations that animals likely can produce in these variables are poorly known.

In this study, we quantify M as a function of wind speed in the presence and absence of simulated solar radiation in rock squirrels, *Spermophilus variegatus*. This diurnal rodent inhabits arid canyons and slopes in Mexico and the western United States (Hall 1983). It is therefore normally exposed to intense solar radiation and substantial variation in wind speeds. Our goal was to quantify the degree to which metabolic rate, animal thermal resistance (insulation), and solar heat gain vary with wind speed. We define the physiologically significant Q_A as the reduction in metabolic heat production produced by exposure to simulated solar radiation.

Methods and materials

Animal collection and maintenance

Animals were trapped during June or July in the Sonoran Desert, in Maricopa County, Arizona. Squirrels were maintained in the laboratory on a 16 h light, 8 h dark photoperiod at $T_{AIR} = 24^\circ\text{C}$, and fed Teklad Rodent Diet (W). Squirrels maintained a mean body mass of 755 g.

Environmental simulation

Metabolic measurements were made both in the presence and absence of simulated solar radiation, with the animal held within a 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 blower circulated air through the test section at speeds ranging from $0.25\text{--}4.0\text{ m}\cdot\text{s}^{-1}$, a range of wind speeds naturally occurring in the Sonoran Desert (Walsberg 1993). Wind speed was measured with a Thermoanemometer HWA-101 thermoanemometer that had been calibrated as described in Walsberg (1988b). Louvers and screens upstream of the test section made air flow more uniform within the chamber. Except within 1 cm of chamber wall, wind speed varied less

than 5% horizontally or vertically within the test section. Turbulence intensity was less than 3% at all wind speeds used, determined using the thermoanemometer with signal output measured with a true root-mean-square voltmeter (Beckman model 850) and computed using the method of Hinze (1959). Temperature within the metabolic chamber was controlled at $15 \pm 1^\circ\text{C}$ by placing it within 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 air stream downwind of the test section. T_{AIR} was measured with a 26 ga, type-T thermocouple connected to a Campbell CR21x datalogger. 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 air mass = 1.0. Irradiance in the test chamber was measured with a LiCor LI200sz pyranometer that had been calibrated against an Oriel model 7080 pyroelectric radiometer. Simulated solar irradiance in the center of the test chamber was maintained at $950\text{ W}\cdot\text{m}^{-2}$, an ecologically realistic level for the Sonoran Desert (Walsberg 1993), and varied less than 5% with time or across the chamber floor. The long-wave radiant environment within the chamber was held nearly constant by painting the walls with flat-black enamel and maintaining their temperature at $15 \pm 2^\circ\text{C}$. Assuming an emissivity of 0.98 and calculating long-wave irradiance by the Stefan-Boltzmann relation, long-wave emission therefore varied less than 6%.

Metabolic rate and evaporative water loss

Metabolic rate was determined from CO_2 production. Air was flowed through the metabolic chamber at $20.1\text{ l}\cdot\text{min}^{-1}$ after being dried and CO_2 removed by a Puregas model CDA1112 H_2O and CO_2 absorber system. Air flow was measured with an Omega FL4002G-HRV rotameter, calibrated to $\pm 1\%$ of full scale with a 5-l soap-bubble flow meter. These high flow rates allowed the entire respiratory apparatus to equilibrate in 12 min, following the calculations of Lasiewski et al. (1966). A $150\text{ ml}\cdot\text{min}^{-1}$ subsample of gas was dried with anhydrous calcium sulphate and passed to a LiCor model 6252 CO_2 analyzer that determined CO_2 concentration to 1 ppm. The analyzer was calibrated daily using both CO_2 -free air and a calibration gas known to contain 0.284% CO_2 .

Animals were exposed to each of five wind speeds (0.25, 0.5, 1.0, 2.0, $4.0\text{ m}\cdot\text{s}^{-1}$) in both the presence and absence of simulated solar radiation. The order in which animals were exposed to particular wind speeds was randomized, and measurements in the presence and absence of solar radiation were made on separate days. All measurements were made during the daylight hours of the animal's daily cycle. During measurements in the absence of simulated solar radiation, animals were provided with fluorescent lighting that allowed normal vision but was thermally insignificant ($< 3\text{ W}\cdot\text{m}^{-2}$). The animal was viewed continuously during experiments using a Magnavox video surveillance system. Each animal was held at each combination of radiation and wind speed for 40–60 min prior to data collection. Data were recorded on a Campbell CR21x datalogger and are 3-min averages following a minimum of 13 min during which the animal rested quietly in the chamber. CO_2 production was calculated using Eq. 3 of Walsberg and Wolf (1995b) and corrected to standard conditions (0°C , 101 kPa). Conversion to units of energy requires knowledge of the respiratory quotient (RQ). Because of high gas flow rates, O_2 depletion was too small for accurate measurement. Therefore, RQ was determined in separate measurements in which animals were placed in a 3.8-l metabolic chamber at 15°C , during their normal active period, but in the dark and without the addition of wind or solar radiation. Dry, CO_2 -free air was flowed into the chamber at $500\text{--}3000\text{ ml}\cdot\text{min}^{-1}$ and CO_2 production and O_2 consumption were measured simultaneously. The O_2 concentration of air entering and leaving the chamber was determined with an Applied Electrochemistry S3a oxygen analyzer. O_2 consumption was calculated using Eq. 3 of Hill (1972) and CO_2 production was

calculated using Eq. 3 of Walsberg and Wolf (1995b). Based upon these measurements, $RQ = 0.92$ (95% confidence interval = 0.099, $n = 7$). The caloric equivalent of CO_2 produced was therefore taken as $22.6 \text{ kJ} \cdot \text{l}^{-1}$ (Kleiber 1961). These measurements of RQ also provided values of metabolic heat production comparable to those obtained in traditional analyses and defined as "resting metabolic rate".

Evaporative water loss was determined by measuring the humidity of effluent chamber air with a Thunder Scientific model PC-2101 hygrometer. This hygrometer was calibrated at low vapor pressures using air first humidified by bubbling through a water column at 23°C , then passed at $50 \text{ ml} \cdot \text{min}^{-1}$ through approximately 2 m of 4 mm internal diameter copper tubing that was immersed in $CaCl_2$ solutions maintained at nine temperatures between -35 and 11°C . Temperature was measured with an Omega HH23 thermocouple thermometer. Vapor densities at these temperatures were obtained from List (1984). Latent heat of evaporation (E) was calculated using a value of $2.42 \text{ kJ} \cdot \text{g H}_2\text{O}^{-1}$. During determinations of animal heat production, hygrometer signal output was measured with the Campbell CR21x data logger, which provided a resolution of $0.01 \text{ mg H}_2\text{O} \cdot \text{l}^{-1}$.

Thermal resistances

Calculating the effect of wind speed upon the total thermal resistance of the animal's body relied upon the relation between M , the body-to-environment temperature gradient, and thermal insulation, as rearranged from Campbell (1977):

$$r_B = \frac{k(T_B - T_E)}{M - E} - r_E \quad (12)$$

Here, r_B is the whole-body thermal resistance ($\text{s} \cdot \text{m}^{-1}$) of the animal's body and subsumes coat insulation and the thermal resistance of peripheral tissues; k is a constant ($1200 \text{ J} \cdot \text{m}^{-3} \cdot ^\circ\text{C}^{-1}$) and T_B is core body temperature, assumed to equal 37°C (Bligh 1973). A rodent exposed to moderately cool conditions is very likely to maintain a T_B near 37°C , and a 1°C variation from this value would alter our calculated values of r_B by only 5–6%. T_E is operative environmental temperature, which was 15°C for experiments conducted in the absence of simulated solar radiation. M is metabolic rate ($\text{W} \cdot \text{m}^{-2}$), expressed on the basis of skin surface area. Surface area (A_{SKIN} ; cm^2) was estimated from body mass (g) using the Meeh equation (1879) with Rubner's (1883) constant of 10:

$$A_{\text{SKIN}} = 10 (\text{body mass})^{0.667} \quad (2)$$

The resulting allometric estimates should suffice for calculations of thermal resistances given the substantial uncertainties in any estimate of the surface area for heat transfer in animals. The effective surface area for heat flow between the skin, the coat, and the environment can readily vary in a single individual, for example, as the skin is stretched or folded (Walsberg and King 1978).

E in Eq. 1 is heat loss by evaporation, also expressed on the basis of skin surface area ($\text{W} \cdot \text{m}^{-2}$); r_E is the effective thermal resistance between the environment and the animal's outer surface, and equals

$$\text{the parallel sum of } r_R \text{ and } r_A \left(= \frac{r_R r_A}{r_R + r_A} \right); r_A \text{ is the thermal resistance of the aerodynamic boundary layer } (\text{s} \cdot \text{m}^{-1}) \text{ and was calculated using the equations of Mitchell (1976) as combined by Webster and Weathers (1988):}$$

$$r_A = 2.7 d^{0.4} \left(\frac{\nu}{u} \right)^{0.6} \quad (3)$$

Here, u is wind speed ($\text{m} \cdot \text{s}^{-1}$), ν is kinematic viscosity of air ($14.6 \text{ mm}^2 \cdot \text{s}^{-1}$), and D_H is thermal diffusivity of air ($20.8 \text{ mm}^2 \cdot \text{s}^{-1}$); d is a characteristic dimension of the animal, taken as 0.08 m ; r_R is

the effective resistance ($\text{s} \cdot \text{m}^{-1}$) to long-wave radiative heat transfer and was calculated following Campbell (1977).

Projected surface area

Comparisons of solar heat gain to radiant flux intercepted by the animal requires determining the cross-sectional area of the beam of simulated solar radiation that is intercepted by the animal. This was estimated by placing animals in the wind tunnel at each wind speed for 20 min, then photographing them from directly overhead through the glass ceiling of the chamber using a Canon EOS ELAN camera with a Tamron 28–200 mm fl lens from a distance of 1.3 m in an optical arrangement that minimized photographic distortions. A grid with wires at 12-mm intervals was placed under the animal and provided a scale for determining surface area. Photographic images were projected and traced (with the tail excluded) on paper of known mass per unit area and the paper weighed to determine projected surface area. Because both the camera and the solar simulator had to occupy the same position, this procedure had to be done after other experiments and the body mass of animals therefore may have differed somewhat from that observed during earlier experiments. Consequently, individual values for particular animals were not used. Rather, we generated a statistically significant (Student's t -test, $P < 0.05$) least-squares regression equation in a form parallel to the Meeh equation that relates projected surface area (A_P ; cm^2) to the two-thirds power of body mass (g):

$$A_P = 2.23 (\text{body mass})^{0.667} \quad (4)$$

Here, range of body masses = 673–972 g, $n = 7$, $r^2 = 0.79$, $S_B = 0.042$, and $S_{Y,X} = 9.41$. There was no statistically significant trend for A_P to vary with wind speed (analysis of variance, $P = 0.32$); therefore, for each of the seven squirrels the average value for all five wind speeds was used as a single datum in the calculation of Eq. 4.

Coat reflectivity

Coat reflectivity to short-wave radiation may change with piloerection (Cena and Monteith 1975). This could not be quantified for live animals within the metabolic chamber, but was assessed for experimental subjects after other measurements were concluded. Animals were sacrificed and reflectivity of the middorsal fur was measured after coats were either manually depressed or erected by brushing with or against the direction the fur tends to lie. Reflectivity was measured while illuminating the animal with the same solar simulator used in metabolic measurements and collecting light using a glass fiber-optic bundle that was paced at a 45° angle to the coat surface. This bundle collected light reflected from an approximately $13 \times 30 \text{ mm}$ elliptical area of the dorsal coat and transmitted it to an Oriel model 7080 pyroelectric radiometer fitted with an 0.1 mm thick fused silica window. This radiometer and window combination has a spectrally neutral response to radiation between 250 and 2500 nm. A plate coated with a 1 mm thickness of Kodak Total Reflectance Paint, which has a reflectance range of 0.96–0.99 over the waveband of 300–1300 nm (average reflectance = 0.98), was used as a standard. Measurements were made once with fur depressed and once with fur erected for each of the seven experimental animals.

Statistical analyses

Wilcoxin pair-sample tests were used for comparison of values for individuals exposed to contrasting conditions (e.g., presence or absence of simulated solar radiation). The Kruskal-Wallis test followed by a nonparametric Tukey-type test was used for multiple contrasts (Zar 1984). For all analyses, statistical significance was accepted at $P < 0.05$. Values are reported as means \pm 95% confidence intervals.

Results

Metabolism and thermal resistance in the absence of sunlight

In the absence of simulated solar radiation, metabolic rate increases 2.2-fold as wind speed is increased from 0.25 to 4.0 $\text{m}\cdot\text{s}^{-1}$ (Fig. 1). Mean M ($\text{mW}\cdot\text{g}^{-1}$) conforms well to linear functions of either the logarithm of wind speed or the square root of wind speed (Table 1). These

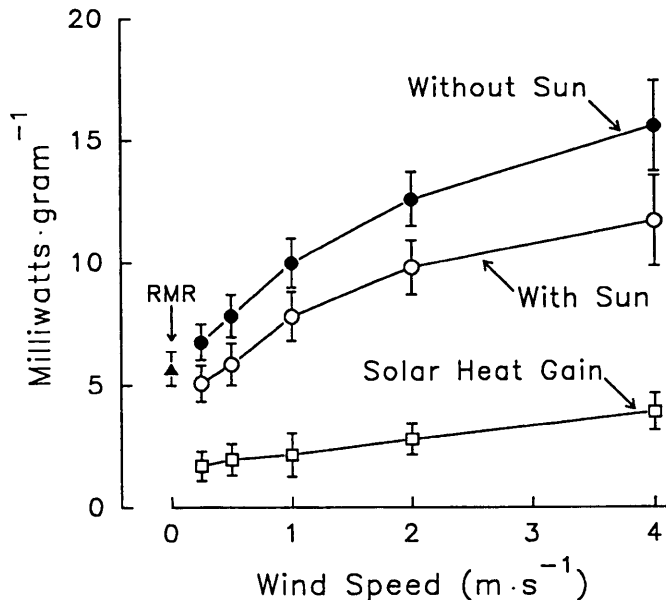


Fig. 1 Metabolic rate and solar heat gain in rock squirrels. Values are either metabolic rate in the absence of solar radiation (but with sufficient illumination to allow vision), metabolic rate in the presence of $950\text{ W}\cdot\text{m}^{-2}$ simulated solar radiation, or solar heat gain calculated as the reduction in metabolic rates associated with the addition of simulated solar radiation. Also shown is the value for resting metabolic rate (*RMR*) of squirrels held in the dark in free convection conditions during daylight hours. Values are means and 95% confidence intervals, with $n = 7$ for each mean. For comparative purposes, note that the equation of Kleiber (1961) predicts a basal metabolic rate of $3.5\text{ mW}\cdot\text{g}^{-1}$ for a 755-g mammal

Table 1 Regression equations describing the relations between wind speed (u ; $\text{m}\cdot\text{s}^{-1}$) and metabolic rate or whole-body thermal resistance (r_B). Equations have the form $Y = a + bX$, where X is either the logarithm or the square root of wind speed. Sample size is seven in each case

Transformation	a	b	r^2	S_B	$S_{Y,X}$
Metabolic rate without sunlight ($\text{mW}\cdot\text{g}^{-1}$)					
$\ln u$	10.3	3.11	0.970	0.317	0.694
$u^{1/2}$	3.85	5.77	0.997	0.169	0.202
Metabolic rate with sunlight ($\text{mW}\cdot\text{g}^{-1}$)					
$\ln u$	8.00	2.38	0.984	0.176	0.385
$u^{1/2}$	3.09	4.36	0.987	0.289	0.345
r_B ($\text{s}\cdot\text{m}^{-1}$)					
$\ln u$	302	-91.0	0.985	6.43	14.1
$u^{1/2}$	484	-161	0.919	27.6	33.0

values describe metabolism by animals provided with illumination that was sufficient for vision but thermally insignificant. Metabolic rate at $0.25\text{ m}\cdot\text{s}^{-1}$ is 19% above that measured for squirrels held in darkness under free-convection conditions ($5.7 \pm 0.72\text{ mW}\cdot\text{g}^{-1}$; Fig. 1).

The minimum heat loss by evaporation ($0.98 \pm 0.18\text{ mW}\cdot\text{g}^{-1}$) occurred at $0.25\text{ m}\cdot\text{s}^{-1}$ and the maximum evaporative loss ($1.47 \pm 0.32\text{ mW}\cdot\text{g}^{-1}$) occurred at $4.0\text{ m}\cdot\text{s}^{-1}$, but there were no statistically significant differences in evaporative loss at different wind speeds ($P = 0.31$). Evaporation accounted for a small percentage of total metabolic heat production; the overall mean was 10% of total heat production for animals not exposed and 11% for animals exposed to simulated solar radiation.

Thermal resistance between the animal surface and the environment (r_E) is calculated to decline from 85 to $23\text{ s}\cdot\text{m}^{-1}$ as wind speed increases from 0.25 to $4.0\text{ m}\cdot\text{s}^{-1}$ (Fig. 2). Whole-body thermal resistance (r_B) declines 56% as wind speed increases from $0.25\text{ m}\cdot\text{s}^{-1}$ (mean $r_B = 428\text{ s}\cdot\text{m}^{-1}$) to $4.0\text{ m}\cdot\text{s}^{-1}$ (mean $r_B = 187\text{ s}\cdot\text{m}^{-1}$; Fig. 2). Similar to the observed increase in M , r_B is well-fitted by a linear function of either the logarithm of wind speed or the square root of wind speed (Table 1).

Solar heat gain

In the presence of $950\text{ W}\cdot\text{m}^{-2}$ simulated solar radiation, metabolic rate increases 2.3-fold as wind speed is

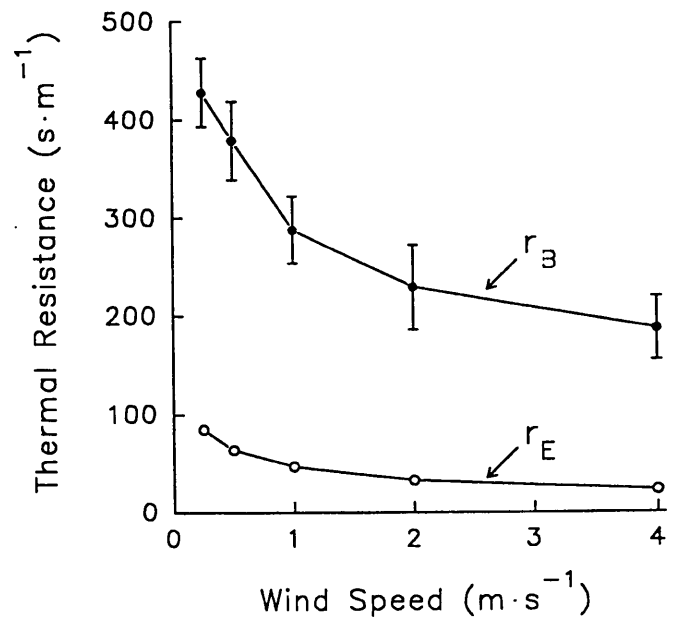


Fig. 2 Whole-body thermal resistance of rock squirrels as a function of wind speed. Values are means and 95% confidence intervals, with $n = 7$ for each mean. Also shown are calculated values for r_E , the effective thermal resistance between the environment and the animal's outer surface

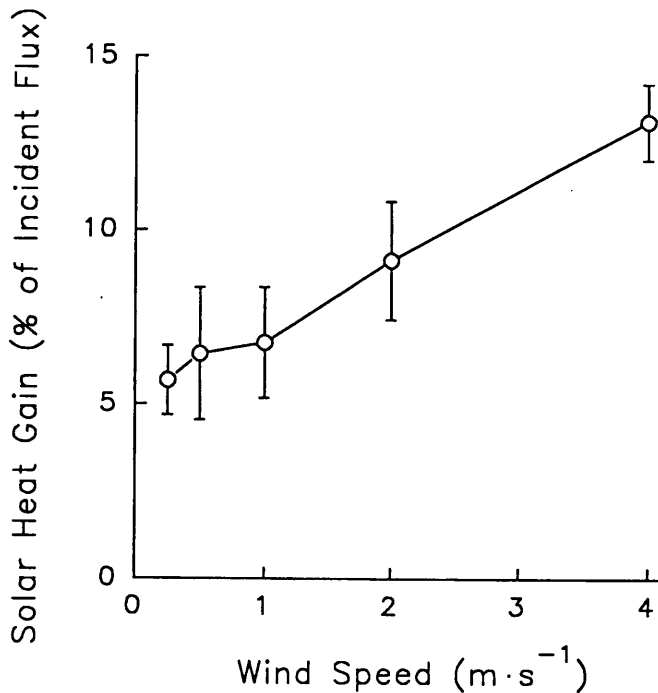


Fig. 3 Solar heat gain to rock squirrels expressed as a percentage of the energy content of the simulated solar radiation intercepted by the animal. Values are means and 95% confidence intervals, with $n = 7$ for each mean

elevated from 0.25 to $4.0 \text{ m} \cdot \text{s}^{-1}$ (Fig. 1). This proportional increase is nearly equal to that observed in the absence of sunlight. Again, M conforms well to a linear function of either the logarithm of wind speed or the square root of wind speed (Table 1).

Solar heat gain, calculated as the reduction in metabolic heat production associated with the addition of simulated solar radiation, significantly increases with wind speed. Heat gain averages $1.26 \text{ mW} \cdot \text{g}^{-1}$ at $0.25 \text{ m} \cdot \text{s}^{-1}$ and $2.92 \text{ mW} \cdot \text{g}^{-1}$ at $4.0 \text{ m} \cdot \text{s}^{-1}$. Calculated as a percentage of radiation intercepted by the animal, mean solar heat gain increases from 5.7% at $0.25 \text{ m} \cdot \text{s}^{-1}$ to 13.1% at $4.0 \text{ m} \cdot \text{s}^{-1}$ (Fig. 3), with the remainder of the energy intercepted apparently being dissipated by processes such as reflection and convection.

Coat reflectivity

Fractional coat reflectivity (ρ) to simulated solar radiation was 0.248 ± 0.062 in depressed coats ($n = 7$). This is 1.8 times the reflectivity of erected coats, which was 0.138 ± 0.022 ($n = 7$; $P < 0.05$).

Discussion

Large-scale disruption of coat insulation by wind

Forced convection can reduce the net thermal resistance between an animal and its environment both by

reducing the thickness of the aerodynamic boundary layer adjacent to the outer coat surface (subsumed in r_E) as well as by penetrating into the coat and reducing coat insulation (subsumed in r_B). Although the latter apparently is important in the heat balance of rock squirrels, it has been little studied in other mammals. Changes in $r_B (\text{s} \cdot \text{m}^{-1})$ often are described as a function of the square root of wind speed (Goldstein 1983):

$$r_B = a + bu^{0.5} \quad (5)$$

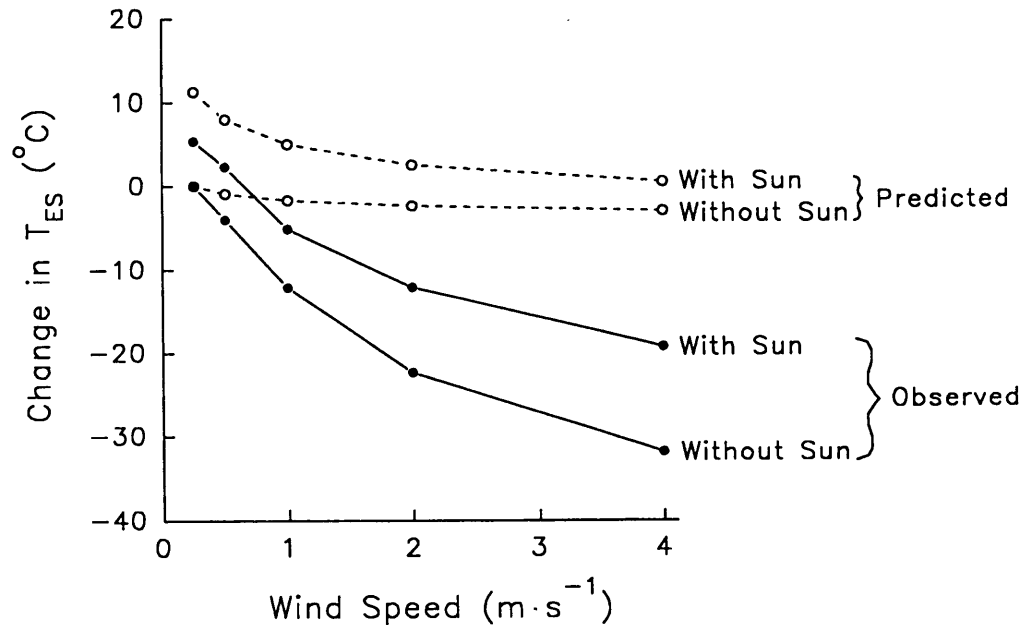
Here, a is an empirically derived constant that describes the r_B value expected at zero wind speed. The coefficient b also is empirically derived and describes the sensitivity of r_B to changes in wind speed. The square-root transformation of wind speed originally was developed for analyses of heat loss from flat plates or cylinders. Although this transformation is not always the best description of wind-induced effects in animals (Goldstein 1983), it does allow convenient comparisons between species and yields a regression equation for *Spermophilus variegatus* that accounts for 92% of the variance in r_B (Table 1). Unfortunately, few data are available describing the relation between r_B and wind speed in other mammals. For domestic sheep and rabbits, respectively, values of the coefficient b in equation 5 are $30 (\text{s} \cdot \text{m})^{1.5}$ and $47 (\text{s} \cdot \text{m})^{1.5}$ (Monteith and Unsworth 1989). Few similar data are available for rodents; $b = 20 (\text{s} \cdot \text{m})^{1.5}$ in *Spermophilus lateralis* and $b = 13 (\text{s} \cdot \text{m})^{1.5}$ in *Spermophilus saturatus* (Walsberg and Wolf 1995a). Data for one other rodent, *Citellus leucurus*, are derived not from live animals, but rather from taxidermic mounts (Chappell and Bartholomew 1981). In this case $b = 34 (\text{s} \cdot \text{m})^{1.5}$. The value of $b = 161 (\text{s} \cdot \text{m})^{1.5}$ for *S. variegatus* is therefore 3–12 times that for other species studied, indicating that body insulation in the rock squirrel is much more sensitive to wind disruption than in these other mammals.

The effects of solar radiation, wind speed, and air temperature on metabolic rates can be compared by calculating T_E and T_{ES} (Bakken 1976; Robinson et al. 1976). In a black-body thermal environment such as produced within our metabolic chamber when sunlight is absent, T_E essentially equals T_{AIR} (Robinson et al. 1976; Campbell 1977). For comparative purposes, it is also useful to stipulate a "standard" convective condition. We define this as $0.25 \text{ m} \cdot \text{s}^{-1}$, the lowest wind speed used in our wind tunnel. Thus, T_{ES} is operationally defined as the air temperature within a black-body environment at $u = 0.25 \text{ m} \cdot \text{s}^{-1}$ and calculated as:

$$T_{ES} = T_B - \frac{(M - E) \cdot r_S}{k} \quad (6)$$

Variables are as defined previously, except that r_S is the sum of r_B and r_E at $u = 0.25 \text{ m} \cdot \text{s}^{-1}$. T_{ES} thus represents the air temperature in the absence of sunlight and at $0.25 \text{ m} \cdot \text{s}^{-1}$ wind that would induce animal heat

Fig. 4 Changes in standard operative temperature (T_{ES}) as a function of irradiance and wind speed. Observed values (solid line) represent mean values calculated from experimental data. Predicted values (dashed line) represent mean values expected if (1) wind does not penetrate into the coat and r_B therefore remains at the value observed at $0.25 \text{ m} \cdot \text{s}^{-1}$, and (2) solar radiation does not penetrate into the coat but rather is absorbed at the outer coat surface. Values are expressed as the difference from standard conditions established when T_{ES} equals T_{AIR} in a black-body thermal environment at $0.25 \text{ m} \cdot \text{s}^{-1}$ wind



production equal to that observed under the radiative and convective conditions actually prevailing.

Such calculations illustrate the impressive sensitivity of rock squirrels to changes in their convective environment. In the absence of sunlight, merely increasing wind speed from 0.25 to $1.0 \text{ m} \cdot \text{s}^{-1}$ produces changes in heat balance equivalent to a decline in air temperature of 12°C (Fig. 4). Elevating wind speed to $4.0 \text{ m} \cdot \text{s}^{-1}$ is equivalent to a 32°C drop in T_{AIR} .

Unexpected increase in solar heat gain at elevated wind speed

In contrast to both theoretical expectations as well as empirical results from skin and coat preparations (Walsberg and Schmidt 1989), solar heat gain in live rock squirrels did *not* decrease with elevations in wind speed. Rather, radiative heat gain more than doubled as wind speed was increased from 0.25 to $4.0 \text{ m} \cdot \text{s}^{-1}$. The effect of solar radiation separated from that of wind is represented by the difference in T_{ES} in the presence and absence of sunlight (Fig. 4). Simulated solar radiation elevates T_{ES} by 5°C at $u = 0.25 \text{ m} \cdot \text{s}^{-1}$. This difference progressively increases with wind speed and is more than doubled at $u = 4 \text{ m} \cdot \text{s}^{-1}$, when solar heat gain increases T_{ES} by 13°C (Fig. 4). At a single air temperature, therefore, the combined changes possible between naturally occurring levels of irradiance and wind speed in the Sonoran Desert can alter T_{ES} by 37°C . This is approximately equal to the entire annual variation in air temperature that occurs in this region.

The bases of this increase in solar heat gain with increased wind speed are as yet unclear, although the following may contribute:

1. Animals could have altered their posture to increase the amount of radiation intercepted at high wind speeds. To account entirely for the effect we observed, A_p would have had to have doubled. This seems unlikely, as no statistically significant change in A , could be distinguished from our data.

2. Animals could have altered the optical properties of their coat. Coat reflectivity is not constant, as commonly assumed, but rather is a function of hair optical characters, fur structure and the degree of hair erection above the skin (Cena and Monteith 1975). In rock squirrels, the average fraction of sunlight absorbed by the coat ($\alpha = 1 - \rho$) increases from 0.75 with the fur depressed to 0.86 with the fur erected. This is produced by exposure of the dark, inner fur layer when the hairs are elevated (Walsberg 1988a). In addition to increased absorptivity, piloerection should increase the depth to which radiation penetrates into the coat. This occurs because the probability per unit coat depth that a photon will be intercepted by a hair is reduced if the hairs are made more vertical. The deeper within a coat that a photon penetrates before being absorbed and generating heat, the smaller the thermal resistance between the point of heat generation and the skin. Consequently, increasing the average depth of radiation penetration into a coat tends to increase solar heat gain to the animal (Kovarik 1964; Hutchinson and Brown 1969; Øritsland 1970; Øritsland and Ronald 1978; Cena and Monteith 1975; Walsberg et al. 1978). The potential importance

of this factor is illustrated by calculating the interception function (I), which equals the probability per unit coat depth that a photon moving downward will strike a hair [Eq. 15 of Cena and Monteith (1975)]:

$$I = nd \tan\left(\cos^{-1} \frac{l_C}{l_H}\right) \quad (7)$$

Here, n is number of hairs per unit skin area, d is hair diameter, l_C is coat depth and l_H is hair length. For a given coat, hair numbers and diameter are constant and the interception function therefore varies only with the ratio of coat depth to hair length. This ratio describes the angle to which the hairs are elevated above the skin. We could not quantify average hair angle for live animals in the wind tunnel, but sample calculations using Eq. 7 are illustrative. For example, coat erection that increases the hair-to-skin angle from 30° to 60° will reduce the interception function by 67%. This would increase by three fold the average distance that a penetrating photon passes before striking a hair, which could substantially increase solar heat gain (Kovarik 1964; Cena and Monteith 1975; Walsberg et al. 1978; Grojean et al. 1980; Gebremedhin et al. 1983).

3. Changes in cutaneous circulation of blood can alter rates of heat transfer across the skin by altering the skin-to-air gradient. Such effects are unquantified in rock squirrels, although in other mammals changes in peripheral circulation are sufficient to alter "tissue" thermal resistance (r_T) by approximately $40\text{--}120 \text{ s} \cdot \text{m}^{-1}$ (Monteith and Unsworth 1989). Particularly at high wind speeds when the contributions of coat thermal resistance and the atmospheric boundary layer are minimized, such changes in tissue thermal resistance could significantly affect heat balance.

4. Changes in T_B can alter rates of heat transfer by modifying either the body-to-air gradient or the amount of heat stored within the body. Although such effects are unquantified in rock squirrels, they seem unlikely to be substantial. Animals were exposed to each combination of wind and radiation for 40–60 min prior to measurement of M and it is not likely that T_B would change significantly after this initial exposure period. Transient effects of heat storage therefore are probably unimportant. Changes in rates of heat transfer could also occur if T_B is altered to new equilibrium values and consequently modifies the thermal gradient between animal and environment. We assume T_B averaged 37°C , yielding a body-to-air temperature gradient of 22°C . For small, nontorpid rodents resting at moderate or cool temperatures, it is likely that T_B did not vary more than about 1°C from this value (Bligh 1973). Such a 1°C change would alter the body-to-air temperature gradient and nonevaporative heat flow by less than 5%. In contrast, dry heat flow was elevated about 140% by increasing wind speed from 0.25 to $4 \text{ m} \cdot \text{s}^{-1}$ and exposure to simulated solar radiation at each wind

speed reduced this heat flow by 20–26%. Changes in T_B are therefore unlikely to be of major importance in alterations of these animals' heat balance.

Implications for analyses of animal heat balance in nature

Both the unexpected increase in solar heat gain at elevated wind speeds and the concurrent disruption of coat insulation suggests that assumptions often used in heat-transfer analyses of animals can produce important errors. Assumptions used by workers vary, but commonly include the expectations that (1) solar radiation is absorbed at the outer coat surface and (2) disruption of coat insulation by wind is sufficiently minor that r_B remains similar to the value measured at very low wind speeds (Porter and Gates 1969; Robinson et al. 1976; Mugaas and King 1981).

The consequences of not accounting for coat disruption and radiation penetration into the coat can be examined by calculating dry heat flow ($M - E$) in the absence of solar radiation by rearranging Eq. 1:

$$M - E = k \frac{T_B - T_E}{r_B + r_E} \quad (8)$$

Here, all values are as previously defined except that r_B is assumed to remain constant at $428 \text{ s} \cdot \text{m}^{-1}$. The resulting value of $M - E$ was then used in Eq. 6 to calculate T_{ES} . Assuming that all absorption of solar radiation occurs at the outer coat surface, the physiologically significant solar heat gain to the animal (Q_A ; $\text{W} \cdot \text{m}^{-2}$) can be calculated following the model of Walsberg (1983):

$$Q_A = \frac{Q_1 r_E}{r_B + r_E} \quad (9)$$

Q_1 ($\text{W} \cdot \text{m}^{-2}$) is the average value for simulated solar radiation intercepted by squirrels in our experiment. The resulting value is then subtracted from nonevaporative heat flow in Eq. 6 and a projected T_{ES} computed.

The consequences of not accounting for wind penetration into the coat are large; T_{ES} can be depressed up to 29°C more than expected if the only effects of wind were to disrupt the atmospheric boundary layer (Fig. 4). Similarly, calculating solar heat gain based upon a surface-action assumption can underestimate changes in T_{ES} by $6\text{--}20^\circ\text{C}$. Such large effects not only alter our view of the magnitude of solar heat gain and convective heat transfer, but also produce qualitatively different conclusions regarding the relative importance of different modes of heat transfer. For example, assumptions such as incorporated in Eq. 9 lead to the common conclusion that solar heat gain becomes relatively unimportant at elevated wind speeds (Porter and Gates 1969; Mugaas and King 1981; Monteith and

Unsworth 1989). This expectation is contrary to our experimental data.

Our data also illustrate the deficiencies of each of three approaches that have been used to analyze heat balance of animals exposed to sunlight. One approach has been to measure the metabolic response of animals to simulated solar radiation in the absence of forced convection (Hamilton and Heppner 1967; Lustick 1969). It is clear, however, that changes in wind speed can substantially alter both solar heat gain and net heat balance for animals in unanticipated directions.

A second approach is the use of detailed biophysical models to analyze solar heat gain (Kovarik 1964; Cena and Moneith 1975; Walsberg et al. 1978; Gebremedhin et al. 1983). Such mathematical models have proved very useful for dissecting the physical determinants of solar heat gain in simplified systems such as coat and skin preparations, including rock squirrels (Walsberg 1988a; Walsberg and Schmidt 1989). However, data for live animals demonstrate that these biophysical models may not even qualitatively predict patterns of solar heat gain in live animals. These unexpected patterns occur even when the animal is prevented from utilizing its full behavioural repertoire of posture and is precluded from microclimate selection that presumably occurs in nature.

A third approach is the use of operative environmental temperature techniques. T_E thermometry does not require complex analytical models or detailed knowledge of the physical properties of the animal. Rather, T_E is commonly estimated using hollow metal casts of an animal's body. These preparations are either painted to match the absorptivity of live birds or mammals (Byman 1985) or, preferably, are covered by its skin and coat (Bakken et al. 1981; Chappell and Bartholomew 1981; Walsberg 1982; Kenagy et al. 1989; Vispo and Bakken 1993). Taxidermic mounts have been used to quantify the thermal balance of a variety of birds and mammals and resulting data have been incorporated into broader scale analyses of animal energetics. The accuracy of such analyses, however, depends upon the degree to which taxidermic mounts duplicate effects observed in live animals, including solar heat gain and wind penetration into the coat. Given that short-term alterations in processes such as fur erection are not produced by T_E mounts, it is striking that the validity of these techniques for estimating the metabolic responses of birds or mammals exposed to solar radiation remains untested. There are *no* data comparing the solar heat gain of live birds or mammals to heat loads acquired by taxidermic mounts. The general importance of processes such as piloerection is unknown, but it seems likely that they can have major effects on both radiative heat gain and passive heat loss. Understanding the role of physiological mechanisms in determining the success of animals in nature clearly is an important goal and the methodological simplifications supplied by operative

temperature techniques are therefore very attractive. Our data, however, strongly suggest that the validity of such analyses will remain unknown and our understanding of the heat balance of animals in nature will be importantly retarded until there exists a significantly expanded data base that describes the metabolic responses of live animals to complex radiative and convective environments and that couples these data with careful physical and physiological analyses.

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