

Seasonal Adjustment of Solar Heat Gain Independent of Coat Coloration in a Desert Mammal

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ABSTRACT

Despite the apparent importance of solar radiation as a source of heat for free-living animals, there exists no substantial body of empirical data describing physiological responses to solar radiation under the range of convective conditions likely to occur in nature. We therefore quantified effects of simulated solar radiation and wind on metabolic heat production in the rock squirrel, *Spermophilus variegatus*. This diurnal mammal inhabits the Sonoran Desert and seasonally replaces its pelage in a fashion in which it retains constant external appearance but incorporates optical and structural changes that are thought to significantly alter heat-transfer properties of the coat. At a given wind speed, the presence of 950 W m^{-2} of simulated solar radiation reduces metabolic heat production by 15% (at a wind speed of 4 m s^{-1}) to 37% (at a wind speed of 0.25 m s^{-1}). Independent of effects of irradiance, metabolic heat production significantly increases with wind speed such that as wind speed is increased from 0.25 m s^{-1} to 4.0 m s^{-1} , metabolic heat production is elevated by 66% (sunlight absent) or 88% (sunlight present). Previous analyses demonstrated that when exposed to identical radiative and convective environments rock squirrels with summer pelages accrue solar heat loads 33%–71% lower than those experienced by animals with winter coats. This reduction of solar heat gain during the extremely hot Sonoran Desert summer apparently constitutes a previously unappreciated mode of thermal adaptation by seasonal adjustment of radiative heat gain without changes in the animal's appearance.

Introduction

Terrestrial habitats arguably represent the most complex and variable thermal environments on earth. Energy and water balance between an animal and its environment can be importantly affected by variation in air temperature and movement, substrate temperature and conductivity, radiation, and humidity. For small animals, changes in position of only a few centimeters in the complex thermal mosaic presented by many terrestrial habitats can significantly alter all of these factors simultaneously.

Of these environmental properties, only the effects of air temperature on metabolic heat production in animals have been studied extensively. Although solar irradiance commonly exceeds 20 times the basal metabolic heat production of birds and mammals (when calculated on the basis of skin surface area), there exists no substantial body of data describing physiological responses to solar radiation under the range of convective conditions likely to occur in nature. Setting radiative heat gain in the context of such conditions is critical, as forced convection (wind) is a conspicuous feature of natural environments and is predicted to be a potent modifier of radiative heat gain in animals.

Most extant analyses of the simultaneous effects of varying wind and radiation are either theoretical explorations (e.g., Porter and Gates 1969) or empirical analyses of the wind-speed dependence of solar heat gain at the level of the skin beneath isolated coat preparations (e.g., Walsberg et al. 1978). In contrast, empirical analyses of metabolic heat production by live animals as a function of varying wind speed and in the presence of short-wave radiation have been conducted for only one bird species (Wolf and Walsberg 1996) and three mammal species (Walsberg and Wolf 1995a, 1995b). One important conclusion from these studies is that, in some cases, effects of wind and radiation are not predicted even qualitatively by theoretical biophysical analyses (Walsberg and Wolf 1995b). Given the potential importance of wind and radiation for animal heat balance in nature (e.g., Chappell and Bartholomew 1981; Bennett et al. 1984), this sparse database importantly limits our understanding of the energetics and behavioral ecology of free-living animals.

In the current analysis, we quantify effects of wind speed on metabolic heat production in the rock squirrel (*Spermophilus variegatus*) in the presence or absence of simulated solar radiation. This diurnal rodent inhabits the Sonoran Desert (Hall 1983), where it is active throughout the year and experiences

marked seasonal changes in weather. Winters in the Sonoran Desert are mild; air temperatures during the coldest month typically range from 0°–4°C at dawn to 18°–22°C during the afternoon. Summers are prolonged and extremely hot. From June through September, air temperatures normally range from 24°–32°C near dawn to 39°–46°C during the afternoon.

Analyses of heat transfer through coat and skin preparations removed from the middorsal region of rock squirrels suggest that seasonal replacement of the pelage is an important component of the animal's adaptive responses to these annual temperature changes (Walsberg and Schmidt 1989). Rock squirrels molt in the spring and fall. Although the summer and winter coats are identical in appearance, their heat-transfer properties are altered, with the result that solar heat gain at the level of the skin is as much as 20% lower beneath summer coats than beneath winter coats (Walsberg and Schmidt 1989).

Such conclusions, however, are based on analyses of isolated skin and coat preparations and are necessarily tentative in the absence of measurements of metabolic responses by live animals. Such responses to wind and insolation previously have been quantified only for rock squirrels with summer coats (Walsberg and Wolf 1995b). In the present analysis, we report parallel measurements for animals with winter coats and quantify the degree to which the seasonal modification of solar heat gain to the level of the skin observed in isolated coat preparations translates to changes in the metabolic intensity of live animals. These data also allow comparison of animal metabolic heat production with predictions of biophysical theory.

Material and Methods

Animal Collection and Maintenance

Animals were trapped between January and March in the Sonoran Desert, in Maricopa County, Arizona. Squirrels were maintained in the laboratory on a 10L : 14D photocycle at an air temperature of 24°C, fed Teklad Rodent Diet W, and supplied ad lib. with water. Mean body mass was 656 g.

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 blower circulated air through the test section at speeds of 0.25–4.0 m s⁻¹, a range of wind speeds naturally occurring in the Sonoran Desert (Walsberg 1993). Wind speed was measured with a Thermonetics HWA-101 thermoanemometer that had been calibrated as described in Walsberg (1988a). Louvers and screens upstream of the test section made airflow more uniform in the chamber. Except within 1 cm of the chamber

walls, wind speed varied less than 5% horizontally or vertically in the test section. Turbulence intensity was less than 3% at all wind speeds used, a fact determined with the thermoanemometer with signal output measured with a true root-mean-square voltmeter (Beckman model 850) and computed with the method of Hinze (1959). Temperature in the metabolic chamber was controlled at 15° ± 1°C 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 with 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 with a LiCor LI22sz pyranometer that had been calibrated against an Oriel pyroelectric radiometer (model 7080). Simulated solar irradiance in the center of the test chamber was maintained at 950 W m⁻². When measured perpendicular to the solar beam, this is an ecologically realistic level of irradiance for the Sonoran Desert during both winter and summer (Walsberg 1993), and it varied 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 by the Stefan-Boltzmann relation, we estimated that long-wave emission varied less than 6%.

Metabolic Rate and Evaporative Water Loss

Metabolic rate was determined from CO₂ production. Air was forced through the metabolic chamber at 20.1 L min⁻¹ after being dried, and CO₂ was removed by a Puregas H₂O and CO₂ absorber system (model CDA1112). Airflow was measured with an Omega FL4002G-HRV rotameter calibrated to ±1% of full scale with a 5-L soap-bubble flow meter. These high flow rates allow the entire respiratory apparatus to equilibrate in 12 min, according to the calculations of Lasiewski et al. (1966). A 150 mL min⁻¹ subsample of gas was dried with anhydrous calcium sulfate and passed to a LiCor CO₂ analyzer (model 6252) that determined CO₂ concentration to 1 ppm. The analyzer was calibrated daily with both CO₂-free air and a calibration gas known to contain either 0.2840% or 0.1550% CO₂.

Animals were exposed to each of five wind speeds (0.25, 0.5, 1.0, 2.0, and 4.0 m s⁻¹) in both the presence and absence of simulated solar radiation. The order in which animals were exposed to particular wind speed 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 ($< 3 \text{ W m}^{-2}$). The animal was viewed continuously during experiments with a Magnavox video surveillance system. Each animal was held at each combination of radiation and wind speed for 30–60 min prior to data collection. Data were recorded on a Campbell CR21x data logger 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 with equation (3) of Walsberg and Wolf (1995c) and corrected to standard conditions (0°C , 101 kPa). Accurate conversion to units of energy requires knowledge of the respiratory quotient (RQ). (See Walsberg and Wolf [1995c] for discussion of the sensitivity of estimates of metabolic heat production to RQ assumptions.) Because of high gas flow rates, O_2 depletion was too small for accurate measurement. Therefore, the RQ was determined from separate measurements of resting metabolic rate at 10°C in the absence of forced convection or insolation. Animals were placed in the dark in a 3.8-L metabolic chamber during their normal active period. Dry, CO_2 -free air flowed into the chamber at $500\text{--}3,000 \text{ mL min}^{-1}$, and CO_2 production and O_2 consumption were determined simultaneously. The O_2 concentration of air entering and leaving the chamber was determined with an Applied Electrochemistry S3a O_2 analyzer. O_2 consumption was calculated with equation (3) of Hill (1972), and CO_2 production was calculated with equation (3) of Walsberg and Wolf (1995c). In addition, CO_2 production was measured in the same apparatus and under the same conditions at air temperatures of 5° , 15° , 20° , 25° , and 30°C . These measurements provided values 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 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 in either a water bath (for temperatures $> 0^\circ\text{C}$) or a slush composed of frozen CO_2 and calcium chloride brines (for temperatures $< 0^\circ\text{C}$). Temperature of the saturated air was measured with an Omega HH23 thermocouple thermometer, and vapor densities at these temperatures were obtained from List (1951). Latent heat of evaporation was calculated with a value of $2.42 \text{ kJ g}^{-1} \text{ H}_2\text{O}$. During determinations of animal heat production, hygrometer signal output was measured with the Campbell CR21x data logger, which provided a resolution of $0.1 \text{ mg H}_2\text{O L}^{-1}$.

Thermal Resistances

Calculating the effect of wind speed on the total thermal resistance of the animal's body relied on the relation between meta-

bolic rate, the body-to-environment temperature gradient, and thermal insulation, as rearranged from Campbell (1977):

$$r_B = [k(T_B - T_E)/(M - E)] - r_E.$$

Here, r_B is the whole-body thermal resistance (s m^{-1}) of the animal's body and subsumes coat insulation and the thermal resistance of peripheral tissues, k is a constant ($1,200 \text{ J m}^{-3} \text{ }^\circ\text{C}^{-1}$), 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 core body temperature 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 heat production (W m^{-2}) expressed on the basis of skin surface area, E is evaporative heat dissipation (W m^{-2}) expressed on the basis of skin surface area, and r_E is the effective thermal resistance between the environment and the animal's outer surface. Surface area (cm^2) was determined after euthanizing the animals with CO_2 , as recommended by the American Veterinary Medical Association and approved by the Animal Care and Use Committee of Arizona State University. The animal's skin was then removed, placed on a paper sheet of known mass per unit area, and its outline traced and cut out. The paper was then weighed to determine skin surface area. To check the accuracy of such measurements, surface area also was independently estimated by analogy to simple geometric shapes. The skin from the head was approximated as a prolate spheroid, that of the neck and torso as the curved sides of cylinders, and that of the appendages as cones. The following dimensions were measured to the nearest 1 mm: head length and breadth, neck length and breadth, torso length and breadth, and appendage length and base diameter. Neck and torso breadth were measured at the middle of their respective lengths, and the diameter of an appendage was estimated as the average of its maximum and minimum width at the base of the appendage. Areas of these surfaces were summed to estimate total skin surface area.

The variable r_E equals the parallel sum of r_R , the effective resistance to long-wave radiative transfer (s m^{-1}) and r_A (i.e., $r_A r_R / [r_A + r_R]$). r_A is the thermal resistance of the aerodynamic boundary layer (s m^{-1}) and was calculated with the equation of Webster and Weathers (1988):

$$r_A = 2.7d^{0.4}(v/u)^{0.6}/D_H.$$

Here, u is wind speed (m s^{-1}), v is the kinematic viscosity of air ($14.6 \text{ mm}^2 \text{ s}^{-1}$), D_H is thermal diffusivity of air ($20.8 \text{ mm}^2 \text{ s}^{-1}$), and d is a characteristic dimension of the animal, taken as 0.08 m. The effective resistance (s m^{-1}) to long-wave radiative heat transfer was calculated following Campbell (1977).

Calculation of Solar Heat Gain and Projected Surface Area

As in previous analyses (Walsberg and Wolf 1995a, 1995b), we define solar heat gain to an animal as the reduction in metabolic heat production produced by exposure to simulated solar radiation. Solar heat gain is expressed in two fashions, 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 between 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 , $W\ m^{-2}$) is computed as

$$Q_A = [(M^- - M^+)/A_p]/Q_i,$$

where M^- is metabolic heat production in the absence of solar radiation (W), M^+ is heat production in the presence of simulated insolation (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 ($W\ m^{-2}$). After the animals were euthanized, A_p was estimated by holding them in a posture simulating that of squirrels occupying the metabolic chamber. Their projected shadow area (excluding the tail) normal to a horizontal surface was then traced on paper of known mass per unit of area. The traced region was then trimmed and weighed to determine area.

Statistical Analyses

Wilcoxon paired-sample tests were used for comparisons 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. Sample size is seven in each case.

Results

Skin Surface Area and Projected Surface Area

The measured skin surface area was $605 \pm 51\ cm^2$. This value differs on the average only 0.3% from the independent geometric estimates of skin surface area, which equaled $607 \pm 37\ cm^2$. Measured values rather than geometric estimates were used in subsequent calculations of body resistance. The projected surface area of squirrels on a plane perpendicular to the solar beam was $150 \pm 26\ cm^2$, which equals 25% of average skin surface area.

RQ and Thermal Equivalent of CO_2 Production

The RQ averaged 0.88 ± 0.034 . Following the calculations of Kleiber (1961), this indicates a thermal equivalent of CO_2 production of $23.5\ kJ\ L^{-1}$, and this value is used in subsequent calculations.

Resting Metabolism in the Absence of Wind and Insolation

Between $20^\circ C$ and $30^\circ C$, metabolic rate remained essentially constant and averaged $0.846\ mL\ CO_2\ g^{-1}\ h^{-1}$, or $5.52\ mW\ g^{-1}$. Below the approximate lower critical temperature of $20^\circ C$, metabolic rate increased linearly with decreasing air temperature (Fig. 1). Using data collected at $20^\circ C$ and below, least squares linear regression yields the equation $M = 11.80 - 0.313T_{AIR}$, where M is metabolic heat production ($mW\ g^{-1}$) and T_{AIR} is the air temperature ($^\circ C$) ($r^2 = 0.997$, $S_{Y,X} = 0.136$, $S_B = 0.0122$, where X is the natural logarithm of temperature and Y is metabolic rate).

Metabolic Heat Production and Body Resistance as Functions of Wind Speed and Insolation

Both in the presence and absence of simulated solar radiation, metabolic heat production significantly increased with wind

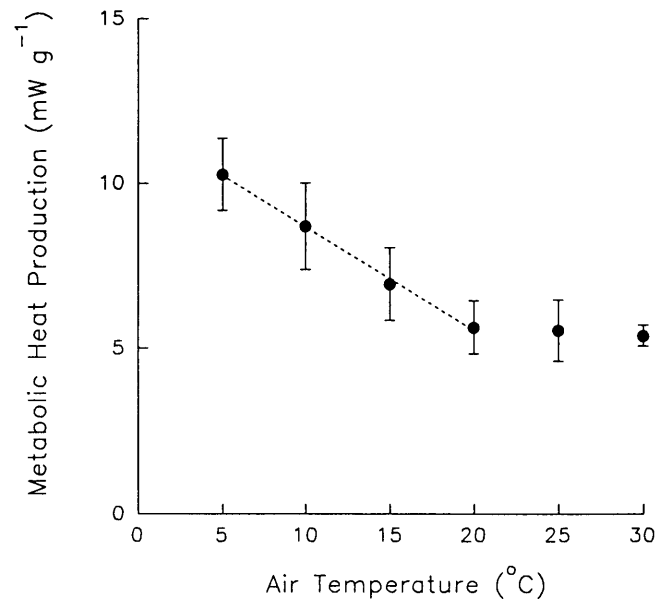


Figure 1. Metabolic rate of rock squirrels in the absence of forced convection and insolation, as a function of ambient temperature. Values are means and 95% confidence intervals; $n = 7$ for each mean. Dashed line was fitted by least squares regression to data collected at $5^\circ - 20^\circ C$.

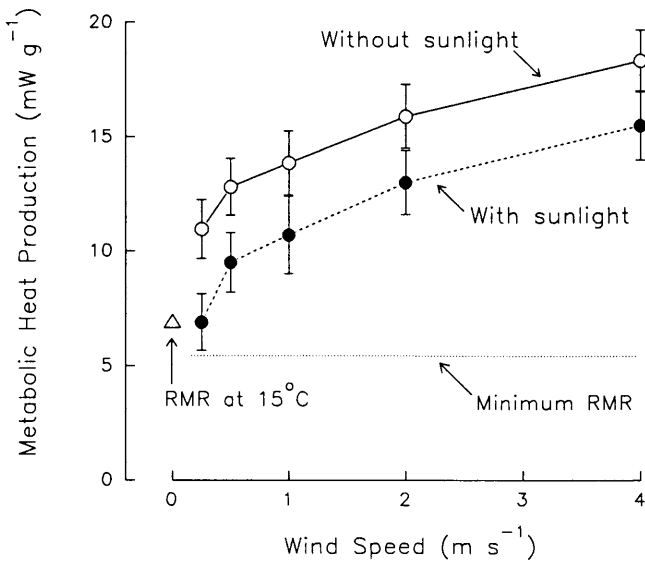


Figure 2. Metabolic rate of rock squirrels as a function of wind speed and irradiance. Metabolic rate in the absence of solar radiation (but with sufficient illumination to allow vision) or metabolic rate in the presence of 950 W m^{-2} simulated solar radiation are presented. Also shown is the value for resting metabolic rate (RMR) of fed squirrels held at an air temperature of 15°C in the dark in free-convection conditions during daylight hours as well as the average minimum RMR measured under these conditions at $20^\circ\text{--}30^\circ\text{C}$. Values are means and 95% confidence intervals.

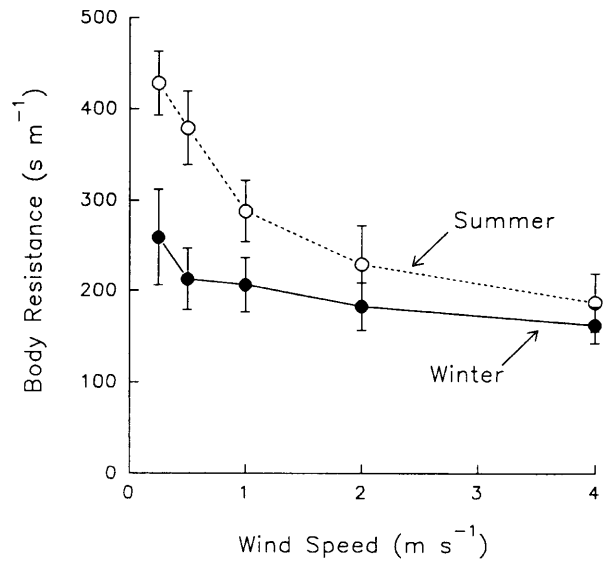


Figure 3. Whole-body thermal resistance of rock squirrels as a function of wind speed. Values are means and 95% confidence intervals. Also shown are values for animals with summer pelages, with data recalculated from Walsberg and Wolf (1995b).

speed (Fig. 2). In the absence of sunlight, metabolic rate increased 66% as wind speed was elevated from 0.25 m s^{-1} to 4.0 m s^{-1} . In the presence of simulated solar radiation, metabolic rate increased 88% over this wind speed range. In both cases, metabolic heat production is a close function (i.e., $r^2 = 0.98\text{--}0.99$) of the logarithm of wind speed, with slopes that are statistically indistinguishable ($P < 0.05$; Table 1).

The presence of simulated solar radiation significantly reduced metabolic heat production at each wind speed (Fig. 2). This metabolic depression apparently is constant with wind speed, given that the lines relating metabolic rate in the presence and absence of simulated solar radiation are parallel (Table 1).

Body resistance declined 37% as wind speed was increased from 0.25 m s^{-1} (body resistance = 259 s m^{-1}) to 4.0 m s^{-1}

(body resistance = 162 s m^{-1}) (Fig. 3). Similar to changes in metabolic heat production, this decline in body resistance is a close function ($r^2 = 0.944$) of the logarithm of wind speed (Table 1).

Discussion

Seasonal Changes in Solar Heat Gain and Body Resistance

Expressed as a percentage of short-wave radiation intercepted by the animal, solar heat gain in rock squirrels with winter pelages averaged 13%–19% of intercepted flux and did not vary significantly with wind speed ($P > 0.05$; Fig. 4). In contrast to these data and to theoretical expectations, radiative heat gain during summer months determined under identical environmental conditions increases with wind speed, from equivalent to 6% of intercepted radiation at 0.25 m s^{-1} to 13% at 4 m s^{-1} (Walsberg and Wolf 1995b; Fig. 4). Prevailing winds in the Sonoran Desert typically are below 4 m s^{-1} (Walsberg 1982,

Table 1: Least squares regression equations describing the relations between logarithmically transformed wind speed (m s^{-1}) and metabolic heat production or body thermal resistance

	<i>a</i>	<i>b</i>	<i>r</i> ²	<i>S</i> _B	<i>S</i> _{Y,X}
Metabolic rate without sunlight (mW g^{-1})	14.36	2.55	.981	.205	.448
Metabolic rate with sunlight (mW g^{-1})	11.12	2.74	.989	.109	.239
Body resistance (s m^{-1})	204.6	-32.3	.944	4.529	7.926

Note. Equations have the form $Y = a + bX$, where *X* is the natural logarithm of wind speed and *Y* is metabolic rate or body resistance.

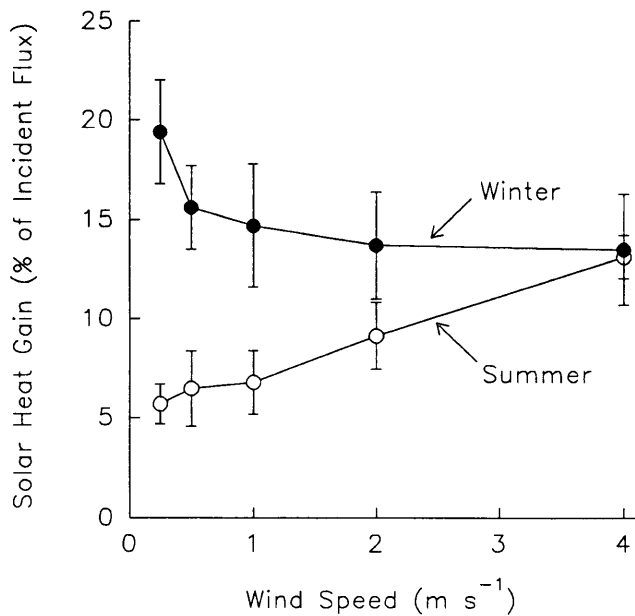


Figure 4. Solar heat gain of rock squirrels expressed as a percentage of the incident flux intercepted by the animal. Values are means and 95% confidence intervals. Also shown are values for animals with summer pelages, with data taken from Walsberg and Wolf (1995b).

1993). When exposed to identical radiative environments at wind speeds of 0.25–2.0 m s⁻¹, rock squirrels with summer pelages experience solar heat loads 33%–71% lower than those experienced by animals with winter coats.

In addition to reduced solar heat gain, the heat load experienced by rock squirrels during summer months should also be reduced by the elevated whole-body thermal resistance occurring during this period (Fig. 3). This conclusion is based on comparisons of body resistance values from the present study with values recalculated from Walsberg and Wolf (1995b). In the present analysis, body resistance was derived by measuring skin surface areas, whereas Walsberg and Wolf (1995b) estimated body surface area for animals collected during summer months with Meeh's (1879) equation $A_{SKIN} = 10 m^{0.667}$, where A_{SKIN} is skin surface area (cm²) and m is body mass (g). Comparison of measured values for animals used in the current analysis, however, to those predicted by this equation suggests that this formula overestimates skin area for this species by an average of 31%. Therefore, we recalculated body resistance from the data of Walsberg and Wolf (1995b) using a revised estimate of skin area. We derived a least squares regression equation relating skin surface area to body mass, using the data for the seven animals used for metabolic measurements plus four additional rock squirrels. Over a body mass range of 619–981 g, skin surface area (cm²) was a significant function of body mass (g): $A_{SKIN} = 99.7 + 0.717m$ ($r^2 = 0.902$, $S_{Y,X} = 25.1$, $S_B = 0.079$; $n = 11$).

These revised estimates indicate that body resistance of rock squirrels during winter or early spring averages 15%–44% below that of animals during summer months (Fig. 3). This parallels seasonal changes observed in the thermal insulation of coats removed from the middorsal region of rock squirrels (Walsberg and Schmidt 1989). Increased insulation during hot summer months may initially appear counteradaptive, but two factors indicate that this is not so. First, air temperatures during the summer in the Sonoran Desert are high throughout the day. During the midday period, temperatures at the approximate squirrel height above the soil surface (5 cm) are often 46°–61°C (G. E. Walsberg, unpublished data). Under such conditions, increased insulation reduces heat gain along the air-to-body gradient and clearly can be beneficial. In addition, increased coat insulation during summer months is an important basis for the reduced solar heat load transmitted to the skin during this period (Walsberg and Schmidt 1989).

It is highly likely that these reduced heat loads on animals with summer coats are adaptive. Reducing environmental heat load during periods in which air temperature is near or above body temperature should lessen the amount of heat that the animal must dissipate by evaporation. This could be critical for species inhabiting subtropical deserts, particularly diurnal mammals that reside in areas devoid of drinking water. Indeed, it is unclear how species such as the rock squirrel meet even minimal water demands during the long summer droughts in which environmental temperatures are highest and succulent vegetation is sparse or absent in many areas they occupy. In addition to alleviating direct physiological stresses, reducing environmental heat loads during the summer may also have important behavioral consequences. To the degree that avoidance of heat stress and conservation of body water are important, lowering the heat load on an animal may importantly ease constraints on the time and intensity of its daily activity as well as the range of microhabitats it can profitably exploit.

Metabolic Effects of Insolation on Live Animals Compared with the Solar Heat Load on the Skin

Although qualitative changes with wind speed in solar heat gain to live animals were similar to those observed for isolated coat samples, values were reduced 69%–76% in live animals compared with the coat preparations (Walsberg and Schmidt 1989). Possible bases for this depression of solar heat gain in live animals include the following. First, the complex and curved nature of whole animals compared with flat coat samples changes the angle of incidence of both sunlight and wind striking the fur and may change the degree to which both sunlight and wind penetrate the coat. Second, short-wave radiation is distributed over the entire upper surface of live animals, but analyses were made only for the middorsal region of coat preparations. Third, in studies of isolated coat samples, heat flux was measured at the skin, and therefore subcutaneous

processes such as alterations in blood flow through peripheral tissues were not subsumed. The addition of any thermal resistance, including tissue thermal resistance between the region of heat generation (e.g., the coat and skin) and the core of the animal, will reduce heat gain. Finally, turbulence in the air-stream was lower in studies of coat preparations than in the current analysis using live animals. Turbulence inherent in the airflow was very low (<0.3%) in measurements of isolated coats, and additional turbulence induced by the sample was too low to be measured (Walsberg and Schmidt 1989). In the current analysis, inherent turbulence was higher (2%–3%), and additional turbulence probably was produced by the animal's presence in the wind tunnel. Turbulence reduces boundary layer resistance, which reduces solar heat gain (Walsberg et al. 1978).

We cannot quantify the importance of the first two sets of these factors, but the approximate role of the latter two can be evaluated with simulations such as those of Walsberg and Wolf (1995a). These analyses noted that the relationship between solar heat gain to the live animal and that to the skin may be expressed as

$$Q_A = Q_S[(r_C + r_E)/(r_C + r_E + r_T)],$$

where Q_S is solar heat gain to the skin ($W m^{-2}$), r_C is coat thermal resistance ($s m^{-1}$), r_E is the thermal resistance between the animal surface and the environment ($s m^{-1}$), and r_T is tissue thermal resistance ($s m^{-1}$).

As in previous comparisons of heat gain of isolated coats and live animals, solar heat gain to the skin was taken as the mean of fractional solar heat gain at each wind speed reported for skin preparations (Walsberg and Schmidt 1989), and the sum of coat thermal resistance and the thermal resistance between the animal's surface and the environment was entered as either 100% or 67% of the values reported by Walsberg and Schmidt (1989). The latter values represent a one-third reduction in these resistances that might be produced by increased turbulence and wind penetration into the coat. Thermal resistance of peripheral tissues was taken as either 50 or 100 $s m^{-1}$, a conservative range of likely values (Monteith and Unsworth 1989).

Simulation results predict a substantial reduction in solar heat gain to live animals compared with that measured at the level of the skin beneath coat samples (Fig. 5). The minimum reduction is predicted from the combination of tissue thermal resistance equal to 50 $s m^{-1}$ and the sum of coat thermal resistance and the thermal resistance between the animal surface and the environment equal to 100% of the values measured in analyses of coat preparations. The maximum reduction is predicted from the combination of tissue thermal resistance equal to 100 $s m^{-1}$ and values for the sum of coat thermal resistance and the thermal resistance between the animal's surface and the environment of 67% of those reported by Wals-

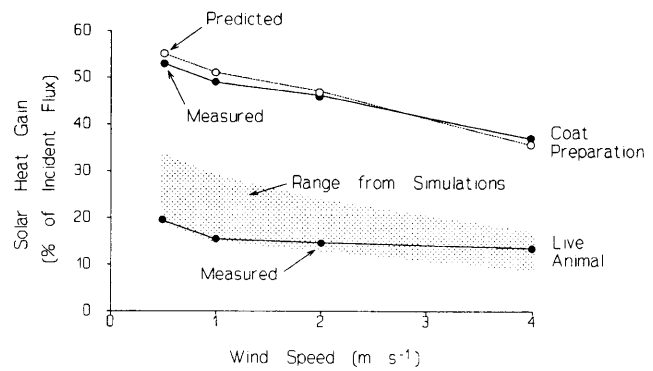


Figure 5. Comparison of solar heat gain values derived from four sources: empirical measurement of solar heat gain to the skin beneath isolated coat preparations (Walsberg and Schmidt 1989), theoretical predictions for heat gain to the skin (Walsberg and Schmidt 1989), empirical measurement of solar heat gain by live animals, and simulation results derived from data for isolated coats projected to expected values for intact animals by accounting for likely effects of changes in boundary layer resistance and tissue thermal resistance. For simplicity of presentation, only mean values are presented. The stippled area represents the range of predictions from simulations.

berg and Schmidt (1989). Other combinations of these resistances produce intermediate levels of reduction.

These predicted values of solar heat gain encompass those actually measured and reveal that reasonable variations that might occur in such thermal resistances are fully capable of producing the differences observed between live animals and coat preparations. The large range of values produced by these simulations also strongly suggests that possible changes in factors such as tissue thermal resistance might greatly alter solar heat gain (Fig. 5).

Concluding Comments

This analysis has demonstrated the importance of the interactive effects of wind and radiation as major determinants of animal heat budgets and illustrated a previously unappreciated mode of thermal adaptation by seasonal adjustment of solar heat gain independent of animal coloration. Perhaps as notable, it also highlights critical weaknesses in our comprehension of the thermal physiology and ecology of animals in nature. Such an understanding requires adequate knowledge and effective integration of the physics and physiology of heat transfer between an animal and its environment. Currently, it is apparently our poor grasp of thermoregulatory physiology rather than that of biophysics that most inhibits our understanding of heat-transfer processes. Previous analyses demonstrated that physical models such as those of Walsberg (1988a) can closely predict environmental heat loads at the level of the skin (Fig. 5; see also Walsberg 1988b, 1990; Walsberg and Schmidt 1989). Equating changes in such environmental heat loads to effects

on whole-animal metabolism, however, requires knowledge of a suite of additional factors, such as those affecting tissue thermal resistance in endotherms (e.g., regional and temporal differences in cutaneous circulation). These remain essentially unexplored.

Acknowledgments

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