

EFFECTS OF SOLAR RADIATION AND WIND SPEED ON METABOLIC HEAT PRODUCTION BY TWO MAMMALS WITH CONTRASTING COAT COLOURS

GLENN E. WALSBURG AND BLAIR O. WOLF

Department of Zoology, Arizona State University, Tempe, AZ 85287-1501, USA

Accepted 20 March 1995

Summary

We report the first empirical data describing the interactive effects of simultaneous changes in irradiance and convection on energy expenditure by live mammals. Whole-animal rates of solar heat gain and convective heat loss were measured for representatives of two ground squirrel species, *Spermophilus lateralis* and *Spermophilus saturatus*, that contrast in coloration. Radiative heat gain was quantified as the decrease in metabolic heat production caused by the animal's exposure to simulated solar radiation. Changes in convective heat loss were quantified as the variation in metabolic heat production caused by changes in wind speed. For both species, exposure to 780 W m^{-2} of simulated solar radiation significantly reduced metabolic heat production at all wind speeds measured. Reductions were greatest at lower wind speeds, reaching 42% in *S. lateralis* and 29% in *S. saturatus*. Solar

heat gain, expressed per unit body surface area, did not differ significantly between the two species. This heat gain equalled 14–21% of the radiant energy intercepted by *S. lateralis* and 18–22% of that intercepted by *S. saturatus*. Body resistance, an index of animal insulation, declined by only 10% in *S. saturatus* and 13% in *S. lateralis* as wind speed increased from 0.5 to 4.0 m s^{-1} . These data demonstrate that solar heat gain can be essentially constant, despite marked differences in animal coloration, and that variable exposure to wind and sunlight can have important consequences for both thermoregulatory stress experienced by animals and their patterns of energy allocation.

Key words: coloration, convection, metabolism, solar heat gain, ground squirrel, *Spermophilus lateralis*, *Spermophilus saturatus*.

Introduction

The surface coloration that an animal presents to its environment can affect its fitness both by determining its conspicuousness and by modifying thermal balance. Visual signals typically rely on mediation of short-wave (solar) radiation reflected from the animal's surface. Solar radiation, however, is sufficiently intense that it can also be a significant source of heat. Even in mammals, in which resting metabolic rate is high compared with that of ectothermic animals, insulation can present an overwhelming component of the heat budget. For example, irradiance perpendicular to the solar beam at the earth's surface commonly exceeds 1000 W m^{-2} (Coulson, 1975). This is more than 20 times the surface-specific basal metabolic heat production of typical mammals (Brody, 1945). The fractional absorptivity of the animal's surface, which is one component of its coloration, determines the proportion of intercepted sunlight that generates heat. Clearly, demands for appropriate appearance and thermal balance can conflict, which could affect the evolution of both coloration and thermoregulatory processes. In addition to postural adjustments and microhabitat selection, a complex set of physical and biological factors determines the solar heat load. For example, the depth to which a photon penetrates into

an animal's coat prior to absorption and generation of heat markedly affects solar heat gain. If radiation absorption occurs largely near the outer coat surface, then a major fraction of the resultant heat will be lost to the environment and will not contribute to the thermal load on the skin (Kovarik, 1964; Cena and Monteith, 1975; Walsberg *et al.* 1978; Grojean *et al.* 1980; Walsberg, 1983). In contrast, coat insulation will importantly retard heat loss to the environment if radiation penetrates deeply into the coat before being absorbed, and a large fraction of the heat generated by irradiation will contribute to the thermal load on the skin. Alteration of the fraction of coat insulation through which radiation penetrates is the primary basis of the apparently adaptive modifications of radiative heat gain observed in several taxa and is affected by coat structure and the optical properties of hairs or feathers (Walsberg, 1988a, 1990; Walsberg and Schmidt, 1989).

Two species of golden-mantled ground squirrels in western North America, *Spermophilus lateralis* and *S. saturatus*, exemplify apparently adaptive alteration of coat properties to modify solar heat gain independent of surface coloration. *S. lateralis* occurs in the United States south of Washington state (Hall, 1983; Hafner, 1984). Populations from Arizona have

relatively pale fur that reflects 29% of solar radiation (Walsberg, 1990). The more northern species, *S. saturatus*, occurs in Washington state and British Columbia (Hall, 1983; Hafner, 1984) and is darker, typically reflecting only 19% of incident sunlight (Walsberg, 1990). The dorsum of both species is brown or greyish-brown and bordered by black and white stripes. Both species are diurnal and occupy coniferous forests, particularly relatively open areas with little undergrowth.

Despite substantial differences in coloration, measurements using isolated coat samples revealed that the effects of differing coat reflectivities are balanced by alterations in the relative depth of penetration of sunlight into the fur. Consequently, solar heat loads transferred to the skin are indistinguishable in the two forms (Walsberg, 1990). This finding of a convergence of solar heat gain between differently coloured species resulted from biophysical analyses that necessarily relied upon the simplified system of an isolated coat sample mounted on a temperature-controlled plate. Although these data strongly suggested that the effects identified were of major importance for intact animals, the gap between studies of isolated coats and comprehending the solar heat gain of live animals is substantial. Even if microclimate selection is not considered, solar heat gain can be affected by factors such as the complex geometry of live animals and their vasomotor processes, which can importantly alter the effective thermal resistance between the skin and the animal's core (i.e. 'tissue resistance'; Campbell, 1977).

Unfortunately, knowledge of the effects of solar radiation upon thermoregulation in animals with insulating coats has heretofore been restricted either to data derived from analyses of isolated skin and coat preparations rather than from intact animals (e.g. Walsberg, 1988*a,b*, 1990) or to data collected in the absence of forced convection (e.g. Hamilton and Heppner, 1967; Lustick, 1969), which is expected markedly to alter solar heat gain (e.g. Bakken, 1976; Campbell, 1977; Walsberg *et al.* 1978). In the following analysis, therefore, we determine whole-animal rates of radiative heat gain and convective heat loss for representatives of two squirrel populations that differ in coloration. 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. Primary questions addressed include the following. (1) Does the similarity in solar heat gain to the skin in isolated coat samples correspond to a similar heat gain by intact animals? (2) What net effects do processes such as variable tissue resistance (produced by changes in peripheral blood circulation) and animal geometry have upon solar heat gain? (3) How is heat balance affected by wind speed?

Materials and methods

Representatives of each population were trapped during June, July or August in one of two locations. *S. saturatus*

Rhoads were collected on Icicle Creek, Chelan Co., Washington, USA. *S. lateralis* Say were trapped on Clear Creek, Coconino Co., Arizona, USA. Squirrels were maintained in the laboratory for 1–4 weeks, on a 13h:11h light:dark photocycle at 24 °C. No animals moulted during this period. Body mass of *S. lateralis* was 202 ± 46 g (mean \pm 95% confidence interval, $N=10$) and that of *S. saturatus* was 332 ± 54 g ($N=10$).

Metabolic measurements were made within a closed-circuit wind tunnel, in both the presence and absence of simulated solar radiation (Fig. 1). This wind tunnel had an effective volume of 541, calculated following Bartholomew *et al.* (1981). A variable-speed blower circulated air through the test section at speeds ranging from 0.5 to 4.0 m s⁻¹, measured with a Thermoanemometer HWA-101 thermoanemometer that had been calibrated as described in Walsberg (1988*b*). Horizontal and vertical louvres upstream of the test section made wind speed more uniform within the chamber. Except within 1 cm of the chamber walls, 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 by measuring the signal output of the thermoanemometer using 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 ± 1 °C by placing it within a temperature-controlled room and by circulating water from a temperature-controlled reservoir through heat-exchange coils located in the chamber walls and in the air flow downstream of the test section. Temperature was measured

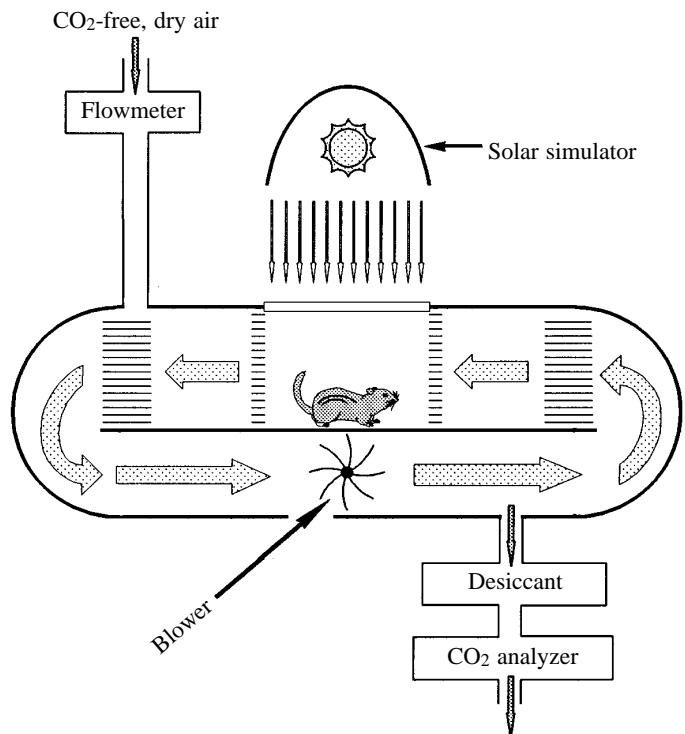


Fig. 1. Apparatus used to measure metabolic responses of ground squirrels to variation in radiation and convection. Not to scale.

with a 26 gauge, type-T thermocouple connected to a Campbell CR21x datalogger. Simulated solar radiation was produced by a Spectral Energy Corp. series II solar simulator, which filters light produced by a xenon arc lamp to simulate direct solar radiation. Radiation was passed through a 4.8 mm flint glass window in the upper portion of the test chamber to block intense ultraviolet radiation which would have burned the animals' skin and eyes. Irradiance in the test chamber was measured with a LiCor LI200sz pyranometer that had been calibrated against an Oriel Corp. pyroelectric radiometer. Simulated solar irradiance in the centre of the test chamber was maintained at 780 W m^{-2} ($\pm 5\%$) and varied less than 5% across the chamber floor. The long-wave radiant environment within the chamber was held nearly constant by painting the walls with flat-black enamel paint 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 relationship, long-wave emission therefore varied less than 6%.

Metabolic rate was determined from carbon dioxide production. Air was passed through the metabolic chamber at $19.9\text{--}20.11 \text{ min}^{-1}$ after being dried and scrubbed of CO_2 by a Puregas model CDA1112 air dryer/ CO_2 absorber system. Air flow was measured with an Omega FL4002G-HRV rotameter, calibrated to $\pm 1\%$ with a 5 l soap-bubble flowmeter. These high flow rates allowed the entire respiratory apparatus to equilibrate in 12 min, following the calculations of Lasiewski *et al.* (1966). A 150 ml min^{-1} subsample of gas was dried with anhydrous calcium sulphate and passed to a LiCor model 6252 carbon dioxide analyzer. CO_2 concentrations in sample gas ranged from 205 to 819 p.p.m. The carbon dioxide analyzer resolved CO_2 concentration to 1 p.p.m., or 0.1–0.5% of measured values. The gas analyzer was calibrated daily using both CO_2 -free air and a calibration gas known to contain 2840 p.p.m. CO_2 .

All measurements were made during the active phase of the animal's daily cycle. Data were collected at each of four wind speeds (0.5, 1.0, 2.0 and 4.0 m s^{-1}) both in the presence and in the absence of simulated solar radiation. Animals were exposed to a given wind speed and radiation regime for 30–45 min. During measurements in the absence of solar radiation, animals were exposed to fluorescent lighting that allowed normal vision but was thermally insignificant (irradiance $< 3 \text{ W m}^{-2}$). All measurements in the presence of solar radiation were made during a single day, and measurements in the absence of solar radiation were made on a separate day. The order in which an animal was exposed to different wind speeds was randomized.

Instrument signals were recorded on a Campbell CR21x datalogger and averaged at 1 min intervals. Animals commonly rested quietly within the chamber, and values reported are those for periods in which the animal was inactive for an entire 12 min equilibration period prior to data collection. Carbon dioxide production was calculated using equation 3 of Walsberg and Wolf (1995) and corrected to STP (0°C , 101 kPa).

This calculation and subsequent 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. In addition, elevation of humidity in the wind tunnel, as measured with a WeatherMeasure HM111RG hygrometer, was too low ($< 1 \text{ mg H}_2\text{O l}^{-1}$) to allow accurate estimation of latent heat loss. Therefore, RQ and the fraction of metabolic power dissipated through evaporation were determined in separate measurements in which animals were placed in a 3.8 l metabolic chamber at 15°C , in the absence of wind or solar radiation. Dry, CO_2 -free air flowed into the chamber at $500\text{--}3000 \text{ ml min}^{-1}$, 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 equation 3 of Hill (1972). CO_2 production was calculated using equation 3 of Walsberg and Wolf (1995). The relative humidity of effluent air from the chamber was measured with the WeatherMeasure hygrometer, calibrated over saturated solutions of LiCl (12% relative humidity) and K_2SO_4 (97% relative humidity) (Winston and Bates, 1960). The temperature of the air flowing over the hygrometer was measured simultaneously, and absolute humidity was calculated using the equation of Campbell (1977). Latent heat of evaporation was calculated using a value of $2.42 \text{ kJ g}^{-1} \text{ H}_2\text{O}$. These measurements were made only for *S. lateralis*. Because diet and experimental conditions were identical for both species, RQ in *S. saturatus* was assumed to be similar to that in *S. lateralis*. Evaporative heat loss constitutes a small fraction of total heat loss ($< 8\%$; see Results) and errors derived from estimating this component are likely to be insignificant. Therefore, the fraction of heat lost through evaporation by *S. saturatus* was assumed to equal that in *S. lateralis*.

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

$$r_B = [k(T_B - T_E)/(M - E)] - r_E. \quad (1)$$

Here, r_B is the total 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 ($1200 \text{ J m}^{-3} \text{ }^\circ \text{C}^{-1}$; Robinson *et al.* 1976; Campbell, 1977) and T_B is core body temperature (assumed to equal 37°C). T_E is operative environmental temperature, which was 15°C for experiments conducted in the absence of simulated solar radiation. M is metabolic rate, expressed on a surface-area basis (W m^{-2}). Deriving this value requires knowledge of skin surface area (A_{SKIN} ; cm^2), which was estimated from body mass (g) using the Meeh equation (1879) with Rubner's (1883) constant of 10:

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

E in equation 1 is heat loss by evaporation, also expressed on the basis of body surface area (W m^{-2}). r_E is the effective thermal resistance between the environment and the animal's

outer surface. It equals the parallel sum of r_R and r_A ($=r_R+r_A/r_R r_A$). r_A is the thermal resistance of the aerodynamic boundary layer (s m^{-1}) and was calculated using the equations of Mitchell (1976) as combined by Webster and Weathers (1988):

$$r_A = 2.7d^{0.4}(\nu/u)^{0.6}/D_H. \quad (3)$$

Here, u is wind speed (m s^{-1}), ν is the kinematic viscosity of air ($14.6 \text{ mm}^2 \text{ s}^{-1}$) and D_H is the thermal diffusivity of air ($20.8 \text{ mm}^2 \text{ s}^{-1}$). d is a characteristic dimension of the animal (Campbell, 1977), taken as 0.12 m for *Spermophilus*. r_R is the effective resistance (s m^{-1}) to radiative heat transfer and was calculated following Campbell (1977).

Comparison of data for intact animals with those previously collected using isolated coat samples requires an estimation of the cross-sectional area of the beam of simulated solar radiation intercepted by the animal. Because the animal moved within the chamber, determining this value is challenging. Because governmental agencies regulating collecting discouraged the animals' subsequent release into the wild and future work requires use of specimens, the animals were killed by exposure to CO_2 , as recommended by the American Veterinary Medical Association and approved by the Animal Care and Use Committee of Arizona State University. The squirrels were then held in a posture simulating that of squirrels occupying the metabolic chamber. Their projected shadow area (excluding the tail) normal to a horizontal surface was traced onto paper of known mass per unit area and the paper was weighed to determine surface area. Because this procedure had to be carried out after all other experiments, body mass may have differed from that measured during experiments. Therefore, values for particular animals were not used. Rather, we generated a statistically significant ($P=0.05$) least-squares regression equation that combines data from both populations and relates projected surface area (A_P ; cm^2) to the two-thirds power of body mass (g):

$$A_P = 1.69(\text{body mass})^{0.667}. \quad (4)$$

Here, body masses ranged from 199 to 416 g, $N=20$, and $r^2=0.84$. Wilcoxon paired sample tests were used for within-species comparisons of values for individuals exposed to contrasting conditions (e.g. the presence or absence of simulated solar radiation). Mann-Whitney U -tests were used for between-species comparisons. 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

Respiratory quotient, latent heat loss and skin surface area

The mean respiratory quotient (RQ) was 0.737 ± 0.069 ($N=10$). On the basis of this value, the thermal equivalent of produced carbon dioxide is estimated as 27 J ml^{-1} (Kleiber, 1961). Heat loss by evaporation equalled $7.9 \pm 0.63\%$ of total

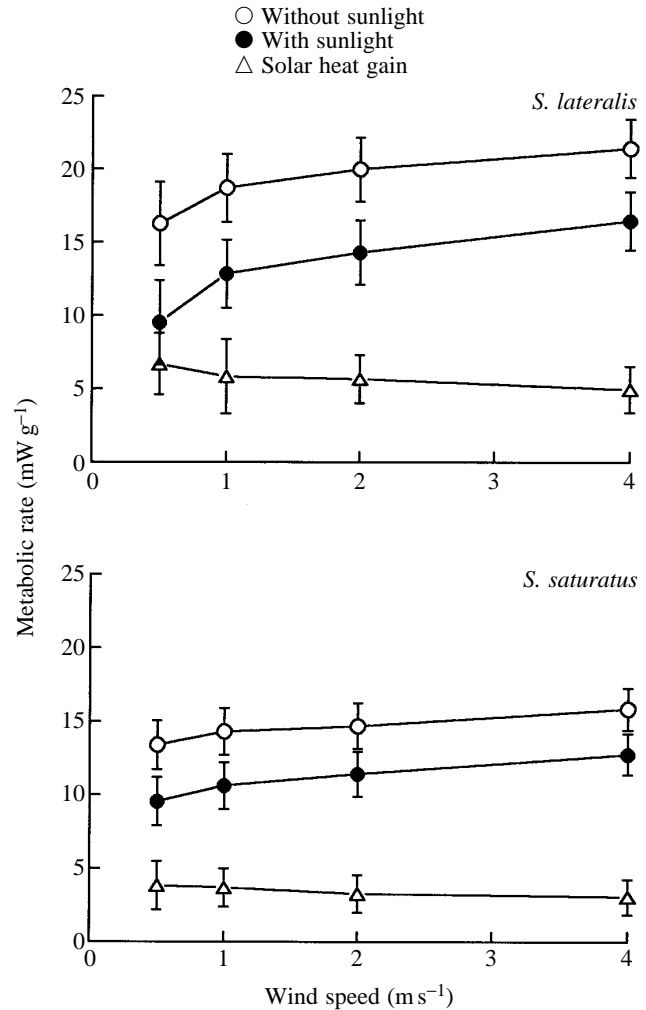


Fig. 2. Metabolic heat production and solar heat gain of golden-mantled ground squirrels as a function of wind speed and the presence or absence of 780 W m^{-2} simulated solar radiation. Values are means \pm 95% confidence intervals, $N=10$.

heat production ($N=10$). Skin surface area was estimated as $335 \pm 69.9 \text{ cm}^2$ in *S. lateralis* and $479 \pm 52.5 \text{ cm}^2$ in *S. saturatus*.

Heat production as a function of wind and irradiance

In the absence of insolation, mass-specific metabolic rates of *S. lateralis* were 31–35% greater than those of *S. saturatus* at all wind speeds above 0.5 m s^{-1} ($P<0.05$) (Fig. 2). Values at 0.5 m s^{-1} did not differ ($P>0.05$). In both species, minimal metabolic rates occurred at 0.5 m s^{-1} . These significantly exceeded expected basal levels, however. During the active phase of the daily cycle, basal metabolic rate (BMR) in *S. saturatus* is about 3.9 mW g^{-1} , based upon measurements by Kenagy and Vleck (1982) and assuming a thermal equivalent of consumed oxygen of 19.9 J ml^{-1} . At 0.5 m s^{-1} , metabolic rate in this species was 3.4 times BMR. Assuming similar mass-specific basal metabolism in *S. lateralis*, the metabolic rate at a wind speed of 0.5 m s^{-1} in the latter species was 4.1 times BMR.

Table 1. Linear regressions of metabolic rate ($mW g^{-1}$) on the logarithm of wind speed ($m s^{-1}$)

Case	a	b	$S_{y,x}$	S_b	r^2
<i>Spermophilus lateralis</i> ; without sun	18.25	2.41	0.414	0.267	0.976
<i>S. lateralis</i> ; with sun	12.17	3.19	0.567	0.366	0.974
<i>S. saturatus</i> ; without sun	14.17	1.11	0.218	0.141	0.969
<i>S. saturatus</i> ; with sun	10.56	1.51	0.169	0.109	0.989

Regression equations have the form: $y=a+bx$, where y is metabolic rate and x is $\ln(\text{wind speed})$.
 $S_{y,x}$ is the standard error of the estimate of y ; S_b is the standard error of the estimate of b .
 All regressions are significant ($P<0.05$).

When simulated solar radiation was present, metabolic rates differed significantly between species only at $4 m s^{-1}$ wind speed. Minimal metabolic rates occurred at $0.5 m s^{-1}$ and were approximately 2.4 times BMR in both species. Regression equations were fitted to these data using untransformed values as well as square-root and logarithmic transformations of wind speed values. Logarithmic transformations provided the greatest explanatory power (i.e. maximum r^2 values) and are the only equations reported (Table 1).

For both species, exposure to solar radiation significantly reduced metabolic heat production at all wind speeds measured, and the reductions were greatest at lower wind speeds ($P<0.05$). Solar heat gain to the animal, defined as the reduction in metabolic rate caused by the addition of simulated solar radiation, was $5.0\text{--}6.7 mW g^{-1}$ in *S. lateralis* (Fig. 2), or a reduction in metabolic rate of 23–42%. In *S. saturatus*, simulated solar radiation reduced animal heat production by $3.0\text{--}3.8 mW g^{-1}$, or 19–29%. When expressed per unit body mass, this heat gain did not differ significantly between the two populations except at a wind speed of $0.5 m s^{-1}$. At this wind speed, heat gain to *S. lateralis* is 74% greater than to *S. saturatus*.

Equation 4 was used to calculate the cross-sectional area of the radiation beam intercepted by an animal, which was $58.0\pm 8.7 cm^2$ in *S. lateralis* and $80.9\pm 10.3 cm^2$ in *S. saturatus*. Solar heat gain in *S. lateralis* therefore averaged 14–21% of the energy intercepted by the animal (Fig. 3). Heat gain in *S. saturatus* equalled 18–22% of the energy contained in the intercepted portion of the beam. At no wind speed did these values differ significantly between species.

Effect of wind on body insulation

Body resistance (r_B) is an index of animal insulation. In both species, r_B declined with increasing wind speed (Fig. 4). The reductions were not large, however, averaging only 10% ($27 s m^{-1}$) in *S. saturatus* and 13% ($32 s m^{-1}$) in *S. lateralis* over the wind speed range $0.5\text{--}4.0 m s^{-1}$. In contrast, the thermal resistance of the aerodynamic boundary layer (r_A) is calculated to decline from 106 to $30 s m^{-1}$ over this range of

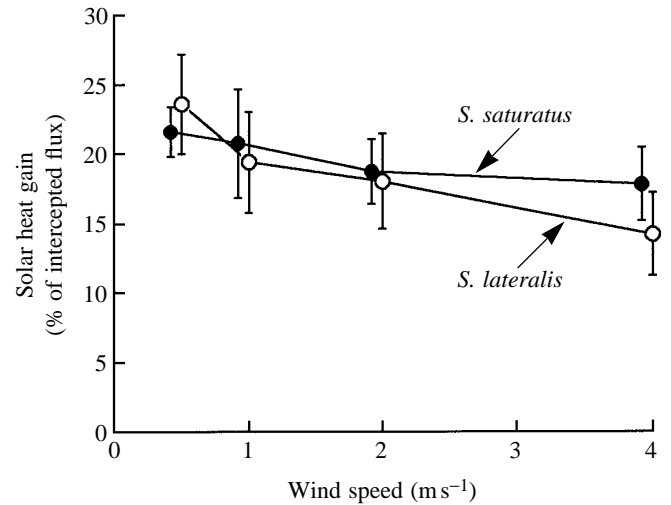


Fig. 3. Solar heat gain by golden-mantled ground squirrels, expressed as a percentage of the power contained within the portion of the beam of simulated solar radiation intercepted by the animal. Values are means \pm 95% confidence intervals, $N=10$. Values for *S. saturatus* are offset along the x -axis for clarity.

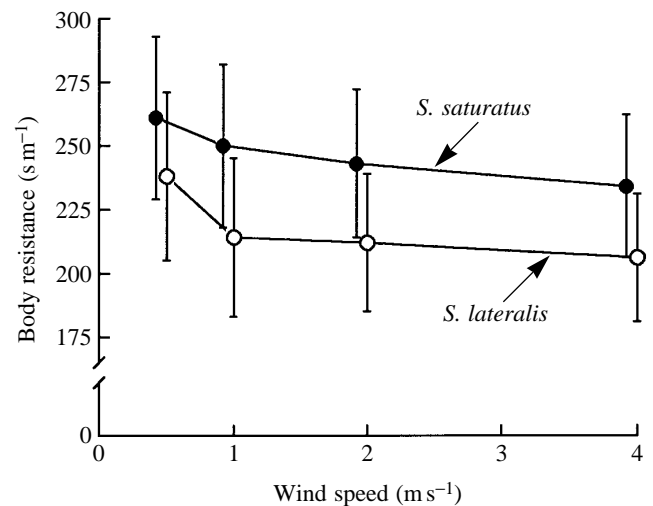


Fig. 4. Body resistance (r_B) of golden-mantled ground squirrels as a function of wind speed. Values are means \pm 95% confidence intervals, $N=10$. Values for *S. saturatus* are offset along the x -axis for clarity.

wind speeds. Thus, increased wind speed reduces total insulation primarily by a reduction of the aerodynamic boundary layer that is 2–3 times greater than the reduction produced by disruption of body insulation.

Discussion

Convergence of solar heat gain in two species with contrasting coat colours

When expressed on the basis of skin surface area, the darker coloration of *S. saturatus* does not impose greater solar heat loads than those experienced by the lighter-coloured *S.*

lateralis. Thus, these results for live animals confirm earlier projections made from analyses of isolated skin and fur preparations (Walsberg, 1990) and therefore demonstrate that solar heat gain can be essentially constant despite marked differences in short-wave reflectivity. These data and those from studies of isolated skin and fur preparations (Walsberg, 1988a, 1990; Walsberg and Schmidt, 1989) contrast with earlier analyses which concluded that darker animals acquire greater radiative heat loads (e.g. Hamilton and Heppner, 1967; Lustick, 1969; Heppner, 1970). However, coat characteristics now known to be important determinants of solar heat gain (e.g. optical properties of the hairs and coat structure) are probably not duplicated by the selective breeding or dyeing used to produce the animals of contrasting coat colours used in pioneering investigations. Clearly, analyses of animals whose physical properties were produced by artificial means must be interpreted cautiously.

Although qualitative relationships in solar heat gain between the two species are as predicted from analyses of isolated coat samples, absolute values of heat gain are only 32–48 % of those measured using coat preparations. Possible bases for this depression of radiative heat gain in live animals are manifold, but include at least the following. (1) Postural and shape effects, reflecting the complex and curved nature of whole animals compared with flat coat samples, change the angle of incidence of both sunlight and wind striking the fur. This may change the degree to which both sunlight and wind penetrate the coat. (2) Radiative heat gain was distributed over the entire upper skin surface of live animals, but was only measured in the mid-dorsal region of isolated coat preparations. (3) In studies of isolated coat preparations, heat flux was measured at the skin. Subcutaneous processes such as alterations in blood flow through peripheral tissues, which may serve as thermoregulatory mechanisms, were not incorporated. In the terminology of operative environmental temperature theory (Campbell, 1977), tissue thermal resistance (r_T) between the skin and body core was not accounted for. Addition of any thermal resistance, including r_T , between the region of heat generation and the core of the animal will reduce heat gain by the intact animal. (4) Turbulence in the air stream was lower in studies of coat preparations than in the current analysis using whole animals. Turbulence inherent in the air flow was very low (<0.3 %) in measurements of coat preparations, and additional turbulence induced by the skin sample was too low to be measured (Walsberg, 1988a). In the current analysis, inherent turbulence was higher (2–3 %). Additional turbulence produced by the animal's presence is unknown, but was probably increased because of the larger and more complex shape of a live squirrel. Turbulence reduces boundary layer resistance (r_A), which will reduce solar heat gain (Walsberg *et al.* 1978).

We are unable to quantify the importance of the first two sets of factors listed above, but the approximate role of the latter two can be evaluated using simple simulations. On the basis of models such as that presented by Walsberg (1983), the relationship between solar heat gain to the animal's core (Q_A ,

$W m^{-2}$) and that to the level of the skin (Q_S , $W m^{-2}$) may be expressed as:

$$Q_A = Q_S[(r_C + r_E)/(r_C + r_E + r_T)] , \quad (5)$$

where r_C is coat thermal resistance ($s m^{-1}$).

For simulations using this model, Q_S was taken as the mean value at each wind speed reported by Walsberg (1988a). The sum r_C+r_E was entered as either 100 % or 67 % of the values reported by Walsberg (1988a). The latter values represent the one-third reduction in these resistances that might be produced by increased turbulence and wind penetration into the coat. The thermal resistance of peripheral tissues (r_T) was taken as either 75 or $100 s m^{-1}$, a conservative range of likely values (Monteith and Unsworth, 1989).

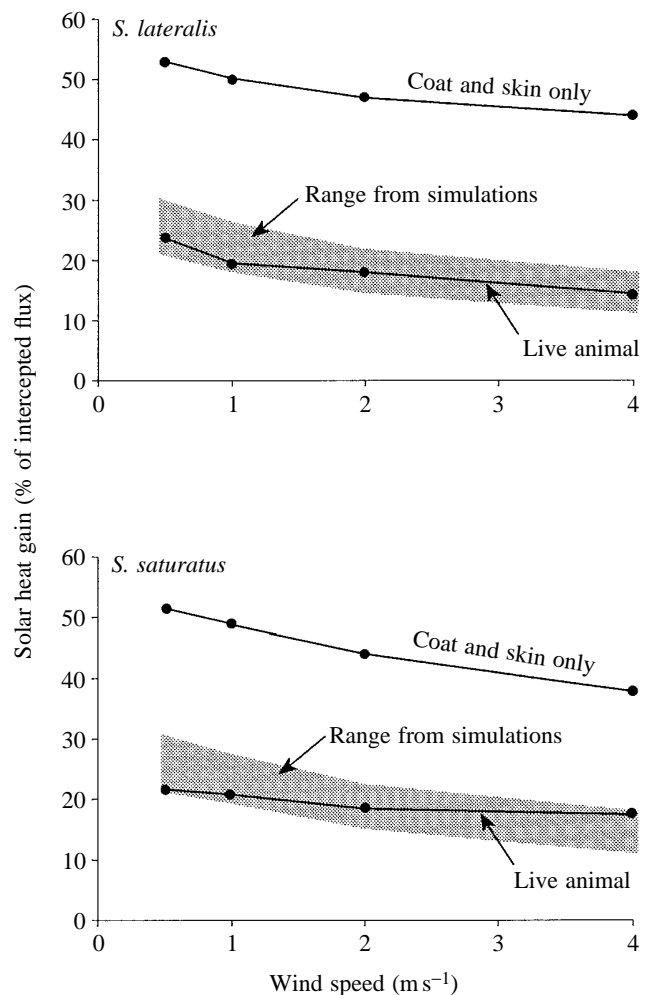


Fig. 5. Comparison of solar heat gain values derived from three sources: (1) empirical measure of solar heat gain at the level of skin beneath isolated coat and skin preparations (Walsberg, 1988a); (2) empirical measures of solar heat gain by intact animals; and (3) simulation results derived from data for isolated coat preparations 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 for empirical measurements are presented. The stippled area represents the range of predictions from simulations.

Simulation results predict a substantial reduction in solar heat gain to live animals compared with that measured at the level of the skin in coat samples (Fig. 5). The minimum reduction is predicted from the combination of $r_T=75 \text{ s m}^{-1}$ and r_C+r_E equal to 100% of the values measured in analyses of coat preparations. The maximum reduction is predicted from the combination of $r_T=100 \text{ s m}^{-1}$ and values of r_C+r_E equal to 67% of those reported by Walsberg (1988a). Other combinations of r_T and r_C+r_E produce intermediate levels of reduction.

These predicted values of solar heat gain to live animals encompass values actually measured. Clearly, such results should not be taken too seriously and do *not* indicate that the only effects operating are changes in the thermal resistance of the aerodynamic boundary layer, the coat or peripheral tissues. However, these results do demonstrate that reasonable variations likely to occur in such thermal resistances are fully capable of producing the differences in solar heat gain observed between live animals and isolated coat preparations.

Potential effects of solar heat gain and wind on animal energy balance

Our analysis provides the first data describing the thermoregulatory consequences for live mammals of simultaneous changes in solar radiation and wind speed. This affords an opportunity to evaluate the consequences of such variation for animal heat production. An animal's thermal microclimate has at least two types of major effects on its energy balance. First, microclimate directly affects the short-term thermal stress experienced by the animal and therefore the energy it must devote to thermoregulation. Second, such energy expended on thermoregulation is a component of an individual's total daily energy expenditure (DEE) and therefore has indirect effects by altering the chemical potential energy that is available for other avenues of expenditure (e.g. locomotion, reproduction). The consequences of microclimatic changes on these two classes of effects may differ greatly because of differing time scales over which the animal responds. The small body size, and consequent small thermal inertia, of most animals dictates that thermoregulatory responses must occur over short periods (e.g. fractions of an hour). In contrast, the chemical potential energy budgets of small endotherms are usually balanced over much longer periods. Even excluding seasonal use of torpor in animals such as golden-mantled ground squirrels, energy budgets are probably balanced over periods of at least a day because foraging typically occurs in 24 h cycles and because even small endotherms can typically store energy sufficient to survive for a few days. We therefore use our data to explore the energetic consequences of wind and solar radiation for both direct and indirect effects; that is, thermoregulatory responses as well as subsequent effects on the daily energy expenditure of free-living animals.

The potential importance of solar heat gain and convective heat loss to short-term thermal demands on golden-mantled ground squirrels can be examined by comparing the effects of

these processes with those produced by changes in air temperature. In a black-body thermal environment, such as that produced by our metabolic chamber with high-emissivity walls, near air temperature and in the absence of sunlight, operative environmental temperature (T_E) essentially equals air temperature. For comparative purposes, it is also useful to stipulate 'standard' convective conditions. We define these as the lowest wind speed used, 0.5 m s^{-1} . Standard operative temperature (T_{ES} ; Bakken, 1976), therefore, is operationally defined as air temperature within a black-body environment at $u=0.5 \text{ m s}^{-1}$ and calculated as:

$$T_{ES} = T_B - (M - E)(r_s)/k. \quad (6)$$

Variables are as defined previously, except that r_s is the sum of r_B and r_E at $u=0.5 \text{ m s}^{-1}$ and in the absence of sunlight. T_{ES} thus represents the air temperature under these conditions that would induce animal heat production equal to that observed under the radiative and convective conditions actually

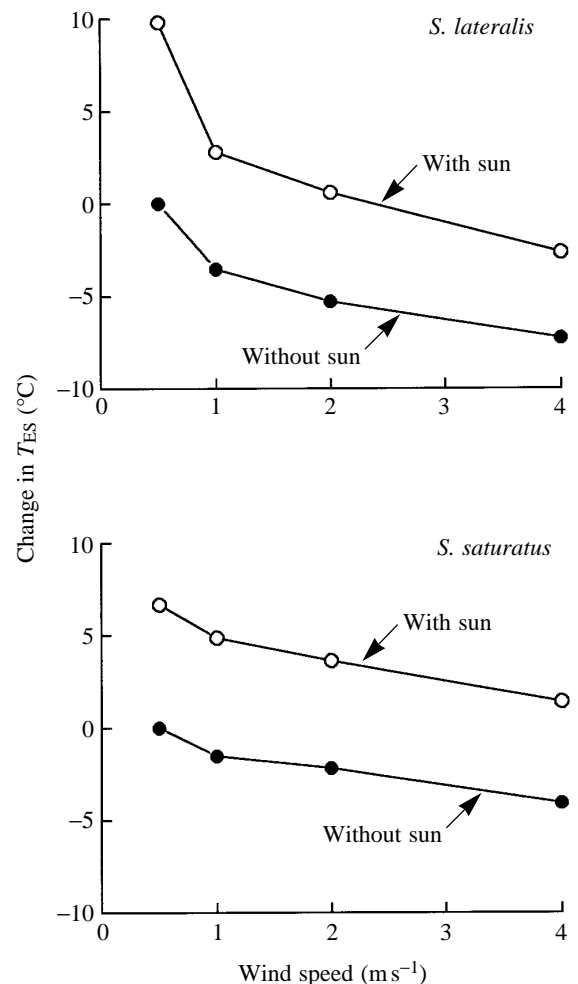


Fig. 6. Changes in standard operative environmental temperature (T_{ES}) produced by variation in wind speed and the presence or absence of 780 W m^{-2} simulated solar radiation. Values presented are means. Standard conditions for computation of T_{ES} are a black-body radiative environment with wind speed of 0.5 m s^{-1} .

prevailing. Values in Fig. 6 are expressed as the difference in T_{ES} from the value of $T_{ES}=15^{\circ}\text{C}$ that existed at $u=0.5\text{ m s}^{-1}$ and no solar radiation.

With wind speed held constant, exposure to moderately intense solar radiation increases the heat load on the animal by an amount equivalent to that produced by 5–8°C elevations of air temperature (Fig. 6). With radiation held constant, increasing wind speed from 0.5 to 4.0 m s^{-1} changes animal heat balance by an amount equal to that produced by 4 to 7°C decreases in T_{AIR} (Fig. 6). In the site at which Kenagy *et al.* (1989) studied *S. saturatus*, average air temperatures during periods of surface activity varied from about 4 to 25°C during the months when animals were not hibernating. Assuming that $T_B=37^{\circ}\text{C}$, the body-to-air temperature gradient therefore averages roughly 12–32°C, and 780 W m^{-2} insolation could have a large effect equivalent to reducing this gradient by 22–67%.

The potential importance of solar heat gain and convective heat loss for an animal's use of chemical potential energy can be explored by comparison with energy allocated to both the animal's basal metabolic rate and its total daily energy expenditure. Solar heat gain for *S. saturatus* exposed to irradiance levels of 780 W m^{-2} was 0.8–1.0 times BMR, depending upon wind speed. Assuming similar mass-specific basal metabolic rate in *S. lateralis*, solar heat gain was 1.3–1.7 times BMR. Increasing wind speed from 0.5 to 4.0 m s^{-1} in the absence of sunlight raises heat production by 5.1 mW g^{-1} in *S. lateralis* and 3.3 mW g^{-1} in *S. saturatus*. These changes equal 1.3 times BMR and 0.8 times BMR, respectively. The total range of mean metabolic rates, from the minima observed at 0.5 m s^{-1} wind in the presence of solar radiation to the maxima observed at 4.0 m s^{-1} wind without solar radiation, averages 1.6 times BMR (*S. saturatus*) or 3.1 times BMR (*S. lateralis*).

Total daily energy expenditure of free-living, non-hibernating *S. saturatus* averages about 840–1340 $\text{J g}^{-1}\text{ day}^{-1}$ (Kenagy *et al.* 1989), depending upon sex, age and phase of the annual cycle. Exposure to sunlight of 780 W m^{-2} can reduce heat production by 11–14 $\text{J g}^{-1}\text{ h}^{-1}$. These ground squirrels spend about 7 h day^{-1} on the surface (Kenagy *et al.* 1989) and the total reduction in heat production associated with solar heat gain could thus equal 77–98 $\text{J g}^{-1}\text{ day}^{-1}$, or 6–12% of DEE. Similar calculations indicate that the change due to variation in wind speed from 0.5 to 4.0 m s^{-1} could be 83 $\text{J g}^{-1}\text{ day}^{-1}$, or 6% of DEE. The total variation observed as a product of change in both wind speed and solar radiation is about 5–12% of DEE in *S. saturatus*.

Daily heat production has not been quantified for *S. lateralis*. Assuming that this species' patterns of time and energy expenditure are similar to those of *S. saturatus*, however, allows rough estimates of the possible effects of changes in exposure to wind or solar radiation. Computations parallel to those described above indicate that varying exposure to 780 W m^{-2} irradiance during a 7 h active period could alter DEE by 9–20%, depending on wind speed. Variation in wind speed in the range 0.5–4.0 m s^{-1} could alter DEE by 10–21%. The total change possible as a product both wind speed and

solar radiation is 22–36% of total daily expenditure in *S. lateralis*.

Although these calculations indicate that solar radiation may have large effects upon both short-term thermoregulatory demands upon the animal and upon total daily energy expenditure, several factors suggest that the exact values described above must be viewed cautiously. First, if air temperatures are sufficiently warm, or the heat production rates of the animals are already high as a result of physical activity, then it is possible that they have no extra thermoregulatory expenses and would, consequently, not benefit energetically from solar heat gain. Second, solar heat gain can increase metabolic rates if the heat load on the animal is sufficiently high to require energetically expensive modes of cooling such as panting. Finally, two considerations suggest that the maximum effects of solar radiation experienced by animals in nature may be substantially greater than these estimates. First, solar heat gain increases with declining wind speed. Wind speeds in nature may often be below 0.5 m s^{-1} and solar heat gain may therefore be elevated. Second, our measurements were made at irradiance values near 780 W m^{-2} , and solar irradiance under clear skies commonly exceeds 1000 W m^{-2} . It is reasonable to expect, therefore, that the effects of solar heat gain for free-living animals may be roughly one-third higher than the values we observed. Clearly, variable exposure to wind and sunlight, as well as the convergence in fractional solar heat gain observed between these two species, can have important consequences for both short-term thermoregulatory stress as well as for patterns of daily energy allocation to competing demands.

We are grateful to Theresa E. Withrow for her assistance in data collection and to Jon F. Harrison for his helpful conversations. This research was supported by NSF grants BSR 91-07470 and IBN 92-24130.

References

- BAKKEN, G. S. (1976). A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. *J. theor. Biol.* **60**, 337–384.
- BARTHOLOMEW, G. A., VLECK, D. AND VLECK, C. M. (1981). Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in sphingid and saturniid moths. *J. exp. Biol.* **90**, 17–32.
- BRODY, S. (1945). *Bioenergetics and Growth, with Special Reference to the Efficiency Complex in Domestic Animals*. New York: Reinhold Publishing Corp.
- CAMPBELL, G. S. (1977). *An Introduction to Environmental Biophysics*. New York, Heidelberg, Berlin: Springer.
- CENA, K. AND MONTEITH, J. L. (1975). Transfer processes in animal coats. I. Radiative transfer. *Proc. R. Soc. Lond. B* **188**, 395–411.
- COULSON, K. L. (1975). *Solar and Terrestrial Radiation*. New York: Academic Press.
- GROJEAN, R. E., SOUSA, J. A. AND HENRY, M. C. (1980). Utilization of solar radiation by polar animals: an optical model for pelts. *Appl. Optics* **19**, 339–346.
- HAFNER, D. J. (1984). Evolutionary relationships of nearctic

- Sciuridae. In *The Biology of Ground-Dwelling Squirrels* (ed. J. O. Murie and G. R. Michener), pp. 1–23. Lincoln: University of Nebraska Press.
- HALL, E. R. (1983). *The Mammals of North America*. New York: John Wiley and Sons.
- HAMILTON, W. J. AND HEPPNER, F. (1967). Radiant solar energy and the function of black homeotherm pigmentation: an hypothesis. *Science* **155**, 196–197.
- HEPPNER, F. (1970). The metabolic significance of differential absorption of radiant energy by black and white birds. *Condor* **72**, 50–59.
- HILL, R. W. (1972). Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. *J. appl. Physiol.* **33**, 261–263.
- HINZE, H. O. (1959). *Turbulence. An Introduction to its Mechanism and Theory*. New York: McGraw-Hill.
- KENAGY, G. J., SHARBAUGH, S. M. AND NAGY, K. A. (1989). Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. *Oecologica* **78**, 269–282.
- KENAGY, G. J. AND VLECK, D. (1982). Daily temporal organization of metabolism in small mammals: adaptation and diversity. In *Vertebrate Circadian Systems* (ed. J. Aschoff, S. Daan and G. A. Gross), pp. 322–338. Berlin: Springer-Verlag.
- KLEIBER, M. (1961). *The Fire of Life: An Introduction to Animal Energetics*. New York: John Wiley and Sons.
- KOVARIK, M. (1964). Flow of heat in an irradiated protective cover. *Nature* **201**, 1085–1087.
- LASIEWSKI, R. C., ACOSTA, A. L. AND BERNSTEIN, M. L. (1966). Evaporative water loss in birds. I. Characteristics of the open flow method of determination and their relation to estimates of thermoregulatory ability. *Comp. Biochem. Physiol.* **19**, 445–457.
- LUSTICK, S. (1969). Bird energetics: effects of artificial radiation. *Science* **163**, 387–390.
- MEEH, K. (1879). Oberflächenmessungen des menschlichen Körpers. *Z. Biol.* **15**, 387–390.
- MITCHELL, J. W. (1976). Heat transfer from spheres and other animal forms. *Biophys. J.* **16**, 561–569.
- MONTEITH, J. L. AND UNSWORTH, M. (1989). *Principles of Environmental Physics*. 2nd edition. London: Edward Arnold.
- ROBINSON, D. E., CAMPBELL, G. S. AND KING, J. R. (1976). An evaluation of heat-exchange in small birds. *J. comp. Physiol.* **105**, 153–166.
- RUBNER, M. (1883). *Die Gesetze des Energieverbrauchs bei der Ernährung*. Leipzig, Vienna: F. Deuticke.
- WALSBERG, G. E. (1983). Coat color and solar heat gain in animals. *Bioscience* **33**, 88–91.
- WALSBERG, G. E. (1988a). The significance of coat structure for solar heat gain in the rock squirrel, *Spermophilus variegatus*. *J. exp. Biol.* **138**, 243–257.
- WALSBERG, G. E. (1988b). Consequences of skin color and fur properties for solar heat gain and ultraviolet irradiance in two mammals. *J. comp. Physiol. B* **158**, 213–224.
- WALSBERG, G. E. (1990). Convergence of solar heat gain in two squirrel species with contrasting coat colors. *Physiol. Zool.* **63**, 1025–1042.
- WALSBERG, G. E., CAMPBELL, G. S. AND KING, J. R. (1978). Animal coat color and radiative heat gain: a re-evaluation. *J. comp. Physiol.* **126**, 211–222.
- WALSBERG, G. E. AND SCHMIDT, C. A. (1989). Seasonal adjustment of solar heat gain in a desert mammal by altering coat properties independent of surface coloration. *J. exp. Biol.* **142**, 387–400.
- WALSBERG, G. E. AND WOLF, B. O. (1995). Variation in the respiratory quotient of birds and implications for indirect calorimetry using measurements of carbon dioxide production. *J. exp. Biol.* **198**, 213–219.
- WEBSTER, M. D. AND WEATHERS, W. W. (1988). Effect of wind and air temperature on metabolic rate in verdins, *Auriparus flaviceps*. *Physiol. Zool.* **61**, 543–554.
- WINSTON, P. W. AND BATES, D. H. (1960). Saturated solutions for the control of humidity in biological research. *Ecology* **41**, 232–237.
- ZAR, J. H. (1984). *Biostatistical Analysis*. Englewood Cliffs, New Jersey: Prentice Hall.