

## DO METABOLIC RESPONSES TO SOLAR RADIATION SCALE DIRECTLY WITH INTENSITY OF IRRADIANCE?

GLENN E. WALSBURG\*, RANDALL L. TRACY AND TY C. M. HOFFMAN  
*Department of Biology, Arizona State University, Tempe, AZ 85287-1501, USA*

*Accepted 20 May 1997*

### Summary

Endotherms exposed to air temperatures below thermal neutrality reduce their metabolic heat production when exposed to sunlight. The physiological effects of this additional source of heat gain from the environment usually are assumed to be proportional to the intensity of irradiance if other factors are held constant. We test this assumption by measuring changes in metabolic heat production produced by exposing a small mammal, the Siberian hamster (*Phodopus sungorus*) to four intensities of simulated solar radiation (0 W m<sup>-2</sup>, 317 W m<sup>-2</sup>, 634 W m<sup>-2</sup> and 950 W m<sup>-2</sup>).

In the absence of solar radiation, metabolic heat production is inversely correlated with air temperature over the measured range of 3–27 °C. The respiratory quotient varies significantly with ambient temperature, indicating that the catabolic substrate and the thermal equivalent of oxygen consumed or carbon dioxide

produced also vary with temperature. The depression of metabolic heat production resulting from exposure to simulated solar radiation is not simply a multiple of the intensity of irradiance. Rather, metabolic responses to higher levels of irradiance are blunted by 14–29% compared with those expected on the basis of the response to less intense irradiance. Because changes in irradiance levels do not have simple linear effects upon the animal's metabolic heat production, even in a simplified situation, significant errors may accumulate in biophysical analyses in which an animal's responses to a restricted set of radiative conditions are measured and the results are extrapolated to a wider range observed in nature.

Key words: metabolic heat production, *Phodopus sungorus*, respiratory quotient, Siberian hamster, solar heat gain, sunlight, thermoregulation.

### Introduction

Under natural conditions, the metabolic heat production required for thermoregulation by endotherms depends upon a complex array of factors that notably includes convective and radiative heat exchange with the environment. During daylight hours, the radiative environment is commonly dominated by solar radiation which, under clear skies, often exceeds 900–1000 W m<sup>-2</sup> on a plane perpendicular to the solar beam. For small animals, this can produce physiological effects equivalent to 10–20 °C elevations in air temperature (e.g. Hamilton and Heppner, 1967; Lustick, 1969; Walsberg, 1982; Wolf and Walsberg, 1996). It is difficult, however, to predict quantitatively the physiological consequences of solar radiation for animals such as birds and mammals that possess insulating coats. Because sunlight penetrates significantly into coats, the heat load transferred to the skin depends importantly not only upon conspicuous factors, such as wind speed and coat color, but also upon a series of much more subtle factors (Kovarik, 1964; Cena and Monteith, 1975a; Walsberg *et al.* 1978; Gebremedhin *et al.* 1983). These include, for example, the microstructure of the coat and the optical properties of individual hairs. Such factors can be of overwhelming

importance in determining the heat load imposed on the skin by insolation (Walsberg, 1988a,b, 1990). Finally, the complexity of the relationship between the intensity of irradiance and the metabolic responses of animals can be further complicated by changes in patterns of peripheral circulation (Walsberg *et al.* 1997).

In the current analysis, we pose a simple, but fundamental, question: do the physiological effects of solar radiation scale directly with the intensity of irradiance? That is, are changes in the intensity of the radiative heat input to the animal's outer surface matched proportionately by changes in the intensity of its physiological responses to such heat input? We address this question by measuring the changes in metabolic heat production in response to exposure to simulated solar radiation in a small mammal, the Siberian hamster (*Phodopus sungorus*). Endotherms exposed to air temperatures below thermal neutrality reduce their metabolic heat production when exposed to solar radiation as a source of additional heat input. The intensity of this depression in thermostatic heat production has been used as a measure of the physiologically significant rate of solar heat gain to the animal (e.g. Walsberg and Wolf,

\*e-mail: walsberg@asu.edu.

1995a,b; Wolf and Walsberg, 1996). In the present study, we exposed hamsters to four intensities of simulated solar radiation and examined the fashion in which their physiological responses scaled with intensity of radiative heat input.

### Materials and methods

#### *Species acquisition and maintenance conditions*

Siberian hamsters, *Phodopus sungorus* (Pallas, 1773), were obtained from a colony at Arizona State University. Animals were maintained on a 12 h:12 h light:dark photocycle at  $T_{\text{air}}=24$  °C, fed Teklad Rodent Diet, and supplied *ad libitum* with water. Mean body mass was 46 g, and all body masses reflect animals with their cheek pouches empty of food.

#### *Metabolic measurements*

Metabolic measurements were made within a closed-circuit wind tunnel, in both the presence and absence of simulated solar radiation (Walsberg and Wolf, 1995a). This wind tunnel had an effective volume of 111, calculated following Bartholomew *et al.* (1981). A variable-speed blower circulated air through the test section at speeds of 0.3, 0.7 and 1.6 m s<sup>-1</sup>, measured using an Omega HHF92 thermoanemometer that had been calibrated as described by Walsberg (1988a). Horizontal and vertical louvers upstream from the test section were used to make wind speed more uniform within the chamber. Except within 1 cm of the chamber walls, wind speed varied by less than 5% horizontally or vertically within the test section. The turbulence intensity was less than 3% at all wind speeds used, determined by measuring the signal output of a Thermoanemometer HWA-101 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 10±1 °C by placing it within a temperature-controlled room and by circulating water from a temperature-controlled reservoir through heat-exchange coils attached to walls of the wind tunnel. Temperature was measured using a 26 gauge, type T thermocouple connected to a Campbell CR21x datalogger. Simulated solar radiation was produced by a Spectral Energy 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 using a LiCor LI200sz pyranometer that had been calibrated against an Oriel pyroelectric radiometer. Simulated solar irradiance in the center of the test chamber was maintained within 2% of four different levels: 950 W m<sup>-2</sup> (100% irradiance), 634 W m<sup>-2</sup> (66.7% irradiance), 317 W m<sup>-2</sup> (33.3% irradiance) and 0% irradiance. In all cases, irradiance varied by less than 5% across the chamber floor. Measurements at 0% irradiance were made with fluorescent room lighting that allowed normal vision but is thermally insignificant (i.e. <3 W m<sup>-2</sup>).

Metabolic rate was determined from the rate of carbon dioxide production. Air was passed through the metabolic chamber at 10.55 l min<sup>-1</sup> after being dried and scrubbed of CO<sub>2</sub>

by an air dryer/CO<sub>2</sub> absorber system (Puregas model CDA1112). Air flow was measured using an Omega FL4002G-HRV rotameter, calibrated to ±1% using a 5 l soap-bubble flow meter. These high flow rates allowed the entire respiratory apparatus to equilibrate in 5 min, following the calculations of Lasiewski *et al.* (1966). A 100 ml min<sup>-1</sup> subsample of gas was dried using anhydrous calcium sulfate and passed to a LiCor model 6252 carbon dioxide analyzer. CO<sub>2</sub> concentrations in the sample gas ranged from 115 to 335 p.p.m. The carbon dioxide analyzer resolved CO<sub>2</sub> concentration to 0.1 p.p.m., or less than 0.1% of measured values. The gas analyzer was calibrated daily using both CO<sub>2</sub>-free air and a calibration gas known to contain 2840 p.p.m. CO<sub>2</sub>.

All measurements were made during the inactive phase of the animal's daily cycle, within 1 h of the animals being removed from access to food. Data were collected at each of the three wind speeds, both in the presence and in the absence of simulated solar radiation. Animals were exposed to a given wind speed and radiation regime for 30–60 min prior to measurements. The order in which an animal was exposed to different wind speeds was randomized.

Instrument signals were recorded on a Campbell 21x 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 5 min equilibration period prior to data collection. The rate of carbon dioxide production was calculated using equation 3 of Walsberg and Wolf (1995c) 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<sub>2</sub> depletion was too small for accurate measurement. Therefore, RQ was determined in separate measurements in which animals were placed in 0.81 metabolic chambers in the absence of wind or solar radiation, with chamber temperature maintained at 3, 10, 20, 25 and 27 °C. Dry, CO<sub>2</sub>-free air flowed into the chamber at 150–510 ml min<sup>-1</sup>, allowing chamber gas composition to equilibrate in 7–25 min (Lasiewski *et al.* 1966). Rates of CO<sub>2</sub> production and O<sub>2</sub> consumption were measured simultaneously. The O<sub>2</sub> concentration of air entering and leaving the chamber was determined using an Applied Electrochemistry S3A oxygen analyzer. All measurements were made during the active phase of the animal's daily cycle, within 1 h of an animal being removed from access to food. O<sub>2</sub> consumption was calculated using equation 2 of Hill (1972). CO<sub>2</sub> production was calculated using equation 3 of Walsberg and Wolf (1995c).

Values are presented as means and 95% confidence intervals. Sample sizes are 10 for measurements of RQ and metabolism made in the absence of wind or simulated solar radiation, with the same individuals being used at each temperature. These data were analyzed by analysis of variance (ANOVA) followed by a Tukey-type test if significant differences were detected (Zar, 1984). Sample sizes are nine for measurements of animals exposed to wind or simulated solar radiation, with the same individuals being used under

each set of conditions. Data were analyzed using three-factor ANOVA followed by Tukey-type tests if significant differences were detected. In all cases, statistical significance was accepted at  $P < 0.05$ .

## Results

### Respiratory quotient

The respiratory quotient (RQ), the ratio of carbon dioxide production to oxygen consumption, varied significantly ( $P < 0.05$ ) with ambient temperature (Fig. 1A). RQ ranged from a mean of 0.76 at 10 °C to 0.86 at 27 °C. This indicates that the catabolic substrate also varied with temperature, and consequently the thermal equivalent of carbon dioxide production or oxygen consumed also varied (Fig. 1B). For estimates of metabolic heat production in subsequent measurements with animals held in the wind tunnel at  $T_{\text{air}} = 10$  °C, metabolic heat production was estimated using the mean RQ (0.776) measured at 3–20 °C and the associated thermal equivalent of CO<sub>2</sub> production (25.9 J ml<sup>-1</sup>)

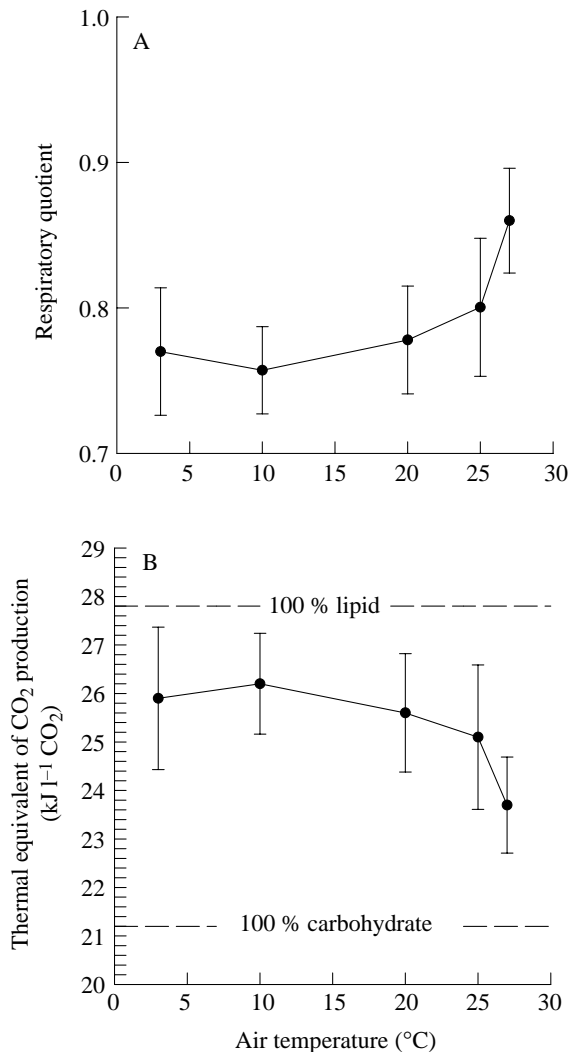


Fig. 1. Respiratory quotients (A) and thermal equivalents of carbon dioxide production (B). Values are means and 95% confidence intervals, with  $N = 10$ .

calculated from the equation of Kleiber (1961). Within this temperature range, RQ did not vary with temperature ( $P > 0.6$ ) and metabolic rates were within the range measured for animals during wind-tunnel experiments.

### Heat production in the absence of wind and short-wave irradiance

Resting rates of oxygen consumption and carbon dioxide production and metabolic heat production were inversely correlated with air temperature over the measured range of 3–27 °C (Fig. 2). No evidence of a thermal neutral zone was detected. Basal metabolic rate, therefore, is presumably attained at air temperatures at or above 27 °C. Our values for rates of oxygen consumption in the absence of wind or solar radiation are very similar to those of Heldmaier (1975); the least-squares regression equation he fitted to his data below 27 °C predicts values within 1% of our mean values.

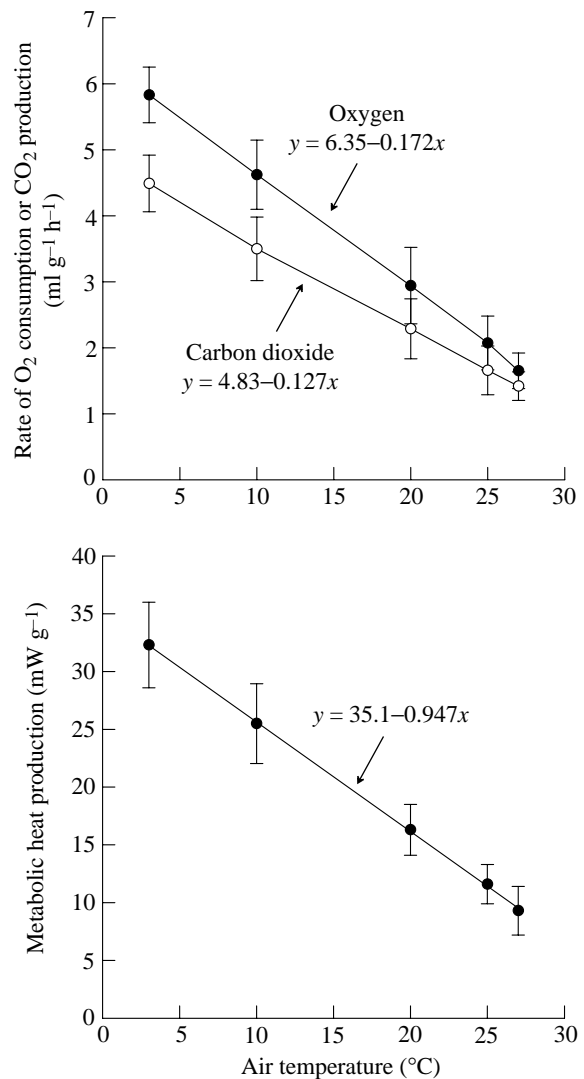


Fig. 2. Resting rates of oxygen consumption and carbon dioxide production and metabolic heat production in the absence of wind and solar radiation. Values are means and 95% confidence intervals ( $r^2 = 0.99$ ;  $N = 10$ ;  $P < 0.05$ ).

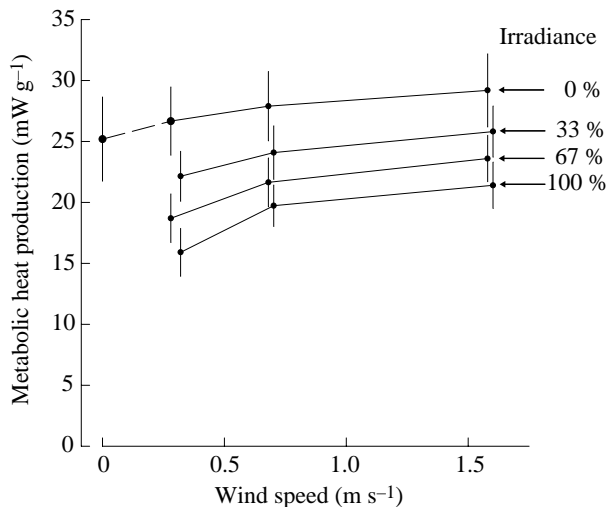


Fig. 3. Metabolic heat production as functions of wind speed and intensity of simulated solar radiation. Irradiance is expressed as a percentage of the maximum used,  $950 \text{ W m}^{-2}$ . Values are means and 95% confidence intervals, with  $N=9$ . The value at 0% irradiance and  $0 \text{ m s}^{-1}$  wind is that reported in Fig. 2 ( $N=10$ ).

#### Heat production as a function of wind and irradiance

Increasing irradiance by amounts equal to or greater than 67% of maximum irradiance ( $950 \text{ W m}^{-2}$ ) significantly depressed metabolic heat production (Fig. 3). That is, metabolic rate was significantly depressed when irradiance was elevated from 0% to 67% of maximum, from 0% to 100% of maximum, or from 33% to 100% of maximum. Increasing irradiance from 0% to 100% significantly depressed metabolic heat production by 27–41%, with the larger fractional reductions occurring at lower wind speeds. Increasing irradiance by only 33% of maximum (i.e. from 0% to 33% of maximum, and from 33% to 67% of maximum) had no statistically significant effects upon metabolic heat production.

At both of the two highest irradiance levels, wind speed significantly affected metabolic rate (Fig. 4). At 67% of full irradiance, metabolic heat production at  $1.6 \text{ m s}^{-1}$  averaged 26% above that at  $0.3 \text{ m s}^{-1}$ . At 100% irradiance, metabolic heat production at  $1.6 \text{ m s}^{-1}$  averaged 35% above that at  $0.3 \text{ m s}^{-1}$ . At the two lower irradiance levels of 0% and 33% of maximum irradiance, wind speed had no statistically significant effects upon metabolic heat production.

## Discussion

### Variation in respiratory quotient with environmental temperature

Unexpectedly, the respiratory quotient varied significantly with ambient temperature. Although relatively constant at low air temperatures, RQ increased rapidly with temperature above  $20^\circ\text{C}$ , despite diet composition being unchanged. This is similar to the observations of Heldmaier (1975), who found RQ in *Phodopus sungorus* to be stable at approximately 0.75 over the temperature range  $-35$  to  $0^\circ\text{C}$  but to increase to

approximately 0.92 at temperatures above  $20^\circ\text{C}$ . The bases of such elevations are unclear, but a likely explanation is that the catabolic substrate varied with changing environmental temperature and that reliance upon lipids increased at lower temperatures. One possibility is that this reflects a shift from a carbohydrate-rich substrate supplied by the diet to one dominated by body lipid stores. Proximate analyses supplied by the manufacturer indicate that the diet consisted of 26.6% protein, 4.8% lipid and 68.6% carbohydrate (ash-free, dry mass). Using the conversion factors of Blaxter (1989), this predicts a respiratory quotient of 0.92 if the animal digested, assimilated and catabolized materials in direct proportion to their abundance in the diet. If, because of increased metabolic demands, animals at low temperatures move more rapidly towards the reliance upon body lipid stores characteristic of fasting metabolism, then the pattern observed in Fig. 1 could

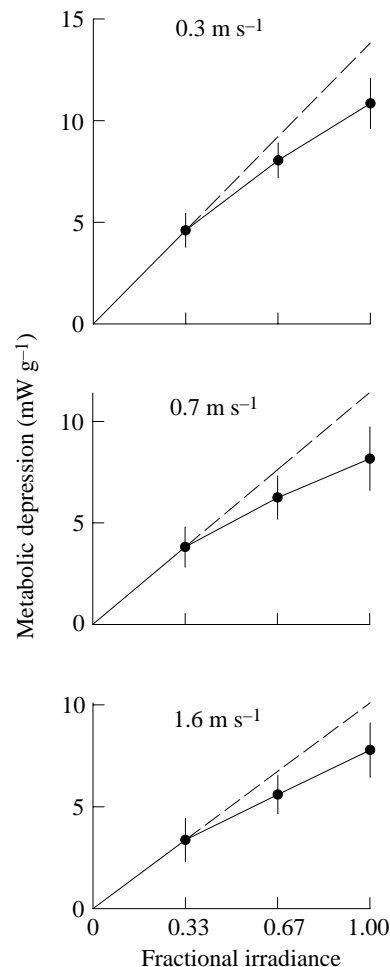


Fig. 4. Depression of metabolic heat production ( $\text{mW g}^{-1}$ ) associated with exposure to simulated solar radiation. Values are calculated for individual animals as the difference between metabolic heat production in the absence of solar radiation and that in the presence of simulated solar radiation, with wind speed constant. Dashed lines represent values expected on the basis of data at 33% irradiance and assuming that the physiological responses of the animal scale linearly with the intensity of irradiance. Values are means and 95% confidence intervals, with  $N=9$ .

result. This would, however, require that animals at moderate air temperatures (e.g. 20 °C) become nearly postabsorptive within 1 h after removal from food, and that animals at higher temperatures (e.g. 27 °C) do not. We cannot evaluate the likelihood of this occurring.

Such variation in the respiratory quotient is probably unimportant for the current analysis in which hamsters in the wind-tunnel metabolic chamber were exposed to environmental conditions that elicited rates of carbon dioxide production similar to those of animals during RQ measurements exposed to air temperatures below 20 °C in the absence of wind and solar radiation. For other studies, however, a significant thermal dependence of RQ upon environmental conditions, independent of diet composition, could create substantial difficulties. The error is smallest when metabolic heat production is estimated from oxygen consumption, as the thermal equivalent of consumed oxygen varies by approximately 12% between pure carbohydrate substrates and pure lipid substrates (Walsberg and Wolf, 1995c). Errors can be much larger when heat production is estimated from measurements of carbon dioxide production, because the thermal equivalent of CO<sub>2</sub> production can vary by approximately 34% with different substrates (Walsberg and Wolf, 1995c). Estimated using the equation of Blaxter (1989) and assuming that animals are not catabolizing protein, the thermal equivalent of carbon dioxide production differs by 11% as RQ changes from 0.76 to 0.86. The greater range observed by Heldmaier (1975) corresponds to a 19% change in the thermal equivalent of CO<sub>2</sub> production. Such variation is much greater than errors likely to occur in either laboratory or field measurements of carbon dioxide production. Well-calibrated laboratory analyses should yield measurements of carbon dioxide production accurate to within 2%, and the doubly labeled water technique for estimating CO<sub>2</sub> production in free-living animals is accurate within 8% (Nagy, 1989). In addition to this temperature-dependence, taxonomic differences, time spent fasting, time of day and diet also produce unexpected variation beyond that normally expected from differing ratios of lipid:carbohydrate:protein. Such variations can lead to rapid and large changes in the estimated thermal equivalent of carbon dioxide production (e.g. >25%; Walsberg and Wolf, 1995c). This suggests that substantial uncertainties exist in our understanding of the relationship between respiratory gas exchange and metabolic heat production, and that it is possible for these to represent large and limiting errors in indirect calorimetry.

#### *Depression of metabolic heat production with increasing irradiance*

The depression of metabolic heat production resulting from exposure to simulated solar radiation is not simply a multiple of the intensity of irradiance. Rather, metabolic responses to higher levels of irradiance are significantly blunted compared with those expected on the basis of the response to 33% irradiance; a doubling or tripling of irradiance does not result in a doubling or tripling of the metabolic depression

experienced by the animal. Instead, depressions of metabolic heat production are 14–29% smaller than expected.

This blunting of metabolic responses to increasing insolation is probably not an adaptive response to reduce the heat load on the animal. The highest heat load on animals was produced by the combination of 0.3 m s<sup>-1</sup> wind and 950 W m<sup>-2</sup> radiation, which elicited a mean metabolic heat production of 15.9 mW g<sup>-1</sup>. This is similar to the value (16.3 mW g<sup>-1</sup>) measured at an air temperature of 20 °C in the absence of solar radiation and wind, and 71% above the minimum measured at an air temperature of 27 °C (Fig. 2). Thus, there is no evidence that irradiance produced heat loads on the animal sufficient to approach thermal neutrality, and it seems unlikely that the animal would elect to reduce heat gain under such circumstances.

Alternatively, it is possible that blunting of the physiological consequences of increasing levels of simulated solar radiation is a passive result of changes in coat or boundary layer insulation. Heat loss from an animal occurs through insulating coats by the coupled processes of long-wave radiation, free convection and forced convection (Cena and Monteith, 1975a,b). Changes in solar irradiance are likely to alter the balance of these processes, because short-wave radiation is not merely absorbed at the outer coat surface, but rather penetrates substantially into the fur. In the case of free convection, increasing short-wave irradiance penetrating into a coat may exacerbate internal thermal gradients driving heat flow within the coat. This would reduce coat thermal resistance, elevating net heat loss from the animal and reducing the metabolic depression associated with exposure to solar radiation.

Another process might be the reduction of the thermal resistance provided by the aerodynamic boundary layer adjacent to the outer coat surface. This is most likely to be significant at wind speeds sufficiently low for free convection to be a dominant mode of heat flow. However, free convection is unlikely to dominate heat flow even at 0.3 m s<sup>-1</sup>, the lowest wind speed used. The relative importance of free and forced convection can be evaluated by calculating the ratio  $Gr/Re^2$ , where  $Gr$  is the Grashof number and  $Re$  is the Reynolds number (Campbell, 1977). This value represents the ratio of buoyant forces in the aerodynamic boundary layer (stimulating free convection) to inertial forces (stimulating forced convection). Assuming a characteristic dimension of 0.06 m and that the surface-to-air temperature gradient is less than 15 °C, calculating  $Gr/Re^2$  for the lowest wind speed of 0.3 m s<sup>-1</sup> indicates that free convection is of only marginal importance ( $Gr/Re^2=0.3$ ). Under such conditions, heat flow by forced convection should occur at a rate approximately three times that by free convection. At higher wind speeds, free convection is likely to be even less important. For temperature gradients of less than 15 °C, forced convection at 1.6 m s<sup>-1</sup> should occur at a rate approximately 80 times that by free convection ( $Gr/Re^2=0.013$ ).

#### *Concluding comments*

Solar radiation can be of overwhelming importance for the

heat balance of animals in nature, but predicting its effects precisely is fraught with difficulties. Currently, three approaches are most common and each incorporates significant difficulties or uncertainties. Mathematical models are available that integrate major modes of heat transfer between animals and their environments and allow computation of net heat loads (e.g. Campbell, 1977). Not only does the use of such models require quantification of the variety of microenvironments occupied by animals in nature (which can be technically challenging) but, for species with insulating coats, the requisite models (e.g. Walsberg *et al.* 1978; Gebremedhin *et al.* 1983) subsume variables such as the microstructure of the fur as well as the optical properties of individual hairs (which is technically challenging). A retreat to simpler models not incorporating such factors leads to large errors in estimates of animal heat balance (Walsberg *et al.* 1978; Walsberg, 1988b).

An alternative approach is the use of taxidermic mounts of animals that consist of a metal cast of the animal's body covered by the animal's integument (Bakken and Gates, 1975). These 'operative temperature thermometers' are supposed to integrate all critical environmental and animal properties, including hair and coat properties, and have become widely used over the past 20 years (e.g. Chappell and Bartholomew, 1981; Bennett *et al.* 1984; Chappell *et al.* 1984; Goldstein, 1984; Weathers, 1986; Kenagy *et al.* 1989; Gibson and Bachman, 1992). However, empirical tests of such mounts reveal that their use without careful calibration can yield large errors (Walsberg and Wolf, 1996a,b). The accuracy of mounts differs greatly among species and among types of mounts for the same species. Therefore, for each particular application involving exposure to sunlight, it is necessary to demonstrate empirically the accuracy of operative-temperature thermometers. Unfortunately, this can require extensive investment of time and resources and has rarely been accomplished (Walsberg and Wolf, 1996a).

A third approach is to measure the animal's responses to a restricted set of radiative conditions and to extrapolate to the continuous range observed in nature. The present study demonstrates the difficulties of this approach. Because changes in irradiance levels do not have simple linear effects upon the animal's metabolic heat production, even in a simplified situation, significant errors can accumulate from such extrapolations. This may substantially complicate biophysical analyses.

### References

- BAKKEN, G. S. AND GATES, D. M. (1975). Heat transfer analysis of animals: some implications for field ecology, physiology and evolution. In *Perspectives of Biophysical Ecology* (ed. D. M. Gates and R. B. Schmerl), pp. 255–290. New York: Springer-Verlag.
- 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.
- BENNETT, A. F., HUEY, R. B., JOHN-ALDER, H. AND NAGY, K. A. (1984). The parasol tail and thermoregulatory behavior of the cape ground squirrel *Xenops inauris*. *Physiol. Zool.* **57**, 57–62.
- BLAXTER, K. (1989). *Energy Metabolism in Animals and Man*. New York: Cambridge University Press.
- CAMPBELL, G. S. (1977). *An Introduction to Environmental Biophysics*. New York, Heidelberg, Berlin: Springer.
- CENA, K. AND MONTEITH, J. L. (1975a). Transfer processes in animal coats. I. Radiative transfer. *Proc. R. Soc. Lond. B* **188**, 337–394.
- CENA, K. AND MONTEITH, J. L. (1975b). Transfer processes in animal coats. II. Conduction and convection. *Proc. R. Soc. Lond. B* **188**, 395–411.
- CHAPPELL, M. A. AND BARTHOLOMEW, G. A. (1981). Standard operative temperatures and thermal energetics of the antelope ground squirrel *Ammospermophilus leucurus*. *Physiol. Zool.* **54**, 81–93.
- CHAPPELL, M. A., GOLDSTEIN, D. L. AND WINKLER, D. W. (1984). Oxygen consumption, evaporative water loss and temperature regulation of California gull chicks (*Larus californicus*) in a desert rookery. *Physiol. Zool.* **57**, 204–214.
- GEBREMEDHIN, K., PORTER, W. P. AND CRAMER, C. O. (1983). Quantitative analysis of the heat exchange through the fur layers of Holstein calves. *Trans. Am. Soc. agr. Eng.* **26**, 188–193.
- GIBSON, R. B. AND BACHMAN, G. C. (1992). The costs of female choice in a lekking bird. *Behav. Ecol.* **3**, 300–309.
- GOLDSTEIN, D. L. (1984). The thermal environment and its constraint on activity of desert quail in the summer. *Auk* **101**, 542–550.
- HAMILTON, W. J. AND HEPPNER, F. (1967). Radiant solar energy and the function of black homeotherm pigmentation: an hypothesis. *Science* **155**, 196–197.
- HELDMAIER, G. (1975). Metabolic and thermoregulatory responses to heat and cold in the Djungarian hamster *Phodopus sungorus*. *J. comp. Physiol.* **102**, 115–122.
- 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. *Oecologia* **78**, 269–282.
- 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.
- NAGY, K. A. (1989). Doubly-labeled water studies of vertebrate physiological ecology. In *Stable Isotopes in Ecological Research: Ecological Studies* vol. 68 (ed. P. W. Rundel, J. R. Ehleringer and K. A. Nagy), pp. 270–287. New York: Springer-Verlag.
- WALSBURG, G. E. (1982). Coat color, solar heat gain and visual conspicuousness in the phainopepla. *Auk* **99**, 495–502.
- WALSBURG, G. E. (1988a). The significance of coat structure for solar heat gain in the rock squirrel, *Spermophilus variegatus*. *J. exp. Biol.* **138**, 243–257.
- WALSBURG, 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., WEAVER, T. O. AND WOLF, B. O. (1997). Color-independent adjustment of solar heat gain in a desert mammal. *Physiol. Zool.* **70**, 150–157.
- WALSBERG, G. E. AND WOLF, B. O. (1995a). Solar heat gain in a desert rodent: unexpected increases with wind speed and implications for estimating the heat balance of free-living animals. *J. comp. Physiol.* **165**, 306–314.
- WALSBERG, G. E. AND WOLF, B. O. (1995b). Effects of solar radiation and wind speed on metabolic heat production by two mammals with contrasting coat colors. *J. exp. Biol.* **198**, 1499–1507.
- WALSBERG, G. E. AND WOLF, B. O. (1995c). Variation in the respiratory quotient of birds and implications for indirect calorimetry using measurements of carbon dioxide production. *J. exp. Biol.* **198**, 213–219.
- WALSBERG, G. E. AND WOLF, B. O. (1996a). An appraisal of operative temperature mounts as practical tools for studies of ecological energetics. *Physiol. Zool.* **69**, 658–681.
- WALSBERG, G. E. AND WOLF, B. O. (1996b). A test of the adequacy of operative temperature thermometers for studies of small ectotherms. *J. therm. Biol.* **21**, 275–281.
- WEATHERS, W. W. (1986). Thermal significance of courtship display by the blue-black grassquit (*Volatinia acarina*). *Natn geogr. Res.* **2**, 291–301.
- WOLF, B. O. AND WALSBERG, G. E. (1996). Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology* **77**, 2228–2236.
- ZAR, J. H. (1984). *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice Hall.