

## EFFECTS OF COMPLEX RADIATIVE AND CONVECTIVE ENVIRONMENTS ON THE THERMAL BIOLOGY OF THE WHITE-CROWNED SPARROW (*ZONOTRICHIA LEUCOPHRYS GAMBELII*)

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### Summary

The energy budgets of small endotherms are profoundly affected by characteristics of the physical environment such as wind speed, air temperature and solar radiation. Among these, solar radiation represents a potentially very large heat load to small animals and may have an important influence on their thermoregulatory metabolism and heat balance. In this investigation, we examined the interactive effects of wind speed and irradiance on body temperature, thermoregulatory metabolism and heat balance in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). We measured changes in metabolic heat production by exposing birds to different wind speeds (0.25, 0.5, 1.0 and 2.0 m s<sup>-1</sup>) and irradiance combinations (<3 W m<sup>-2</sup> and 936±11 W m<sup>-2</sup>; mean ± s.d.) at an air temperature of 10 °C.

Body temperature was not affected by wind speed, but was significantly higher in animals not exposed to simulated solar radiation compared with those exposed at most wind speeds. In the absence of solar radiation, metabolic heat production was strongly affected by wind speed and increased by 30% from 122 to 159 W m<sup>-2</sup> as wind speed increased from 0.25 to 2.0 m s<sup>-1</sup>. Metabolic heat production was even more strongly influenced by wind speed in the presence of simulated solar radiation and increased by 51% from 94 to 142 W m<sup>-2</sup> as wind speed increased from 0.25 to 2.0 m s<sup>-1</sup>. Solar heat gain was

negatively correlated with wind speed and declined from 28 to 12 W m<sup>-2</sup> as wind speed increased from 0.25 to 2.0 m s<sup>-1</sup> and, at its maximum, equaled 11% of the radiation intercepted by the animal. The overall thermal impact of the various wind speed and irradiance combinations on the animal's heat balance was examined for each treatment. Under cold conditions, with no solar radiation present, an increase in wind speed from 0.25 to 2.0 m s<sup>-1</sup> was equivalent to a decrease in chamber air temperature of 12.7 °C. With simulated solar radiation present, a similar increase in wind speed was equivalent to a decrease in chamber air temperature of 16 °C. Overall, shifting environmental conditions from a wind speed of 0.25 m s<sup>-1</sup> and irradiance of 936 W m<sup>-2</sup> to a wind speed of 2.0 m s<sup>-1</sup> with no short-wave radiation present was equivalent to decreasing chamber air temperature by approximately 20 °C.

The sensitivity to changes in the convective environment, combined with the complex effects of changes in irradiance levels revealed by re-analyzing data published previously, significantly complicates the task of estimating the heat balance of animals in nature.

Key words: white-crowned sparrow, *Zonotrichia leucophrys gambelii*, thermoregulation, convection, radiation, heat transfer, metabolic heat production, solar heat gain, body temperature.

### Introduction

The maintenance of high body temperatures is a costly enterprise for small endotherms and in many species may account for a major portion of their daily energy expenditure. The basal metabolic and thermoregulatory costs of small birds, for example, typically account for 40–60% of their total daily energy expenditure. These rates of energy expenditure are strongly influenced by characteristics of the physical environment or the 'microclimates' the animal occupies. Surprisingly, of the physical environmental factors that define an animal's microclimate (e.g. air temperature, solar radiation and wind speed), only the effects of air temperature are well

studied (for a review, see Calder and King, 1974). The effects of wind speed on avian thermoregulatory metabolism have also received some attention, and convective heat transfer clearly plays a significant role in determining the heat balance and thermoregulatory costs in small birds (for a review, see Goldstein, 1984; see also Bakken et al., 1991; Buttemer, 1981; Webb and Rogers, 1988; Webster and Weathers, 1988; Wolf and Walsberg, 1996).

Solar radiation represents a potentially overwhelming heat load to small animals and may therefore significantly influence thermoregulatory metabolism; under clear skies, it commonly

exceeds  $900\text{--}1000\text{ W m}^{-2}$  on a plane perpendicular to the solar beam. To date, only a handful of studies have focused on the effects of solar radiation on heat balance and thermoregulation in small birds (DeJong, 1976; Hamilton and Heppner, 1967; Heppner, 1970; Lustick, 1969, 1971; Lustick et al., 1970), all these studies being carried out in the absence of wind (e.g. under free-convective conditions).

Taken together, these analyses provide important insight into the thermoregulatory responses of small birds to challenges from their thermal environment, but impart an incomplete picture of how animals respond physiologically to complex natural environments. Especially lacking is an understanding of the interactive effects between solar radiation and forced convection on the heat balance and thermoregulatory costs of wild birds; empirical data are available from only a single study of the desert-dwelling verdin, *Auriparus flaviceps* (Wolf and Walsberg, 1996). These data suggest that the convective environment has a significant influence on radiative heat loads transferred from the animal's plumage surface to its skin. Unfortunately, it is difficult to generalize how forced convection affects radiative heat transfer from a single study. In addition, the available data set may be not indicative of a generalized response because of the extremely small body size (approximately 6.5 g) of the verdin and its light insulation (e.g. plumage mass was 29% lower than allometric predictions; Webster and Weathers, 1988).

Radiative heat flow from the plumage surface to the bird's skin is affected by variations in wind speed because of alterations in boundary layer and plumage heat transfer resistance. In birds, incident radiation does not simply interact with feather elements at the plumage surface to produce heat, but may penetrate more deeply into the plumage. Thus, the heat load that the skin receives is influenced not only by such conspicuous factors as wind speed and coat color but also by more subtle properties such as the microstructure and optics of the feather elements. In mammals, such factors have been found to have an overwhelming effect on the heat load transferred to the skin (Walsberg and Wolf, 1995b). Finally, other factors, such as changes in peripheral circulation and pilo- or ptilo-erection in response to irradiation, may greatly modify the total thermal resistance of the animal's coat. Unfortunately, it is a difficult task to integrate these factors and to estimate accurately, or to model in a simple manner, the effects of varying convective environments on the radiative heat loads experienced by animals that possess fibrous pelts or plumages.

In this investigation, we examine how complex radiative and convective environments affect thermoregulatory costs and heat transfer in a small bird. We focus on the following questions. (i) How does solar radiation and wind speed affect metabolic heat production in a small finch? (ii) To what degree does forced convection affect physiologically significant solar heat gain? Physiologically significant solar heat gain (SHG) 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 different wind speeds. (iv) How much intercepted radiation is utilized by the animal, as shown by concurrent reductions in metabolic rate associated with irradiation? (v) How is body temperature affected by differing convective and radiative regimes? We chose the white-crowned sparrow (*Zonotrichia leucophrys gambelii*) as a study animal because of the extensive background research on its thermoregulatory processes and physiology (e.g. DeJong, 1976; Ketterson and King, 1977; King, 1964; Mahoney and King, 1977; Paladino and King, 1984; Robinson et al., 1976).

## Materials and methods

### *Experimental animals*

White-crowned sparrows *Zonotrichia leucophrys gambelii* were captured with mist nets in Apache Junction, AZ, USA, during January 1995. The birds were transported to Arizona State University, Tempe, Arizona, where they were housed individually in BioQuip  $0.2\text{ m}^3$  folding insect cages in a temperature-controlled environmental room. The room temperature was maintained at  $24\pm 0.5^\circ\text{C}$  and the photoperiod was held at 10h:14h L:D. Sparrows were maintained on an *ad libitum* diet of chick starter and wild bird seed. Water and grit were also freely available.

### *Environmental simulation*

Metabolic measurements were made both in the presence and absence of simulated solar radiation with the sparrows placed in a closed-circuit wind tunnel, described by Walsberg and Wolf (1995b). This wind tunnel had an effective volume of 451, calculated following Bartholomew et al. (1981). A variable-speed direct-current blower circulated air through the chamber test section at wind speeds ( $u$ ) ranging from  $0.25$  to  $2.0\text{ m s}^{-1}$ , as measured using a Thermoanemometer HWA-101 thermoanemometer that had been calibrated as described by Walsberg (1988). Vertical and horizontal louvers installed upstream of the test section were adjusted to ensure uniform airflow within the chamber. Wind speed varied less than 5.0% vertically and horizontally except within 1 cm of the chamber walls. Turbulence intensity was 3% or less at all wind speeds, as determined using a thermoanemometer with the signal output measured by a true-root-mean-square voltmeter (Beckman model 850) and computed using the method of Hinze (1959).

Simulated solar radiation was produced by a Spectral Energy Corp. series II solar simulator, which filters light produced by a 1 kW xenon arc lamp to simulate direct solar radiation at an air mass of 1. Irradiance within the test section of the chamber was maintained at  $936\pm 11\text{ W m}^{-2}$  (mean  $\pm$  s.d.) (high irradiance) and was measured using a LiCor LI200sz pyranometer that had been calibrated against an Oriel Corp. model 7080 pyroelectric radiometer. Simulated solar radiation passed through a 4.8 mm flint glass window installed in the top of the chamber test section and onto the animal. The flint glass blocked the intense ultraviolet radiation produced by the lamp,

which could potentially have burned the eyes and skin of the experimental animal. Wind tunnel measurements in the absence of simulated solar radiation (low irradiance) were carried out under fluorescent room lighting at an irradiance of less than  $3 \text{ W m}^{-2}$ .

Chamber air temperature was maintained at  $10 \pm 0.5 \text{ }^\circ\text{C}$  by placing it within a temperature-controlled room and by circulating water from a constant-temperature reservoir through heat-exchange coils located in the walls of the test section and in the airstream downwind of the test section. Chamber air temperature was measured using a 26 gauge type T thermocouple calibrated at two points, at  $0 \text{ }^\circ\text{C}$  in a distilled water ice bath and at  $35 \text{ }^\circ\text{C}$  in a water bath against a mercury thermometer traceable to National Bureau of Standards and recorded by a Campbell model CR21x datalogger. The long-wave radiant environment in the test section of the chamber was held nearly constant by painting the walls of the chamber flat black. Assuming an emissivity of 0.98 and calculating the long-wave irradiance using the Stefan-Boltzmann relationship, we estimated that long-wave emission varied less than 6%.

#### *Carbon dioxide production and body temperature measurements*

A Puregas model CDA1112 air dryer/ $\text{CO}_2$  scrubber system provided dry,  $\text{CO}_2$ -free air that ventilated the metabolic chamber at a rate of  $12028 \pm 65 \text{ ml min}^{-1}$  (mean  $\pm$  S.D.). Incurrent flow was measured using an Omega FL 3404T-HRV rotameter, calibrated to  $\pm 1\%$  of full scale with a 51 soap-bubble flowmeter. These flow rates allowed the gas mixture within the metabolic chamber to reach 99% equilibrium in approximately 17 min, as calculated following Lasiewski et al. (1966). A sample of chamber effluent air was dried, by passing it through a column of anhydrous calcium sulphate at  $150 \text{ ml min}^{-1}$ , and then passed into a LiCor model 6252 infrared  $\text{CO}_2$  analyzer that determined  $\text{CO}_2$  concentration to  $\pm 1.0$  p.p.m. The  $\text{CO}_2$  analyzer was zeroed and spanned daily using dry  $\text{CO}_2$ -free air and a calibration gas known to contain 0.1570%  $\text{CO}_2$ . Instrument signals were recorded on a Campbell model CR21x datalogger and averaged at 1 min intervals.

Metabolic measurements were made during the photophase within the closed-circuit wind tunnel, both in the presence and absence of simulated solar radiation. Measurements were made on 10 adult white-crowned sparrows (mean body mass  $\pm$  S.D.,  $22.9 \pm 1.5 \text{ g}$ ) between January and May 1995. Sparrows were blindfolded during measurements, to minimize locomotor activity, with a  $1 \text{ cm} \times 3 \text{ cm}$  black Lycra strip that covered their eyes and through which their bill protruded; an elastic thread stretched around the back of the skull held the blindfold in place. Birds were placed on a dowel perch in the center of the test section of the chamber 2.5 cm above the chamber floor and rested quietly for approximately 60 min at each wind speed ( $u=0.25, 0.5, 1.0$  or  $2.0 \text{ m s}^{-1}$ ) while  $\text{CO}_2$  production was measured. The order in which animals were exposed to wind speed/irradiance combinations was randomized, and sparrows were exposed to only a single wind speed and irradiance combination on a single day. We report data for the minimum

1 min average values for  $\text{CO}_2$  production measurements taken during the last 7 min of each 1 h run. All measurements were corrected to standard conditions ( $0 \text{ }^\circ\text{C}$ , 101 kPa) using equation 6.5 of Mclean and Tobin (1987) for flow measurements using rotameters. A Magnavox CCD camera surveillance system mounted above the chamber test section monitored the activity of each bird during the experiments; runs in which birds did not sit quietly on the perch were excluded from analyses.

The body temperatures of sparrows were obtained, within 1 min of the end of each run, after the bird's removal from the metabolic chamber. An 18 gauge Physitemp Teflon sheathed thermocouple with a time constant of 0.1 s was inserted approximately 15 mm into the sparrow's cloaca, until a slight withdrawal did not result in a decrease in temperature. Thermocouple temperatures were read using an Omega model HH23 digital thermocouple thermometer.

#### *Respiratory quotient measurements and total evaporative water loss*

Respiratory quotients (RQ) and total evaporative water loss (TEWL) were measured in a separate series of experiments because the high flow rates used in the wind tunnel experiments precluded accurate measurements of oxygen consumption. Methods used are outlined below, and details of calibration procedures and of the apparatus used can be found in Walsberg and Wolf (1995a). Measurements were made between 09:00 and 15:00 h on recently fed (not post-absorptive) birds ( $N=12$ ) held in the dark at  $10 \text{ }^\circ\text{C}$ . Birds were placed in 21 metabolic chambers and rested quietly on  $1.3 \text{ cm}^2$  mesh hardware cloth above 2 cm of mineral oil used for the collection of fecal material. Dry,  $\text{CO}_2$ -free air flowed through the metabolic chamber at a rate of  $505 \text{ ml min}^{-1}$ . A sample of chamber effluent air passed over a Thunder scientific humidity evaluation module (model PC-2101) and was dried by passing it through a column of anhydrous calcium sulphate at  $100 \text{ ml min}^{-1}$  and into a LiCor model 6252  $\text{CO}_2$  analyzer that determined  $\text{CO}_2$  concentration to  $\pm 1.0$  p.p.m. After leaving the  $\text{CO}_2$  analyzer, efflux air was dried and scrubbed of  $\text{CO}_2$  by passing it through a small column of anhydrous calcium sulphate and Ascarite, and oxygen concentration was determined using an Applied Electrochemistry S3a oxygen analyzer calibrated using the procedures of Walsberg and Wolf (1995a).

We report data for the minimum 1 min average values for evaporative water loss,  $\text{CO}_2$  production and oxygen consumption on measurements taken during the last 7 min of each 1 h run. Instrument signals were recorded on a Campbell model CR21x datalogger that averaged the values for each minute. The activity of each bird was monitored during the experiments using a Magnavox CCD camera surveillance system. We calculated oxygen consumption rates using equation 2 of Hill (1972) and  $\text{CO}_2$  production rates using equation 3 of Walsberg and Wolf (1995a). Measurements were corrected to standard conditions ( $0 \text{ }^\circ\text{C}$ , 101 kPa) using equation 6.5 of Mclean and Tobin (1987) for flow measurements using rotameters.

### Analyses

We computed metabolic heat production from  $\dot{V}_{\text{CO}_2}$  using  $20.9 \text{ J ml}^{-1}$  as the thermal equivalent of carbon dioxide. We divided these values by plumage surface area estimated from body mass (g) using the Meeh equation, as modified by Walsberg and King (1978), to obtain surface-area-specific heat production ( $\dot{H}_m$ ).

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

$$r_b = [k(T_b - T_e)/(\dot{H}_m - \dot{H}_e)] - r_e. \quad (1)$$

The animal's total body thermal resistance ( $r_b$ ) subsumes coat insulation and the thermal resistance of the peripheral tissues.  $k$  is a constant ( $1200 \text{ J m}^{-3} \text{ K}^{-1}$ ) and  $T_b$  is body temperature, measured immediately following each metabolic trial.  $T_e$  is operative temperature ( $10^\circ\text{C}$  for experiments conducted in the absence of solar radiation).  $\dot{H}_e$  is heat loss by evaporation, also expressed on the basis of plumage surface area ( $\text{W m}^{-2}$ ). We assumed that latent heat loss was not affected by wind speed at temperatures below  $20^\circ\text{C}$ , as demonstrated for small birds by Robinson et al. (1976) and Buttemer (1981).

For all wind speeds, we assumed that forced convective heat loss from the plumage surface approximated heat transfer from a sphere of similar size. The equivalent parallel resistance between the environment and the animal's outer surface ( $r_e$ ) equals the parallel sum of a radiative resistance ( $r_r$ ) and the resistance of the aerodynamic boundary layer ( $r_a$ ):

$$r_e = (r_r r_a / r_r + r_a). \quad (2)$$

$r_a$  ( $\text{s m}^{-1}$ ) was calculated using the equations of (Mitchell, 1976) as combined by Webster and Weathers (1988):

$$r_a = 2.7d^{0.4}(v/u)^{0.6}/D_H, \quad (3)$$

where  $u$  is wind speed ( $\text{m s}^{-1}$ ),  $v$  is the kinematic viscosity of air ( $1.46 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$ ),  $D_H$  is the thermal diffusivity of air ( $2.08 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$ ) and  $d$  is the characteristic dimension of the animal, taken as  $0.035 \text{ m}$  for the white-crowned sparrow. The effective resistance to radiative heat transfer,  $r_r$  ( $\text{s m}^{-1}$ ), was calculated following Campbell (1977):

$$r_r = k/4\sigma\epsilon T_a^3, \quad (4)$$

where  $k$  is a constant ( $1200 \text{ J m}^{-3} \text{ K}^{-1}$ ),  $\sigma$  is the Stefan-Boltzmann constant ( $5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$ ),  $\epsilon$  is the emissivity of the animal's surface, assumed to be  $0.98$ , and  $T_a$  is chamber air temperature.

### Statistical analyses

Values are presented as means  $\pm 95\%$  confidence intervals except where otherwise noted. Mean values for body temperature measurements taken in the presence and absence of simulated solar radiation were compared at each wind speed using a paired two-sample Student's  $t$ -test using Microsoft Excel. Analyses of covariance and least squares regression

were carried out using JMP statistical software. We did not use a repeated-measures analysis of covariance (ANCOVA) because only two birds were used in all eight wind speed/irradiance treatments. Thirteen birds were used during the course of the study.

## Results

Daytime RQ averaged  $1.01 \pm 0.01$  ( $N=12$ ). On the basis of this value, the thermal equivalent of carbon dioxide produced is estimated as  $20.9 \text{ kJ l}^{-1}$  (Brody, 1945). Total evaporative water loss averaged  $9.3 \pm 0.5 \text{ mg g}^{-1} \text{ h}^{-1}$  ( $N=12$ ), and latent heat loss averaged  $22.8 \text{ W m}^{-2}$ , calculated using a value of  $2.42 \text{ kJ g}^{-1} \text{ H}_2\text{O}$ .

### Body temperature variation

Fig. 1 presents  $T_b$  as a function of wind speed and irradiance. We found no correlation between  $T_b$  and wind speed, so we pooled  $T_b$  data for all wind speeds at a given irradiance level.  $T_b$  differed significantly with irradiance level at all wind speeds tested except  $1.0 \text{ m s}^{-1}$  (Fig. 1). At  $T_a=10^\circ\text{C}$ , and at the low level of irradiance,  $T_b$  averaged  $42.5 \pm 0.4^\circ\text{C}$ ; at the high level of irradiance,  $T_b$  averaged  $41.8 \pm 0.3^\circ\text{C}$ .

### Variation in metabolic heat production with wind speed and irradiance level

We examined differences in the relationships between metabolic heat production and wind speed at our two

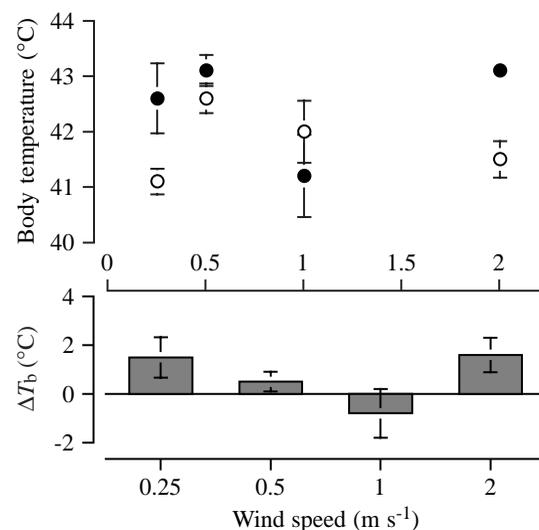


Fig. 1. Variation in body temperature with wind speed and irradiance in white-crowned sparrows.  $N=10$  for each wind speed and irradiance group. The upper panel shows mean body temperature  $\pm 95\%$  confidence intervals for birds exposed to  $936 \pm 11 \text{ W m}^{-2}$  (mean  $\pm$  s.d.) of simulated solar radiation (open circles) and to normal room lighting at less than  $3 \text{ W m}^{-2}$  (filled circles). Chamber air temperature ( $T_a$ ) was held at  $10^\circ\text{C}$  for all treatments. The lower panel shows the difference in body temperature ( $\Delta T_b$ ) and  $95\%$  confidence intervals between irradiance treatments as a function of wind speed. Body temperature for the high- and low-irradiance treatments were significantly different at all wind speeds except  $1.0 \text{ m s}^{-1}$ .

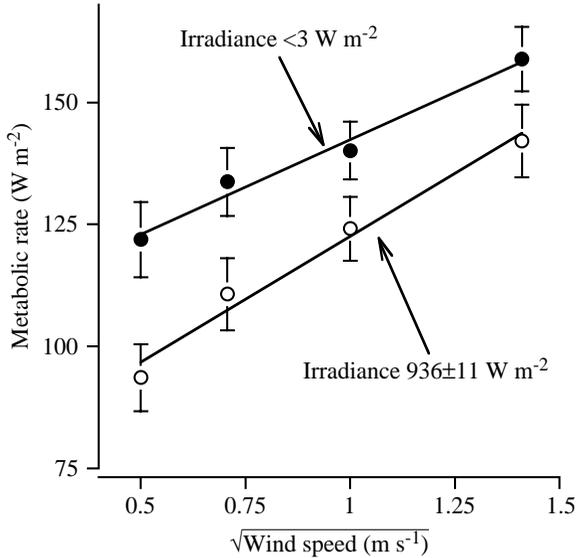


Fig. 2. Metabolic heat production ( $\dot{H}_m$ ) of white-crowned sparrows as a function of the square root of wind speed in the presence (open circles) and absence (filled circles) of simulated solar radiation. Chamber air temperature ( $T_a$ ) was held at  $10^\circ\text{C}$  for all treatments. Values are presented as means  $\pm 95\%$  confidence intervals, with  $N=10$  for all wind speeds and irradiance groups.

experimental irradiances (Fig. 2) using ANCOVA. Metabolic heat production increased linearly with the square root of wind speed ( $r^2=0.67$  for low irradiance and  $r^2=0.75$  for high irradiance;  $P<0.0001$ ). Using the square root of wind speed provided a better linear fit than using untransformed wind speed, as noted by Webster and Weathers (1988). Between  $0.25$  and  $2.0 \text{ m s}^{-1}$ , metabolic heat production increased by 30 and 51% at the low and high irradiances, respectively. Metabolic heat production  $\dot{H}_m$  as a function of the square root of wind speed  $u$  for low and high irradiance levels can be described by the following linear model:

$$\dot{H}_m = \beta_0 + \beta_1 u^{0.5} + \beta_2 x_2 + \beta_3 u^{0.5} x_2, \quad (5)$$

where  $\beta_0$  is metabolic heat production at zero wind speed and high irradiance,  $\beta_1$  is the slope of the relationship between metabolic rate and wind speed at high irradiance,  $\beta_2$  is the difference between the metabolic rates of birds exposed to high and low irradiances at zero wind speeds,  $\beta_3$  is the difference in slopes of the wind speed *versus* metabolic rate relationship at high and low irradiances, and  $x_2$  is a nominal variable that codes for the level of irradiance. When irradiance was high,  $x_2$  was set to 0; when irradiance was low,  $x_2$  was set to 1. We tested for the effect of wind speed by examining whether  $\beta_1$  equaled zero, and for the effect of irradiance and of irradiance  $\times u^{0.5}$  interactions (slope) by testing whether  $\beta_2$  and  $\beta_3$  equaled zero.

Both wind speed and irradiance level had a significant effect on metabolic heat production ( $F_{1,76(\sqrt{u})}=193$ ,  $P<0.0001$ ;  $F_{1,76(\text{Irradiance})}=26.4$ ,  $P<0.0001$ ). However, we found no significant interaction between wind speed and irradiance level

( $F_{1,76(\text{Interaction})}=3.4$ ,  $P=0.067$ ). At all wind speeds measured, metabolic heat production was higher for low than for high irradiance levels. However, the differences between these two irradiance treatments declined as wind speed increased. At the low level of irradiance, metabolic rate ( $\dot{H}_m$ ;  $\text{W m}^{-2}$ ) increased with increasing wind speed according to the following relationship:

$$\dot{H}_{m,\text{low}} = 103.7 + 38.7u^{0.5}. \quad (6)$$

In the presence of simulated solar radiation, metabolic rate increased with increasing wind speed and was described the following equation:

$$\dot{H}_{m,\text{high}} = 71.7 + 50.5u^{0.5}. \quad (7)$$

For statistical purposes, we analyzed the solar heat gain data using a reduced data set in which we had obtained data from both irradiance treatments from the same individuals at each wind speed. A single data point at  $2.0 \text{ m s}^{-1}$  that was more than 4 confidence intervals from the mean ( $44 \text{ W m}^{-2}$ ) was removed from the analysis. Solar heat gain (SHG), defined as the decrease in metabolic heat production induced by the animal's exposure to simulated solar radiation, resulted in a  $28.1 \text{ W m}^{-2}$  reduction in metabolic rate at  $0.25 \text{ m s}^{-1}$  (Fig. 3). SHG declined significantly (ANOVA,  $F_{1,27}=12.38$ ,  $P=0.0016$ ) to  $12.3 \text{ W m}^{-2}$  (56%) as wind speed was increased to  $2.0 \text{ m s}^{-1}$ .

Body resistance ( $r_b$ ) decreased significantly from  $334.5$  to  $270.9 \text{ s m}^{-1}$  as wind speed was increased from  $0.25$  to  $2.0 \text{ m s}^{-1}$  (regression analysis,  $F_{1,39}=15.7$ ,  $P=0.0003$ ) (Fig. 4). A greater relative decrease was observed in the thermal resistance of the aerodynamic boundary layer ( $r_e$ ), which declined by 64% from  $70$  to  $25 \text{ s m}^{-1}$  over the same range of wind speeds. Addition of body and boundary layer resistances ( $r_b+r_e$ ), yielded total resistance ( $r_T$ ) to heat flow between the animal and

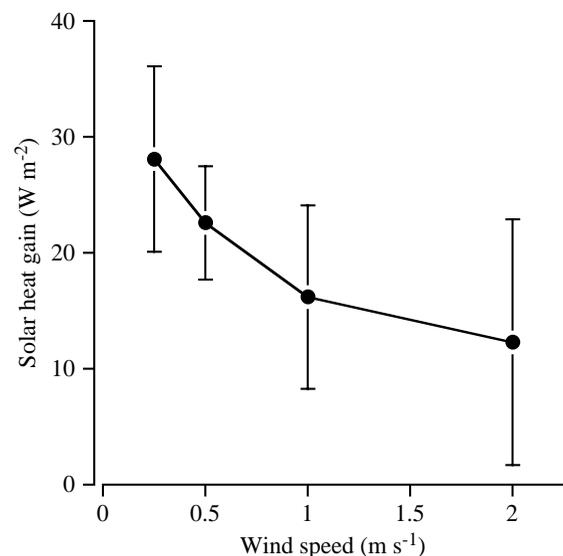


Fig. 3. Solar heat gain ( $\text{W m}^{-2}$ ) of white-crowned sparrows as a function of wind speed. Values are presented as means  $\pm 95\%$  confidence intervals. Sample sizes are  $N=8$ , 8, 7 and 6 for wind speeds of  $0.25$ ,  $0.5$ ,  $1.0$  and  $2.0 \text{ m s}^{-1}$ , respectively.

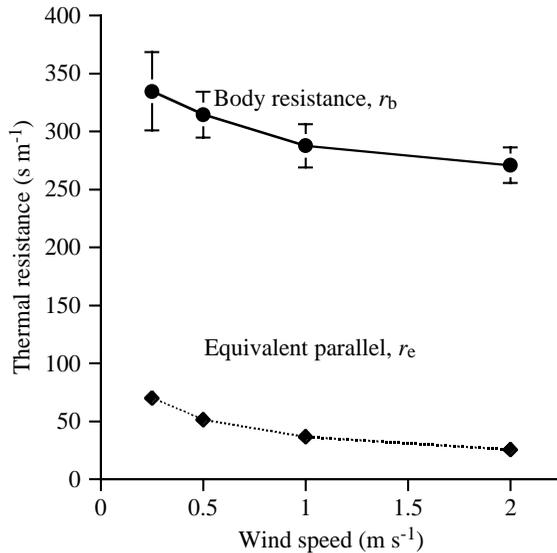


Fig. 4. Body resistance ( $r_b$ ) and equivalent parallel resistance ( $r_e$ ) of white-crowned sparrows as a function of wind speed. Values are presented as means  $\pm 95\%$  confidence intervals with  $N=10$  at all wind speeds.  $r_e$  represents the radiative resistance to heat transfer and the thermal resistance of the aerodynamic boundary layer.

environment.  $r_T$  showed an overall decline of 27% from 404.5 to 295.8 s m<sup>-1</sup> as wind speed increased from 0.25 to 2.0 m s<sup>-1</sup>.

## Discussion

### Body temperature variation

Body temperatures of birds did not vary systematically with wind speed, but were significantly affected by irradiance level at all wind speeds except 1.0 m s<sup>-1</sup> (Fig. 1). Body temperatures

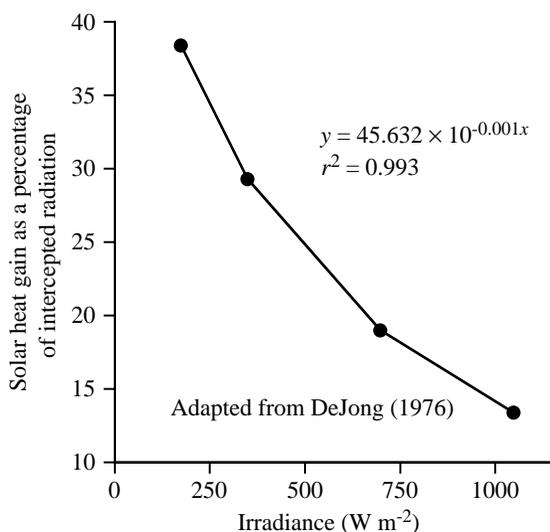


Fig. 5. Mean solar heat gain for white-crowned sparrows as a function of irradiance level for animals held at 10°C in the presence of 174, 349, 698 and 1047 W m<sup>-2</sup> of simulated solar radiation. Data are from DeJong (1976), and solar heat gain values were calculated using equation 8, as described in the text.

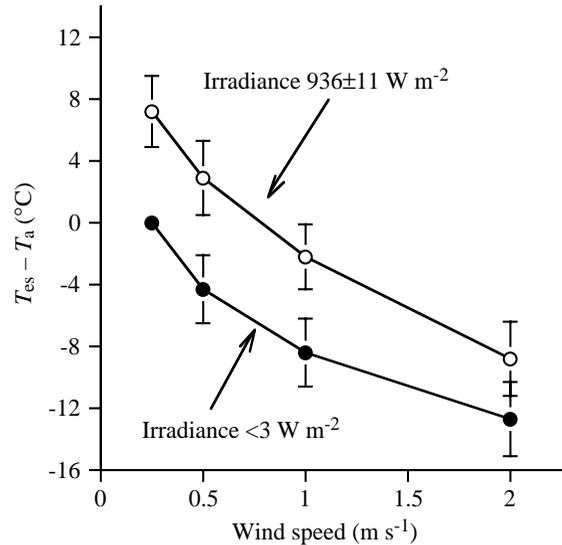


Fig. 6. Change in standard operative temperature ( $T_{es}$ ) as a function of wind speed in the presence and absence of simulated solar radiation. Standard conditions used for the calculation of  $T_{es}$  were air temperature ( $T_a$ )=10°C and wind speed=0.25 m s<sup>-1</sup>. Values are presented as means  $\pm 95\%$  confidence intervals, with  $N=10$ .

were typically highest under the conditions of greatest cold stress (e.g. in the absence of solar radiation). We cannot explain why, in general, the physical mechanism causing the changes in thermal stress (i.e. wind speed *versus* irradiance level) had different effects on  $T_b$ . Webster and Weathers (1988) found no correlation below 30°C between  $T_b$  of verdins and wind speed, although  $T_b$  did increase with increasing air temperature  $T_a$ . Similar results were reported by Goldstein (1983) for Gambel's quail (*Callipepla gambelii*).

Paladino and King (1984) found that exercising white-crowned sparrows increased their body temperature as work load and rates of oxygen consumption increased at a given temperature. In the same birds at rest, body temperatures increased erratically with declining air temperature and increasing rates of oxygen consumption. The available evidence suggests that  $T_b$  is unaffected by changes in the convective environment, but our data suggest that specific mechanisms of heat transfer (i.e. convection *versus* radiation) have differing effects on  $T_b$ .

### Variation in metabolic heat production with wind speed in the absence of simulated solar radiation

Our measurements of metabolic heat production for white-crowned sparrows in the absence of simulated solar radiation are 18–28% higher than those reported by Robinson et al. (1976) over a similar range of wind speeds and air temperatures. Differences in experimental conditions among these studies largely explain this variation. The measurements of Robinson et al. (1976) were made on birds during the rest phase of their daily cycle and would therefore be expected to be 20–25% lower than those measured during the animal's active phase (Aschoff and Pohl, 1970; Calder and King, 1974).

In addition, the birds of Robinson et al. (1976) were in a post-absorptive condition and held in a darkened wind tunnel for 3 h before any measurements were started. In our study, the birds were fed and held in the light for approximately 55 min before measurements. Furthermore, the birds in our study were blindfolded during trials so they perched quietly in the illuminated chamber. We found that normal room illumination ( $<3 \text{ W m}^{-2}$ ) in non-blindfolded birds resulted in an approximately 10% increase in metabolic heat production above that in darkened conditions; all treatments were therefore carried out under some illumination (e.g.  $<3$  or  $936 \text{ W m}^{-2}$ ). Published resting metabolic rates for white-crowned sparrows at  $10^\circ\text{C}$  under free-convection conditions are variable, with DeJong (1976) reporting  $106 \text{ W m}^{-2}$  for a post-absorptive bird under room lighting during the active phase of its daily cycle and King (1964) reporting  $85 \text{ W m}^{-2}$  for post-absorptive birds held in the dark during their rest phase. Extrapolation of our data (Fig. 2; equation 7) to zero wind speed in the absence of short-wave radiation yields an estimated metabolic rate of  $103.7 \text{ W m}^{-2}$ .

#### Thermal insulation

As expected, thermal insulation decreased with increasing wind speed (Fig. 4); our values are lower than those reported for white-crowned sparrows by Robinson et al. (1976). Body resistances are calculated from rates of metabolic heat production and, as discussed above, rates of metabolic heat production reported in this study are 18–28% higher than those reported by Robinson et al. (1976). Body thermal resistance values from the present study reflect these differences and are approximately 13% lower than those reported by Robinson et al. (1976). However, sparrows from both studies showed very similar relative changes in  $r_b$  with increasing wind speed; as wind speed was increased from  $0.5$  to  $2.0 \text{ m s}^{-1}$ , the  $r_b$  of sparrows in the present study declined by approximately 19%. Robinson et al. (1976) reported a 15% decline in  $r_b$  under similar conditions. The total thermal resistance ( $r_T = r_b + r_E$ ) of the animals in this study declined by 27% from  $404.5$  to  $295.8 \text{ s m}^{-1}$  as wind speed increased from  $0.25$  to  $2.0 \text{ m s}^{-1}$ .

#### Solar heat gain and variation in metabolic heat production with wind speed in the presence of simulated solar radiation

The net solar heat gain (SHG) measured in white-crowned sparrows during this study declined by 56% as wind speed was increased from  $0.25$  to  $2.0 \text{ m s}^{-1}$  (Fig. 3). In a previous study (Wolf and Walsberg, 1996), net solar heat gain in verdins was found to be even more sensitive to changes in wind speed; SHG declined by more than 90% as wind speed was increased from  $0.4$  to  $3.0 \text{ m s}^{-1}$ . Extrapolating from the white-crowned sparrow data to zero wind speed, solar heat gain is estimated to equal  $32 \text{ W m}^{-2}$  or 63% of the sparrow's basal metabolic rate ( $\text{BMR} = 51 \text{ W m}^{-2}$ ) reported by King (1964). This value is similar to the solar heat gain value reported by DeJong (1976) of  $38.4 \text{ W m}^{-2}$  for white-crowned sparrows held at  $10^\circ\text{C}$  and an irradiance of  $1047 \text{ W m}^{-2}$  under free-convective conditions.

At  $2.0 \text{ m s}^{-1}$ , solar heat gain declined substantially and equaled 24% of BMR.

To estimate the percentage of intercepted radiation that represented an effective heat load to the skin, we compared the radiant flux intercepted by the animal with the solar heat gain at each wind speed. To calculate the radiation intercepted ( $Q_d$ , W), we used the animal's projected shadow area ( $A_p$ ) on a plane perpendicular to the solar beam multiplied by short-wave irradiance ( $S_p$ ,  $\text{W m}^{-2}$ ):

$$Q_d = A_p S_p. \quad (8)$$

Here,  $A_p$  was calculated using the shape factor (0.28) used by DeJong (1976) which assumes that the shape of a perching sparrow approximates a prolate spheroid with the major axis at an angle of  $60^\circ$  to the solar beam and with major and minor axes of 70 mm and 35 mm, respectively. This shape factor was multiplied by the animal's total plumage surface area, estimated from Walsberg and King (1978), to obtain  $A_p$ . By dividing SHG (W) by  $Q_d$  and multiplying by 100, we expressed solar heat gain as a percentage of flux intercepted by the animal. In this study, at  $0.25 \text{ m s}^{-1}$ , only approximately 10.8% of the intercepted radiation was transferred to the skin surface and observed as a reduction in metabolic heat production; as wind speed increased to  $2.0 \text{ m s}^{-1}$ , this value declined to 4.6%. Extrapolating our data to a zero wind speed yields a value of 12.2%. This value agrees closely with DeJong's (1976) measurement that 13.4% of the intercepted radiation was apparent as a reduction in metabolic rate.

Previously, we found that verdins experience large heat loads from solar radiation and that a very large proportion of the intercepted radiation is transferred to the skin and is seen as a reduction in metabolic rate (Wolf and Walsberg, 1996). If we assume the same shape factor used for the present study (0.28) (previously, and in error, we used a shape factor of 0.44) and apply the above equation to the verdin data for a wind speed of  $0.4 \text{ m s}^{-1}$  and an irradiance of  $500 \text{ W m}^{-2}$ , we find that approximately 44% of the intercepted radiation is used physiologically and is seen as a heat load to the skin. DeJong's (1976) data suggest that the large disparity in the percentage of intercepted radiation transferred to the skin in verdins *versus* white-crowned sparrows and expressed as SHG may largely be due to the different irradiance levels used in the two studies. In the present study, sparrows were exposed to an irradiance of  $936 \text{ W m}^{-2}$ ; previously, we exposed verdins to an irradiance of  $500 \text{ W m}^{-2}$  (Wolf and Walsberg, 1996). A reappraisal of DeJong's (1976) data indicate that solar heat gain does not scale directly with irradiance level (Fig. 5), but is a negative power function of irradiance level. DeJong's (1976) data for white-crowned sparrows suggest that doubling irradiance from  $500$  to  $1000 \text{ W m}^{-2}$  in the absence of wind increases solar heat gain by only approximately 50%. Walsberg et al. (1997) reported very similar results for a small mammal in a direct test of the effect of irradiance level on solar heat gain. As suggested by Walsberg et al. (1997), increased irradiance levels are likely to alter the heat balance of the system. Because heat loss through an insulating coat or plumage occurs by the

coupled processes of long-wave radiation and free and forced convection, changes in irradiance level may alter the balance between these processes. Increased irradiance may result in increased penetration of radiation into the plumage and may therefore increase the thermal gradients within the plumage that drive heat flow. This could result in a decrease in plumage insulation and a concurrent reduction in solar heat gain.

*An evaluation of the combined thermal effects of radiation and wind speed on heat balance in white-crowned sparrows*

Because of the interactive nature of heat transfer processes, we use operative temperature theory to examine the combined thermal impact of different complex radiative and convective conditions on the heat balance of white-crowned sparrows. We calculated the standard operative temperature ( $T_{es}$ ) (Bakken, 1976), which equals the thermal conditions produced by radiative and convective heat transfer in natural environments, with the thermal condition produced by changes in air temperature ( $T_a$ ) in a metabolic chamber under standardized convective conditions. This allows an appraisal of the thermal conditions imposed on an animal by a diverse array of natural microhabitats. In a black-body thermal environment, such as that produced by our metabolic chamber with high-emissivity walls when sunlight is absent,  $T_{es}$  equals air temperature under stipulated 'standard' convective conditions, which we define as  $0.25 \text{ m s}^{-1}$ .  $T_{es}$  (Bakken, 1976) is calculated as:

$$T_{es} = T_b - (\dot{H}_m - \dot{H}_e)(r_s)/k. \quad (9)$$

$\dot{H}_m$  is the surface-area-specific metabolic heat production ( $\text{W m}^{-2}$ ),  $\dot{H}_e$  is evaporative heat loss ( $\text{W m}^{-2}$ ),  $k$  is a constant ( $1200 \text{ J m}^{-3} \text{ K}^{-1}$ ) and  $r_s$  is the sum of  $r_b$  and  $r_e$  at  $u=0.25 \text{ m s}^{-1}$  and in the absence of sunlight. Thus,  $T_{es}$  represents the  $T_a$  at a wind speed of  $0.25 \text{ m s}^{-1}$  that would produce the metabolic response equivalent to that elicited by the radiative and convective conditions actually prevailing in the natural environment. At  $0.25 \text{ m s}^{-1}$ , the addition of  $936 \text{ W m}^{-2}$  of simulated solar radiation is equivalent to increasing  $T_a$  by  $7.2^\circ\text{C}$  (Fig. 6). At higher wind speeds, this response is somewhat blunted; at  $2.0 \text{ m s}^{-1}$ , the addition of  $936 \text{ W m}^{-2}$  of simulated solar radiation is equivalent to increasing  $T_a$  by only approximately  $3.9^\circ\text{C}$ . Wind speed alone has a significant effect on  $T_{es}$ , and increasing wind speed from  $0.25$  to  $2.0 \text{ m s}^{-1}$  is equivalent to decreasing in the cold (or increasing in the heat)  $T_a$  by  $12.7^\circ\text{C}$ . The combined effects of wind speed and irradiance level are particularly striking: a white-crowned sparrow moving from a sunlit microsite with a wind speed of  $0.25 \text{ m s}^{-1}$  and an irradiance of  $936 \text{ W m}^{-2}$  to a shaded microsite at the same  $T_a$  but with a wind speed  $2.0 \text{ m s}^{-1}$  would experience a change in thermal condition equivalent to a  $19.9^\circ\text{C}$  change in  $T_a$ .

*Concluding comments*

In this study, we have examined how complex radiative and convective environments affect thermoregulatory costs and heat balance in a small bird. Body temperature is affected by irradiance level, but not by wind speed. Thus, different types of thermal loads have different effects on the animal's body

temperature. Wind speed had marked effects on solar heat gain. Increases in wind speed from  $0.25$  to  $2.0 \text{ m s}^{-1}$  reduced SHG by approximately 56%. This sensitivity of radiant heat loads to changes in the convective environment appears quite variable interspecifically, as shown by our previous study (Wolf and Walsberg, 1996). We also found significant variability in the proportion of intercepted radiation that affected the animal's thermal balance. This varies both with wind speed and with the intensity of irradiance. For example, a fourfold increase in irradiance results in only an approximately 50% increase in metabolic savings to the animal (calculated from DeJong, 1976). That is, low-intensity irradiance has much greater proportional effects on the animal's heat balance than do high levels of irradiance. Such phenomena add a new layer of complexity to efforts to predict the effects of complex radiative and convective environments on the heat balance and energetics of animals in nature.

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