Thermal Effects of Radiation and Wind on a Small Bird and Implications for Microsite Selection

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Abstract. The physical environmental factors (air temperature, solar radiation, wind speed) that define specific microclimates and their effects on water and energy budgets of small birds are of major importance to our understanding of avian thermal biology. We examined the effects of solar radiation, wind speed, and their interaction on metabolic rates in the Verdin, Atricapillus flaviceps. Daytime resting metabolic rates and evaporative water loss rates as a function of air temperature, as well as basal metabolic rate, were also measured to allow estimation of water and energy flux rates in diverse microclimates.

In the absence of solar radiation, as wind speed was increased from 0.4 to 3.0 m/s, metabolic rate increased 14%. Exposure to simulated solar radiation significantly reduced metabolic heat production at all wind speeds measured except 3.0 m/s. Solar heat gain (SHG) was estimated for an irradiance of 1000 W/m², similar to that commonly observed in nature. At 0.4 m/s wind speed and 1000 W/m² irradiance, SHG may reduce metabolic rate by 46%. SHG declines precipitously as wind speed is increased, and at 3.0 m/s, metabolic rate is only reduced by 3%.

Analyses of changes in thermostatic costs associated with microclimate selection in winter suggest that Verdins may reduce metabolic rate by as much as 50% by shifting from a shaded, windy site to one protected from the wind and exposed to 1000 W/m² solar radiation. Similar analyses for Verdins during the summer suggest that microsite selection can result in significant water savings. By remaining out of the sun and wind, Verdins can reduce their rate of evaporative water loss by at least a factor of four. This analysis clearly demonstrates the potential importance of daytime microclimate selection to balancing water and energy budgets in small birds.

Key words: Atricapillus flaviceps; effects of wind and solar radiation; energetics; microclimate; microsite selection; thermal biology; thermoregulation; Verdin; water balance.

Introduction

The physical environmental factors (air temperature, solar radiation, wind speed) that define specific microclimates and their effects on water and energy budgets of small birds is of major importance to our understanding of avian thermal biology (Walsberg 1985, 1993). Basal and thermoregulatory costs in small birds typically account for 40–60% of total daily energy expenditure (Calder and King 1974, Walsberg 1983). Consequently, by selecting microclimates that minimize thermoregulatory costs, small birds may reduce their energy requirements or reallocate conserved time or energy to other vital processes (Calder 1973, Bartholomew et al. 1976, Buttemer 1985, Walsberg 1985, 1986, 1993, Webb and Rogers 1988). In this investigation, we focus on the effects of solar radiation and wind speed, as well as their interaction, on the thermal biology of a very small songbird, the Verdin Atricapillus flaviceps. As a consequence of their small mass and high surface-area-to-volume ratios, the maintenance of high body temperatures in small passerines such as the Verdin requires high mass-specific rates of energy expenditure. In addition, their low thermal inertia dictates that small birds must respond rapidly to changes in the thermal environment if they are to remain homeothermic. No previous study has examined the interaction between convective and radiative heat transfer and their combined effects on metabolic heat production in intact animals.

The effects of air temperature on metabolic rates in birds are well known (Calder and King 1974) and the effects of wind have also received some scrutiny (Buttemer 1981, Goldstein 1983, Webb and Rogers 1988, Webster and Weathers 1988, Bakken et al. 1991). However, only a few studies have examined the effects of solar radiation on avian metabolic rates (Lustick 1969, Heppner 1970, Lustick et al. 1970, De Jong 1976), and their methodology constrains the applicability of several of these studies to free-living animals. These investigations were carried out in the absence of forced convection and typically used radiation sources that deviated significantly from solar radiation in their spectral energy distribution. In some, animals were used in which important properties such as natural plumage coloration were altered.

In this investigation, we focus on the following ques-

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tions: (1) How does solar radiation and wind speed affect metabolic rate production in small birds? (2) 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 produced by the animal’s exposure to simulated solar radiation. Similarly, changes in convective heat loss are quantified as the variation in metabolic heat production produced by exposure to different wind speeds. Measurements of basal metabolic rate (BMR) were made to establish a basis for comparison. Finally, we used operative temperature theory (Bakken 1976) and measurements of daytime resting metabolic rate (RMR) and evaporative water loss rate (EWL) as a function of air temperature, to explore how complex microclimates potentially effect fluxes of energy and water in free-living birds.

METHODS

Experimental animals

Verdins are very small (∼7.0 g) insectivorous passerines that reside year-round in the deserts of the southwestern United States and northern Mexico. Birds used for the solar heat gain experiments were captured from their roost nests in the Superstition Mountains of central Arizona in May 1993. Verdins used for measurements of RMR, BMR, and EWL were captured in the Goldfield Mountains during May and June of 1992. Birds were transported to Tempe, Arizona, where they were housed individually in BioQuip 0.2-m³ folding insect cages in a temperature-controlled environmental room. The room was reprogrammed weekly to simulate the current photocycle and thermal regime of the nearby desert. We maintained birds on a diet of mealworms and seedless grapes, supplemented once weekly with vitamins (Webster and Weathers 1988). All birds maintained mass while in captivity.

Measurements of daytime resting metabolic rate and evaporative water loss as a function of air temperature

Daytime resting metabolic rate (RMR) and rates of evaporative water loss (EWL) were measured during August and September 1992. Measurements were made simultaneously on four birds using four 600-mL glass metabolic chambers with inlets connected to a common supply header. Chambers were housed in a temperature-controlled room. Air dried with Drierite was pumped through each chamber at rates of 250–1200 mL/min. Inlet flow rates for each chamber were adjusted by Omega model FL3402G-HRV rotameters to maintain chamber dew points below 7.0°C. Birds rested quietly on 0.5-cm wire mesh placed 3 cm above an ∼2-cm layer of paraffin oil used for the collection of fecal material. A 100 mL/min subsample of effluent gas from each chamber was pumped through a manifold that directed a sample from one of the chambers past a Vaisala humidity probe (Weathermeasure Corporation, Sacramento, California) accurate to ±1% relative humidity, then through a small column of Drierite and into an Anarad model AR-411 (Santa Barbara, California) that determined CO₂ concentration to ±10 μL/L. The CO₂ analyzer was zeroed and spanned daily using CO₂-free air and a calibration gas known to contain 0.456% CO₂. The Vaisala probe was calibrated daily over saturated solutions of LiCl and NaCl. Chamber air temperature was measured by a 0.4 mm (26 gauge), type-T thermocouple and recorded by a Campbell model CR21x datalogger (Logan, Utah).

RMR and EWL were measured during photophase for birds sitting in the dark at 10°, 20°, 30°, and from 32° to 48° ± 0.75°C in 2° increments. The order of temperatures selected was randomized. Each bird was used only once during any 24-h period and the order in which each bird was used each day was varied at each temperature. Verdins (n = 12; mean body mass 7.03 ± 0.06 g) were placed in metabolic chambers and allowed to rest quietly for 30 min before starting measurements, except at 46° and 48°C where birds were only given 15 min to adjust to the chamber in order to minimize stress on the animal. During the measurement period, chamber efflux gases were sequentially sampled for 7 min each, twice in succession, and the lowest 1-min value of each run was used to determine RMR and EWL. Instrument signals were recorded on a Campbell model CR21x datalogger, that averaged the values for each minute. CO₂ production was calculated using Eq. 3 of Walsberg and Wolf (1995). Respiratory quotient (RQ) was measured in a separate series of experiments because the high flow rates used in the wind tunnel experiments precluded accurate measurements of oxygen consumption. Mean daytime RQ equaled 0.738 (n = 8) as measured from 0.5 to 2.5 h after removal from food (Walsberg and Wolf 1995). Based on this value, the thermal equivalent of produced carbon dioxide is estimated as 26.74 J/mL (Kleiber 1961, Gessaman and Nagy 1988).

Basal metabolic rate measurements

Measurements of basal metabolic rate were made using the same techniques, apparatus, and birds (n = 12; mean body mass 7.13 ± 0.12 g) as described above, with the following exceptions. Basal metabolic rate was determined from measurements at 34°, 36°, and 38° ± 0.5°C starting 3 h after the onset of darkness. Dry, CO₂-free air flowed through the metabolic chambers at a controlled rate of 250 mL/min. Oxygen concentration was determined from a 100-mL/min subsample of chamber efflux air, after it was dried (Drierite) and scrubbed of CO₂ (Aesarite), using an Applied Electrochemistry S3a oxygen analyzer (Sunnyvale, California) calibrated using the procedures of Walsberg and Wolf (1995). We assumed room air had a fractional oxygen concentration of 0.2094%. Oxygen consumption was calculated using Eq. 2 of Hill (1972). Mean nighttime
Fig. 1. Wind tunnel metabolic chamber used to vary the radiative and convective environment and measure Verdin metabolic responses.

RQ equaled 0.76 \((n = 7)\) as measured from 0.5 to 12 h after lights out (Walsberg and Wolf 1995). Based on this value, the thermal equivalent of oxygen consumed is estimated as 20.1 J/mL (Kleiber 1961).

**Solar heat gain measurements**

*Environmental simulation.*—Rates of carbon dioxide production were measured for birds using a closed-circuit wind tunnel with a volume of 11 L (Fig. 1). A variable speed DC blower circulated air through the chamber test section at speeds ranging from 0.4–3.0 m/s, as measured with a Thermometrics HWA-101 thermoanemometer (San Diego, California) that had been calibrated as described by Walsberg (1988). Wind speed varied <10% laterally within 2 cm of the perch in the chamber test section. Turbulence intensity was 5% or less at all wind speeds used, 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 Corporation Series II solar simulator (Hillsdale, New Jersey), which filters light produced by a 1-kW xenon arc lamp to simulate direct solar radiation at an air mass = 1. Irradiance within the test section of the chamber was maintained at 500 ± 25 W/m² and was measured with a LI-COR LI200sz pyranometer (Lincoln, Nebraska) that had been calibrated against an Ortel Corporation model 7080 pyroelectric radiometer (Stratford, Connecticut). 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 would have burned the eyes and skin of the experimental animal. Wind tunnel measurements in the absence of simulated solar radiation were done with normal fluorescent room lighting at an irradiance of <3 W/m². Chamber air temperature was maintained at 15° ± 0.5°C by placing it within a temperature-controlled room and by heating the chamber air with an electrical resistance heater. Chamber air temperature was measured by a 0.4 mm (26 gauge), type-T thermocouple and recorded by a Campbell model CR21x datalogger.

*Carbon dioxide measurement system.*—A Puregas model CDA1112 air dryer/CO₂ scrubber system (Westminster, Colorado) provided dry, CO₂-free air that ventilated the metabolic chamber at a rate of 4838–4940 mL/min. Incurrent flow was measured using an Omega FL 3404T-HRV rotameter, calibrated to ±1% of full scale with a 2-L soap-bubble flowmeter. These flow rates allowed the gas mixture within the metabolic chamber to reach 99% equilibrium in ≈10 min, as calculated using the equation of Lasiewski et al. (1966). A sample of chamber effluent air passed through a column of Drierite at 150 mL/min and into a LI-COR model 6252 CO₂ analyzer that determined CO₂ concentration to ±1 µL/L. The CO₂ analyzer was zeroed and spanned daily using CO₂-free air and calibration gas known to contain 0.2840% CO₂. Instrument signals were recorded on a Campbell model CR21x datalogger, that averaged the values for each minute.

*Experimental protocol.*—Metabolic measurements were made during photophase within the closed-circuit wind tunnel, both in the presence and absence of simulated solar radiation. Metabolic measurements were made on eight adult Verdins (mean body mass 7.13 ± 0.26 g) during September and October 1993, after the completion of molt. Birds were placed in the chamber 30 min prior to the start of measurements. Verdins were then held for 30 min at each of four wind speeds (0.4, 0.9, 1.7, 3.0 m/s) and CO₂ production measured. Wind speed orders were varied from run to run and each bird was measured twice (in the presence and absence of simulated solar radiation) at each wind speed on different days. We report data for the minimum 1-min average values for CO₂ production taken from the last 10 min of each wind speed. Carbon dioxide production was calculated using Eq. 3 of Walsberg and Wolf (1995) and corrected to standard conditions (0°C, 101 kPa) using Eq. 6.5 of Mclean and Tobin (1987) for flow measurements using rotameters. Activity of each bird during the experiments was monitored with a Magnavox CCD camera surveillance system. Birds that exhibited more than a occasional perch change were excluded from the analyses.

**Results**

*Basal metabolic rate, daytime resting metabolic rate, and rate of evaporative water loss*

Basal metabolic rate averaged 54.0 ± 4.9 W/m² at 36°C. Daytime resting metabolic rate varied from av-
Fig. 2. Daytime resting metabolic rates as a function of air temperature for Verdins sitting in the dark. Means and 95% confidence intervals are shown at each temperature.

Fig. 3. Evaporative water loss rates for Verdins resting in the dark. Means and 95% confidence intervals are shown at each temperature.

Fig. 4. Metabolic rates of Verdins as a function of wind speed in the presence and absence of simulated solar radiation at an air temperature of 15°C. Values are means and 95% confidence intervals with n = 7 at 0.4 m/s and n = 8 at all other wind speeds.

Metabolic heat production as a function of wind and irradiance

In the absence of insolation, metabolic rate increased 14% from an average of 11.4 mL CO₂·g⁻¹·h⁻¹ or 202 W/m² to 13.0 mL CO₂·g⁻¹·h⁻¹ of 228 W/m² as wind speed increased from 0.4 m/s to 3.0 m/s (Fig. 4). Exposure to simulated solar radiation significantly reduced metabolic heat production at all wind speeds measured except 3.0 m/s (paired two-sample Student’s t test; 0.4 m/s, P = 0.0002; 0.9 m/s, P = 0.0002; 1.7 m/s, P = 0.009; 3.0 m/s, P = 0.19). In the presence of solar radiation, metabolic rate increased from an average of 8.0 mL CO₂·g⁻¹·h⁻¹ or 140 W/m² at 0.4 m/s to 12.6 mL CO₂·g⁻¹·h⁻¹ or 222 W/m² at 3.0 m/s. Solar heat gain to the animal, defined as the reduction in metabolic rate produced by the addition of simulated solar radiation, was 3.4 mL CO₂·g⁻¹·h⁻¹ or 62 W/m² at a wind speed of 0.4 m/s. Solar heat gain declined to 0.4 mL CO₂·g⁻¹·h⁻¹ or 7 W/m² at a wind speed of 3.0 m/s (Fig. 4).

Effects of wind on thermal resistance

Body resistance (r_b) (see Appendix for calculations) did not change significantly with wind speed (ANOVA, df = 3, 24, F = 2.86, P = 0.058) (Fig. 5). Thermal resistance of the aerodynamic boundary layer (r_a) declined by 70% from 63 to 19 s/m as wind speed increased from 0.4 to 3.0 m/s. Total thermal resistance to heat flow between animal and environment (r_t), the
Fig. 5. Body resistance \( r_b \) of Verdis and equivalent parallel resistance \( r_p \) as a function of wind speed. Values for \( r_b \) are means and 95% confidence intervals with \( n = 7 \) at all wind speeds.

sum of \( r_b \) and \( r_e \), decreased by 13% from 161 s/m to 141 s/m as wind speed increased from 0.4 to 3.0 m/s.

**DISCUSSION**

**Variation in thermal resistance with wind speed**

Body resistance \( r_b \) did not change with wind speed (Fig. 5), in contrast to the decline in \( r_b \) with increasing wind speed observed for other species (Robinson et al. 1976, and others cited therein). Webster and Weathers (1988) found that the body resistance of Verdis declined by <10% over a similar range of wind speeds and temperatures. Increasing wind speed and the subsequent disruption of the thin plumage apparently has only minor effects on body resistance in Verdis. Occasional perch hopping or other activities such as preening observed during the experiment may have increased metabolic rate and lowered estimates of \( r_b \) below those for resting birds (Webster and Weathers 1988). Peripheral vaso-constriction may also increase \( r_b \) and thus compensate for the effects of plumage disruption (Monteith 1973).

Our data confirm that total thermal resistance \( r_T = r_b + r_e \) values are low for Verdis compared to those of similar-sized birds (Webster and Weathers 1988). \( r_T \) is 161 s/m at 15°C and wind speed of 0.4 m/s, and decreases to 141 s/m as wind speed is increased to 3.0 m/s. Values for other species of similar size, such as the Bushtit *Psaltriparus minimus* (283 s/m, Chaplin 1982) and the Black-rumped Waxbill *Estrilda troglodytes* (210 s/m, Weathers and Nagy 1984), are 30–80% higher than our values. Insulation values for Verdis are also much lower than the allometric predictions of 306–390 s/m calculated by Webster and Weathers (1988) from Robinson et al. (1976) and Aschoff (1981). These low \( r_T \) values are in part due to a relatively thin feather coat that has a mass 29% less than predicted allometrically (Webster and Weathers 1988).

**Effects of wind speed on metabolic rate in the absence of insolation**

Metabolic rates in the absence of solar radiation were relatively insensitive to changes in wind speed. As wind speed increased from 0.4 to 3.0 m/s, metabolic rate increased only 14% or 28 W/m² (Fig. 4). These values are similar to those of Webster and Weathers (1988) for Verdis. Using their Eq. 8 for an air temperature of 15°C, metabolic rate is calculated to increase by 17% or 36 W/m² over the same range of wind speeds.

The metabolic rates of our birds at each wind speed are 8–14% higher than those of Webster and Weathers (1988). This probably results from differences in the experimental conditions between the two studies. Our measurements were made on recently fed birds held under normal room lighting. In contrast, Webster and Weathers (1988) made measurements on post-absorptive birds held in the dark, which are expected to have lower metabolic rates than recently fed birds held in the light (Aschoff and Pohl 1970, Calder and King 1974).

**Solar heat gain and effects of wind speed**

To examine SHG in a ecologically relevant context, heat balance should be estimated for irradiances normally encountered by free-living Verdis. Typically, direct short-wave irradiance on a clear day in the Sonoran Desert ranges from 900–1100 W/m² and varies both with time of day and season. For example, during June, these levels of irradiance are commonly present for 9 h of the 13-h day. During December, insolation values reach these levels for ~6 of the 10-h day. Potential metabolic savings from SHG during the winter, therefore, are reduced early in the morning and late in the afternoon due to lower irradiance levels. In contrast, during the summer, lower irradiances early in the morning and late in the afternoon can result in water savings due to reduced rates of evaporative water loss. Projecting SHG values from the experimental irradiance of 500 W/m² to an irradiance of 1000 W/m² using biophysical modeling (e.g., Campbell 1977) requires doubling the absorbed radiation term and the value for radiative heat gain at each wind speed. Although empirical data are sparse and not definitive, De Jong's (1976) data for White-crowned Sparrows suggests that doubling irradiance from 500 to 1000 W/m² in the absence of wind increases radiative heat gain by only ~50%. For the following analyses, we use De Jong's (1976) data as a conservative guide for estimating solar heat gain at 1000 W/m². We also use Verdin BMR as a basis for comparing the magnitude of SHG to the Verdin's overall rate of energy expenditure.

The sensitivity of solar heat gain to changes in the convective environment can be analyzed by comparing
the radiant flux intercepted by the animal to the physiologically significant heat gain. To calculate the radiation intercepted \( Q_{\text{R}} \) (in watts), we use the ratio \( R \) of the animal’s projected shadow area on a plane perpendicular to the solar beam, to the total plumeage surface area. This value is multiplied by the product of the total plumeage surface \( A_{\text{plumeage}} \) (m²) and short-wave irradiance \( S_p \) (W/m²) (Campbell 1977):

\[
Q_d = (R)A_{\text{plumeage}}S_p.
\]

Here, \( R = 0.44 \) and is calculated assuming that the shape of a perching Verdin approximates a prolate spheroid at an angle 50° from horizontal (Campbell 1977), with a major axis of 54 mm and a minor axis of 24 mm. Dividing SHG (in watts) by \( Q_d \) and multiplying by 100 expresses solar heat gain as a percentage of flux intercepted by the animal. Such a comparison emphasizes the sensitivity of SHG to changes in the convective environment (Fig. 6). Solar heat gain at 0.4 m/s, equals 28% of the intercepted radiant flux, but as wind speed is increased to 3.0 m/s, solar heat gain declines to only 3% of the intercepted flux. At 0.4 m/s wind speed and 1000 W/m² irradiance, SHG would reduce metabolic rate by 46%, assuming that a 100% increase in irradiance produces only a 50% increase in SHG. This reduction equals 1.7 times the basal metabolism of the Verdin. SHG declines precipitously as wind speed is increased and at 3.0 m/s metabolic rate is reduced by only 3%, or 0.2 times BMR at an irradiance of 1000 W/m².

Potential effects of solar heat gain and wind on Verdin energy and water balance

The thermal microclimate can have major influences on an animal’s time, water and energy budgets. Small endothermic vertebrates have a low thermal inertia and a limited capacity to store vital resources such as water or energy. When coupled with high body temperatures and high surface-area-to-volume ratios, small endotherms are, therefore, forced to respond rapidly to changes in microclimates. In the short term, these thermoregulatory responses may result in deficits of either water or energy. Over a longer period, the energy used for thermoregulation is not available for other activities or processes (i.e., social behavior, reproduction, somatic maintenance). Additionally, time spent acquiring energy may limit the time available for other activities or expose the animal to increased risk of predation and so lower the animal’s fitness. In the following analyses, we examine the potential importance of solar heat gain and convective heat transfer to water and energy expenditure in Verdins.

Short-term costs of thermoregulation for Verdins can be examined by calculating standard operative temperature \( T_{\text{oa}} \) (Bakken 1976). \( T_{\text{oa}} \) equates the thermal stress produced by radiative and convective heat transfer in natural environments with the thermal stress produced by changes in air temperature \( T_{\text{an}} \) in a metabolic chamber under standardized convective conditions. In a black-body thermal environment such as produced by our metabolic chamber with high-emissivity walls when sunlight is absent, \( T_{\text{oa}} \) equates air temperature under stipulated “standard” convective conditions, which we define as 0.4 m/s. \( T_{\text{es}} \) (Bakken 1976) is calculated as:

\[
T_{\text{es}} = T_h - (M - E)(r_e)/k
\]

Variables are as defined previously and in the Appendix, except that \( r_e \) is the sum of \( r_e \) and \( r_c \) at \( u = 0.4 \) m/s and in the absence of sunlight. Thus, \( T_{\text{es}} \) represents the \( T_{\text{oa}} \) at a wind speed of 0.4 m/s that would produce the metabolic response equivalent to that elicited by the radiative and convective conditions actually prevailing in the natural environment.

In the absence of solar radiation, increasing wind speed from 0.4 to 3.0 m/s produces a change in metabolic heat production or \( T_{\text{es}} \) equivalent to that produced by decreasing \( T_{\text{oa}} \) by 4°C (Fig. 7). With solar radiation present (500 W/m²), increasing wind speed from 0.4 to 3.0 m/s produces a much greater effect and is equivalent to decreasing \( T_{\text{oa}} \) by 11°C over the same range of wind speeds (Fig 7). SHG for irradiances typical in the Sonoran Desert (1000 W/m²) would likely be at least 50% greater than we measured. For example, at the single wind speed of 0.4 m/s with an irradiance of 500 W/m², simply shifting from a perch in the shade to one in full sun would produce a change in heat load equivalent to raising \( T_{\text{oa}} \) by 8°C (Fig. 7). At an irradiance of 1000 W/m² the same movement may be equivalent to raising \( T_{\text{oa}} \) by 12°C or more.

Measurements of RMR (Fig. 2) and EWL (Fig. 3) as a function of air temperature can be used to illustrate the effects that differing microclimates can have on energy and water utilization. During winter, Verdins spend 75–95% of their active day searching for food.
dehydration tolerance (11% of body mass; B. O. Wolf, unpublished data) in only 1.6 h. These high operative temperatures are common and prolonged during the summer and free water typically is not available. These extremely hot periods therefore may well represent a bottleneck during which natural selection reduces populations and may cause especially high mortality among juvenile birds that are less efficient at obtaining food and water than the adults. Finally, birds, unlike many other desert animals do not retreat underground to escape the heat.

**Effects of body size on solar heat gain, energetics, water economy, and microsite selection**

Solar heat gain and heat transfer by convection between an animal and its physical environment are intimately tied to body size. Body size is an important characteristic because it partially defines a suite of animal properties. Of major importance is the animal’s surface-area-to-mass ratio. For very small birds such as the Verdin, this ratio is high (i.e., 4.1 cm²/g). In contrast, surface-area-to-mass ratios for a 35-g and 70-g bird are 2.5 cm²/g and 2 cm²/g, respectively (Walsberg and King 1978). Lower surface-area-to-mass ratios in larger birds require lower mass-specific metabolic rates and less frequent ventilation of respiratory surfaces. In cold environments, larger animals receive less benefit from solar radiation and experience lower mass-specific metabolic savings. In hot environments, however, this lower solar heat gain is probably beneficial, as it results in lower rates of mass-specific evaporative water loss.

In addition, larger birds have a greater thermal inertia and relatively larger capacity for storage of vital resources such as water or energy. The higher thermal inertia and storage ability may allow larger birds to exploit different strategies from smaller birds to maintain homeostasis. For example, facultative hypothermia and heat storage can reduce water loss when environmental temperatures are above body temperature. In cold environments, larger birds have a greater fasting ability, accompanied by their lower mass-specific metabolic rates (Calder and King 1974). Larger species thus must balance energy budgets over time periods of hours or days vs. minutes to hours for smaller birds.

In contrast, smaller species may be more able to exploit small-scale spatial variation in their environments. Such small forms also have lower total water and energy requirements, which could be critical in environments or seasons in which such resources are limited.

Clearly, seasonal changes in the thermal environment may alter the availability or utilization of vital resources such as energy or water. During winter, the combination of low environmental temperatures and reduced energy availability require that the Verdin forage almost continuously (Austin 1976, 1978, Webster and Weathers 1990). In contrast, summer activity is severely curtailed when environmental temperatures

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**Fig. 7.** Change in standard operative temperature (Tₙₐ) as a function of wind speed in the presence and absence of solar radiation. Standard conditions for the calculation of Tₙₐ are a black-body radiative environment with a wind speed of 0.4 m/s.

(Austin 1976, 1978, Webster and Weathers 1989). Short episodes of inclement weather or periods of reduced prey availability could, therefore, have serious effects on the bird’s ability to survive, and energy-saving strategies may be of major importance. Natural selection may well favor individuals that select microclimates that reduce their rate of energy expenditure. For example, a Verdin perched in the shade and exposed to a 3.0 m/s wind at a T₉₀ of 15°C (Tₛₐ = 11°C) would experience a reduction in resting metabolic rate of at least 50% by simply shifting to a perch exposed to 1000 W/m² sunlight and protected from the wind (Tₛₐ = 27°C) (Fig. 2).

Summer in the Sonoran Desert presents different challenges; high operative temperatures (40°–60°C) may severely tax an animal’s ability to dissipate heat and balance its water budget. Verdins drastically reduce activity and seek shaded microclimates as air temperatures increase (Austin 1976, 1978; B. O. Wolf, unpublished data). When T₉₀ is below 35°C, Verdins spend equal time in shaded and sunlit microclimates and forage 75% of each hour. As T₉₀ increases above 40°C, rates of foraging decline to 9–21% of each hour and birds spend 95% of their time in shaded sites (Austin 1976, 1978). A Verdin sitting in a shaded microclimate at a moderate (for subtropical deserts) Tₛₐ of 40°C evaporates water at a rate of 16 mg·g⁻¹·h⁻¹, or 1.7% of its body mass per hour (Fig. 3). In the absence of wind, shifting from this shaded microclimate (Tₛₐ = 40°C) to a sunlit one could increase Tₛₐ to 52°C or higher. This would produce at least a fourfold increase in the rate of evaporative water loss. At a Tₛₐ of 50°C, a Verdin’s evaporative water loss rate is 71 mg·g⁻¹·h⁻¹, and results in the loss of 7% of its body mass per hour (Fig. 3). This could drive the bird beyond its limits of
are high and the need to conserve water may constrain behavior (Austin 1976, 1978). These different patterns of resource utilization may have an important effect on an animal's allocation of time to vital activities. Our data clearly demonstrate that shifts between microsites that require movements of only a few centimeters can have major effects on an animal's heat balance and thermoregulatory costs.

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Literature Cited


APPENDIX

Analysis.—Calculating the relation between wind speed and total thermal resistance of the animal’s body relied on the relation between metabolic rate, the body-to-environment temperature gradient, and thermal insulation, as rearranged from Campbell (1977):

\[ r_s = \frac{k(T_b - T_e)(M - E)}{r_e} \]  

(A.1)

The animal’s total body thermal resistance \( r_s \) subsumes coat insulation and the thermal resistance of the peripheral tissues. \( k \) is a constant (1200 J m\(^{-1}\)K\(^{-1}\)) and \( T_b \) is body temperature, calculated using Eq. 7 of Webster and Weathers (1988). \( T_e \) is operative temperature, (15°C for experiments conducted in the absence of solar radiation). \( M \) is metabolic rate, in the absence of simulated solar radiation, expressed on a surface-area basis (watts per square metre). Deriving this value requires knowledge of plumage surface area, \( A_{	ext{plumage}} \) (in square centimetres), which is estimated from body mass (grams) using the Meeth equation as modified by Walsberg and King (1978) to estimate plumage surface area:

\[ A_{	ext{plumage}} = 8.11 \text{(body mass)}^{0.667} \]  

(A.2)

\( E \) in Eq. A.1 is heat loss by evaporation, also expressed on the basis of plumage surface area (watts per square metre). Evaporative water loss at 15°C was estimated as 7 mg g\(^{-1}\) h\(^{-1}\) based on measurements at 10°C and 20°C (Fig. 3). Latent heat loss, calculated using a value of 2.42 kJ/g H\(_2\)O, was 11.3 W/m\(^2\). We assumed that latent heat loss was not affected by wind speed at temperatures below 20°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. \( r_e \) is the equivalent parallel resistance between the environment and the animal’s outer surface. It equals the parallel sum of \( r_s \) and \( r_e \):

\[ r_s = (r_s + r_e) \]  

(A.3)

\( r_s \) is the thermal resistance of the aerodynamic boundary layer (seconds per metre) and was calculated using the equations of Mitchell (1976) as combined by Webster and Weathers (1988):

\[ r_s = 2.7d^0.4(\nu/\mu)^0.4/D_h \]  

(A.4)

Here, \( \mu \) is wind speed (metres per second), \( \nu \) is the kinematic viscosity of air (1.46 \times 10^{-5} \text{ m}^2/\text{s}), and \( D_h \) is the thermal diffusivity of air (2.08 \times 10^{-5} \text{ m}^2/\text{s}). \( d \) is the characteristic dimension of the animal, taken as 0.024 m for Verdins. \( r_e \) is the effective resistance (seconds per metre) to radiative heat transfer and was calculated following Campbell (1977):

\[ r_e = k/4\pi T_w^4 \]  

(A.5)

\( k \) is a constant (1200 J m\(^{-1}\)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 0.980), and \( T_w \) is chamber air temperature.

Statistical analyses.—Values are presented as means ±95% confidence limits. Sample sizes for the solar heat gain experiment were seven at 0.4 m/s and eight at 0.9, 1.7, and 3.0 m/s. Mean values for measurements taken in the presence and absence of simulated solar radiation were compared at each wind speed using a paired two-sample Students \( t \) test. Significance was accepted at \( P < 0.05 \). Microsoft Excel was used for statistical analyses.