

The Role of the Plumage in Heat Transfer Processes of Birds¹

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SYNOPSIS. The plumage of birds provides a critical thermal buffer between the animal and its environment. Rates of energy expenditure are strongly influenced by the thermal properties of the environment or the microclimates the animal occupies. Current data suggest that the addition of solar radiation is equivalent to three to four-fold changes in wind speed and that solar heat gain can be extremely sensitive to changes in wind speed.

Dry heat transfer through the plumage occurs by three avenues 1) conduction and free convection through air 2) conduction along the solid elements of the plumage and 3) radiation. Overall, about 95% of the total heat flow is evenly divided between the first two avenues. Radiative heat transfer accounts for only about 5% of total heat flow. Plumage color, as well as the microstructure and micro-optical properties of plumage elements, when combined with environmental properties (e.g., wind speed), determine the radiative heat loads that birds acquire from solar radiation. Although plumage color or reflectivity determines the fraction of incident solar radiation that is absorbed by the plumage and generates heat, the fraction of this heat that contributes to the thermal load on the animal can vary greatly. In a fibrous coat such as a plumage, there is some variable penetration into the coat, with absorption over a range of coat depths. Factors such as feather micro-optics and structure are critical determinants of radiation penetration into avian coats. Significant differences in solar heat loads can also result from behavioral adjustments in plumage thickness.

INTRODUCTION

The plumage of birds provides a critical thermal buffer between the animal and its environment. Feathers serve to retard convective and radiative heat flow from an animal's skin surface to the environment. In addition, plumage color, structure and optical properties, when combined with environmental properties (e.g., wind speed), determine the radiative heat loads that birds acquire from solar radiation. Thus, a suite of animal and environmental properties combine to determine the thermoregulatory costs, in terms of energy and water, that birds must assume during their day to day lives. These costs are substantial, as basal metabolic and thermoregulatory costs in

small birds typically account for 40 to 60% of their total daily energy expenditure (Walsberg, 1983). In hot environments, rates of evaporative water loss can exceed 5.0% of total body mass per hour (Wolf and Walsberg, 1996a, b).

This paper was not conceived as an exhaustive review, but instead provides an overview of heat transfer processes in avian plumages. Many selective forces have interacted to ultimately determine the physical characteristics of plumages. Feathers reduce drag (Homburger and de Silva, 2000), provide lift and propulsion, function in social signaling and crypsis (Stettenheim, 2000) and provide insulation to support the endothermic lifestyle of birds (Ruben, 2000). Because of these potentially competing demands, it is important to understand how feather and plumage structure and coloration are influenced by thermoregulatory constraints. We focus on three areas relating to the role of avian plumages in heat transfer processes in birds. First, we

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TABLE 1. Mean conductances \pm SD ($mW m^{-1} ^\circ C^{-1}$) of avian plumage preparations for Gambel's Quail, *C. gambelii*, Crissal Thrasher, *T. dorsale* and the House Finch, *C. mexicanus* from Walsberg (1988a).*

	With air present	Without air present	Mean difference	Coat depth (m)	Interception prob. (m^{-1})	Radiative conductance
<i>C. gambelii</i>	73.7 \pm 8.8	39.6 \pm 6.5	34.1	0.0094 \pm 0.0016	0.31 \pm 0.048	2.7
<i>T. dorsale</i>	79.6 \pm 7.2	42.4 \pm 6.3	37.2	0.0065 \pm 0.0004	0.42 \pm 0.050	2.0
<i>C. mexicanus</i>	70.1 \pm 10.4	33.9 \pm 6.1	38.2	0.0048 \pm 0.0032	0.30 \pm 0.041	2.8

* Also shown are measurements of plumage depth and estimates of interception probability (p).

examine the relative importance of different avenues of heat loss from the animal's skin surface to the external plumage surface. We discuss heat transfer by aerial conduction, conduction through the solid elements of the feathers, and radiation. Second, we look at how plumage color, structure, and optical properties combine with properties of physical environmental (*e.g.*, wind speed) to determine radiative heat loads to the skin from direct solar radiation. We also illustrate how solar heat loads are potentially de-coupled from plumage color. Then, we look briefly at the potential for behavioral adjustments of plumage thickness, through fluffing and sleeking of the feathers, to alter both plumage resistances and radiative heat loads to the skin. Finally, we look at the integration of animal and environmental properties and see how these combine to affect thermoregulatory metabolism in small birds.

HEAT FLOW THROUGH PLUMAGES

Heat transfer through the plumage occurs by several avenues, these include: 1) conduction and free convection through air, 2) conduction along solid elements of the feathers and 3) radiation (see Walsberg, 1988a for review). Identification of the relative importance of each of these avenues of heat transfer provides the basis for understanding how animals interact with their physical environments and how diverse evolutionary factors have interacted to produce the plumage of modern birds. To date, only a single study in wild birds has addressed the relative importance of these avenues of heat loss in avian plumages (Walsberg, 1988a).

Walsberg (1988a) quantified heat flow

from the skin to the surface of the plumage by using plumage preparations affixed to a aluminum plate heated to 40°C and a heat flux transducer situated on the outer plumage surface without a guard ring. Measurements were taken both in air (shielded from forced convection), and in a vacuum of 0.1 torr. Heat flow was quantified in plumage preparations from Gambel's quail (*Callipepla gambelii*), Crissal Thrashers (*Toxostoma dorsale*) and House Finches (*Carpodacus mexicanus*). The total conductances measured in air for these preparations were 2.6 to 3 times that of an equivalent thickness of still air (Table 1). These data indicated that the overall plumage insulation is equal to only 33–39% of the insulation provided by an equivalent depth of unstirred air.

When the plumage preparations were placed in a vacuum, heat transfer rates were reduced by one half and thermal conductances reduced by 46–52%. These differences in conductances for measurements made in air versus a vacuum indicate that approximately one-half of the total heat flow probably occurs through aerial conduction (Table 1). Interestingly, the values for aerial heat transfer are 26–41% greater than those predicted for aerial conduction through an equivalent depth of unstirred air ($27 mW m^{-1} ^\circ C^{-1}$). These data suggest that under the experimental conditions used (15°C thermal gradient), which roughly mimic the conditions found in a living bird, that free convection within the plumage may augment aerial heat transfer by 30 to 50%. However, this enhancement represents only a modest portion of the total thermal conductance of the plumage and accounts

for 10–16% of the overall heat flow between the skin and plumage surface.

The remainder of this heat flux (Table 1) can be attributed to conduction through the solid elements of the feathers and to radiative heat transfer. These two avenues of heat transfer can be segregated by estimating a radiative conductance for each species using the equations of Cena and Monteith (1975). These estimates incorporate measurements of the radiation interception function (p), which determines the probability of photon interception per meter of plumage depth for each plumage preparation (Walsberg *et al.*, 1978). In this study, values of p for the Gambel's quail, Crissal Thrasher and House Finch tested ranged from 0.30–0.42 m^{-1} indicating that photons travel only a short distance (0.0004–0.0007 m) before being absorbed by a plumage element. These values are significantly greater than those measured in mammalian pelts (Cena and Monteith, 1975). The large differences seen between mammals and birds are probably due to the layered ramiform structure typical of avian plumages. The more open structure of the mammalian pelt allows a photon to travel a much greater distance than in a bird plumage before absorption by a coat element. As a consequence, radiative conductances for the plumages examined in this study were extremely low and accounted for only about 5% of the total plumage conductance. Overall, conductances and rates of heat transfer from Walsberg, (1988a) were evenly divided between conduction and free convection through air, and conduction through the solid elements of the plumage.

SOLAR HEAT LOADS TO THE SKIN:
INFLUENCES OF PLUMAGE COLOR,
STRUCTURE, OPTICS, AND BEHAVIOR

In nature, a variety of selective factors compete to determine an animal's surface coloration. Among these are the need for visual communication, the maintenance of crypsis and the facilitation of thermoregulatory processes. Plumage color, microstructure, optical properties, and behavior all can interact to modify heat transfer from the external environment to an animal's skin surface. Solar radiation is a critical en-

vironmental property that can have an overwhelming affect an animal's heat balance. Under clear skies, heat input from the sun often exceeds 1,000 $W m^{-2}$ on a plane perpendicular to the solar beam. This is about 10 to 20 times the average area-specific basal metabolic rate of a small bird (Calder and King, 1974). About 40% of this solar energy lies in the visible wavelengths (*i.e.*, 400–900 μ) where plumage color has the opportunity to influence an animal's heat balance (Campbell, 1977). These environmental and animal properties suggest that thermoregulatory needs potentially exert a strong selective influence on the evolution of plumage traits.

Although plumage color or reflectivity determines the fraction of incident solar radiation that is absorbed by the plumage and that generates heat, the fraction of the heat that contributes to the thermal load on the skin can vary greatly. Traditional views, through analogies with simple surfaces (Lustick, 1971; Hamilton, 1973; Lustick *et al.*, 1978), generally furthered the premise that darker coats (*e.g.* those with higher absorptivities) acquire greater heat loads from solar radiation than do lighter plumages. Early measurements supported this view (Hamilton and Heppner, 1967; Lustick, 1969; Heppner, 1970), but there was also theoretical (Kovarik, 1964) and empirical work (Øristland, 1970) that suggested that other factors besides coat color had an important influence on solar heat loads. Equation 1, simplified from Walsberg *et al.* (1978), shows in general terms the factors that help determine the proportion of absorbed energy that is transferred to the skin surface.

$$H_s = (I_s)(1 - \rho^*)(r_E + r_Z)/(r_E + r_C) \quad (1)$$

Here, H_s is the heat load acquired at the skin surface, I_s is equal to the incident radiation flux, where ρ^* is reflectivity of the plumage. r_E is the equivalent parallel resistance to radiative and convective heat flow, and as such includes the resistance of the air boundary layer on the plumage surface. It is therefore affected by environmental properties such as wind speed. r_Z represents the plumage resistance to outward heat flow

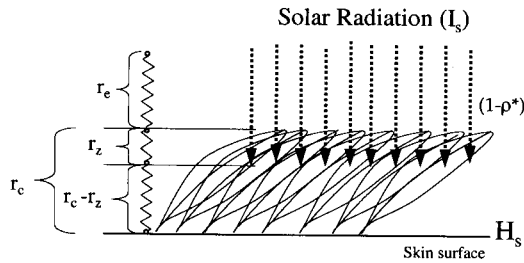


FIG. 1. Electric circuit analogs of factors affecting solar heat gain in plumages (adapted from Walsberg, 1983). This figure illustrates the scenario in which radiation penetrates to some average depth into the plumage before absorption and heat generation. H_s is the heat load on the skin from solar radiation, I_s is the solar irradiance at the outer coat surface, $1 - \rho^*$ is the coat absorptivity, r_e is the equivalent parallel resistance and includes the apparent radiative resistance of the air boundary layer. r_c is coat resistance, and r_z is the average coat resistance above the point of radiation absorption.

due to the penetration of radiation into the plumage and r_c is the plumage resistance.

For the remainder of this discussion we use heat transfer resistances to illustrate how physical environmental factors, such as wind speed and solar radiation, potentially affect an animal's heat balance. The use of heat transfer resistances facilitates the use of electric circuit analogs to model heat transfer processes (Campbell, 1977). Heat transfer resistances can be related to thermal conductances by equation 2

$$r = 1/(\rho c_p/k) \quad (2)$$

Where r is the resistance to heat transfer in (sec m^{-1}), l is the depth of the insulation in m , k is thermal conductivity in $\text{W m}^{-1} \text{K}^{-1}$, and ρc_p is the volumetric heat capacity of air ($1,200 \text{ J m}^{-3} \text{K}^{-1}$). The component conductances through different pathways can be summed to give a total conductance and converted to total resistance using equation 2. For example, *C. gambelii*, has a total plumage conductance (h) of $0.0737 \text{ W m}^{-1} \text{K}^{-1}$ and a plumage depth of 0.0094 m (Table 1); applying equation 2 to these values yields a total plumage resistance of 153 sec m^{-1} .

We can use Figure 1 and equation 1, to compare the fate of heat generated from radiation absorption at the plumage surface with a more realistic scenario where radia-

tion penetrates to some depth z into the plumage before absorption by a feather element. In the simplest scenario and the one used in early analyses (Lustick, 1971; Hamilton, 1973; Lustick *et al.*, 1978), all radiation is absorbed at the plumage surface. Thus, the solar heat load that reaches the skin is determined by: (I_s) the incident flux, $(1 - \rho^*)$ the coat absorptivity, and $(r_e)/(r_e + r_c)$ the proportion of the total resistance opposing heat flow away from the skin surface over the total resistance of the system. With absorption and heat generation at the plumage surface, $r_z = 0$. Consequently, the entire coat resistance (r_c) opposes heat flow towards the skin.

In a fibrous coat such as a plumage, however, we would expect some variable penetration into the coat, with absorption over a range of coat depths (Fig. 1). If the average depth of radiation penetration equals z ; then the coat resistance opposing the outward flow of heat equals r_z . Thus, heat flow away from the skin will now be proportional to $(r_e + r_z)/(r_e + r_c)$. Under these circumstances, the thermal resistance opposing heat flow away from the skin is equal to the sum of $r_e + r_z$, and the proportion of the total resistance opposing outward heat flow increases.

These effects, are potentially large (Fig. 2) and have been shown to increase solar heat loads to the skin by 600% in pigeons (Walsberg, 1983). At low wind speeds, solar heat loads are much greater in pigeons with black plumages ($\rho^* = 0.1$) than in those with white plumages ($\rho^* = 0.7$), regardless of whether the feathers are depressed or erected (Walsberg *et al.*, 1978). Interestingly, increased wind speeds have a much greater effect on the heat loads acquired by dark plumages than by white plumages. In dark plumages, 90% of the radiation absorption occurs in the upper 20% of the coat and none of the radiation penetrates beyond the upper 25% of the coat. In contrast, in light plumages, a full 10% of the radiation intercepted penetrates through more than 80% of the coat before it is absorbed. Consequently, in lighter plumages, heat generated by irradiation is largely insulated from loss to the environment. Strikingly, at high wind velocities,

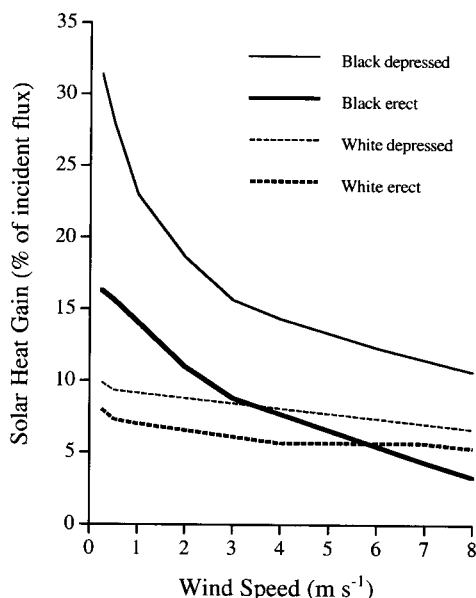


FIG. 2. Range of solar heat loads acquired by the skin for black and white pigeon plumages as a function of wind speed. Upper boundary for plumages of either color represents heat loads for completely depressed plumages. Lower boundaries represent heat loads for fully erected plumages. Data presented are mean values from Walsberg *et al.* (1978).

differences in radiation penetration into the plumage can even reverse the effects of large differences in plumage color. As detailed in Figure 2, for depressed plumages, increased wind speeds lead to greater solar heat loads in white plumages than in black ones above wind velocities of 5.5 m s^{-1} .

There can also be significant differences in solar heat loads as a result of behavioral adjustments in plumage thickness. In pigeons, where plumage depth varied from 8.0 to 31 mm, ptilo-erection increased plumage thermal resistance by about 50% in both light and dark plumages over a broad range of wind speeds (Walsberg *et al.*, 1978). Although these changes in the thermal insulation due to feather erection and depression are equal, the heat loads acquired by light and dark plumages are very different. In dark plumages, especially at low wind speeds, ptilo-erection results in huge decreases in solar heat loads to the skin (Fig. 2). In contrast, ptilo-erection results in only small decreases in solar heat

loads to the skin in lighter plumages at low wind speeds.

Which properties of the feathers or plumage determine the depth to which radiation can penetrate into the plumage? Radiation penetration into the coat is a function of the structural and micro-optical properties of plumage elements. A number of structural characteristics determine the depth to which a photon penetrates before interacting with a feather element. These may include the density, number and placement of feathers on the skin, the fraction of feather surface that is comprised of open space (the feather may be seen as a somewhat porous surface composed of a lattice of interlocking barbs and barbules), and the angle of the feathers relative to the incident radiation. These parameters are described by the interception probability function (p) for which there are few empirical data (Walsberg, 1983). p is the probability per unit of plumage depth that a ray will strike a plumage element and has units of m^{-1} (Walsberg *et al.*, 1978). For the Gambel's Quail, Crissal Thrasher, and House Finch, p varies by about 30% (Walsberg, 1988b), with no apparent relationship of p to body size. Walsberg (1988b) also used simulations to show the potential effects of the intercept function (p) on radiative heat loads for light and dark pigeon plumages. Halving the distance that a ray traveled before being intercepted by a plumage element reduced solar heat gain by 5% in both light and dark plumages. But because overall levels of solar heat gain were greater in dark versus light plumages there were different fractional decreases in the heat load for light ($\sim 41\%$) versus dark ($\sim 25\%$) plumages.

In mammals, there appears to be significant variation in the value of p , *e.g.*, 120 times greater in rat (0.8 m^{-1}) than in goat pelts (0.007 m^{-1}) (Cena and Monteith, 1975; Walsberg, 1988a). In spite of this variability, p appears to be largely independent of coat reflectivity (Cena and Monteith, 1975), suggesting that interception probability can affect solar heat loads without influencing an animal's coat color.

Feather micro-optics are also important in determining the depth to which radiation penetrates into the plumage. Overall plum-

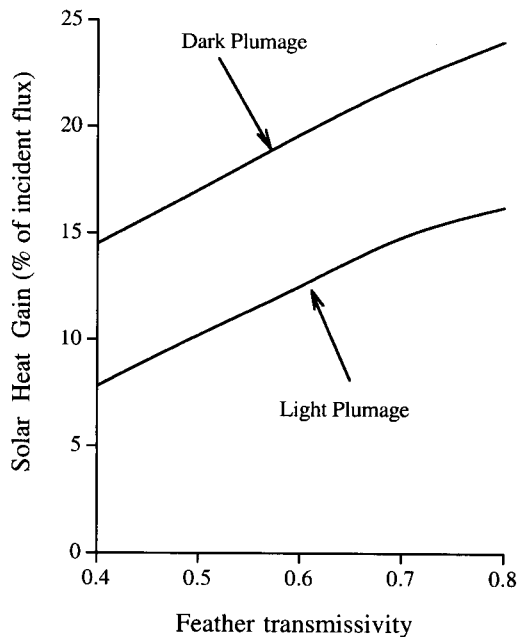


FIG. 3. Simulated effect of variation in feather transmissivity on solar heat gain in dark ($*\rho = 0.1$) and light ($*\rho = 0.7$) plumages (from Walsberg, 1988b). Heat gain at the skin level is calculated as the percentage of solar radiation incident at the outer coat surface. Calculated from equation 1 of Walsberg (1988b), equation 11b of Cena and Monteith (1975) and data from Walsberg *et al.* (1978) for pigeon plumages exposed to a wind velocity of 3 m sec^{-1} .

age color is a function of the ratio of absorptivity (α) to reflectivity (ρ) of the whole plumage. Solar heat loads acquired at the skin, in contrast, are greatly dependent on the optical properties (α , ρ and τ , transmissivity) of individual coat elements. Theoretically, two plumages may be of similar color, *i.e.*, have similar α/ρ ratios, but the absolute values of these parameters may be very different. For example, one plumage may have absolute values of α and ρ which are very small and a large τ with the concomitant forward scattering (transmission) of radiant energy. In this case, because of forward scattering, the high τ results in much greater solar heat load to the skin than might be seen in a plumage with a small τ and greater absolute values for α and ρ . Figure 3 shows the potential effects of transmissivity or forward scattering on solar heat loads in light and dark plumages. Over a range of τ (0.4–0.8) each 0.1 in-

crease in τ results in about a 2% in solar heat load to the skin for both light and dark plumages.

INTERACTIVE EFFECTS OF SOLAR RADIATION AND WIND ON THE THERMOREGULATORY METABOLISM OF SMALL BIRDS

Thus far, we have focussed on heat transfer processes within the plumages of birds by looking at 1) the specific attributes of plumages and how they mediate heat loss to the environment and 2) how solar heat loads are affected by behavioral adjustments of plumage depth, structural characteristics of plumage elements, and the micro-optical properties of feathers. For the remainder of this paper, we focus on the integrative effects of wind and solar radiation on the heat balance and thermoregulatory metabolism of a small bird.

Rates of energy expenditure are strongly influenced by the thermal properties of the 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 understood (reviewed by Calder and King, 1974). Less extensive research has examined the effects of wind speed on avian metabolic rates and has shown that convective heat transfer plays a significant role in determining thermoregulatory costs in small birds (reviewed by Goldstein, 1983) see also (Webb and Rogers, 1988; Webster and Weathers, 1988; Bakken *et al.*, 1991; Wolf and Walsberg, 1996). Fewer researchers have focussed on the potential effects of solar radiation on thermoregulatory costs in small birds (Hamilton and Heppner, 1967; Heppner, 1970; Lustick, 1969, 1971; Lustick *et al.*, 1970; De Jong, 1976).

Here, we briefly examine the role of complex radiative and convective environments on the thermoregulatory metabolism of the Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) (Wolf *et al.*, 2000). We present data on metabolic rates and changes in body thermal resistances as a function of wind speed and irradiance. We also look at solar heat gain as a function of incident flux and wind speed.

The methods used for this analysis were similar to those of Wolf and Walsberg (1996) and detailed in Wolf *et al.* (2000). Briefly, we measured rates of CO₂ production in captive White-crowned Sparrows by using a closed circuit wind tunnel metabolic chamber. A variable speed DC blower recirculated air through the chamber test section. Simulated solar radiation was produced by a Spectral Energy Corporation series II solar simulator, passed through a flint glass window, and irradiated an animal perched in the chamber test section. Sparrows ($n = 8$ for each wind speed and irradiance level) perched quietly in the chamber test section, and their rates of CO₂ production were measured at wind speeds of 0.25, 0.5, 1.0 and 2.0 m sec⁻¹, both in the presence ($936 \pm 11 \text{ W m}^{-2}$) and absence of simulated solar radiation. Chamber air temperatures were held at 10°C for all treatments.

As expected, metabolic rates increased sharply with increasing wind speed (Fig. 4). In the absence of solar radiation, between wind speeds of 0.25 and 2.0 m sec⁻¹, metabolic rates increased by 30% (or 90% of basal metabolic rate, 51 W m^{-2} [King, 1964]) and with solar radiation present metabolic rates increased by 52% (or 120% of basal metabolic rate). Solar heat gain, defined as the reduction in metabolic rate associated with the addition of solar radiation, varied from 36 W m^{-2} to 21 W m^{-2} , between wind speeds of 0.25 and 2.0 m sec⁻¹. These values are equal to approximately 71% and 41%, respectively, of the sparrow's basal metabolic rate. At low wind speeds (0.25 m sec⁻¹), solar heat gain resulting from the addition of 936 W m^{-2} produces a change in metabolic rate equivalent to a reduction in wind speed from 2.0 m sec⁻¹ to just under 0.5 m sec⁻¹ in the absence of solar radiation. These data suggest that the addition of solar radiation is equivalent to three to four-fold changes in wind speed (Wolf *et al.*, 2000).

These changes in metabolic rate with wind speed and irradiance are largely due to changes in the thermal resistance of the interface between the animal and its environment. Between 0.25 and 2.0 m sec⁻¹, r_B declines by a modest 14% (Fig. 5). In con-

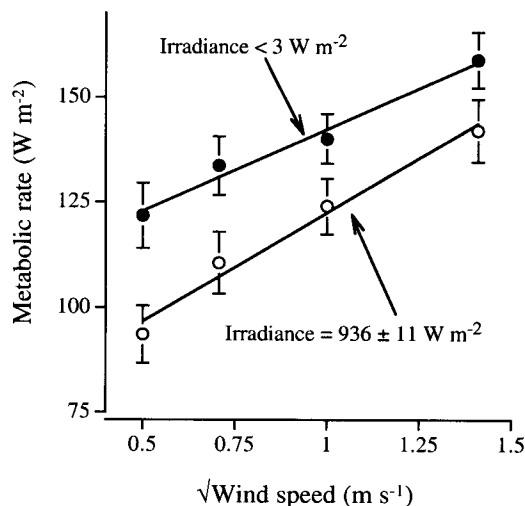


FIG. 4. White-crowned sparrow metabolic rates as a function of the square root of wind speed and irradiance (from Wolf *et al.*, 2000). Metabolic rates are presented on a plumage surface-area specific basis where plumage surface is equal to $A_p = 8.11 \text{ (m}^{0.667}\text{)}$ (Walsberg and King, 1978). Means \pm 95% confidence intervals are presented for an $n = 8$ at each wind speed and irradiance combination. Solar heat gain, is calculated as the reduction in metabolic rate, at a given wind speed, associated with addition of simulated solar radiation.

trast, r_E declines by 64% over the same range of wind speeds. The observed decline in r_E is due solely to the disturbance of the air boundary layer at the plumage surface. Reductions in r_B as wind speed increases probably represent disruption of the plumage itself. As a result of these shifts there is a 52% increase in metabolic rate between 0.25 and 2.0 m sec⁻¹ in sparrows exposed to solar radiation (Fig. 5).

How much intercepted radiation is translated physiologically into a savings of energy? We examine this question by calculating the solar heat gain for each wind speed as a percentage of the intercepted flux. It is clear that interspecific differences in solar heat gain can be substantial (Fig. 6). In Verdins, *Auriparus flaviceps*, intercepted radiation has very large physiological effects, but these are extremely sensitive to increases in wind speed. This may partially be explained by their small size (6.5 g) and lesser insulation (~50% less than that estimated from allometric equa-

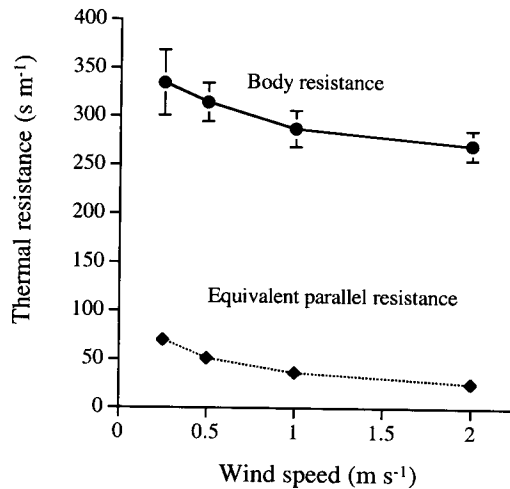


FIG. 5. Body resistance (r_b) (mean \pm 95% confidence intervals) and equivalent parallel resistance (r_E) as a function of wind speed (from Wolf *et al.*, 2000).

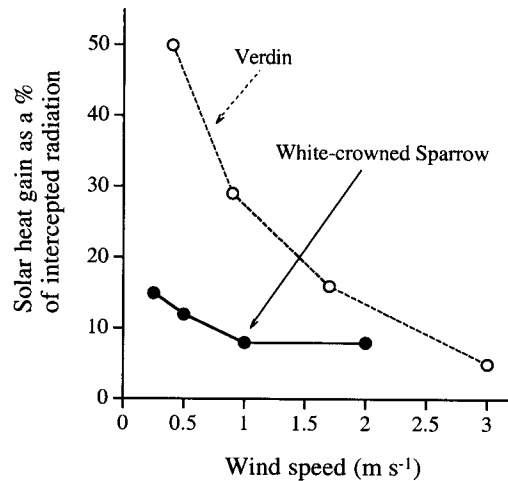


FIG. 6. Solar heat gain (as a percentage of intercepted radiation flux) as a function of wind speed for White-crowned Sparrows (from Wolf *et al.*, 2000) and Verdins (Wolf and Walsberg, 1996b).

tions) compared to passerines of similar size (Webster and Weathers, 1988). This species builds and occupies domed roost nests throughout the year (Taylor, 1971). These nests confer a significant metabolic savings by shielding the animal from the wind and reducing convective heat losses (Buttemer *et al.*, 1987). White-crowned sparrows, in contrast, are a larger (25 g) boreal species that breeds in Alaska. They do not show the same sensitivity as Verdins to changes in wind speed, nor do they derive the same physiological benefits from solar radiation. White-crowned Sparrows, for example, are able to use only about 16% of the intercepted radiation.

CONCLUDING COMMENTS

Understanding heat transfer processes in avian plumages is a significant undertaking. Although measurements are sparse, current data (DeJong, 1976; Wolf and Walsberg, 1996; Wolf *et al.*, 2000) indicate that solar heat gain has significant effects on the heat balance and thermoregulatory metabolism of small birds. These data also suggest that there is significant variability among species in the effects of forced convection on solar heat gain. Heat transfer is importantly affected by plumage structure, which in

turn determines the relative proportion of heat transferred by radiation, conduction through the solid elements of the feathers, aerial conduction and convection through the feathers. Many of these factors vary among species and may be under behavioral control (*e.g.*, ptilo-erection). Ample opportunity exists, as suggested by Figures 2 and 3, for changes in plumage color, structure and micro-optics to de-couple plumage coloration from solar heat gain; although the actual occurrence of these phenomena are largely undescribed for birds (but see Walsberg, 1980, 1982, 1993). Limited work on small mammals has found differences in the color, structure or optical properties of pelages that lead to adaptive shifts in thermoregulatory metabolism (Walsberg, 1988c; Walsberg and Schmidt, 1989; Walsberg, 1990; Walsberg and Wolf, 1995a, b; Walsberg *et al.*, 1997). If the variation found in mammals is common to avian species, then feather micro-optical and structural properties could de-couple thermoregulatory and social pressures that drive the evolution of plumage color. Currently, the natural variation in plumage properties and heat transfer processes of birds living in the diversity of complex natural environments remains largely unexplored.

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APPENDIX 1.

α	plumage absorptivity
H_s	heat load acquired at the skin surface ($W\ m^{-2}$)
I_s	incident radiation flux ($W\ m^{-2}$)
k	thermal conductivity ($W\ m^{-1}\ K^{-1}$)
l	insulation depth (m)
p	radiation interception function (m^{-1})
r	heat transfer resistance ($s\ m^{-1}$)
r_B	body resistance ($s\ m^{-1}$)
r_C	coat resistance ($s\ m^{-1}$)
r_E	equivalent parallel resistance to radiative and convective heat flow ($s\ m^{-1}$)
r_E	radiation penetration resistance ($s\ m^{-1}$)
ρc_p	volumetric heat capacity of air ($1200\ J\ m^{-3}\ K^{-1}$)
ρ^*	plumage reflectivity
τ	plumage transmissivity
