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Coat Color and Solar Heat Gain in Animals

Glenn E. Walsberg

The relation between coat color and solar heating in birds and mammals varies greatly; darker colors either may increase or decrease heat gain. This relation depends upon a suite of environmental and organismal properties that may vary independently of color and be open to adaptive adjustment. *(Accepted for publication 24 September 1982)*

A recent analysis of the relation between animal coat color and solar heat gain stated "there still is a question as to whether dark or light plumage is more effective in utilization of direct solar radiation" (Lustick et al. 1980). This may surprise some, since common experience indicates that dark surfaces acquire greater heat loads when exposed to solar radiation than do light surfaces. For animals such as birds or mammals that possess insulating coats of fur or feathers, however, recent studies have shown that the thermal consequences of coloration present the potential for widely varying effects that have not been generally appreciated by biologists.

It is clear that an animal's surface coloration might importantly affect heat exchange with its environment and thus its thermoregulatory demands. Surface coloration arises from differential reflection or transmission of short-wave radiation (the longest wavelength visually perceived by animals typically is near 700 nm). That radiation not reflected or transmitted by the surface is absorbed, resulting in sensible heat generation. With the exception of bioluminescence, the only important natural sources of short-wave radiation are very hot objects, notably stars such as the sun. The intensity of solar radiation reaching the earth's surface varies, but under clear skies often reaches values of about 1000 W/m^2 on a plane perpendicular to the solar beam. Roughly one-half of this energy lies in visible wavelengths and hence is of sufficient magnitude that coat color might significantly modify an animal's heat balance.

EARLY ANSWERS AND RECENT QUESTIONS

Through analogy with the properties of simple surfaces, biologists (e.g., Hamilton 1973, Lustick 1971, Lustick et al. 1978) have generally accepted the view that animals with dark-colored pelages or plumages, and hence obstensibly greater absorptivity for short-wave radiation, acquire greater heat loads from solar radiation than do animals with light-colored coats. In spite of some empirical evidence (e.g., Øristland 1970) and theoretical arguments to the contrary (e.g., Kovarik 1964), pioneering measurements of the relation between radiative heat gain and coat color generally supported this expectation (e.g., Hamilton and Heppner 1967, Heppner 1970, Lustick 1969). These analyses typically involved comparison of the thermoregulatory performance of light and dark plumaged birds confined in metabolic chambers and exposed to short-wave radiation. Simulated solar radiation at intensities resembling natural levels affected the animals' heat budgets significantly, and darker forms acquired greater radiative heat loads. For example, Hamilton and Heppner (1967) found that in zebra finches (*Poephila castanotis*) held at an air temperature of 10°C, exposure to 860 W/m^2 of short-wave radiation reduced resting metabolism 6% in albino finches and 27% in those that had been dyed black.

The generalization that darker coat colors are necessarily associated with increased solar heat loads has been questioned seriously on both theoretical and experimental bases (e.g., Cena and Monteith 1975, Øristland 1970, Walsberg et al. 1978). These analyses focused on the confounding effects of radiation penetrating into an insulating fur or feather coat. The role of such radiation penetration can be examined using a model simplified from Walsberg et al. (1978) (Figure 1). For illustrative purposes, the distribution of radiation absorption within a coat is characterized by a single average level of ray penetration (Z in Figure 1). Assuming that a steady state prevails, heat generated at level Z will flow toward the skin or the environment in inverse proportion to the relative magnitude of the insulation opposing its flow in a particular direction. That is, if thermal resistance from the level of radiation penetration to the environment is one-half of that to the skin, twice as much heat will flow to the environment as to the skin. One can therefore divide the total insulation from skin to environment into two components. The thermal resistance opposing heat loss to the environment is the sum of the coat's resistance from the level of radiation penetration to the outer coat surface (r_Z) and the resistance to heat transfer from the outer coat surface to the general environment (r_E). The latter term subsumes qualities such as the insulative character of the atmospheric boundary layer adjacent to the outer coat surface and is influenced by factors including wind velocity and body size and shape. The thermal resist-

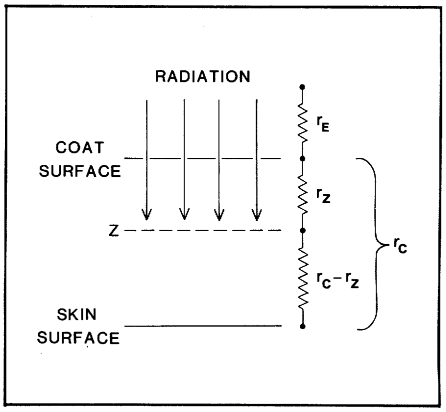

Figure 1. An electrical circuit analogue of factors affecting solar heat gain in a fur or feather coat.

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ance opposing heat transfer to the skin is that fraction of the coat resistance (r_C) between the level of radiation penetration and the skin ($= r_C - r_Z$). Thus, the heat load on the skin from solar radiation (H_S) will equal the product of solar irradiance at the outer coat surface (I_S), the fraction of solar radiation which is not reflected by the coat, and the fraction of the total thermal resistance that opposes heat loss to the environment from the site of radiation absorption:

$$H_S = (I_S)\ (1 - \rho^*)\ (r_E + r_Z)/(r_E + r_C)$$

Here, ρ^* is the fractional reflectivity of the coat to solar radiation, which is an index of coat color. This equation illustrates that reflectivity is only one of many factors determining the solar heat load accrued by an animal. If solar radiation did not penetrate animal coats ($r_Z = O$), then two animals that differed only in coat color and were exposed to the same microclimate would acquire solar heat loads inversely proportional to coat reflectivity. If radiation penetration is significant, however, then variation in r_Z can oppose the thermal consequences of variation in ρ^*. For example, a dark coat may absorb most solar radiation impinging on it. However, if such absorption occurs largely near the outer coat surface, then a large fraction of the resulting heat will be lost to the environment and will not contribute to the thermal load on the skin. In contrast, a white coat may reflect most solar radiation, but the radiation that is not reflected may penetrate readily through unpigmented hairs or feathers and pass deep into the coat before being absorbed. In this case, a large fraction of the heat generated by irradiation will contribute to the thermal load on the skin.

The thermal effects of short-wave radiation penetrating into a coat can be substantial. In cattle, Hutchinson and Brown (1969) have shown that such penetration into either brown or white coats increases the heat load at the skin up to 300% over that expected if all radiation were absorbed at the upper coat surface. In pigeons (*Columba livia*), short-wave penetration increases heat gain up to 30% in black plumages and up to 600% in white plumages (computed from data in Walsberg et al. 1978). This difference is large enough under proper conditions to result in white plumages acquiring greater radiative heat loads than black plumages. Thus, the little-known determinants of radiation penetration can be of major thermal importance and can reverse the relation between solar heat gain and coat color.

DETERMINANTS OF RADIATION PENETRATION INTO COATS

Factors affecting radiation penetration may be divided into bulk properties of coat structure, which determine the likelihood of a penetrating ray being intercepted by a coat element (hair or feather barbule), and optical properties of individual hairs or feathers, which modify the fate of the intercepted ray.

Coat Structure

The structure of an insulating coat determines the probability per unit coat depth that a penetrating ray will be intercepted by a coat element. In a fur coat, this interception probability (P) is determined by the number, length, and diameter of the hairs as well as the angle of the hairs relative to incident radiation (Cena and Monteith 1975). Important determinants of P in birds should include the density and placement of feathers on the skin, as well as the fraction of the microscopic lattice of feather barbs and barbules that is composed of open space. Few data are available describing this function, but P undoubtedly varies widely both between and within species. For example, Cena and Monteith (1975) cite a value of 0.7 cm^{-1} for a goat pelt, but I have calculated a value of 84 cm^{-1} for a laboratory rat (unpublished data). Thus, a light ray penetrating a unit depth of fur is 120 times more likely to be intercepted by a hair in a rat pelt than in that of a goat. This interception probability can be behaviorally modified. In black-tailed hares (*Lepus californicus*), for example, piloerection results in an approximate doubling of the distance a penetrating ray travels through the fur before striking a hair (Walsberg, unpublished data).

Considering this substantial range of variation, it is notable that coat reflectivity appears to be nearly independent of the interception function (Cena and Monteith 1975). Thus, variation in this factor can affect solar heat gain without importantly affecting coat color.

Optical Properties of Hair and Feathers

A ray that is intercepted by a coat element will either be absorbed by that element, generating sensible heat; transmitted or scattered toward the skin; or scattered or reflected away from the skin. The greater the degree to which intercepted radiation is scattered deeper into the coat toward the skin, the greater the consequent solar heat load on the animal. Thus, important variables affecting solar heat gain are the fractions of incident solar radiation that an individual coat element absorbs (α), reflects or scatters backward (ρ), and transmits or scatters forward (τ). (Note that $\alpha + \rho + \tau = 1$.) These properties of individual hairs or feathers should not be confused with bulk properties of the coat, such as the fractional reflectivity of the coat to solar radiation. Indeed, coat reflectivity (ρ^*) apparently is almost independent of the absolute values of the optical variables of individual hairs (i.e., α, ρ, τ), but rather is largely a function of the ratio α/ρ (Cena and Monteith 1975). The absolute values of α, ρ, and τ do, however, importantly affect radiation penetration into a coat and, thus, solar heat gain. The relation between these optical properties and solar heat gain is complex, but a theoretical solution has been derived for the case in which the coat is of uniform structure and insulation increases linearly with depth. In this situation, solar heat gain to the animal is an inverse function of the quantity $\alpha + 2\rho$ (Walsberg et al. 1978). (Readers of Walsberg et al. [1978] should note that $1/[\alpha + 2\rho]$ is equivalent to the expression α/η^2 incorporated in their equation 15.)

Thus, the observation that two coats are of similar reflectivity may indicate only that the ratio α/ρ is similar, but the absolute values of these optical properties may differ sharply between coats. For example, one coat may be composed of hairs in which forward scattering (τ) predominates and the absolute values of hair absorptivity (α) and reflectivity (ρ) are very small. In this case of very transparent hairs, the value $\alpha + 2\rho$ will be low. Thus, the solar heat load acquired by radiation penetrating into the coat will be higher than that experienced by a coat of similar color in which hair transmissivity is low and the absolute values of α and ρ are high.

The extent to which such phenomena are important in nature is unknown, though it has been suggested that arctic mammals such as polar bears (*Thalarctos maritimus*), Weddell seals (*Leptonychotes weddelli*), and harp seals (*Pagophilus groenlandicus*) employ very transparent hairs to increase their rate of solar heat gain (Grojean et al. 1980, Øristland 1970, 1971, Ray and Smith 1968). In polar bears, for example, Grojean et al. (1980) have proposed that hollow, transparent hairs act as light

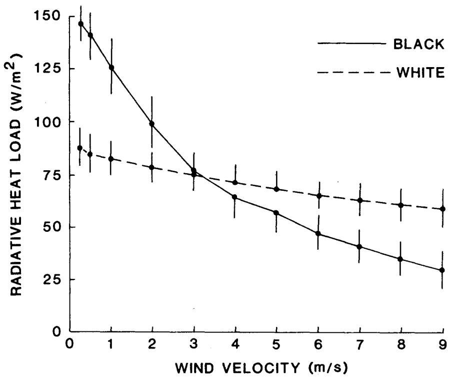

Figure 2. Radiative heat load transferred to the skin under black or white pigeon plumages as a function of wind velocity. Plumages were maximally erected and exposed to 900 W/m^2 of simulated solar radiation. Values are $\bar{x} \pm$ S.D., n = 5. See Walsberg et al. (1978) for methods and original data.

guides to preferentially scatter solar radiation toward the dark skin, thus increasing the depth of radiation penetration and consequent heat gain. Unfortunately, measurements of the efficacy of this arrangement in increasing solar heating are not available. In spite of the sparse data base, however, it is clear that substantial natural variation exists in hair optical properties (Cena and Monteith 1975, Øristland and Ronald 1978). For example, Øristland and Ronald (1978) report values for three mammals (*Mustela* sp., *Enhydra lutris, Callorhinus ursinus*) that possess dark brown coats. Though coat reflectivity is similar in these species (= 0.30–0.35), hair transmissivity varies twofold. Thus, even if other coat characters such as bulk structure and insulation were similar in these animals, different solar heat loads would be expected. This variable relation between coat reflectivity and the transmissivity of individual hairs is not restricted to these species, for analysis of Øristland and Ronald's (1978) data indicates no significant correlation between ρ^* and τ in 16 mammal species (Student's t-test; $P > 0.40$, $r^2 = 0.05$). These considerations substantially increase the technical difficulties encountered in analyses of the relation between solar heat gain and coat color. Such studies often entail use of animals whose coat color was produced by artificial dying, bleaching, or selective breeding of domestic populations (e.g., Finch et al. 1980, Hamilton and Heppner 1967, Lustick 1969, Marder 1973). The degree to which the optical and structural characters of the resulting hair or feathers resemble those of coats occurring in natural populations is unknown. Without such information, one cannot determine the extent to which data generated by these experiments applies to animals in nature.

MEASUREMENTS OF RADIATIVE HEAT GAIN

As might be expected from these physical considerations, empirical analyses demonstrate that the relation between animal coat color and radiative heat gain is quite variable. For example, several experimental studies have concluded that darker color is associated with increased heat gain. These analyses examined the effect of short-wave radiation upon a variety of birds and mammals (e.g., *Larus argentatus*, Lustick et al. 1980; *Poephila guttata*, Hamilton and Heppner 1967, Heppner 1970, Lustick 1969; *Capra hircus*, Finch et al. 1980). Such measurements typically have been made under a restricted set of environmental conditions in which complicating effects, such as those due to forced convection, are largely excluded.

In contrast, Øristland (1970) concluded that lighter fur color increased solar heat gain in the harp seal. These seals are light gray or yellowish with patches of dark fur. Øristland quantified thermal effects of such variation in coat color by measuring the subcutaneous temperature of detached portions of pelts that were mounted outdoors on a styrofoam block and exposed to solar radiation. The higher temperatures occurring under areas of light-colored fur were attributed to increased penetration of radiation into these coats.

These analyses indicate that for different species and settings, darker coat color may either increase or decrease solar heat gain. Such qualitative variation also may occur within a single species. In pigeons (*Columba livia*), the heat gain of black plumages exposed to simulated solar radiation is much greater than that of white plumages when wind velocities are low (Figure 2) (Walsberg et al. 1978). However, because radiation penetrates deeply into white plumages (Figure 3), heat generated by irradiation is substantially insulated from loss to the environment, and radiative heating of these plumages is less dependent on wind speed than that of black plumages. Thus, the radiative heat loads of black and white coats rapidly converge as wind speed increases. This effect is seen most prominently when the feathers are fully erected and white plumages acquire greater radiative heat loads than black plumages at wind velocities above 3 m/s (Figure 2).

The degree to which such effects occur in other animals is unknown, since the relationship between radiative heat gain and wind velocity depends upon a suite of factors including body size, coat structure, and the optical properties of the feathers. My colleagues and I have noted, however, that at least some species appear to take advantage of the effects described above (Walsberg et al. 1978). For example, most gulls (*Larus* spp.) have white bodies with light gray backs, but a few desert-nesting species are conspicuous exceptions in that they are primarily dark gray over most of their body. The best studied species is the gray gull (*Larus modestus*), which nests during the summer in the Atacama Desert of Chile (Howell et al. 1974). Solar radiation in this tropical desert is intense and air temperatures often reach 38°C. This species' dark color apparently serves to minimize radiation penetration and associated solar heat gain during the hot and windy afternoon. Conversely, the white plumages characteristic of arctic birds may reduce cold stress by increasing solar heating.

The sensitivity of solar heat gain to moderate variation in environmental var-

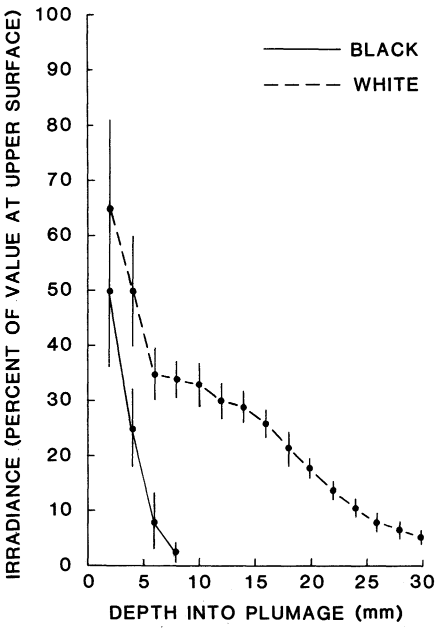

Figure 3. Penetration of short-wave radiation into black or white pigeon plumages. Plumages were erected to a depth of 30 mm and irradiance measured under a diffuse incandescent lamp using a blue-enhanced silicon cell mounted at the base of a 40 mm long, 16 ga. blunt hypodermic needle. A small hole was cut in the skin of the horizontally mounted plumage preparation and the needle passed vertically through the plumage, with irradiance measured at 2 mm intervals. Values are $\bar{x} \pm$ S.D., n = 5. (G. E. Walsberg and J. R. King, unpub. data).

iables such as wind velocity demonstrates the necessity to evaluate the thermal significance of coat color in the context of a particular species' natural environment and coat properties. This rarely has been accomplished, which prompted me to quantify the effect of plumage color upon the energy balance of a desert bird, *Phainopepla nitens*, under natural conditions (Walsberg 1982). This species is a small (about 25 g) songbird that normally is exposed to intense solar radiation, since it resides in the Sonoran Desert. In addition, it is sexually dimorphic in plumage coloration. With the exception of light wing patches that are concealed when the bird perches, males are black (solar reflectivity = 10%) and females are gray (solar reflectivity = 22%) (Walsberg 1980). Thus, the female's reflectivity is close to that typical of the cryptic gray or brown hues common to birds. In contrast, the male is an example of the pattern noted by a number of authors (e.g., Buxton 1923, Meinertzhagen 1954) that black animals are the most common exceptions to the rule that desert species are cryptically colored. When exposed to natural conditions likely to maximize the effect of differences due to coat color, the heat load on the black male is only slightly greater than that on the gray female and is equivalent to the increase in heat load that would be produced by a 1–2°C increase in air temperature. At least for one species, therefore, variation in heat gain due to differences in coat color probably is insignificant compared to that produced by simple postural adjustments and selection between available microclimates (Walsberg 1982).

CONCLUDING COMMENTS

It is apparent that no general answer is possible to the common question of whether animals with dark or light coats acquire greater solar heat loads. Both theoretical considerations and empirical measurements demonstrate that there is no simple relation, even in a qualitative sense, between coat color and radiative heat gain. A darker coat may acquire either a larger or smaller solar heat load depending upon a complex suite of organismal and environmental properties that often are independent of pelage or plumage color. Many of these factors vary between species and may be under behavioral control by an individual (e.g., by ptilo- or piloerection). It is quite possible, for example, that two fur coats of similar color and insulation may transfer substantially different solar heat loads to the skin due to differing degrees of hair transmissivity. Little is known regarding many of these factors except that substantial variation occurs. In addition, a number of other potentially significant variables have received little attention. Animal coats, for example, frequently are not uniform in color or structure throughout their depth. One case occurs in snowshoe hares (*Lepus americanus*), which, during portions of their annual cycle, appear brown only because long, dark guard hairs protrude through and conceal a shorter, dense white fur. The effects of such a complex coat structure upon radiation exchange have yet to be evaluated. Adaptive adjustment of heat-transfer relations may be further complicated by selection pressures related to the other functions of animal coats, such as social signaling and crypsis, water repellency, and maintenance of appropriate aerodynamic or hydrodynamic qualities (Burtt 1981).

Perhaps the most salient conclusion to be drawn from this analysis is that the initial question of the qualitative relation between animal coat color and solar heat gain does not currently have substantial scientific utility. Since there apparently are ample opportunities for natural selection to adjust this relation, more productive approaches to understanding the ecology of animal coloration or the interactions of birds and mammals with their radiative environments could be developed from other perspectives, such as quantifying the degree to which animals in their natural setting acquire solar heat loads and determining the major environmental properties and animal adaptations affecting such heat gain.

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