Black Pigmentation: Adaptation for Concealment or Heat Conservation?

A recent report by Hamilton and Heppner (*1*) on some possible functions of surface coloration (albedo) in birds once again states the possible involvement of physiological processes with varying light or energy absorption in organisms having differing coefficients of reflectivity.

Because the theoretical conclusions that might be drawn from these data could be interpreted as disproving or at least as denigrating the classical views of the definitive function of surface coloration, and its function under natural selection and in evolution, I am constrained to argue that despite the demonstrable 22.9 percent metabolic conservation obtained (*1*) in insolated blackened birds, other conclusions can be derived from the experimental results on white and artificially blackened Australian zebra finches (*Poephila castanopsis*).

Many workers have repeatedly noted and confirmed the selective value of concealing albedos and coloration. Of course even extremes in albedos might serve one, two, or even more selectively effective roles in nature; nonetheless, even if one (or more) function is served, this fact does not by itself require substitution of one for the other, and especially not of a lesser use for a greater one, nor especially for the overlooked, but probably definitive effects.

In this instance difficulties chiefly due to semantics may have contributed to the conflicting viewpoints and interpretations of otherwise unarguable experimental observations. As long as inappropriate or confusing words are used, there will probably be additional conflicts in the interpretation of data. In discussions of energy conservation and body temperature it is semantically advantageous to substitute the dynamically expressive terms endotherm and endothermic (*2*) which direct attention to the source of energy and heat, for homoiotherm, which merely denotes a more or less static condition resulting from endothermy. This usage has particular value in the comparison of the internally heated mammals and birds with the externally heated reptiles and amphibia (the ectotherms) or with the basking heliotherms. Under the usual conditions prevailing in and around endotherms, and particularly in birds, the thermal gradient usually slopes steeply from the body toward the environment. Under these conditions, excessive heat loss from birds is prevented chiefly by the notable insulative qualities of their feathers.

Interpreting the observations of Hamilton and Heppner, according to the picture evoked by use of the concept of endothermy, and in conjunction with the insulative effectiveness of bird plumage, I find it scarcely possible that even the notable metabolic economy amounting to 22.9 percent could be attributed to the transfer into the body of surface heat impinging on black feathers. Such transfer is implied by the statement, "These results indicate that homeothermic animals can absorb and utilize radiant solar energy and that dark pigmentation facilitates this process." Is it not equally possible that the heated surface might reverse the normal thermal gradient and thus interpose a barrier to an otherwise extravagant heat loss?

In the absence of any temperature measurements of the body at the skin surface, and outwardly to the insolated surface layer of feathers, it is impossible to follow and evaluate the precise processes of heat movement. In the absence of this thermal information and with due regard to the minute amounts of solar energy available at dawn and dusk, when external heat is supposedly needed and used, the feathers, regardless of color, might even occlude the needed supplementary external heat precisely when it would be most beneficial.

An additional conclusion is drawn by the authors, "The same evidence is applicable to the coloration of man. Dark human skin coloration may maximize the absorption of solar radiation in situations where energy must be expended to maintain body temperature, as at dawn and dusk in otherwise hot climates."

It seems probable that just because solar energy is so effectively absorbed by the dark skins of most tropical races, a low albedo (which might not be helpful even for brief periods at dawn and dusk) also would expose the possessor to the handicap of an excessive external heat load for all the rest of the daylight hours. This alternative effect raises a serious objection to the theoretical energy-conserving benefits of blackness in man or finch. To me it seems scarcely possible that maximizing the absorption of solar radiation in animals living in hot climates in summation could have any but a deleterious effect.

Under the conditions in which dark pigmentation is supposed to exert a favorable effect it would be necessary to have a readily changeable albedo from light-absorbing dark hue, to a heat-reflecting white so as to modulate the absorption of environmental heat. Without such a mechanism black pigment would be a distinct disadvantage, not only in direct proportion to its efficiency for heating during the fleeting "dawn" and "dusk" hour or so, but also according to the number of hot hours per day. In hot climates where the sunlight is very intense, a dark skin might cause a serious heat burden for as many as 10 hours a day, or more, over a period of at least several months each year. And these hot hours of intense insolation also are precisely those when many diurnal creatures often must generate internal heat while foraging, evading enemies, defending territories, and even in conducting respiratory cooling, or, except for man, carrying on most of the mating activities. Blackness in conjunction with the notable penalties of heat absorption and overheating would seem to outweigh the evanescent benefits by at least ten or more times. But even the suggested benefits at dawn and dusk of surface heating as a result of black color seem exceedingly dubious, since the light intensities and the total insolated energy at these critical hours are, except for total darkness, at their lowest levels. The facts concerning the effects of black pigmentation on energy conservation can be ascertained only by plotting the metabolic and external heat conditions throughout a 24-hour period under natural radiative and behavioral circumstances.

If some other explanation for black plumage and pelage and for the dark skins of human beings in tropical countries must be sought, then that of concealment seems most plausible. Viewed from this classical interpretation of natural selection via effective concealment, the surface coloration or albedo which absorbs most of the incident light and reflects the least, simultaneously results in providing minimum visibility in an object. Thus dark or black bodies that reflect almost none of the incident light rays that would be necessary for stimulation of the retinal cells of a potential predator, will be least visible or invisible. Furthermore, under crepuscular conditions when predation is usually most intense, a black object is more apt to be overlooked than one that reflects light. If a dark object is detectable at all, it is only against a light or reflective background. My observations (*3*) in hot climates lead me to believe that even during the daylight hours man, other mammals, and birds frequent the shade during the heat of the day, and that in the somnolent midday hours and in shady retreats either a color matching with the environment or one with low light reflectivity would offer maximum concealment.

Despite the fact that black color also might expose its possessor to serious thermal problems in deserts and other intensely insolated areas, it is significant that the sedentary inhabitants of black lava landscapes, the hottest known environments, have evolved a concealing dark-to-black coloration whereas their adult, varietal, or subspecific equivalents living only a short distance away, sometimes only a few meters, still match the prevailing desert pallor of their environment. Even if color or albedo matching changes occur sometime during the ontogeny of certain reptiles and insects, this requisite matching and concealment despite the entailed exposure to heat, would constitute even more emphatic evidence of the definitive factor in the evolution of light-absorbing surfaces.

Other arguments in favor of the theory of concealment rather than for any definitive physiological advantages (these doubtless occur but are less important) have been proposed (*3*), but it seems probable that need for concealment almost invariably takes precedence over any attendant metabolic benefits or dangers and that this may have been true for the evolution of some prototypal human skin color.

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References

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2. R. B. Cowles, *ibid.* **135**, 670 (1962).
3. ———, *Amer. Natur.* **93**, 283 (1959).

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The direction of a species' evolution is guided by the total effect of all the selective forces acting upon it. An optimum response to one selective force can be disadvantageous with respect to another, and a compromise may be required. An animal's color is a case in point.

Predator pressure may force selection for a concealing color. However, a drab concealing color is not the most effective one for visual communication in sexual or group behavior. Two opposing pressures can thus act in the selection of color. The camouflaged animal must have some compensation, either behavioral, physiological, or morphological, to overcome its communication handicap. Conversely, the brightly colored animal must have compensation for its greater exposure to predation. We would argue that in addition to the pressures exerted by the need to avoid predation and to communicate, a third pressure, energy conservation, may be able to influence color. In some cases, energy conservation may be of prime importance; in others it may be of no importance. We do not think that any one of these factors is "definitive" for all animals, nor do we rule out the possibility that other forces can influence color under certain conditions. Only study of a particular animal can show which, if any, of these pressures is of primary importance for that animal.

We stated that "homoiothermic animals can absorb and utilize radiant solar energy." We believe that the experimental results show that this is a reasonable conclusion; the means by which the energy absorbed by the surface is translated into a metabolic economy is still subject to investigation. Cowles's suggestion of a reversal of thermal gradient may well be correct, and does not rule out our conclusion. We found the term homoiotherm to be more useful than endotherm in this particular case because we needed a term to describe a state of relative temperature constancy without making a commitment to the source of heat.

Cowles's suggestion that the surface which absorbs the most incident light is the least effective visual stimulus does not seem to consider that discontinuities and contrasts are important visual stimuli, and in most terrestrial environments black animals provide a rich supply of these cues. The basic principle of concealment by matching the general background appears to be that maximum concealment is obtained by reflecting the same quantity and quality of light as the background. In some special environments, such as lava flows, burnt vegetation, or dark soils, this may involve dark or even black coloration, but black birds, mammals, and men are not restricted to these environments. In other environments black animals are relatively more conspicuous than species that match the background, and some other explanation for their blackness must be offered. Nor does the principle of concealment by background matching change at low light intensities, as Cowles implies. Discontinuities and contrasts with the environment continue to be effective stimuli at night. However, at night our own eyes provide less reliable information about the situation. There are relatively few black nocturnal birds and mammals. Most nocturnal animals heavily involved in predator-prey relationships are background matching rather than black. Since these nocturnal animals generally obtain shelter during the day and are thus not exposed to "the notable penalties of high [radiation] absorption and overheating" we are led to ask why they have adopted their background-matching colors rather than black. For these reasons Cowles's conclusion that black coloration is in the vast majority of cases an adaptation to concealment seems vulnerable.

Cowles is probably right in stating that a sunbathing black animal would face a heat load problem at midday in the tropics. The solution to this problem, as he pointed out, is to get out of the sun. In the shade, color is probably irrelevant to heat exchange, since both black and white animals have similar radiative properties in the far infrared, as Kelly, Bond, and Heitman (*1*) observed. In the early hours of the day, solar radiation may enable homoiotherms not only to reduce maintenance metabolism requirements but also to restore body temperatures which have fallen during the night. In hot climates, particularly at dawn, a wide variety of sunbathing homoiotherms can be found, many of them orienting black surfaces to the sun.

We wish to take this opportunity to correct an error in the second sentence of the caption of Table 1. It should read, "Units are milliliters of oxygen per gram of body weight per *hour*." This correction in no way influences the conclusions from the experiment.

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