

THE METABOLIC SIGNIFICANCE OF DIFFERENTIAL ABSORPTION OF RADIANT ENERGY BY BLACK AND WHITE BIRDS

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The surface color of homeotherms is commonly thought to have two possible functions: concealment (Cott 1957) and communication (Lorenz 1935; Tinbergen 1948). Hamilton and Heppner (1967) proposed a third possible function for dark, or black, homeotherm coloration: the reduction of the metabolic cost of homeothermy by maximization of absorption of radiant solar energy. This hypothesis proposed that the integument of black animals absorbs more of the visible and near infrared components of solar energy than does the integument of lighter-colored animals, and that this greater absorption may permit them to reduce their heat loss when ambient temperatures are below their lower critical temperature.

Hamilton and Heppner reported that black-dyed, white Zebra Finches (*Poephila castanotis*) demonstrated a significant metabolic economy over undyed birds when both were exposed to artificial sunlight while in a moderately cold (10°C) metabolism chamber. I now report the results of experiments relating the metabolic differences between blackened and white birds observed by Hamilton and Heppner to the difference in amount of radiant energy absorbed by the black and white birds in our experiments, and discuss a physical mechanism whereby dark-colored birds might achieve a metabolic advantage over lighter counterparts.

DETERMINATION OF DIFFERENCES IN ABSORBED ENERGY

Of paramount importance is the quantitative relationship between the difference in requirements for chemical energy of the white and blackened birds, and the different rates of energy absorption from the artificial sun. This relationship can be determined by comparing the difference in heat production, expressed in calories, between the white and blackened birds, with the difference in the amount of energy absorbed at the surface of birds in the two color conditions.

The undyed birds exposed to radiant energy consumed a mean of 2.00 ml O₂/min, while the dyed birds exposed to radiant energy had a mean consumption of 1.44 ml O₂/min. By assuming a thermal quotient of 4.8 cal/ml O₂ (King and Farner 1961), the heat production of the blackened birds was 6.9 cal/min, and the heat production of the white birds was 9.6 cal/min, a difference of 2.7 cal/min. It is this difference that must be accounted for in calculating the difference in the amount of radiant energy absorbed by the blackened and white birds.

DETERMINATION OF TOTAL AMOUNT OF ENERGY FALLING ON SURFACE

As reported earlier, the rate of energy falling on the surface of a bird in the metabolism chamber was 1.23 cal/cm²-min, as determined by a 50-junction Eppley pyroheliometer. The metabolism chamber, which was made of Plexiglas, had a lid fitted with an ultraviolet transmitting glass filter. During a metabolism test, the chamber was submerged in a water bath, with 1 cm of water over the top surface of the chamber lid.

The spectrum of the light energy that fell on a bird in the chamber, after passing through the lid and the water over the lid, was determined by employing a Beckman DK-2 spectrophotometer set up in a spectroradiometry configuration. A Sylvania DWY "Sun-Gun" lamp, which was the artificial sun in the metabolism experiment, was mounted over the entrance port of the spectrophotometer. Spectrum measurements were then made (fig. 1) over the range 0.350–2.900 μ of: (A) the light of the lamp alone, (B) the light passing through the lid of the metabolism chamber, which was mounted between the lamp and the spectrophotometer, and (C) the light passing through both the lid and a 1-cm layer of tap water which was created by making a rim of masking tape around the edge of the chamber lid and then pouring water on the lid. The area under the curves can be expressed as the amount of energy falling on a unit of surface per unit of time. The lid had little effect on

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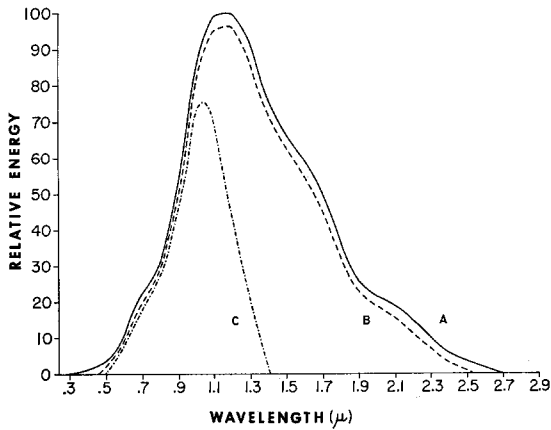


FIGURE 1. Spectrum measurements of Sun-Gun artificial sun (A, Sun-Gun; B, Sun-Gun through filter; C, Sun-Gun through filter and water).

the energy passing through it (curve 1B) over the spectrum range measured, but the water cut off radiation beyond 1.400μ and shifted the energy peak to about 1.050μ (curve 1C). This curve represents the spectrum of the light energy falling on the surface of a bird in the metabolism chamber. From the pyroheliometer measurements, it was known that the energy falling on the bird had an absolute value of $1.23 \text{ cal/cm}^2\text{-min}$. This value is equivalent to the area under curve 1C.

If the fraction of energy absorbed by the surface is determined for each wavelength, and this fraction then multiplied by the fraction of total energy emitted by the source at that wavelength, a new curve will be obtained, the area under which will be the energy absorbed by the surface. This area can be measured by a mechanical integrator (planimeter), and compared with the area under the curve of the emission spectrum, the absolute value of which is known ($1.23 \text{ cal/cm}^2\text{-min}$). The new value obtained will be the energy absorbed by the surface of the bird.

The absorption characteristics of the birds' surfaces were determined by setting up the Beckman DK-2 spectrophotometer in a spectroreflectometer configuration. Live white Zebra Finches and newly dyed, blackened Zebra Finches were anaesthetized with a gas anaesthetic and strapped to the sample port of the integrating sphere of the spectrophotometer. The reflection and absorption characteristics were compared to a white reference block of magnesium carbonate. Because there were slight differences in absorption at different locations on the back, measurements were taken at five locations. The absorption frac-

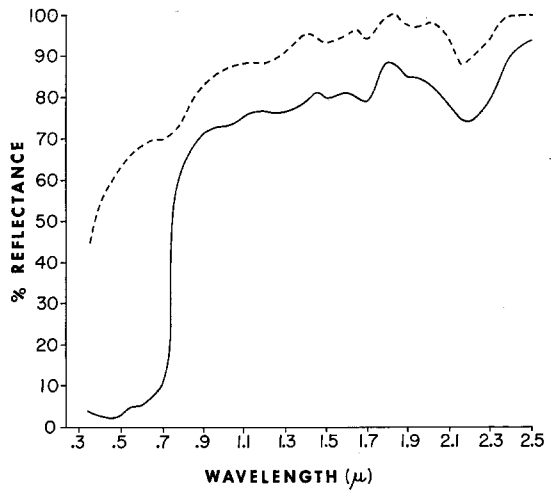


FIGURE 2. Absorbance characteristics of the surfaces of white and black-dyed Zebra Finches (solid line, black bird; dashed line, white bird).

tions at the five locations were then averaged at 0.100μ intervals and a composite curve was hand drawn for each bird (fig. 2).

The shapes of both curves are generally similar, both birds tending to be "white" beyond 1.000μ , but there is a sharp difference in absorbance from 0.350 to 0.800μ , with the blackened bird absorbing more, as would be expected.

In figure 3 the emission spectrum of the lamp is again shown with the curves produced by multiplying the absorption fractions of the black and white birds at 0.100μ intervals times the height of the emission curve at the same wavelength. The area under these curves, compared with the area under the curve representing the energy falling on the bird, indicates what fraction of the energy falling on the bird is actually absorbed.

The areas under the three curves were measured with a planimeter. It was found that the area under the curve representing the energy absorbed by the black bird was 33.2 per cent of the total energy falling on the bird, and the area under the curve for the white bird, 16.0 per cent.

From the pyroheliometer measurements, the area under the curve representing energy falling on the bird is equivalent to $1.23 \text{ cal/cm}^2\text{-min}$. The black bird absorbed 33.2 per cent of this energy, or $0.41 \text{ cal/cm}^2\text{-min}$, and the white bird 16.0 per cent, or $0.20 \text{ cal/cm}^2\text{-min}$.

Finally, to determine the difference in total energy absorbed by the black and white birds, it is necessary to know the area upon which

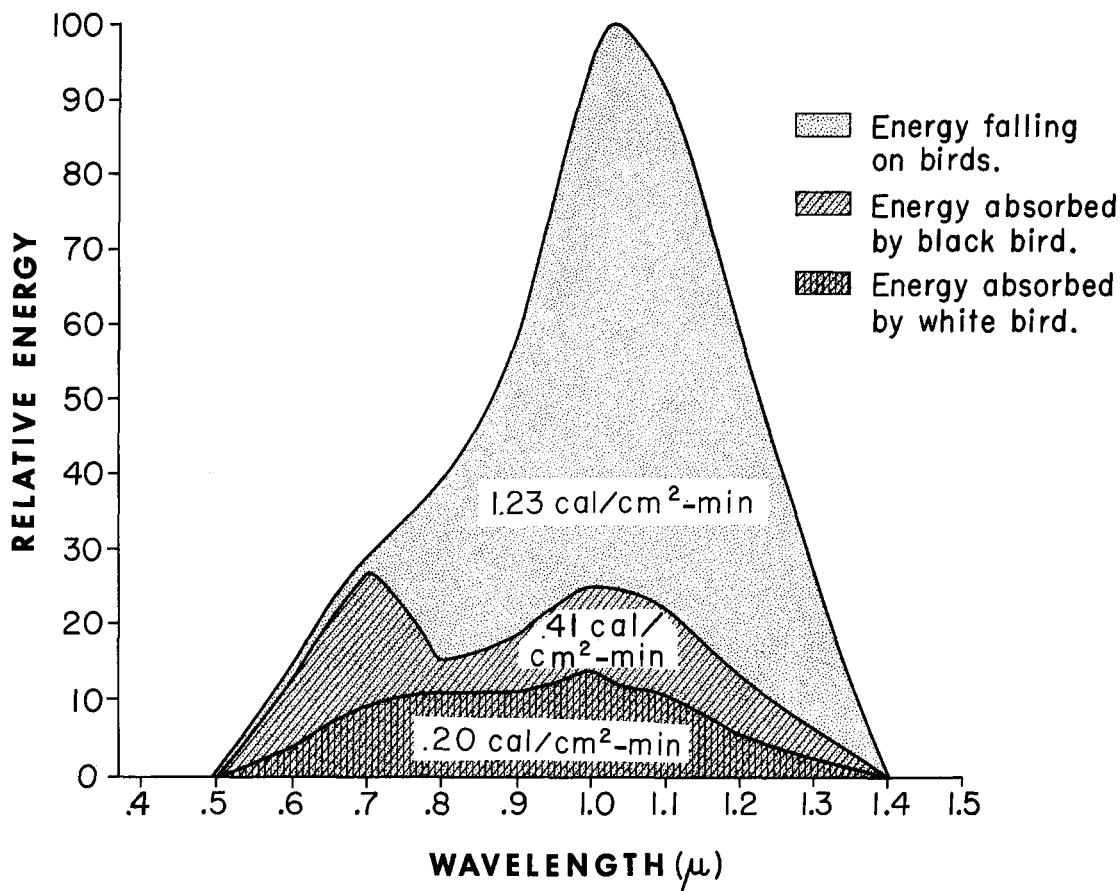


FIGURE 3. Energy falling on the surface of birds, and energy absorbed by black and white birds.

the radiation is falling. This cannot be measured precisely, because there are reflections from the bottom of the chamber that will irradiate the ventral surface of the bird, postural variations, and differences in feather erection which will alter the effective area exposed to direct radiation. An estimate can be obtained by projecting the dorsal view of the bird on a plane surface, and measuring the area of this projection. The dorsal projected area of three birds (excluding the tail) was 13.8, 15.2, and 15.2 cm^2 , or a mean of 14.7 cm^2 . These areas were obtained by measuring the projected area with a planimeter.

Using 14.7 cm^2 as the "absorbing" surface area, it is calculated that the white birds absorbed 2.9 cal/min while the black birds absorbed 6.0 cal/min, or 3.1 cal/min more than the white birds. The 3.1 cal/min difference in absorption of energy may be compared with the metabolic economy of 2.7 cal/min demonstrated by black birds in the metabolism experiment reported earlier. The value of 3.1 cal/min as the difference in energy absorbed between the black and white birds is probably

conservative. The effective absorbing area of the birds is probably larger than the 14.7 cm^2 obtained by projecting the dorsal surface of the bird on a plane, since there will be some reflections in the experimental universe that will impinge on all surfaces of the bird, although the intensity of these reflections is probably small. A larger surface area than estimated here would increase the absolute value of the difference in energy absorbed by black and white birds. Even with a conservative value, it appears that the difference in energy absorbed is sufficient to account for the metabolic economy demonstrated by the blackened birds.

DETERMINATION OF TEMPERATURE UNDER THE FEATHERS

To interpret the results of the metabolism experiment and the experiment reported above, it was desirable to obtain information about the heat flow from the bird's skin to the environment, under conditions that approximated the experimental setup of the metabolism experiments. Temperature measurements can

TABLE 1. Temperatures (°C) in three positions under the feathers of a stuffed black and white Yellow-billed Magpie (ambient temperature, 15.6°C).

	Black feathers	White feathers
Under surface	41.7	37.5
Middle	38.0	35.4
Next to skin	35.0	34.9

indicate the steepness of the gradient from the skin of a bird to the environment, and thus furnish an idea of the rate of heat flow. Two experiments were performed which suggested what the heat flow conditions of the metabolism experiments might have been.

STUFFED BLACK AND WHITE BIRD

A cotton-stuffed museum specimen of a Yellow-billed Magpie (*Pica nuttalli*) was placed ventral side up on a piece of corrugated cardboard. The top of the chamber used in the metabolism experiment was then mounted above it and the lamp used in that experiment placed above the chamber lid, 25 cm from the ventral surface of the magpie. A layer of water 1 cm deep was made above the filter in the chamber lid, to simulate submersion in a water bath. Yellow Springs Instrument Co. thermister probes were placed at various locations under the feathers and connected to a YSI thermometer.

The experimental setup was located in a walk-in controlled temperature room which was set at 15.6°C. The magpie specimen was allowed to come to ambient temperature; then the Sun-Gun lamp was turned on, and temperature readings were made after the temperature at the various locations had reached a state of equilibrium where the incoming heat produced by radiation was balanced by the heat reradiated, and carried off by convection.

Temperatures under both the black and the white breast feathers were measured under (1) the first layer of feathers from the surface, (2) approximately in the middle of the feathers, and (3) next to the skin of the specimen. The results are recorded in table 1.

WHITE AND BLACK-DYED LIVE BIRD

The feathers on half the breast of a white Zebra Finch were dyed black in the manner of the metabolism experiments. The experimental setup was the same as in the stuffed-bird experiment, except that the ambient temperature was 10.0°C and the lamp was 35 cm from the surface of the bird. The plumage of the bird was only slightly thicker than the diameter of the probe, so it was possible to

TABLE 2. Temperatures (°C) in two positions under the feathers of a live white and black-dyed Zebra Finch (ambient temperature, 10.0°C).

	Lamp off		Lamp on	
	Black	White	Black	White
Under surface	26.1	26.1	32.8	28.8
Next to skin	37.8	37.8	37.8	37.8

obtain only readings next to the skin, and just under the first layers of feathers. Measurements were made under both the white and the black feathers with the Sun-Gun on, and off. The bird was anaesthetized with ether and placed on its back with the ventral side exposed to the lamp. The results are recorded in table 2.

DISCUSSION OF TEMPERATURE EXPERIMENTS

The results of these experiments, although not useful in a quantitative sense because of differences in experimental conditions between the metabolism and temperature experiments, suggest a mechanism by which the heat economy demonstrated by black birds in the metabolism experiment might be accomplished (fig. 4). For a bird of any color in a cold environment, in the absence of sunlight (fig. 4A), the direction of heat flow is from the interior of the bird to the environment, and the rate of heat flow, indicated by the length of the arrow, is governed chiefly by the insulative properties of the feathers.

In the case of a black bird in the presence of sunlight (fig. 4B), the outer layer of feathers is warmed by the sun, thereby reducing the gradient between the skin of the bird and the outer layer of feathers, with the result that

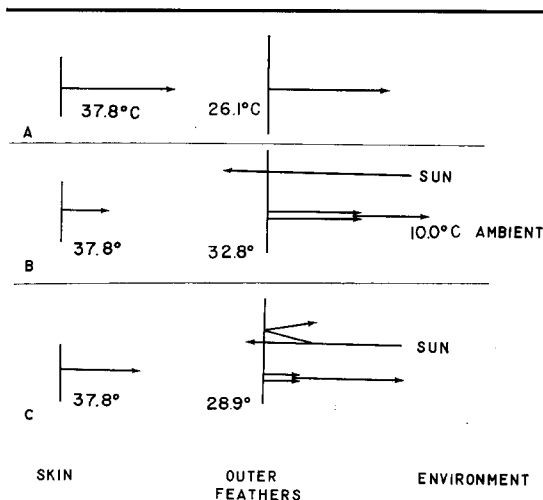


FIGURE 4. Heat flow in black and white birds under different conditions. For explanation see text.

the rate of heat flow from the skin of the bird to the outer feathers is decreased. At the same time the gradient between the outer feathers and the environment is increased, increasing the heat flow from outer feathers to the environment. However, a portion of the heat that flows from the outer feathers is energy that has been reradiated off as a consequence of the feathers being warmed by sunlight. The net result is that the outward flow of metabolic heat is reduced in the presence of sunlight. A double line indicates reradiated heat. The situation in the white bird is basically the same (fig. 4C), but the quantities are different, since the white bird reflects a portion of the incoming solar energy.

Birkebak (1966) has derived a set of general equations for heat exchange in animals which are useful for illustrating this proposed mechanism.

$$Q_{\text{cond}} + Q_e = Q_{\text{conv}} + R_s^* - R^* + S_D^* + S_a^*, \quad (1)$$

where Q_{cond} is the heat conducted from the interior of the body to the integument surface, Q_e is heat lost by evaporation, Q_{conv} is heat lost by convection, R_s^* is infrared energy absorbed by the animal from its surroundings, R^* is infrared energy emitted by the animal, S_D^* is direct solar energy absorbed by the animal, and S_a^* is diffuse solar energy absorbed by the animal. Q might be expressed as cal/unit time.

The heat conducted from the interior of the body to the integument surface is expressed as

$$Q_{\text{cond}} = \sum_{k=1}^n k_k f_k(r_b, r_o, L)(T_b - T_a), \quad (2)$$

where k is thermal conductivity of the integument, $f_k(r_b, r_o, L)$ is the geometrical form factor for a given body shape, T_b is the deep body temperature, and T_a is the temperature at the surface of the body. An increase in the temperature of the body surface might thus slow the flow of body heat to the environment.

Absorbed direct solar energy, the sixth term in equation (1) is expressed by

$$S_D^* = \alpha S_D A_D, \quad (3)$$

where α is the absorptance of the surface, S_D is the direct solar radiation and A_D is the projected area of the surface. A similar equation applies to S_a^* , the diffuse solar radiation.

The heat lost by convection is expressed by

$$Q_{\text{conv}} = \sum h_k A_k (T_a - T_{\text{air}}), \quad (4)$$

where h_k is the average heat transfer coefficient for the k th part of the body and A_k is its surface area.

The thermal radiation emitted by the surface is given by

$$R^* = \epsilon_a \sigma A_a T_a^4, \quad (5)$$

where ϵ is the infrared emittance of the surface, A_a is the surface area, σ is a constant (1.376×10^{-15} kcal/cm²-sec-°K⁴), and T_a is the surface temperature in °K.

Equation (1), written in more specific form, where relevant to consideration of the effects of differential absorption of solar energy, is then

$$\begin{aligned} \sum_k k_k f_k(r_b, r_o, L)(T_b - T_a) + Q_e \\ = \sum_k h_k A_k (T_a - T_{\text{air}}) + R_s^* - R^* \\ + \alpha S_D A_D + S_a^*. \end{aligned} \quad (6)$$

An increase in α , the absorptance of solar energy, might affect the other terms of equation (6) in several ways, one way being to increase the rate of heat loss in infrared emission, as an effect of the heating of the surface, while decreasing the rate of conduction of body heat from the interior to the surface, as a result of the decreased gradient between the interior and the surface.

The smaller the gradient is between the skin and the outer feathers, the slower will be the loss of metabolic heat from the bird. Maximizing the amount of solar energy absorbed by the outer feathers will maximize the heat economy.

DISCUSSION

The sun radiates energy that potentially could be used by warm-blooded animals to reduce the energy cost of maintaining a body temperature higher than that of its surroundings. The great absorption of short wave-length solar energy by black feathers can serve to decrease the temperature gradient between the skin of the bird and the outer feathers, thus slowing the flow of heat from the bird to its surroundings. In the absence of solar radiation, as in the shade and at night, the black bird would not necessarily radiate off more heat than a lighter counterpart, because the energy emitted by a surface at the temperature of the outer feathers of a bird is chiefly in the form of long wavelength infrared. As will be discussed later, the emissive properties of black and non-black feathers with respect to these wavelengths appear to be nearly the same. Thus it might be possible for a black bird to show a net energy advantage over a similar, but non-black bird, because the black bird would lose less heat during the day than the non-black bird, and lose about the same amount as its lighter counterpart at night.

The amount of energy available for absorption depends on many factors, including latitude, altitude, season, and atmospheric conditions, but under certain conditions represents a potentially significant amount to a small animal whose surface/volume ratio is large. Gates (1966) presents data for the level of solar radiation at the earth's surface under various conditions. It is not unusual to find levels of 1.00 cal/cm²-min at temperate latitudes. A small bird whose dorsal surface area (excluding tail) is 10 cm² potentially could absorb 600 cal/hr under these conditions. When this is compared with the approximately 400 cal/hr resting metabolic rate of a 30-g passerine bird (Lasiewski and Dawson 1967), it is clear that radiant energy absorption represents a potentially important factor in the overall energy balance. The larger the animal, the less important absorption of energy should be, owing to the lessening of the surface/volume ratio, although a 2-kg chicken, whose resting metabolic rate is 5.5 kcal/hr (Barott and Pringle 1941) and whose dorsal surface area, excluding the tail, is about 300 cm² has 18 kcal/hr of solar energy falling on its back under the conditions described above. How much of this energy is actually absorbed by the feathers will depend on the characteristics of the feathers, and the posture and orientation of the bird relative to the sun.

The physiological effects of sunbathing at moderately low temperatures were explored by Adolph and Molnar (1946), who compared various physiological parameters (heart rate, surface temperature, deep body temperature, oxygen consumption, urine production, evaporative water loss, and blood chemistry) of nude men under various conditions of ambient temperature, cloudiness, humidity, and working conditions (at rest, working, etc.). Their most significant measurement with reference to the present discussion was that of oxygen consumption, hence energy metabolism, measured under conditions of sun and shade outdoors in the fall at Rochester, New York. They found that lying in sunlight with a radiation intensity of approximately 1.00 cal/cm²-min, as opposed to lying in the shade, had the same functional effect upon the subjects as raising the ambient air temperature 6°C in the range between 1.1° and 26.7°C. That is, the threshold of shivering was raised, skin surface temperature was raised, and heat production was lowered. The difference between sun and shade was lessened when work was done, but the total energy production in both cases was greater than while resting.

In terms of absolute values, they found that a nearly nude, resting man saved about 80 kcal/hr by being in the sunshine as opposed to being in the shade. This figure represents 20–25 per cent of the total energy output at that temperature. The posture of the man appeared to make little, if any, difference in this figure.

Contrary to Blum's (1945) prediction that a man shaded from sunshine is appreciably influenced by radiation from sky and ground, Adolph and Molnar found no appreciable differences in heat production between men who were shielded from the sun's rays, but exposed to ground and sky radiation, and unshielded men outdoors at night, at the same ambient air temperature as the daytime measurements. This finding does not necessarily mean that ground and sky radiation are unimportant to a smaller animal whose surface/volume ratio is greater than man's.

The experiments of Adolph and Molnar were chiefly concerned with examining the effects of solar radiation at low-to-moderate air temperatures. It might be asked whether solar radiation also affects physiology at higher ambient temperatures.

Craig and Cummings (1962) examined the thermal influence of sunshine and clothing on men walking in humid heat. They found that the same physical strain, in terms of heart rate, blood pressure, and sweating, was found in heavily clothed men walking outdoors in an ambient temperature of 29.4°C, and a solar radiant energy level of 1.00 cal/cm²-min as was produced indoors at a temperature 5.6° C higher, when the work load was the same. The clothing was a dark olive drab on the outside. This 5.6°C increment at 29.4°C is quite comparable to the values found by Adolph and Molnar at lower temperatures. Relative to energy metabolism, then, exposure to sunshine appears to have the same functional effect as raising the ambient temperature. The degree to which this effect is produced will depend on the characteristics of the incoming radiation, and the properties of the surface upon which it falls.

According to Kirchoff's Law, a surface which is a good absorber is also a good emitter. It is therefore reasonable to ask whether a black animal that has gained a thermal advantage during the day by sunbathing might not lose that advantage at night by emitting more heat than its more lightly colored counterpart.

This question was posed, in a different reference, by Hesse et al. (1937) and Hamil-

ton (1939) who speculated that the white color of arctic animals is an adaptation for heat conservation. Two experimental tests of this hypothesis have been made, with differing results.

Stulken and Heistand (1953) measured the oxygen consumption of C-57 black mice, Swiss albino mice, and Swiss albino mice which had been dyed black with a commercial hair dye. Oxygen consumption was measured at various temperatures from 30°C to 5°C. They found that in all cases oxygen consumption increased as the temperature decreased, but the rate increased faster in the black mice and the black-dyed mice. Their conclusion was that the black mice were radiating off more energy than the white mice and thus needed a higher metabolic rate to maintain a constant body temperature.

There are several factors that preclude a clear interpretation of these results. The C-57 black mouse is a very active strain (Thompson 1953) and might react differently to cold than the albino strain. If the C-57 black mice became more active as the temperature decreased, they would also show a higher oxygen consumption. In the case of the black-dyed mice, the dye might have produced undetected changes in the insulative characteristics of the fur, thus permitting a greater loss of heat than in the undyed animals. In the experiment of Hamilton and Heppner (1967) there were no significant differences in metabolism between white and black-dyed animals when the artificial sun was off, thus suggesting that the dye did not affect the insulative properties of the feathers.

Svihla (1956) measured the food consumption of white and black-dyed rats at 25°C and 5°C. He found no significant difference between the two, and concluded that color had no effect on heat loss.

It is necessary to reexamine Kirchoff's Law to clarify the question of the effect of color on heat loss. Whereas Kirchoff's Law states that a good absorber is also a good emitter, the law applies only for a particular wavelength. A good absorber of 2 μ wavelength energy is not necessarily a good emitter of 3 μ energy. Thus a visual impression of blackness or whiteness furnishes no information about the emissivity of the surface in other regions of the spectrum. In living animals, the radiant energy that is emitted lies principally in the 4–20 μ region, or the infrared (Hammel 1956).

Emissivity is expressed on a scale from 0.0 to 1.0; a surface with an emissivity of 0.0 absorbs or emits no energy (but reflects all

energy falling upon it), and a surface with an emissivity of 1.0 absorbs all energy falling upon it (and reflects none). Hardy and Muschenheim (1934), Hardy (1939), and Barnes (1963), using different techniques, report that human skin has an emissivity of 0.98 to 0.99. This means that for that region of the spectrum in which the skin is radiating energy (4–20 μ), the surface behaves almost like a black body. Hammel (1956) measured the emissivity of the pelage of light and dark forms of arctic mammals and birds, and found that both had an emissivity of close to 1.00. Hammel concluded that there should be no difference in heat loss between light- and dark-colored forms of an animal.

Kelly et al. (1954) studied the role of color and solar radiation in the thermal environment of swine. They contrasted the amount of solar radiant energy absorbed by black and by white pigs and found that black pigs absorb 90 per cent more than white pigs over the range 0.4–3 μ , which is approximately the range of direct solar radiation, and 50 per cent more over the range 0.4–50 μ , which includes atmospheric and diffuse sky radiation. Their values for the difference in absorption of direct solar energy between black and white pig skins compare closely with the value reported here for differences in absorption between white and black-dyed feathers under similar conditions.

They also reported no differences in absorptivity or emissivity between black and white swine in wavelengths beyond 3 μ . They concluded that black and white animals in the shade would have the same rate of radiative heat exchange, but that black animals would absorb more than white animals when in the sun. Their discussion was aimed at considering the problems of heat load upon animals in hot surroundings, but the same physical principles apply to low ambient temperatures.

Thus it is possible that a black animal might enjoy an advantage over a white animal during the daytime by absorbing the relatively short wavelength energy of the sun, without losing the advantage at night, since both black and white animals would radiate longer wavelength energy at the same rate.

Buxton (1923) was puzzled by the observation that the only apparent exceptions to the rule that desert animals were colored to match the background were animals that were colored black. Craig and Cummings' (1962) study of the effect of solar radiation on humans in the presence of high ambient temperatures does suggest that exposure to solar radiation

at high temperatures might impose more of a heat load on a black animal than a white animal. This problem might be solved by an examination of the behavior of these animals under natural conditions. A black animal in the shade on a very hot day is probably no worse off than a white animal, since the radiation component of heat exchange is decreased in importance. Also, although the midday temperatures in desert regions are often so hot as to preclude much activity in the open sun, the early morning ambient temperatures, when much foraging is often done, especially by birds, may be below the thermoneutral point of the animal, and an advantage might be gained by maximizing the absorption of solar energy.

Jaeger (1957) notes that in the Colorado Desert of North America there is a 16.7°C daily difference between maximum and minimum daily temperatures. Cloudsley-Thompson and Chadwick (1964) report daily ranges of 32.3°C at In Salah, Algeria, and a record 37.8°C daily range at Bir Mighla, Tripoli. Under such conditions, energy expenditure might be reduced by adopting a black color to capitalize on morning sunlight when the ambient temperature was below thermoneutrality; then shade could be sought in the middle of the day if heat stress became a threat. This suggestion might explain the atypical black coloration of desert wheatears and chats noted by Buxton.

A similar situation may occur in tropical jungles. Schaller (1964), in his study on the mountain gorilla, notes that the early morning temperatures often approached freezing in the highland area, while afternoon temperatures were warm. He also states that the black gorillas are frequent baskers, and, "If gorillas had a religion, they would surely be sun worshippers."

Black birds in hot non-desert regions do not always seek shade during periods of peak temperature. I have often seen Brewer's Blackbirds (*Euphagus cyanocephalus*) and Common Crows (*Corvus brachyrhynchos*) foraging in the sun on days when the ambient temperature was above 39.4°C. Shaded foraging areas were nearby, but the birds moved from sun to shade and back indiscriminately. The birds were panting, but otherwise showed no apparent discomfort. This behavior is a puzzle, since under those conditions the birds might be expected to be running the risk of a dangerously high heat load.

Most black, or nearly black, birds are relatively free from predation, either by virtue of

their size (crows, vultures, ravens) or because of their flocking tendencies (blackbirds, starlings, mynahs). These factors reduce the necessity for a background-matching coloration; and it may be that the energy advantages offered by blackness have resulted in a selection for black coloration, rather than grayish or brownish coloration, in those birds that live in climatic conditions where black might be metabolically useful. Where predator pressure is strong, a neutral, background-matching color will be selected. Cowles (1959) and Cowles et al. (1967) argue that black is a background matching color in dense jungle, but it is difficult to see how black could serve such a function in more open surroundings, such as the typical habitats for blackbirds, crows, and several other black birds.

White birds present different problems with reference to the effects of insolation. A white bird reflects most, although not all, of the energy in the visible spectrum that falls on it. White or whitish birds would thus be expected to receive a lesser advantage from the sun than black birds in those cases where absorption of radiant energy is of value, but also be less subject to high heat loads where insolation is at a high level.

Only one experiment has been reported that relates to the effects of insolation on the energy budget of feral small birds. Morton (1967) observed the feeding behavior of flocks of wild White-crowned Sparrows (*Zonotrichia leucophrys*) on sunny and cloudy days in the state of Washington. He noted that on cold, cloudy days there was only a slight decrease in feeding activity during midday, but on warm sunny days foraging tended to be more curtailed during midday. Some birds were then captured, held in outdoor cages, and their feeding pattern was observed. Their food intake was significantly less on a sunny morning than on a cloudy morning, although ambient temperatures were similar.

Finally, Morton compared the feeding pattern and activity of White-crowned Sparrows irradiated with energy from an infrared sun lamp with those which were not. Both groups were tested under the same ambient temperature conditions, and two test temperatures, 20°C and 7°C, were used. At 20°C, the feeding pattern of the birds exposed to the infrared was nearly identical to that of the control birds, and their pattern and total amount of locomotor activity was like that of the control birds. At 7°C the food intake of the birds exposed to the infrared was relatively lower than the controls, but again there was

no significant difference in locomotor activity between birds exposed to radiant energy and nonirradiated birds. Morton's findings indicate that insolation can be a significant factor in the energy metabolism of dark colored, but non-black, birds. His results are in substantial agreement with those reported here.

Black coloration in birds appears to be a specialized adaptation that functions to reduce the energy cost of homeothermy in those situations where there is low predator pressure, daytime ambient temperatures below thermo-neutrality, and sufficient insolation to significantly alter the heat exchange between the bird and its environment. Black coloration might also serve a concealing function in certain situations, such as in dense foliage, but the determination of which of these factors has guided selection for blackness can only be made by studying the ecology of a species in question.

SUMMARY

Hamilton and Heppner (1967) found that black-dyed, white Zebra Finches (*Poephila castanotis*) demonstrated a 23 per cent metabolic economy over undyed birds when both were exposed to artificial sunlight at 10°C. It is here reported that the difference in radiant energy absorbed between the blackened and white birds in the previous experiment was sufficient to account for their observed metabolic differences. Spectrum and radiometric analysis of the light energy absorbed by the surface of the birds showed that the black birds absorbed 3.1 cal/min more than the white birds while the white birds had a metabolic heat production 2.7 cal/min greater than the black birds.

Temperature measurements made under blackened and undyed white feathers of a live Zebra Finch exposed to artificial sunlight suggest that the warming of the outer feathers of the black bird reduces the temperature gradient from the skin of the bird to the surface feathers, and thus slows the loss of metabolic heat to cold surroundings.

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