COAT COLOR, SOLAR HEAT GAIN, AND CONSPICUOUSNESS IN THE PHAINOPEPLA

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ABSTRACT.—The effect upon solar heat gain of substantial differences in plumage color was quantified for a desert bird, the Phainopepla (*Phainopepla nitens*), under natural conditions. This was accomplished by measuring the operative temperature of the environment acting upon gray female and black male Phainopeplas. When exposed to conditions likely to maximize the effect of differences due to coat color, the operative temperature acting on the black male averages only 0.9–2.3°C higher than that on the gray female. This change is small compared to that produced by simple postural changes and selection between available microclimates. An analysis of the optical properties of desert habitats suggests that dark coloration may be advantageous because it maximizes visual conspicuousness while the animal is active, hence facilitating social communication, and minimizes conspicuousness during inactive periods, thus reducing dangers of predation. *Received 30 September 1981, accepted 12 December 1981.*

RADIATION is a major mode of heat transfer for animals in nature, and it has been customarily assumed that forms with dark-colored surfaces acquire substantially greater solar heat loads than do those with light-colored surfaces. Though some theoretical analyses suggested otherwise (Kovarik 1964), pioneering studies of radiative heat gain in small birds supported this expectation (e.g. Hamilton and Heppner 1967, Lustick 1969). These studies, however, necessarily were conducted within a limited range of conditions, because measurements were made in the greatly simplified environment of a metabolic chamber. Recent laboratory studies (Walsberg et al. 1978) demonstrated that in ecologically realistic circumstances the generally conceived relation of coat color to solar heat gain can be reversed: black plumages may acquire heat loads substantially lower than those of white plumages. This study demonstrated that the net effect of coat color on solar heat gain is an important product of both differences in coat reflectivity to radiation and the degree to which radiation penetrates into the coat. In a light-colored coat, a substantial fraction of incident short-wave (300–2,500 nm) radiation is reflected away. That radiation that is not reflected, however, tends to penetrate deeply into the insulating coat, and the average level of ray absorption and consequent heat generation is nearer to the skin than in dark coats. In dark coats, a large fraction of incident short-wave radiation is absorbed, but that absorption tends to occur very near the outer surface of the pelage or plumage. Thus, much of the heat generated by irradiation is lost to the environment by reradiation or convection from the coat surface. The net effect of opposing shifts in radiation absorption and penetration is a function of a number of meteorological and species-specific factors in addition to and independent of coat color (e.g. wind velocity, plumage insulation, feather microstructure, and feather optics). Depending upon the manner in which these factors are combined, darker coat colors may either increase or decrease the solar heat load on an animal (Walsberg et al. 1978).

It is clear, therefore, that the thermal significance of coat color must be evaluated in the context of a particular species' natural environment. In this study, I quantify the effect of substantial differences in plumage color upon the energy balance of a desert bird, *Phainopepla nitens*, under natural conditions. The Phainopepla is a small (about 25 g) songbird in the family Ptilogonatidae that breeds in a variety of arid habitats in North America. Two aspects of its biology make it attractive for study. First, it normally is exposed to intense solar radiation, because it resides in deserts and frequently perches in the open on top of tall shrubs or small trees. Second, there is a substantial sexual dimorphism in coat color. With the exception of white wing patches, which are concealed when the bird perches, males are glossy black and have a solar reflectivity of 6.7–10%, depending on the angle of incidence

(Walsberg 1980). The female is gray and has a solar reflectivity of 17–23%, depending on the angle of incidence (Walsberg 1980). This reflectivity is close to that typical of the cryptic gray or brown hues common to birds [e.g. values for such species summarized by Calder and King (1974) typically range from 20 to 30%]. Thus, one may compare the effects within a single species of a shift from the moderate solar reflectivity exhibited by many species to a substantially lower reflectivity.

The difference in radiative heat loads on male and female Phainopeplas under natural conditions can be estimated using recently refined and tested biophysical techniques and theory that allow an estimation of the operative temperature of the environment (T_E) for a particular species and setting (Bakken and Gates 1975, Robinson et al. 1976, Campbell 1977, Mahoney and King 1977, Bakken et al. 1981). T_E represents the sum of air temperature and a temperature increment subsuming radiative and convective factors. The difference between body temperature (T_B) and T_E equals the net thermal gradient between animal and environment. Net heat flux is proportional to this gradient divided by the total resistance to heat flow of the animal/environment system. This resistance is determined by properties of both the animal (e.g. plumage insulation) and environment (e.g. wind velocity). Thus, a total description of the bird's thermal environment requires a determination of both the operative thermal resistance and the $T_B - T_E$ gradient. In the following comparison, only the $T_B - T_E$ gradient is analyzed, because all animal and environmental properties important for heat transfer other than coat color are similar for males and females.

An alternative statement of the concept that the $T_B - T_E$ difference defines the net thermal gradient operating on an animal is that the net effect of a homeotherm's endogenous heat production and evaporative water loss is to maintain a T_B different from T_E. If a bird maintained its normal heat-transfer properties at its interface with the environment yet produced no heat internally and evaporated no water, then the body would thermally equilibrate with the environment, and T_B would equal T_E. This is the theoretical basis for the use of taxodermic mounts to measure T_E (Bakken and Gates 1975, Bakken 1976). A type of mount appropriate for use as a T_E-thermometer consists of a hollow copper cast of the bird's body covered by the animal's integument (Bakken and Gates 1975). If constructed properly, such a model has essentially the same heat transfer properties as a live bird (e.g. size, shape, plumage qualities), yet is thermally passive. When allowed to equilibrate with a particular microclimate, such models should exhibit an internal temperature very near the value of T_E for the particular species and environment studied. The most serious potential error encountered when using such devices is that the surface temperature of the model may differ from the surface temperature of a live animal due to the living animal's metabolic heat production and cutaneous evaporation of water (Bakken 1976). Bakken (1976) analyzed this problem and concluded that the error in the estimate of T_E probably is about 5% of the difference between the surface temperatures (T_S) of the model and a live bird. The difference in surface temperatures between a model and a live bird should be minimized when both are exposed to intense radiation. Even if this difference were 10°C, however, the error in T_E probably would be only about 0.5°C. Other errors may accrue from surface-temperature effects if free convection prevails, yet even the lowest wind velocities in this study were sufficiently high to prevent this. This conclusion is based upon analyses using surface-temperature measurements of taxodermic mounts made with a Mikron 15D infrared thermometer. Mounts were placed 1.5 m above ground, but other conditions were similar to those used in the rest of the study. Measurements were made on all 18 mounts at 2-h intervals over a 4-day period. If mean surface temperature (T_S) is estimated as the average of the temperature of the side of the model's torso exposed to the direct solar beam and that of the shaded side of the model, then the maximum average surface-to-air temperature gradient was 13°C. This occurred on male mounts at wind velocities near the lowest measured in this study (0.3 m/s). Using these data and assuming a characteristic dimension of 0.035 m (typical midtorso diameter of a Phainopepla), one may calculate Grashof (Gr) and Reynolds (Re) numbers as indices of convection regimes. Such an analysis indicates that forced convection was dominant even at these lowest wind velocities (i.e. $Gr/Re^2 = 0.01$) [see Monteith (1973) or Campbell (1977) for a discussion of this type of analysis].

Methods and Materials

Construction of T_E-thermometers.—Phainopeplas were collected about 20 km south of Apache Junction, Maricopa County, Arizona. Taxodermic mounts were constructed using the technique described in Bakken and Gates (1975). Briefly, this entails removing the intact skin and plumage, then producing a hollow copper duplicate of the bird's defeathered body as it is held in the normal posture of a perching Phainopepla. The skin and feathers are then placed on the copper cast. The skin was sealed to the copper cast with cyanoacrylate adhesive. Nonfeathered portions of the tarsi were removed and replaced with 2 mm diameter wooden dowels inserted into the apex of the remaining portions of the mount's legs. These dowels were attached to larger (1.3 cm diameter) dowels that served as a perch for the mount. The plumage was arranged carefully before the skin dried, and the resultant mounts closely resembled live Phainopeplas perching in normal posture on the 1.3-cm diameter dowel. Internal temperature was measured using 26-gauge copper-constantan thermocouples placed in the upper abdominal region of the hollow cast. Nine models of each sex were constructed.

Fieldwork.—All data were collected in the Sonoran Desert 48 km east of Gila Bend, along Vekol Wash at an elevation of about 935 m in Maricopa County, Arizona. This normally dry watercourse is lined with a variety of large shrubs and small trees [e.g. Palo Verde (*Cercidium floridum*), Ironwood (*Olneya tesota*), Catclaw Acacia (*Acacia greggi*)] and represents typical breeding habitat for the Phainopepla (Walsberg 1977).

Measurements were made on 10 cloudless days in April 1981. Only calm, nearly windless days were chosen in order to minimize the relative importance of convective heat flux and maximize effects due to differences in radiative heat loads on males and females. The "perch" dowels of the models were attached to vertical poles and all models were oriented so that the long axis of the body was at a normal angle for a perching Phainopepla (approximately 55° above horizontal). The models were arranged so that they formed a single row facing one direction. Males and females were alternated along the row, and individual models were placed 10 cm apart. The entire group was then elevated to the top of a 3 m high *Cercidium floridum*, where the mounts were exposed to full sunlight. This is a typical perch site occupied by territorial male or female Phainopeplas (Walsberg 1977).

Measurements were made with the models in two orientations. Initially, all models were oriented with their dorsal surface toward the sun's azimuth. The internal temperature of the models was measured after an equilibration period of 20 min; then the orientation of the models was reversed so that their ventral surface faced the sun's azimuth. Temperatures were recorded again after a 20-min equilibration period. Such measurements were made at 2-h intervals throughout daylight hours, using a Campbell Scientific Co. CR5 data logger that had been calibrated with a standard thermometer (calibration traceable to U.S. National Bureau of Standards).

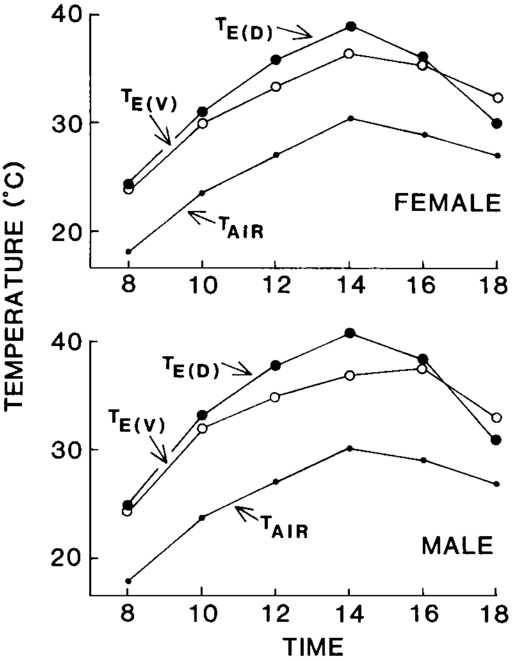

Fig. 1. Average air (T_{AIR}) and operative environmental temperatures (T_E) for Phainopeplas perched in full sun during 10 days in April in the Sonoran Desert. $T_{E(D)}$ and $T_{E(V)}$ refer to birds perched so that their dorsal or ventral surface, respectively, is directed toward the solar azimuth.

Meteorological data were recorded using the Campbell CR5 data logger over 40-min periods encompassing both 20-min equilibration periods required for the two orientations of the mounts. Total downward short-wave radiation (300–2,500 nm wavelength) was measured in the open, using an Eppley pyranometer. Downward scattered short-wave radiation was measured midway through each period with a disc held about 20 cm above the sensor surface to occlude direct solar radiation. Direct short-wave radiation was computed as the difference between total and scattered short-wave radiation. Radiation perpendicular to the solar beam was computed using Lambert's cosine law. Upward short-wave radiation was measured using an Eppley pyranometer placed 10 cm below the center of the group of taxodermic mounts. A Fritschen net radiometer, modified as described by Idso (1971), was placed adjacent to this pyranometer and used to measure upward all-wave radiation. Downward all-wave radia-

TABLE 1. Meteorological data.[a]

						Radiation (W/m^2)				
				A_P[c] (cm^2)						
Time[b] (MST)	Statistic	Air temperature (°C)	Wind velocity (m/s)	Dorsal orientation	Ventral orientation	Direct shortwave[d]	Downward diffuse shortwave[c]	Upward diffuse shortwave[e]	Downward longwave[e]	Upward longwave[e]
0800	$\bar{x}$	18.0	0.63	33.3	19.7	741	70	87	286	422
	SD	8.41	0.57	3.4	2.4	116.1	20.0	49.7	109.8	94.6
1000	$\bar{x}$	23.8	0.62	34.1	15.1	850	110	124	311	466
	SD	6.62	0.42	5.5	2.1	68.4	25.4	57.4	59.5	51.7
1200	$\bar{x}$	27.3	0.53	30.7	16.3	799	106	149	280	423
	SD	6.93	0.21	4.0	2.6	51.9	38.7	63.8	90.1	85.0
1400	$\bar{x}$	30.2	0.58	32.1	15.7	933	136	167	338	517
	SD	7.40	0.49	4.8	1.6	97.8	49.0	63.8	94.8	85.1
1600	$\bar{x}$	29.0	0.67	35.3	16.4	853	105	122	355	490
	SD	9.92	0.34	5.3	1.8	96.4	23.2	42.5	92.8	82.7
1800	$\bar{x}$	27.4	0.63	29.0	23.2	520	70	54	351	450
	SD	10.49	0.32	4.6	2.7	100.1	40.0	61.2	82.0	89.8

[a] Data collected 1, 2, 3, 11, 12, 13, 14, 15, 22, 23 April 1980. For each statistic, $n = 10$.

[b] Data were collected for 40-min periods commencing 20 min prior to the time cited.

[c] Projected surface area of mannequin on a plane perpendicular to the solar beam.

[d] Irradiance perpendicular to the solar beam.

[e] Irradiance on a horizontal surface.

tion was measured by placing a modified Fritschen net radiometer facing upward in the open. Long-wave radiation (wavelength >2,500 nm) was calculated as the difference between all-wave radiation and short-wave radiation. Air temperature was measured using a shielded thermocouple placed at the same height as the taxodermic mounts. Wind velocity was measured adjacent to the mounts using miniature cup anemometers (starting speed about 0.1 m/s).

The cross-sectional area of the solar beam intercepted by the mounts (A_P) was measured by tracing the shadow cast by the taxodermic mounts onto a sheet of paper attached to a board that was mounted perpendicular to the solar beam. The tail was considered of minor thermal significance, and its portion of the shadow was excluded. Proper orientation of the mounting board was assured by use of a shadow rod. Shadow area was determined by outlining the shadow on paper of known mass per unit area and weighing the paper. A_P was determined for a different mount on each of the 10 days of study.

RESULTS

Table 1 lists meteorological data, and average values for the operative environmental temperature (T_E) are summarized in Fig. 1. Operative temperatures for Phainopeplas were elevated over air temperature an average of 3.9–10.8°C in males and 2.6–8.6°C in females, depending on time of day and orientation. Maximum elevations of T_E over T_A occurred at 1400, when the mount's dorsal surface was directed toward the solar azimuth. Minimum elevations occurred in the same posture at 1800. Reversing the mount's orientation, from dorsum to venter being directed toward the solar azimuth, changed T_E an average of 0.1–3.6°C in males and 0.5–2.3°C in females.

For either sex, T_E in the dorsal orientation typically was above that in the ventral orientation. This pattern usually reversed in the late afternoon (Fig. 1), and at 1800 the ventral orientation produced a significantly higher T_E than the dorsal orientation for both males and females on 8 of the 10 sample days (ANOVA; $P < 0.05$). The higher value of T_E in the dorsal orientation through most of the day reflects differences in the projected surface area of the taxodermic mount on a plane perpendicular to the solar beam (A_P). This equals the cross-sectional area of the solar beam intercepted by an object and thus is an important determinant of solar heat loads. Through most of the day, A_P was about twice as large in the dorsal orientation than in the ventral orientation (Table 1). By 1800, the values converged, and a mount in the dorsal orientation intercepted only 26% more of the direct solar beam than when it was in the opposite posture. Considering only A_P, one thus would expect that T_E for the two postures would become more similar at 1800 and that the dorsal orientation should produce the highest operative temperature. T_E in the ventral orientation, however, was about 2° higher. This reversal probably reflects differences in plumage insulation. The decreased heat load when the bird's dorsum is directed toward the solar beam may be produced by the shielding effect of the wings, which are folded over the bird's back and add an additional layer of insulation that should reduce radiative heat gain.

The black male bird acquires a slightly greater heat load than the gray female (Fig. 2). The difference in operative temperature is not large, however, and during the average day ranges from 0.9 to 2.3°C. When data for a particular time of day are compared, lumped values for all 10 days reveal no statistically significant differences between males and females (ANOVA; $P > 0.05$). This probably is due in part to variance induced by differing meteorological conditions between days. When values are compared for a particular time, day, and orientation (10 days, 6 times of measurement per day, 2 orientations), statistically significant differences (ANOVA; $P < 0.05$) are observed in 31 of the 120 pair-wise comparisons between sexes (when making 120 pairwise comparisons, 6 such significant differences at the 0.05 level are expected by chance alone).

The small, but persistent elevation of T_E for males compared to females is not simply a function of low wind velocity. Preliminary indications of the influence of wind velocity on solar heat gain were obtained on 5 April 1981, when wind velocity at Vekol Wash averaged 10–15 m/s. Only limited measurements were made to avoid wind damage to the mounts. However, measurements made at 1200 MST (direct solar radiation = 985 W/m^2, average wind velocity = 10.8 m/s, T_A = 20.1°C) and 1400 MST (direct solar radiation = 855 W/m^2, average wind velocity = 11.6 m/s, T_A = 22.2°C) showed that T_E for males averaged 0.4°C (1200 MST) or 0.3°C (1400 MST) higher than T_E for females; the difference is not statistically significant (ANOVA, $P > 0.05$). Thus, there is as yet no indication that the qualitative effect of coat color on solar heat gain is reversed at high wind velocities for Phainopeplas in normal perching posture.

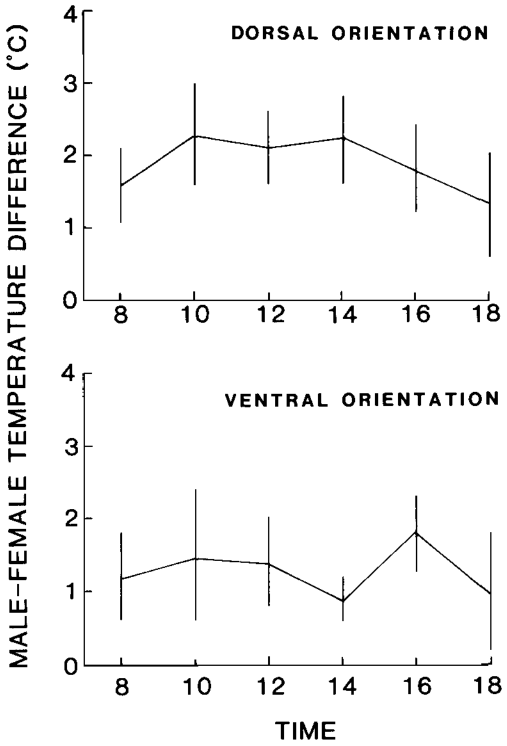

Fig. 2. Difference between operative environmental temperatures acting on male and female Phainopeplas exposed to full sunlight. Values are calculated as male value minus female value and plotted as $\bar{x}$ ± SD.

Discussion

These results indicate that males are exposed to consistently higher operative temperatures than are females. Are these differences biologically significant? Under the conditions examined, sexual differences in solar heat gain should be maximal, yet the difference observed in T_E was only about 1–2°C. Other climatic conditions to which Phainopeplas are exposed should decrease this difference. Increased wind velocity above the low levels observed in the study would increase the relative importance of convective heat flux and decrease the importance of differences in radiative transfer. Any degree of shading or cloud cover also would decrease the observed differences.

The maximum effect of the Phainopepla's sexual dichromatism should occur when the birds are very inactive and thermoregulation makes its greatest fractional contribution to total power consumption. Under cold stress, a 1–

2°C decrease in T_E could produce at most a 5–10% increase in energy expenditure (Walsberg 1977). A greater effect is observed under heat stress, when a 1–2°C increase in T_E could force the bird to commence thermal panting. This would result in up to a 32–64% increase in power consumption (Walsberg 1977). Evaporative water loss also would increase substantially, but data are not available to quantify this change. These estimates not only reflect reactions to maximum differences in solar heat gain that occur only under a restricted set of environmental conditions but probably are exaggerations, because they are based upon data for postabsorptive birds. It is clear, however, that if the bird is near its upper critical temperature, a small change in T_E can force the bird to initiate panting and may substantially affect its energy and water budget. It is also clear, however, that microhabitat selection or simple postural shifts are much more likely to be of major importance and can easily overwhelm effects of differences in coat color.

The microclimate used in this study is characterized by exposure to intense solar radiation and probably presents the highest T_E value available to a Phainopepla. The complete range of microclimates available for this species in this habitat has not yet been quantified, but another common condition can be estimated. This would occur when T_E is near air temperature. During daylight hours, this situation probably is approached in the center of dense vegetation, where the radiative environment may be composed mainly of leaves with surface temperatures close to that of the air. Such areas of dense vegetation typically are occupied by Phainopeplas through much of the late morning and afternoon hours. Thus, the microclimates normally occupied probably are characterized by a range of operative temperatures from at least air temperature to the T_E reported in Fig. 1. T_E in these two different microclimates typically differs from 3 to 11°C, depending on time of day. The variation in operative temperature available to a bird at a particular time of day through behavioral selection of microclimates, therefore, is about 3–8 times as large as the difference imposed by the dimorphism in coat color.

Postural shifts within the same microclimate also can compensate for differences in solar heat loads induced by dichromatism. The reversal of the body's orientation toward the solar azimuth represents a type of simple postural shift that produces a 0.1–3.6°C change in T_E in males and a 0.2–2.3°C change in females. For example, the maximum increase of operative temperature over air temperature occurs at 1400. When males' dorsal surfaces are directed toward the solar azimuth, their T_E is elevated 2.2°C over that for females. A male that reversed his orientation so that his dorsum was directed away from the solar azimuth would decrease T_E 3.6°C, however, and thus would experience an operative temperature 1.4°C below that of the lighter colored female in the opposite orientation. These are conservative estimates of the importance of postural shifts, because they are based upon a single postural change out of the large repertoire available to a live bird. The variation in operative temperature that can be produced by such postural changes and selection between available microclimates suggests that the thermal consequences of sexual dichromatism are minor compared to other determinants of the bird's heat balance.

What, then, are the selective pressures that have resulted in the evolution of this dimorphism in coat color? The male Phainopepla is an example of the pattern noted by a number of authors that black animals are the most common exceptions to the generalization that desert species are cryptically colored (Buxton 1923, Meinertzhagen 1954). For some species, black coloration may be advantageous, because it allows the animal to be conspicuous during daylight hours (Hamilton 1973). In the Phainopepla, visual conspicuousness serves as an energetically inexpensive mode of social signalling that is important in territorial defense and courtship behavior (Walsberg 1977). In such a species, it also probably is advantageous to reduce risks of predation by being inconspicuous at night and during inactive portions of the day. One important mechanism used to generate conspicuousness is the maximization of visual contrast with the local environment (Hailman 1977). An important optical property of desert habitats is the presence of an intense and highly directional short-wave radiation field. This field is highly directional during the day because it is dominated by the direct solar beam, with scattered solar radiation typically accounting for 20% or less of the short-wave radiation on a surface perpendicular to the solar beam. Because the sky is luminous, maximum contrast under these conditions is produced by an object that emits or reflects little light (i.e. a black surface). Black surfaces also are likely to produce high contrast against desert vegetation or soils. The degree of contrast may be estimated by comparing the visual albedo of desert vegetation with that of an animal. Here, visual albedo is defined as the fraction of visible solar radiation that is reflected, with the range of wavelengths visible assumed to be 400–700 nm. Using these criteria, one may estimate the visual albedo of desert vegetation and soils typically to be about 0.25–0.30 (List 1951). The visual albedo of a male Phainopepla is 0.08 (calculated using the data of Walsberg 1980). Because visual contrast differences typically are perceived as a function of proportional differences in the radiative flux from objects (Cornsweet 1970), an important index of a bird's contrast against its environment should be the ratio of the albedos of the animal and its background. For a male Phainopepla contrasted against a background of desert vegetation, there is about a 3–4 fold difference in albedos (0.25/0.85–0.30/0.08). If the visual albedo of a white bird is about 0.8 (estimated from Fig. 2 in Lustick 1969), such animals may achieve similar proportional differences in albedo with desert vegetation (i.e. 0.8/0.25 = 3.2). Thus, white and black species may contrast to a similar degree with desert vegetation or soil. Species with intermediate visual albedos will tend to exhibit less contrast and be less conspicuous. When the bird is viewed against the background of a bright sky, black coloration should maximize contrast.

Specular effects and advantages of nocturnal crypsis also may favor black coloration in desert areas. Specular reflection is most conspicuous in dark-colored birds and is responsible in an important way for the glossy, gleaming appearance of such species (Walsberg 1980). This may increase their conspicuousness substantially. Such specular effects represent a strong angular-dependence of reflection and are noticeable only when the visual radiation field has an important directional component, such as occurs when the animal is exposed to the direct solar beam. In a diffuse radiation field, where there is no important contribution made by the direct solar beam, such as at night or in a diurnal roost surrounded by dense vegetation, glossiness produced by specular effects will disappear. Under these conditions, a glossy, black bird may be quite inconspicuous, while a white individual is likely to remain the brightest object in its local environment, making it vulnerable to predation during inactive periods.

Finally, thermal relations may select against the evolution of white-plumaged species in deserts. Walsberg et al. (1978) demonstrated that under appropriate environmental conditions light-colored species may acquire substantially greater solar heat loads than dark-colored species. This effect was not found in the current study but is much more likely to be important in white species than in gray birds such as the female Phainopepla, because radiation may penetrate deeply into white plumages (Walsberg et al. 1978). Such penetration increases the heat load on the bird, because the site of radiation absorption and consequent heating is nearer to the skin. White plumages therefore can substantially increase solar heat gain, which may be deleterious for desert species.

Thus, under typical desert conditions black coloration should maximize conspicuousness due to increased visual contrast and exhibition of specular effects. Under some conditions, white species could achieve similar degrees of visual contrast. This alternative method of achieving conspicuousness may have distinct thermal disadvantages, however, as well as creating a potentially dangerous conspicuousness during inactive portions of the daily cycle.

Acknowledgments

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