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Abstract

Metabolism, body temperature (T_b), and feather reflectance was measured for dark Louisiana herons (LOU), little blue herons (LB), snowy egrets (SE), and cattle egrets (CE); only LOU nest preferentially in shade. The reflectance of LOU and adult LB was 13%-15%; it was 80%-82% for SE, CE, and immature (white) LB. T_b for all four species approximated 40 °C; hypothermy was never observed. Basal metabolism (H_b) was 107% of the expected level for LOU, 85% for SE and CE, and 66% for LB. Minimal thermal conductance (C) was calculated as approximately 131% of the expected value for LOU, 115% for SE and CE, and 110% for LB. Metabolism and solar radiation may combine to produce heat stress in hot climates, particularly in dark birds; reduced H_b allows LB and other dark birds to nest in exposed sites. High values for C suggest a heat dissipation function; the relatively lower values are found in species with relatively lower H_b's, thus preventing or reducing increases in T₁, the lower limit of thermoneutrality. White plumage is thermally advantageous in tropical/subtropical birds nesting in open habitat, but dark coloration is not; other evolutionary explanations must be sought to explain the occurrence of dark birds in hot climates.

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METABOLISM AND SOLAR RADIATION IN DARK AND WHITE HERONS IN HOT CLIMATES¹

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(Accepted 3/3/80)

Metabolism, body temperature (T_b), and feather reflectance was measured for dark Louisiana herons (LOU), little blue herons (LB), snowy egrets (SE), and cattle egrets (CE); only LOU nest preferentially in shade. The reflectance of LOU and adult LB was 13%–15%; it was 80%–82% for SE, CE, and immature (white) LB. T_b for all four species approximated 40 C; hypothermy was never observed. Basal metabolism (\dot{H}_b) was 107% of the expected level for LOU, 85% for SE and CE, and 66% for LB. Minimal thermal conductance (C) was calculated as approximately 131% of the expected value for LOU, 115% for SE and CE, and 110% for LB. Metabolism and solar radiation may combine to produce heat stress in hot climates, particularly in dark birds; reduced \dot{H}_b allows LB and other dark birds to nest in exposed sites. High values for C suggest a heat dissipation function; the relatively lower values are found in species with relatively lower \dot{H}_b 's, thus preventing or reducing increases in T_b , the lower limit of thermoneutrality. White plumage is thermally advantageous in tropical/subtropical birds nesting in open habitat, but dark coloration is not; other evolutionary explanations must be sought to explain the occurrence of dark birds in hot climates.

INTRODUCTION

The heat balance of endotherms is often described by the relation

$$\dot{H}_m = C(T_b - T_a), \quad (1)$$

where \dot{H}_m is metabolism and represents the heat produced, C is thermal conductance, and T_b and T_a are body temperature and

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ambient temperature, respectively. The term $C(T_b - T_a)$ represents heat loss when C is considered to be wet thermal conductance (McNab 1974). The distinction between “wet” and “dry” conductance normally has little importance at low to moderate T_a since evaporative heat loss is low. Scholander et al. (1950a) concluded that C was very important in controlling an endotherm's response to climate, whereas basal metabolism (\dot{H}_b) was considered virtually nonadaptive in many endotherms (particularly terrestrial mammals); they noted, however, that such a statement required further study in the case of birds. After a decade of further study by many investigators, McNab and Morrison (1963) asserted that both mammals and birds showed climatic adaptation of their basal metabolic rates.

Equation (1) is obviously a simplification; many extrinsic factors can affect the heat balance in endotherms (Porter and Gates 1969; Calder and King 1974; McNab 1974). One of these factors is solar radiation. There has been considerable interest recently re-

garding the interaction between solar radiation and dark feathers or skin of birds (Hamilton and Heppner 1967; Lustick 1969; Heppner 1970; Lustick, Talbot, and Fox 1970; Lustick 1971; Ohmart and Lasiewski 1971; Bateman and Balda 1973; Lustick, Battersby, and Kelty 1978; Walsberg, Campbell, and King 1978; Wunder 1979). Many of these authors demonstrated that dark birds are able to reduce their metabolic expenditure at T_a below their lower limit of thermoneutrality (T_1) when exposed to solar radiation. Hamilton (1973) in fact argues convincingly that black color in birds has often been selected to achieve this thermal benefit. When a dark bird is exposed to solar radiation at $T_a < T_1$, there is a reduction in the feather surface to skin surface thermal gradient. Heat loss is thus minimized; that is, C is reduced (Cowles 1967; Lustick 1969; Dawson and Hudson 1970; Heppner 1970). It can be seen from equation (1) that a reduction in C results in a lowered \dot{H}_m at any $T_a < T_1$. This reduced C also results in a lowered T_1 which may be accompanied by a lowered upper limit of thermoneutrality (Lustick 1969; DeJong 1976). That is, the zone of thermoneutrality (TNZ) tends to shift down when thermal conductance is reduced under conditions of insolation. Within the TNZ, metabolism is basal (\dot{H}_b) when the animal is quiescent and postabsorptive and cannot be further reduced without a fall in T_b .

It is significant that of the studies of birds and solar radiation cited above, all but the last two, which will be discussed later, were done for birds occupying cool or seasonally cool temperate environments where $T_a < T_1$. However, when $T_a > T_1$, as in warmer climates, the thermal gradient between feather and skin surfaces is much diminished and ultimately reversed (Lustick et al. 1970). If this thermal gradient is reversed, solar radiation acts as an external heat load to be added to the bird's internal metabolic heat production. Yet many dark, often black, birds breed in the tropics, subtropics, and seasonally warm temperate environments exposed to high levels of insolation.

They must compensate for this heat stress behaviorally and/or physiologically.

Herons (Ardeiformes, Ardeidae) include species that are predominantly tropical or subtropical in distribution and that seasonally invade warm temperate climes. These species vary greatly in plumage color: cattle egrets (*Bubulcus ibis*) and snowy egrets (*Egretta thula*) are white; Louisiana herons (*Hydranassa tricolor*) are dark gray on their dorsal surface; little blue herons (*Florida caerulea*) are dark slaty blue. Little blue herons are unique among ardeids in that their plumage is white during their first year but dark as adults. The juvenal plumage of the other three species here resembles the adult color. At least three of these herons are closely related; Dickerman and Parkes (1968) and Curry-Lindahl (1971) considered snowy egrets, Louisiana herons, and little blue herons all to be congeneric in *Egretta*. Payne and Risley (1976) have also included the cattle egret in this worldwide genus. In Florida, all four species nest together in mixed heronries during the spring when insolation is most intense. They provide a natural test for the effect of solar radiation on dark and white birds in a hot climate where T_a often exceeds 35 C and wind-shielded black bulb temperatures may exceed 60 C.

MATERIAL AND METHODS

ANIMALS

At least two individuals of all four species were examined, including a little blue heron in juvenal plumage. All the herons except cattle egrets 4 and 5 (the latter was found with a broken wing) were raised from nestlings in captivity and weighed about 20% less than wild herons. A weight difference between wild and captive-reared birds has also been noted for the redhead (*Aythya americana*) by Weller (1957). The cattle egrets were daily fed stunned mice which were swallowed whole. The other three species were fed smelt in pans of water daily with a weekly vitamin (particularly thiamine) supplement. The birds were all housed indoors in hardware cloth cages no smaller than $2.0 \times 1.5 \times 2.0$ m and con-

taining a maximum of two animals. The cages contained tree branches on which the birds usually roosted when not feeding. Window light provided a natural photoperiod. Louisiana heron 3, a juvenile, was killed at night by a slow loris in a neighboring cage before the anticipated end of metabolic studies.

ENERGETICS

Feather reflectances were measured on a Beckman DK-2A spectrophotometer using a reflectance sphere attachment in the "diffuse" mode with a white MgO standard. Feather reflectance was measured over a 300–2,700-nm range on the dorsal surface of mounted skins.

Solar radiation was measured at 178 nests with a dome solarimeter (Science Associates model no. 615) that integrated all direct shortwave radiation over a wavelength range of 300–3,500 nm. The solarimeter had a sensitivity of 25.8 mV/cal·cm² and a cosine response of $\pm 2\%$ from 0° to 65° and $\pm 4\%$ from 65° to 80° incidence. The leveling and recording apparatus used in association with the solarimeter is described elsewhere (Ellis, forthcoming). All measurements were made between 1000 and 1500 hours Eastern Standard Time when insolation was most intense.

Resting metabolism was measured in birds that had not been fed at least 14 h before testing during daylight hours using a Beckman G2 paramagnetic oxygen analyzer connected in open circuit (Depocas and Hart 1957). Air flow of about 1,400 cm³/min was pulled through the chamber and measured by a Brooks precision rotameter, after CO₂ and water were removed. The rotameter was calibrated with a Brooks 500 cm³ Vol-U-Meter. Oxygen consumption was calculated at standard temperature and pressure, dry (STPD). Body temperatures of herons were taken with a Schultheis fast response thermometer inserted 3–5 cm into the cloaca within about a minute of the final metabolic measurement.

CALCULATIONS

Thermal conductance.—Minimal C can be calculated in various ways. In an endotherm

whose total response to $T_a < T_1$ is chemical (metabolic) regulation, C is the slope of the regression of \dot{H}_m on decreasing T_a . In this case C extrapolates to T_b in accordance with equation (1). This is rarely the case in birds, however. Most birds show a mixing of chemical and physical (posture, feather erection, etc.) regulation at $T_a < T_1$. This manifests itself as a steadily decreasing C as T_a decreases (Drent and Stonehouse 1971; Schmidt-Nielsen 1979, p. 247). As a result, the slope of the regression of \dot{H}_m on T_a extrapolates to a temperature exceeding T_b . Such a slope will be an underestimate of minimal C . Two solutions are possible for estimating C in birds that mix chemical and physical regulation at $T_a < T_1$ (Ellis 1976): (1) C may be presented as a family of slopes that decrease with decreasing T_a and that converge at a T_b representing T_b for all $T_a \leq T_1$ (as in figs. 2–4). Minimal thermal conductance would be the lowest of these slopes; it is determined by the lowest T_a values and estimates purely chemical responses to decreased T_a . (2) The same points which determine minimal conductance in the first solution may be used a different way to determine C . Each metabolic value at low T_a can be regressed on its own T_b . A family of slopes, whose average is an estimate of minimal C , results. The more accurate of these methods is the one that extrapolates more closely to actual T_b (McNab 1980). The second method is used in this paper for that reason. All measures of C in this paper represent minimal values and are symbolized by C/m (where m is mass in g) to emphasize their mass-specific nature.

Statistics.—All measures of variation presented here are standard errors of the means (Snedecor and Cochran 1967). Comparisons between two means, including those involving pooled data, were made using t -tests (Simpson, Roe, and Lewontin 1960). All comparisons were considered statistically significant at a level of $P < .05$.

RESULTS

REFLECTANCE AND SOLAR RADIATION

The effect of solar radiation on a bird can be described by the term $SA(1 - r_t)$ (modi-

fied from Gates 1962), where S is solar radiation, A is the animal's surface area, and r_f is the reflectance of its feathers; transmission through the plumage is probably negligible in very dark birds, although it probably is not in very light ones (Walsberg et al. 1978). Maximum potential S is the same for little blue herons, snowy egrets, cattle egrets, and Louisiana herons because they all live together. All are approximately the same size, so A is similar for all species. If these birds experience different maximum solar loads, then it is a consequence of their different reflectances.

Figure 1 shows the percent reflectances

for all these species as a function of wavelength. Because the reflectance of these birds is spectral dependent and because wavelength is not a direct measure of energy (Wald 1965), the average feather reflectance, or r_f (table 1), was calculated by integrating the area under a reflectance curve based on wave numbers and corrected for sunlight actually reaching sea level (Gates 1965). The white birds all have a reflectance of about 80%, although they are not equally reflective at all wavelengths. Little blue herons in juvenal plumage, for example, were more reflective in infrared but less reflective in visible light than either

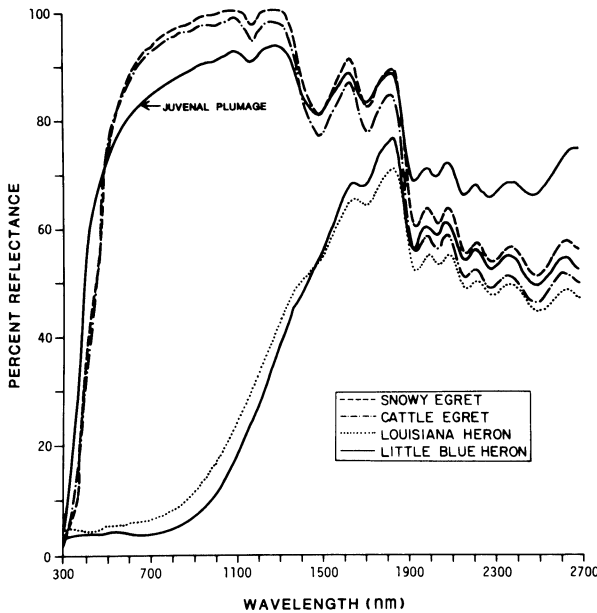


FIG. 1.—Feather reflectances in four species of herons. Little blue herons have white plumage, here labeled “juvenal plumage,” for at least their first year.

TABLE 1
MAXIMAL POTENTIAL SOLAR LOADS

	S (cal/cm ² ·min)	A (cm ²)	r_f	$SA(1-r_f)$ (cal/min)
Snowy egret.....	1.43	187.68	.82	48.31
Cattle egret.....	1.43	181.75	.81	49.38
Little blue heron (immature)..	1.43	(178.14?)	.80	(50.95?)
Little blue heron (adult).....	1.43	178.14	.13	221.62
Louisiana heron (sun).....	1.43	186.05	.15	226.14
Louisiana heron (shade).....	.046	186.05	.15	7.27

NOTE.—See text for definitions of symbols.

snowy egrets or cattle egrets. Little blue heron adults and Louisiana herons were markedly less reflective than the white birds, particularly in the visible and very near infrared wavelengths; their average reflectance was only 13%–15%.

Table 1 shows how the maximal potential solar loads were calculated. The wavelength ranges used in determining S (300–3,500 nm) and r_f (300–2,700 nm) are fairly compatible because very little energy penetrates the earth's atmosphere between 2,700 and 3,500 nm (Gates 1962, 1965). In table 1, A was calculated using a modified Meeh approximation (Walsberg and King 1978):

$$A = (8.11m^{0.667})/2, \quad (2)$$

where m is mass in grams. The Walsberg and King modification allows calculated A to approximate feather surface (the surface of heat exchange with the environment) rather than the somewhat larger skin surface. Affected surface area (cm^2) is given as half of the total since it is unlikely that solar radiation would impinge on more than 50% of a bird's surface; in fact, this surely represents a maximal value. The highest value for S normally recorded in the field during the breeding season was 1.43 cal/ $\text{cm}^2 \cdot \text{min}$ (998 W/ m^2). This value is used in table 1 and probably represents the maximum S to which these herons are normally exposed.

Louisiana herons have apparently adopted a strategy of nesting in the shade to cope with the potential thermal load their dark plumage confers upon them, whereas the other three species appear to nest without reference to incident sunlight (Ellis 1976 and forthcoming). Because Louisiana herons rarely experience the maximum potential S at their nest, table 1 also includes a value for this species in deep shade. This "shade" value of 0.046 cal/ $\text{cm}^2 \cdot \text{min}$ (32 W/ m^2) was the lowest value recorded at a nest of this species in the field; it should not be mistaken for the average value for Louisiana heron nests, which is about 0.50 cal/ $\text{cm}^2 \cdot \text{min}$ (352 W/ m^2).

METABOLISM AND CONDUCTANCE

Metabolism.—Resting metabolism was measured during the (daylight) phase for adults of all four species of herons. Daytime metabolic measurements are a better estimate of heron energetics in the field when the birds experience thermal stress. Resting metabolism measured within the thermoneutral zone is treated here as "basal" (\dot{H}_b), although nighttime measurements approximate the 20%–25% metabolic rate reduction reported by Aschoff and Pohl (1970a, 1970b). A few nighttime measurements of metabolism in one cattle egret (CE 1) showed C unchanged but \dot{H}_b 24% lower than in the daytime.

Figures 2–5 show the metabolism of all four species as a function of ambient temperature. Table 2, which summarizes these results, shows that \dot{H}_b/m (measured as a mass-specific rate) for the smaller individual of a species pair is always significantly higher than for the larger individual. This is a consequence of the fact that metabolism is a function of body size. For nonpasserines this may be expressed as

$$\dot{H}_b/m = 4.6m^{-0.28} \quad (3a)$$

whereas in passerines, the proper equation is

$$\dot{H}_b/m = 7.5m^{-0.28} \quad (3b)$$

where \dot{H}_b/m is in $\text{cm}^3\text{O}_2/\text{g} \cdot \text{h}$ and mass (m) is in g (Lasiewski and Dawson [1967], as modified by McNab [1974]).

Equation (3) can be used to predict standard rates of metabolism. In table 3, observed \dot{H}_b/m is compared with predicted values and expressed as a percent. Louisiana herons, which usually nest in the shade, were the only birds whose basal rate of metabolism exceeded the predicted value (107% of expected). This species can be compared with the other three that nest without reference to the sun. Average snowy egret \dot{H}_b was 85% of expected. Although the range was large (77% and 93%), the average was quite close to the 85.5% average of the cattle egrets (whose range was small). Both of these species are white or nearly so. Little blue herons had an

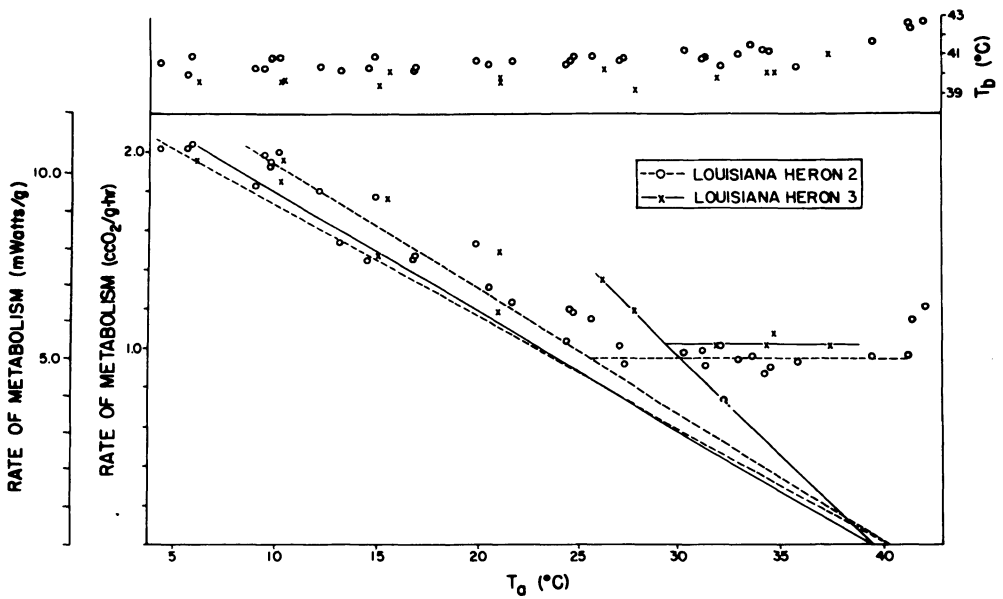


FIG. 2.—Louisiana heron metabolism and body temperature (T_b) as a function of ambient temperature (T_a).

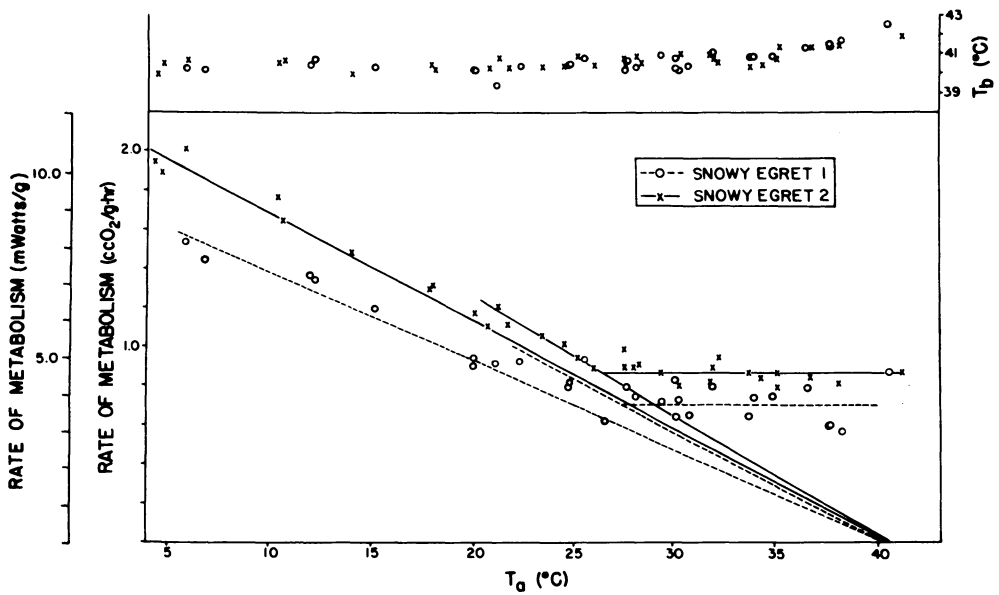


FIG. 3.—Snowy egret metabolism and body temperature (T_b) as a function of ambient temperature (T_a)

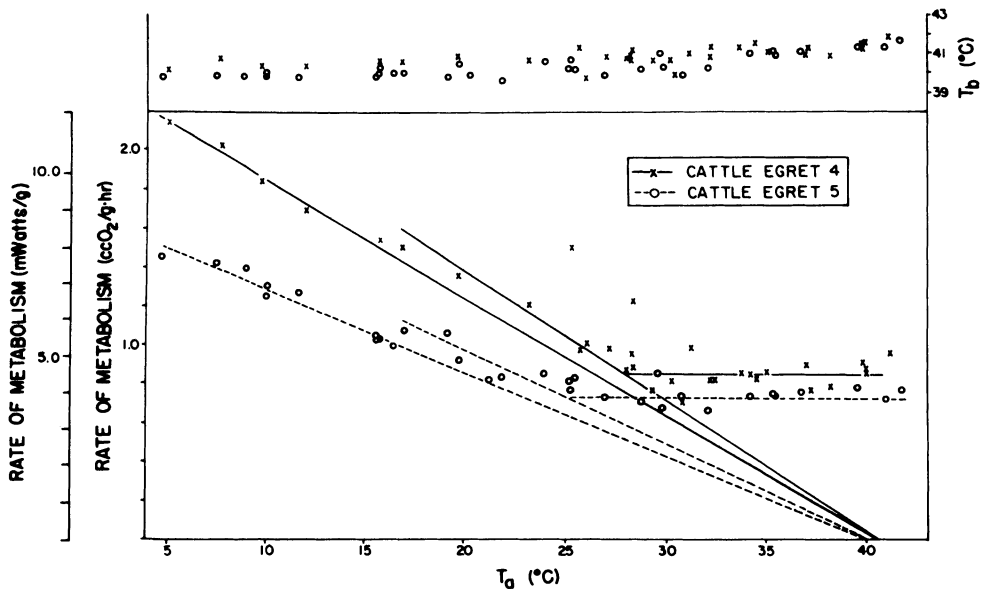


FIG. 4.—Cattle egret metabolism and body temperature (T_b) as a function of ambient temperature (T_a)

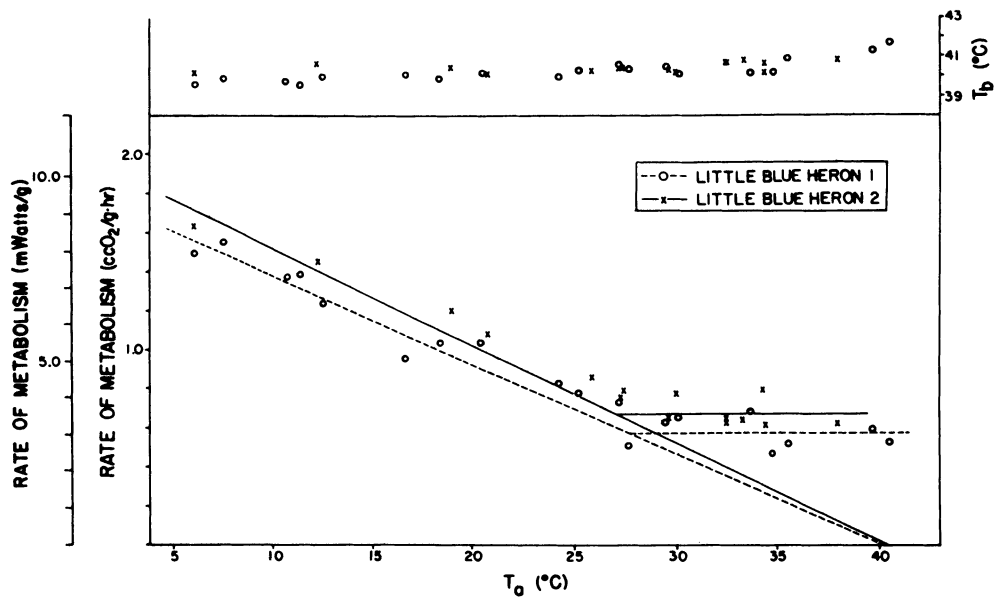


FIG. 5.—Little blue heron metabolism and body temperature (T_b) as a function of ambient temperature (T_a).

average \dot{H}_b/m of 66% of expected and have a dark plumage. A few measurements on a yearling little blue heron with white plumage were equally low. Of course, basal rates for all these herons would be even lower had they been measured at night.

Thermal conductance.—Table 2 summarizes the data provided in figures 2–5 for minimal thermal conductance, C/m (a mass-specific measure). Table 3 compares these values with the conductances predicted in the allometric relationship described by Lasiewski, Weathers, and Bernstein (1967):

$$C/m = 0.85m^{-0.51}, \quad (4)$$

where C/m is in $\text{cm}^3\text{O}_2/\text{g}\cdot\text{h}\cdot^\circ\text{C}$ and m is in g. In every species C/m is greater than expected. There is a clear trend in these values similar to the data for \dot{H}_b/m . Louisiana herons have the highest C/m (130.7%) and nest in the shade. The white snowy egrets and cattle egrets which may

nest in the sun have intermediate values of 113.7% and 115.5%, respectively. The dark little blue herons, which often nest in the sun, have a minimal conductance of 109.9%.

Body temperature.— T_b averages about 40.5 C for all species (table 4). The lowest daytime T_b (=39.3 C) ever recorded was for a juvenile Louisiana heron (LOU 3) at $T_a = 28.0$ C. Average $T_b = 40.6$ for cattle egrets compares favorably with the 40.46 C reported elsewhere for wild and captive cattle egrets (Siegfried 1968). Wetmore (1921) reported a value of about 40.2 C for snowy egrets and 40.8 C for Louisiana herons as compared with 40.6 C and 40.8 C, respectively, reported here. None of these herons ever showed signs of hypothermia.

DISCUSSION

METABOLISM AND INSOLATION

Previous information on solar radiation and metabolism in warm climates has suggested for turkey vultures (Heath 1962)

TABLE 2
METABOLIC RELATIONSHIPS IN FOUR SPECIES OF HERONS

Animal ^a	<i>m</i> (g)	\dot{H}_b/m ($\text{cm}^3\text{O}_2/\text{g}\cdot\text{h}$)	<i>C/m</i> ($\text{cm}^3\text{O}_2/\text{g}\cdot\text{h}\cdot^\circ\text{C}$)	T_b^b ($^\circ\text{C}$)	T_1 ($^\circ\text{C}$)
LOU 2.....	343.31 ± 2.59	.951 ± .012	.0575 ± .0005	40.4 ± .1	25.8
LOU 3.....	276.50 ± 5.75	1.033 ± .014	.0616 ± .0011	39.7 ± .1	... ^c
SE 1.....	333.73 ± .61	.700 ± .020	.0464 ± .0007	40.2 ± .1	26.5
SE 2.....	294.23 ± 1.51	.869 ± .012	.0566 ± .0006	40.4 ± .1	26.0
CE 4.....	271.67 ± 3.09	.850 ± .015	.0641 ± .0014	40.6 ± .1	28.0
CE 5.....	326.79 ± 1.04	.745 ± .014	.0431 ± .0004	39.9 ± .1	25.2
LB 1.....	299.63 ± 1.88	.571 ± .010	.0482 ± .0013	40.0 ± .1	27.8
LB 2.....	281.06 ± 1.57	.670 ± .025	.0553 ± .0017	40.4 ± .1	27.2

^a LOU = Louisiana Heron, SE = snowy egret, CE = cattle egret, LB = little blue heron.

^b Body temperature where $T_a \leq T_1$.

^c Not enough data to determine T_1 .

TABLE 3
RELATIONSHIP OF OBSERVED AND EXPECTED VALUES OF
METABOLISM AND THERMAL CONDUCTANCE^a

Species	\dot{H}_b/m	$\dot{H}_b\%$ ^b	<i>C/m</i>	<i>C%</i> ^c
Louisiana heron.....	.992	107.5	.0596	130.7
Snowy egret.....	.784	85.3	.0515	113.7
Cattle egret.....	.798	85.6	.0536	115.5
Little blue heron.....	.620	66.0	.0518	109.9

^a Based on two individuals of each species.

^b Percentage of expected \dot{H}_b ; from eq. (3).

^c Percentage of expected *C*; from eq. (4).

TABLE 4
COMPARATIVE ENERGETICS OF HERONS^a

Animal	\dot{H}_b/C	$(\dot{H}_b/C)_e^b$	F^c	T_b^d	T_1	$(T_b - T_1)$
LOU 2.....	16.539	20.721	.798	40.7	25.8	14.9
LOU 3.....	16.769	19.715	.851	40.9
SE 1.....	15.086	20.586	.733	40.6	27.5	13.1
SE 2.....	15.353	19.998	.768	40.7	26.0	14.7
CE 4.....	13.261	19.641	.675	40.9	28.0	12.9
CE 5.....	17.285	20.487	.844	40.4	25.2	15.2
LB 1.....	11.846	20.096	.589	40.1	27.8	12.3
LB 2.....	12.116	19.789	.612	40.5	27.2	13.3

^a Symbols as in table 2 unless otherwise noted.

^b Expected $\dot{H}_b/C = 5.41 m^0.22$ as determined by eqq. (3) and (4).

^c Ratio of observed \dot{H}_b/C to expected \dot{H}_b/C .

^d Includes values at all T_a unless above thermoneutrality.

and shown for roadrunners (Ohmart and Lasiewski 1971) that insolation may supplement internal heat production in maintaining normal body temperatures. However, turkey vultures and roadrunners live in only seasonally warm environments, and they utilize basking in conjunction with hypothermia (Heath 1962; Ohmart and Lasiewski 1971). The herons studied here exhibit neither basking behavior nor hypothermia. These herons, throughout most of their range, are faced with high T_a 's as well as intense solar radiation year round. Furthermore, any heat stress they undergo in their environment will be exacerbated by nesting in open areas where, for reasons of incubation and protection of eggs and nestlings, they cannot leave the vicinity of their nests. All four herons have normal $T_b \simeq 40$ C. Insolation at high T_a can only make these birds hyperthermic; their T_b rises as they store heat. Although moderate hyperthermia may allow a bird some respite from heat stress (Calder and King 1974), it is unclear how long a bird will be able to regulate a hyperthermic T_b if it is unable to leave the nest. Because lethal T_b for most birds is around 46 C (Dawson and Hudson 1970), there exists only a small margin for error in hyperthermic birds. The rate of change in body temperature ($\Delta T_b / \Delta t$) of a bird that is receiving solar radiation in a hot environment is a function of internal heat production and external heat load. The external heat load will be trans-

mitted through the thermal gradient between feather surface and skin.

The main external heat load differentially affecting dark and white birds is shortwave radiation from the sun striking the feathers. Measuring skin temperatures, Lustick et al. (1978) found solar heat gain to the body from the feathers to be higher with dark plumage than white plumage, although this difference may not hold at air speeds > 3 m/s (Walsberg et al. 1978). Heat gain from direct shortwave radiation was also found to be considerably higher in black goats than in white goats inhabiting hot deserts (Finch et al. 1980). Potential solar loads can be estimated by $SA(1 - r_f)$, although this may cause some underestimate in white birds where some energy is transmitted beyond the feather surface. Birds at high T_a and with relatively high \dot{H}_m may reduce their rate of T_b increase ($\Delta T_b / \Delta t$) by reducing the solar radiation striking them. This may be accomplished by staying in shade (Louisiana herons), thus lowering S , or by having a highly reflective (white) plumage (snowy egrets and cattle egrets), thus lowering $(1 - r_f)$. Conversely, dark birds in the sun (little blue herons) which cannot reduce $SA(1 - r_f)$ can reduce the rise in T_b by having a low \dot{H}_m .

Figure 6 shows the relationship between expected \dot{H}_b taken from table 3 as a function of potential solar loads, $SA(1 - r_f)$, taken mainly from table 1. The line is speculative, but reflects the presumption

that although basal metabolism decreases with increasing heat load, there is a minimal level (probably set by the energy requirements for survival) below which \dot{H}_b 's are not selected for. Values to the right of this line would result in rapid increases in T_b . Such should be the case for Louisiana herons nesting in the sun. Actually, the average Louisiana heron is somewhat to the right of this line which was developed using the limiting case of a bird in deep shade. Values to the left of the line would result in slower increases in T_b . Presumably young (white) little blue herons would have a low $\Delta T_b/\Delta t$, although it was not plotted in figure 6 due to insufficient measurements of body size and \dot{H}_b .

Relatively little information has been reported on the metabolic rates of dark-plumaged birds residing in warm climates and spending appreciable time in open habitats. Table 5 summarizes what is known

to date about dark birds in these conditions. Of these eight species, all have basal rates of metabolism considerably below the rates predicted by equations (3a) and (3b). The two cultures are the most temperate in distribution and do not normally nest in the sun, although they spend considerable periods of time feeding and roosting in direct sunlight (personal observation). As scavengers, they probably have unpredictable food supplies, which seem to be correlated with low \dot{H}_b (McNab 1969, 1974). On the other hand, little blue herons, anhingas, magnificent frigatebirds, sooty terns, and both passerines, all nest in relatively open habitat, remain at lower latitudes (except lark buntings), and, with the possible exception of frigatebirds (Nelson 1976), have stable or at least predictable food supplies. Apparently, dark birds nesting in the sun in hot (generally low latitude) climates often, perhaps invariably, have

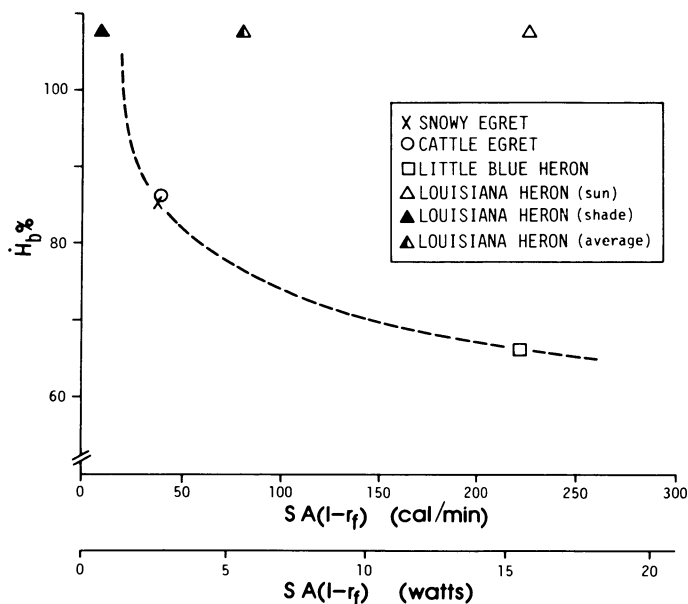


FIG. 6.—The relationship between the percentage of expected basal metabolism (\dot{H}_b) and solar load [$SA(1 - r_f)$]. The values for (\dot{H}_b) are taken from table 3; most of the values for solar load come from table 1. However, the value for Louisiana heron (average) is based on the average solar radiation ($S = 0.505 \text{ cal/cm}^2 \cdot \text{min}$) striking that species' nests (no. = 33). The sun value assumes maximum S , the condition which also defines solar load for all other species here. The shade value is defined in the text. The line is speculative. Values to the right of the line are assumed to be at a thermal disadvantage relative to those on or to the left of the line (see text). Apparently, among Louisiana herons, only those that nest in sites more shaded than the average will not be at some disadvantage.

TABLE 5

COMPARATIVE METABOLISM OF DARK-PLUMAGED BIRDS IN HOT, SUNNY CLIMATES

Species	No.	m (g)	\dot{H}_b (%)	Source
Nonpasserines: ^a				
<i>Fregata magnificens</i> (magnificent frigatebird)	4	1,080	69.4	Enger 1957
<i>Cathartes aura</i> (turkey vulture)	2	1,100	70.4	Enger 1957
<i>Coragyps atratus</i> (black vulture)	2	1,700	79.6	Enger 1957
<i>Sterna fuscata</i> (sooty tern)	6	148	86.3	MacMillen, Whittow, Christopher, and Ebisu 1977
<i>Florida caerulea</i> (little blue heron)	2	290	66.0	Present study
<i>Anhinga anhinga</i> (anhinga)	2	1,055	85.0	Hennemann, unpublished data
Passerines: ^b				
<i>Corvus corax ruficollis</i> (brown-necked raven)	22	610	76.6	Marder 1973a
<i>Calamospiza melanocorys</i> (σ) (lark bunting)	6	33	83.1	Wunder 1979

^a \dot{H}_b % based on eq. (3a).^b \dot{H}_b % based on eq. (3b).

low \dot{H}_b 's. In contrast, the dark-backed herring gull which mainly nests at higher, cooler latitudes, under intense solar radiation (maximum $S \approx 1.55$ cal/cm²·min), experiences thermal stress at "moderate T_a 's"; yet these birds have a basal metabolism of about 130% of that expected from their mass (Lustick et al. 1978). This comparison does not, however, reflect a simple latitudinal effect. Some open-nesting white birds (royal terns [*Sterna maxima*], masked boobies [*Sula dactylatra*]) in low latitudes have high \dot{H}_b 's (Ellis, unpublished data).

THERMAL CONDUCTANCE

Dawson and Hudson (1970) hypothesized that birds in very hot environments could restrict their environmental heat gain by reducing thermal conductance. Nevertheless, birds living in hot environments tend to have values of C/m approximately equal to or higher than levels predicted by equation (4), presumably for reasons of heat dissipation (Dawson and Hudson 1970; Yarbrough 1971). The herons studied here conform to this pattern: minimal C/m ranges from about 110% to over 130% of expected values (table 3). Particularly interesting is that little blue herons have the lowest minimal conductance, whereas Louisiana herons have the highest.

A relatively low minimal conductance in the little blue heron has two related func-

tions. First, given its large solar load and low reflectance, a low C will reduce its heat load as Dawson and Hudson (1970) suggested. This is less important in the cattle egret and snowy egret which reflect much of their solar load. A relatively low conductance is still less of an advantage for the Louisiana heron which incurs only a modest solar load while nesting. Second, as suggested by Scholander et al. (1950b), a reduction in C reduces the lower limit of thermoneutrality (T_1). This is particularly important to a species like the little blue heron with its low \dot{H}_b .

When an endotherm is at its lower limit of thermoneutrality, metabolism is basal, and equation (1) becomes

$$\dot{H}_b = C(T_b - T_1) \quad (5)$$

(McNab 1970, 1974; Calder and King 1974). This can be rearranged to

$$\dot{H}_b/C = T_b - T_1 = \Delta T_1. \quad (6)$$

Thus ΔT_1 , the temperature differential below which metabolism is no longer basal, is a function of \dot{H}_b and C . Also T_1 is determined by \dot{H}_b and C if T_b is constant, as it is in these herons. A reduction of \dot{H}_b at a constant T_b would raise T_1 unless compensated by a reduced C . Thus a lower C can be the means by which an endotherm maintains a low T_1 (a wide ΔT_1) even while

decreasing its heat production. A low T_1 may be important to a tropical or subtropical bird that seasonally invades temperate areas. Early in the breeding season in Florida, herons often encountered T_a 's of 18 C or lower at night. Comparably low T_a 's are occasionally reached even in the tropics. Thus a relatively low C (compared with the C 's of the other herons) allows little blue herons to maintain nearly as low a T_1 as the other three species. Even so, its ΔT_1 (12.0 ± 0.1 C) is significantly smaller than the other species (15.7 ± 0.6 C) when calculated as \dot{H}_b/C (see table 4). If little blue herons had the same C as Louisiana herons (130.7% of expected), their \dot{H}_b/C would only be 10.1 C, and T_1 would be 2 C higher than is the case. Of course, if C were still lower, T_1 could be further reduced. Perhaps this is not the case because too low a thermal conductance might jeopardize the bird's ability to dissipate heat, especially in still air. A comparable situation may be found in poorwills. Poorwills nest in the sun and have a very low (49%) \dot{H}_b (Bartholomew, Hudson, and Howell 1962). They also have a C of 94%. The decreased C may be useful in extending the bird's thermoneutral zone to help it in a fluctuating environment.

Empirically determined ΔT_1 's in little blue herons (12.8 ± 0.5 C) are smaller but not significantly different from those of the other herons when pooled (14.2 ± 0.5 C). This may be due to small sample size. However, Louisiana herons, snowy egrets, and cattle egrets all reduce C with decreasing T_a . Consequently, their actual T_1 's are higher (therefore, their ΔT_1 's are smaller) than they would be if C were minimal at all T_a 's below TNZ (as appears to be the case in little blue herons).

Scholander et al. (1950*b*) showed that tropical birds have a higher T_1 than arctic birds. Yarbrough (1971) argued that tropical or desert (i.e., warm habitat) birds have a small ΔT_1 and show a related low F value [his (M_b/C_r)]. McNab (1970) also cited data showing that birds from warm climates have a low F , where F is the ratio between observed and expected \dot{H}_b/C . As such, F

represents the variation in ΔT_1 among species not attributable to mass (at least as mass affects \dot{H}_b and C) (McNab 1978). The F values in table 4 are in fact low (< 1.000) with the little blue heron's (0.601 ± 0.012) being significantly lower than the pooled F of the other species (0.778 ± 0.028). The fact that F and ΔT_1 are relatively low even in the Louisiana heron, whose \dot{H}_b is not low, indicates that it is their high C that is responsible for these warm habitat properties.

COLOR DIFFERENCES: EVOLUTIONARY IMPLICATIONS

The question of why white and black are common colors among many groups of birds has perplexed biologists at least since Darwin (1896). One explanation advanced is thermal adaptiveness. Hamilton (1973), and more recently Kushlan (1978), argued that white color afforded a degree of protection from heat stress in species living in high insolation environments. This investigation adds additional weight to that argument. However, Hamilton's arguments concerning dark coloration are less convincing. The fact that dark color aids birds by reducing their metabolic output at low T_a 's is irrelevant in hot climates where birds confront heat stress, rather than heat loss, problems.

Marder (1973*b*), and more recently Walsberg et al. (1978), have proposed that black plumage is specifically adaptive in hot, sunny climates. Walsberg et al. argue that at wind speeds exceeding 3 m/s, white birds gain more heat than black birds with erected plumage. This is because radiant energy penetrates white plumage more than black plumage (particularly when erected) and hence is less easily ameliorated by forced convection at the surface (this model assumes that all birds in hot, sunny climates fully erect their feathers). Walsberg et al. also demonstrate, however, that the radiant heat load on both colors is relatively low at wind speeds > 3 m/s, but can be high at wind speeds < 3 m/s. At wind speeds < 3 m/s, they show the radiant energy load to be substantially higher on black birds than on white ones. The transition wind

speed of 3 m/s is based on pigeons (*Columba livia*) and may differ for other species; nevertheless, the general analysis here should not be affected. Although very calm days are uncommon during the nesting season of these herons (and probably most other birds), they do occasionally occur. Dark birds on unsheltered nests on hot, sunny, windless days are faced with severe heat loads, as suggested by Cowles (1967). This is particularly true when the incidence of solar radiation is normal to the feather surface (Lustick, Adam, and Hinko 1980), as when exposed birds incubate at mid-day, although herons, especially little blue herons, may reduce that solar load by changing posture (Ellis, forthcoming). Abandoning the nest, even briefly, to escape the heat puts a bird's whole reproductive effort in jeopardy (e.g., to predation). This probably explains the fact that every dark bird that lives in hot, sunny climates and for which metabolic data are available shows lower than expected basal rates of metabolism (table 5). This is compounded by the fact that on hot, sunny days, even in light breezes (wind speed unknown), dark little blue herons (despite their lower \dot{H}_b) always began gular flutter before white snowy and cattle egrets (Ellis, personal observation). Wunder (1979) has shown that dark (male) lark buntings (*Calamospiza melanocorys*) have greater evaporative water loss at high T_a when irradiated. Furthermore, his data indicate that this species tolerates a high external heat load by maintaining a low internal heat production (table 5).

If dark coloration represents a thermal problem, the question still remains why

many low latitude birds, including ardeids like little blue herons and Louisiana herons, are dark. Ellis (1976), Kushlan (1978), and Mock (1980) reviewed several explanations of why herons are white or dark. One theory that cannot be easily dismissed states that white and black (dark) colors promote conspicuousness in gregarious species (Darwin 1896, p. 493; Meyerriicks 1960; Moynihan 1960, 1968). All four herons species investigated here are colonial nesters. Little blue herons, Louisiana heron, and snowy egrets, regardless of taxonomic schemes, are closely enough related to hybridize on rare occasions (Dickerman and Parkes 1968). Perhaps their very different adult plumages represent the result of selection for reproductive isolation without sacrificing conspicuousness.

In any event, while white coloration is useful in hot (usually low latitude) climates (and only found in herons inhabiting them), dark plumage confers a thermal penalty in such climates, if combined with open nesting habits. However, the fact that certain dark birds (e.g., little blue herons) can exist under these conditions because of their low metabolic rates suggests a conclusion of causality that is not yet warranted. The question of whether low \dot{H}_b is a specific adaptation to these climates or exists for other reasons but allows nesting in a hot, high insolation environment awaits further study. The nesting in shaded sites by Louisiana herons having relatively high metabolic rates does seem to be a behavioral adaptation to an extreme climate (Ellis, forthcoming).

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