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ENERGETICS AND SPREAD-WINGED BEHAVIOR OF ANHINGAS IN FLORIDA

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ABSTRACT.—Metabolic rates and body temperatures of four captive Anhingas (*Anhinga anhinga*) were measured over a range of ambient temperatures. In addition, Anhingas were observed in the field in an attempt to correlate the frequency of behaviors, such as wing-spreading, with environmental conditions, such as the intensity of solar radiation and ambient temperature. Anhingas have low basal metabolic rates and high thermal conductances for their mass. The frequency of spread-winged behavior increases at higher solar intensities and is inversely correlated with ambient temperature. Anhingas assuming spread-winged postures orient with their backs to the sun, maximizing the surface area exposed to insolation and maintaining an angle of incidence of approximately 90°. In contrast, birds engaged in gular flutter face into the sun, thereby minimizing the surface area exposed to insolation and increasing the angle of incidence. Anhingas spread their wings to dry the plumage and to absorb solar energy during cool weather. They thereby supplement their low metabolic rates, compensate for their high thermal conductances, and replace heat lost via evaporation and convection due to wetting of the plumage.

Although spread-winged behavior is well known in darters, its function is not established (Clark 1969, Kennedy 1969). Suggested functions include the synthesis of vitamin D (Kennedy 1968, 1969); the removal of ectoparasites (Kennedy 1969); skin conditioning during molt (Potter and Hauser 1974); feather maintenance (Kahl 1971); wing-drying (Rijke 1968, Siegfried et al. 1975, Berry 1976); and thermoregulation (Heath 1962, Clark 1969, Kennedy 1969). The wing-drying hypothesis is especially attractive because Casler (1973) and Rijke (1968) found that these birds possess wettable plumage, which allows water to penetrate the air spaces next to the skin. This reduces their buoyancy and facilitates underwater stalking of prey.

I examined the metabolism of Anhingas (*Anhinga anhinga*) in the laboratory, and their behavior in the field, to determine if the birds use spread-winged behavior in drying the wings or in thermoregulation.

METHODS

I hand-raised four Anhingas (two adult females with an average weight of 1.12 kg; two juvenile females averaging 0.93 kg), housed them in an outdoor aviary in which they were exposed and became acclimated to weather conditions of Gainesville, Florida, and maintained them on a diet of whole smelt and minnows. I measured temperature-specific rates of metabolism for each individual over a range of ambient temperatures (0 to 40°C) in an open flow system employing a Beckman G2 or Applied Electrochemistry S-3A oxygen analyzer. Measurements were made in a constant-temperature chamber with a volume of 326 l, through which air flowed at rates of 4.4 to 6.8 l/min. (Flow rates were measured with a Brooks R215-B rotameter after the removal of CO_2 and water; all values were corrected to STPD.) I measured metabolic rates when the subjects were in a postabsorptive state between the hours of 09:00 and 18:00 during fall, 1979. Metabolic runs were terminated only after steady state conditions had been reached (Christensen 1947, Heusner 1955). I monitored the birds' deep body temperatures during metabolic measurements using Mini-mitters (Mini-mitter Co., Indianapolis, IN): miniature, temperature-sensitive, AM radio transmitters, which were coated with beeswax and fed to the subjects. I also measured cloacal temperatures after each metabolic trial using a Schultheis thermometer. Both methods of measuring body temperature yielded statistically similar results and data obtained by the two methods are used interchangeably throughout the text.

Mean basal rates of metabolism were estimated from independent measurements of the minimal rate of oxygen consumption within the region of thermoneutrality. At temperatures below thermoneutrality, I estimated minimal thermal conductances (C_m) for each bird from the relationship $C_m = M/(T_b - T_a)$ using simultaneous measurements of its metabolic rate (M), body temperature (T_b), and ambient temperature (T_a). I then compared measured values for mean basal metabolic rate (M_b) with the value expected from body mass

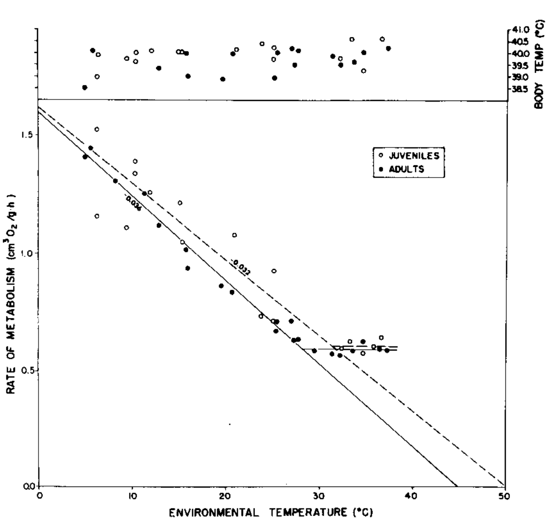

FIGURE 1. The relationship of metabolic rate and body temperature of four Anhingas to environmental temperature. Measurements were made during daylight hours in fall, 1979. Each symbol represents one measurement for one individual. The dashed line describes the relationship for juveniles, the solid for adults. The number above each line is its slope.

(W) for a nonpasserine in the active phase of its diurnal cycle, using the equation of Aschoff and Pohl (1970) $M_b = 5.14\ W^{-0.27}$ in which M_b is in $cm^3\ O_2/g \cdot h$ and W is in g. I also compared the mean measured values of C_m with the value predicted for a bird of this body mass using the equation of Lasiewski et al. (1967) $C'/W = 0.85\ W^{-0.51}$ in which C′ is "wet thermal conductance" in $cm^3\ O_2/g \cdot h \cdot °C$ (McNab 1974); W is in g.

I watched the activities of a resident population of 10–15 Anhingas at Lake Alice in Gainesville. Observations were made at all times of the day and in all seasons during 1978 and 1979. At 5-min intervals I recorded (1) the amount of time that each bird under observation spent in such activities as wing-spreading, preening, foraging, and gular flutter, (2) the orientation of each individual with respect to sun and wind, (3) ambient (shade) temperature, and (4) the intensity of solar radiation measured with an Epply PSP radiometer. The behavior recorded at the end of each 5-min period was considered one observation of that behavior. If the individual under observation behaved in more than one way during the 5-min period, I recorded the fraction of time devoted to each action. I then calculated the frequency of each behavior in percent, i.e., (no. of observations of the behavior)/(total no. of observations) × 100, under each specific set of environmental conditions. For example, if I made 20 observations of Anhingas while the intensity of solar radiation was below 222 W/m^2 and T_a was between 0 and 5°C, and if birds were preening during two of them, then preening was considered to represent 10% of the behavior observed under those environmental conditions. I then examined these data for correlations between the frequency of certain behaviors and environmental conditions.

RESULTS

The relationship between the metabolic rates and body temperatures of adult and juvenile Anhingas and ambient temperature is presented in Figure 1. Basal metabolic rates, thermal conductances, and data concerning body temperature are listed in Table 1. Daytime T_b ranged from 38.5 to 42.0°C in both age groups. I did not see gular flutter during any of the metabolic trials. The slopes of the regression lines fitting the data presented in Figure 1 cannot be used as estimates of thermal conductance because they do not extrapolate to T_b. This suggests that Anhingas combine physical (i.e., postural and plumage adjustments) with chemical (i.e., metabolic) thermoregulation (McNab 1980).

At low T_a, both in the field and during metabolic trials, Anhingas commonly folded their necks in a tight S-shape and pressed them tightly against the upper body. Occasionally, birds laid the head and neck along the back and covered them with the wings. Both postures should reduce thermal conductance by reducing surface area and I, therefore, labelled them *heat conserving postures* (Table 2).

My field observations are summarized in

TABLE 1. Thermoregulation in adult and juvenile Anhingas.*

	M_b ($cm^3O_2/g \cdot h$)	M_b as a percent of predicted M_b**	T_b (°C)	T_{lc} (°C)	C_m ($cm^3O_2/g \cdot h \cdot °C$)	C_m as a percent of predicted C_m***
Adults	0.59	77	39.1	28.0	0.0446	190
Juveniles	0.60	74	39.9	32.0	0.0401	177
Combined	0.59	76	39.8	29.5	0.0454	184

* M_b = basal metabolic rate, T_b = body temperature, T_{lc} = lower critical temperature, C_m = minimal thermal conductance.
** M_b predicted by the equation of Aschoff and Pohl (1970).
*** C_m predicted by the equation of Lasiewski et al. (1967).

Table 2. Behavior in general, and wing-spreading in particular, was highly dependent on weather. Anhingas assumed spread-winged postures much more frequently during cool than during warm weather. The frequency of this behavior was negatively correlated with T_a (Fig. 2, $r = -0.85$, $P < 0.01$, 9 df), but positively influenced by the intensity of solar radiation (Table 2). When the intensity was less than 222 W/m^2 (cloudy days with mostly diffuse radiation), wing-spreading constituted only 3.8% of the observed behavior, but it accounted for 47.1% of the latter when intensity exceeded 222 W/m^2 ($T_a < 30$°C in both cases, $P < 0.001$, test for the equality of two percentages, Sokal and Rohlf 1969). When solar radiation was low (e.g., during early evening), birds just emerging from the water often fanned their wings and tail continuously (*fan drying,* Table 2) rather than hold them steady (as was usually the case).

Thirty-four percent of the observed wing-spreading involved birds that appeared to be wet, 49% involved individuals that appeared to be dry, and 17% involved individuals whose plumage condition could not be determined. Wet birds usually held their wings completely outstretched, whereas dry individuals often held them closer to the body or occasionally drooped at their sides. During such behavior Anhingas commonly held their wings and body perpendicular to the incident sunlight, flattening out when the sun was high, standing erect when the sun was low. Most birds spreading their wings also oriented with their backs to the sun: in only 16 or 3.4% of 468 observations did they orient differently. In these 16 cases, all of the birds had wet plumage, most (14/16) were facing into the wind, and most (14/16) were noted when the intensity of solar radiation was less than 222 W/m^2. The frequency with which Anhingas oriented with backs to the sun was also negatively correlated with T_a (Fig. 2; $r = -0.83$, $P < 0.01$, 9 df).

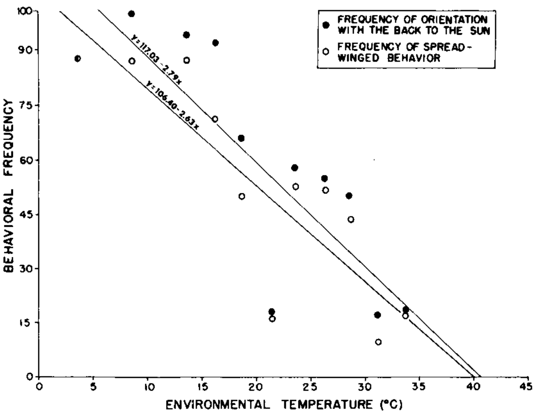

FIGURE 2. Frequency with which Anhingas orient away from the sun and exhibit spread-winged behavior as a function of environmental temperature. The behavioral frequency (ordinate) is the percent of the bird's total behavior devoted to orienting away from the sun or spreading its wings within a specific range of temperatures (abscissa). Each symbol represents the mean of at least 30 observations. The upper line describes the frequency of orientation away from the sun; the lower line the frequency of spread-winged behavior. The equation above each line describes the relationship. The half-filled symbol indicates that the frequencies of both behaviors were identical.

Anhingas oriented differently while heat-stressed (gular fluttering), facing into the sun 53% of the time, obliquely (side to the sun) 36% of the time, and away from the sun only 11% of the time (55 observations). This orientation is statistically nonrandom ($\chi^2 = 43.12$, $P < 0.001$, 2 df). Gular flutter occurred when T_a was between 25 and 30°C, but only when the intensity of solar radiation exceeded 700 W/m^2. All other observations of gular flutter occurred when T_a was above 30°C. It was significantly more common in bright sunlight, being 5.6% of the observed behavior when radiation was less than 222 W/m^2 as compared to 23.8% of the behavior when it exceeded 222 W/m^2 ($T_a > 30$°C; test for the equality of two percentages, $P < 0.01$). Gular flutter was

TABLE 2. Frequencies for the behavior of Anhingas under various environmental conditions.

Environmental conditions		Frequency of behaviors (%)[a]								
Solar radiation (W/m^2)	T_a (°C)	Total number of observations	Sunning[b]	Sunning and preening[c]	Preening	Perching	Using gular flutter	Swimming	Using heat conserving postures	Fan drying
>222	<30	860	40.8*	6.3	9.7	22.1	2.6	16.9	1.6	0.0
<222	<30	387	1.6	2.2	13.0	43.6	0.0	5.4*	31.8*	2.5*
>222	>30	111	8.8	0.0	17.1	32.0	23.8*	18.2	0.0	0.0
<222	>30	25	10.0	0.0	28.0	39.5	5.6	16.9	0.0	0.0
		1,383	26.5	4.6	11.8	29.1	3.5	14.0	9.4	1.1

[a] Behavioral frequency refers to the incidence of a specific behavior expressed as a percentage of the total number of behavioral observations (see text for further explanation).
[b] *Sunning* refers to spread-winged behavior in the absence of preening.
[c] *Sunning and preening* refers to spread-winged behavior accompanied by preening.
* Significantly different ($P < 0.05$) from the other percentages in the column (test for the equality of two percentages, Sokal and Rohlf 1969).

never accompanied by wing-spreading. Orientation during gular flutter (predominately facing the sun) was similar to that during exposure to strong winds in which individuals usually faced into the wind, thereby exposing a minimum of surface.

Anhingas spent only 14.0% of the time foraging in the water during the study. Most of their time (more than 80% of the total observations) was spent perching (preening, sunning, or just sitting). They spent significantly less time in the water when T_a was below 25°C (9.8% of 783 total observations) than when it exceeded 25°C (18.8% of 600 total observations, test for the equality of two percentages, $P < 0.001$).

After leaving the water, Anhingas shook excess water from their plumage and almost invariably spread their wings. However, they also spread their wings before entering the water (with dry plumage). Seventy-one percent of all trips to the water, and 90% of all such trips when solar radiation exceeded 222 W/m^2, was preceded by wing-spreading. This value increased to 94% when considering only those occasions when T_a was below 30°C and solar radiation exceeded 222 W/m^2.

DISCUSSION

My observations indicate that Anhingas are highly effective predators, often capturing three to five fish in a period of 5 to 10 min. This may explain why most of their time is devoted to activities other than foraging. Anhingas, therefore, can be considered as "time minimizers" with respect to feeding habits (Schoener 1971). Their reduced buoyancy, due to water-absorbing plumage, may improve their efficiency as underwater predators by allowing them to remain relatively motionless underwater. However, the temporary increase in thermal conductance that must result from having a layer of water adjacent the skin must subject them to thermoregulatory stress, especially on cold days (Mahoney, in press; Hennemann, pers. observ.), a predicament similar to that suffered by land birds exposed to heavy rains (Kennedy 1970). This too may explain why Anhingas spend so little time in the water, especially during cool weather. Considering the high rates of heat loss that must occur in individuals with water-saturated plumage, it would be energetically advantageous for Anhingas to dry as quickly as possible after foraging, thereby re-establishing a layer of air next to the skin. Wing-spreading may be a behavioral adaptation to this end. Such a function is suggested by the appearance of this behavior in wet birds on overcast days, and by their fan-drying behavior, which almost certainly dries the plumage rapidly when sunlight is unavailable. Anhingas often expose the skin during wing-spreading by erecting wing and back feathers, especially while wet. Rapid drying should be facilitated by a combination of feather erection, the black feather pigmentation, and exposure of the maximum surface area to the sun via wing extension and orientation. Although the remiges may not adsorb water to the extent of the breast feathers studied by Casler (1973) and Rijke (1968), the wing coverts may be wettable and it may be these which a bird is attempting to dry by fanning when the sky is overcast. Although the wings appear water laden when birds leave the water, the contention that Anhingas must dry their plumage before they can fly (McAtee and Stoddard 1945) is not supported by my observations of birds flying, albeit weakly, from the water's surface. This suggests that wing-drying serves primarily as an adaptation to conserve metabolic heat.

Other data suggest that spread-winged behavior also has an overlapping thermoregulatory function:

(1) Dry Anhingas spread their wings more often than do wet birds.

(2) The frequency of this behavior was inversely correlated with T_a and might comprise as much as 88% of the behaviors observed when T_a was less than 10°C (Fig. 2). In contrast, the frequency was only 15% at temperatures above 30°C.

(3) Anhingas are jet black on the back and wings. Dark plumage may absorb more solar radiation than pale (Hamilton and Heppner 1967, Lustick 1969) depending on the wind speed (Walsberg et al. 1978) and the angle of incidence (Lustick 1980). That Anhingas normally gain heat by means of insolation is obvious because gular flutter appeared in free-living birds when T_a was between 25 and 27.5°C and the intensity of solar radiation was moderate, but did not appear in my captive birds even when chamber temperatures exceeded 37°C.

(4) Most birds oriented away from the sun (and perpendicular to the incident radiation) while spreading their wings, but faced the sun during heat stress (gular flutter). Orienting perpendicular to incident radiation would enable Anhingas to take full advantage of the heat absorbing qualities of the black plumage by increasing the surface exposed to the sun and by optimizing the angle of incidence (Lustick 1980). Orienting toward the sun would reduce the amount of surface exposed to it, as demonstrated for Herring Gulls (*Larus argentatus*; Lustick et al. 1978), and maximize the angle of incidence, making the birds effectively

white with respect to the absorption of radiant energy (Lustick 1980).

(5) Anhingas have a high C_m in air (177–190% of that predicted for a nonpasserine of their mass; Table 1) and this increases when they are wet. This high rate of heat loss could be offset by the absorption of radiant energy during insolation.

(6) Anhingas also have a low M_b (74–77% of that predicted for a nonpasserine of their mass; Table 1), which may reduce heat stress in summer, but may be maladaptive in cool or wet weather.

(7) Anhingas spread their wings before entering the water. This may enable them to store heat passively to offset the high thermal conductance associated with wetting.

(8) Anhingas have a high lower critical temperature (Table 1, Fig. 1) and probably encounter temperatures below thermoneutrality for most of the winter in northern Florida. Consequently, they may have difficulty making up heat losses via metabolism and balancing their energy budgets in many parts of their winter range.

That birds can take advantage of solar radiation to reduce the metabolic costs of endothermy is well documented (Morton 1967; Heppner 1969, 1970; Lustick 1969, 1971; Ohmart and Lasiewski 1971; De Jong 1976). The high C_m and wettable plumage of Anhingas may cause thermoregulatory problems during cool or wet periods, but may be beneficial in preventing heat stress during tropical summers. The spread-winged posture offers a metabolically inexpensive, behavioral means of reducing heat loss (thermal conductance). In Gainesville, Anhingas are near the northern limit of their winter range (Palmer 1962). The data on M_b and C_m presented here (Fig. 1) suggest that *Anhinga* is poorly adapted to cool climates and may explain why it only occurs in tropical and subtropical areas. Spread-winged behavior may be an essential adaptation in balancing the energy budgets of these birds, supplementing metabolic energy with insolation, compensating for heat lost via evaporation and convection due to the wetting of the plumage, and reducing daily energy requirements so that less time need be spent foraging (i.e., wet).

Wing-spreading of Anhingas is not a mechanism for "dumping heat" since it never accompanies gular flutter. In addition, spread-winged sunning in Anhingas is not simply a means for realigning the feathers after soaring as proposed for vultures and other soaring birds by Houston (1980). Although Anhingas occasionally soar, they maintain spread-winged postures for much longer periods than would be required for this purpose, and the appearance of wing-spreading is not in any way associated with soaring.

Although wing-spreading apparently has both thermoregulatory and wing-drying functions in Anhingas, it may have different functions in other birds. (The use of such behavior for thermoregulation in Anhingas may be an evolutionary result of the development of water adsorbing plumage as a foraging aid.) Cormorants also have plumage that holds water, but only the distal portions of their feathers are wettable, and they consequently maintain a layer of air next to the skin while foraging (Casler 1973). This difference in feather structure affords cormorants greater insulation while immersed and may explain why they appear to spend more time in the water than do Anhingas. This, plus data on the Cape Cormorant (*Phalacrocorax capensis*; Siegfried et al. 1975) on four species of South African cormorants (*P. capensis, P. neglectus, P. lucidus,* and *P. africanus*; Berry 1976), and my personal observations of the Double-crested Cormorant (*P. auritus*), all of which indicate that cormorants orient into the wind when they assume spread-winged postures, suggest that such behavior functions only in drying the wings.

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LITERATURE CITED

Aschoff, J., and H. Pohl. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. J. Ornithol. 111:38–47.

Berry, H. H. 1976. Physiological and behavioral ecology of the Cape Cormorant *Phalacrocorax capensis.* Madoqua 9:5–55.

Casler, C. L. 1973. The air-sac systems and buoyancy of the Anhinga and Double-crested Cormorant. Auk 90:324–340.

Christensen, B. G. 1947. A simple apparatus for simultaneous measurement of the standard metabolism and the respiratory quotient in small laboratory animals, supplemented with investigations on normal and hypophysectomised rats. Acta Physiol. Scand. 12:11–16.

Clark, G. A., Jr. 1969. Spread-wing postures in Pelecaniformes, Ciconiiformes, and Falconiformes. Auk 86:136–139.

De Jong, A. A. 1976. The influence of simulated solar radiation on the metabolic rate of White-crowned Sparrows. Condor 78:174–179.

Hamilton, W. J., III, and F. Heppner. 1967. Radiant solar energy and the function of black homeotherm pigmentation: an hypothesis. Science 155:196–197.

Heath, J. E. 1962. Temperature fluctuation in the Turkey Vulture. Condor 64:234–235.

HEPPNER, F. H. 1969. Bird feathers and radiation. Science 164:202.

HEPPNER, F. H. 1970. The metabolic significance of differential absorption of radiant energy by black and white birds. Condor 72:50–59.

HEUSNER, A. 1955. Technique de mésure de courte durée de la consommation d'oxygène et de l'activité du rat. Etude du circuit de Benedict. C. R. Soc. Biol. Paris 149:2254–2257.

HOUSTON, D. C. 1980. A possible function of sunning behavior by Griffon Vultures, *Gyps* spp., and other large soaring birds. Ibis 122:366–369.

KAHL, M. P. 1971. Spread-wing postures and their possible functions in the Ciconiidae. Auk 88:715–722.

KENNEDY, R. J. 1968. The role of sunbathing in birds. Br. Birds 61:320–322.

KENNEDY, R. J. 1969. Sunbathing behavior of birds. Br. Birds 62:249–258.

KENNEDY, R. J. 1970. Direct effects of rain on birds; a review. Br. Birds 63:401–414.

LASIEWSKI, R. C., W. W. WEATHERS, AND M. H. BERNSTEIN. 1967. Physiological responses of the Giant Hummingbird, *Patagona gigas*. Comp. Biochem. Physiol. 23:797–813.

LUSTICK, S. 1969. Bird energetics: effects of artificial radiation. Science 163:387–390.

LUSTICK, S. 1971. Plumage color and energetics. Condor 73:121–122.

LUSTICK, S. 1980. Interaction between posture, color and the radiative heat load in birds. Science 208: 1052–1053.

LUSTICK, S., B. BATTERSBY, AND M. KELTY. 1978. Behavioral thermoregulation: orientation toward the sun in Herring Gulls. Science 200:81–82.

MAHONEY, S. Thermal energetics of Anhingas and Double-crested Cormorants. *In* Proceedings of South African Seabird Symposium. Capetown Univ., Capetown. In press.

MCATEE, W. C., AND H. L. STODDARD. 1945. Wettable water birds. Auk 62:303–304.

MCNAB, B. K. 1974. The energetics of endotherms. Ohio J. Sci. 74:370–380.

MCNAB, B. K. 1980. On estimating thermal conductance in endotherms. Physiol. Zool. 53:145–156.

MORTON, M. L. 1967. The effects of insolation on the diurnal feeding patterns of the White-crowned Sparrows (*Zonotrichia leucophrys gambelii*). Ecology 48:690–694.

OHMART, R. D., AND R. C. LASIEWSKI. 1971. Roadrunners: energy conservation by hypothermia and absorption of sunlight. Science 172:67–69.

PALMER, R. S. 1962. Handbook of North American birds. Vol. 1. Yale Univ. Press, New Haven, CT.

POTTER, E. F., AND D. C. HAUSER. 1974. Relationship of anting and sunbathing to molting in wild birds. Auk 91:537–563.

RIJKE, A. M. 1968. The water repellency and feather structure of cormorants, Phalacrocoracidae. J. Exp. Biol. 48:185–189.

SCHOENER, T. W. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369–404.

SIEGFRIED, W. R., A. J. WILLIAMS, P. G. H. FROST, AND J. B. KINAHAN. 1975. Plumage and ecology of cormorants. Zool. Afr. 10:183–192.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. Freeman, San Francisco.

WALSBERG, G. E., G. S. CAMPBELL, AND J. R. KING. 1978. Animal coat color and radiative heat gain: a re-evaluation. J. Comp. Physiol. 126:211–222.

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