

RESPONSES TO HIGH TEMPERATURE IN NESTLING DOUBLE-CRESTED AND PELAGIC CORMORANTS

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ADULT and nestling cormorants are often subject to overheating from insolation at the nest. Their generally dark plumage, exposed nest sites, and reradiation from surrounding rocks aggravate the thermal stress. Young nestlings must be shielded from the sun by their parents. Older nestlings and adults compensate for heat gain through behavioral adjustments and modulation of evaporative cooling by panting and gular fluttering.

This study was undertaken to examine some of the responses to high temperature in nestlings of two species of cormorants, the Double-crested Cormorant, *Phalacrocorax auritus*, and the Pelagic Cormorant, *P. pelagicus*. The evaporative cooling responses in birds have been studied in some detail in recent years (see Bartholomew et al., 1962; Lasiewski et al., 1966; Bartholomew et al., 1968; Calder and Schmidt-Nielsen, 1968, for more detailed discussions), although much still remains to be learned.

MATERIALS AND METHODS

The nestling cormorants used in this study (four *Phalacrocorax pelagicus* and four *P. auritus*) were captured from nests on rocky islands off the northwest coast of Washington. As their dates of hatching were not known it was impossible to provide exact ages. From comparisons of feather development with descriptions in the literature (Bent, 1922; Palmer, 1962), we judged that the *pelagicus* chicks were approximately 5, 5, 6, and 6 weeks old, while the *auritus* chicks were 3.5, 3.5, 4.5, and 6 weeks of age upon capture.

The nestlings were taken to the laboratories at Friday Harbor, Washington on the day of capture and housed in three 4' × 4' × 4' chicken wire cages. The cages were equipped with plywood platforms for the birds to sit on and covered on top and two sides to shield birds from wind and rain. The cormorants were fed whole and cut fish twice daily and the cages were washed after feedings. By the end of the first day in captivity, they learned to accept fish presented at the end of a stick and within 3 days after capture, all birds were eating fish thrown into cages.

The *auritus* weighed from 1,640 to 1,870 g upon capture and 4 weeks later weighed between 2,140 and 2,610 g. They were quite tame and easily handled, voracious, rarely fought over food, and showed little aggression towards the handlers. The *pelagicus* weighed from 750 to 1,180 g when captured. They remained nervous throughout, were extremely excitable, fought constantly over food, and were aggressive toward any person or object moving near them. Although we handled them rarely and they gained some weight, they did not adjust to captivity, and none survived more than 2 weeks.

Birds were exposed to controlled temperature conditions by placing them in a 9.5 ft³ incubator that could be regulated at a desired temperature $\pm 0.5^{\circ}\text{C}$. Humidity was maintained between 11–15 mm Hg water vapor pressure by drawing room air through the chamber at variable rates using a vacuum cleaner and variable trans-

former. Chamber humidity was monitored with a Hydrodynamics Universal Indicator used in conjunction with wide range humidity sensors (± 1.5 per cent RH).

A 30-gauge copper-constantan thermocouple was inserted at least 4 cm into the cloaca, and secured with two surgical clips to a retriex, and with dental wax to ventral body feathers caudad to the cloaca. We assume that cloacal temperature is equivalent to core body temperature (T_B). Ambient temperature (T_A) and T_B were monitored by attaching thermocouples to a Honeywell Elektronik 16 potentiometric recorder.

Temperatures of evaporating surfaces were obtained in two ways: 1) fine 40-gauge thermocouples were sewn into place so that the bimetallic junction rested on the surface, 2) a 30-gauge thermocouple was pressed to the surfaces of buccal and gular regions or wall of trachea, or inserted through an 18-gauge needle into the interclavicular air sac and then pressed against sac walls.

The chamber was lighted by a 15-watt incandescent bulb, and the bird was observed through a double glass port from a dimly lighted room. Breathing rates were timed with a stopwatch while gular flutter rates were determined with a Strobotac (General Radio Co.). All cloacal temperatures, breathing, and gular flutter rates reported were obtained from birds that had maintained a stable cloacal temperature ($\pm 0.1^\circ\text{C}$) for at least 15 minutes. All birds studied were presumably postabsorptive, as their last meal was no less than 14 hours prior to onset of experimentation.

RESULTS

Description of gular flutter.—When *P. auritus* are not heat stressed they usually have their mouths closed (Figure 1, pose 1) and breathe slowly (10–12/min). The hyoid is held in the floor of the buccal cavity in the same plane as the mandibles. The glottis is positioned between the two horns of the hyoid just anterior to the hinge of the jaw. Under these conditions the major sites of evaporation will be the buccal cavity and trachea, since without gular flutter little or no air movement occurs in the pharynx and esophagus posterior to the glottis.

When exposed to low heat loads Double-crested Cormorants open their mouths slightly and commence gular fluttering (Figure 1, pose 2). The glottis and hyoid are depressed 1–1.5 cm ventral to the lower line of the mandible and the hyoid is flared laterally. This creates an open chamber bounded by the buccal and pharyngeal surfaces and those of the anterior portion of the esophagus. The tidal air from respiratory movements passes over the buccal, pharyngeal, and tracheal surfaces. Independent from respiratory air movements, a rapid, repetitive bowing of the hyoid (10–11/sec) brings additional external air (plus some respiratory air) across the moist membranes of the mouth, pharynx, and esophagus. There may be some increase in respiratory rate during low heat loads, although we observed gular flutter in some birds that were breathing at resting levels.

When *auritus* are subjected to high heat loads, the hyoid is depressed 3.5–4.0 cm below the lower margin of the mandible and the glottis is located approximately one cm below the hyoid. This depression and flaring of the hyoid creates a considerably larger cavity than that found during low heat loads, expanding the buccal and pharyngeal areas as well

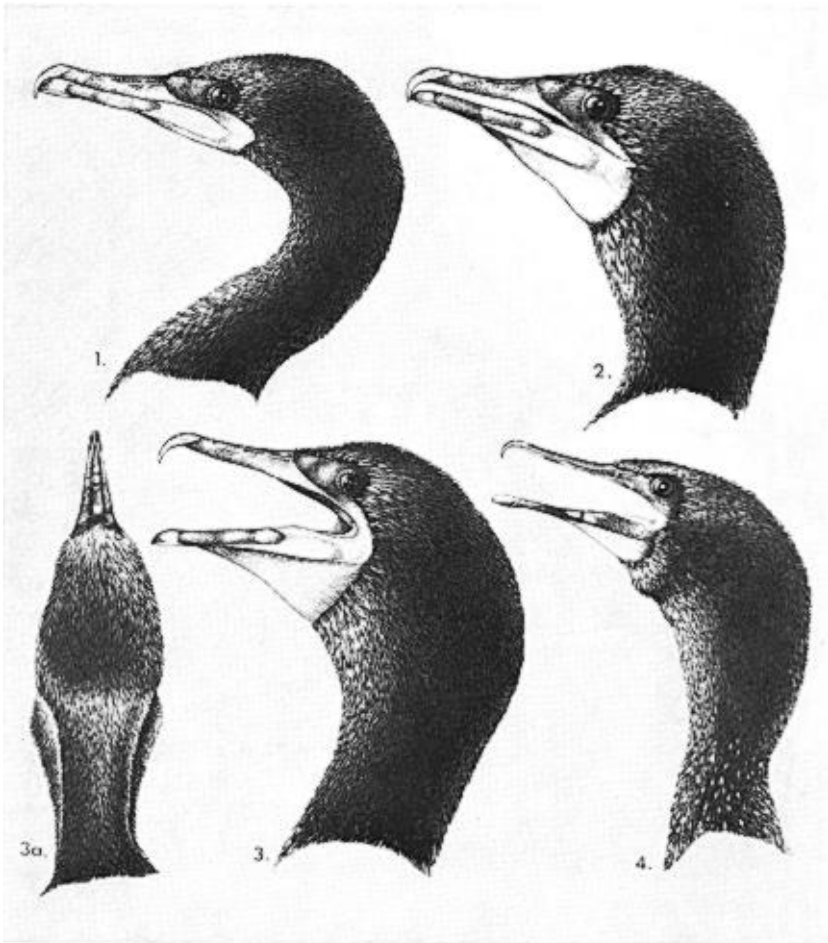


Figure 1. Typical attitudes assumed by cormorants subjected to different heat loads. Pose 1 shows a Double-crested Cormorant at rest and not heat stressed. Pose 2 represents a Double-crested Cormorant subjected to low heat loads soon after the onset of low amplitude gular flutter. Poses 3 and 3a illustrate Double-crested Cormorants, exposed to high heat loads, engaged in a maximal evaporative cooling effort. Pose 3a is a dorsoposterior view showing lateral flaring of hyoid and esophagus during high amplitude gular flutter. The Pelagic Cormorant in Pose 4 is subjected to high heat load, but the area moved by gular flutter is considerably less than that in Double-crested Cormorants.

as exposing a greater portion of the esophagus (Figure 1, poses 3, 3a). The hyoid movements (and resultant vibrations of esophageal membranes) move larger amounts of air across the moist surfaces than during lower heat loads even though gular flutter rate increases only slightly (see Figure

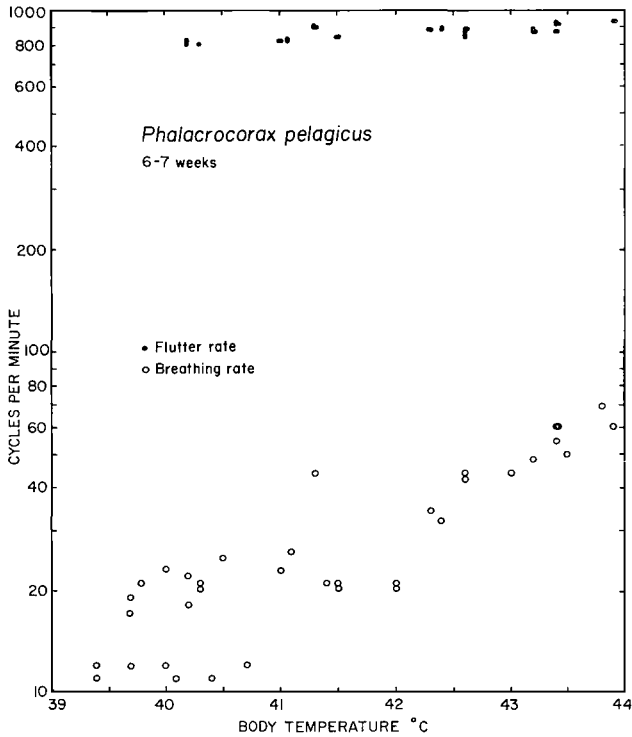


Figure 2. The relation of rates of gular flutter and breathing to body (cloacal) temperature in 6- to 7-week-old Pelagic Cormorant nestlings.

3). The amplitude of hyoid movement laterally is 1–1.5 cm, which moves the upper 15 cm of the esophagus (almost all of the thin-walled area of the esophagus). The rate of respiration increases with increasing body temperature (see Figures 2 and 3).

Qualitatively *pelagicus* behaved similarly to *auritus* at comparable temperatures, although the extent of the esophageal area fluttered and the amplitude of flutter were not as great even during maximum heat stress (Figure 1, pose 4).

Rates of gular flutter and breathing.—In nestlings of both species studied, the rates of gular flutter were relatively independent of heat stress and T_B , while breathing rates increased with T_B . Rates of gular flutter range from 790–920/min in *pelagicus* (Figure 2), and showed a slight increase with increasing T_B . Breathing rates of resting *pelagicus* nestlings were 11–12/min and increased with T_B , to 68 breaths/min at T_B of 43.8°C.

No differences were observed between 4.5- to 5.5- and 7.5- to 9-week-old *auritus* with respect to gular flutter or breathing rates. Gular flutter rates

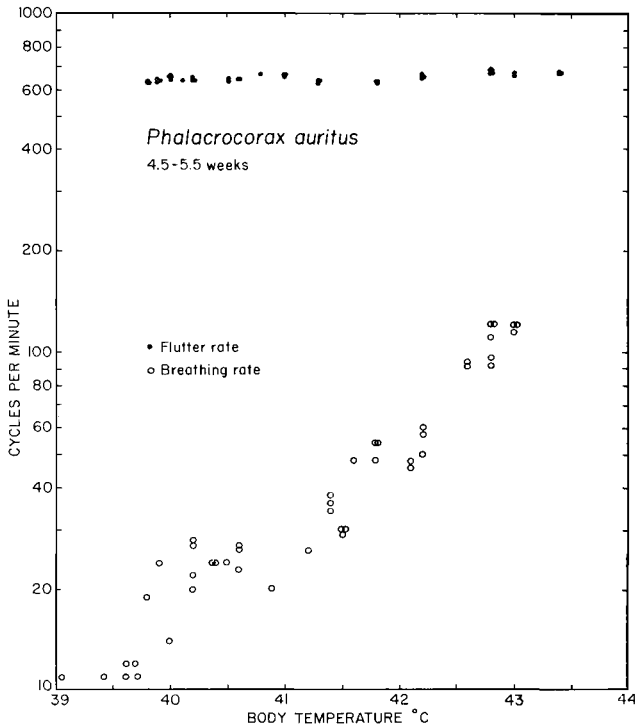


Figure 3. The relation of rates of gular flutter and breathing to body (cloacal) temperature in 4.5- to 5.5-week-old Double-crested Cormorant nestlings.

ranged from 615–677/min and increased slightly with T_B (Figure 3). Breathing rates varied from 11–12/min in the resting birds to 120/min when T_B reached 42.6°C.

Sites of evaporation.—When T_B equals T_A , there is no net gain or loss of heat via avenues of radiation, conduction and convection. If a bird is to maintain a constant T_B under such conditions, it must evaporate sufficient water to dissipate an amount of heat equivalent to the metabolic heat production. Sites of evaporation may have temperatures appreciably below that of the core T_B (making it possible to identify these areas). Measuring surface temperatures does not, however, permit quantification of evaporation since the temperatures attained by the evaporative surfaces will be influenced by rates of blood flow through the area as well as rates of evaporation. Figure 4 presents representative temperatures recorded from potential evaporative surfaces of two 6.5-week-old *auritus* nestlings with $T_A = T_B$. Surface temperatures of 0.9 to 5.1°C lower than T_B were recorded in buccal and pharyngeal regions, tracheal walls, and that portion

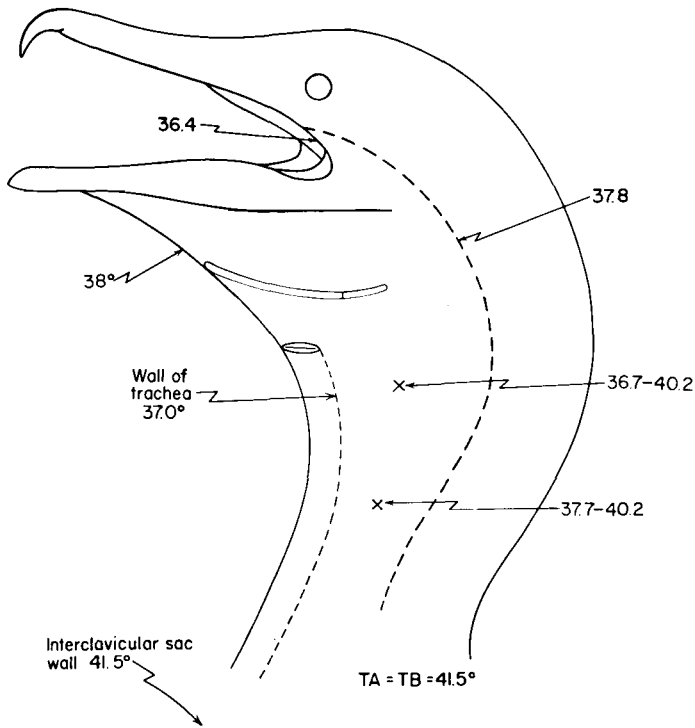


Figure 4. Representative evaporative surface temperatures from two 6.5-week-old Double-crested Cormorants. Ambient temperature was held at body temperature (41.5°C) during these measurements.

of the esophagus moved during gular flutter, implicating these areas as sites of evaporation. In these studies the interclavicular sac wall temperatures recorded did not differ from T_B .

Body temperatures.—Pelagic Cormorant nestlings 6–7 weeks old were unable to maintain constant body temperatures during heat stress as indicated by the fact that T_B was generally higher or equal to T_A over the range studied (Figure 5). It is uncertain whether the inability of these nestlings to regulate body temperature in the face of heat stress was due to their physiological characteristics or to the nervousness of individuals of this species, or both.

Nestling *auritus* were studied at two stages of development; 4.5 to 5.5 weeks and 7.5 to 9 weeks after hatching. Nestlings of both age classes maintained relatively constant T_B below T_A of 40°C (Figure 6). At T_A above 40°C , body temperatures of the 4.5- to 5.5-week-old chicks were near that of the environment although one bird was able to regulate

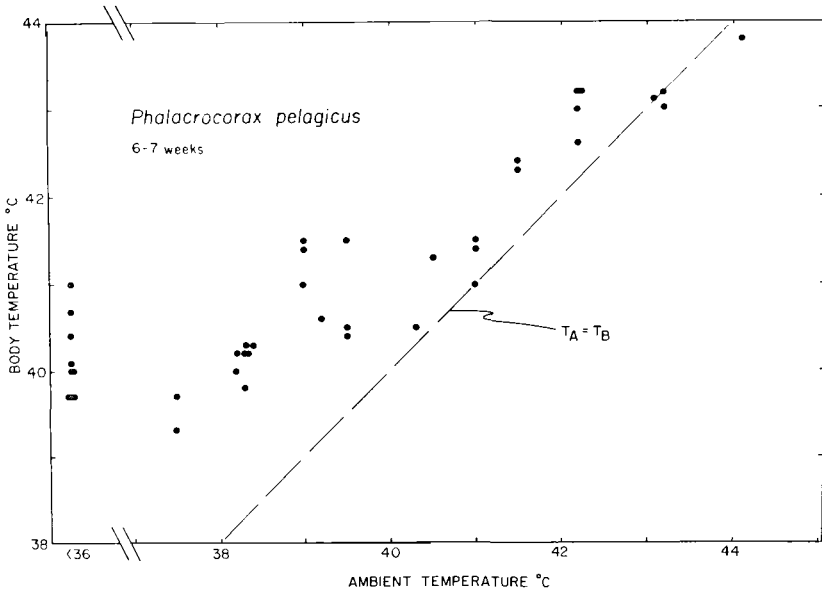


Figure 5. The relationship between body (cloacal) temperature and ambient temperature in 6- to 7-week-old Pelagic Cormorant nestlings. Water vapor pressure maintained between 11-15 mm Hg.

its T_B 1.0 to 1.8°C below T_A for almost 50 minutes. As the *auritus* nestlings grew and matured, they showed enhanced abilities to maintain T_B below high environmental temperatures (Figure 6). When, for example, one 9-week-old chick was exposed to a T_A of 45°C, it was able to maintain a T_B below 42°C for over 1 hour without any apparent stress.

DISCUSSION

Modulation of evaporative cooling.—Several patterns of evaporative cooling responses in birds have thus far emerged: panting alone, synchronized panting and gular flutter, and panting and gular flutter at different rates. Both cormorants we studied flutter at a high and relatively constant rate and pant at a slower rate that increases gradually with T_B . This pattern was established earlier in Pelecaniformes by Bartholomew et al. (1968) in the Double-crested Cormorant and Brown Pelican, *Pelecanus occidentalis*, and by Calder and Schmidt-Nielsen (1968) in the White Pelican, *Pelecanus erythrorhynchos*.

The occurrence of rates of gular flutter that are relatively independent of heat load have been described previously in the Common Nighthawk, *Chordeiles minor* (Lasiewski and Dawson, 1964), Poor-will, *Phalaenoptilus nuttallii* (Lasiewski and Bartholomew, 1966), Domestic Pigeon, *Columba*

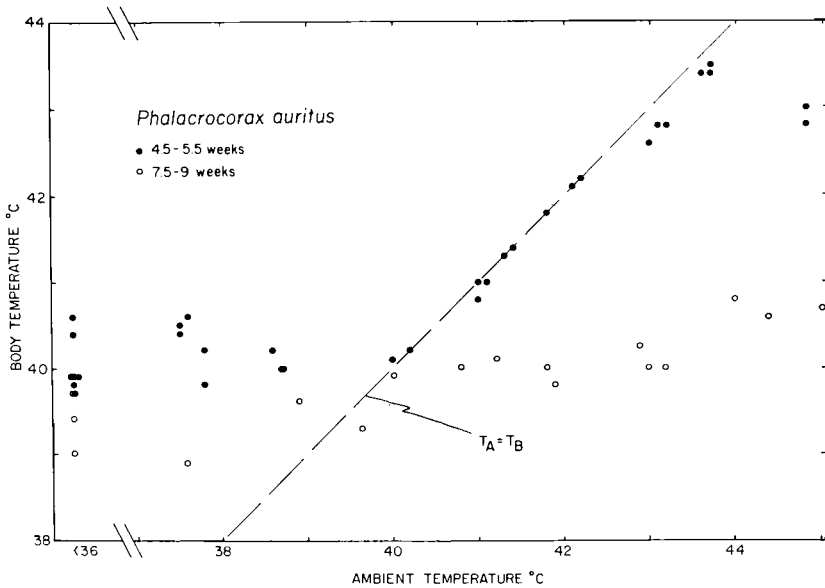


Figure 6. The relationship between body (cloacal) temperature and ambient temperature in two age classes of Double-crested Cormorant nestlings. Water vapor pressure maintained between 11–15 mm Hg.

livia (Calder and Schmidt-Nielsen, 1966), Roadrunner, *Geococcyx californianus* (Calder and Schmidt-Nielsen, 1967) and the Double-crested Cormorant, Brown Pelican, and Mourning Dove, *Zenaidura macroura* (Bartholomew et al., 1968). The relative independence of gular flutter frequencies from heat loads is presumably related to the fact that the gular regions are driven at their resonant frequencies thereby reducing the metabolic cost of evaporative cooling. Crawford (1962) demonstrated that dogs pant at the natural resonant frequencies of their thoracic cages and suggested that use of the natural frequency was advantageous in permitting evaporative cooling at a minimal metabolic cost.

Bartholomew et al. (1962), Lasiewski and Dawson (1964), MacMillen and Trost (1967), and Calder and Schmidt-Nielsen (1967) have documented the low energy cost of gular flutter. The muscles driving the hyoid during gular flutter are relatively small in comparison to the metabolically active mass of a bird, and we can assume, *a priori*, that the energy required for gular flutter is low in comparison to total metabolism. Furthermore, lowering and flaring of the hyoid in cormorants requires relaxation of some associated muscles, and this may partially offset the cost of gular flutter.

The cormorants we studied exhibited respiratory rates that increased

gradually with increasing T_B . This correlation is similar to that demonstrated in two species that pant, the House Sparrow, *Passer domesticus* (Kendeigh, 1944) and the Tawny Frogmouth, *Podargus strigoides* (Lasiewski and Bartholomew, 1966) as well as in several species that combine gular flutter and panting: the Domestic Fowl, *Gallus domesticus* (Frankel et al., 1962), the Brown Pelican and Double-crested Cormorant (Bartholomew et al., 1968), and the White Pelican (Calder and Schmidt-Nielsen, 1968). The pattern of a gradual increase in breathing rate contrasts with the more rapid shift to high panting frequencies found in dogs (Hemingway, 1938; Crawford, 1962), in Domestic Pigeons and Roadrunners (Calder and Schmidt-Nielsen, 1967), and in Ostriches, *Struthio camelus* (Crawford and Schmidt-Nielsen, 1967).

The resting rates of respiration in both species of cormorants were approximately 10–12/min, which compares favorably with breathing rates predicted for nonpasserine birds of this size by Calder (1968). Double-crested Cormorants had higher breathing rates at comparable hyperthermic body temperatures than did Pelagic Cormorants, which may partially explain their superior ability at thermoregulating under heat stress.

The gular flutter response permits evaporation from surfaces not normally exposed to the tidal air of respiratory movements (i.e. variable portions of the pharynx and esophagus). Evaporation from gular flutter in cormorants is modulated primarily by controlling the volumes of air moved per flutter. It is difficult at present to assess either the relative contributions of panting and gular flutter to evaporative cooling, or the relative metabolic costs of panting and gular flutter.

Sites of evaporation.—The importance of gular flutter and respiration as mechanisms of evaporative cooling in Double-crested and Pelagic Cormorants is corroborated by records of surface temperatures lower than cloacal temperatures (see Figure 4) in the buccal, pharyngeal, tracheal, and esophageal regions. Kallir (1930) demonstrated temperatures of evaporating surfaces in birds which were below T_B , as did Wilson et al. (1952). Hutchinson (1955) concluded that the temperatures of the evaporative surfaces of heat stressed Domestic Fowl must be 2 to 4° below that of the body. Lasiewski and Bartholomew (1966) demonstrated gular temperatures of 1.5 to 3°C lower than T_B during gular flutter in the Poor-will, and showed that as T_A increased, the gular surface temperatures decreased. Calder and Schmidt-Nielsen (1968) and Schmidt-Nielsen et al. (1969) recorded lower evaporative surface temperatures in the White Pelican and Ostrich, respectively. Measurements on the Ostrich revealed that the buccal and tracheal surfaces and possibly those of the postthoracic and interclavicular air sacs were important sites of evaporation. Our data on the cormorants did not reveal lowered temperatures on the

walls of the interclavicular air sac, although this cannot be used as evidence against the role of the air sacs in evaporative cooling in these birds.

Body temperatures.—In our studies, the *auritus* nestlings were better able to thermoregulate during heat stress than *pelagicus* nestlings. This specific difference is in part due to the larger size of *auritus* (and subsequent lower surface-to-volume ratio) and the greater amounts of air moved during flutter and panting, although we cannot evaluate the importance of the nervousness of the *pelagicus*.

Cormorant chicks are altricial at hatching and almost certainly show little capacity for thermoregulation. The 4.5- to 5.5-week-old *auritus* nestlings were near adult weights when studied, and yet showed limited thermoregulatory ability during heat stress. At this stage, the bodies of the nestlings were completely covered with down, although wing and tail feathers were developed. As they gained weight and replaced the body down feathers with juvenal plumage, the nestlings demonstrated enhanced physiological capacities to regulate T_B during heat stress. Bartholomew (1966) has shown the ontogenetic development of homeothermic capacities during heat stress in another Pelecaniform bird, the Masked Booby, *Sula dactylatra*.

The behavior of adult Pelecaniform birds in brooding and shielding their young from thermal stress is critical to the survival of younger nestlings. Occasionally young White Pelicans die from overheating without the attendant care of adults (Bartholomew et al., 1953). During periods of intense insolation, the reluctance of adult Brown Pelicans "to leave their young was very conspicuous" (Bartholomew and Dawson, 1954). Similar chick-adult responses have been noted in the Masked Booby (Bartholomew, 1966), and Double-crested Cormorant (Bent, 1922; Palmer, 1962). Advanced nestlings of many Pelecaniforms show considerable motility and may seek shade or enter the water to relieve heat stress.

Nestlings of both species of cormorants we studied show elevated body temperature (hyperthermia) when exposed to high ambient temperatures. This seems to be a general avian response to heat stress, i.e. almost all species of birds studied in this respect become hyperthermic. Hyperthermia during heat stress may be important in the conservation of water. When T_A exceeds T_B , birds must expend water for evaporation at a rate roughly proportional to heat gain. Hyperthermia reduces heat gain by reducing the thermal gradient between the body and environment, thereby lowering necessary evaporative water losses.

Our study suggests that when Double-crested and Pelagic Cormorant nestlings, taken from the same area, are exposed to heat stress, the Double-crested Cormorants exhibit superior thermoregulatory abilities. This finding is in accord with the following considerations. Double-crested

Cormorants are larger than Pelagic Cormorants and have a lower surface-to-volume ratio. Their anatomy and size permit exposure of a larger gular, pharyngeal, and esophageal surface for evaporative cooling and they pant at higher frequencies. Double-crested Cormorants have a more southern distribution and tend to feed closer to shore. Double-crested Cormorants generally nest in more exposed situations, while Pelagic Cormorants nest in remote or precipitous sites.

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SUMMARY

Double-crested and Pelagic Cormorant nestlings pant and gular flutter when heat stressed. Nestlings of both species gular flutter at high and relatively constant rates and pant at slower rates that increase gradually with body temperature. Gular flutter supplements respiratory evaporation. Evaporation during gular flutter in cormorants is modulated primarily by controlling the volume of air moved per flutter. Surface temperatures of 0.9 to 5.1°C lower than body temperature were recorded in buccal and pharyngeal regions, tracheal walls, and that portion of the esophagus moved during gular flutter, implicating these areas as important sites of evaporative cooling. Double-crested Cormorant nestlings are able to expose larger gular, pharyngeal, and esophageal surfaces for evaporation than Pelagic Cormorant nestlings, and show superior thermoregulatory ability during heat stress.

At ambient temperatures below 40°C, nestlings of both species maintained relatively constant body temperatures. At ambient temperatures above 40°C, Pelagic Cormorant nestlings 6 to 7 weeks old had body temperatures generally higher than or equal to ambient temperatures. When exposed to ambient temperatures above 40°C, 4.5- to 5.5-week-old Double-crested Cormorant nestlings had body temperatures equal to environmental temperatures, while 7.5- to 9-week-old nestlings of this species maintained relatively constant body temperatures.

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