# PATTERNS OF PANTING AND GULAR FLUTTER IN CORMORANTS, PELICANS, OWLS, AND DOVES

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Most birds pant when subjected to heat stress, but some supplement evaporation from the respiratory tract by fluttering the gular area. Gular flutter occurs in at least the following taxa: cormorants, pelicans, boobies, anhingas, frigate-birds, herons, owls, doves, roadrunners, colies, and many gallinaceous species.

The mechanics of gular flutter have been examined only in the Poor-will, *Phalaenoptilus nuttallii* (Lasiewski and Bartholomew 1966), but data on rates of gular flutter are available for a number of species, including the Common Nighthawk, *Chordeiles minor* (Lasiewski and Dawson 1964), Domestic Pigeon (*Columba livia* (Calder and Schmidt-Nielsen 1966), Bobwhite (*Colinus virginianus*), Gambel's and California Quail (*Lophortyx gambelii* and *L. californicus*), Painted Quail, *Excalfactoria chinensis*, Screech Owl, *Otus asio*, and Mourning Dove, *Zenaidura macroura* (Lasiewski *et al.* 1966b). The ability of birds that employ gular flutter to dissipate all of their metabolic heat through evaporation has been demonstrated in the Poor-will (Bartholomew *et al.* 1962), Common Nighthawk (Lasiewski and Dawson 1964), Domestic Pigeon (Calder and Schmidt-Nielsen 1966), Inca Dove, *Scardafella inca* (MacMillen and Trost 1967), and the Painted Quail (Lasiewski *et al.* 1966a).

In caprimulgids the rate of flutter is independent of heat load and appears to be determined by the resonant properties of the gular area, just as the panting rate of dogs is determined by the resonant properties of the thoraco-abdominal region (Crawford 1962).

The present study was undertaken to examine aspects of gular flutter and breathing in several birds of widely differing morphology and behavior. Through the cooperation of the staff of the San Diego Zoological Gardens, we were able to make measurements on a Double-crested Cormorant (*Phalacrocorax auritus*), a Brown Pelican (*Pelecanus occidentalis*), a Horned Owl (*Bubo virginianus*), and a Barn Owl (*Tyto alba*). Mourning doves (*Zenaidura macroura*) and a Horned Owl were studied on the Los Angeles Campus of the University of California.

## MATERIALS AND METHODS

The methods and instruments for controlling ambient temperatures ($T_A$), recording cloacal temperatures ($T_B$), restraining the birds, and making stroboscopic measurements of gular flutter rate were the same as those described in Lasiewski and Bartholomew (1966), modified as needed to accommodate birds of different sizes. Breathing rates of all species and the flutter rates of the Brown Pelican and Horned Owls were counted visually and timed with a stopwatch. Motion pictures of the responses to heat stress were taken of the owls, pelican, and cormorant to assist in analysis of gular movements. Heat load was imposed by holding the incubator temperatures at various levels between 30 and 48° C. Humidity was not controlled, but in all cases water-vapor pressure remained between 10.4 and 16.3 mm Hg as indicated by a Hygrodynamics Universal Humidity Indicator.

## RESULTS

Although the patterns of gular flutter differed in the various birds, certain common features were apparent in all species studied. (1) Under slight heat load, gular flutter was intermittent, of low amplitude, and involved only a small portion of the gular region. (2) As heat load increased, the amount of time occupied by gular flutter increased as did the gular area involved. (3) Under severe heat stress gular flutter was continuous, of large amplitude, and involved the greatest gular area.

When subjected to severe heat stress all species drooped the wings and held them away from the sides of the body. The pelican and cormorant also elevated the scapular feathers.
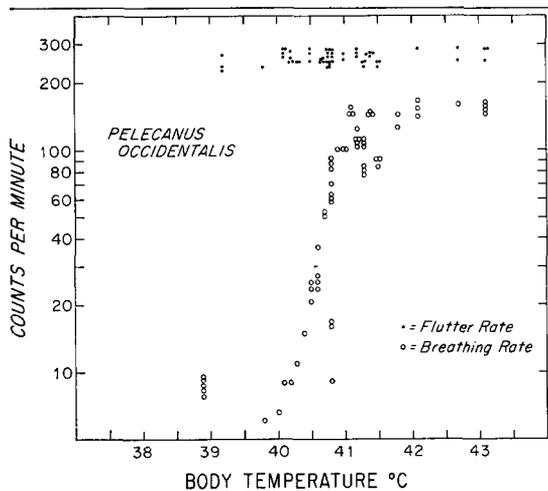
FIGURE 1. The relation of rates of gular flutter and breathing to body (cloacal) temperature in a Brown Pelican weighing 3.13 kilograms.

## BROWN PELICAN

The rate of gular flutter varied between 230 and 290 per minute and was independent of ambient temperature, body temperature, and breathing rate. The rate and amplitude of breathing increased with rising body temperature. The breathing rate increased tenfold between body temperatures of 40.2° and 41.0° with a continuous series of intermediate rates between the minimal and maximal values (fig. 1). Above $T_B$ of 41° breathing rate remained constant, but the amplitude of breathing movements increased markedly.

The fluttering of the gular area is driven by flexing movements of the hyoid apparatus that is suspended in the skin of the gular pouch. The horns of the hyoid lie below and behind the glottis and are connected anteriorly. Along each horn of the hyoid there is a slim, spirally arranged muscle, the contractions of which flex the horns and cause the gular skin to flutter. During gular flutter the mandibles are gaped slightly but remain motionless.

The inner lining of the gular pouch is normally moist, but after several hours of fluttering it became dry to the touch. The skin of the pouch is thin, translucent, and vascular. Under conditions of heat stress the blood vessels of the pouch are conspicuously engorged with blood. Flutter facilitates evaporative cooling from the moist internal surfaces of the gular pouch, and when external gular temperatures exceed ambient temperature it increases heat loss by forced convection.

After the pelican had maintained gular
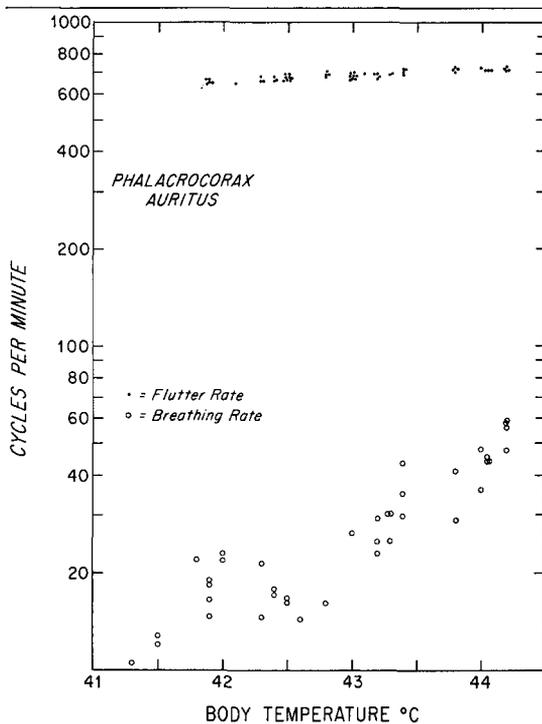


FIGURE 2. The relation of rates of gular flutter and breathing to body (cloacal) temperature in a Double-Crested Cormorant weighing 1.34 kilograms.

flutter continuously for several hours, its nasal gland began to secrete. This is circumstantial evidence that the fluttering and heavy breathing caused sufficient loss of water to increase the tonicity of the body fluids.

## DOUBLE-CRESTED CORMORANT

The rate of gular flutter varied from 645 to 730 per minute and was relatively constant over a wide range of ambient temperatures, body temperatures, and breathing rates. In the absence of heat stress, the breathing rate was about 15 per minute, and respiratory movements were barely visible. Rate and amplitude of breathing increased regularly and gradually with increasing body temperature (fig. 2).

Gular flutter in cormorants is driven by the hyoid, which is relatively larger than in pelicans. During flutter the gular region is lowered and the hyoid is flared laterally. Under severe heat stress the area fluttered extends at least 15 cm down the ventral and lateral surfaces of the neck, and includes feathered as well as unfeathered skin.

### MOURNING DOVE

The rate of gular flutter was independent of ambient temperature, and varied between 680
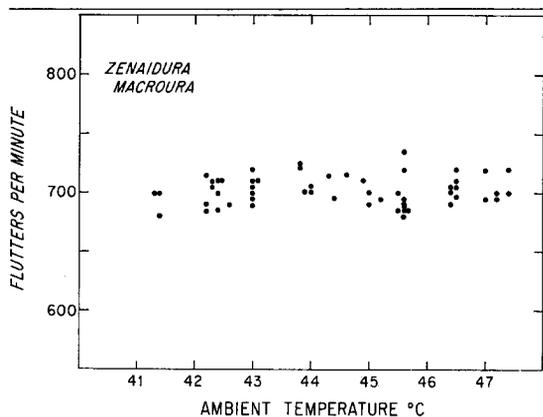
FIGURE 3. The relation of rate of gular flutter to ambient temperature in two Mourning Doves.

TABLE 1. Gular flutter rate, body temperature, and ambient temperature in a Horned Owl, *Bubo virginianus*.

| Ambient temp. °C | Body temp. °C | Mean flutter rate (counts/min.) |
|---|---|---|
| 31.0 | 39.8 | — |
| 36.4 | 39.6 | — |
| 38.6 | 39.8 | 210[a] |
| 40.2 | 40.2 | 240 |
| 42.4 | 40.5 | 240 |
| 44.2 | 40.9 | 240 |
| 47.6 | 41.6 | 255 |

[a] Intermittent flutter.

and 735 per minute in the two birds measured (fig. 3).

HORNED OWL

Flutter rate varied from 210 to 255 per minute and increased slightly with increasing heat load (table 1). The change in rate, however, was much less conspicuous than the change in amplitude and the increase in area fluttered.

The Horned Owls were effective in evaporative cooling. The bird that was subjected to a heavy heat load kept body temperature below ambient for over two hours even at ambient temperatures as high as 47.6° C. During flutter, the mandibles were gaped but remained almost motionless, while the tongue moved forward and back in synchrony with flutter.

We were unable to discern breathing movements when the owls were exposed to moderate heat stress. However, when $T_A$ exceeded $T_B$, breathing became clearly visible and was synchronous with gular flutter. Palpation of the abdomen and thorax showed that the entire visceral mass was moving at the same rate as the gular area. Under severe heat stress this species pants and flutters simultaneously and synchronously.

BARN OWL

The rate of flutter ranged between 245 and 285 per minute. When ambient temperature approached body temperature, the entire contents of thorax and abdomen moved strongly with each breath and were driven at the same rate as the gular flutter. The lower mandibles moved in synchrony with flutter.

DISCUSSION

The birds considered in the present study resemble the Common Nighthawk and the Poor-will in having gular flutter frequencies that are relatively independent of heat load. This independence is presumably related to the gular regions being driven at their resonant frequencies. The exploitation of the resonant characteristics of the gular areas should minimize the metabolic cost of evaporative cooling. The low energetic cost of gular fluttering has been documented in the Poor-will (Bartholomew et al. 1962) and the Common Nighthawk (Lasiewski and Dawson 1964), two caprimulgids that are particularly effective in heat dissipation through evaporation.

The comparative efficiencies of evaporative cooling in birds cannot be quantitatively evaluated at present, since the data available in the literature were obtained under a variety of conditions of humidity, and the ability of birds to dissipate heat through evaporation is markedly affected by the ambient water vapor pressure (Lasiewski et al. 1966a and b).

Gular flutter permits evaporation from areas that are not involved in respiratory ventilation, because it moves air across the moist mucosa of the buccal cavity and esophagus posterior to the glottis.

The synchronization of panting and gular fluttering under high heat load that we observed in the Horned Owl and the Barn Owl also occurs in the Domestic Pigeon (Calder and Schmidt-Nielsen 1966). Panting in these three species resembles that in dogs; the panting frequency seems to be related to the resonant characteristics of the thoraco-abdominal cavity and remains almost constant over a wide range of ambient temperatures.

Since the gular area has a small mass, relatively little energy is required to move it. Even in the absence of information on the physical properties of the gular and the thoraco-abdominal complexes, it is reasonable to suggest that the rate at which the two are synchronously driven is determined by the

thoraco-abdominal structures because of their relatively greater mass. In contrast to the owls and pigeon, cormorants, pelicans, and caprimulgids have relatively enlarged gular areas, and their rates of panting and gular flutter are markedly different and the two are asynchronous.

The breathing rates of the Brown Pelican during heavy panting are approximately ten times higher than resting values, although the two ranges are connected by a continuous series of intermediate rates. The transition from "low" to "high" breathing rates occurs over a narrow range of body temperatures, and the transition values would not be apparent if the rates had been measured at large and predetermined intervals of ambient temperature.

In contrast to the Brown Pelican, breathing rates in the Double-Crested Cormorant increased gradually with increasing heat load, as they do in the Domestic Fowl (Hutchinson 1955). In this respect, the cormorants resemble many birds that do not flutter, but gradually increase the rate and amplitude of ventilation in response to heat stress.

## SUMMARY

Responses of the Brown Pelican, Double-Crested Cormorant, Horned Owl, Barn Owl, and Mourning Dove to heat stress were studied. All five species employ both panting and gular flutter to enhance evaporative cooling, and the rates of flutter were relatively independent of heat load. In the owls panting and flutter were synchronous and occurred at the same rates. In the pelican and cormorant gular flutter and panting were asynchronous, and flutter was much more rapid than panting. In all five species the duration and amplitude of gular flutter increased with ambient temperature as did the extent of the gular region moved.

The independence of rate of gular flutter from heat load is probably related to exploitation of the resonant frequencies of the gular regions. We suggest that when flutter and panting are synchronous, the rate is determined by the resonant properties of the thoraco-abdominal region.

## ACKNOWLEDGMENTS

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