EVAPORATIVE COOLING IN THE POOR-WILL AND THE TAWNY FROGMOUTH

ROBERT C. LASIEWSKI and GEORGE A. BARTHOLOMEW

When ambient temperatures exceed body temperature most birds pant, and by increasing the rate and amplitude of their breathing they increase their rate of evaporative cooling. However, the energetic cost of panting is high in relation to the calories dissipated through evaporation, and most birds that pant are unable to keep their body temperatures from rising when exposed to heat stress. Birds of several orders supplement panting by holding the mouth open and rapidly fluttering the gular area. The energy required for this gular flutter is small in relation to the amount of water evaporated, and some birds that use gular flutter are able to maintain body temperature near 42°C for hours in environmental temperatures exceeding 47°C (Bartholomew et al., 1962; Lasiewski and Dawson, 1964). Gular fluttering has been reported in pelicans and herons (Bartholomew and Dawson, 1954a), doves (Bartholomew and Dawson, 1954b), boobies (Howell and Bartholomew, 1962), caprimulgids (Cowles and Dawson, 1951; Bartholomew et al., 1962; Lasiewski and Dawson, 1964), and it is known to occur in cormorants, owls, and the Roadrunner (Geococcyx californianus).

Although it has been shown that gular flutter offers an effective way for a bird to unload heat, little is known about the mechanism involved. The panting rate of dogs occurs at a frequency that is determined by the resonant characteristics of the thoracic region (Crawford, 1962). Dawson and Schmidt-Nielsen (1964) and Schmidt-Nielsen (1964) have suggested that the flutter rate in birds may occur at a resonant frequency fixed by the physical properties of the gular area. Lasiewski and Dawson (1964) have partly substantiated this suggestion by demonstrating that the rate of gular flutter in the Common Nighthawk (Chordeiles minor) is relatively independent of ambient temperature; independence of ambient temperature should be a characteristic of a biological system that has one frequency at which it is most easily driven.

The present study undertakes to elucidate some aspects of the mechanism of evaporative cooling in members of two families of the order Caprimulgiformes, the Poor-will, Phalaenoptilus nuttallii (Family Caprimulgidae), which flutters the gular area at high ambient temperatures, and the Tawny Frogmouth, Podargus strigoides (Family Podargidae), which pants when subjected to heat stress.

METHODS

The two Poor-wills used in this study were kept in good condition for many months on a diet of Tenebrio larvae, dried dog food, and newborn mice. They were periodically permitted to fly, and both vocalized regularly at night. One of the birds was taken at Malibu, California, and the other was captured near Stockton, California.

When gular flutter was to be studied, a Poor-will was placed in a cage made of wire mesh painted flat black and measuring 10 × 15 × 20 cm. This cage allowed the bird to move about and change its posture without letting it move out of the area of focus of the stroboscope and optical system described below. Experimental temperatures were maintained to within 0.2°C by an Aminco incubator. All temperatures were measured to the nearest 0.1°C with copper-constantan thermocouples used in conjunction with a multichannel recording potentiometer. Relative humidities were not controlled but in all cases remained between 27 and 41 per cent.

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The Poor-will was allowed to adjust to a given test temperature for 10 to 30 minutes before its rate of gular flutter was determined. Repeated measurements of flutter rate were made at each temperature with an electronic stroboscope (Strobotac, General Radio Co.) accurate to within 1 per cent. The flash duration over the range of frequencies used was 1.2 microseconds. The flashes of light were directed through one window of the darkened incubator, reflected onto the bird by a mirror, and observations were made through a second window. The rate of gular flutter was determined by varying the rate of flashing of the stroboscope until the motion of the gular area appeared to stop.

The extreme regularity of the gular flutter permitted us to slow down its apparent rate of movement at will by adjusting the stroboscope so that it was slightly out of phase with the frequency of flutter. Thus it was possible to observe the details of the movement of the gular area. We measured the amplitude of the flutter in relation to air temperature by placing a millimeter scale behind the bird and watching its gular area through a $3\times$ lens positioned in front of the holding cage. By aligning the eye of the observer, the optical axis of the lens, the gular area of the bird, and the millimeter scale, problems of parallax were minimized, and readily reproducible measurements of amplitude of movement were conveniently made.

The effects of changing the weight of the gular complex on the rate and amplitude of flutter were studied by fastening several No. 3 lead split shot to the shafts of the feathers immediately adjacent to the skin of the gular area and then using the techniques described above.

The relative amounts of time spent with mouth closed, mouth open but without gular flutter, and fluttering were recorded simultaneously with ambient and body temperature. A vinyl-sheathed 30-gauge copper-constantan thermocouple was inserted into the large intestine and secured in place by attaching the leads to the rectrices with surgical clips. The bird was allowed to equilibrate at the desired test temperature for 30 minutes in the incubator. Then, illuminated by a 25-watt incandescent bulb, it was observed continuously for a 30-minute period, and the intervals occupied by each of the three activities indicated above were recorded on a Sanborn 320 Oscillograph with three different outputs from a Grass SD5 stimulator.

Temperatures of the gular region were obtained by sewing a butt-welded 40-gauge Cu-Cn thermocouple through the floor of the mouth, and positioning the bimetallic junction at the midline between the base of the tongue and the glottis. The leads emerged ventrally through the gular region, one on each side about 5 mm from the midline. The wires were then looped up behind the head and secured to the feathers at the nape of the neck with sealing wax to prevent the thermocouple from being moved by changes in posture of the bird. The thermocouple leads were then soldered to 30-gauge duplex thermocouple wire connected to the recorder.

Heart rates were obtained by securing three gold-plated safety pins subcutaneously, one each in the right and left pectoral regions, and a third, as ground, on the right thigh. The leads from these electrodes were connected either to a Cambridge Versascribe Electrocardiograph or to a Honeywell Visicorder System, and the electrocardiograms during periods with flutter and without flutter were recorded. Breathing rates were determined visually and timed with a stop watch while the bird was maintained at desired environmental temperatures in the incubator. Observations and measurements were made from a darkened room, so that the birds received minimal visual stimuli from the experimenters or experimental procedures.

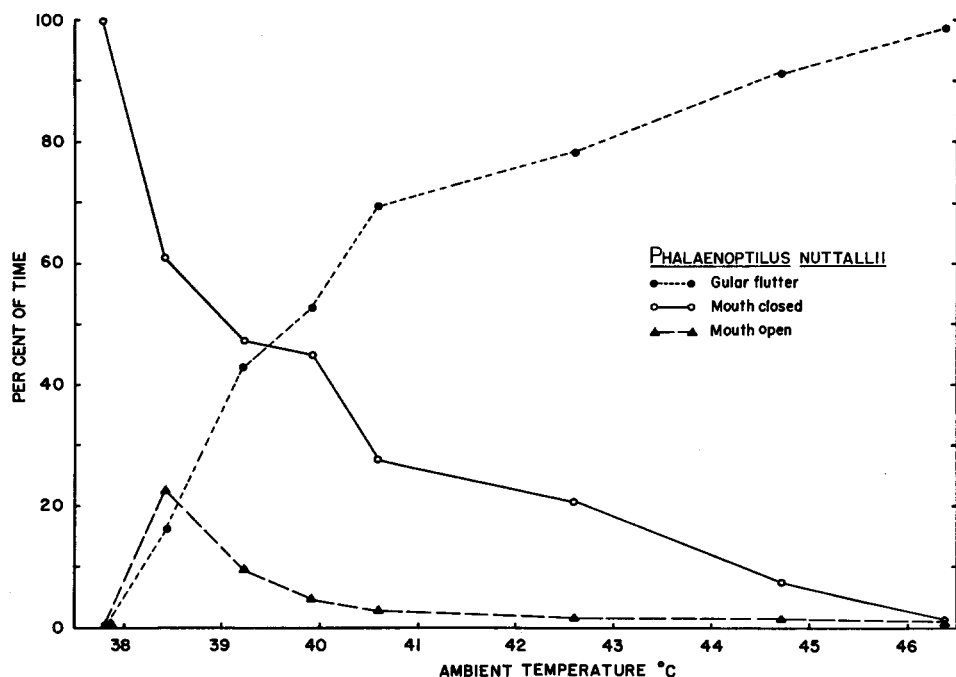We were able to obtain some measurements related to evaporative cooling from

Figure 1. The relationship between ambient temperature and the amount of time spent with mouth closed, mouth opened but without gular flutter, and with gular flutter in a Poor-will.

two Tawny Frogmouths with the help of K. C. Lint, Curator of Birds at the San Diego Zoo. The pair was captured in the Blue Mountains, New South Wales, Australia, in 1958, and had been maintained on a diet of mice in an outdoor aviary at the San Diego Zoo. Breathing rates at rest were determined visually with a stop watch from the birds sitting quietly in their aviary. To study the response to heat stress, the female, which weighed 675 g, was removed to a laboratory dark room and placed on a perch in a fiberglass cage closed on three sides and measuring approximately $60 \times 60 \times 60$ cm. Heat was applied to the cage and bird by a 250-watt infrared heat lamp and by a hot-air blower. Body temperatures during the heating were obtained without otherwise disturbing or handling the bird by slipping a vinyl-sheathed thermistor into the wide-open mouth and down the gullet, and reading the temperature on a YSI temperature indicator. Breathing rates were determined visually and timed with a stopwatch.

<div align="center">RESULTS</div>

Poor-will. At ambient temperatures (T_A) below 38°C, the Poor-will maintained a uniform body temperature without opening its mouth. When T_A was 38 to 39°C, the Poor-will was able to dissipate enough heat to maintain thermal equilibrium merely by opening the mouth and without gular flutter. When T_A exceeded 39°C, the birds employed gular flutter. The amount of time spent fluttering increased directly with temperature, while the amount of time with mouth closed, or with mouth open but without gular flutter, decreased (fig. 1). At environmental temperatures above 46.5°C, gular flutter was almost continuous and was interrupted only briefly and infrequently by yawning movements.
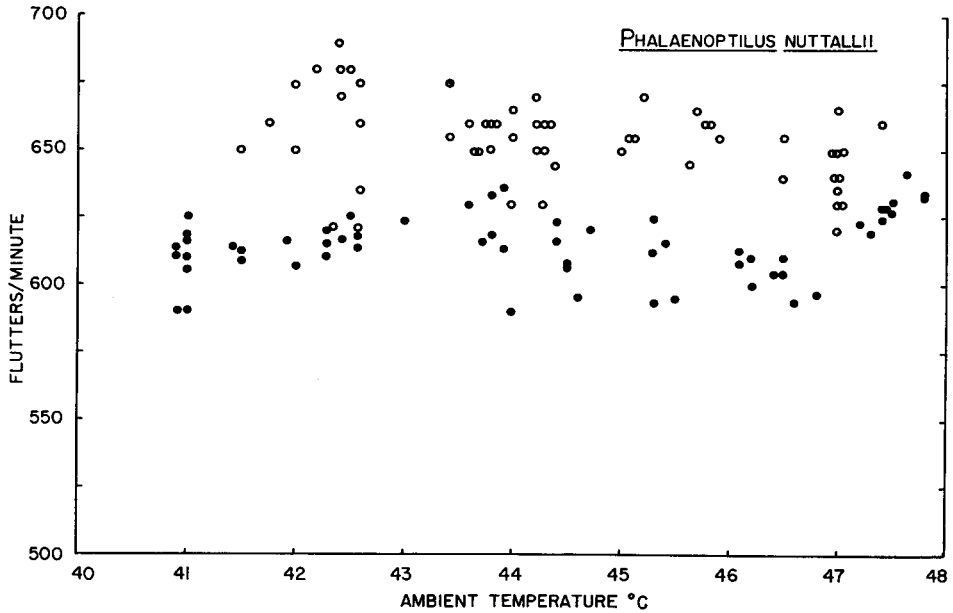
Figure 2. The frequency of gular flutter in the Poor-will in relation to ambient temperature. Values from bird captured at Malibu, California, are represented by shaded circles, while those obtained from Poor-will taken near Stockton, California, are indicated by unshaded circles.

Duration is only one of the characteristics of gular flutter that can be varied by birds in coping with different heat loads, and it is obvious that the rate of flutter and its extent and amplitude are important parameters which need to be considered. The rate of gular flutter in Poor-wills was independent of heat load; it remained constant over ambient temperatures extending from 40.9 to 47.8°C. Flutter rates were from 590 to 690 per minute, with values from one Poor-will generally higher than those of the other (fig. 2).

The horizontal amplitude, which is one measure of the extent of gular flutter, increases directly with environmental temperature (fig. 3). In addition to increased amplitude of the movement of the gular region, the total area of the gular region being fluttered also increased directly with temperature.

Weighting the gular region with either 3.1 or 3.6 g of lead shot did not change the basic frequency of the flutter, but did decrease its horizontal amplitude at any given temperature. More effort appeared to be required to drive the weighted gular area, since when the weights were added, the whole head moved during fluttering, while fluttering of the unweighted gular area rarely evoked such head movements.

Cloacal temperatures, ambient temperature, gular temperatures, and periods of fluttering were recorded simultaneously. As ambient temperature increased, the temperature of the gular surface decreased (fig. 4), presumably reflecting increased rates of evaporation of water. The gular temperature was from 1.5 to 3.0°C lower than the body (cloacal) temperature, substantiating the importance of the gular region as a site of heat loss. The temperature of the gular area was remarkably sensitive to gular flutter. Whenever the mouth was closed, the temperature of the gular area immediately increased. Within seconds after the onset of gular flutter, the temperature dropped.
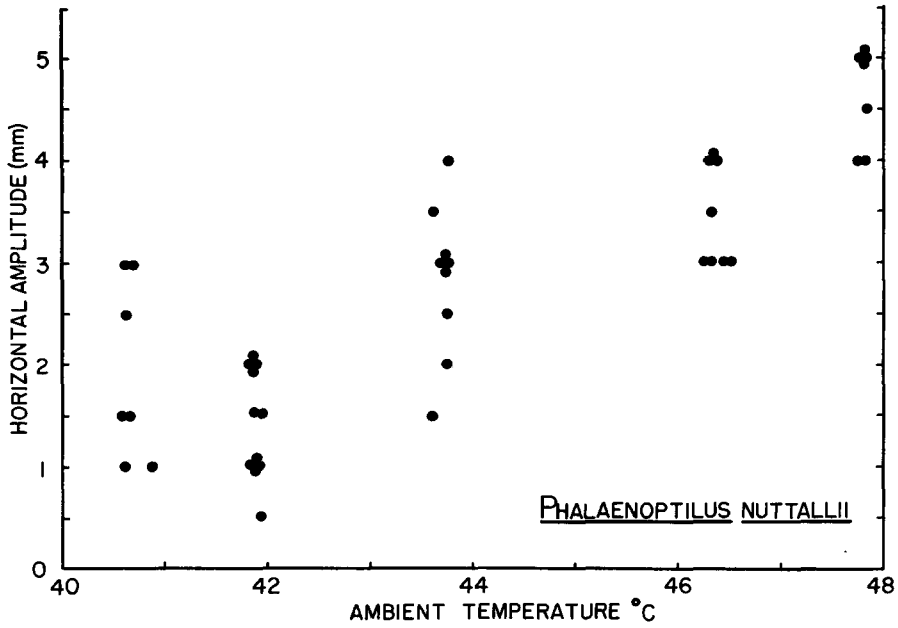
Figure 3. Horizontal amplitude in millimeters as a measure of the extent of gular flutter in the Poor-will in relation to ambient temperature.
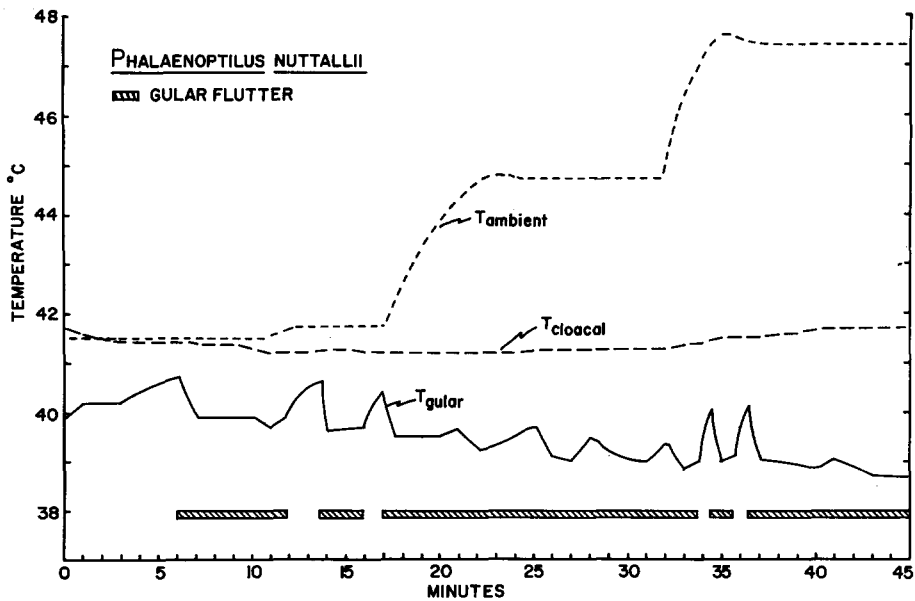

Figure 4. Gular temperature, cloacal temperature, and intervals of gular flutter in the Poor-will in relation to ambient temperature.
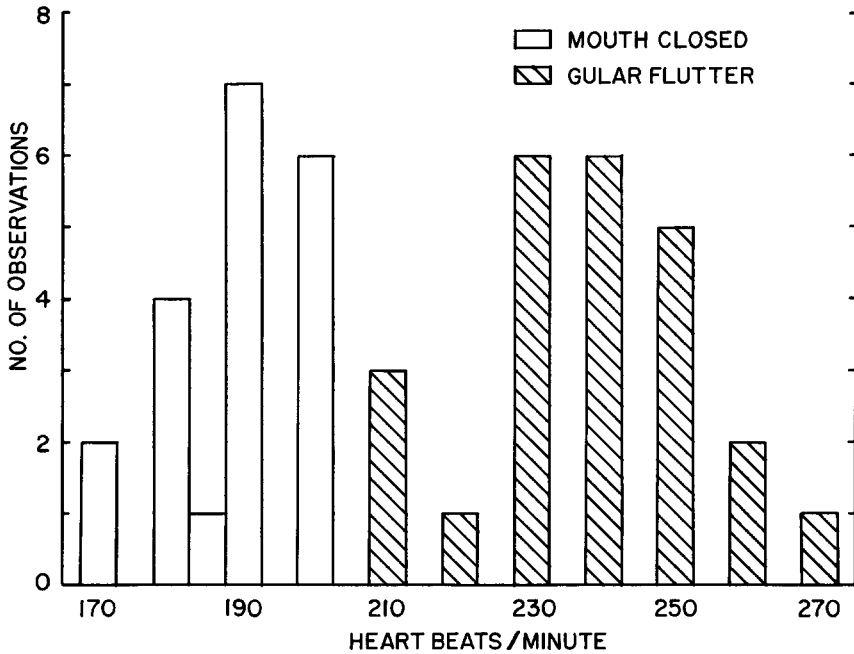
Figure 5. Heart rate in the Poor-will during periods of gular fluttering (crosshatched) and periods without flutter.

Heart rate increased during gular flutter and decreased again when flutter stopped, even under conditions of intermittent flutter (fig. 5). Breathing rate of quiet Poor-wills in the thermoneutral zone was only 14.5 to 18 breaths/minute. Our data on the relation of gular flutter to breathing rates are equivocal. In some cases there was a clear difference between breathing rates during and after fluttering, while in other cases there was none.

Tawny Frogmouth. The breathing rates of two frogmouths sitting quietly in the shade (T_A 20.9°C) ranged from 19 to 21 breaths per minute. When the 675-g female was heated by infrared lamp and blower, her body temperature (T_B) and breathing rate gradually increased. Breathing rate increased with increased body temperature and reached a maximum of 100 breaths per minute (fig. 6). At breathing rates above 60 per minute, the bird opened its mouth and lowered the gular area. In the absence of heat stress, breathing was barely perceptible and seemed to be mainly abdominal. As the body temperature increased, the amplitude of breathing deepened and the rate increased. The breathing movements during hyperthermia involved the entire thoracic areas and moved the entire body. At T_B of 42.5°C the frogmouth lowered and slightly spread her wings and compressed the feathers along the body surface. Mucous was seen hanging from the side of the mouth, and there was an obvious engorgement of blood vessels in the mouth area.

DISCUSSION

Gular flutter is a rapid vibration of the gular area, apparently driven by the hyoid apparatus. It differs from panting in that it does not involve trachea, lungs, and air sacs. Birds that use gular flutter can also respond to an increased heat load
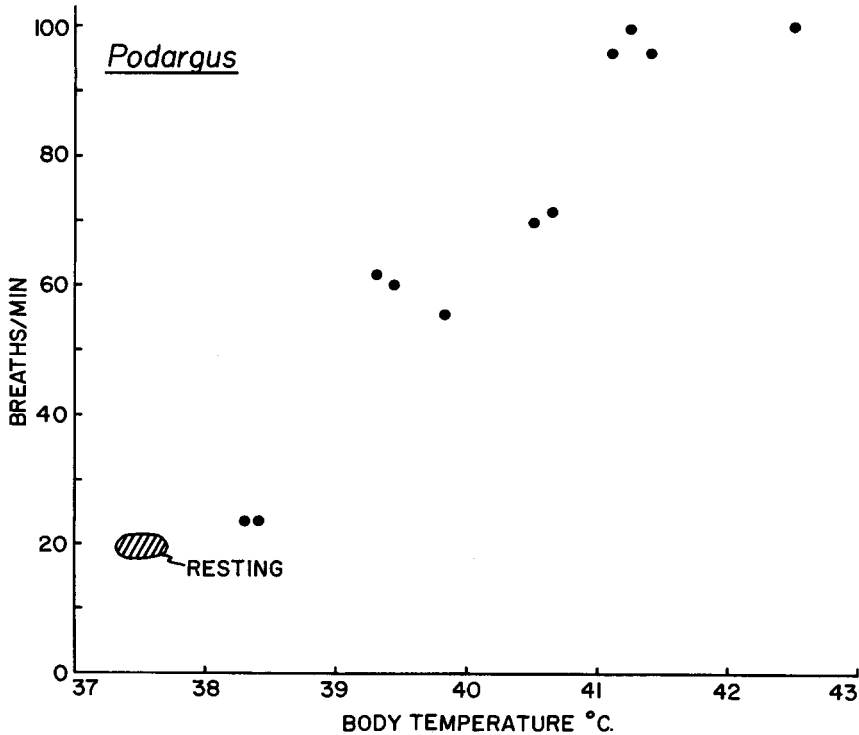
Figure 6. Breathing rate in the Tawny Frogmouth in relation to body temperature.

by panting (*i.e.*, increasing the rate and amplitude of the breathing movements). Gular flutter is metabolically relatively less costly than panting, presumably because the thin floor of the buccal and pharyngeal cavities, and anterior portions of the esophagus, can be moved more easily than can the thoracic cage.

In the two species for which data are available (Poor-will and Common Nighthawk), the amount of energy required for heat dissipation through evaporation of water by gular flutter plus breathing is significantly less than from birds that only pant. In these two caprimulgids heat loss by evaporation during gular flutter exceeds the total heat produced by resting metabolism plus that required to drive the evaporative mechanism (fig. 7). This allows members of both species to maintain body temperature below ambient temperatures of 45°C or more for long periods.

In the Poor-will the extent of the gular area fluttered increases with the heat load. When the heat load is small, only the buccal area is involved. As the heat load is increased, progressively greater portions of the pharyngeal and esophageal areas participate in the movements. Thus the extensive moist areas of the upper parts of the digestive tract, posterior to the tongue and glottis, act as additional evaporative surfaces. This is presumably also the case in other birds that use gular flutter.

Crawford (1962) has shown that panting in dogs occurs at the natural resonant frequency of the respiratory system and has discussed the implications of this relationship to temperature regulation. The fact that flutter rate in caprimulgids is independent of ambient temperature shows that these birds have taken advantage of
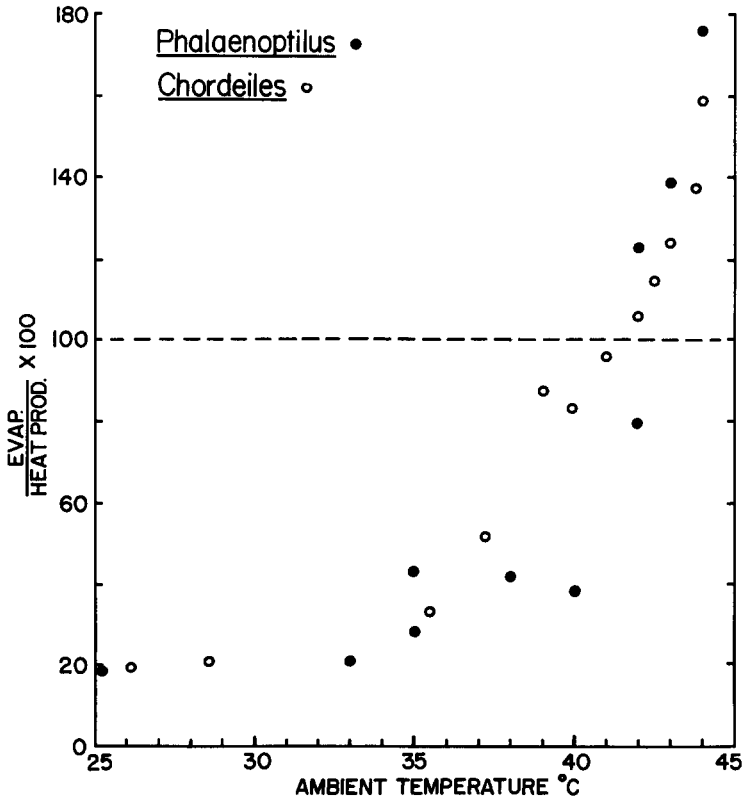
Figure 7. The ratio of evaporative cooling to metabolic heat production in relation to ambient temperature in two caprimulgids. Values greater than 100 indicate that the bird can dissipate all its metabolic heat plus some of the heat gained from the environment. Data redrawn from Bartholomew *et al.* (1962) and Lasiewski and Dawson (1964).

the mechanical properties of the gular area and drive it at a rate that appears to be the resonant frequency of the system. Supporting evidence for this assumption is offered by the data from experiments in which the gular region was weighted with lead shot. The additional weight did not alter the basic frequency, but it decreased the amplitude of movement, which is the result that would be expected in a simple physical resonating system. We have been unable to devise a method for directly determining the resonant frequency of the gular system by driving it externally, as Crawford was able to do with the thoracic cage of dogs.

Since flutter rate is independent of temperature, Poor-wills adjust their evaporative loss to different heat loads by varying (1) the amount of time spent fluttering, (2) the amplitude of excursion of the gular area during flutter, and (3) the area of the gular region involved in the flutter. The second and third of these parameters are interrelated, an increase in the amplitude of fluttering generally accompanying an increase in the area fluttered. When the heat load is small, the gular region is fluttered only intermittently; the flutter is of small amplitude and involves only the most anterior parts of the gular region. When the heat load is high, gular flutter is

essentially continuous, of high amplitude, and involves a large part of the upper digestive tract.

During gular fluttering there is a conspicuous engorgement of the blood vessels in the buccal area and presumably also in more posterior regions, and the heart rate increases. Thus effective conditions for cooling the blood as it passes through the gular area are available, and as shown in figure 4, the gular area is as much as 3°C below the deep body temperature, and as much as 9° below air temperature. These temperatures clearly indicate the importance of the gular area as a site of heat loss.

In the thermoneutral zone the breathing rate of the Poor-will is only 15 to 18 per minute, which is remarkably low for a 40- to 45-g bird. The Tawny Frogmouth, which weighs about 15 times as much and does not use gular flutter, has a breathing rate at rest of from 19 to 21 breaths per minute.

The rate of gular flutter in the Poor-wills studied varied between 590 and 690 per minute, which is essentially the same as that of the Common Nighthawk, which weighs approximately twice as much as the Poor-will. The original data on the Common Nighthawk (Lasiewski and Dawson, 1964) indicated that the rate of gular flutter averaged about 300 per minute. However, a recent re-examination of flutter rate in this species with more adequate instrumentation by these authors indicates that the original stroboscopic measurements halved the true frequency. Although the Common Nighthawk and the Poor-will are of very different weights, the sizes of the head and gular regions of the two species are similar, and flutter rate should be dependent upon gular area.

SUMMARY

The Poor-will is able to maintain a normal level of body temperature at an ambient temperature of 38°C without gular flutter and with mouth closed. When environmental temperature exceeds 39°C, gular flutter begins, and the amount of time spent fluttering increases with increasing temperature.

The frequency of gular flutter is independent of heat load, and the movements are apparently driven at a rate determined by the natural resonating frequency of the gular complex. Supporting evidence for this assumption is offered by the fact that adding weights to the gular region leaves the rate of flutter unchanged but causes its amplitude to decrease.

Poor-wills adjust rate of evaporative water loss to heat load by varying (1) the amount of time spent fluttering, (2) the amplitude of excursion of the gular region, and (3) the area involved. All three parameters increase with increasing heat loads.

Heart rate increases during periods of flutter, and there is a conspicuous engorgement of the blood vessels in the buccal region. The gular area may be maintained 3°C below body temperatures, and as much as 9°C below air temperatures, clearly demonstrating the importance of this region as a site of heat loss.

The breathing rate of a 675-g Tawny Frogmouth increased linearly with increasing body temperatures as the bird was subjected to heat. Breathing rates varied from 22/minute at a body temperature of 37.6°C to 100/minute at a body temperature of 42.5°C. As body temperature increased, the frogmouth opened its mouth, lowered the gular area, increased the flow of blood to the buccal area, and increased air flow across the moist buccal surfaces by increasing the amplitude as well as the rate of breathing.

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