

TEMPERATURE REGULATION IN THE LITTLE PAPUAN FROGMOUTH, *PODARGUS OCELLATUS*

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The avian order Caprimulgiformes has proved to be of unusual physiological interest. Physiological data are available from five genera of caprimulgids (*Phalaenoptilus*, *Chordeiles*, *Caprimulgus*, *Eurostopodus*, and *Nyctidromus*) and one podargid (*Podargus strigoides*). Members of the order tend to have low and variable body temperatures, and, under some circumstances, can enter a state of torpidity (see Bartholomew et al. 1957; and Dawson and Fisher 1969, for pertinent references).

Oxygen consumption has been measured in four genera of caprimulgids (Scholander et al. 1950; Bartholomew et al. 1962; Lasiewski and Dawson 1964; Dawson and Fisher 1969; Lasiewski 1969), and the standard metabolic rates of *Phalaenoptilus*, *Chordeiles*, and *Eurostopodus* are conspicuously lower than those of most birds of their size. Under conditions of heat stress, birds of these three genera facilitate evaporative cooling by fluttering the gular area. Gular flutter is an energetically economical method of achieving such cooling, and this, together with a relatively low metabolism, allows these birds to tolerate high ambient temperatures. Indeed, they attain the highest ratios of evaporative heat loss to heat production of any birds so far studied (Bartholomew et al. 1962; Lasiewski and Dawson 1964; Dawson and Fisher 1969; Lasiewski 1969). The only physiological data on podargids of which we are aware are those of Lasiewski and Bartholomew (1966) on the relation of breathing rate to body temperature in the Tawny Frogmouth, *Podargus strigoides*, a species that pants but does not gular flutter at high temperatures.

During the 1969 Alpha Helix Expedition to New Guinea, we had the fortunate opportunity to examine in some detail the physiological responses of podargids to heat stress. The two adult Little Papuan or Marbled Frogmouths (*Podargus ocellatus*) that we studied

were captured in mist nets set in a primary rain forest near our camp, approximately 32 km N of Madang, (5° 2' S), Territory of Papua and New Guinea. Members of this species occur in small numbers in forests from sea level to 5000 ft in New Guinea, Northern Queensland, and adjacent islands (Rand and Gilliard 1967). They take much of their food from the ground at night. During the day they often sleep in trees with their bills pointing upward, thereby simulating a broken branch.

MATERIALS AND METHODS

The frogmouths were housed in small cages placed in an outdoor shelter. They were fed by hand on meal worms, a variety of locally captured insects, and small pieces of fresh meat. They maintained weight, averaging approximately 145 g, and remained in good condition throughout the period of study, May-June 1969.

All observations were made during the daytime on postabsorptive birds that had been maintained under the desired conditions of temperature and humidity for at least one hour. The birds were remarkably quiet and docile, and remained virtually motionless during most periods of measurement. Oxygen consumption and evaporative water loss were measured with an open-flow system similar to that described by Dawson and Fisher (1969). Flow rates were adjusted between 300 and 3000 cc/min so as to maintain humidity in the metal respirometer chamber (24 × 24 × 30 cm) as nearly uniform as possible. Above ambient temperatures of 20°C, only those runs in which water vapor pressures remained between 10 and 18 mm Hg, as calculated with the equation of Lasiewski et al. (1966), were used for analysis.

Oxygen consumption was determined from the rate of air flow into the chamber and the difference in concentrations of oxygen between the outflowing and inflowing air (each dried and CO₂-free). All gas volumes are corrected to STP, and all temperatures are expressed in degrees Centigrade.

Ambient temperatures were controlled to within 0.3° with a constant temperature cabinet. Ambient temperatures, including those in the respirometer chamber, were measured to within 0.1° with 30-ga copper-constantan thermocouples connected to a 12-channel Honeywell Electronik 16 recorder. At ambient temperatures below 40°, body temperatures were

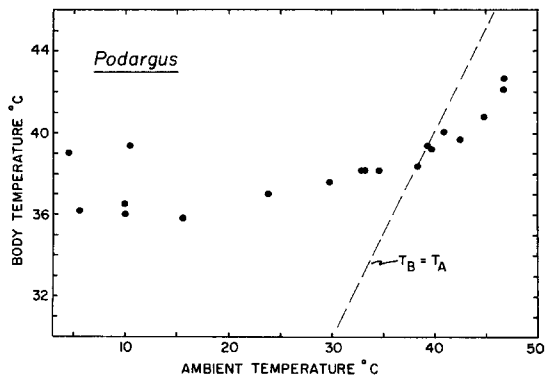


FIGURE 1. The relation between body temperature and ambient temperature in *Podargus ocellatus*. Values were obtained following measurements of oxygen consumption on animals that had been maintained for at least 90 min at a given ambient temperature.

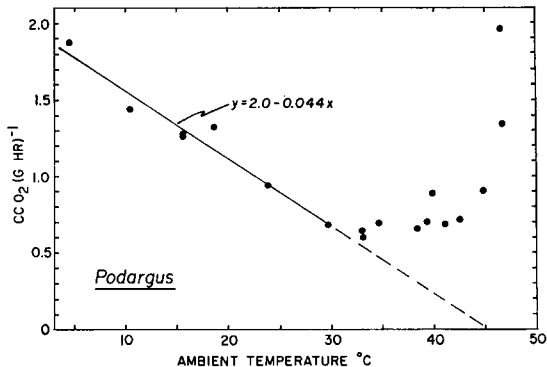


FIGURE 2. The relation between oxygen consumption of *Podargus ocellatus* and ambient temperature.

measured with a quick-acting mercury thermometer immediately following open-flow measurements of oxygen consumption and evaporative water loss. At higher ambient temperatures, body temperature was monitored continuously with a 30-ga copper-constantan thermocouple enclosed within a sphere of sealing wax 2 mm in diameter. This thermocouple was inserted through the cloaca into the large intestine to a depth of at least 2 cm and was held in place by securing the leads to the rectrices with surgical wound clips. At higher ambient temperatures, where hyperthermia developed, oxygen consumption and evaporative water loss were measured only after body temperature had stabilized, generally within two hours.

As the investigation progressed, it became desirable to characterize the sites of evaporative cooling by making continuous measurements of temperatures within the pharynx and mouth. One fine (40-ga) enamelled copper-constantan thermocouple was sewn onto the midline of the floor of the mouth 12 mm posterior to the symphysis of the lower mandibles. Another was sewn through the wall of the pharynx 4 mm lateral to the trachea and 10 mm caudad to the posterior edge of the horny floor of the mouth. The 40-ga leads to the couples were held in place with dental wax, so that the junctions rested directly on the surfaces being measured. The leads were soldered to 30-ga duplex wire which was secured to the feathers on the back of the bird with surgical clips and then connected to the recorder.

The behavioral responses of the birds to heat were observed through an insulated window in the temperature cabinet. Humidities within the cabinet were measured with a Hygrodynamics Universal Indicator used with a wide-range sensor. Breathing rates were counted visually and timed with a stop-watch.

Heart rates were monitored on a Hewlett-Packard 180/AR oscilloscope used in conjunction with a Grass P-8 a.c. preamplifier and a Grass AM-4 Audio-monitor. The electrocardiograms were taken from two leads attached subcutaneously on the lateral surfaces of the pectoral muscles. A third lead attached to one of the legs served as a ground. During measurements of heart rate the bird rested in the dark at ambient temperatures of 31.0–36.5°C.

An outdoor experiment was performed to measure the responses of a frogmouth to mid-day sun and air movements. Temperatures and humidities were mea-

sured with a YSI multichannel telethermometer and a sling psychrometer respectively. Air movements were measured with a vane anemometer.

RESULTS

Body temperatures. At the ambient temperatures (25–35°) prevailing in the lowland tropical forests where our experimental animals were obtained, the body temperatures of resting *P. ocellatus* were between 37 and 38.2° (fig. 1), which are low compared with those of most birds of comparable size (approximately 39–43°). However, they are similar to values reported for other members of the order Caprimulgiformes (Bartholomew et al. 1962; Lasiewski and Dawson 1964; Peiponen 1966; Dawson and Fisher 1969). At ambient temperatures above 40° the birds were able to maintain stable body temperatures as much as 4° below ambient, although some hyperthermia developed. At ambient temperatures below 15° the body temperatures of resting birds were variable, with the minimal values (35.8–36.5°) being 1–2° lower than those measured at 30–35°. Our data indicate a thermoregulatory capacity more than adequate to cope with the thermal environment which this species normally encounters. The physiological basis of this capacity is examined below.

Oxygen consumption. The zone of thermo-neutrality lies between 30 and 40°, but its upper and lower limits are not sharply defined (fig. 2). The minimal rate of oxygen consumption of *P. ocellatus* resting in the dark within the zone of thermal neutrality approximated 0.7 cc O₂ (g hr)⁻¹. At ambient temperatures above 40°, the birds maintained their body temperatures below ambient by augmenting evaporative water loss through increased respiratory rates (see below). The cost of this augmentation is reflected in a rise in oxygen consumption.

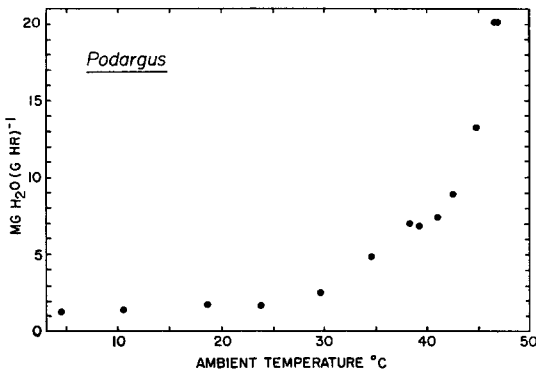


FIGURE 3. The relation of evaporative water loss of *Podargus ocellatus* to ambient temperature. At temperatures above 20°, water vapor pressure was maintained between 10 and 18 mm Hg.

Oxygen consumption was inversely related to ambient temperatures below approximately 30°. The relationship appears to be linear and is described by the following equation, derived by least squares regression analysis:

$$y = 2.00 - 0.044x \pm 0.07$$

where y is oxygen consumption, x is ambient temperature, and ± 0.07 represents the standard error of estimate.

Evaporative water loss. Evaporative water loss (fig. 3) increased more than 15 fold over the range of ambient temperatures studied (4.5–46.8°). About two-thirds of the increase occurred above 40°, where the animals panted vigorously (see below).

Breathing rate. At rest, breathing was almost imperceptible and minimal rates approximated 10 breaths per min. At body temperatures above 39°, the rate and amplitude of breathing increased regularly, the former being maximal at 100–107 breaths per min at body temperatures of 42° and above (fig. 4).

Heart rate. The heart rate of resting birds maintained in the dark for 3.5 hr at ambient temperatures of 31–36.5° were between 124 and 148 per min, with a mean of 133 ± 5.3 sd.

Buccal and pharyngeal temperatures during evaporative cooling. Simultaneous measurements were made of ambient, cloacal, buccal, and pharyngeal temperatures in one of the frogmouths. The tongue and floor of the mouth are cornified in frogmouths and do not appear to be important sites of evaporative cooling; however, we observed increased vascularity in the underlying tissues during heat stress, and this should enhance convective heat transfer when the temperature gradient is favorable. As respiratory rate increased at high ambient temperatures, the buccopharyn-

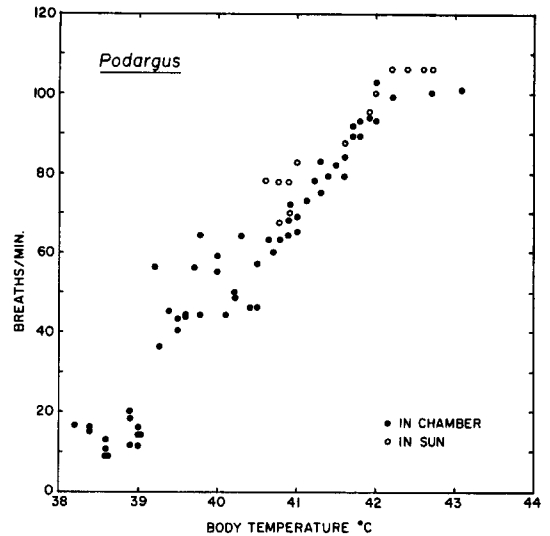


FIGURE 4. The relation of breathing rate to body temperature in *Podargus ocellatus*. Shaded circles represent rates obtained while the birds were in a constant temperature cabinet. The unshaded circles show values obtained while a bird was exposed to direct solar radiation.

geal cavity was conspicuously enlarged, thereby exposing the richly vascularised mucosal surfaces of the upper digestive tract to enhanced movements of tidal air. The moist mucosa of the pharynx had a markedly reduced surface temperature during active panting (fig. 5). In the absence of panting, the glottis rests just behind the posterior margin of the horny floor of the mouth. As the panting response develops, the glottis moves back into the cavity created by the expanded pharynx. This facilitates the direct movement of air over the moist pharyngeal surfaces and should contribute to the enhancement of evaporation in panting frogmouths, in a manner similar to the changes in location of the glottis during gular flutter in heat-stressed cormorants described by Lasiewski and Snyder (1969).

Effects of solar radiation on body temperature. Since the specific situations in which *P. ocellatus* spend the hours of daylight are poorly known, it seemed reasonable to examine their responses to the most extreme conditions of solar radiation and air temperature available in their general habitat. A frogmouth was tethered to a wooden perch, 1 m above the grass in full sun between 13:30 and 15:00 on 30 May 1969. It was oriented so that its back was approximately perpendicular to the sun's rays. The course of body temperature during the test is shown in figure 6. During the initial exposure to direct sun and a gentle

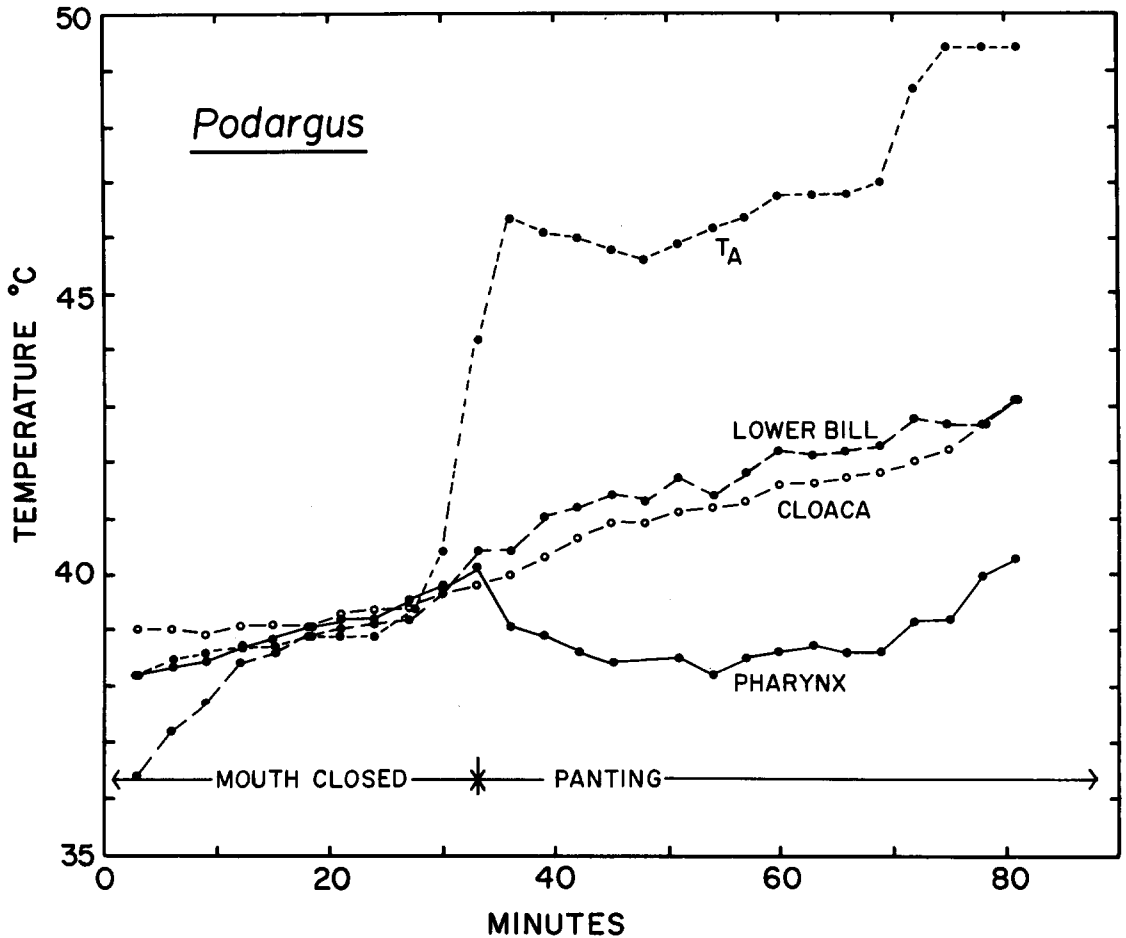


FIGURE 5. The relation of the temperatures of the cloaca, pharynx, and lower bill to ambient temperature in *Podargus ocellatus*. Between min 75–81 the bird was restless and struggled intermittently.

breeze varying between 0.3 and 1.3 m/sec, body temperature rose and stabilized near 41°. When body temperature had remained stable for approximately 15 min, we reduced air movement around the bird by placing a series of 4 × 8-ft panels of fibrous insulating board on the windward side of the bird. The consequent reduction in forced convective cooling resulted in a sharp and sustained rise in deep body temperature, despite progressively more vigorous and rapid panting by the bird. During this phase of the experiment, the temperature on the surface of the shoulder feathers reached 49.8°. To avoid excessive hyperthermia, when the cloacal temperatures reached 43° we removed the wind baffles and provided shade for the bird. The resulting increase in convection, together with the reduced radiant heat load, permitted a decline in body temperature of about 0.1° per min. Breathing rates were measured throughout the experiment. Despite the radiant heat load, the relation of breathing rate to body temperature was

not significantly different from that obtained in the laboratory where the heat load was imposed predominantly by convection (fig. 4). From this test, we conclude that, at rest, *P. ocellatus* can adequately regulate its body temperature, even in full sun at the ambient temperatures prevailing during the warmest part of the day in its habitat, as long as moderate air movement is present.

DISCUSSION

Little Papuan Frogmouths are remarkably lethargic, and values for the physiological functions we measured fall far below those of other birds of similar size (table 1). Like other members of the order Caprimulgiformes which have been studied in detail, the frogmouth has a low standard metabolic rate (less than two-thirds that predicted for similar-sized nonpasserine species). Breathing and heart rates are also remarkably low. Evaporative water loss, on the other hand, is only about 10 per cent below the predicted level, although

TABLE 1. Comparison of values for physiological parameters measured in *Podargus ocellatus* and those predicted for a 145-g bird.

Physiological parameters	Equation	Source	Predicted for 145-g bird ^a	Observed in <i>P. ocellatus</i>	% of predicted
Standard metabolism (kcal/day)	$\log M = \log 78.3 + 0.723 \log \text{kg}$	Lasiewski and Dawson 1967	19.4	11.7	60
Evaporative water loss at 25°C (g H ₂ O/day)	$\log E = \log 0.351 + 0.613 \log g$	Crawford and Lasiewski 1968	7.3	6.6	89
Heart rate (beats/min)	$f_h = 763 g^{-0.23}$	Calder 1968	242	124	51
Breathing rate (breaths/min)	$f_b = 146 g^{-0.31}$	Calder 1968	31.2	10	32

^a All values are calculated from equations for nonpasserine birds, with the exception of that for heart rate, which is from an equation for all birds.

the available data for evaporative water loss in birds are not well standardized.

The data on resting body temperatures of birds are too variable and unstandardized to allow the development of adequate predictive curves. Nevertheless, it is clear that the body temperatures of resting *P. ocellatus* (37–38°) are distinctly lower than those of most land birds of similar size.

Many birds exposed to heat stress appear to benefit significantly from hyperthermia for this frequently allows them to remain warmer

than the environment, thereby facilitating heat loss via heat transfer and reducing the requirements for evaporative water loss. Its low resting body temperature and its tolerance of hyperthermia (see figs. 1, 6) in theory afford *P. ocellatus* the possibility of storing significant quantities of heat in warm environments. The situation, however, is complicated by the tendency of this species to initiate active evaporative cooling at relatively low ambient and body temperatures (fig. 3). *Podargus ocellatus* is unusual among birds in achieving parity

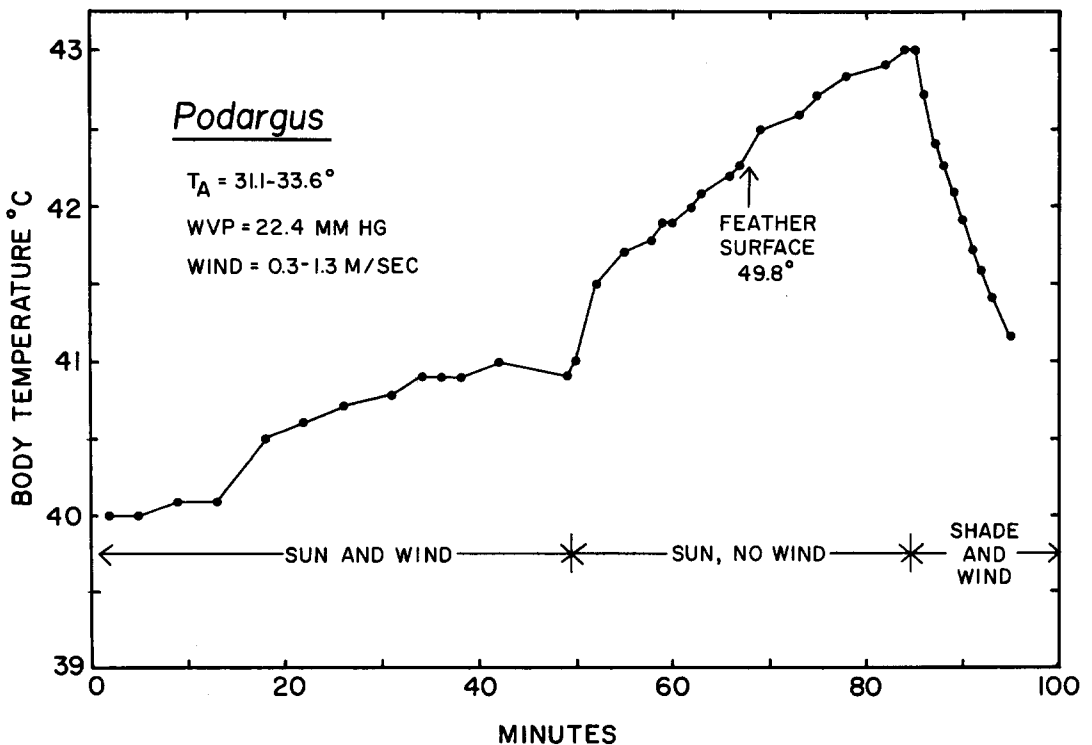


FIGURE 6. The course of body temperature in *Podargus ocellatus* during exposure to various combinations of wind and solar radiation.

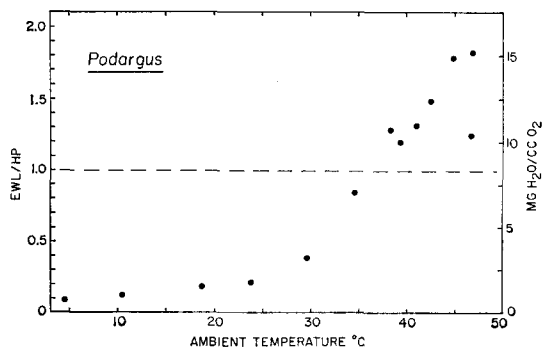


FIGURE 7. The relation of the ratio of calories dissipated by evaporation and calories produced (EWL/HP) to ambient temperature in *Podargus ocellatus*.

between evaporative cooling and heat production at the low ambient temperature of 37–38° (fig. 7). Most birds attain such parity only at much higher (42–45°) ambient temperatures (Lasiewski et al. 1966). The effectiveness of thermoregulation of *P. ocellatus* at high temperatures is linked with its inherently low level of heat production and the low cost of its panting. The latter is of particular interest because most birds that rely solely on panting are unable to achieve ratios of EWL/HP (i.e., calories dissipated through evaporation over calories produced) much higher than 1.0 (Lasiewski et al. 1966). *Podargus ocellatus*, on the other hand, reached the unprecedented value for panting birds of 1.8. (It should be noted that we maintained humidity below 18 mm Hg water vapor pressure, whereas in most other studies humidity has been relatively uncontrolled.) EWL/HP ratios of this magnitude have previously been associated with birds employing gular flutter (Bartholomew et al. 1962; Lasiewski and Dawson 1964; Calder and Schmidt-Nielsen 1967; Dawson and Fisher 1969; Lasiewski 1969).

The metabolic rate of *P. ocellatus* rises very little with panting except at the most extreme ambient temperatures to which we subjected them. Since a portion of the augmented metabolism at higher temperatures must reflect the acceleration of metabolism with increasing body temperature, the cost of panting in *P. ocellatus* must be low indeed.

A gradual increase of breathing rate with body temperature in *P. ocellatus* is similar to that described by Lasiewski and Bartholomew (1966) for *P. strigoides*, and by Kendeigh (1944) for the small passerine, *Passer domesticus*. This contrasts with the pattern reported for the Ostrich, *Struthio camelus* (Crawford and Schmidt-Nielsen 1967; Schmidt-Nielsen et

TABLE 2. Thermal conductance in *Podargus ocellatus*.

Ambient temperature °C	Total thermal conductance ^a	Dry thermal conductance ^b	
	cc O ₂ × (g hr °C) ⁻¹	cal × (g hr °C) ⁻¹	kcal × (m ² hr °C) ⁻¹
4.5	0.053	0.24	1.32
10.3	0.049	0.21	1.15
18.7	0.072	0.29	1.60
23.9	0.072	0.27	1.49
29.7	0.086	0.25	1.38
34.7	—	0.16	0.88
42.5	—	0.35	1.93
44.7	—	0.84	4.62
45.3	—	0.35	1.93
46.8	—	1.27	7.00
Predicted ^c	0.068	—	—

^a Total thermal conductance was computed as $M/(T_B - T_A)$, where M is metabolism in cc (g hr)⁻¹, T_B is body temperature, and T_A is ambient temperature.

^b Dry thermal conductance was computed as $(M - E)/(T_B - T_A)$, where M is metabolism (1 cc O₂ = 4.8 cal), E represents calories evaporated (1 mg H₂O = 0.58 cal). Surface area was computed from the formula, $S = 0.1 W^{0.67}$, where S is surface area in m², and W is weight in kg.

^c Minimum total thermal conductance predicted for a 145-g bird by the equations of Herreid and Kessel (1967) and Lasiewski et al. (1967).

al. 1969), which pants at a relatively constant level, several times higher than resting rates. During panting in *P. ocellatus* the dilation of the upper digestive tract and the caudad movement of the glottis mobilize additional mucosal surfaces for evaporative cooling.

Values for total and dry thermal conductance in *P. ocellatus* are given in table 2. Dry thermal conductance reaches its minimal levels (i.e., insulation is maximal) at temperatures below 30°. Total thermal conductance is about 70 per cent of that predicted for a 145-g bird by the equations of Herreid and Kessel (1967) and Lasiewski et al. (1967). The values for dry conductance show no tendency to return to minimum levels at ambient temperatures between 42.5 and 46.8°, indicating that this species does not maximize its insulative capacities at high ambient temperatures in a manner serving to reduce heat gain. This contrasts with the pattern noted by Dawson and Schmidt-Nielsen (1966) in the jack-rabbit, *Lepus alleni*, but is consistent with the information available for other birds (see, for example, Calder and Schmidt-Nielsen 1967; and Dawson and Fisher 1969).

Podargus ocellatus possesses a complete and effective repertoire of thermoregulatory responses although it lives in a uniform, equable, tropical environment. The effectiveness of the thermoregulation of this species at high ambient temperatures demonstrates with unusual clarity one benefit of an inherently low level of metabolism.

SUMMARY

Standard metabolism of *Podargus ocellatus* approximated $0.70 \text{ cc O}_2 (\text{g hr})^{-1}$ which is 60 per cent of that predicted for 145-g nonpasserine birds. Below 30° metabolism increased linearly at $0.044 \text{ cc O}_2 (\text{g hr } ^\circ\text{C})^{-1}$. Near 40° and above, frogmouths enhance evaporative cooling by increased respiratory rates (panting). Evaporative water loss ranged from 1.3 to $20.2 \text{ mg H}_2\text{O} (\text{g hr})^{-1}$ at 4.5 and 46.8° , respectively, and increased markedly above 38°C . The low metabolic cost of panting, together with the low metabolic rate, enabled frogmouths to maintain body temperatures below environmental temperatures of 40° and above. *P. ocellatus* achieved parity between heat lost through evaporation and metabolic heat at the relatively low temperatures of 37 – 38° . At 46.8° the ratio of evaporative heat loss metabolic heat reached the unprecedented level for panting birds of 1.8.

Resting breathing rates approximated 10/min, and increased regularly with body temperature to 100–107/min at 42° . Resting heart rates averaged 133/min. Breathing and heart rates of resting *P. ocellatus* were 32 and 51 per cent, respectively, of levels predicted for 145-g birds.

ACKNOWLEDGMENTS

This research was carried out during the 1969 Alpha Helix Expedition to New Guinea and supported by NSF Grants GB8400, GB8445, GB5139, and GB3656.

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Accepted for publication 16 October 1969.