RESPONSES TO TEMPERATURE BY THE SPOTTED NIGHTJAR (EUROSTOPODUS GUTTATUS)

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Caprimulgid birds have proved to be intriguing subjects for physiological research. Some, the Poor-will (*Phalaenoptilus nuttallii*), the Common Nighthawk (*Chordeiles minor*), and the European Nightjar (*Caprimulgus europaeus*), have been observed to become dormant under appropriate conditions in the field or laboratory (Jaeger 1948, 1949, 1954; Thorburg 1953; Marshall 1955; Novrup 1956; Bartholomew et al. 1957; Howell and Bartholomew 1959; Bartholomew et al. 1962; Lasiewski and Dawson 1964; Peiponen 1965, 1966). Several, the Poor-will, Common Nighthawk, and Lesser Nighthawk (*Chordeiles acutipennis*), have been found to excel in their resistance to heat (Cowles and Dawson 1951; Bartholomew et al. 1962; Lasiewski and Dawson 1964; Lasiewski and Bartholomew 1966). Acquisition of two Spotted Nightjars (*Eurostopodus guttatus*) has afforded us the opportunity for examining the physiological responses to temperature of an additional caprimulgid. Some of our observations pertain to hotter conditions than those utilized in previously published studies. The additional perspective our data provide concerning thermoregulatory capacities in the family and the fact that circumstances will prevent us from obtaining any more Spotted Nightjars in the foreseeable future prompt us to present our results in this report. We acknowledge that a larger sample of these birds would have been desirable.

MATERIAL AND METHODS

The Spotted Nightjar is resident over most of Australia, except for the mesic parts of the east coast, southeast, and southwest. It is also reputed to occur on the Aru Islands and New Ireland (see Cayley et al. 1959), but this has been questioned by Peters (1940:190). The male and female used in this study were obtained on 30 December 1967 from a mist net that had been left standing overnight near a water hole at Thundelarra Station (approximately midway between Yalgoo and Payne's Find), Western Australia. This area is in the mulga (principally *Acacia aneura*) belt. The Spotted Nightjar also occurs in mallee and in desert scrub. The two birds weighed between 85 and 90 g at capture and were undoubtedly adjusted to the hot conditions of the austral summer. They were transferred within a week to the Department of Zoology, University of Western Australia, Nedlands, for study. A scarcity of moths in the vicinity forced considerable experimentation to establish a satisfactory diet. This consisted principally of cockroaches and a vitamin mixture, which were ultimately supplemented by grasshoppers and an occasional moth. These items were administered by hand nightly in sufficient quantity so that the female had actually gained a couple of grams by the end of the three-week period of study. The situation regarding the male is outlined subsequently in connection with observations on torpidity.

Oxygen consumption and evaporative water loss were measured simultaneously while the birds were resting in a postabsorptive state during the day, the normal period of quiesence in these nocturnal animals. An open-circuit metabolism system was used in which air passed successively via tygon tubing through a drying train of silica gel and then Drierite (anhydrous $CaSO_4$), a suitably calibrated rotameter, and a chamber fashioned from a new 2-gal paint can. The temperature in this chamber, at the level of the bird, was measured with a thermocouple used in conjunction with a recently calibrated Brown recording potentiometer. The bird rested in the chamber on a wire mesh platform over a 1.5-cm layer of mineral oil which served to cover any droppings voided during an experiment, thus preventing them from adding water vapor to the system. Evaporative water loss was determined by connecting two or (at high temperatures) three tubes containing Drierite in series with the outflow line from the chamber. The gain in weight of these tubes over a precisely timed interval was determined with a Mettler balance of appropriate sensitivity. This gain, when reduced by a small correction value determined in a blank run preceding the experiment, represented the water evaporated by the bird. The Drierite in the tubes recovered all but a small fraction of one per cent of known amounts of water vapor introduced into the metabolism system with rates of air flow corresponding to those used in the experiments. These rates ranged from approximately 700 to 2600 cm^3/min (ambient conditions) and were held constant in the individual experiments at levels that maintained the humidity within the chamber near the following average values: 20°–30°C, 19 per cent (relative humidity) and 5 mm Hg (vapor pressure of water); 30°–40°C, 20 per cent and 8 mm Hg; 40°–45°C, 16 per cent and 10 mm Hg; 45°–50°C, 16 per cent and 13 mm Hg; 52.8°C, 18 per cent and 17 mm Hg; 56.5°C, 20 per cent and 25 mm Hg. These values were determined using the equation employed by Lasiewski (1964) and standard physical tables.

Measurement of oxygen consumption required diverting a portion of the air stream passing from the drying tubes through a train containing Ascarite (a CO_2 absorbent) and Drierite to a Beckman paramagnetic oxygen analyzer of appropriate sensitivity. The oxygen consumption was determined from the
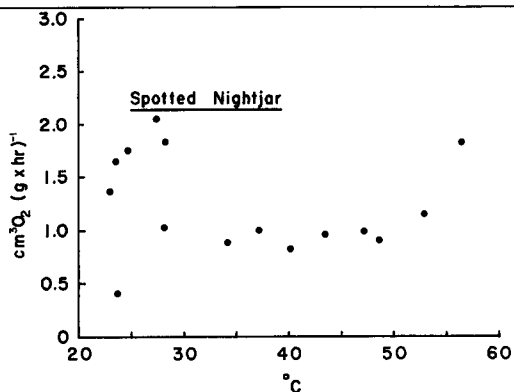
FIGURE 1. Rates of oxygen consumption by Spotted Nightjars resting and fasting at various ambient temperatures. The value of 0.4 cm³ O₂ $(g \times hr)^{-1}$ observed at 23.7°C pertains to a torpid individual with a body temperature of 29.6°C (see text).

flow rate registered by the rotameter and from the difference in the fractional concentrations of oxygen between this air sample and pure air (both dried and CO₂-free). The applicable equation from Depocas and Hart (1957) was used. All gas volumes expressed in connection with metabolic rate have been corrected to 0°C and 760 mm Hg.

Experiments typically lasted four or five hours with determinations of oxygen consumption and evaporative water loss being made during the last hour. At that time the bird had fasted approximately 16 hours. Below 42°C the temperature in the chamber was held constant throughout the experiment. For studies at higher temperatures a modified procedure was used to prevent excessive water loss over the four- to five-hour period. The bird was allowed an hour or so to adjust to the chamber while it was at a moderate temperature. The chamber was then brought to the desired high temperature over the next hour. A measurement period lasting 15 to 30 min was begun when the bird had been at the desired ambient temperature for 1½ to 2 hr. Above 50°C a 15-min measurement starting at the end of the first hour was also made. Body temperature was measured at the end of each experiment using a thermometer designed for small-animal work. The nightjars proved exceedingly tractable experimental subjects.

RESULTS AND DISCUSSION

The rates of oxygen consumption by the nightjars at various ambient temperatures are illustrated in figure 1. The basal level of metabolism is estimated to be 0.83 cm³ O₂ $(g \times hr)^{-1}$. This is 63 per cent of the value predicted for an 88-g bird using Lasiewski and Dawson's (1967) equation relating basal metabolic rate and body weight in nonpasserine birds. This relatively low level of metabolism is consistent with the situation noted in the two caprimulgid birds on which detailed observations have been made (Bartholomew et al. 1962; Lasiewski and Dawson 1964). The basal rates of the Poor-will (40 g) and Common Nighthawk (75 g), respec-

tively, amount to 49 and 79 per cent of the values characterizing most other nonpasserine birds of comparable size. The metabolic pattern of the Spotted Nightjar resembles the patterns for these other two species in another important respect—oxygen consumption and hence heat production increases relatively little at high temperatures. It reached only 1.4 times the basal rate at 52.8°C. Much of this rise is probably associated with the moderately increased body temperatures noted at high ambient temperatures (see fig. 4). The relatively low energy requirement of evaporative cooling reflects the use of gular fluttering by the nightjar. The nature and significance of this mechanism have most recently been reviewed by Lasiewski and Bartholomew (1966) and Bartholomew et al. (1968). We lacked equipment to determine the flutter frequency employed by the nightjar, but it appeared to be in the same range (approximately 600 cycles per minute) as that characterizing the Poor-will and Common Nighthawk (see Lasiewski and Bartholomew 1966). Only at 56.5°C, an ambient temperature that produced fatal overheating of the female nightjar after 100 min, did the metabolic rate become conspicuously elevated with exposure to heat. This development is best considered in relation to the fact that the drying power of air is determined both by its water content at inspiration and its temperature at expiration. In the experiment at 56.5°C, the vapor pressure of water in the inspired air approximated 25 mm Hg. Prior to heat injury, this air was probably expired by the nightjar at a temperature somewhere near 42°C; Lasiewski and Bartholomew (1966) found mucosal temperatures in the gular area to fall between 39° and 40°C in a Poor-will studied at ambient temperatures of 44°–47.5°C. At 42°C the effective saturation deficit of the air inspired by the nightjar would approximate only 37 mm Hg, corresponding to 40 per cent relative humidity. It is therefore not surprising that the nightjar was forced to expend far more vigorous efforts in evaporative cooling at 56.5°C than at somewhat cooler ambient temperatures where both the thermal differential between body and air and the absolute humidity were less.

Heat production in the nightjar begins to rise as ambient temperature falls below approximately 32°C. The onset of chemical thermoregulation, i.e., regulation primarily by adjustment of heat production, at this relatively high temperature level is associated with the relatively low level of basal metab-

olism. Considerable scatter is evident in the metabolic data for temperatures below 32°C. This appears to reflect some lability in body temperature; rates exceeding 1.5 cm³ O₂ (g × hr)⁻¹ were linked with body temperatures ranging from 38.4° to 39.5°C, whereas those between 1.0 and 1.4 cm³ O₂ (g × hr)⁻¹ involved body temperatures of 37.3° and 36.2°C (see fig. 4).

It is always of interest to determine whether or not caprimulgid birds will readily enter a torpid state. We did not make serious efforts in this direction because we lacked facilities for maintaining low ambient temperatures and because our birds were adjusted to summer conditions. However, the failure of the male to maintain weight while we were still in the process of developing a satisfactory diet resulted in a situation bearing on the question of whether or not the Spotted Nightjar possesses a capacity for dormancy. The bird declined from 86 to 75 g in body weight over the course of a week. On the last day of this period, it was placed in the metabolism chamber at 11:45, where it remained at an ambient temperature of 23.7°C for five hours. Its metabolic rate and body temperature at the end of this period were 0.4 cm³ O₂ (g × hr)⁻¹ and 29.6°C, respectively. It did not open its eyes when removed from the chamber. After 50 more minutes undisturbed at 23.7°C, the nightjar had warmed to 37.2°C and was normally alert. It is of interest that this bird had lost but 13 per cent of its initial weight at the time of entry into torpor, for Common Nighthawks did not become torpid until they had lost 28–34 per cent of theirs (Lasiewski and Dawson 1964). Marshall (1955) concluded that Lesser Nighthawks and Poor-wills would not enter torpor until they had undergone a loss of weight amounting to at least 20 per cent. The figure for the European Nightjar is as low as 8 per cent in one instance (Peiponen 1966).

The occurrence of torpor suggests that it would be profitable to undertake studies of dormancy in the Spotted Nightjar that parallel those that have been conducted on the Poorwill (Bartholomew et al. 1957, 1962; Howell and Bartholomew 1959). Such studies are rendered of additional interest by the fact that the nightjar is in the size range where shortterm torpor may become impractical; Lasiewski and Lasiewski (1967) estimate that an 80- to 100-g bird would require approximately 12 hr just to cool to and rewarm from an ambient level of 20° C.

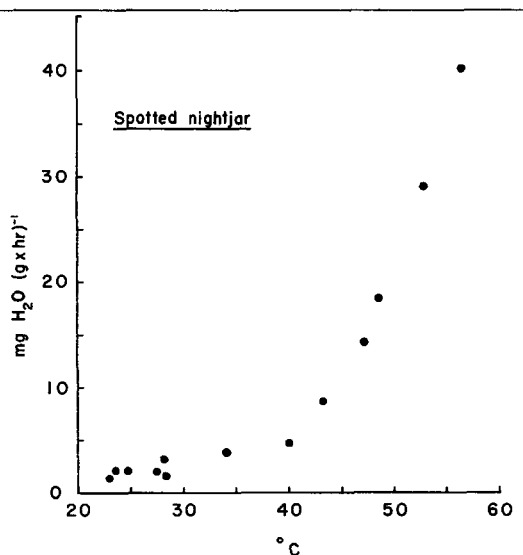The evaporative water loss by the nightjar

FIGURE 2. Rates of evaporative water loss by euthermic Spotted Nightjars resting and fasting at various ambient temperatures. All values shown were obtained in conjunction with measurements of oxygen consumption.

at various ambient temperatures is shown per unit of weight in figure 2. The average weight-relative value for nontorpid individuals between 23° and 25° is 1.9 mg (g × hr)⁻¹. This is 67 per cent of the value predicted for an 88-g bird using Crawford and Lasiewski's (1968) equation relating evaporative water loss and body weight in nonpasserine birds: $E = 0.351W^{0.613}$, where E is water loss (g/day) and W is weight (g). This situation parallels that noted previously concerning the relation of basal metabolic rate of the Spotted Nightjar to the value predicted for a bird of its weight. The form of the evaporative water loss-temperature relation (fig. 2) resembles that for most other birds that have been studied, although the conspicuous augmentation of water output commences at a higher ambient temperature (ca. 40° C) than in most other species, including the Common Nighthawk (Lasiewski and Dawson 1964). Like other birds, the nightjar does not increase its evaporative water loss at moderate ambient temperatures where oxygen consumption begins to rise with the onset of chemical thermoregulation. This situation has been commented on previously in other species (see, for example, Lasiewski and Dawson 1964; Lasiewski et al. 1966). The capacity of the nightjar for augmenting evaporative water loss in hot environments is impressive; the value recorded at 56.5° C exceeds those for 23°–25° by a factor of approximately 20.
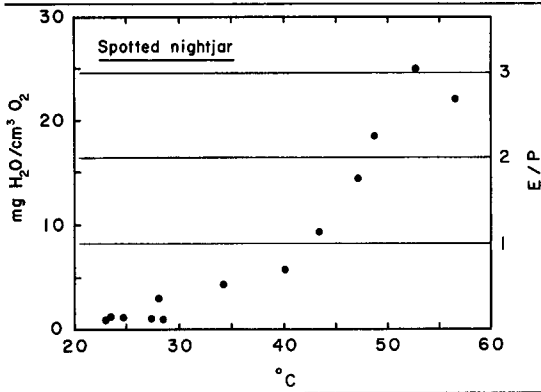
Evaporative water loss per unit of metab-

FIGURE 3. Evaporative water loss (data from fig. 2) per unit of oxygen consumption (data from fig. 1) in euthermic Spotted Nightjars. Conversion of data on these functions to caloric terms (1 mg H_2O = 0.57 cal; 1 cm^3 O_2 = 4.7 cal) permits expression of evaporative cooling (E) per unit of heat production (P) on the right ordinate.

FIGURE 4. Body temperatures of euthermic Spotted Nightjars resting and fasting at various ambient temperatures. $T_B = T_A$ along diagonal line.

olism exceeds 1 mg/cm^3 O_2 at all temperatures studied (fig. 3). The values obtained are in general agreement with those reported for corresponding temperatures in the Poor-will and Common Nighthawk (Bartholomew et al. 1962; Lasiewski and Dawson 1964), but differences in humidity among the three sets of experiments hinder detailed comparisons. Oxidative water production is inadequate to offset evaporative water loss at moderate temperatures in all three species and the situation is even less favorable at higher temperatures. The insectivorous habits of these birds must contribute to rectification of this situation by making available relatively large amounts of preformed water. The Spotted Nightjar also appears to drink on the wing at water holes (Fisher, unpublished data).

Water loss through evaporation and oxygen consumption can both be converted to calories (we have used 0.57 cal/mg of H_2O and 4.7 cal/cm^3 O_2). Consequently, it is possible to evaluate the evaporative cooling of the Spotted Nightjar in relation to metabolism, as indicated on the right-hand ordinate of figure 3. This bird can dissipate slightly more than three times its heat production at high ambient temperatures. This is a larger factor than those obtained in published studies of the Poor-will and Common Nighthawk (Bartholomew et al. 1962; Lasiewski and Dawson 1964), but these other birds were studied at lower temperatures and different humidities. The fact that the nightjar can dissipate significantly more heat than it produces allows it to remain substantially cooler than its surroundings at very high ambient temperatures (fig. 4). The relatively low level of metabolism
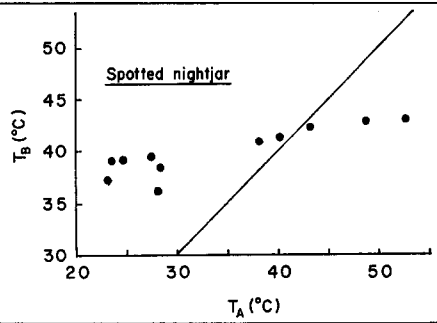
and the fairly effortless character of the gular flutter of this species contribute to this capacity.

The availability of simultaneous measurements of oxygen consumption (fig. 1) and water loss (fig. 2) permit calculation of values for the thermal conductance of the nightjar, corrected for evaporative cooling. These are expressed in surface-relative terms in table 1, body surface being calculated from the equation $S = 0.1W^{0.67}$, where S is surface in m^2 and W is weight in kg. Thermal conductance provides an index of insulation (insulation = conductance^{-1}) at the various ambient temperatures studied. The minimum conductance value obtained for the nightjar, 1.7 kcal m^{-2} $hr^{-1}°C^{-1}$, is similar to that estimated for the Poor-will (40 g), rather than that (approximately 2 kcal $m^{-2}hr^{-1}°C^{-1}$) for the Common Nighthawk, a caprimulgid more nearly its size. The maximal value (4.9 kcal $m^{-2}hr^{-1}°C^{-1}$) obtained for the nightjar exceeds the minimal value by a factor of 2.9. The comparable factor for the Roadrunner (Geococcyx californianus), a 285-g bird occupying regions with temperature regimes approximating those for the area in which the Spotted Nightjar

TABLE 1. Thermal conductance[a] of the Spotted Nightjar at various ambient temperatures.

Bird	Ambient temp. °C	Thermal conductance (kcal m^{-2} hr^{-1} °C^{-1})
♂	23.0	1.7
♀	23.5	1.9
♀	24.7	2.2
♀	27.4	3.3
♂	28.1	1.6
♂	28.3	3.3
♀	40.1	4.0
♀	43.3	2.8
♀	48.6	4.5
♀	52.8	4.9

[a] Thermal conductance = $\dfrac{\text{heat produced} - \text{heat evaporated}}{(\text{body temp.} - \text{ambient temp.})\ (m^2)}$

occurs, is about 2.7 (Calder and Schmidt-Nielsen 1967).

It is of interest that the thermal conductance of the nightjar reached its highest level at ambient temperatures exceeding body temperature. Increasing conductance would be advantageous as ambient temperature rises to near body temperature, assuming that the animal is not exposed to intense solar radiation. However, a continued increase as ambient temperature exceeds body temperature would appear deleterious, since it would facilitate gain of heat from the environment. The possibility exists that the rise in conductance is associated with the increased rates of air flow employed at high ambient temperatures. However, the velocity of the air within the chambers even at a flow rate of 2600 cm³/min should be less than 10 cm/min, with the cross sectional area of the 2-gal paint cans used. Perhaps the relatively high conductance (and, therefore, low insulation) noted at 48.6° and 52.4°C results from the movements and postural adjustments associated with rapid evaporative cooling.

SUMMARY

The Spotted Nightjar is a bird with superior powers of heat defense which depend principally on an extensive capacity for evaporative cooling via gular fluttering and a relatively low level of metabolism. Body temperature tends to be rather labile at moderate ambient temperatures and a capacity for dormancy is indicated, although it remains to be established whether or not nightjars become torpid in nature. The Spotted Nightjar resembles the somewhat smaller Poor-will in those aspects of its physiology that have been investigated. This is consistent with the ecological similarities between the two birds.

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