TEMPERATURE REGULATION IN THE SPECKLED MOUSEBIRD, *COLIUS STRIATUS*

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Mousebirds, or colies, comprise a monogeneric order, Coliiformes, containing six species, all of which are confined to subsaharan Africa. Field observations of the communal roosting of colies, their frequent sunbathing, and occasional instances of hypothermia (often in birds with wet plumage), have led to the suggestion that they may undergo periods of torpor (McAtee 1947; Bartholomew et al. 1957; Cowles 1959). Their thermoregulatory capacity, however, has never systematically been studied, and despite their abundance and the many unusual features of their structure and behavior, only isolated fragments of data are available on any aspect of their physiology. The best source of information on their biology is the comprehensive treatment by Rowan (1967) of *Colius striatus*, *C. colius*, and *C. indicus* in southern Africa.

MATERIALS AND METHODS

The Speckled Colies (*C. s. minor*) used in this study were reared in an aviary and were two and three generations removed from the wild. The original stock was captured in Natal, South Africa, by Dr. Raymond B. Cowles who kindly gave us four second-generation individuals. Our physiological measurements were made on two of the second-generation birds and on five third-generation individuals reared by Bruce Bartholomew. During the period of study, 12 July 1966–16 June 1967, all of the birds were at least two years old and in excellent condition. They were maintained on lettuce, fresh fruit, and commercial mockingbird food. Water was available ad libitum.

During most of the study the birds were housed in a shaded outdoor aviary on the roof of the Life Sciences Building at UCLA. During the study of torpor the birds were kept in individual wire cages (1.0 × 0.5 × 0.5 m), in a windowless room on a 12-hr photoperiod (lights on, 10:00–22:00). To facilitate handling and to allow the colies to fit easily into the confined space of the respirometer chamber, their long tail feathers were cut to a length of about 4 cm. Under conditions of captivity with food freely available the body weight of the colies varied between 50 and 55 g. The species shows no sexual dimorphism and the sex of the experimental birds was not determined.

Oxygen consumption and evaporative water loss were measured simultaneously. A bird was fasted for at least 2 hr, then placed on a wire mesh platform in a 1-gal glass respirometer chamber. Any excreta produced fell through the platform and sank beneath a 2-cm layer of mineral oil in the bottom of the chamber, thus minimizing fecal contributions to the measurement of evaporative water loss. The respirometer chamber was equipped with ports for the introduction and removal of air, a thermocouple, and an electric humidity sensor. Dried air was passed through the respirometer chamber at 700 cc/min at ambient temperatures of 5–40°C; at 42°C the rate was increased to 1500 cc/min. Evaporative water loss was determined from the change in weight of tubes of Drierite (anhydrous $CaSO_4$) through which the effluent air was passed for either 30 or 60 min. Oxygen consumption was measured by passing a fraction of the dried effluent air (CO_2 not removed) through a Beckman G-2 recording paramagnetic oxygen analyzer. The values used represent the minimum stable levels attained during a period of at least 2 hr. Ambient temperature was controlled to within 0.2°C by an Aminco bacteriological incubator. Temperatures were measured to within 0.1°C with 20-gauge copper-constantan thermocouples connected to a recording potentiometer, with a thermistor telethermometer, or with a quick registering mercury thermometer. Heart rates were recorded on a Grass Polygraph from EKG leads secured to right and left pectoral areas and to the scapular region. Breathing rates were counted by eye and timed with a stop watch or, in some cases, determined from EKG records.

Body temperatures were measured cloacally. Continuous records were obtained by inserting a vinyl-sheathed thermocouple to a depth of at least 3 cm and securing the leads to the shafts of the rectrices with surgical clips.

Rates of gular flutter were determined by repeated measurements at each test temperature on birds put in a cylinder of wire mesh painted flat black and placed in the darkened incubator. The flashes from a Strobotac electronic stroboscope were directed onto the bird through the window of the incubator and their rate varied until the gular movement appeared to stop.

RESULTS

BODY TEMPERATURE (T_B)

During daytime measurements of oxygen consumption at ambient temperatures (T_A) of 5–35°C, normothermic mousebirds maintained relatively stable body temperatures of

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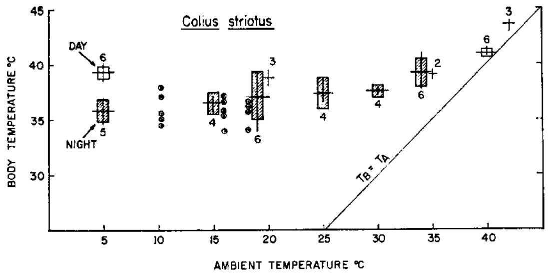

FIGURE 1. The relation of body temperature (T_B) to ambient temperature (T_A). The circles represent temperatures of individual birds huddled in an outdoor aviary at night. All other body temperatures were determined at the end of periods of measurement of oxygen consumption, either during daytime (unshaded) or at night (shaded). Vertical lines show ranges; horizontal lines show means; rectangles enclose the 95 per cent confidence interval ($\bar{x} \pm t \times \text{SE}$). For graphic purposes the symbols for the night T_B at 20 and 35°C are plotted 1° below the T_A at which they were measured.

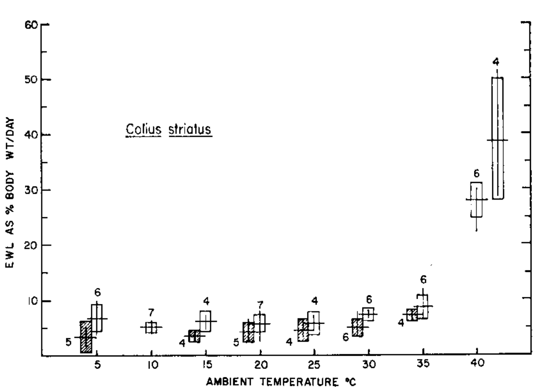

FIGURE 3. The relation of evaporative water loss (EWL) to T_A. Symbols and displacement of nocturnal values as in figure 1. See text for humidities.

about 39°C, but at ambient temperatures above 35°C they became hyperthermic (fig. 1). During the nocturnal measurements of oxygen consumption, body temperatures were more variable and lower than during the day. Most of the measurements fell between 35 and 38°C and T_B varied directly with T_A between 5 and 35°C. Body temperatures of birds huddled in groups at night in the outdoor aviary ranged from 34 to 38°C (mean = 35.7°).

OXYGEN CONSUMPTION ($\dot{V}O_2$)

The general shape of the curve describing the relation of $\dot{V}O_2$ to T_A is typical of that for small birds (fig. 2). The thermal neutral zone extends approximately from 25° to beyond 40°C. The mean minimal daytime oxygen consumption (1.2 cc/g-hr) of the six birds measured was about 25 per cent lower than the value predicted by the equation of Lasiewski and Dawson (1967) for nonpasserine birds. Oxygen consumption at all temperatures measured was slightly lower at night than during the day.

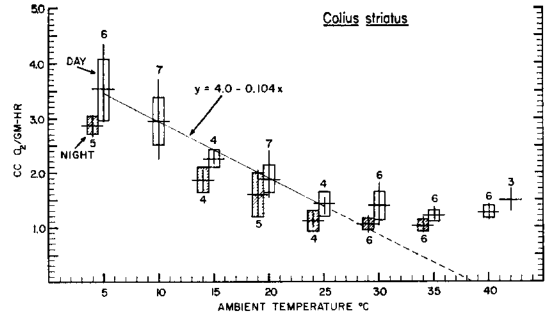

FIGURE 2. The relation of oxygen consumption to T_A. Symbols and displacement of nocturnal values as in figure 1. The line was fitted by the method of least squares to daytime values.

The slope of the least squares regression of daytime $\dot{V}O_2$ on T_A below thermal neutrality extrapolates to zero at a temperature of 38.5°C which is very close to the mean body temperature at rest. Thermal conductance ($\dot{V}O_2/T_B-T_A$) below neutrality was constant at 0.1 cc O_2/g-hr-°C during the day and decreased slightly to 0.09 at night. These figures are slightly but insignificantly lower than the value (0.12 cc O_2/g-hr-°C) predicted by the equations of Herreid and Kessel (1967) and Lasiewski et al. (1967).

EVAPORATIVE WATER LOSS (EWL)

Evaporative water loss (fig. 3) was independent of ambient temperatures of 5–30°C and was of the magnitude (5–6 per cent of body weight per day) expected for 50-g nonpasserine birds (Crawford and Lasiewski 1968). Above 35°C, evaporative water loss increased markedly. At all temperatures measured, it averaged lower at night than during the day. The humidity in the respirometer chamber, which is a function of the flow rate and rate of water loss by birds, was approximately 2.0 g H_2O/m^3 at all ambient temperatures of 5–30°C, and increased to 15.8 at 40°. At 42° the rate of air flow was changed from 700 to 1500 cc/min, which reduced the humidity in the chamber to 11.5 g H_2O/m^3 despite the increased water loss by the birds.

The fraction of metabolic heat dissipated by

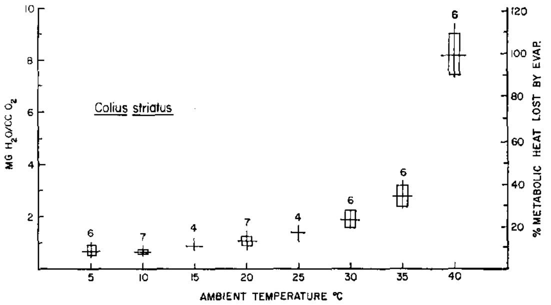

FIGURE 4. The ratio of evaporative water loss to oxygen consumption and the relation of evaporative cooling to metabolic heat production as functions of T_A. It is assumed that the oxidation of 1 cc of O_2 yields 4.8 cal and that 0.58 cal are required to evaporate 1 mg of H_2O. See text for humidities.

evaporation increased slowly from less than 10 per cent at 5°C to 33 per cent at 35°C. When exposed to heat stress the birds employed gular flutter (see below), and at 40°C and a water vapor pressure of 17 mm of Hg they were able to lose all of their metabolic heat by evaporation (fig. 4).

BREATHING RATE AND GULAR FLUTTER

At ambient temperatures of 5–35°C breathing rate averaged about 50 per min, but between 35 and 40°C it increased approximately two fold (fig. 5). The increase in breathing rate at the higher ambient temperatures was associated with an increase in amplitude of breathing and a progressive elevation in body temperature. However, under the conditions of measurement there was no regular relation between breathing rate and degree of hyperthermia (fig. 6).

Like members of several other nonpasserine orders, colies employ gular flutter as a device for enhancing evaporative cooling under conditions of heat stress (Bartholomew et al. 1968). Occasional brief and intermittent episodes of gular flutter occurred at ambient temperatures of 35°C. At higher ambient temperatures the duration of the periods of gular flutter increased but the rate of flutter remained relatively uniform (fig. 5). At ambient temperatures of 35–40°C, the birds occasionally twitched the gular area slightly at a frequency of about 200 per min with the mouth either open or closed, and they often gaped the mouth without gular flutter. At ambient temperatures above 40°C gular flutter was almost continuous.

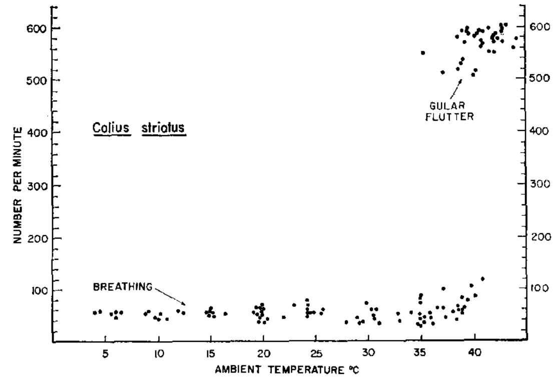

FIGURE 5. The rates of breathing and gular flutter in relation to T_A.

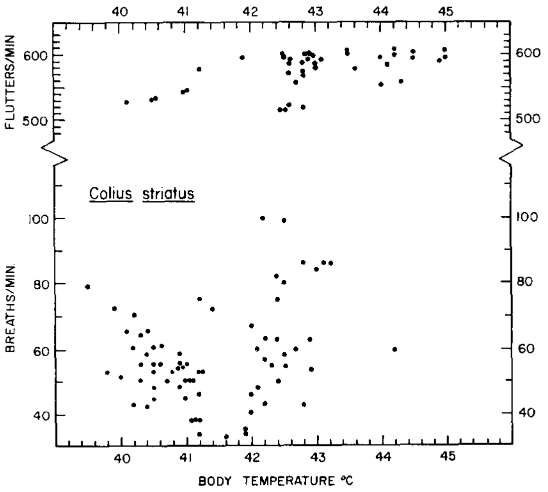

FIGURE 6. The rates of breathing and gular flutter in relation to T_B.

Intermittent gular flutter was observed in birds with body temperatures as low as 40.1°C. Sustained gular flutter commenced at body temperatures of 42.5° and was characteristic of all body temperatures above this level. The frequency of gular flutter appears to be virtually independent of extent of hyperthermia or degree of heat stress (fig. 6) and probably is a function of the natural resonant frequency of the gular area (see Lasiewski and Bartholomew 1966 for discussion).

HEART RATE

Minimal resting heart rates were inversely related to ambient temperature between 5 and 35° (fig. 7). The slopes of the least squares regressions of heart rate on T_A for the two birds from which complete sets of data could be obtained were similar and, unlike the curve for $\dot{V}O_2$, do not extrapolate to zero at $T_A = T_B$. The mean minimal resting heart rates of four

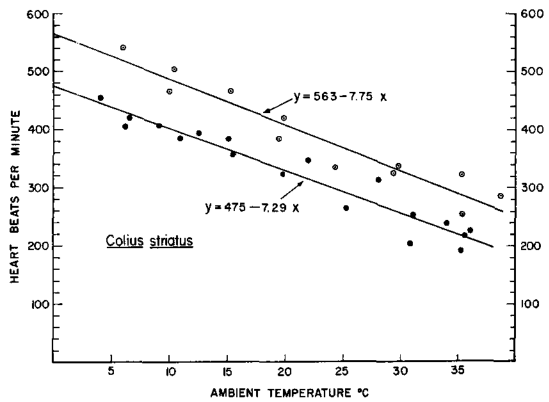

FIGURE 7. The minimal heart rates of two mousebirds in relation to T_A. The lines are fitted by the method of least squares.

individuals in the zone of thermal neutrality was 244 per min (range, 220–285). No systematic effort was made to determine maximal heart rates. However, the maximum rates observed were 580–590 per min. Both the minimal and maximal rates are lower than expected on the basis of size.

TORPIDITY

Although the significance of the phenomenon under natural conditions cannot yet be assessed, in the laboratory *C. striatus* can successfully enter and arouse from a state of torpor in which oxygen consumption is far below normal levels and body temperature falls 15°C or more (figs. 8 and 9).

We were able to induce daily cycles of torpor by gradually reducing the food ration until the weight of the birds fell 10–15 per cent below their customary weight of about 50 g. The onset of torpor always occurred during the night and arousal usually preceded the time when the lights came on in the morning. The colies were able spontaneously to increase their oxygen consumption while in a condition of profound hypothermia and produce sufficient heat by their own metabolism to arouse to normal levels of body temperature within 60–90 min in ambient temperatures of 19–20°C. During arousal, oxygen consumption rose to more than twice the standard level at 20°C and peaked prior to the attainment of the normothermic body temperatures (fig. 9).

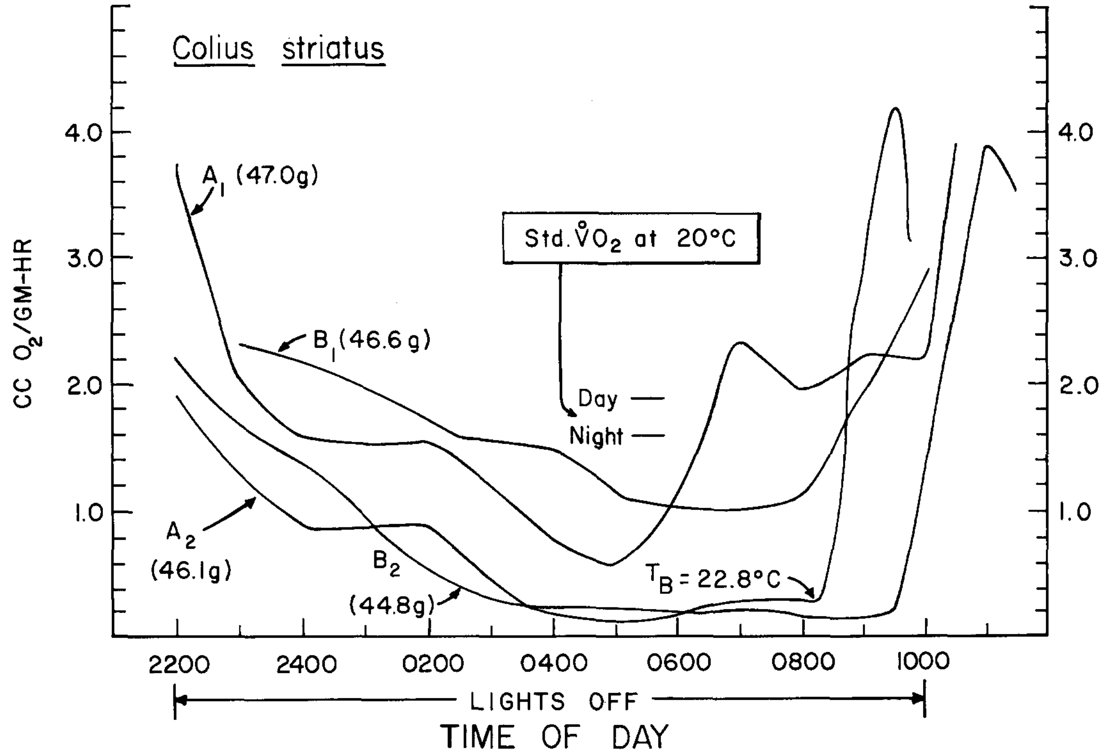

FIGURE 8. Continuous records of $\mathring{V}O_2$ of two mousebirds (A and B) on consecutive nights in a T_A of 19.2°C. The daily food ration was insufficient for weight maintenance and the birds were about 10 per cent below their usual weights. Three of the four arousals were spontaneous, but one (A_2) was caused by the attachment of a cloacal thermocouple. A detailed record of the course of T_B and $\mathring{V}O_2$ in A_2 is shown in figure 9.

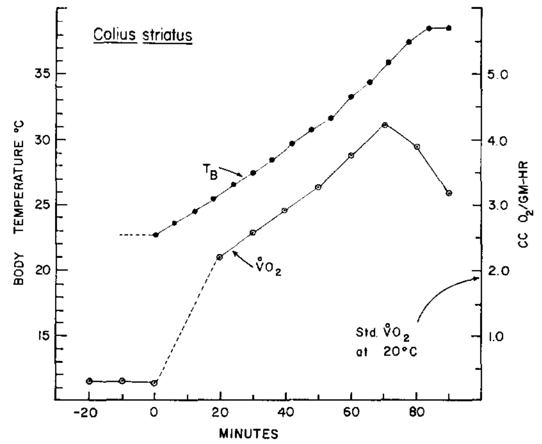

FIGURE 9. The course of T_B and $\mathring{V}O_2$ during arousal of A_2 (see fig. 8) in a T_A of 19.2°C. The torpid bird was removed from the respirometer at minute zero, a cloacal thermocouple was attached, and the bird was returned to the respirometer chamber by minute 3.

DISCUSSION

Even from this limited and exploratory study it is apparent that in thermoregulation, as in behavior and anatomy, colies are of unusual interest. Their body temperature, weight-relative oxygen consumption, and heart rate all average lower than those of passerines of similar size. Like other birds which employ fixed-frequency gular flutter they are able to use evaporative cooling at a minimal metabolic cost (Lasiewski and Bartholomew 1966; Bartholomew et al. 1968). Indeed, at an ambient temperature of 40°C and water vapor pressure of 17 mm Hg they dissipated by evaporation all of their metabolic heat at such small energetic cost that it was not measurable under the experimental conditions employed (fig. 2). However, like all birds, colies become hyperthermic when ambient temperatures approach or exceed the usual range of body temperatures. Hyperthermia, of course, facilitates heat loss by conduction and convection and reduces dependence on evaporative cooling.

The most interesting result of the present study is the demonstration that adult colies, like some humming birds, swifts, and caprimulgids, can enter a state of torpor in which body temperature falls 15°C or more below normothermic levels, and are then capable of arousing from this profound hypothermia by means of their own metabolic heat production without the addition of heat from any external source. The potential energy saving in birds of such a capacity has been considered elsewhere (e.g., Pearson 1950, 1960; Bartholomew et al. 1962; Lasiewski 1963) and need not be re-examined here. However, it is noteworthy that colies are neither very small, like hummingbirds, nor do they feed on airborne insects, like swifts and caprimulgids. Consequently, they do not have the necessity of maintaining a very high weight-relative metabolism, nor do they face the problem of short-term food shortages associated with poor weather, which presumably favor the evolution of the capacity for torpidity. Except for the instances mentioned above, experimental documentation for a nocturnal decline in body temperature of as much as 15°C is available only for the Inca Dove (*Scardafella inca*), and this species has extremely limited capacity for arousal to normothermic temperatures (MacMillen and Trost 1967).

The ecological importance of the capacity of colies to become torpid remains unknown. Their torpor cannot be attributed to an inability to thermoregulate. Our data and the observations of Rowan (1967:80) show that colies remain normothermic in temperatures near 0°C. The experimental instances of torpor were induced neither by cold nor wet, but occurred after a modest loss in body weight caused by a reduction in daily food ration. However, nothing is known about weight variation in colies under natural conditions. Cowles (1959:134) has pointed out that colies are almost exclusively vegetarian, and Rowan (1967:89) has emphasized that because of their relatively generalized food habits they are normally assured of an adequate "succession of indigenous fruit throughout the year."

About all that can be said at present is that individuals of one species of mousebird have the capacity for nocturnal torpidity at ambient temperatures near 20°C and that the ecological importance of this capacity awaits further study.

SUMMARY

Body temperature in quiet normothermic mousebirds averaged about 2°C lower than in passerine birds of similar size and showed a more marked nocturnal decline. The standard oxygen consumption for this nonpasserine species (1.2 cc/g-hr) was about 25 per cent less than predicted on the basis of weight, and thermal conductance (0.1 cc O_2/g-hr-°C during the day, and 0.09 at night) was slightly but insignificantly lower than the predicted value. Oxygen consumption was essentially independent of ambient temperature from 25° to

beyond 40°C, but evaporative water loss increased markedly at ambient temperatures above 35°C. Below 35°C, evaporative water loss was of the magnitude expected on the basis of body weight. Mousebirds employ gular flutter. At an ambient temperature of 40°C and a water vapor pressure of 17 mm Hg they were able to dissipate all of their metabolic heat by evaporation of water, at a negligible metabolic cost. The frequency of gular flutter, which is probably related to the natural resonant frequency of the gular area, was independent of the degree of heat stress or extent of hyperthermia.

Heart rate was inversely related to body temperature below the thermal neutral zone, and the mean minimal resting rate in thermal neutrality was 244 per min.

Captive colies maintained at about 20°C on a reduced food ration will enter a state of nocturnal torpor in which body temperature falls almost to air temperature and oxygen consumption is profoundly reduced. They are capable of arousing to a normothermic state in 60–90 min by metabolically produced heat. The significance of their capacity for dormancy in nature remains to be assessed.

ACKNOWLEDGMENTS

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