

Metabolic rate and body temperature of an African sunbird, *Nectarinia chalybea*: daily rhythm and the effect of ambient temperature

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The oxygen consumption ($\dot{V}O_2$) of the lesser double-collared sunbird, *Nectarinia chalybea*, was measured at ambient temperatures (T_a) from 7 to 35°C. The diel variation in body temperature (T_b) and wet thermal conductance (C) was also determined. The sunbirds (mean mass 8.36 g \pm S.E. 0.21 g) showed a pronounced diel cycle of $\dot{V}O_2$, with a mean reduction of 50% at night. Basal metabolic rate was estimated to be 3.23 ml $O_2/g.h$, which is 88% of the predicted value for a passerine bird of this size. There was a mean reduction in T_b of 3.6°C at night. Both day and night values of T_b decreased with decreasing T_a , as did individual values of C . Winter breeding in the south-west Cape is energetically stressful for lesser double-collared sunbirds, but they have the physiological capacity to reduce their energy expenditure substantially at night.

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In Africa, the smallest nectarivorous birds are the passerine sunbirds (family Nectariniidae). They occupy a similar niche to the hummingbirds of the Americas. Of the 118 species world-wide, most occur in the southern latitudes of the Old World, with 21 species in southern Africa (Skead 1967; Maclean 1993).

A large body of literature has accumulated on the energetics of nectarivorous birds, especially the hummingbirds (Trochilidae) and the Australian honeyeaters (Meliphagidae). Both field and laboratory measurements have been made of energy intake and expenditure. For some sunbirds from east and southern Africa, time-budget data and predictive equations from the literature on avian energetics have been used to estimate energy expenditure by free-ranging birds (e.g. Wolf 1975; Wolf, Hainsworth & Gill 1975; Gill & Wolf 1975; Frost & Frost 1980; Collins 1983). More recently, Williams (1993) used doubly labelled water to measure field metabolic rates in incubating *Nectarinia violacea*.

The only laboratory data on sunbird energetics and temperature regulation are from the preliminary study of Wolf *et al.* (1975) on *N. kilimensis*, and the work of Prinzinger and colleagues. Prinzinger, Lübben & Schuchmann (1989) investigated the metabolic physiology of 13 sunbird species, although their sample sizes were very small. Subsequently, Prinzinger, Schäfer & Schuchmann (1992) compared the smallest of the 13 species, *Aethopyga christinae*, with a hummingbird of the same body mass (about 5 g). In these studies metabolism of the sunbirds was lower than that of hummingbirds and within the range of expected values. Torpor was observed in all hummingbirds investigated, but in none of the sunbirds (Krüger, Prinzinger & Schuchmann 1982; Prinzinger *et al.* 1989, 1992).

The lesser double-collared sunbird, *Nectarinia chalybea*, has a wide distribution in southern Africa. Within South

Africa it ranges from the semi-arid west coast, through the coastal fynbos of the south-west Cape, to eastern forest habitats. In the winter rainfall region of the south-west Cape, *N. chalybea* breeds in winter (mainly July to September; Maclean 1993) when nectar is most abundant. Although the energy requirements of perching sunbirds are less than those of hovering hummingbirds, physiological mechanisms of energy conservation will be particularly important in the breeding season when foraging is constrained by low ambient temperatures, short photoperiod, and winter storms. The aim of this study was to investigate possible adaptations for conserving energy in *N. chalybea*, by measuring metabolic rate and body temperatures over the range of ambient temperatures experienced by these birds.

Materials and Methods

Capture and maintenance

Seven *N. chalybea* (two females and five males, body mass 8.36 \pm 0.21 g, mean \pm S.E.), were captured in mist nets at the Cape of Good Hope Nature Reserve during December. They were housed individually in cages measuring 50 \times 40 \times 30 cm, covered by 30% shade cloth. Each cage had several perches, a feeder and a dish of water for bathing or drinking. The birds were housed indoors with natural photoperiod and uncontrolled room temperatures. They were fed *ad lib.* with a mixture, renewed twice daily, of sucrose, water and Complan health food (Lotz & Nicolson 1996). Occasionally they were also given insects or spiders. The birds were kept in captivity for at least three weeks prior to any experimentation. All experiments were completed between January and April.

Metabolic rate

Rates of oxygen consumption ($\dot{V}O_2$) were measured in a

temperature-controlled room (accuracy $\pm 0.5^\circ\text{C}$) with a controlled photoperiod of 13L:11D. The respirometer was a 3 l sealable perspex metabolism chamber fitted with inlet and outlet ports, a thermocouple port, a feeder containing 11% (w/w) sucrose solution (Complan was omitted from the diet during experiments) and a single perch. A grid was placed in the bottom of the chamber to separate the bird from cloacal fluid voided during the experiment. The chamber was large enough for the bird to change position but too small to allow flight. The sucrose solution was available *ad lib.* during all experimental runs, but the birds do not feed during the dark period.

Measurements of $\dot{V}\text{O}_2$ were made with an open-flow system, using one channel of a two-channel Applied Electrochemistry S-3A oxygen analyser (Lighton 1985). Outside air was drawn through the metabolism chamber and dried before passing through a Hastings mass flowmeter. Thereafter, air was passed over CO_2 and H_2O absorbents before entering the oxygen analyser. Air flow rate was adjusted between 170 and 200 ml/min with higher flow rates being used at colder ambient temperatures. A copper-constantan thermocouple within the chamber, connected to a Bailey Bat 12 digital thermometer, measured ambient temperature (T_a). Recordings of oxygen concentration and T_a were made using either a data logger (Esterline Angus PD 2064), programmed to record at 10-min intervals, or a BBC microcomputer programmed to sample the voltage output of the oxygen analyser every 2 min and to convert this value to fractional concentration of oxygen. Control or baseline readings were taken at the beginning and end of each run without the bird in the chamber and corrections made for any baseline drift, assuming a linear change. Steady state $\dot{V}\text{O}_2$ values were calculated using the formula $\dot{V}\text{O}_2 = V(\text{FIO}_2 - \text{FEO}_2)/(1 - \text{FIO}_2)$, where FIO_2 and FEO_2 are incurrent and excurrent fractional concentrations of oxygen and V is the flow rate of dry air in ml/min. The error incurred by not absorbing CO_2 before the flowmeter was calculated to be a maximum overestimate of 1% in oxygen consumption, with the flow rates used and assuming RQs of either 1 or 0.75 (Withers 1977). All gas volumes were converted to STPD.

Oxygen consumption was measured at ambient temperatures ranging from 7–35°C. The initial 1.5 h of recordings after the birds had been introduced into the respirometer were considered as an equilibration period and the data discarded. All measurements of $\dot{V}\text{O}_2$ were continued for at least 12 h, incorporating part of both light and dark phases of the daily cycle, and some experimental runs lasted 24 h. Minimum values of metabolic rate were calculated separately for light and dark periods, as the mean of the six lowest consecutive values (i.e. over 1 h), and were expressed as ml $\text{O}_2/\text{g}\cdot\text{h}$. The body mass of each bird was recorded at the beginning and end of each run and the mean value used as the actual body mass for calculation of $\dot{V}\text{O}_2$. The effect on metabolic rate of continuous light and reversal of the light cycle was also tested.

Body temperatures

These experiments were run after those on oxygen consumption. Three birds were used (one female, 8.2 g; two males, 8.9 and 9.1 g). In order to facilitate handling, they were housed individually in small cylindrical cages (9.5 cm diameter \times

17.0 cm high) covered with shade cloth and containing a perch and feeder. Body temperatures (T_b) were measured every 3 h over 24-h periods at T_a 's from 10 to 35°C. A fine copper-constantan thermocouple was inserted about 1 cm into the cloaca for each measurement, and T_b was measured within 30 s of handling. The thermocouple was connected to a Bailey Bat thermocouple thermometer, and the system was calibrated against an accurate mercury thermometer prior to use. Birds were always handled with woollen gloves, kept at the same T_a , to minimise conductive heat transfer.

Statistics

Mean values are expressed \pm S.E. Least squares regression was used to determine the relationship between two variables. Slopes and elevations of regression lines were compared using a variant of the Student's t test (Zar 1996). Results were considered significant at $p < 0.05$.

Results

Diurnal cycle of oxygen consumption

Once the birds had become used to the experimental procedure and the metabolism chamber, they were remarkably quiet when subsequently introduced into the chamber. The sunbirds showed a distinct diel rhythm in $\dot{V}\text{O}_2$ at all T_a 's tested. Metabolism during the day (active or light phase) was always conspicuously higher and more variable than at night (passive or dark phase) (Figure 1). Night values ranged between 36.0 and 69.8% of the mean lowest values recorded during the day, with an average of $50.5 \pm 1.0\%$. The birds responded almost immediately to a reversal in lighting, irrespective of the time of day, by either increasing (light turned on) or decreasing (light turned off) their metabolic rate. When the birds were kept in constant light, however, an endogenous cycle of metabolic rate was apparent (Figure 2). The abrupt change in metabolic rate which occurred under normal lighting conditions was replaced by a gradual reduction in metabolic rate, beginning at around 20h00, reaching its lowest

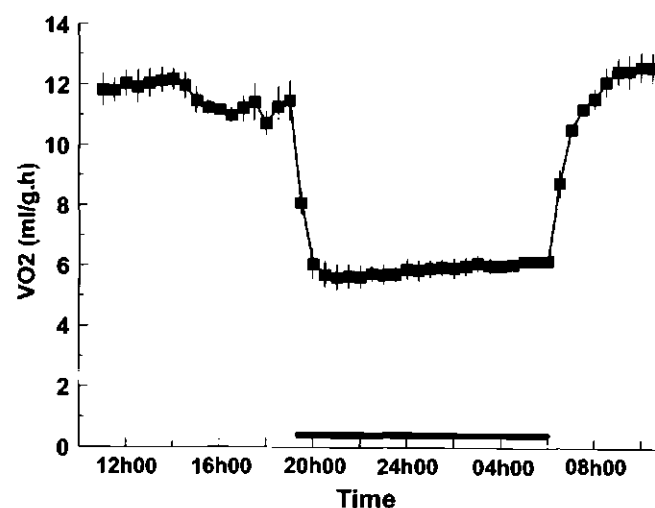


Figure 1 Diurnal cycle of oxygen consumption (ml/g.h) of *Nectarinia chalybea* ($n = 4$) at 22°C. Horizontal line indicates dark period. Standard errors larger than symbol diameter are indicated by vertical bars.

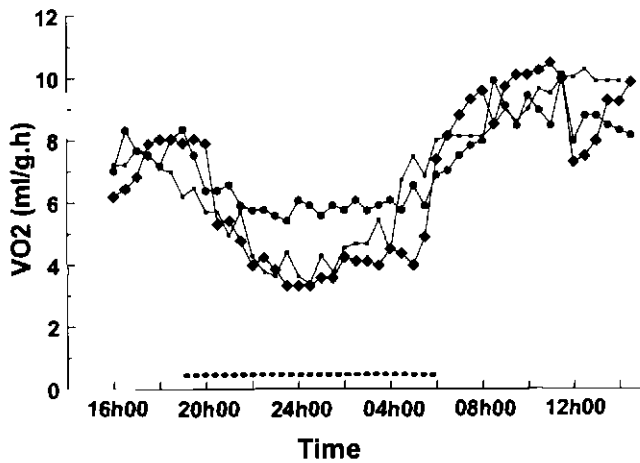


Figure 2 Oxygen consumption (ml/g.h) of three *N. chalybea* maintained in continuous light at 29°C. Dashed line indicates normal dark period.

value around midnight, and increasing gradually from about 05h00. The change in amplitude was, however, similar to that measured under normal lighting conditions.

Oxygen consumption at different ambient temperatures

At night, at the lower limit of thermoneutrality of about 33°C (see Figure 3), the basal metabolic rate of *N. chalybea* was estimated to be 3.23 ± 0.09 ml O₂/g.h (65.1 ± 1.9 J/g.h). The lowest metabolic rate recorded during the day was 7.30 ± 0.26 ml/g.h (146.8 ± 5.3 J/g.h) at a Ta of 35°C (thermoneutrality during the day was not readily apparent, but probably lies around 35°C). These values can be compared with those calculated from the predictive equations of Aschoff & Pohl (1970) for a passerine bird weighing 8.36 g: 3.69 ml/g.h for the resting phase and 5.03 ml/g.h for the active phase. Using the equation of Prinzinger *et al.* (1989) for sunbirds gives a lower estimate, 2.78 ml/g.h, for the resting phase.

When Ta was below thermoneutrality, mass-specific metabolic rate at night increased according to the equation:

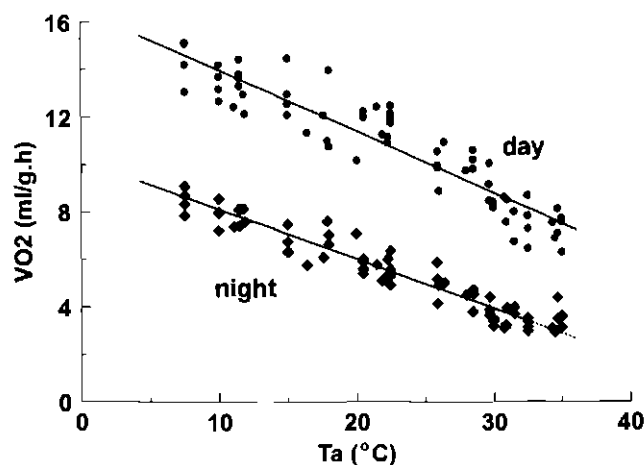


Figure 3 Rates of oxygen consumption (ml/g.h) of *N. chalybea* as a function of ambient temperature. Regression equations for day values, and for night values below 33°C, are given in the text.

$$\dot{V}O_2 \text{ (ml/g.h)} = 10.10 - 0.207T_a \text{ (}^\circ\text{C)}$$

$$(n = 61; r^2 = 0.92; p < 0.001).$$

The equation for the regression of daytime values of $\dot{V}O_2$ on Ta (Figure 3) was:

$$\dot{V}O_2 \text{ (ml/g.h)} = 16.48 - 0.255T_a \text{ (}^\circ\text{C)}$$

$$(n = 68; r^2 = 0.86; p < 0.001).$$

The slopes of these two regression lines were significantly different ($p < 0.001$), as were the intercepts ($p < 0.01$).

Body temperatures

Body temperatures (Tb) showed a diel rhythm, with values at night being consistently lower (by $3.6 \pm 0.2^\circ\text{C}$) than those during the day (Figure 4). Both day and night values of Tb were labile and were positively correlated with Ta, according to the equations:

$$\text{Day: } T_b \text{ (}^\circ\text{C)} = 36.36 + 0.172T_a \text{ (}^\circ\text{C)}$$

$$(n = 18; r^2 = 0.86; p < 0.001)$$

$$\text{Night: } T_b \text{ (}^\circ\text{C)} = 31.73 + 0.216T_a \text{ (}^\circ\text{C)}$$

$$(n = 18; r^2 = 0.88; p < 0.001).$$

The slopes and intercepts of these lines were significantly different ($p < 0.001$).

Although nocturnal Tb was always above 30°C in the three birds whose Tb was measured over 24 h, the lowest value recorded in any of the birds was 29.3°C at a Ta of 10°C (but see Discussion). The highest individual Tb was 42.9°C at a Ta of 35°C.

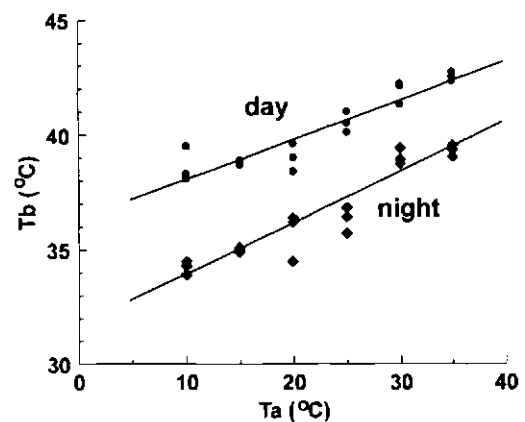


Figure 4 Body temperature of three *N. chalybea* as a function of ambient temperature. Each point is the mean of 5 (day) or 4 (night) measurements of Tb in an individual bird (Tb was measured at 3-h intervals in 3 birds, from 11h00 to 11h00). Regression equations for day and night values are given in the text.

Conductance

The slope of the regression of night $\dot{V}O_2$ on Ta could not be used as an estimate of minimal wet thermal conductance (C), since extrapolation of this line meets the x-axis (see Figure 3) at a temperature (48.8°C) well above the highest Tb measured in the sunbirds. Neither could McNab's (1980) correction factor be applied to the present situation, because the Tb of *N.*

chalybea is not constant. Therefore, C was calculated at each Ta below thermoneutrality from measurements of $\dot{V}O_2$ and Tb for individual birds, according to the equation $C = \dot{V}O_2 / (T_b - T_a)$ (McNab 1980). These results should be viewed with caution, since the $\dot{V}O_2$ and Tb data were acquired in separate experiments. The calculated values of C were positively correlated with Ta (Figure 5), but the scatter was such that the slopes and intercepts of the regression lines for day and night values did not differ significantly ($p > 0.05$):

Day: $C(\text{ml/g.h.}^\circ\text{C}) = 0.26 + 0.016T_a (^\circ\text{C})$
($n = 15$; $r^2 = 0.81$; $p < 0.001$)

Night: $C(\text{ml/g.h.}^\circ\text{C}) = 0.23 + 0.006T_a (^\circ\text{C})$
($n = 15$; $r^2 = 0.52$; $p = 0.002$)

The mean of the lowest values for calculated C (those at night at Ta's of 10, 15 and 20°C) was assumed to be the minimal wet thermal conductance at $0.32 \pm 0.01 \text{ ml O}_2/\text{g.h.}^\circ\text{C}$. This is 45% higher than the predicted minimal wet thermal conductance ($0.22 \text{ ml/g.h.}^\circ\text{C}$) for a passerine of 8.36 g for the passive phase (Aschoff 1981). However, our calculated value is in good agreement with estimates of 0.31 and $0.29 \text{ ml/g.h.}^\circ\text{C}$ from the prediction equations of Herreid & Kessel (1967) and Lasiewski, Weathers & Bernstein (1967) respectively. The lowest conductance calculated for the day phase was $0.44 \pm 0.02 \text{ ml/g.h.}^\circ\text{C}$ at 10°C, but this was unlikely to be minimal since the curve of conductance vs Ta had not yet flattened out. This value is 38% higher than the predicted value of $0.32 \text{ ml/g.h.}^\circ\text{C}$ for the day phase (Aschoff 1981).

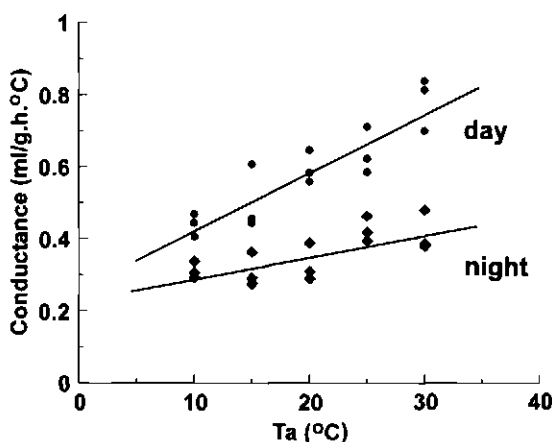


Figure 5 Calculated conductance ($\text{ml/g.h.}^\circ\text{C}$) of *N. chalybea* as a function of ambient temperature. Regression equation for day and night values are given in the text.

Discussion

Lesser double-collared sunbirds showed a clear diel rhythm in metabolism, like the sunbirds studied by Prinzing *et al.* (1989). At ambient temperatures from 7–35°C, the reduction in $\dot{V}O_2$ at night averaged 50%. Over an 11 h dark period, this represents a substantial energy saving. For example, the four birds whose diel cycle at 22°C is illustrated in Figure 1 would have used 45.7–49.9 kJ of energy in 24 h if their daytime rates of $\dot{V}O_2$ were maintained at night. Actual daily energy use was 34.5–38.4 kJ, a saving of about 23%. Energy savings

calculated from the regression equations of $\dot{V}O_2$ on Ta, assuming a 13L:11D light cycle, vary from 19% at 5°C to 29% at 35°C, when the nocturnal reduction in $\dot{V}O_2$ is greatest (Figure 1). A similar 50% drop in metabolic rate in finches at night represents daily energy savings of about 33% and 18% in winter and summer respectively, owing to the longer daily duration of hypometabolism in winter (Saarela, Klapper & Heldmaier 1995).

Daytime $\dot{V}O_2$ values are elevated by the specific dynamic effect of ingested food as well as higher Tb and increased activity. The 50% difference in metabolic rate between active and resting phases of the daily cycle is twice that expected for passerine birds (25%; Aschoff & Pohl 1970). In previous work on sunbirds, this was ascribed to the fact that the birds were able to fly in large (8.7 l) metabolic chambers (Prinzing *et al.* 1989, 1992). Powers (1991) used an even larger metabolism chamber for hummingbirds and measured high and very variable $\dot{V}O_2$ during the day. Our 3-l respirometer precluded flight and daytime $\dot{V}O_2$ was much less variable (Figure 1), but still approximately double the night-time values.

Probably because of the high level of activity of the hummingbirds in his experiments, Powers (1991) found laboratory energy expenditure to be as high as that measured in the field using doubly labelled water. The only measurement of field metabolic rate in sunbirds is that of Williams (1993), who obtained a value of 66 kJ/day in female *N. violacea* (9.5 g) incubating eggs in winter. This can be compared with our laboratory data for a 13L:11D light cycle and constant temperature: 45 and 36 kJ/day at 10 and 20°C respectively. When maintained in the laboratory at a constant 20°C, *N. chalybea* ingest 2.1 g of sucrose daily, representing an energy intake of 37 kJ (C.N. Lotz, unpublished). Using time budgets and predictive equations, other authors have estimated daily energy expenditure of sunbirds as 71 kJ, 54 kJ and 55 kJ in territorial *N. famosa* (13.5 g), *N. reichenowi* (15.0 g) and *N. olivacea* (12.1 g) respectively (Wolf 1975; Gill & Wolf 1975; Frost & Frost 1980), and as 53 kJ in *N. violacea* (9.9 g; Collins 1983). In the territorial birds, 6–13% of the energy was expended on defence (Frost & Frost 1980). The assumption was made that Tb is not lowered at night, which means that overnight costs may have been overestimated, as pointed out by Gill & Wolf (1975). This caution is justified by the data of Prinzing *et al.* (1989) and the present study.

The reduction in metabolic rate at night was accompanied by a lowering of Tb by 3.6°C on average. This is a slightly larger day-night difference than the 3.2°C predicted for an 8.36-g passerine (Aschoff 1982). Prinzing *et al.* (1989) also observed nocturnal hypothermia in sunbirds, but not daily torpor. However, $\dot{V}O_2$ and Tb were later measured simultaneously overnight in the same lesser double-collared sunbirds used in the present study, after they had been deprived of food for 3 h before the start of the dark period, and five out of six birds apparently entered torpor at a Ta of 10°C (J.R.B. Lighton & B. Leon, unpublished data). Their minimum Tb's were in the range 24.3–26.5°C, and $\dot{V}O_2$ in four of the birds was reduced to only 3.3–3.6 ml/g.h (cf. the night values of about 8 ml/g.h at 10°C in Figure 3). The birds were able to arouse spontaneously. When Ta was 20°C, only two out of five birds tested reduced their Tb to this extent. It thus appears that torpor may be utilised as an energy-saving mech-

anism when reserves fall below the threshold needed for overnight energy expenditure (Hainsworth, Collins & Wolf, 1977). Two previous publications have suggested that sunbirds become hypothermic: on cold nights in montane regions of Kenya, Cheke (1971) found Tb of several sunbird species dropped 5–17°C lower than daytime values, and Williams (1993) measured an egg temperature of about 29°C for over 3 h under an incubating female *N. violacea* presumed to be in negative energy balance. Moderate nocturnal hypothermia in two species of manakins (small tropical frugivores) studied by Bartholomew, Vleck & Bucher (1983) was shown to result in substantial energy savings. These authors present a model relating energy savings to the degree and duration of nocturnal hypothermia: according to this model, a reduction in Tb of 3.6°C for 11 h results in energy savings of 23%, which is in excellent agreement with our data.

The Tb of *N. chalybea* was depressed at low Ta, being approximately 34°C at night at a Ta of 10°C (Figure 4). Similarly, Lasiewski (1964) found that non-torpid hummingbirds resting in the dark in a postabsorptive state regulated their Tb between 34.4 and 41.2°C over a wide range of Ta's. Two species of honeyeaters show mild hypothermia at low Ta, with measured Tb's as low as 32–34°C when Ta is below 12°C (Collins, Cary & Payne 1980).

The nocturnal decrease in thermal conductance is a result of nocturnal hypothermia and changes in posture and ptile-erection of the plumage which result in more effective insulation. Conductance also decreases at lower Ta's in *N. chalybea*. MacMillen (1974) found that calculated thermal conductance in the Hawaiian honeycreeper *Loxops virens* was directly related to Ta, and considered this to be of ecological significance in reducing heat loss at night in a forest habitat where Ta frequently drops below 10°C.

Small nectar-feeding birds are especially susceptible to energetic stress because of their high metabolic costs and low storage capacity. In the south-west Cape winters, *N. chalybea* needs extra energy for reproduction and for thermoregulation at low Ta, while at the same time its food intake is reduced by short photoperiods and relatively low nectar concentrations. We have shown that under laboratory conditions *N. chalybea* has a basal metabolic rate less than predicted on the basis of body mass and further reduces its metabolic rate dramatically at night. Controlled hypothermia at night and at low Ta reduces the temperature gradient between bird and environment, and decreases metabolism through the Q₁₀ effect. Heat loss is also reduced by decreasing thermal conductance at night and at low Ta. *Nectarinia chalybea* thus has the physiological capacity to reduce its energy expenditure substantially under conditions of energetic and thermal stress.

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