THERMOREGULATION AND NOCTURNAL HETEROTHERMY IN THE WHITE-BACKED MOUSEBIRD (*COLIUS COLIUS*).

by

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PREFACE

The experimental work described in this dissertation was carried out in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from February 1997 to November 1998, under the supervision of Dr Barry G. Lovegrove.

These studies represent original work on my part and have not otherwise been submitted in any form for any degree or diploma to any University. During the course of interpreting the data, an alternative interpretation was suggested to me by Dr Lovegrove. I have chosen to apply this interpretation to some of the data, and have subsequently developed several of the arguments presented below based on this interpretation. Where use has been made of the work of others it is duly acknowledged in the text.

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ABSTRACT

Thermoregulatory patterns, the use of rest-phase heterothermy, the energetic significance of clustering behaviour, and the role of sunning behaviour in thermoregulation were assessed in the white-backed mousebird *Colius colius*, an southern African arid zone species. I hypothesised that *C. colius* makes significant rest-phase energy savings by means of clustering behaviour, and has the ability to reduce diurnal energy costs by utilising solar radiation. I tested these hypotheses using indirect calorimetry and surgically implanted temperature-sensitive telemeters, and by simulating solar radiation in a constant-environment chamber.

Rest-phase body temperature (T_b) was highly labile, with rest-phase T_bs of down to 26°C being recorded. During the rest-phase, T_b was not regulated with respect to a setpoint temperature, as typically occurs in endotherms. Rather, rest-phase T_b patterns were characterised by periods of linear decreases (passive cooling) at a rate dependent on ambient temperature and the number of individuals in a group. I did not observe any instances of torpor, as described in the literature. When T_b depression did occur, it appeared to be the result of passive heat loss, and not the metabolic down-regulation which typically precedes a torpor bout. These findings, together with the phylogenetic position of the Coliidae, raise questions regarding the evolution of torpor. The inability of individual mousebirds to maintain a rest-phase setpoint T_b suggests that in *C. colius* the physiological mechanism responsible for the defence of a rest-phase setpoint T_b is replaced by a behavioural mechanism, namely clustering behaviour.

The birds in this study showed a basal metabolic rate 40% below the predicted allometric values, and a circadian amplitude of body temperature (T_b) of 5.2°C, 195% of the predicted value. The use of linear independent contrasts revealed that these deviations from the expected allometric values are not due to the phylogenetic relationships of the Coliiformes, and hence are likely to represent adaptation. These conservative metabolic traits offer opportunities for significant energy savings and are presumed to be adaptive in the unpredictable habitat of this species.

The birds were able to make significant energy savings by means of huddling behaviour. At an ambient temperature of 15 °C, the energy expenditure of birds in a group of six was 50% of that of single birds. The energy savings the birds were able to make were dependent on ambient temperature and the number of birds in the group. The ability to lower energy requirements by means of huddling behaviour is likely to be highly adaptive when dealing with low nocturnal temperatures in an environment where food supplies are spatially and temporally unpredictable.

When allowed access to simulated solar radiation, individual mousebirds showed 15 - 30% reductions in their energy expenditure, while maintaining a constant body temperature. These reductions in energy expenditure hence represent thermoregulatory savings. My results support the hypothesis that solar radiation may be important in the energy budgets of some bird species. The ability to reduce food requirements by means of absorbing solar radiation is likely to be strongly selected for in the arid areas inhabited by *C. colius*, which are characterised by large circadian fluctuations in ambient temperature, in addition to resource unpredictability. Thermoregulation in *C. colius* appears to involve an interaction of behavioural patterns and physiological traits.

ACKNOWLEDGEMENTS

My sincere thanks go to my supervisor, Dr Barry Lovegrove, for his enthusiasm and interest in my project. I believe that I have learnt valuable academic skills from studying under his supervision, and that these skills will benefit me greatly during future research. During the course of my studies, Dr Lovegrove kindly paid for me to attend a conference in Finland. This was a valuable experience for which I am grateful.

Several farmers provided me with accommodation and permission to work on their farms during the course of this study. I would like to thank Graham Koster (Withart), Ralph and Diana Koster (Mimosa Lodge), Edwin and Danielle Jackson (Omdraaisvlei), Julian and Maritisan Theron (Wonderboom) and Mike and Gail Hall for their hospitality. In addition, I would like to thank Richard and Sue Dean, for their hospitality and for allowing me to use Tierberg Research Station, Christiaan de Wit (Laer Scholzkloof) for permission to trap on his farm, and Leighton Hare for permission to carry out behavioural observations in the Karoo National Park. Several people at the University of Natal provided assistance at various stages of the project. Colin Everson kindly trained me in the use of a spectroradiometer, and Prof. Mike Savage and Gastao Lukango helped me use a pyranometer. Jaishree Raman fed my birds during my frequent absences from the Department. This work was partly funded by the Foundation for Research Development.

Finally, and most importantly, I would like to thank my parents for their continuing support. This project represents a considerable financial investment on their part, and without their assistance would not have been possible. Through-out my university career they have been a source of advice and encouragement, and I am extremely grateful to them.

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CHAPTER 1. THERMOREGULATION, NOCTURNAL HETEROTHERMY AND THE ENERGETIC SIGNIFICANCE OF CLUSTERING BEHAVIOUR.

INTRODUCTION

Clustering (or huddling) behaviour is important in the thermoregulation of many endotherms, and is common in small mammals and birds (Reinertsen, 1983). Generally, the energetic value of clustering is directly proportional to the temperature gradient between the animal and its environment and the number of animals forming the cluster (Davenport, 1992; Boix-Hinzen & Lovegrove, 1998). Vickery & Millar (1984) examined the energetics of clustering using a mathematical model and suggested that this behaviour becomes energetically advantageous whenever ambient temperature and nest temperature decrease below the thermoneutral zone. These benefits also apply if the animal enters torpor, provided that body temperature does not approach nest temperature (Vickery & Millar, 1984).

Clustering is particularly important for species permanently resident in temperate and sub-arctic regions subject to strong seasonal patterns of cold and food availability (Reinertsen, 1983; du Plessis, Weathers & Koenig, 1994). Typically, the onset of winter is associated with an increase in thermoregulatory energy demands coinciding with a decrease in food availability and quality (Karasov, 1983). Clustering is also important for young mammals and birds in which endothermy has not yet developed fully (Davenport, 1992).

The energetic benefits of communal roosting are particularly significant in small bird species (Chaplin, 1982; Walsberg, 1990). In small birds, the high rates of heat loss associated with small size are decreased by a reduction in the surface area: volume ratio resulting from clustering (Weatherhead, Sealy & Barclay, 1985). The potential risks of huddling have been discussed by Weatherhead *et al.* (1985) and Davenport (1992).

The adaptive value of clustering is not limited to high latitudes. Boix-Hinzen & Lovegrove (1998), for example, have shown that Afrotropical red-billed woodhoopoes *Phoeniculus purpureus* significantly reduce energy expenditure during the rest-phase by huddling.

Clustering behaviour is particularly common in the mousebirds (Coliiformes), an order endemic to the Afrotropics (Rowan, 1967). The Coliiformes diverged approximately 100 million years B.P., and are not closely related to any other avian order (Sibley & Ahlquist, 1990). All six species form tight clusters of up to 14 individuals during cold weather or even during the hottest hours of the day (Yamagishi & Kabango, 1986). Brown & Foster (1992) investigated the energetic value of clustering in the speckled mousebird *Colius striatus* and concluded that clustering resulted in significant energetic savings at night or in cold, wet weather. These authors suggested that clustering during warm weather probably serves a social function.

The white-backed mousebird (*Colius colius*) occupies the most arid habitat of all six mousebird species (with the possible exception of the white-headed mousebird *C. leucocephalus*), and is endemic to the western regions of southern Africa where it occurs in arid to semi-arid scrub and riverine bush (Fry, Keith & Urban, 1988; Maclean, 1993). These Karoo regions, typical of semi-arid deserts, are characterised by erratic rainfall patterns and low productivity (Noy-Meir, 1973; Lovegrove, 1993). Such environmental conditions are likely to be important in the selection for physiological traits resulting in energy conservation.

Mousebirds generally display low basal metabolic rates (Bartholomew & Trost, characterised by unpredictable fluctuations in resource availability , it is likely that metabolic traits that conserve energy have evolved in this species. In this study I test several predictions concerning the energetic significance of clustering behaviour and energy-conserving physiological traits. I predicted that *C. colius* should show conservative metabolic traits, manifested as a lower BMR and higher circadian amplitudes of T_b and MR than those predicted by standard allometric equations. I also predicted that *C. colius* should make significant energy savings by means of nocturnal clustering behaviour and that the extent of these savings should be related to firstly, the number of birds in a cluster and secondly, the ambient temperature at which the clustering takes place.

MATERIALS AND METHODS

Thirty white-backed mousebirds were trapped in the Karoo, South Africa during April 1997 using mist-nets and walk-in traps baited with fruit. The birds were caught at a) Tierberg Research station near Prince Albert, b) the farm Laer Scholzkloof near Prince Albert, and c) the farm Omdraaisvlei approximately 70km south-east of the Orange River at Prieska. Upon capture, the birds were weighed and marked with celluloid split rings for individual identification. Upon capture, the mean body mass was 40.2 ± 6.2g. In captivity, M_b dropped by approximately 13% before stabilising. They were transported by road to the Department of Zoology and Entomology at the University of Natal, and housed in two outdoor aviaries (1m wide x 1m high x 3m long). The positioning of the aviaries allowed the birds to sun themselves at any time between sun-rise and sun-set. They were fed chopped spinach, apples, bananas, grapes and pears, together with a protein supplement (Avi-Plus; Denrob, Durban). Water was available in the aviaries *ad libitum*, although the birds were not observed to drink. Experiments were conducted during July and August 1997.

Measurement of T_b

Temperature-sensitive telemeters (Model XM, Mini-mitter Co., Sunriver, Oregon) calibrated with a standard mercury thermometer (0.05 °C) in a water bath at temperatures from 5 - 45 °C were implanted into the intra-peritoneal cavities under inhalation anaesthesia (Isoflourane in oxygen; induction and maintenance, 2%; flow rate, *ca* $1 \ell.\text{min}^{-1}$). The mini-mitters weighed approximately 1.2 after being encased in wax, and measured 12mm in length and 7mm in diameter. Hence the weight of each mini-mitter was equivalent to approximately 3.4% of the M_b of the mousebirds. The mini-mitter signals were detected using dual antennae attached to perspex sleeves surrounding the respirometers. The signals were converted to TTL waves using a monostable multi-vibrator and then converted to voltages using a frequency-to-voltage converter. Ambient temperatures in the cabinet and the respirometers were measured with thermistor probes, calibrated in a similar way.

Metabolic measurements

Metabolic rate was measured indirectly as oxygen consumption (VO_2). All metabolic measurements were made in respirometers constructed from clear perspex under a light:dark cycle matched to the natural photoperiod prevailing at the time i.e. that in the aviaries. The mean M_b of the birds at the time the experiments were undertaken was 35.1 ± 5.3g. Measurements of single birds and two birds were made in 4dm^3 respirometers (22cm high, 12cm wide, 15cm long), whereas measurements of four or six birds were made in 17,5 dm^3 respirometers (35cm high, 20cm wide, 250cm long). The respirometers were placed in a 1 m^3 sound-proof constant environment cabinet. Measurements of VO_2 were made using an open flow-through system. Atmospheric air, acting as the control gas, was pumped from outside the building, partially dried using silica gel, and pumped into the cabinet at approximately 5ℓ.min^{-1} (relative humidity < 50%). This air was drawn through the respirometers at flow rates chosen to maintain less than one percent oxygen depletion between the incurrent and excurrent air. Flow rates were adjusted according to the number of birds in each respirometer and varied from *ca.* 0.6 to 2.5 ℓ.min^{-1}. Air was drawn into each respirometer at the base and removed at the top, hence maintaining a constant flow of air past the bird(s). Flow rate was measured with a Brooks thermal mass flow meter (Model 5810) factory calibrated to STP at sea level. The use of solenoid valves and a pump for each respirometer allowed up to five respirometers, as well as a control channel, to be used simultaneously. The excurrent air from each respirometer was passed via CO_2-proof tubing through a water condenser and a CO_2 scrubber to remove water vapour and CO_2 gas respectively. After passing through pumps, relay valves, filters and the mass flow meter, the excurrent air was subsampled with an oxygen analyser (Model S-3A/1, Ametek) and an oxygen sensor (Ametek N-22M) to determine the fractional concentration of oxygen in the dry air. The fractional concentration of oxygen in the control channel was measured every cycle (6 minutes or less, depending on number of respirometers being used) and O_2 measurements for the experimental channels were subtracted from this control value. In this way the inherent problem of long-term drift in the output of the O_2 analyser was limited to that which could occur over a maximum of 6 min, thus permitting long-term measurements of VO_2. Analog signals from the thermistor probes, mini-mitters, mass flow meter and oxygen analyser were digitised using an A/D converter and recorded on a multi-channel WINDOWS-based recording program written by Dr Barry Lovegrove. The sampling interval for each respirometer varied from 3 min to 6 min, depending on the number of respirometers used at any one time. Metabolic rates were calculated using the equation $VO_2 = V_E(F_{I\,O2} - F_{E\,O2}) / (1 - F_{I\,O2})$ where VO_2 = metabolic rate (m$\ell O_2.h^{-1}$), V_E = flow rate (mℓ.min^{-1}), $F_{I\,O2}$ = incurrent fractional O_2 concentration and $F_{E\,O2}$ = excurrent fractional O_2 concentration (Withers, 1977).

Experimental Protocol

Determination of zone of thermoneutrality

The lower critical limit of thermoneutrality (T_{lc}) was determined (28.8 ± 2.4°C) to permit subsequent circadian measurements of metabolic and T_b parameters to be made at thermoneutrality. Nine birds were placed in respirometers at approximately 16h15 and measurements commenced at 16h30. During two 10-hour sessions on subsequent nights, each bird spent 2 hours at each ambient temperature (15, 18, 21, 24, 27, 28, 30, 32, 34 and 36°C), and resting metabolic rate (RMR) was calculated as the mean of the three lowest consecutive data points during the last 30 min at each temperature. Linear regressions of RMR as a function of T_a at $T_a \leq 27°C$ were calculated for each bird using the method of least squares fit (Zar, 1984). The lower critical limit of thermoneutrality (T_{lc}) was calculated for each bird as the intercept of this regression line on the lowest observed VO_2 value (assumed to represent BMR) for that individual.

Minimum wet thermal conductance (C_{min}) was taken as the slope of the regression line for RMR as a function of T_a at $T_a < T_{lc}$, as described by McNab (1980). This method expresses C_{min} as a measure of the ease of heat flow between an organism and it's environment in mℓ O_2.(g.h.°C)$^{-1}$ and has been extensively employed for more than four decades (Scholander, Hock, Walters & Irving, 1950; Tucker, 1965; Herreid & Kessel, 1967; Bradley & Deavers, 1980; McNab, 1980; Aschoff, 1981; Dawson & Dawson, 1982). Theoretically, conductance should be expressed as the rate of heat transfer per unit area (W.cm^{-1}.°C) (Dawson & Schmidt-Nielsen, 1966; Ward & Pinshow, 1995). However, this method requires an accurate determination of the surface area of the animal. I opted for the former method because of the practical difficulties of accurately determining the surface area of a mousebird, and for ease of comparison with data published in the literature.

Circadian measurements

To determine circadian measures of DEE and associated metabolic parameters, oxygen consumption and T_b were measured for 24 hours in nine birds. The BMR, daily energy expenditure (DEE), and the amplitude of circadian T_b cycles (R_t) were calculated from these data.

Energetics of clustering

To assess the energetic significance of clustering, single birds or groups of birds were placed in the respirometers at *ca.* 16h00, at least 90 min prior to the experimental scotophase. Measurements of RMR, rest-phase energy expenditure and various T_b parameters were made at $T_a = 5$, 15 and 25°C. At each T_a, measurements were made in nine single birds, five groups of two birds, four groups of four birds and three groups of six birds. The only exception were the data for single birds at $T_a = 5$°C. Of the nine birds tested, four suffered visible hypothermia, and hence data for the five remaining birds were used in the analyses. Where groups of birds were used, only one bird in each group was implanted with a telemeter and was the source of T_b data for that group. This restriction was imposed by the amplitude-modulated nature of the mini-mitter signals.

Data analysis

Yeager & Ultsch (1989) have proposed a procedure for objectively determining where a deviation or inflexion from steady state physiological measurement occurs. The method is based upon the sum of the variance of simple linear equations fitted to each side of potential inflexion points. I used this method to identify the components of a typical circadian rhythm of various physiological variables; the steady-state rest-phase (ρ) and active phases (α), and the two transition periods between α and ρ. The values during the transitional phase were ignored, except when total daily energy expenditure was calculated. Once the components of the circadian rhythm were identified using the procedure of Yeager & Ultsch (1989), it was possible to calculate various metabolic and T_b parameters for the active and rest phases. Mean values were calculated within points of inflexion, and maximum and minimum values within active and rest phases were objectively calculated as the three lowest or highest consecutive points between calculated transition inflexion points, respectively. The BMR for each individual was calculated as the mean of the three lowest consecutive ρ values.

It became apparent during data analysis that the mousebirds seldom maintained steady-state body temperatures during the rest-phase. Typically, body temperature decreased steadily during the scotophase at a rate influenced by ambient temperature and cluster size. Since the pattern of cooling appeared to be linear, I estimated cooling rates by calculating linear regressions of T_b as a function of time for periods where a drop in T_b was evident. Passive cooling curves for ectothermic bodies generally follow a curvi-linear pattern (Withers, 1992). However, if the gradient between T_b and T_a is large, the cooling pattern more closely approximates a linear pattern (Withers, 1992). As this appeared to be the case with the cooling patterns displayed by *C. colius*, I fitted linear lines to the passive cooling curves. The onset of "passive cooling" was subjectively judged to commence following the metabolic down-regulation typical of the onset of the rest-phase, and was judged to end prior to the endogenous increase in metabolic heat production associated with the end of the rest phase. Two VO_2 values, and their corresponding T_b values, within the range shown by each bird during the scotophase were estimated from the regression and used to calculate the Q_{10} during periods of passive cooling. Because it was impossible to measure VO_2 for individual birds in a group, Q_{10} values for groups of birds are based on mass-specific VO_2 measurements for the entire group and T_b measurements for a single bird implanted with a mini-mitter. All RMR values refer to the lowest VO_2 value recorded, and hence were usually measured near the end of the rest-phase. Q_{10} values for single birds were also calculated for the transition period between active-phase and rest-phase metabolic rate and T_b.

The standard conversion factor of 20.083 kJ per litre O_2 was used to convert VO_2 to values of energy expenditure (Schmidt-Nielsen, 1990). Mass specific energy expenditures were calculated by integrating mass-specific VO_2 data over the appropriate component of the circadian cycle. Energy expenditure values were calculated for the entire active- and rest-phases (excluding transition periods), as well as for complete circadian cycles (including transition periods) for the data obtained from the circadian measurements at the T_{lc}.

Where ever possible, values are presented as mean ± S.D. Results were analysed using a two-way multi-factor analysis of variance (MANOVA) to test the influence of temperature and cluster size on the data set for various physiological variables.

Comparisons with allometric data in the literature were made by calculating 95% confidence intervals for the data, following Zar (1984).

Observed BMR, rest-phase T_b, and C_{min} data were compared with predicted values using independent linear contrasts (Felsenstein, 1985; Garland, Harvey & Ives, 1992). This method is based upon the use of standardized independent contrasts calculated as the phenotypic differences between sister species or nodes divided by the patristic distance between them (Garland, Dickerman, Janis & Jones, 1983). Such independent contrasts may be regarded as drawn from a normal distribution with mean zero and variance one, hence overcoming the problem of statistical non-independence (Felsenstein, 1985). My analysis was performed at the family level, using one species datum for each family. Metabolic data were obtained from Appendix 2 in Bennett & Harvey (1987), conductance data from Aschoff (1981) and McNab & Bonaccorso (1995), and rest-phase T_b data from Prinzinger, Preßmar & Schleucher, (1991). Additional data for the Phoeniculidae, Zosteropidae and Coliidae were obtained from Boix-Hinzen & Lovegrove (1998), Maddocks & Geiser (1997), and the present study, respectively (Appendix 1). When data for more than one species were available for a family, one species was chosen at random. The taxonomy and phylogeny, including divergence times, were obtained from Sibley & Ahlquist (1990). Although the phylogeny of Sibley & Ahlquist (1990) has received some criticism, it is generally considered to be robust to phylogenetic analyses (see Rolland, Danchin & de Fraipont, 1998). Phylogenetically independent linear contrasts were calculated and standardised, after which linear regressions of standardised phylogenetically independent linear contrasts of $\log_{10}$ BMR, rest-phase T_b and C_{min} were calculated using the program PDTREE (Garland *et al.*, 1993). For each variable, a phylogenetically corrected regression was then calculated using the technique described in Reynolds & Lee (1996). Each variable for *C. colius* was considered to deviate significantly from the predicted value if it lay outside the 95% confidence intervals for the respective phylogenetically corrected regressions.

RESULTS

General behaviour

Groups of bird exhibited clustering behaviour at all three T_as. Generally clustering would commence immediately following the beginning of the experimental scotophase, although at $T_a = 5\,°C$, some birds did cluster prior to lights-off. In all cases observed, clustering behaviour occurred throughout the rest phase and terminated after lights-on.

Body temperature and thermal conductance

Data from the initial measurements during the scotophase at $T_a \leq 27\,°C$ suggested that the mousebirds did not maintain rest-phase T_b with respect to a setpoint T_b (Figure 1, p 14). During these measurements, T_b decreased as T_a increased (Figure 2a, p 16), and also increased with time elapsed since the commencement of the rest-phase (Figure 2b, p 16). However, this time-dependent decrease in T_b was attenuated at *ca.* $T_a = 31\,°C$, thereafter, T_b increased steadily with increasing T_a (Figure 1b, p 14).

The minimum wet thermal conductance was 0.16 ± 0.03 mℓ $O_2.(g.h.°C)^{-1}$ (n = 9). The regression for the phylogenetically corrected linear contrasts of C_{min} as a function of body mass was $\log_{10}C_{min} = -0.689(\log_{10}M_b) + 0.148$, based on literature data for 10 species. My data for *C. colius* lay outside the 95% confidence intervals for this regression, and were hence assumed to deviate significantly from the predicted value. However, the gradual decrease in T_b at T_as $\leq 27\,°C$ makes it highly likely that VO_2 showed a concomitant decrease due to Q_{10} or temperature effects not associated with T_a. Hence conductance values calculated as the slope of the T_a - VO_2 regression may be underestimated. My C_{min} value should therefore be evaluated accordingly.

Body temperatures during the circadian measurements at T_{lc} (28.8 °C) showed a marked circadian amplitude in T_b between the rest and active phases, indicating a clear pattern of elevated diurnal body temperatures (Table 1, p 15; Figure 3, p 17). The regression equation of linear contrasts for 48 species of ρT_bmin as a function of body mass was $T_b = -4.3X10^{-6}M_b + 38.52$. The ρT_bmin for *C. colius* again lay outside the 95% confidence intervals of this equation, and was hence assumed to deviate significantly from predicted values.

Although ρT_bmin during clustering decreased significantly with decreasing T_a ($F_{2,53} = 37.87$; $p << 0.05$), there was no significant effect of cluster size ($F_{3,53} = 1.79$; $p > 0.05$; Figure 4, p 18). An *a posteriori* Tukey Multiple Range Test revealed that ρT_bmin at T_a = 5°C was significantly lower than at T_a = 15°C and T_a = 25°C. The mean ρT_b also decreased significantly with T_a ($F_{2,52} = 1.36$, $p > 0.05$) but not with cluster size ($F_{3,52} = 20.61$, $p << 0.05$). In this case, ρT_bmean was significantly lower at 15°C and at 5°C than at 25°C, and was also significantly lower at 5°C than at 15°C (Tukey Multiple Range Test). On several occasions, single birds at T_a = 5°C appeared to enter pathological hypothermia after the onset of the active phase following the end of the experimental scotophase. Of nine birds tested, one bird died and three showed signs of severe hypothermia. The latter three birds recovered after being heated with an artificial heat source. The lowest T_b that was recorded in a bird that was able to reheat following passive cooling, was 26.06°C.

Rates of linear body temperature cooling and Q_{10} values

Unlike most birds, the T_b of the mousebirds was not maintained or regulated with reference to a rest-phase setpoint body temperature. At all three experimental ambient temperatures used during the clustering measurements, T_b decreased steadily throughout the scotophase after the initial circadian T_b decrease following the end of the active phase. In most cases, coefficients of determination of regressions of T_b and time during the scotophase revealed that more than 70% of the T_b trend could be explained by a linear model fitted to the data (Table 2, p 19). The cooling rates increased significantly as T_a decreased ($F_{2,44} = 45.99$; $p \ll 0.05$) and decreased significantly as cluster size increased ($F_{3,44} = 3.296$; $p < 0.05$; Table 2, p 19).

The relationship between the thermal gradient of body temperature and ambient temperature (T_b - T_a) and T_a did not follow the pattern typical of endothermic thermoregulation (Figure 5, p 20). (T_b-T_a) values at lower T_as were lower than would be expected if the birds had defended a setpoint rest-phase T_b (Figure 5, p 20).

Average Q_{10} values calculated using expected values of VO_2 and T_b from linear regressions of VO_2 and T_b during passive cooling bouts were 2.74 ± 0.92 at $T_a = 15°C$, and 2.19 ± 0.70 at $T_a = 5°C$. Q_{10} values did not change significantly with increasing cluster size at $T_a = 15°C$ ($F_{3,24} = 1.42$, $p > 0.05$). At $T_a = 5°C$, changes in Q_{10} with increasing cluster size were similarly non-significant ($F_{3,28} = 2.16$, $p > 0.05$). There was no significant difference between the Q_{10} values at $T_a = 5°C$ and $T_a = 15°C$ ($F_{1,36} = 1.93$, $p > 0.05$).

The mean Q_{10} value for the period of metabolic down-regulation associated with the commencement of the rest-phase (i.e. within the first *ca.* 30 min) at all three T_as was 7.1 ± 3.8.

The decreases in VO_2 associated with T_b cooling therefore clearly influence thermoregulatory responses of the mousebirds, since both VO_2 and T_b were dependent on the elapsed time from the commencement of the rest phase (Figure 6, p 23). The regression line plotted using VO_2 data recorded at a range of T_as $\leq 27°C$ differed from the regression line plotted using data recorded during the final hour of scotophase after the birds had spent an entire scotophase at constant T_a (Figure 6, p 23).

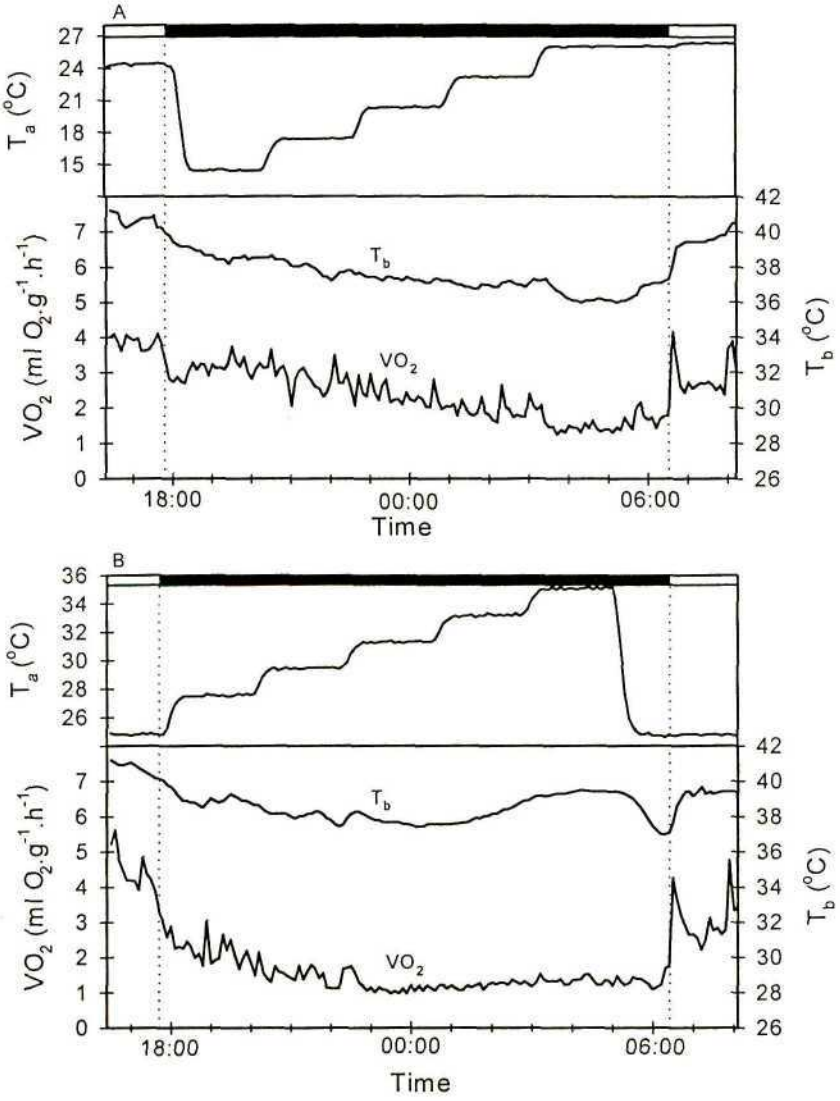

Figure 1. Representative traces of T_a, VO_2 and T_b in an individual white-backed mousebird *Colius colius* recorded at a range of ambient temperatures ≤ 27°C (A) and ≥ 28°C (B). These data were recorded in a ramped T_a design in order to establish the relationship between VO_2 and T_a. However, they reveal clearly a decrease in body temperature in (A), despite the concomitant increase in ambient temperature. This pattern is indicative of passive cooling. In graph B, the passive cooling is arrested only when $T_a > 32$°C i.e. as T_a approaches T_b.

Table 1. Mean ± SD oxygen consumption and body temperature measurements in white-backed mousebirds *Colius colius*. All measurements are from single birds at thermoneutrality i.e. at $T_a = T_{lc}$ (28.8 °C).

Oxygen Consumption	$m\ell\ O_2.g^{-1}.h^{-1}$	n
αVO_2max	3.511 ± 0.186	9
αVO_2mean	2.475 ± 0.694	9
αVO_2min	1.951 ± 0.284	9
ρVO_2max	1.738 ± 0.170	9
ρVO_2mean	1.256 ± 0.741	9
ρVO_2min (BMR)	0.905 ± 0.128	9
[1] R_{VO2}	2.605 ± 0.694	9

Body temperature	°C	n
αT_bmax	40.2 ± 0.8	8
αT_bmean	39.5 ± 0.6	8
αT_bmin	37.7 ± 1.1	8
ρT_bmax	37.4 ± 1.2	8
ρT_bmean	36.3 ± 0.7	8
ρT_bmin	35.0 ± 0.6	8
[2] R_T	5.2 ± 1.1	8

[1] $R_{VO2} = \alpha VO_2max - \rho VO_2min$

[2] $R_T = \alpha T_bmax - \rho T_bmin$

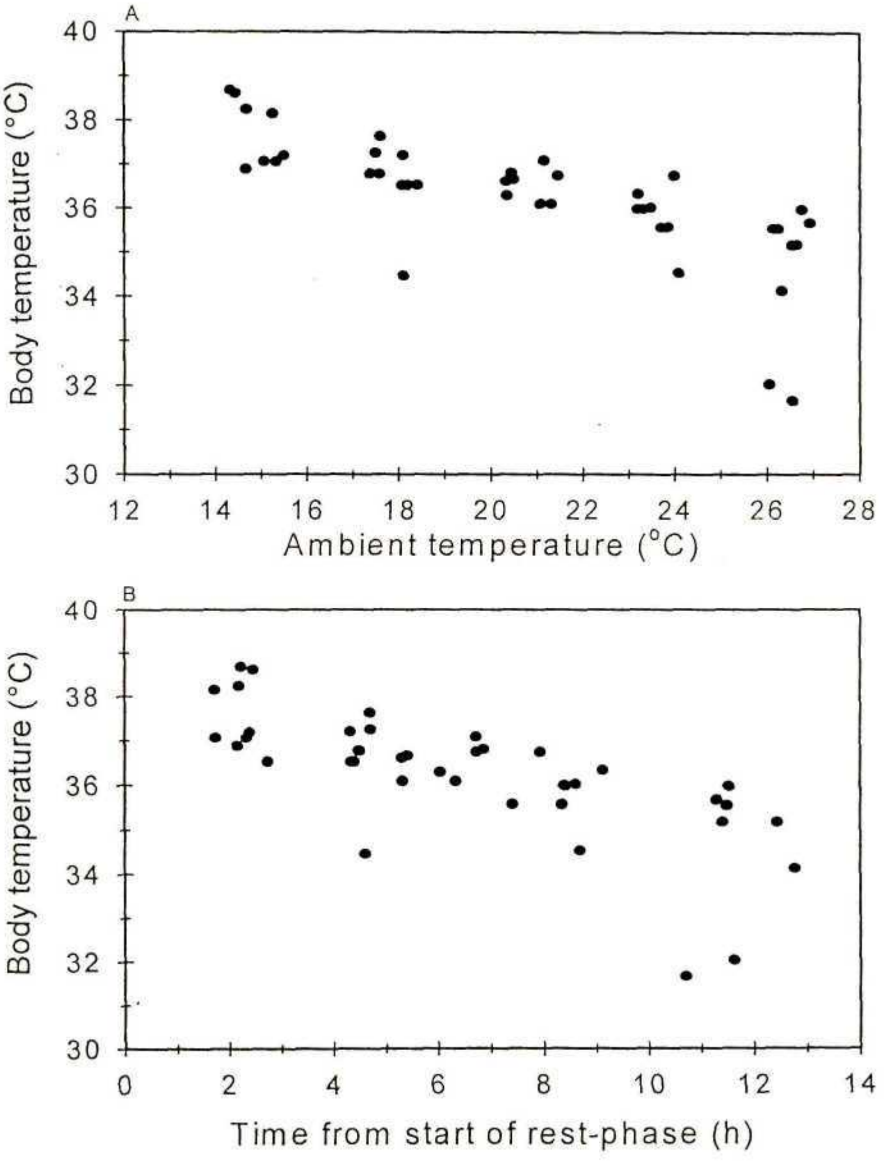

Figure 2. The relationship between body temperature and ambient temperature (A), and elapsed time after the commencement of scotophase (B), during measurements at ambient temperatures between 14°C and 28°C in *C. colius*. These data show that, despite ramping of T_a during the VO_2 measurements (see Figure 1), T_b was not maintained at a constant temperature, but decreased in a time-dependent pattern.

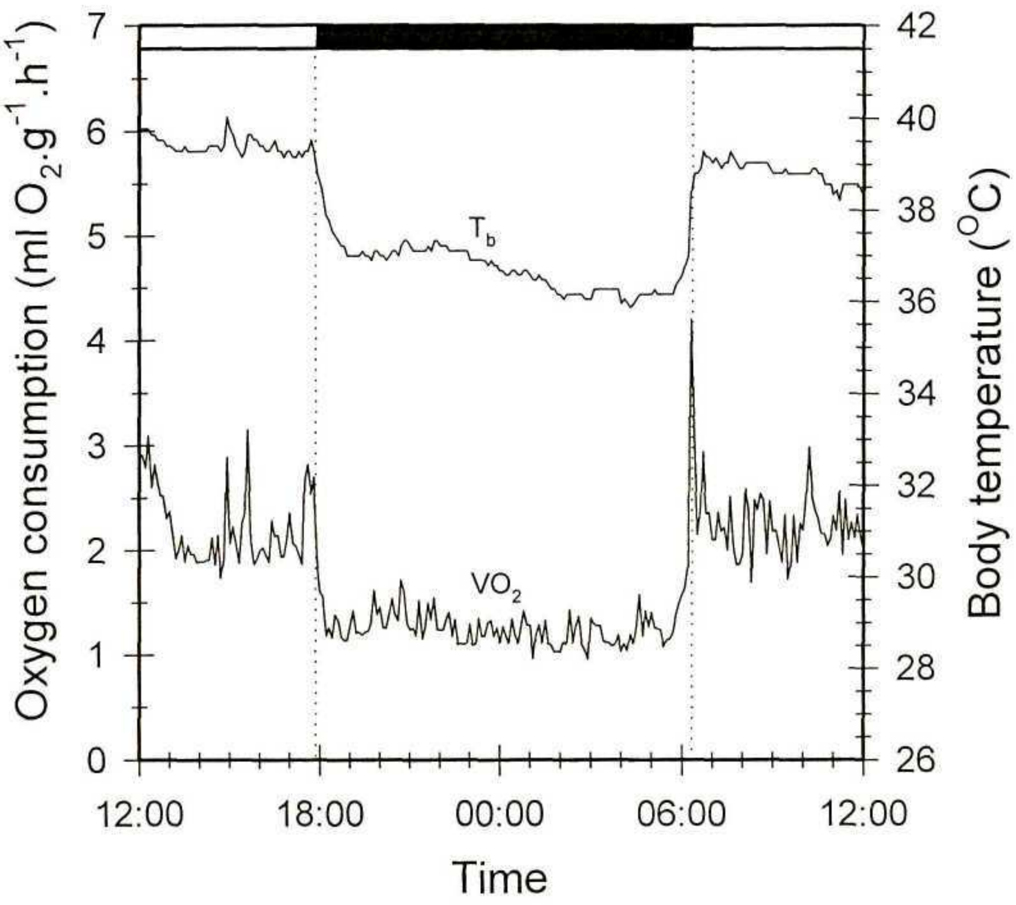

Figure 3. Representative 24 hour plot of metabolic rate and body temperature of a single white-backed mousebird *Colius colius*, recorded at thermoneutrality (T_a = 28.8 °C).

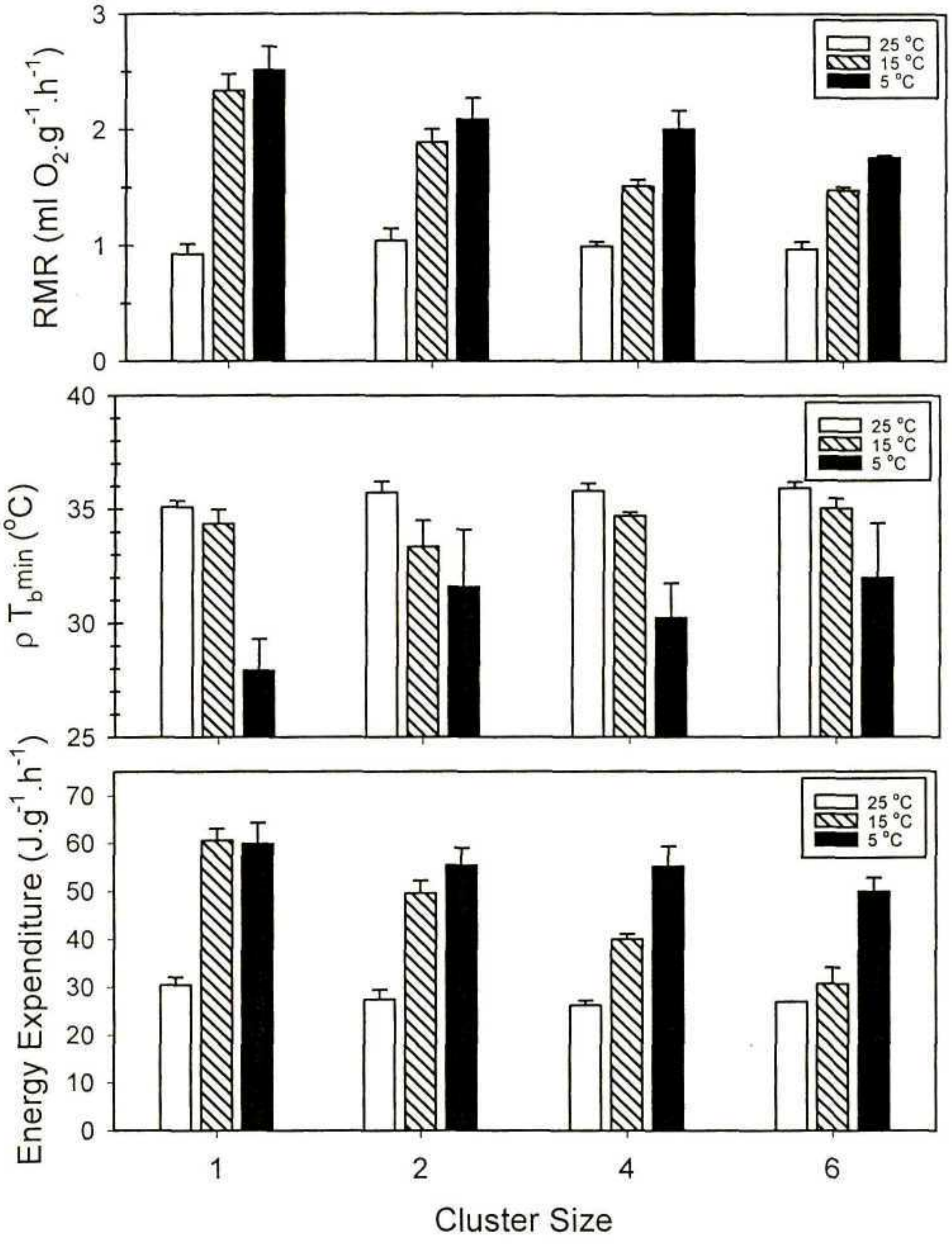

Figure 4. Minimum rest-phase body temperature, resting metabolic rate, and rest-phase energy expenditure in white-backed mousebirds *Colius colius* at three ambient temperatures. Individual measures of RMR and ρ$T_b$min were taken as the lowest values attained during the scotophase. Ambient temperature was held constant throughout the scotophase. Generally, the lowest values occurred towards the end of the scotophase.

Table 2. Cooling rates in groups of white-backed mousebirds *Colius colius* at three ambient temperatures. The rates were calculated from the slopes of linear regressions fitted to rest-phase T_b as a function of time.

Group size	5°C		15°C		25°C	
	Cooling rate (°C.h^{-1})	r^2	Cooling rate (°C.h^{-1})	r^2	Cooling rate (°C.h^{-1})	r^2
1	0.83±0.06	0.915	0.30±0.14	0.817	0.23±0.18	0.732
2	0.50±0.24	0.862	0.25±0.17	0.928	0.13±0.09	0.410
4	0.77±0.02	0.973	0.25±0.10	0.826	0.10±0.00	0.506
6	0.50±0.17	0.788	0.28±0.06	0.684	0.17±0.06	0.746

Coeffecient of determination (r^2) indicates strength of linear relationship

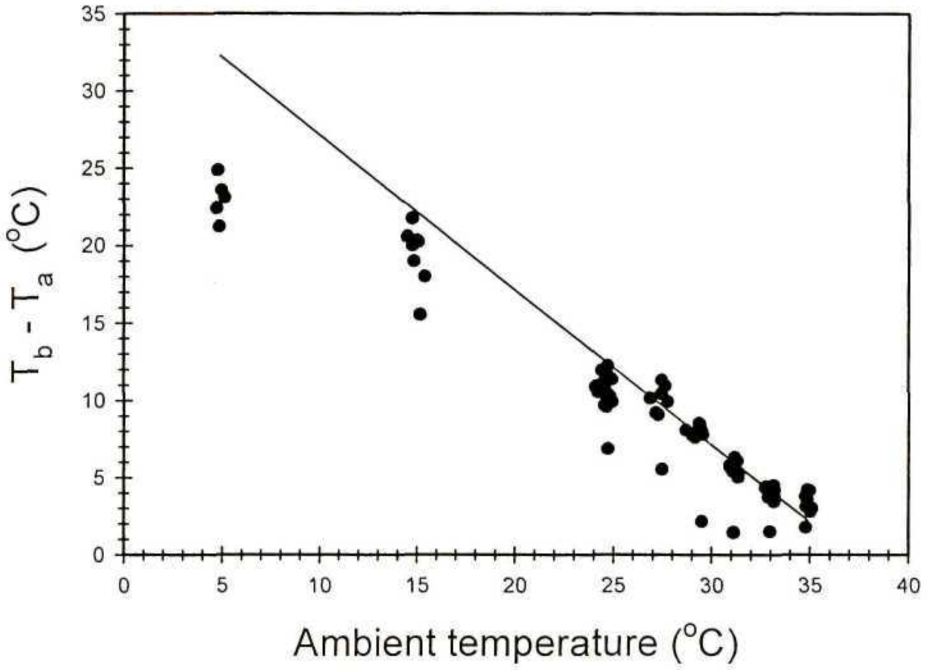

Figure 5. Relationship between the rest-phase body temperature and ambient temperature gradient and ambient temperature in the white-backed mousebird *Colius colius.* The solid line indicates the relationship that would have been observed had the birds defended a constant rest-phase setpoint temperature i.e. that attained following the photophase-mediated down regulation of VO_2 immediately following the onset of the scotophase. The very low outlier values at ambient temperatures from 25 °C to 35 °C were recorded in a small, young individual, that consistently displayed low metabolic rates and body temperatures.

Oxygen consumption

At thermoneutrality, oxygen consumption showed a marked diurnal, circadian pattern similar to that of T_b (Table 1, p 15, Figure 3, p 17). The regression equation of linear contrasts of BMR and body mass (Figure 7, p 24) was $\log_{10}BMR = 0.695\log_{10}M_b + 2.057$, calculated for 61 species. The BMR contrast for *C. colius* lay outside the lower 95% confidence intervals of the equation, and was hence assumed to deviate significantly from the predicted allometric trend (Figure 7, p 24).

RMR decreased significantly with increasing cluster size ($F_{3,55} = 6.13$, $p < 0.05$), but increased significantly with decreasing temperature ($F_{2,55} = 64.27$, $p << 0.05$; Figure 4, p 18). However, there was no significant difference between RMR at 15°C and 5°C (Tukey Multiple Range Test).

At $T_a = 25°C$, there was no decrease in RMR with increasing cluster size. However, at 15°C, large reductions in RMR with increasing cluster size were observed. Single birds used 2.33 ± 0.44 mℓ $O_2.g^{-1}.h^{-1}$ (n = 9), whereas the mean value for birds in clusters of six was 1.48 ± 0.05 mℓ $O_2.g^{-1}.h^{-1}$ (n = 3 groups; 18 birds). Similarly, decreases in RMR occurred with increasing cluster size at $T_a = 5°C$, from 2.51 ± 0.54 mℓ $O_2.g^{-1}.h^{-1}$ (n = 9) in single birds, to 1.76 ± 0.03 mℓ$O_2.g^{-1}.h^{-1}$ (n = 3 groups, 18 birds) for clusters of six birds. Representative circadian oxygen consumption and T_b patterns at 15°C and 5°C are illustrated in Figures 8 and 9 (p 25). From these graphs it is evident that at $T_a = 15°C$, birds in larger groups showed lower VO_2 values at higher T_bs (i.e. near the commencement of passive cooling bouts) than single birds and groups of two individuals. This would suggest that a greater degree of metabolic down-regulation occurred in these larger groups, since the observed VO_2 values are lower than would be expected on the basis of Q_{10} effects alone.

Energy Expenditure

The DEE during the circadian measurements at T_{lc} was 25.56 ± 7.11 $J.g^{-1}.hr^{-1}$ ($n = 9$). The active phase energy expenditure (excluding transition phases) was 16.26 ± 4.71 $J.g^{-1}.hr^{-1}$ ($n = 9$), compared with 8.22 ± 2.21 $J.g^{-1}.hr^{-1}$ ($n = 9$) during the rest phase.

The rest phase energy expenditure decreased significantly with increasing cluster size ($F_{3,55} = 9.65$, $p << 0.05$), and increased significantly with decreasing T_a ($F_{2,55} = 72.98$, $p << 0.05$; Figure 4, p 18). Significant increases in rest phase energy expenditure occurred at $T_a = 15°C$ compared with $T_a = 25°C$, as well as at $T_a = 15°C$ compared with $T_a = 5°C$ (Tukey Multiple Range Test).

Decreases in rest phase energy expenditure occurred as cluster size increased at $T_a = 25°C$ from 30.39 ± 4.93 $J.g^{-1}.hr^{-1}$ ($n = 9$) in single birds to 26.94 ± 0.12 $J.g^{-1}.hr^{-1}$ ($n = 3$ groups; 18 birds) in clusters of six birds. At $T_a = 15°C$ the energy expenditure of single birds was 60.56 ± 7.35 $J.g^{-1}.hr^{-1}$ ($n = 9$), compared with 30.65 ± 5.93 $J.g^{-1}.hr^{-1}$ ($n = 3$ groups; 18 birds) in clusters of six birds. At $T_a = 5°C$, however, decreases in energy expenditure with increasing cluster size were minimal.

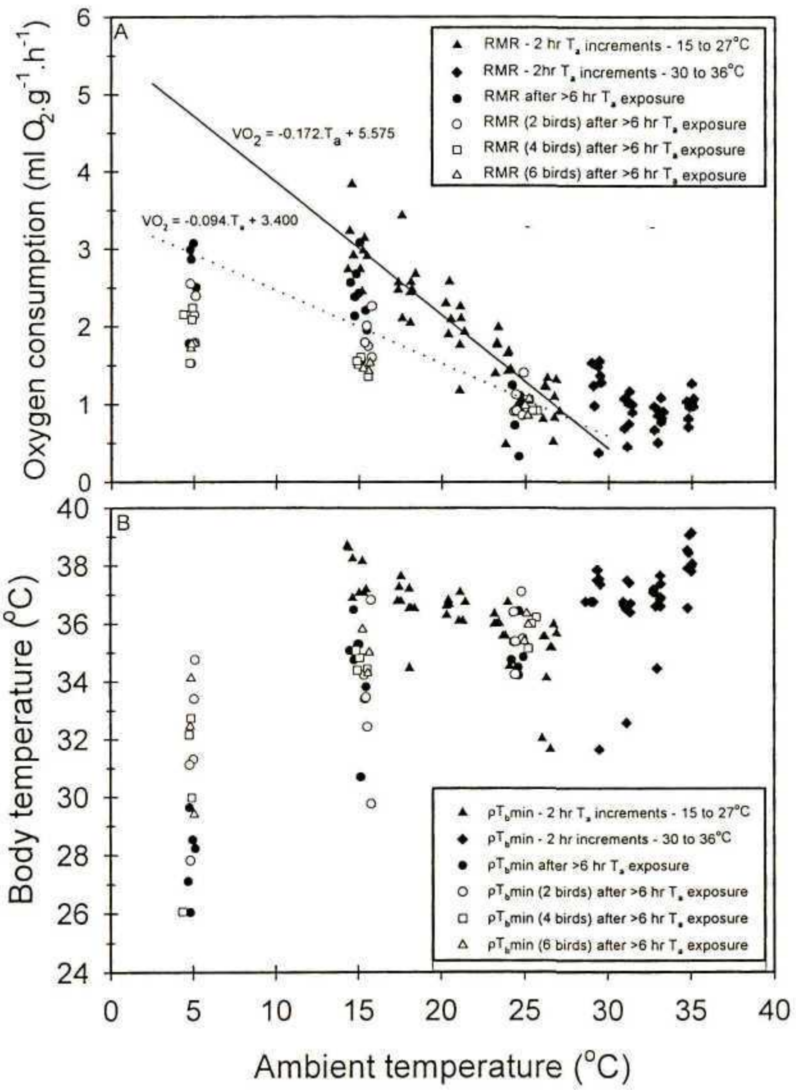

Figure 6. Scatterplot of resting metabolic rate and minimum rest-phase body temperature in white-backed mousebirds *Colius colius,* measured at a range of ambient temperatures. The solid line indicates a linear regression of data recorded during the measurements at ambient temperatures ≤ 27°C, and the dotted line indicates a linear regression of data taken during the final hour of the rest-phase during the clustering measurements. Note that the pattern shown by the ρT_bmin data recorded during 2 hour T_a increments from 15 to 27°C represents largely a time dependency effect.

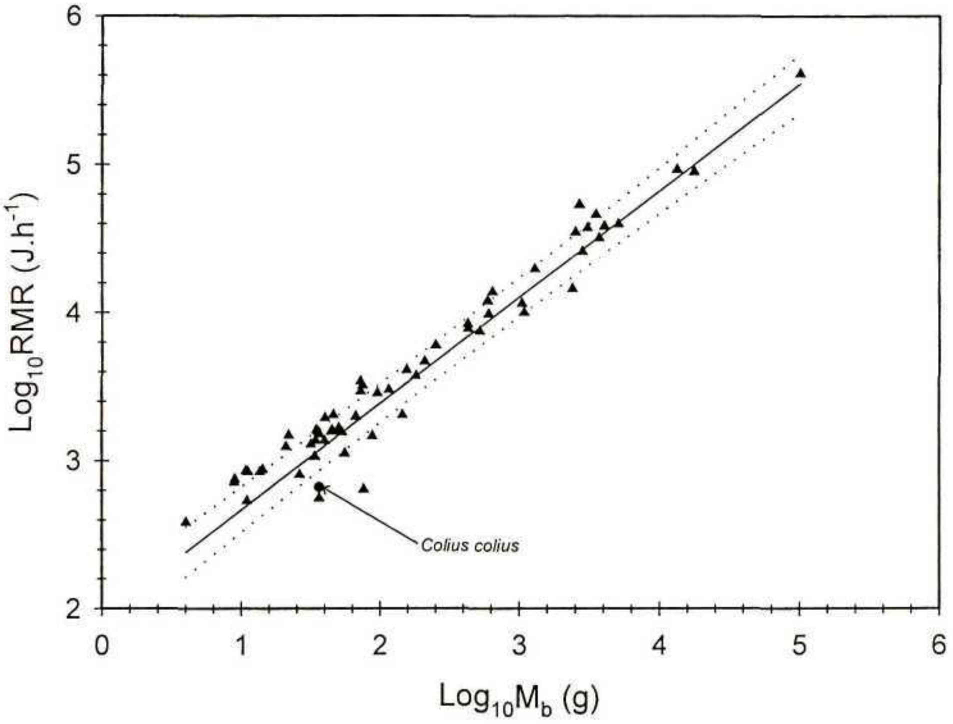

Figure 7. Phylogenetically-corrected regression for basal metabolic rate as a function of body mass in 61 bird species, based on independent linear contrasts method. The datum for *C. colius* is indicated by a closed circle; all other data by closed triangles. The species used are listed in Appendix 1. The dotted lines indicate the 95% confidence intervals, calculated following Zar (1984).

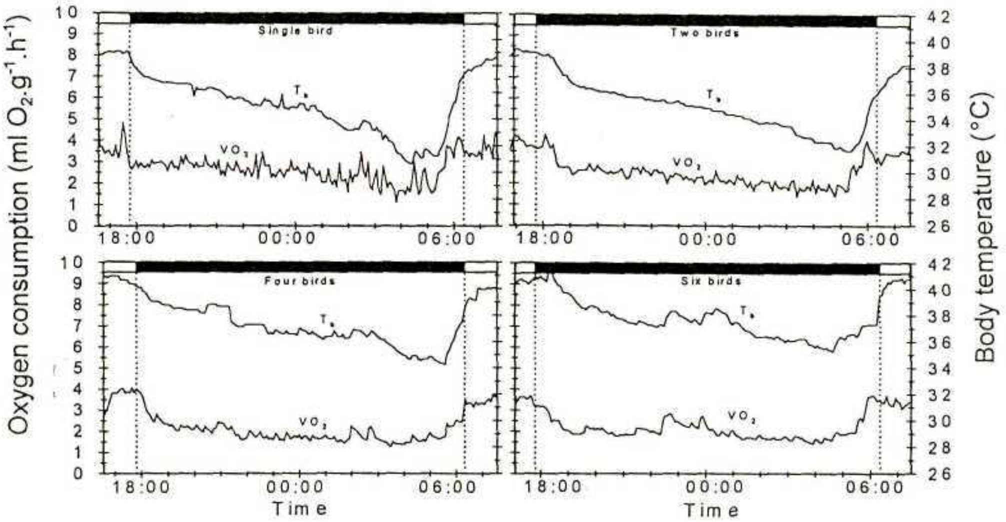

Figure 8. Representative plots of VO_2 (average value for groups of 2, 4 and 6 individuals) and T_b (single individuals) in white-backed mousebirds *Colius colius* of various cluster sizes at T_a = 15°C.

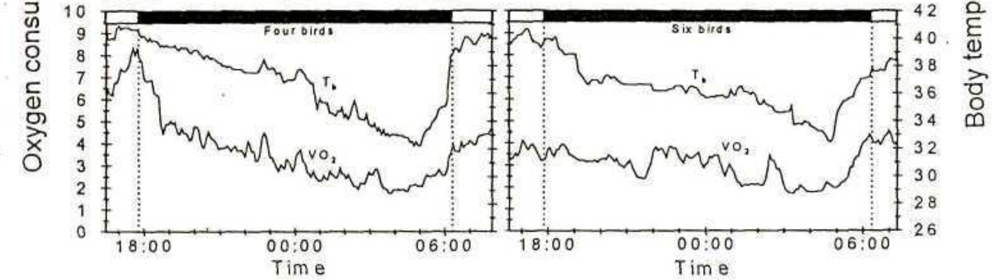

Figure 9.Representative plots of VO_2 (average value for groups of 2, 4 and 6 individuals) and T_b (single individuals) in white-backed mousebirds *Colius colius* of various cluster sizes at T_a = 5°C. Note that cooling rates, and the minimum rest-phase body temperature attained, depended on the number of individuals in a group.

DISCUSSION

Thermoregulation in the white-backed mousebirds did not appear to follow the typical endothermic pattern of maintenance of rest-phase T_b with reference to a set-point T_b. A high degree of rest-phase heterothermy was evident, characterised by periods of linear cooling. The birds exhibited low basal metabolic rates and were able to significantly reduce energy expenditure and rest-phase cooling rates by means of clustering behaviour.

Body temperature and basal metabolic rate

The mousebirds displayed lower T_bs at thermoneutral ambient temperatures than Prinzinger *et al.* (1991) report for all birds. Although T_b was considered to be independent of M_b by Aschoff (1982), Prinzinger *et al.* (1991) have shown that a correlation exists between M_b and T_b, evident mainly during the active phase and during periods of high activity. Both αT_b (Paired T-test; $t = -2.34$; $p < 0.05$) and ρT_b (Paired T-test; $t = -9.18$; $p \ll 0.05$) were significantly lower in *C. colius* than predicted by these authors' equation for 26 orders. Again, by using the independent linear contrasts method, I was able to confirm that the low rest-phase T_bs recorded for *C. colius* at thermoneutrality do not appear to represent an inherited trait, and hence may well indicate physiological adaptation.

The αT_b values recorded in this study were similar to Prinzinger *et al.*'s (1991) value of 39.5 ± 1.21 °C for the Coliiformes. However, the mean ρT_b I measured for *C. colius* was lower than the reported value of 38.2 ± 0.93 °C for the Coliiformes. Furthermore, my ρT_b values are lower than rest-phase T_bs measured in other mousebirds; 39.8 °C in *C. striatus* (Brown & Foster, 1992), 38.5 °C in *C. castonotus* (Prinzinger, Göppel, Lorenz & Kulzer, 1981) and 38.6 °C in *Urocolius macrourus* (Prinzinger, 1988).

The birds displayed a large amplitude of circadian cycles of T_b (R_t) at thermoneutrality, which was on average 195% of the values calculated from Aschoff's (1982) equation for R_t in non-passerines.

The basal metabolic rates of the mousebirds during circadian measurements were 40.7 ± 8.9% below the values predicted by Bennett & Harvey (1987), based on birds from 78 families. A comparison with published data for other mousebird species revealed that *C. colius* displayed a lower BMR than *C. striatus* (Bartholomew & Trost 1970, Brown & Foster, 1992) and *C. castonotus* (Prinzinger *et al.*, 1981). The BMR recorded in this study is also lower than the RMRs recorded in euthermic (non-torpid) *C. striatus*, *C. castonotus*, *Urocolius indicus* and *U. macrourus* by Hoffmann & Prinzinger (1984). A phylogenetically corrected regression of BMR as a function of body mass (Figure 7, p 24) shows that the BMR of *C. colius* falls outside the 95% confidence intervals of the regression, confirming a value that was significantly lower than expected. The low metabolic rate of this species is not due to the phylogenetic relationships of the mousebirds, and is more likely to have evolved in response to environmental selection. The fact that a complete phylogeny for the six species of the Coliidae has not been published prevented me from comparing the metabolic rates of mousebirds as a group to those of other avian orders using this method.

Thermoregulation in *C. colius* appears to differ from typical endothermic thermoregulation (Schmidt-Nielsen, 1990; Withers, 1992). At T_as below the thermoneutral zone, ρT_b is not maintained with reference to a set-point T_b. This lack of thermogenic regulation results in ρT_b gradually decreasing until immediately prior to the commencement of the α-phase. The Q_{10} values of 2-3 calculated for the rest phase are typical of temperature-induced reduction of biological reactions during nocturnal heterothermy (Geiser, 1988) and suggest a process of passive time-dependent cooling. These data suggest that rest-phase heterothermy represents a temperature effect, rather than active metabolic inhibition, or down-regulation, generally characterised by Q_{10} values > 3 (Geiser, 1988). The Q_{10} values calculated for the period of metabolic down-regulation associated with the immediate commencement of the rest-phase (within *ca.* min) clearly indicate that two discrete metabolic processes are involved. Following the initial "circadian entry" phase, metabolic down-regulation is attenuated, perhaps with reference to a rest-phase setpoint T_b. However, for the rest of the maintenance phase, linear passive cooling occurs at a rate commensurate with the T_b - T_a gradient and cluster size. I assume that the initial down-regulation during the onset of the scotophase represents a normothermic circadian response to photoperiod.

The passive cooling observed in my study has, to the best of my knowledge, not been recorded previously in birds, and does not conform to any of the hypothermic states discussed by Prinzinger *et al.* (1991) or Reinertsen (1983). However, the VO_2 traces of two speckled mousebirds *(C. striatus)* shown in Figure 8 in Bartholomew & Trost (1970) are similar to the VO_2 traces recorded in my birds, possibly indicating similar patterns of passive cooling. In the latter study, however, linear cooling was attenuated as the T_b - T_a gradient attained *ca.* 5°C. Considering the T_a at which their measurements were made (19.2°C), I assume that the attenuation of the linear reduction of VO_2 occurred as the T_b - T_a gradient decreased sufficiently to prevent further heat loss. Unfortunately, the lack of continuous T_b recordings in the latter paper prevents any firm conclusions being drawn. Should a similar mechanism operate in other mousebird species, my results demonstrate the need for continuous monitoring of rest-phase T_b in any study of T_b in mousebirds. It is possible that previous cloacal T_b measurements such as those of Brown & Foster (1992) were made near the onset of passive cooling bouts, and hence are unlikely to indicate minimum T_bs attained during the rest-phase. They probably reflect intermediate T_bs at some unknown point between the commencement and termination of a passive cooling bout. It should also be noted that, since T_b depends on the amount of time allowed for passive cooling to take place (Figure 2, p 16), as well as the (T_b - T_a) gradient, the experimental procedure of exposing birds to a range of T_as during the course of a single night may in some cases produce misleading results. It is likely that the relationship between T_b and T_a will be confounded by the time dependency effect, and any values obtained in this way should hence be treated with caution.

Torpor, nocturnal hypothermia or poor thermoregulation?

Certain characteristics of the nocturnal heterothermy I have observed in *C. colius* are inconsistent with those of typical avian and mammalian torpor bouts. (Lyman, Willis, Malan & Wang, 1982; Schmidt-Nielsen, 1990; Withers, 1992). Typically, torpor commences with an entry phase, followed by a maintenance phase and an arousal phase.

The mechanism responsible for rapid reduction in metabolic rate and T_b characteristic of the entry phase has been examined by Geiser (1988; 1993), Song, Körtner & Geiser (1995; 1997) and Geiser, Song & Körtner (1996). Although the topic remains debatable, it is becoming clear that the regulation of the active-phase metabolic rate with respect to a αT_b setpoint is terminated at the onset of the scotophase (Song *et al.*, 1995; 1997; Geiser *et al.*, 1996). Active metabolic down-regulation follows, with a concomitant rapid reduction in T_b, until the metabolic rate is again regulated with respect to a torpor setpoint body temperature, i.e. the onset of the maintenance phase (Geiser, 1988; 1993).

The white-backed mousebirds do not appear to display an obvious entry or maintenance phase. There is indeed initial metabolic down-regulation to *ca.* 70% of the active-phase VO_2 within the first 30 mins or so, but this I suspect may reflect the endogenous, normothermic circadian rhythm. Typically, VO_2 is reduced to < 30% of normothermic BMR values during the maintenance phase of torpor in mammals and birds (Geiser & Ruf, 1995). Moreover, during the maintenance phase, there is clearly a lack of effective thermogenic defence of either a normothermic or torpor rest-phase setpoint body temperature. In other words, rest-phase thermoregulation seems to be inhibited, and as a consequence the birds cool passively at a rate commensurate with the T_b - T_a gradient and the number of birds in a cluster. The birds are capable of generating endogenous heat at the onset of the photophase, but only if body temperature does not fall below *ca.* 26°C. Below this body temperature the birds become pathologically hypothermic, and cannot attain normothermic active-phase body temperatures without an exogenous source of heat.

To my knowledge, endotherms that regularly employ daily torpor become pathologically hypothermic only if they have insufficient energy resources to meet the high costs of thermogenesis during arousal. From the traces of VO_2 (Figures 8 and 9, p 26), it is obvious that my birds made no attempt to defend a constant rest-phase body temperature at any time during the scotophase, yet clearly they had the energetic resources to reheat and arouse at the end of the scotophase.

Prinzinger *et al.* (1991) considered moderate ρT_b depression of down to 25°C to be a discrete physiological mechanism to torpor that they called "controlled rest-phase hypothermia". They argued that controlled rest-phase hypothermia is generally a response to food deprivation and/or cold load (Prinzinger *et al.* 1991). The authors listed six orders, two families (including Coliidae) and 38 - 40 species in which controlled rest-phase hypothermia has been described, based on depressed ρT_bmin, with a lower limit of 25°C. Interestingly, the Coliidae were listed as showing ρT_bmin values down to 35°C only. Results from the present study suggest that ρT_bmin in *C. colius* can fall to considerably lower temperatures, with a lowest recorded value of 26.08 °C, although such T_b depression is not a consequence of the mechanisms discussed by Prinzinger *et al.* (1991).

Thermal conductance

The lack of rest-phase T_b maintenance prevented me from obtaining a meaningful estimate of thermal conductance for *C. colius*. Nevertheless, the value I obtained is higher than predicted by Aschoff's (1981) equation for ρ-phase C_{min} in non-passerines, lying outside the 95% confidence intervals for the C_{min} predicted for a bird with a M_b = 35.1g (mean M_b of experimental individuals). Although no conclusions can be drawn from my estimate, for reasons discussed above, I believe that several physiological characteristics of *C. colius* suggest a high thermal conductance. At T_a = 5 °C four out of nine birds suffered pathological hypothermia. The high rates of heat loss experienced by these individuals allude to rapid heat flux between the birds and their environment, and hence a high thermal conductance. In addition, *C. colius* can utilise simulated solar radiation to reduce active-phase energy expenditures (see Chapter 2). This ability to efficiently absorb solar radiation, together with the apparent thermal stress that individual birds experience at low T_as, clearly suggests that rates of heat flux between the birds and their environment is high. Given these observations, it seems reasonable to suggest that the thermal conductance of *C. colius* is indeed high.

There are two obvious advantages of a high C_{min}, or conversely, a low thermal insulation. Firstly, a poor insulation facilitates the absorption of solar radiation during the frequent bouts of sunning behaviour characteristic of this order (Rowan, 1967). Secondly, a poor insulation promotes heat flux between closely huddling birds thus effectively reducing the surface area for heat loss in individual birds (Canals, Rosenmann & Bozinovic, 1997).

My results suggest that the thermoregulatory abilities of individual white-backed mousebirds are poor, and that a high thermal conductance does not permit individual mousebirds to maintain a constant rest-phase T_b, particularly at low T_as.

Effects of clustering

The effects of clustering behaviour on energy expenditure and T_b varied according to the T_a at which measurements were made. At $T_a = 25\,°C$, a decrease in energy expenditure of 11.4% suggests that even at T_as a few degrees below the T_{lc}, individual mousebirds are able to make significant energetic savings by means of clustering. At $T_a = 15\,°C$, the average rest-phase energy expenditure of individuals in clusters of six birds was equivalent to 50.6% of that shown by single birds. The observation that energy savings were greater at $T_a = 15\,°C$ than at $T_a = 25\,°C$, and that energy savings increased with cluster size, support my initial predictions. It should also be noted that clusters in the wild often consist of up to 14 birds (Rowan, 1967), and it may be that considerably greater energy savings are possible in clusters consisting of more than six individuals. A possible avenue for future research would involve the determination of the optimal cluster size for maximising energy savings.

At $T_a = 5\,°C$, the decreases in energy expenditure were smaller than I expected. This observation presumably relates to the temperature effects associated with rest-phase heterothermy as discussed above, and may arise because the energetic advantages of huddling are proportional to body temperature (Vickery & Millar, 1984). The savings that the birds were able to make by clustering presumably decreased due to the observed T_b depression. This is probably due to the effect of a reduced T_b-T_a gradient and consequent changes in heat flux rates.

Although Brown & Foster (1992) suggested that diurnal clustering serves largely a social function in *C. striatus*, my results suggest that *C. colius* derive more fundamental thermoregulatory benefits from such diurnal clustering at medium T_as. My observations in the field at Tierberg Research Station showed that, early in the morning and late in the afternoon, the birds perched regularly in several favourite trees to sun themselves. However, as soon as the sun was obscured by a cloud, the entire group would exhibit huddling behaviour.

Brown & Foster (1992) found that individual speckled mousebirds in a cluster of six at $T_a = 16\,°C$ showed an energy expenditure equivalent to 66% of that used by single birds. An individual in a cluster of three red-backed mousebirds *C. castanotus* used 45.1% less energy than a euthermic single bird at $T_a = 8\,°C$, whereas at $T_a = 4\,°C$ a heterothermic single bird used 26.6% more energy than a bird in a cluster of three (Prinzinger, 1988). Walsberg (1990) calculated that communally roosting blacktailed gnatcatchers *Auriparus flaviceps* make a 61% reduction in energy expenditure. Putaala, Hohtola & Hissa (1995) found that grey partridges (*Perdix perdix*) could reduce energy expenditure by 24% by forming a cluster of nine individuals at an T_a of -30 °C. These data clearly confirm that clustering behaviour is highly effective as an energy-saving measure in many birds, and that mousebirds appear to be able to make greater energy savings than the majority of bird species investigated.

Furthermore, my results show that clustering behaviour is an important thermoregulatory mechanism in *C. colius*. The observation that four out of nine single birds suffered adverse effects of hypothermia following a night at 5 °C suggests that clustering is critical for survival at low ambient temperatures. I would argue that clustering behaviour is obligatory in the white-backed mousebird at low ambient temperatures, due in part to the constraints of a high thermal conductance. The birds appear to lack the thermoregulatory mechanism required to defend a rest-phase set-point T_b and instead rely on clustering behaviour to reduce rates of heat loss and to regulate rest-phase T_b. A trade-off appears to exist in *C. colius* between a high thermal conductance, which presumably facilitates efficient absorption of solar radiation during frequent bouts of sunning behaviour (see Chapter 2), and reliance on clustering behaviour to regulate body temperature at low ambient temperatures.

General

A major observation of this study is the apparent lack of true torpor in *C. colius.* Several authors have discussed torpor in mousebirds, and it is considered to be common in the Coliidae (Rowan, 1967; Bartholomew & Trost, 1970; Finke, Misovic & Prinzinger 1995). However, I did not detect torpor (*sensu* Prinzinger *et al.,* 1991; Geiser & Ruf, 1995) in the birds used in my study. I observed rest-phase heterothermy at T_as below thermoneutrality, but in no cases was torpor, characterised by T_b approaching *ca.* 17°C (Geiser & Ruf, 1995), observed. As previous studies of mousebird thermoregulation have largely relied on rectal, rather than telemetric measurement of T_b, I suggest that torpor in mousebirds should be reevaluated. However, my study investigated thermoregulation in mousebirds fed *ab libitum* only, and I have not investigated the possibility that *C. colius* may utilise torpor under conditions of food deprivation, or at T_as < 5°C.

Malan (1996) has proposed that hibernation and torpor may be pleisiomorphic (ancestral) physiological patterns, and not adaptive traits which have arisen independently in a polyphyletic assemblage of mammals and birds. Several ectotherms employ behavioural thermoregulation to maintain circadian T_b cycles of relatively high amplitude, and Malan (1996) has suggested that the normothermic circadian patterns of T_b shown by endotherms represent an inhibition of the primitive tendency to a wide-amplitude daily cycling of T_b. However, Geiser (1998) has pointed out that in birds heterothermy is generally found in more modern groups, and particularly those which are small and whose food supplies tend to fluctuate. Geiser (1998) has argued that the evolution of torpor and hibernation may indeed be polyphyletic and that the occurrence of heterothermy in an avian taxon may also depend on size and food resources. These two view points provide a framework in which to examine the evolutionary implications of the observed patterns of thermoregulation in *C. colius*.

The Coliiformes diverged from the Cuculiformes and Psittaciformes approximately 100 million years B.P., and are hence a relatively old lineage (Sibley & Ahlquist, 1985). In addition, they are the oldest group of birds in which torpor has been described (see phylogeny in Geiser, 1998). In contrast with most endotherms, *C. colius* does not maintain normothermic rest-phase T_b with reference to a set-point T_b. Furthermore, I found no evidence of true torpor in *C. colius,* but rather patterns of rest-phase T_b characterised by periods of linear passive cooling. These patterns differ from typical torpor bouts in that active metabolic down-regulation of T_b to a torpor set-point does not appear to occur, and that a set-point T_b is not maintained. My results showing the apparent reliance on clustering behaviour for thermoregulation by *C. colius* suggest that thermoregulation in this species may show several characteristics intermediate between typical endothermic circadian patterns of metabolism and Malan's (1996) proposed ancestral characteristics. In this respect *C. colius* may provide insights into the evolution of thermoregulatory systems and adaptive heterothermy (e.g. torpor) in birds. The physiological mechanism responsible for the defence of a set-point T_b during the "maintenance" phase of either torpor or a normothermic rest phase in most endotherms does not appear to be shown by *C. colius*.

Instead, they employ a behavioural mechanism, namely clustering, which may represent an intermediate step between individual behavioural thermoregulation found in some ectotherms, and the thermogenesis characteristic of endotherms.

In terms of Geiser's (1998) argument, it is noteworthy that the Coliiformes are the oldest group with a body mass less than 50g. If Geiser's (1998) hypothesis is correct, then the thermoregulatory pattern shown by *C. colius* may represent an evolutionary stage between the euthermy shown by old groups of relatively large birds, and the frequent use of torpor by more modern groups consisting of small species, such as the hummingbirds and the passerines.

Under natural conditions, free-ranging mousebirds may not show the low rest-phase body temperatures exhibited by single birds in captivity. Rather, the use of clustering behaviour should allow the birds to maintain their rest-phase body temperatures near normothermic levels. The ability to tolerate passive cooling and to subsequently raise T_b to active-phase levels, as observed under laboratory conditions, is likely to be strongly selected for in certain situations, for example if an individual were to be separated from it's flock for any period of time, or during the breeding season when individuals could be subjected to low temperatures or loss of insulation because of cold weather and/or rain while on a nest.

Several of the metabolic traits of *C. colius* are highly conservative, such as the low BMR and large amplitude of circadian T_b fluctuations. Lovegrove & Heldmaier (1994) have discussed the possible adaptive value of circadian energetic rhythms to endotherms and have argued that a large R_t may be indicative of energy conservation during the rest phase, and is likely to be highly adaptive in regions in which resource availability is temporally and spatially unpredictable. The large amplitude of circadian patterns of T_b in *C.*

colius at thermoneutrality, together with a low BMR, suggest that this species has undergone a high degree of selection for energy conservation. Although McNab (1983, 1986) found that folivorous and frugivorous mammals generally show low BMRs, Elgar & Harvey (1987) pointed out that these are also taxonomic correlates, and hence may be due to phylogenetic effects rather than the energetic constraints of a largely folivorous diet. Bennett & Harvey (1987) found no significant associations between variation in relative RMR and differences in diet across avian families. However, folivory is relatively rare in birds and the possible relationship between the conservative metabolic traits shown by *C. colius* and its folivorous diet requires further investigation.

Huddling or clustering behaviour has a number of ecological advantages over torpor as an energy-saving mechanism (Prinzinger, 1988). Because the decrease in T_b required to save a given percentage of an individual's energy expenditure is less when the individual is in a cluster, the individual is better able to respond rapidly to weather changes or predators (Prinzinger, 1988). The obligatory nature of clustering behaviour in mousebirds raises questions regarding the evolution of sociality in this group. Did sociality evolve in tandem with endothermy in *C. colius,* thereby obviating selection for rest-phase thermoregulation, or has the latter mechanism been subsequently lost in this species in lieu of the thermoregulatory benefits of huddling?

During approximately 100 hr of behavioural observations at Tierberg and in the Karoo National Park, not a single incidence of attempted predation was observed. The mousebirds at Tierberg do not appear to defend territories and are not subjected to significant avian predation (W.R.J. Dean, *pers. comm.*). During periods of sunning behaviour, very low levels of vigilance were evident, with every bird in the flock sunning in an exposed position.

The apparent importance of clustering behaviour for the survival of *C. colius* individuals at low T_as, challenge the commonly held view that energetic benefits represent secondary benefits of sociality, with the primary benefits being territory and predator defence (Alexander, 1974; Siegfried & Underhill, 1975; Bertam, 1980; Rubenstein & Wrangham, 1986; Stacey & Koenig, 1990).

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Appendix 1 - Bird families and species used for independent linear contrasts analyses of basal metabolic rate, rest-phase body temperature and thermal conductance. Sources: 1 = Bennett & Harvey (1987); 2 = data set for Prinzinger *et al.* (1991); 3 = Aschoff (1981); 4 = Boix-Hinzen & Lovegrove (1998); 5 = present study; 6 = Maddocks & Geiser (1997); 7 = McNab & Bonaccorso (1995).

Basal metabolic rate

Family	Species	M_b(g)	RMR (kCal/d)	Source
Struthionidae	*Struthio camelus*	10^6	2350	1
Casuariidae	*Casuarius bennetti*	17600	1302	1
Apterygidae	*Apteryx australis*	2380	83.2	1
Cracidae	*Crax daubentoni*	2800	148.4	1
Phasianidae	*Meleagris galloparvo*	3700	184	1
Anatidae	*Anas crecca*	250	34.4	1
Picidae	*Jynx torquilla*	31.8	7.4	1
Upupidae	*Upupa epops*	67	11.4	1
Phoeniculidae	*Phoeniculus purpureus*	71.4	11.6	4
Trogonidae	*Trogon rufus*	53	8.9	1
Meropidae	*Merops viridis*	33.8	6.1	1
Alcedinidae	*Alcedo atthis*	34.3	7.8	1
Coliidae	*Colius colius*	35.1	3.9	5
Cuculidae	*Cuculus canorus*	111.6	17.3	1
Psittacidae	*Neophema bourkii*	40	11.1	1
Apodidae	*Apus apus*	44.9	9	1
Trochilidae	*Calypte anna*	4	2.2	1
Strigidae	*Strix aluca*	520	43	1
Podargidae	*Podargus ocellatus*	145	11.7	1
Caprimulgidae	*Eurostopodus guttatus*	88	8.4	1
Columbidae	*Streptopelia turtur*	154	23.5	1
Rallidae	*Crex crex*	96	16.3	1
Gruidae	*Anthropoides paradisea*	4030	220	1
Thinocoridae	*Thinocorus rumicivorus*	55.5	6.4	1
Scolopacidae	*Scolopax rusticola*	430	44.6	1
Charadridae	*Charadrius dubious*	36	8.6	1
Laridae	*Larus canus*	428	48	1
Falconidae	*Falco subbuteo*	208	17	1
Accipritidae	*Gypaetus barbatus*	5070	228	1
Phaethontidae	*Phaethon rubricauda*	593.2	68.7	1
Sulidae	*Sula dactylatra*	1289	113.7	1
Anhingidae	*Anhinga anhinga*	1120	76.1	1
Phalacrocoracidae	*Phalocrocorax atriceps*	1330	130.2	1
Ardeidae	*Botaurus lentiginosus*	600	56	1
Phoenicopteridae	*Phoenicopterus ruber*	3040	215	1
Threshkiornidae	*Eudocimus albus*	940	85	1
Ciconiidae	*Mycteria americana*	2500	201	1
Pelecanidae	*Pelecanus occidentalis*	3510	264	1

Spheniscidae	*Aptenodytes patagonica*	13270	534.6	1
Procellaridae	*Pterodroma hypoleuca*	180	21.4	1
Furnariidae	*Xiphorhynchus guttatus*	45.2	9.2	1
Formicaridae	*Thamnophilus punctatus*	21	7.1	1
Tyrannidae	*Tyrannus tyrannus*	35.7	9	1
Meliphagidae	*Lichmera indistincta*	9	4.3	1
Irenidae	*Chloropsis sonnerati*	39.7	7.8	1
Laniidae	*Lanius excubitor*	72.4	16.8	1
Corvidae	*Corvus cryptoleucus*	640	79	1
Bombycillidae	*Bombycilla garrulus*	72.5	19.7	1
Cincilidae	*Cinclus mexicanus*	50.2	9.5	1
Muscicapidae	*Saxicola rubetra*	14.3	5	1
Sturnidae	*Sturnus vulgaris*	67	18.1	1
Sittidae	*Sitta canadensis*	11.2	4.8	1
Paridae	*Parus ater*	10.8	4.9	1
Aegithalidae	*Aegithalos caudatus*	8.9	4.1	1
Hirudinidae	*Riparia riparia*	13.6	4.8	1
Pycnonotidae	*Pycnonotus finlaysoni*	26.3	4.6	1
Zosteroptidae	*Zosterops lateralis*	11	3.23	6
Alaudidae	*Alauda arvensis*	46.1	11.6	1
Nectarinidae	*Arachnothera flavigaster*	36.3	6.2	1
Passeridae	*Passer montanus*	22	8.5	1
Fringillidae	*Psittirostra baileui*	34.8	9.2	1

Rest-phase body temperature

Family	Species	M_b(g)	T_b(°C)	Source
Struthionidae	*Struthio camelus*	10^6	38.1	2
Casuariidae	*Casuarius bennetti*	17600	39	2
Spheniscidae	*Aptenodytes patagonica*	16000	37.7	2
Ciconiidae	*Leptoptilos javanicus*	5710	39.6	2
Gaviidae	*Gavia immer*	3588	39.5	2
Pelecanidae	*Pelecanus occidentalis*	3130	38.9	2
Tinamidae	*Nothura maculosa*	2340	39.2	2
Apterygiidae	*Apteryx haasti*	2000	38.1	2
Sulidae	*Sula dactylatra*	1900	37.1	2
Podicipedidae	*Aechomophorus occidentalis*	1470	38.5	2
Anatidae	*Branta nigricans*	1390	37.1	2
Lariidae	*Larus argentatus*	919.5	39.5	2
Ardeidae	*Nycticorax nycticorax*	670	38.7	2
Accipiteridae	*Buteo buteo*	920	38.5	2
Phaethontidae	*Phaethon aethereus*	616.4	38.5	2
Procellaridae	*Puffinus pacificus*	360	37.7	2
Phoeniculidae	*Phoeniculus purpureus*	71.3	37.95	4
Tytonidae	*Tyto alba*	315	38.9	2
Podargidae	*Podargus strigoides*	269	37.6	2
Falconidae	*Falco tinnunculus*	200	39.7	2

Strigidae	*Otus asio*	190	38	2
Ceryliidae	*Megaceryle alcyon*	150	39.2	2
Columbiidae	*Leptotila verreauxi*	131	38.6	2
Psittacidae	*Myiopsitta monachus*	80.4	38.1	2
Sturniidae	*Sturnus vulgaris*	70	38.8	2
Caprimulgidae	*Caprimulgus europaeus*	70	37.4	2
Piciidae	*Picoides articus*	65	39	2
Turniciidae	*Turnix suscitator*	58.1	37.5	2
Scolopacidae	*Phalaropus fulicaria*	55.4	38.2	2
Charadriidae	*Charadrius hiaticula*	54	38.3	2
Trogonidae	*Trogon rufus*	53	38.1	2
Fringillidae	*Pipilo aberti*	47	39.5	2
Apodidae	*Aeronautes saxatilis*	38.7	38.6	2
Coliidae	*Colius colius*	35.1	35	5
Trochillidae	*Oreotrochilus estella*	8.7	38.8	2
Phasianidae	*Excalifactoria chinensis*	33	37.5	2
Passeridae	*Passer montanus*	23	39.6	2
Thamnophidae	*Thamnophilus punctatus*	21	39.3	2
Hirudiniidae	*Delichon urbica*	18.8	38.5	2
Muscicapidae	*Erithacus rubecula*	18.1	38.5	2
Furnariidae	*Xiphorhynchus guttatus*	45.2	39.3	2
Tyrannidae	*Manacus vittelinus*	15.5	37.5	2
Troglodytidae	*Troglodytes aedon*	11.1	39.5	2
Paridae	*Parus montanus*	11	39.3	2
Corvidae	*Corvus corax*	610	39.4	2
Zosteropidae	*Zosterops lateralis*	11	36.9	6

Thermal conductance

Family	Species	M_b (g)	C_{min} ($mlO_2.g^{-1}.h^{-1}.°C$)	Source
Apodidae	*Collocalia esculenta*	6.8	0.318	7
Zosteropidae	*Zosterops lateralis*	11	0.2	6
Tyrannidae	*Pipra mentalis*	14.2	0.315	3
Coliidae	*Colius colius*	35.1	0.16	5
Columbidae	*Scardafella inca*	41.5	0.122	3
Caprimulgidae	*Caprimulgus macrurus*	68.6	0.0641	7
Phoeniculidae	*Phoeniculus purpureus*	71.3	0.048	4
Strigidae	*Speotyto cunicularia*	138	0.055	3
Podargidae	*Eurostopodus mystacalis*	162	0.0468	7
Phasianidae	*Bonasa umbellus*	644	0.016	3

CHAPTER 2. THE THERMOREGULATORY ROLE OF SUNNING BEHAVIOUR.

INTRODUCTION

Mousebirds (Coliidae) spend long periods of time sun-bathing during the day (Rowan 1967; Decoux 1988, pers. ob.). Typically, the mousebirds cling to a suitable perch with their underparts orientated towards incident radiation. During sunning bouts, the belly feathers are raised to expose the skin to incident radiation (Rowan, 1967; pers.ob.). Dean & Williams (in press) have shown that a negative correlation exits between ambient temperature and the duration of sunning bouts, with white-backed mousebirds spending more time sunning at lower ambient temperatures.

Several authors have alluded to the possible importance of sunning behaviour in the energy budgets of birds (Hamilton & Heppner, 1967; Lustick, 1969; Wolf & Walsberg, 1996). Furthermore, Ohmart & Lasiewski (1971) have pointed out that solar radiation is one of the most dependable energy sources for organisms living in arid areas. Despite this, few authors have attempted to experimentally quantify and evaluate the importance of solar radiation in the energy budgets of birds. Several other roles for sunning behaviour have been suggested, such as the control of ectoparasites (Blem & Blem, 1993; Moyer & Wagenbach, 1995). These authors have proposed that birds sunbathe, even at high ambient temperatures, since these high temperatures serve to kill and/or discourage ectoparasites such as mites and lice. In addition, it is possible that the UV component of sunlight may have pesticidal effects (Blem & Blem, 1993). Dean & Williams (in press) have hypothesized that sunning behaviour in mousebirds has a digestive function. They suggest that by maintaining a higher T_b by means of sunning behaviour, the birds are able to increase the rates of enzymatic reactions in their digestive system.

I was not able to accurately measure the thermal conductance of the *C. colius*, since this species does not appear to maintain a constant rest-phase body temperature (see Chapter 1). The relationship between oxygen consumption and ambient temperature is hence confounded by a Q_{10} effect associated with decreases in body temperature caused by periods of passive heat loss, making it impossible to accurately calculate thermal conductance (see Chapter 1) However, the high rates of heat loss exhibited by individual mousebirds at low ambient temperature, and the obligatory nature of clustering behaviour in this species, suggest that thermal conductance in *C. colius* is indeed high (see Chapter 1). I have suggested that a high conductance facilitates the absorption of solar radiation during the frequent sunning bouts characteristic of this species.

This study was undertaken to experimentally investigate the possible thermoregulatory role of sunning behaviour in *C. colius*. I tested the hypothesis that white-backed mousebirds derive direct thermoregulatory benefits from sunning behaviour by reducing endogenous heat production. Specifically, I predicted that the energy expenditure of individual mousebirds is lower when they are allowed access to simulated solar radiation at constant ambient temperature.

MATERIALS AND METHODS

Field observations and measurement of operative environmental temperatures

Behavioural observations of white-backed mousebirds were made at Tierberg Research Station (33 07'S; 22 16'E) in the southern Karoo, South Africa during April 1997. To assess the extent to which mousebirds can alter their operative environmental temperature (T_e) by means of postural adjustments, I measured T_e using copper mousebird models covered with mousebird skins (see Bakken, Erskine & Santee, 1983). Three models were placed in a bush which a local flock was often observed to use as a perch during sunning bouts. One model faced east in a typical sunning posture for early morning sunning, a second model was placed facing west in a typical late afternoon sunning posture, and the third model was placed in the centre of the bush and was shaded throughout the day. Temperatures inside each model, as well as ambient temperature, were measured every 15 minutes and recorded using a MCS 120-02EX Data Logger (MC Systems, Cape Town).

A total of sixty white-backed mousebirds were trapped using mist-nets and walk-in traps baited with fruit. The birds were caught at Tierberg Research station near Prince Albert, the farm Laer Scholzkloof near Prince Albert, the farm Omdraaisvlei approximately 70km south-east of the Orange River at Prieska, and near Kimberley. Upon capture, the birds were weighed ($M_b = 40.8 \pm 5.05$g) and marked with celluloid split rings for individual identification. The birds were transported to the Department of Zoology & Entomology at the University of Natal in Pietermaritzburg and housed in two outdoor aviaries (1m wide X 1m high X 3m long). The positioning of these aviaries allowed the birds to sun themselves at any time between sun-rise and sun-set. They were fed *ad libitum* on chopped spinach, apples, bananas, pears and grapes, together with a protein supplement. Water was available in the aviaries, although the birds were not observed to drink.

Artificial radiation source and measurement of VO_2 and T_b

In the laboratory, artificial radiation was provided using an Osram bulb (Halogen Superphot, 650-watt, colour temperature 3400°K), suspended under a tin foil reflector from the roof of a 1 m^3 soundproof constant environment chamber, in which all experiments were conducted. The emission spectrum of the bulb was measured using a portable spectroradiometer (LI-1800, Li-Cor, Lincoln, NE). The bulb provided radiation in the visible and IR spectra at wavelengths >400nm, with a peak at *ca.* 1020 nm. All recording equipment in the chamber was shielded from radiation using tin foil. Background lighting in the chamber was provided by a flourescent bulb, with negligible radiation output. The photoperiod in the chamber was matched to the prevailing natural photoperiod. Hence the birds experienced approximately the same photoperiod in the constant environment chamber as they experienced in the aviaries. Each bird was placed in a $6dm^3$ respirometer, designed so that the upper glass surface was orientated at 90° to radiation emitted from the lamp. The inside surfaces of each respirometer were covered with matt black cardboard, except for half of the surface facing the lamp. A piece of wire mesh was attached inside each respirometer onto which the birds clung. The birds were hence able to choose between perching in a shaded portion of the respirometer and perching in a position exposed to the incident radiation from the lamp. This design ensured that exposure to incident radiation occurred voluntarily. The respirometers were placed equidistantly from the lamp at a distance of 50cm. Radiant energy from the lamp was measured using a pyranometer (CM-11, Kipp & Zonen, Delft, Netherlands). While in the respirometers, the birds experienced $242W.m^{-2}$. Outdoor measurements revealed that the lamp supplied radiant energy at a similar intensity to that the birds would experience at approximately 06:45 on a clear day in summer in Pietermaritzburg.

Measurements of oxygen consumption (VO_2) were made using an open flow-through system. Atmospheric air, acting as the control gas, was pumped from outside the building, dried using silica gel, and pumped into the cabinet at approximately 5 $\ell.min^{-1}$ (relative humidity < 50%). This air was drawn through the respirometers at flow rates chosen to maintain less than one percent oxygen depletion between the incurrent and excurrent air. Flow rates were approximately 1 $\ell.min^{-1}$, which maintained O_2 depletion between incurrent and excurrent air of < 1% Flow rate was measured with a Brooks Thermal Mass Flow Meter (Model 5810) calibrated to STP at sea level. The use of solenoid valves and a pump for each respirometer allowed up to five respirometers as well as a control channel to be used simultaneously. The excurrent air from each respirometer was passed via CO_2-proof tubing through a water condenser and a CO_2 scrubber to remove water vapour and CO_2 gas respectively. After passing through pumps, relay valves, filters and the mass flow meter, the excurrent air was subsampled with an oxygen analyser (Model S-3A/1, Ametek) and an oxygen sensor (Ametek N-22M) to determine the fractional concentration of oxygen in the dry air. Analogue signals from the thermistor probes, body temperature telemeters, mass flow meter and oxygen analyser were digitised using an A/D converter and recorded on a multi-channel WINDOWS-based recording program written by BGL, with the sample interval for each respirometer varying from 3 min to 6 min, depending on the number of respirometers in the chamber. Metabolic rates were calculated using the equation $VO_2 = V_E(F_{I\,O2} - F_{E\,O2}) / (1 - F_{I\,O2})$ where VO_2 = metabolic rate ($m\ell\ O_2.h^{-1}$), V_E = flow rate ($m\ell.min^{-1}$), $F_{I\,O2}$ = incurrent fractional O_2 concentration and $F_{E\,O2}$ = excurrent fractional O_2 concentration (Withers, 1977).

For T_b measurements, temperature-sensitive telemeters (Model XM, Mini-mitter Co., Sunriver, Oregon) calibrated with a standard mercury thermometer (0.05 C) were implanted into the peritoneal cavity under inhalation anaesthesia (isoflourane; induction and maintenance, 2%; flow rate, *ca* 1 $\ell.min^{-1}$). The signals transmitted by the mini-mitters were detected using dual antennae attached to perspex sleeves surrounding the respirometers, converted to TTL waves using a monostable multi-vibrator and then converted to voltages using a frequency-to-voltage converter. Ambient temperatures in the cabinet and the respirometers were measured with thermistor probes, calibrated similarly.

Experiment 1

Ten birds were weighed and placed in the respirometers at *ca.* 08:00, with the cabinet T_a set at 15 °C. The birds were not fed on the morning of the experiment and were hence assumed to be post-absorptive. Metabolic measurements commenced immediately after the birds were placed in the respirometers. After two hours, the lamp was switched on, and cabinet T_a set to 11.6 °C. This cabinet T_a was found to compensate for heat production by the lamp, and maintained respirometer T_a within 1 °C of the initial temperature with the lamp off. Immediately after the lamp was turned on, respirometer T_a rapidly rose by 2 - 3 °C, and then stabilised within 1 °C of the earlier respirometer T_a after 10 - 20 minutes. If respirometer T_a was found to change by more than 1 °C, the data were not used in the analyses. Measurements were continued for a further two hours, with each bird spending a total of four hours in the respirometer.

The data for the second and fourth hours (i.e. the hour prior to the lamp being switched on, and the hour prior to the end of the experiment) of each run were used in the analyses. Data from these periods were compared using an one-way analysis of variance (ANOVA), following Zar (1984).

Experiment 2

Ten birds (different individuals to those used in experiment 1)were placed in the respirometers at *ca.* 16h30 on the day prior to the experiment and spent the night in the respirometers. They were also post-absorptive. Data analyses were restricted to the period between the start of the photophase and *ca.* 0900, as this is the period during which solar radiation is most likely to play a thermoregulatory role. To obtain metabolic and body temperature measurements without the influence of an external radiation, a set of measurements were made with the lamp was left turned off for this period. During the second set of measurements, the lamp was turned on *ca.* 20min after lights-on to simulate the effects of morning sun. The first and second set of measurements were made at a constant T_a = 15 C. The heat production of the lamp was compensated for as described above for experiment one. The third and fourth set of measurements were made using the procedure described above, but with a cabinet T_a program simulating an ambient temperature profile recorded overnight at Tierberg during April 1997 (Figure 1, p 57). In all cases, data were tested for significant differences using an ANOVA (Zar, 1984).

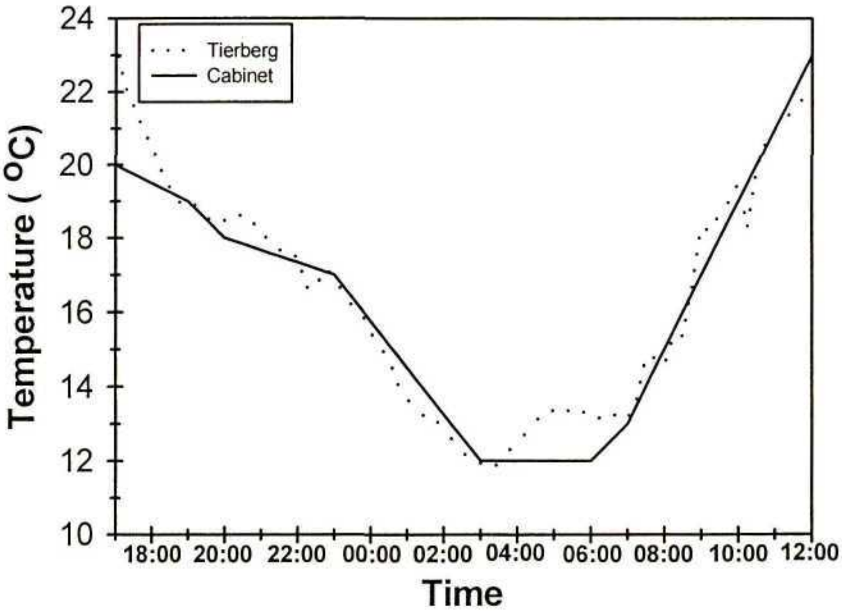

Figure 1. Constant-environment cabinet temperature profile (solid line) used to simulate overnight temperature profile (dotted line) recorded at Tierberg Research Station during April 1997.

RESULTS

Operative environmental temperature

Daily patterns of T_e showed considerable variation depending on the position of the model. Patterns typical of sunny days during April 1997 (southern hemisphere autumn) were characterised by rapid increases in the T_e of the east-facing model during the morning, and similar increases in the west-facing model in the afternoon (Figure 2, p 59). For example, the east-facing model typically attained a temperature of 25 - 30 °C by 09h00, whereas that of the west-facing model remained below 18 °C. Similarly, whereas the east-facing model typically cooled to *ca.* 25 °C by 16h00 in the late afternoon, the west-facing model maintained a T_e greater than 35 °C. Models simulating an individual engaged in morning or afternoon sunning behaviour experienced consistently higher T_es than the shaded model (Figure 2, p 59).

Behaviour during laboratory experiments

During periods when the lamp was switched on and the birds allowed exposure to artificial radiation, all the experimental individuals were observed to assume a sunning posture im the exposed portion of the respirometer and maintain this posture for most of the experiment.

Experiment 1

When allowed access to simulated solar radiation, the birds displayed significant reductions in VO_2mean ($F_{1,18} = 10.094$; $p < 0.05$), VO_2max ($F_{1,18} = 6.276$; $p < 0.05$) and energy expenditure ($F_{1,18} = 9.735$; $p < 0.05$) (Table 1, p 61, Figure 3, p 60). The percentage

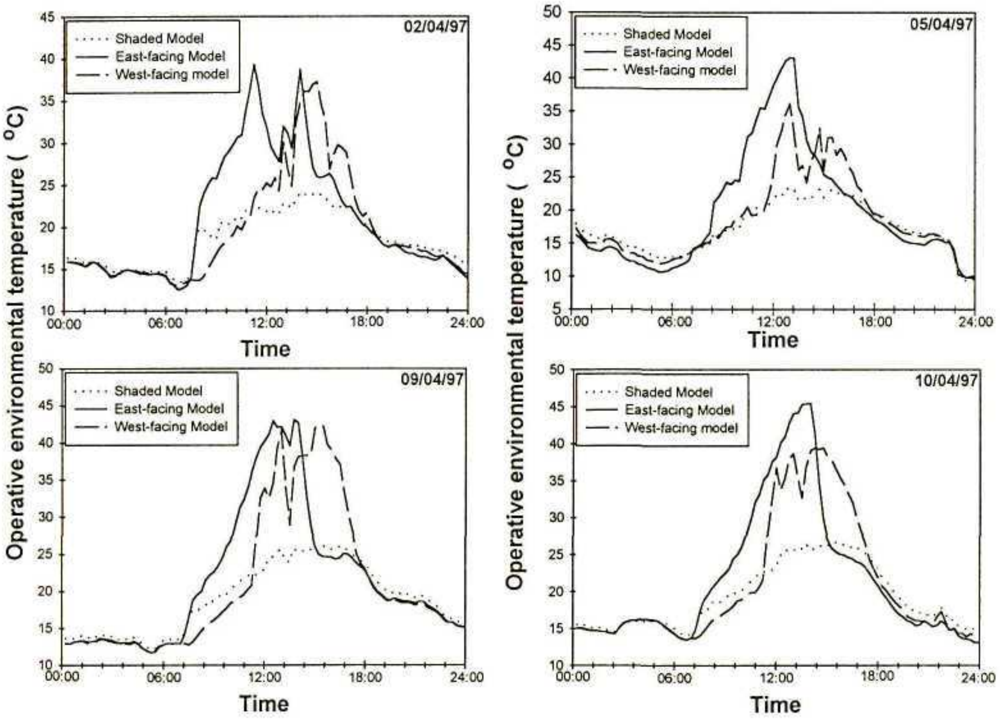

Figure 2. Standard operative temperatures experienced by three copper mousebird models placed in favourite sunning site at Tierberg Research Station.

depression in the various VO_2 parameters ranged from 15 - 21%, and was not accompanied by a reduction in $T_b$min ($F_{1,16} = 0.122$; $p > 0.05$), $T_b$mean ($F_{1,16} = 0.005$; $p > 0.05$) or $T_b$max ($F_{1,16} = 0.001$; $p > 0.05$) (Table 1, p 61; Figure 3, p 60).

Experiment 2

Similar patterns of reduced energy expenditure and maintenance of a constant T_b were observed at a constant cabinet T_a = 15 °C (Table 1, p 61), as well as when the cabinet T_a followed a temperature profile typical of that experienced at Tierberg (Table 1, p 61). At a constant cabinet T_a = 15 °C, significant reductions occurred in VO_2min ($F_{1,18} = 15.470$; p <

0.05), VO_2mean ($F_{1,18} = 21.637$; $p < 0.05$), VO_2max ($F_{1,18} = 20.533$; $p < 0.05$) and energy expenditure ($F_{1,18} = 20.093$; $p < 0.05$). There were significant reductions in $T_b$min ($F_{1,18} = 1.144$; $p > 0.05$), $T_b$mean ($F_{1,18} = 0.105$; $p > 0.05$) or $T_b$max ($F_{1,18} = 0.647$; $p > 0.05$).

Similar results were obtained under T_a conditions simulating those recorded in at Tierberg. Significant reductions in VO_2min ($F_{1,18} = 13.427$; $p < 0.05$), VO_2mean ($F_{1,18} = 19.398$; $p < 0.05$), VO_2max ($F_{1,18} = 6.636$; $p < 0.05$) and energy expenditure ($F_{1,18} = 19.632$; $p < 0.05$) were observed. No significant changes in $T_b$min ($F_{1,18} = 0.222$; $p > 0.05$), $T_b$mean ($F_{1,18} = 0.084$; $p > 0.05$) or $T_b$max ($F_{1,18} = 0.144$; $p > 0.05$) were observed.

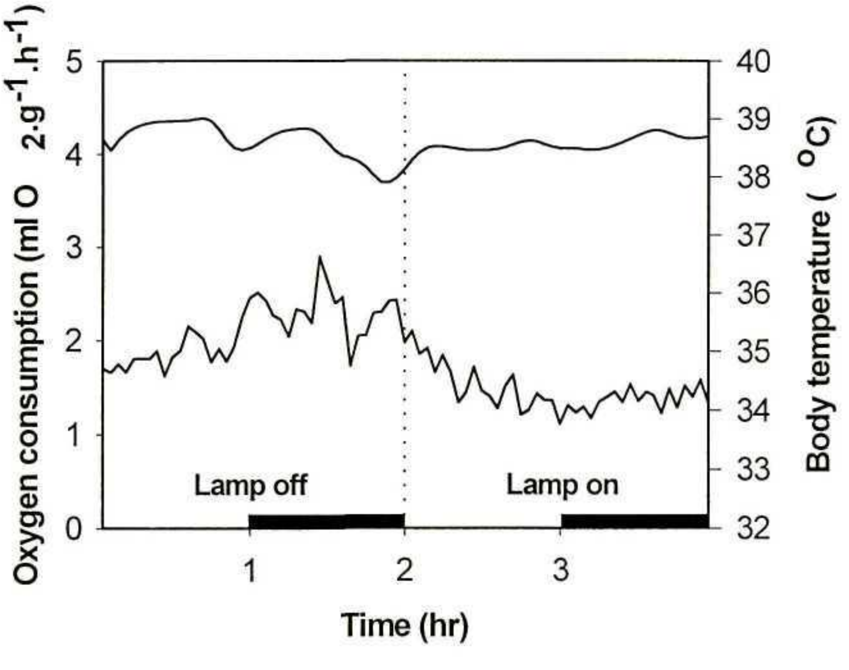

Figure 3. Oxygen consumption (lower line) and body temperature (upper line) in a white-backed mousebird *Colius colius* allowed access to simulated solar radiation.

Table 1. Changes in oxygen consumption (ml $O_2.g^{-1}.h^{-1}$), energy expenditure ($J.g^{-1}.h^{-1}$) and body temperature (°C) associated with access to simulated solar radiation in white-backed mousebirds *Colius colius*.

	Lamp off (n)	Lamp on (n)	% difference
Experiment 1			
VO_2min	1.608 ± 0.358 (10)	1.361 ± 0.346 (10)	15.3
VO_2mean	2.148 ± 0.314 (10)	1.698 ± 0.318 (10)	20.9
VO_2max	2.705 ± 0.464 (10)	2.247 ± 0.345 (10)	16.9
[1]Energy Exp.	43.13 ± 6.31 (10)	34.40 ± 6.20 (10)	20.2
$T_b$min	39.15 ± 0.88 (9)	39.27 ± 0.58 (9)	-0.3
$T_b$mean	39.58 ± 0.67 (9)	39.60 ± 0.49 (9)	-0.1
$T_b$max	39.89 ± 0.60 (9)	39.88 ± 0.47 (9)	0.0
Experiment 2 (T_a = 15 °C)			
VO_2min	2.552 ± 0.404 (10)	1.906 ± 0.326 (10)	25.3
VO_2mean	3.170 ± 0.346 (10)	2.447 ± 0.350 (10)	22.8
VO_2max	3.908 ± 0.341 (10)	3.007 ± 0.528 (10)	23.0
[1]Energy Exp.	62.34 ± 6.92 (10)	48.20 ± 7.19 (10)	22.7
$T_b$min	37.95 ± 1.00 (10)	38.33 ± 0.54 (10)	-1.0
$T_b$mean	39.07 ± 0.63 (10)	38.99 ± 0.54 (10)	0.2
$T_b$max	39.85 ± 0.52 (10)	39.59 ± 0.88 (10)	0.7
Experiment 2 (Tierberg T_a profile)			
VO_2min	2.087 ± 0.437 (10)	1.448 ± 0.337 (10)	30.6
VO_2mean	2.918 ± 0.412 (10)	2.120 ± 0.335 (10)	24.8
VO_2max	3.767 ± 0.435 (10)	3.273 ± 0.444 (10)	13.1
[1]Energy Exp.	55.43 ± 7.99 (10)	39.62 ± 7.97 (10)	28.5
$T_b$min	37.26 ± 1.12 (9)	36.98 ± 1.33 (8)	0.8
$T_b$mean	38.81 ± 0.74 (9)	38.67 ± 1.23 (8)	0.4
$T_b$max	39.75 ± 1.10 (9)	39.53 ± 1.34 (8)	0.6

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1. Energy Exp. = energy expenditure during experimental period.

DISCUSSION

White-backed mousebirds significantly reduced their oxygen consumption by 15 - 30% when allowed access to artificial radiation. Despite these reductions in VO_2, T_b did not show any significant changes. Hence, the reductions in VO_2 reduce thermoregulatory costs through ectothermy. The reduction in energy expenditure was greatest (28.5%) when the birds were exposed to an ambient temperature pattern simulating a pattern recorded in the field at Tierberg. My data suggest that solar radiation may be important in the energy budgets of wild white-backed mousebirds, and hence provide support for the hypothesis of Hamilton and Heppner (1967) that birds may utilise solar radiation to reduce metabolic costs.

Several studies have examined the absorption of solar radiation by birds. The majority have focussed on the effect of pelage colour (Hamilton & Heppner, 1967; Lustick, 1969). Ohmart & Lasiewski (1971) found that hypothermic roadrunners (*Geococcyx californianus*) conserve energy by utilising solar radiation to raise T_b to normal levels following periods of nocturnal hypothermia. *C. colius* appears to utilise exogenous heat as a means of reducing metabolic costs while maintaining a constant body temperature, whereas *G. californianus* employs exogenous heat as a means of reducing the metabolic costs of arousal from rest-phase hypothermia (Ohmart & Lasiewski, 1971). The latter study recorded energy savings of 41% associated with sunning behaviour, compared with 20 - 30% in the present study. Morton (1967) found that at lower T_as white-crowned sparrows (*Zonothrichia leucophrys*) reduced their food intake when allowed access to simulated solar radiation. Morton's (1967) study highlights the adaptive value of using solar radiation to reduce thermoregulatory energy expenditure. The ability to reduce food requirements by means of sun-bathing behaviour is likely to be selected for in areas where food resources show a high degree of spatial and temporal unpredictability, such as the Karoo and Namib areas inhabited by *C. colius*. Furthermore, the results of the present study allow us to hypothesize that *C. colius* should spend more time sunning during periods in which food availability (or quality) is low.

Several interesting similarities exist between *G. californianus* and *C. colius*. Firstly, both species inhabit arid areas, and are hence exposed to unpredictable fluctuations in food availability. Secondly, both species routinely show hypothermia (*sensu* Reinertsen, 1983) during the rest-phase (Ohmart & Lasiewski, 1971; see Chapter 1). Thirdly, both species possess a very dark skin, suggesting that dark skin pigmentation facilitates their ability to utilise solar radiation as an energy source, as originally proposed by Hamilton & Heppner (1967). Hamilton & Heppner's (1967) hypothesis offers a possible adaptive explanation for the dark skin exhibited by some birds, but requires rigorous testing using phylogenetically independent analyses.

Blem & Blem (1993) and Moyer & Wagenbach (1995) have convincingly demonstrated that black noddies (*Anous minutus*) and violet-green woodswallows (*Tachycineta thallisina*) sunbathe to kill ectoparasites, such as lice and mites. Sun-bathing may also serve this function in *C. colius*, which, like other members of the Coliidae, has an unusually high incidence of ecto- and endoparasites (Rowan, 1967). The high parasite load may result from frequent contact between individuals during clustering behaviour, which I have shown to be obligatory in *C. colius* to avoid pathological hypothermia (see Chapter 1).

I have suggested that the apparently high thermal conductance of *C. colius* may facilitate exogenous heat absorption (see Chapter 1). I have also found that *C. colius* displays patterns of rest-phase T_b characterised by linear decreases in T_b (passive cooling) at a rate dependent on ambient temperature and group size. Clustering behaviour in *C. colius* significantly reduces rest-phase energy expenditure and passive cooling rates, and substantially improves the birds' ability to regulate T_b during the rest-phase (see Chapter 1). Furthermore, it would appear that such huddling behaviour is vital for survival at low ambient temperatures, due to the high rates of heat loss that *C. colius* exhibits (see Chapter 1). It would hence appear that a trade-off exists in *C. colius* between the maintenance of strict homeothermy and the capacity to absorb exogenous heat. I suggest that whereas a high conductance facilitates exogenous heat absorption in *C. colius*, it necessitates obligatory huddling to reduce heat loss at low T_as.

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