Thermoregulation under semi-natural conditions in speckled mousebirds: the role of communal roosting

Andrew E. McKechnie*, Gerhard Körtner† & Barry G. Lovegrove

School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, 3209 South Africa

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Mousebirds (Coliiformes) exhibit well-developed communal roosting behaviour as well as a pronounced capacity for facultative hypothermic responses. We recorded body temperature ($T_b$) in speckled mousebirds ($Colius striatus$) under semi-natural conditions in outdoor aviaries, and examined interactions between behavioural and metabolic thermoregulation by experimentally manipulating food availability and communal roosting behaviour. When food was available ad libitum, mousebirds roosting in a cluster maintained approximately constant rest-phase $T_b$, with $32°C < T_b < 42°C$. By contrast, rest-phase $T_b$ in single mousebirds decreased at $0.5°C/hr$ and minimum rest-phase $T_b$ was significantly lower than when clustering. When food availability was restricted, the mousebirds exhibited facultative hypothermic responses that were less pronounced in clustering groups (minimum rest-phase $T_b = 33.3°C$, circadian amplitude of $T_b = 9.5°C$) compared to single birds (minimum rest-phase $T_b = 30.7°C$, circadian amplitude of $T_b = 11.8°C$). When clustering, rest-phase $T_b$ was highly synchronized among individuals. Our data reveal that communal roosting has profound consequences for rest-phase thermoregulation in $C. striatus$, and provide further insights into the potential role of physiological constraints in the evolution of avian sociality.

Key words: body temperature, sociality, communal roosting, facultative hypothermic responses, torpor.

INTRODUCTION

Maintaining a constant, high body temperature during the inactive or rest phase of the circadian cycle can be energetically costly, particularly for small endotherms in thermally challenging environments. During conditions of low air temperature ($T_a$), wind and/or rain, for instance, birds roosting in relatively exposed arboreal or terrestrial sites need to balance rapid heat loss to the environment with endogenous heat production that may require metabolic rates equivalent to several times basal levels (Dawson & Whittow 2000). Birds can reduce their rest-phase energy demands through behavioural and/or physiological avenues, including the selection of thermally buffered microclimates (Walsberg 1985; Ferguson et al. 2002), communal roosting (Walsberg 1990; McKechnie & Lovegrove 2001b), and facultative hypothermic responses such as torpor (Prinzinger et al. 1991; McKechnie & Lovegrove 2002).

The mousebirds (Coliformes) are a phylogeneti-
phase \( T_b \) that decreased at 0.8°C/hr over the course of a night and ranged from 26–38°C, whereas groups of 6–12 individuals cooled at only 0.2°C/hr and maintained rest-phase \( T_b >32°C \) (McKechnie & Lovegrove 2001b; McKechnie et al. 2004).

In this study, we examined interactions between energy supply (food availability), behavioural thermoregulation, and metabolic thermoregulation in speckled mousebirds (Colius striatus) exposed to natural cycles of air temperature (\( T_a \)), photoperiod, and solar radiation. We predicted that rest-phase \( T_b \) and patterns of thermoregulation should vary with food availability and roosting behaviour (roosting alone versus clustering).

**MATERIALS & METHODS**

Ten C. striatus were trapped in Pietermaritzburg, South Africa, during June 1999 using a walk-in trap baited with fruit. They were housed in an outdoor aviary (3 m long, 2 m high, 1 m wide) in the School of Biological and Conservation Sciences at the University of KwaZulu-Natal. They were fed *ad libitum* on a variety of fruit, including pawpaws, bananas, grapes, apples and tomatoes. Each bird was ringed with coloured celluloid split rings for identification. The birds were weighed every second day during *ad libitum* feeding, and daily during restricted feeding. All experiments were carried out during August 1999.

**Body temperature**

We used temperature-sensitive frequency-modulated transmitters (Sirtrack, Havelock North, New Zealand) with an average mass of 1.6 g and frequencies between 146.0 and 146.5 MHz to measure \( T_b \) in the mousebirds. The transmitters were calibrated in a water bath at temperatures between 10°C and 45°C, using a standard mercury thermometer (accurate to 0.05°C, traceable to the US National Bureau of Standards), and were then implanted into the peritoneal cavities of the mousebirds under inhalation anaesthesia (Isoflurane in oxygen; induction and maintenance, 2.5%; flow rate, c. 0.5 l/min). Signals from the transmitters were recorded using a custom-built multi-channel data logger. This data logger controlled a single side-band mode communications receiver (Model IC-R10, Icom, Bellevue, Washington) and recorded pulse intervals of all 10 transmitters in 10-minute intervals. Air temperature (\( T_a \)) in the aviary was recorded by the data logger using a monolytic temperature transducer (LM335). Data were stored on an electronically erasable programmable read-only memory (EEPROM) chip and downloaded daily. Electronics and software were developed by the authors.

**Experimental protocol**

Body temperature recording commenced immediately after implantation on 3 August 1999 and continued for 3–4 weeks, depending on transmitter battery life. Data recorded within 48 hours of surgery were excluded from the analyses. All 10 birds were kept in a single aviary (‘group aviary’) for seven days after implantation. Thereafter, during a five-day period, each bird in the group was removed from the group aviary and placed in a separate aviary overnight, before being returned to the group aviary the following day. Two birds were placed in separate aviaris each night, leaving eight birds in the group aviary. Each bird spent an entire circadian \( T_b \) cycle (12:00–12:00) away from the group.

To investigate the effects of a reduction in food availability, we deprived the mousebirds of food for one day. This procedure was repeated three times while all the birds were in the group aviary, with a minimum of five days between each food deprivation period. Finally, we placed each bird in a single aviary (as described above) and deprived it of food for 24 hours. Some of the transmitter batteries ran flat during this period and we were able to obtain reliable \( T_b \) data for only five individuals.

**Data analysis**

We subjectively judged the rest-phase to commence following the rapid reduction in \( T_b \) that typically occurred shortly after sunset. Single birds generally did not exhibit well-defined \( T_b \) downregulation at the onset of the rest-phase, and we assumed that the rest-phase commenced at the same time as that of clustering birds on the same evening. The rest-phase was subjectively judged to end immediately prior to the rapid rewarming that occurred before sunrise.

Since temporal variation in rest-phase \( T_b \) in C. colius and C. striatus is best described by linear models (McKechnie & Lovegrove 2001a,b), we fitted least-square linear regressions (Zar 1999) to \( T_b \) as a function of time during the rest-phase. The coefficients of these regressions were used as cooling rates. We calculated the circadian amplitude of \( T_b \) rhythms as the difference between minimum rest-phase \( T_b \) and the maximum active-phase \( T_b \),
following Aschoff (1982).

Values are presented as means ± S.E. To determine the effects of clustering and food availability we used repeated-measures analyses of covariance (RM-ANCOVA; Zar 1999), with the minimum and average Tₐ between sunset and sunrise as covariates. Assumptions concerning the homogeneity of variances/covariances were confirmed using Sen and Puri’s nonparametric test.

RESULTS

Random visits to the aviaries at night indicated that the mousebirds clustered from shortly after sunset until immediately before sunrise the next morning. Some movement occurred within the clustering group, and an individual’s position in the cluster varied during the course of the night. The mousebirds’ body mass (Mₐ) during ad libitum feeding was 52.4 ± 1.4 g, and decreased to 46.3 ± 1.0 g when food was removed for a day, equivalent to Mₐ loss of 11.7 ± 0.8%.

Rest-phase thermoregulation during ad libitum feeding

Clustering mousebirds exhibited typical endothermic circadian Tₐ rhythms, namely rapid cooling at the end of the active phase followed by the defence of an approximately constant rest-phase Tₐ (Fig. 1a–d). By contrast, Tₐ in birds roosting alone decreased gradually during the rest-phase, reaching a minimum shortly before sunrise (Fig. 1e–h). The horizontal bars indicate the period between sunset and sunrise. The data shown were recorded in different individuals at various times during the study.

When food was available ad libitum, clustering speckled mousebirds (Colius striatus) downregulated body temperature (Tₐ) at the end of the active phase, and thereafter maintained approximately constant rest-phase Tₐ (A–D). By contrast, Tₐ in birds roosting alone decreased gradually during the rest-phase, reaching a minimum shortly before sunrise (E–H). The horizontal bars indicate the period between sunset and sunrise. The data shown were recorded in different individuals at various times during the study.

![Figure 1](image-url)

**Fig. 1.** When food was available ad libitum, clustering speckled mousebirds (Colius striatus) downregulated body temperature (Tₐ) at the end of the active phase, and thereafter maintained approximately constant rest-phase Tₐ (A–D). By contrast, Tₐ in birds roosting alone decreased gradually during the rest-phase, reaching a minimum shortly before sunrise (E–H). The horizontal bars indicate the period between sunset and sunrise. The data shown were recorded in different individuals at various times during the study.
Rest-phase cooling rates in single birds were equivalent to approximately three times those in clustering birds, and were significantly higher (RM-ANCOVA, $F_{1,135} = 55.852, P < 0.05$; Table 1). The maximum circadian $T_b$ amplitude of single birds was significantly greater than that of clustering birds (RM-ANCOVA, $F_{1,135} = 16.143, P < 0.05$; Table 1).

**Rest-phase thermoregulation during restricted feeding**

When the mousebirds were deprived of food and lost c. 12% of their $M_b$, the circadian amplitude of $T_b$ rhythms increased in both clustering (RM-ANCOVA, $F_{1,149} = 97.473, P < 0.05$) and single birds (RM-ANCOVA, $F_{1,2} = 96.856, P < 0.05$). Clustering birds did not maintain a constant rest-phase $T_b$ following the initial downregulation at the onset of the rest-phase (Fig. 4a–d). Rather, they exhibited linear cooling that was quantitatively similar to that observed in single birds during *ad libitum* feeding (Table 1). Both clustering and single birds showed a wider range of rest-phase $T_b$ than when fed *ad libitum* (Fig. 2c,d). Moreover, modal rest-phase $T_b$ decreased (Fig. 2c,d). Similarly, the minimum rest-phase $T_b$ of clustering (RM-ANCOVA, $F_{1,149} = 82.339, P < 0.05$) and single mousebirds (RM-ANCOVA, $F_{1,2} = 203.931, P < 0.05$) decreased significantly compared to when food was available *ad libitum* (Table 1). The cooling rates of birds in clusters were significantly higher (RM-ANCOVA, $F_{1,149} = 82.454, P < 0.05$) than during the *ad libitum* treatment, although no differences were evident in single birds (RM-ANCOVA, $F_{1,2} = 1.623, P > 0.05$; Table 1). The widest range in rest-phase $T_b$ (c. 29–43°C) was exhibited by single mousebirds during the restricted food treatment (Fig. 2d). The lowest $T_b$ we observed was 29.1°C in a single mousebird (Fig. 4e). Minimum rest-phase $T_b$ was
significantly lower in single birds than in clustering birds (RM-ANCOVA, $F_{1,14} = 10.312, P < 0.05$) and the circadian $T_b$ amplitude was significantly greater (RM-ANCOVA, $F_{1,14} = 4.854, P < 0.05$).

**Active-phase thermoregulation**

The mousebirds maintained approximately constant $T_b$ during the active-phase, with a mean active $T_b$ of $41.5 \pm 0.1^\circ C$ during the *ad libitum* food treatment.

The maximum active-phase $T_b$ exhibited during the course of the study was $43.6 \pm 0.2^\circ C$. Daily $T_b$ maxima typically occurred between 09:00 and 11:00 on sunny days, and appeared to coincide with bouts of basking behaviour. Neither the maximum, mean, nor minimum active-phase $T_b$ differed significantly during the restricted food treatment.

**DISCUSSION**

The patterns of thermoregulation exhibited by the mousebirds during *ad libitum* feeding reveal that communal roosting is a vital component of homeothermic thermoregulation. When clustering, speckled mousebirds exhibited temporal variation in $T_b$ that was similar to that exhibited by most birds, namely an initial decrease from active-phase to rest-phase $T_b$, followed by an approximately constant rest-phase $T_b$, and finally an increase back to active-phase levels (Dawson & Whittow 2000). The typical avian pattern in clustering mousebirds contrasts with the non-steady-state rest-phase $T_b$ and lack of initial downregulation exhibited by single birds (Fig. 1). It is unclear why single birds did not downregulate their $T_b$ at the onset of the rest-phase. One possibility is that metabolic suppression was facultatively inhibited.
in order to minimize the over-night reduction in rest-phase $T_b$. The cooling rates and rest-phase $T_b$ range exhibited by single speckled mousebirds during ad libitum feeding were consistent with previous laboratory observations (McKechnie & Lovegrove 2001a). Collectively, these differences in thermoregulation between clustering and single mousebirds reveal that communal roosting is obligatory for the maintenance of typical avian endothermic circadian $T_b$ rhythms in $C. striatus$, as is the case in the closely-related $C. colius$ (McKechnie & Lovegrove 2001b; McKechnie et al. 2004).

Mousebirds respond to restricted food availability and/or challenging thermal environments with facultative reductions in $T_b$ under both laboratory and natural conditions (Bartholomew & Trost 1970; Prinzinger et al. 1981; McKechnie & Love-

Table 1. In speckled mousebirds ($Colius striatus$) held under semi-natural conditions, rest-phase thermoregulatory parameters differed between birds clustering (roosting communally) and birds roosting alone. The data are means ± S.E., and numbers in brackets refer to the number of individuals (first number) and the total number of overnight body temperature ($T_b$) traces analysed (second number). The relevant statistics are provided in the text.

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<th>Clustering</th>
<th>Alone</th>
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<tr>
<td><strong>Minimum rest-phase $T_b$ (°C)</strong></td>
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<tr>
<td>Ad libitum feeding</td>
<td>35.9 ± 0.1 (10, 145)</td>
<td>34.9 ± 0.6 (9, 9)</td>
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<tr>
<td>Restricted feeding</td>
<td>33.3 ± 0.2 (10, 23)</td>
<td>30.7 ± 1.2 (5, 5)</td>
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<td><strong>Amplitude of circadian $T_b$ rhythm (°C)</strong></td>
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<tr>
<td>Ad libitum feeding</td>
<td>6.9 ± 0.1 (10, 145)</td>
<td>8.1 ± 0.6 (9, 9)</td>
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<tr>
<td>Restricted feeding</td>
<td>9.5 ± 0.2 (10, 23)</td>
<td>11.8 ± 0.5 (5, 5)</td>
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<td><strong>Cooling rate (°C/hr)</strong></td>
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<tr>
<td>Ad libitum feeding</td>
<td>0.14 ± 0.0 (10, 145)</td>
<td>0.49 ± 0.1 (9, 9)</td>
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<tr>
<td>Restricted feeding</td>
<td>0.42 ± 0.0 (10, 23)</td>
<td>0.47 ± 0.1 (5, 5)</td>
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Recent empirical and theoretical studies have revealed that several birds and mammals bask during rewarming from torpor, and that radiative heat gain can significantly reduce the costs of rewarming to normothermic Tb. This suggests that thermoregulatory constraints may play a role in mediating survival in white-backed mousebirds. At Ta = 5°C, four out of nine single C. colius exhibited unregulated, apparently irreversible decreases in Tb, and had to be artificially rewarmed (McKechnie & Lovegrove 2001b). Although the labile patterns of rest-phase Tb exhibited by single mousebirds could conceivably represent regulated, reversible facultative responses, the adverse effects suffered by four out of nine C. colius argues against this possibility. Collectively, the available data suggest that communal roosting is an obligatory component of homeothermic thermoregulation in at least two species. The mousebirds hence provide strong evidence that physiological constraints can play a role in shaping avian social systems, and thereby potentially influence the evolution of associated traits such as cooperative breeding (Du Plessis 2004).
the mousebirds. Speckled mousebirds maintained higher, more stable $T_b$ at $T_a < 15^\circ$C under laboratory conditions than white-backed mousebirds (McKechnie & Lovegrove 2001a,b), suggesting that the latter species is more reliant on communal roosting at low $T_a$. This is a surprising observation given the respective distributions of these two species: $C. colius$ inhabits the colder western regions of southern Africa, whereas $C. striatus$ is widespread in the milder eastern and northern regions (Harrison et al. 1997). One possible explanation concerns the generally arid, unpredictable habitat of $C. colius$. Endotherms inhabiting deserts have evolved more conservative energetic traits than their mesic counterparts (Lovegrove 2000; Tieleman & Williams 2000; Lovegrove 2003). Other physiological and behavioural traits that reduce energy expenditure are also likely to be selected for in arid environments, and we hypothesize that $C. colius$ has experienced stronger selection for reductions in rest-phase energy expenditure through communal roosting than $C. striatus$, which in turn has favoured a greater reliance on this form of behavioural thermoregulation. However, adaptation cannot be inferred from two-species comparisons (Garland & Adolph 1994), and data from additional mousebird species are needed to test this hypothesis.

The quantitative and temporal synchronicity of $T_b$ in clustering mousebirds (McKechnie et al. 2004; present study) raises questions about inter-individual variation in rest-phase energy expenditure. In a clustering group, individuals near the centre are completely surrounded by flock-mates, but individuals on the periphery are partly exposed to the surrounding air (A.E. McKechnie, pers. obs.). Since their $T_b$s are similar, individuals on the periphery of the cluster presumably have higher rates of convective and radiative heat loss, and hence greater energy expenditure, than individuals near the centre. The energetic benefits of clustering are presumably greatest for individuals that position themselves near the centre of a cluster, particularly when individuals on the periphery experience rapid convective heat loss in windy conditions. Do individuals attempt to position themselves within a cluster so as to minimize their energy expenditure? If so, how is the position of an individual (centre versus periphery) determined? Inefficient foraging can be a major constraint on time and energy allocation, and hence survivorship, in young birds (Weathers & Sullivan 1989). By positioning themselves in the centre of a cluster, young mousebirds could conceivably offset limited diurnal energy gains. Answering these questions requires a detailed study of mousebird cluster dynamics.

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University of Alaska, Fairbanks, Alaska


