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Heterothermic responses in the speckled mousebird (*Colius striatus*)

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Abstract We investigated normothermic thermoregulation and heterothermic responses to restricted food in the speckled mousebird *Colius striatus*, in the context of the widely accepted distinction between normothermia, rest-phase hypothermia, and torpor. Normothermic thermoregulation differed from typical endothermic patterns in that rest-phase body temperature (*T*<sub>b</sub>) was not maintained with respect to a constant setpoint. Instead, *T*<sub>b</sub> decreased during the course of the rest-phase, with the highest cooling rates observed at moderate ambient temperatures (*T*<sub>a</sub>). Restricted food was associated with significant reductions in rest-phase *T*<sub>b</sub> and metabolic rate. The lowest *T*<sub>b</sub> recorded in a bird which was able to arouse spontaneously, was 18.2 °C. However, we were unable to clearly discern between normothermic, hypothermic and torpor *T*<sub>b</sub> ranges. Furthermore, heterothermic responses did not accord with the patterns typically observed in birds and mammals. Metabolic suppression normally associated with entry into torpor and the defence of a torpor *T*<sub>b</sub> setpoint was largely absent. The mousebirds significantly reduced their energy expenditure when heterothermic at moderate *T*<sub>a</sub>s only. We suggest that the observed patterns of thermoregulation in *C. striatus*, as well those previously reported in *Colius colius*, are associated with pleiomorphic clustering behaviour in the Coliiformes, and the tandem evolution of behavioural and metabolic thermoregulation.

Keywords Mousebirds  ·  Normothermia  ·  Heterothermic responses  ·  Torpor  ·  Clustering

Abbreviations *α* active phase  ·  BMR basal metabolic rate  ·  CR cooling rate  ·  *M*<sub>b</sub> body mass  ·  *T*<sub>a</sub> ambient temperature  ·  *T*<sub>b</sub> body temperature  ·  *T*<sub>lc</sub> lower critical limit of thermoneutrality  ·  *ρ*<sub>1</sub> first hour of rest-phase  ·  *ρ*<sub>2</sub> final hour of rest-phase  ·  *VO*<sub>2</sub> oxygen consumption  ·  *VCO*<sub>2</sub> carbon dioxide production

Introduction

Normothermic metabolic rate and body temperature (*T*<sub>b</sub>) cycles in endotherms are characterised by circadian fluctuations about a stable, long-term mean (Aschoff 1982). Controlled heterothermic responses are marked exaggerations of these cycles, and have been described in a variety of endotherms (Lyman et al. 1982; Boyer and Barnes 1999). These heterothermic responses are usually divided into daily torpor (daily heterothermy) and hibernation (seasonal heterothermy; Lyman et al. 1982; Geiser and Ruf 1995). Torpor and hibernation are distinguishable on the basis of several characteristics, including the extent of metabolic down-regulation, minimum *T*<sub>b</sub>, and bout duration (Geiser and Ruf 1995).

Hibernation is typically a seasonal response, and is characterised by metabolic depression to ca. 5% of basal metabolic rate (BMR), long bout lengths (mean = 355 h) and a mean minimum *T*<sub>b</sub> of 5.8 °C (Geiser and Ruf 1995). Hibernation appears to be a predominantly mammalian phenomenon, and has been reported in only one bird species, the common poorwill *Phalaenoptilus nuttallii* (Jaeger 1948, 1949).

Daily torpor is characterised by shorter bouts (mean = 11.2 h), metabolic depression to ca. 27% of BMR and a mean minimum *T*<sub>b</sub> of 17.4 °C (Geiser and Ruf 1995). Daily heterothermy has been described in several mammalian (e.g. Rodentia, Insectivora, Carnivora, Primates, Macroscelidea) and avian (e.g. Apodiformes, Caprimulgiformes, Coliiformes) orders (Geiser and Ruf 1995).

A third, supposedly independent heterothermic response, rest-phase hypothermia, is also recognised in
birds (Reintersen 1983, 1996; Prinzinger et al. 1991). During rest-phase hypothermia, $T_b$ is typically reduced by $< 10$ °C, and has been recorded in response to cold (e.g. Haftorn 1972; Reintersen 1983; Reintersen and Haftorn 1986) and food deprivation (e.g. Bartholomew et al. 1983; Graf et al. 1989).

Although the evolutionary link between daily torpor and hibernation is still the subject of debate (Malan 1996; Geiser 1998), similarities exist in the patterns of metabolic rate and $T_b$ associated with these two heterothermic responses (Geiser and Ruf 1995). Both involve initial reductions of $T_b$ associated with metabolic suppression, followed by a maintenance phase during which $T_b$ is regulated with respect to a setpoint considerably lower than that during normothermia (Geiser and Ruf 1995). Body temperature returns to normothermic levels during the arousal phase, characterised by rapid increases in endogenous heat production which are usually entrained to the light-dark cycle (Geiser and Ruf 1995).

In contrast, the distinction between rest-phase hypothermia and daily heterothermy in birds has not been rigorously examined. Prinzinger et al. (1991) suggested that $T_{ps} < 25$ °C are indicative of torpor, whereas Reintersen (1996) proposed $T_{ps} < 30$ °C. The distinction between rest-phase hypothermia and torpor on the basis of bout duration, extent of metabolic rate reduction, etc., remains similarly unresolved.

Torpor has been well-documented in the mousebirds (Coliiformes), which are endemic to sub-Saharan Africa (Fry et al. 1988). Torpor has been described in response to low body mass (M_b) in four species; the speckled mousebird *Colius striatus*, the red-backed mousebird *Colius castanotus*, the blue-naped mousebird *Urococcyx macrourus*, and the red-faced mousebird *Urococcyx indicus* (Bartholomew and Trost 1970; Prinzinger et al. 1981a, 1981b; Hoffmann and Prinzinger 1984; Prinzinger 1988). Mousebirds are also known for their huddling behaviour (clustering) which has been shown to be important for reducing energy expenditure (Brown and Foster 1992; McKechnie and Lovegrove 2001; Prinzinger et al. 1981b). In the white-backed mousebird (*Colius colius*), clustering behaviour is essential for effective thermoregulation and the avoidance of pathological hypothermia at low ambient temperatures ($T_{a}$s) (McKechnie and Lovegrove 2001).

While investigating thermoregulation in the white-backed mousebird *C. colius*, we observed patterns of non-steady state metabolic rate and the apparent lack of a constant normothermic $T_b$ setpoint in single birds during the rest-phase (McKechnie and Lovegrove 2001). These patterns did not accord with typical avian normothermia, hypothermia, or torpor, leading us to regard them as atypical normothermic cycles (McKechnie and Lovegrove 2001). However, we did not investigate the effects of food deprivation, and were hence unable to rule out the possibility that at least some of the patterns represented heterothermic responses.

These observations highlighted the lack of a clear distinction between the various avian hypothermic states. In this study, we investigated rest-phase thermoregulation in the speckled mousebird *C. striatus* under ad libitum and restricted food treatments. The objective of the study was to assess the heterothermic responses of *C. striatus* in the context of the distinction between normothermia, rest-phase hypothermia and torpor.

**Materials and methods**

Twelve speckled mousebirds were trapped in Pietermaritzburg, South Africa, using a walk-in trap baited with fruit. They were housed in outdoor aviaries (3 m long×2 m high×1 m wide) at the School of Botany and Zoology at the University of Natal. They were fed ad libitum on a variety of fruit, including pawpaws, bananas, grapes, apples and tomatoes. Each bird was marked with coloured celluloid rings for identification. All experiments were carried out during July and August 1999.

**Measurement of $T_b$**

Ten temperature-sensitive telemeters (Model XM, Mini-Mitter, Sunriver, Ore.) with an average mass of 1.2 g were calibrated with a standard mercury thermometer (0.05 °C) in a water bath at temperatures from 5-45 °C. These were implanted into the intra-peritoneal cavity under inhalation anaesthesia (Isoflurane in oxygen; induction and maintenance, 2%; flow rate, ca. 0.5 L.min⁻¹). The birds were allowed 7 days to recover from surgery before any measurements were made. The Mini-Mitter signals were detected using dual antennae attached to Perspex sleeves surrounding the respirometers. Ambient temperatures in the cabinet and the respirometers were measured with thermistor probes, calibrated in a similar way.

**Metabolic measurements**

We measured oxygen consumption ($\dot{V}_O_2$) as an indirect measure of metabolic rate. 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 (ca. 11L:13D). Measurements were made in 3.96-l respirometers (22 cm high, 12 cm wide, 15 cm long). The respirometers were placed in a 1-m³ sound-proof temperature cabinet.

Measurements of $\dot{V}_O_2$ and carbon dioxide production $\dot{V}_C_O_2$ were made using an open flow-through system, as described in McKechnie and Lovegrove (2001), with the addition of a CO₂ analyser (Model WA-445-MK3; Analytical Development) placed upstream from the O₂ analyser. Air was drawn through the respirometers at flow rates of ca. 0.8 L.min⁻¹, chosen to maintain less than 1% oxygen depletion between the incident and excurrent air. Metabolic rates were calculated using Eq. 3a in Withers (1977). The birds were weighed before and after each experiment. Mass-specific $\dot{V}_O_2$ was calculated assuming a linear decrease in $M_b$ during the measurements.

**Experimental protocol**

For all experiments, birds were placed in the respirometers at ca. 1530 hours, to allow sufficient time to equilibrate before the onset of the rest-phase. Birds were removed from the respirometers at least 2 h after lights-on the following morning, to ensure that $T_b$ and $\dot{V}_O_2$ attained normothermic active-phase levels.

Measurements of $T_b$, $\dot{V}_O_2$ and $\dot{V}_C_O_2$ were made in eight to ten birds at $T_a$=0, 5, 10, 15, 20, 25, 28, 31 and 34 °C in a randomly chosen sequence. The birds were maintained in the respirometers for the entire rest-phase at each $T_a$. 
