

Thermoregulation in free-ranging ground woodpeckers *Geocolaptes olivaceus*: no evidence of torpor

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Heterothermic responses characterised by pronounced hypometabolism and reductions in body temperature (T_b) are one of the most effective ways in which small endotherms can offset the energetic cost of endothermic homeothermy. It remains unclear, therefore, why daily torpor and hibernation are restricted to only a subset of avian lineages. To further our understanding of the phylogenetic distribution of avian torpor, we investigated winter thermoregulation in the southern African ground woodpecker *Geocolaptes olivaceus*. We considered this species a good candidate for heterothermy, because it is resident year-round in mountainous regions with cold winters and reliant on small ectothermic prey. We recorded T_b patterns in free-ranging individuals and measured T_b and metabolic rates in captive individuals. Neither free-ranging nor captive woodpeckers showed any indication of daily torpor or even shallow rest-phase hypothermia. All birds maintained bimodally distributed T_b characteristic of classic endothermic homeothermy, with a mean rest-phase T_b of $37.9 \pm 0.2^\circ\text{C}$ and no data below 37.0°C . The mean circadian amplitude of T_b was 4.2°C , equivalent to approximately twice the expected value. There was some evidence of seasonal acclimatisation in T_b , with a small decrease in rest-phase T_b with the onset of the austral winter. Captive birds showed patterns of resting metabolic rate and T_b consistent with the classic model of endothermic homeothermy. The apparent absence of torpor in *G. olivaceus* supports the notion that, unlike the case in mammals, many avian taxa that may a priori be expected to benefit from deep heterothermy do not use it.

Endothermy evolved independently in birds and mammals (Ruben 1995, Lovegrove 2016). The elevated energy demands associated with endothermic homeothermy, particularly in cold environments, have led to both classes evolving a number of behavioural and physiological mechanisms of energy conservation. One of the most effective is heterothermy, a term usually used to refer to a spectrum of facultative hypometabolic states during which body temperature (T_b) is reduced below the range characteristic of normothermic circadian rhythms (Lyman et al. 1982). Heterothermy is generally categorized on the basis of bout duration and the extent of reductions in T_b and metabolic rate as hibernation, daily torpor or shallow rest-phase hypothermia, with hibernation generally characterised by bout lengths > 24 h, torpor by both lengths < 24 h and reductions in T_b by $> 10^\circ\text{C}$ below normothermy, and shallow rest-phase hypothermia by less pronounced reductions in T_b (Prinzinger et al. 1991, Geiser and Ruf 1995, Ruf and Geiser 2015). Many authors use specific threshold T_b values (e.g., $T_b \approx 30^\circ\text{C}$; Reinertsen 1996, Barclay et al. 2001) to distinguish torpor from shallower responses, but cases where the T_b ranges associated with two discrete physiological states overlap (Merola-Zwartjes and Ligon 2000) suggest that this approach may be problematic in practise.

The physiology, ecology and evolution of heterothermy among birds have received far less attention than has been

the case for mammals (Heldmaier and Klingenspor 2000, Barnes and Carey 2004, Lovegrove and McKechnie 2008). Nevertheless, the available data reveal that avian heterothermy occurs in many species and in a variety of ecological contexts where birds need to avoid mismatches between energy supply and demand (Prinzinger et al. 1991, McKechnie and Lovegrove 2002, Schleucher 2004). Daily torpor appears to be most common in phylogenetically older avian taxa, particularly those that feed on spatially and/or temporally unpredictable food resources such as aerial insects or nectar (Prinzinger et al. 1991, McKechnie and Lovegrove 2002). Shallow rest-phase hypothermia, in contrast, occurs throughout the avian phylogeny and appears to be particularly common in passerines (Prinzinger et al. 1991, McKechnie and Lovegrove 2002).

Several major gaps remain in our understanding of avian heterothermy, among the most prominent of which concerns the phylogenetic distribution of daily torpor. Although heterothermy has been reported in 16 orders (Brigham and McKechnie 2017), investigations of daily torpor in birds have focused disproportionately on a small number of taxa in which torpor is known to be common, particularly the caprimulgids, hummingbirds and the mousebirds (Bartholomew and Trost 1970, Carpenter 1974, Withers 1977, Hoffmann and Prinzinger 1984, Hiebert 1990, Brigham 1992, Bech et al. 1997, McKechnie and Lovegrove

2001a, Smit et al. 2011). One of the many understudied taxa in this respect is the order Piciformes; to the best of our knowledge the only record of heterothermy in this group involves a single record of $T_b \approx 31^\circ\text{C}$ in an African barbet (McKechnie and Smit 2010).

One family that is potentially a good candidate for torpor is the woodpeckers (Piciformes: Picidae). Woodpeckers are part of the supraorder Coraciimorphae (Prum et al. 2015), which includes several groups known to possess the capacity for torpor, such as mousebirds and todies (Bartholomew and Trost 1970, Hoffmann and Prinzinger 1984, Merola-Zwartjes and Ligon 2000, McKechnie and Lovegrove 2001a). The thermal physiology of woodpeckers in general remains poorly studied (Weathers et al. 1990, Du Plessis et al. 1994), but heterothermy is a distinct possibility in this group on account of most species' generally small size, reliance on ectothermic prey, non-migratory life histories, and in several parts of the world (including southern Africa) the climatic unpredictability generated by the El Niño Southern Oscillation (Lovegrove 2000). Moreover, several woodpecker species inhabit environments where torpor might be expected to result in substantial energetic benefits but incur few ecological costs, such as increased vulnerability to predation; under these conditions, selection is likely to favour the use of deep heterothermy (McKechnie and Lovegrove 2006).

We investigated thermoregulation during mid-winter in the ground woodpecker *Geocolaptes olivaceus*, a ~ 106-g species endemic to southern Africa and whose range is restricted to high-lying, mountainous areas. This species, which is primarily terrestrial, has a specialised diet consisting almost entirely of ants throughout the year (Oatley et al. 1989), and roosts in pairs or small groups in tunnels 0.5–1 m long, located in gullies and cliff edges (Tarboton 2005), often in locations inaccessible to potential predators such as mongooses and small felids (R. Kemp pers. obs.).

Material and Methods

Study site

The study took place in the Drakensberg mountains, in South Africa's Free State Province between Golden Gate Highland National Park ($28^\circ30'S$, $28^\circ33'E$) and Clarens ($28^\circ30'S$, $28^\circ26'E$), at elevations of 1700–2400 m a.s.l. between March and June 2016. The vegetation at the site consists predominantly of montane grasslands and *Leucosidea sericea* spread across boulder-strewn mountains with cold winters and occasional snow, with mean daily T_a minima and maxima of $-0.35 \pm 2.87^\circ\text{C}$ and $16.39 \pm 2.89^\circ\text{C}$ respectively during June (austral winter). A portable weather station (Vantage Pro2™, Davis Instruments, Hayward, CA) was erected at the field station to measure air temperature (T_a). We also measured T_b within roost burrows by placing iButtons (calibrated as described below) ~ 25 cm from the entrance of burrows. Birds were captured by locating active roosting holes and placing a handheld net or a mist net over the entrance when the birds emerged at first light. Group sizes were easily determined by observing birds entering a roost hole in

the evening. The mean body mass was 106.36 ± 6.12 g ($n = 31$).

Body temperature measurements in free-ranging birds

The T_b of free-ranging woodpeckers was recorded using miniature temperature loggers (iButton [3.5g] Maxim Semiconductors, model DS1922L, Dallas, USA), with a resolution of 0.0625°C . Prior to implantation, each iButton was calibrated in a circulating water bath against a digital thermocouple reader (model RDXL12SD, Omega, Stamford, CT, USA) over temperatures ranging from 10°C to 45°C in 5°C increments. Each iButton was programmed to record temperature every 20 min, and was coated with biological surgical wax (Elvax, Mini Mitter) before being implanted in the abdominal cavity of the bird under anesthetic (Isoflurane) at the Maloti Veterinary Clinic in Bethlehem, South Africa. Each iButton weighed less than 5% of the bird's body mass. The surgery took place approximately 2 h after capture, and birds were kept in captivity for another 2 h thereafter, before being released at their site of capture. The first 2 d of T_b data were excluded from the analyses. iButtons were recovered from 10 birds, but the failure of three units meant that our final sample size was seven. Data were obtained per bird for periods varying from 23–55 d.

Metabolic rate and body temperature measurements under laboratory conditions

Following capture, birds were temporarily held in an indoor cage (0.8 m^3) constructed from shade cloth, provided with an ad libitum supply of water and hand-fed with mealworms at regular intervals. Food was removed at least 3 h before respirometry measurements to ensure that birds were post-absorptive (predicted mean digesta retention time for a 106-g bird = 80 min; Karasov 1990).

We measured oxygen consumption (\dot{V}_{O_2}), carbon dioxide production (\dot{V}_{CO_2}) and T_b in a field laboratory using two open-flow respirometry systems. Woodpeckers were placed individually in 9-L airtight plastic containers, with birds perching on a plastic mesh platform positioned 10 cm above a ~1 cm layer of mineral oil to prevent evaporation from urine and faeces. An air pump (model DOA-P13-BN, Gast Air pumps, Benton Harbour MI, USA) supplied scrubbed atmospheric air (series of columns containing silica gel and drierite) to the chamber, which was placed in one of two cooler boxes (50–75 L), within which T_a was controlled by a Peltier device (model AC-162, TE Technology Inc., Traverse City MI, USA) and a custom-built controller, or by a PELT-5 Peltier effect temperature controller (Sable Systems, Las Vegas NV, USA). A thermistor probe (model TC-100, Sable system, Las Vegas NV, USA) was inserted through a hole sealed with a rubber grommet in the lid of each metabolic chamber, and connected to an analog-digital converter (model UI-2 universal interface, Sable systems, Las Vegas NV, USA) to measure the T_a within each chamber.

Incurrent atmospheric air was split into a baseline channel (flow rate of ~ 1.5 L min^{-1} maintained with a needle valve; model RFU 482-1/8, Camozzi, Brescia Italy) and two experimental channels with flow rates of ~ 2.5 L min^{-1} regulated

by Alicat mass-flow controllers (model MC10SLPM, Alicat Scientific Inc., Tucson AZ, USA). Baseline and excurrent air from the experimental chambers was sequentially sub-sampled using a multiplexer (MUX Flow-Multiplexer, Sable system, Las Vegas NV, USA), and then pulled using a custom-built pump through an additional Drierite column to scrub water vapour. The filtered air was then pulled through the CO₂/H₂O (model LI-840A, LI-COR, Lincoln NE, USA) and O₂ (FC – 10A, Sable Systems, Las Vegas NV, USA) analysers. A personal computer with Expedata software (Sable System, Las Vegas NV, USA) was used to acquire data, with voltage outputs from the various analysers converted to digital signals using an analog-digital convertor (model UI-2, Sable systems, Las Vegas NV, USA) at a 5-s interval.

Abdominally-injected temperature-sensitive passive integrated transponder (PIT) tags (Biomark, Biose ID, USA) were used to measure T_b every 10 seconds via a portable transeiver system (model 2001F-ISO, Biomark, Boise, ID, USA) connected to an external antenna placed adjacent to each metabolic chamber. Prior to fieldwork, 10 PIT tags were calibrated in a circulating water bath against a digital thermocouple reader (model RDXL12SD, Omega, Stamford, CT, USA) over temperatures ranging from 25°C to 50°C in 5°C increments.

\dot{V}_{O_2} and \dot{V}_{CO_2} were recorded at T_a values of 0°C to 30°C in 5°C increments in a random order. All measurements took place between sunset and sunrise during the woodpeckers' rest phase, with measurements for either one or two birds per night. A total of 14 individuals (9 males and 5 females) were used for measurements of T_b and MR under laboratory conditions. Six of these individuals were recaptured and measurements conducted again at combinations of T_a values different to the first time they were captured. A minimum of 4 d elapsed between release and recapture, with the exception of one individual that was recapture on consecutive days. Each bird spent less than 48 h in captivity at a time, and each respirometry run lasted approximately 12 h. During each run, birds experienced two T_a values, the first from 18:00 to 00:00 and then the second from 00:00 to 06:00. Data collected during the first hour at each T_a were excluded from analyses. Measurements involved repeating cycles, consisting of a 10-min baseline, each metabolic chamber sampled for 30 min, followed by a second 10-min baseline.

Data analyses

Values are presented as mean ± SD. For T_b data from free-ranging birds, the five daily lowest and highest data points were used to calculate the average minimum rest-phase T_b (ρT_{bmin}) and maximum active-phase T_b (αT_{bmax}). The ρT_{bmin} and αT_{bmax} were used to determine the amplitude of the circadian T_b cycle (R_T; Aschoff 1982). Total thermal conductance (C_{total}) was calculated following Noakes et al. (2013). The heterothermy index (HI) was calculated following Boyles et al. (2011). To assess seasonal changes in thermoregulation and test for an effect of group size, we analysed the relationships among log₁₀-transformed response variables (T_{b-min}, R_T and HI) and predictor variables (T_a, Julian day and group size) with individual as a random predictor,

using linear mixed effect models (nlme package; Pinheiro et al. 2007) in R 2.13.1 (R Core Team). The best model was selected based on Akaike information criterion (AIC) values (MuMIn package; Bartoń 2016). Mean values were used to conduct post hoc test of multiple comparison (Tukey contrasts for mixed-effects models). Interaction effects were excluded because no interaction influenced the response variables significantly.

Baseline [O₂] and [CO₂] values were used to correct for drift using the relevant algorithms in Expedata software (Sable System, Las Vegas NV, USA). The lowest 5-min sample period of average \dot{V}_{O_2} and \dot{V}_{CO_2} was used to calculate RMR and BMR of each individual, for both T_a values during an overnight run. Equations [9.4] – [9.6] from Lighton (2008) were used to calculate \dot{V}_{O_2} and \dot{V}_{CO_2} values and using equation [9.3] for excurrent flow rate estimates in all calculations.

Respiratory exchange ratio (RER) was calculated as $\dot{V}_{CO_2} / \dot{V}_{O_2}$. Measurements of gas exchange were converted to metabolic rates (W) using joule equivalence values from Table 4-2 in (Withers 1992). RER for RMR data at 0°C ≤ T_a ≤ 30°C averaged 0.67 ± 0.08 however, RER = 0.71 was assumed if RER < 0.71 (Noakes et al. 2017).

Linear mixed effect models (nlme package; Pinheiro et al. 2007) were fitted to the data using R 2.13.1 (R Core Team). Potential predictor variables and interactions between these variables were initially included in the models, however, the best model was selected based on Akaike information criterion (AIC) values (MuMIn package; Bartoń 2016). Sex and interaction effects were excluded from the model as neither significantly influenced the response variables. To estimate inflection points in RMR as a function of T_a, we fitted segmented linear regression models to the data using the SiZer package (Sonderegger 2012) in R 2.13.1 (R Core Team).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.82jk8>> (Kemp et al. 2017).

Results

Thermoregulation in free-ranging woodpeckers

There was no indication of torpor or hibernation in free-ranging *G. olivaceus*, with T_b decreasing to levels characteristic of these pronounced heterothermic responses at no stage during our study. The single lowest T_b datum we recorded was 37.0°C. Free-ranging birds showed a typical avian circadian rhythm of T_b, decreasing sharply immediately after sunset and thereafter decreasing more gradually to a $\rho T_{bmin} = 37.84 \pm 0.17^\circ\text{C}$ (n = 7), typically just after midnight (Fig. 1). Thereafter, T_b increased gradually until sunrise, after which it increased rapidly back to diurnal levels, with a mean active phase T_b of $41.62 \pm 0.24^\circ\text{C}$ (n = 7; Fig. 1) and maximum active phase T_b of $42.01 \pm 0.26^\circ\text{C}$. The mean R_T was $4.20 \pm 0.33^\circ\text{C}$ (Fig. 2; Supplementary material Appendix 1), and mean HI was $2.37 \pm 0.26^\circ\text{C}$.

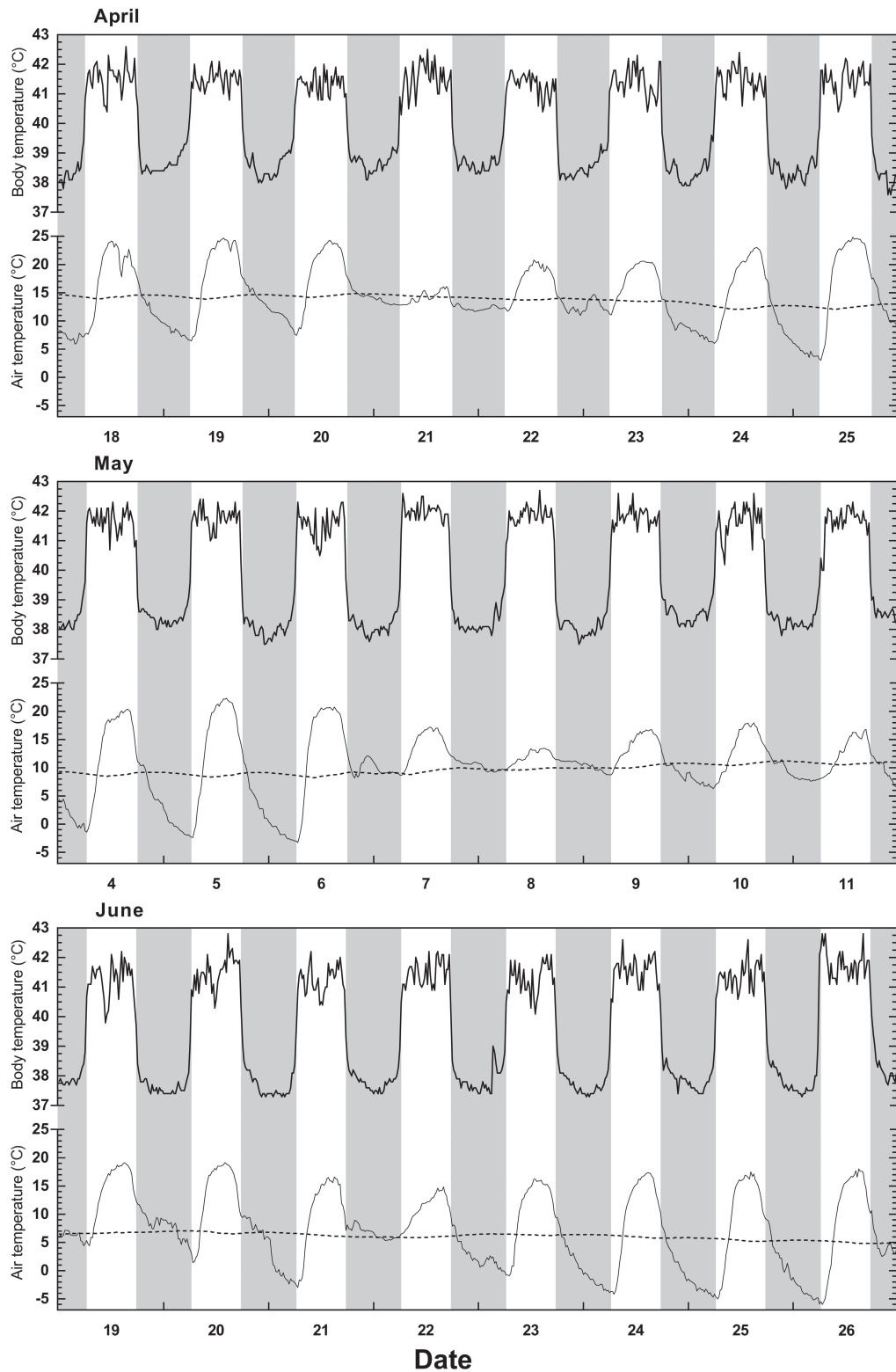


Figure 1. Representative body temperature (T_b ; dark solid line) circadian rhythms of free-ranging ground woodpeckers *Geocolaptes olivaceus* during April, May and June 2016 in the Drakensberg Mts of South Africa. For each period, outside air temperature (T_a ; thin solid line) and roost burrow temperature (T_{Roost} ; dashed line) are also shown. The white bars represent day (i.e., sunrise to sunset), the grey bars night.

Minimum T_b was not significantly influenced by group size ($F_{2,4} = 0$, $p = 0.718$), but decreased significantly during the course of the study period ($F_{1,192} = 20$, $p < 0.001$; Fig. 3).

R_T increased significantly with both group size ($F_{2,4} = 7.677$, $p < 0.043$; Fig. 3) and Julian day ($F_{1,191} = 34.016$, $p < 0.001$; Fig 3). HI did not significantly vary with group

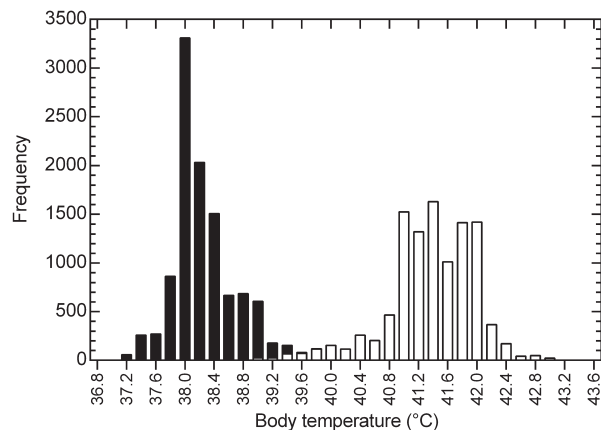


Figure 2. Frequency distribution of body temperature (T_b) in seven free-ranging ground woodpeckers *Geocolaptes olivaceus* during April–June 2016 in the Drakensberg Mts, South Africa. Black bars represent nocturnal T_b and white bars diurnal T_b .

size (ANOVA, $F_{2,4} = 3.218$, $p = 0.147$), but increased with Julian day ($F_{1,192} = 76.501$, $p < 0.001$).

Thermoregulation under laboratory conditions

There was also no indication of torpor or hibernation during laboratory measurements. The mean T_b varied between 36.4°C and 39.8°C over the range of T_a we investigated and was not significantly correlated with T_a (Pearson product-moment $r = 0.278$, $p = 0.105$; Fig. 4a). A clear thermoneutral zone (TNZ) was evident between $T_a \approx 15^\circ\text{C}$ and 30°C . The model provided a significant fit to the RMR data and identified an inflection point at $T_a = 16.1 \pm 0.8^\circ\text{C}$ (SegReg software; <www.waterlog.info/segreg.htm>; Fig. 4b). RMR was significantly related to T_a below the inflection point ($F_{1,9} = 31.471$, $p < 0.001$), but not above it ($F_{1,12} = 0.149$, $p = 0.707$). The minimum RMR value within the TNZ, which we interpret as the basal metabolic rate (BMR) of *G. olivaceus*, was 0.857 ± 0.127 W ($n = 3$) at $T_a = 30^\circ\text{C}$. Thermal conductance was approximately constant at T_a below the TNZ, with a mean of 0.229 ± 0.052 $\text{mW}^\circ\text{C}^{-1} \text{cm}^{-2}$ ($n = 5$) at $T_a \approx 15^\circ\text{C}$. Within the TNZ, C_{total} increased to a maximum of 0.589 ± 0.100 $\text{mW}^\circ\text{C}^{-1} \text{cm}^{-2}$ ($n = 3$) at $T_a \approx 30^\circ\text{C}$.

Discussion

Ground woodpeckers inhabiting the Drakensberg mountains of southern Africa did not show torpor or any obvious heterothermic responses during our study period. Instead, both free-ranging and captive birds regulated a rest-phase T_b set point of $\sim 38^\circ\text{C}$, and never reduced T_b to levels characteristic of torpor or even shallow rest-phase hypothermia. The absence of heterothermic responses during winter in this high-altitude endemic species with a specialised diet is, a priori, difficult to explain. Although the M_b of Ground Woodpeckers (~ 106 g) is larger than that of many species in which torpor has been reported (McKechnie and Lovegrove 2002), it is well below those of several species in which heterothermy associated with $T_b < 30^\circ\text{C}$ occurs,

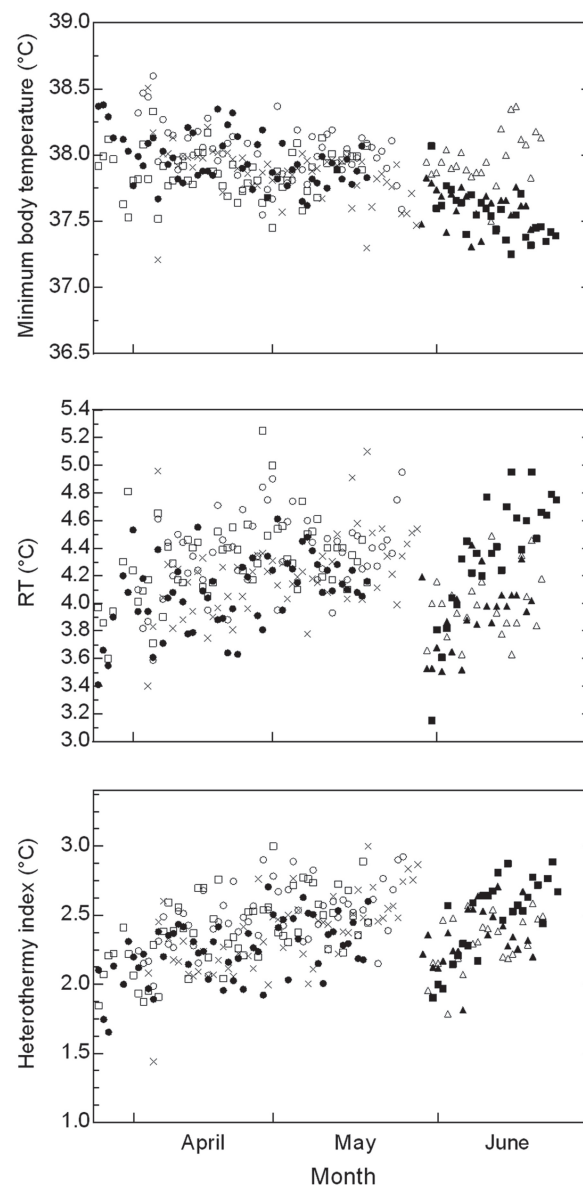


Figure 3. Free-ranging ground woodpeckers *Geocolaptes olivaceus* ($n = 7$), showed a significant decrease in minimum body temperature ($pT_{b\text{min}}$; top panel), a significant increase in the amplitude of the circadian body temperature cycles (R_T ; middle panel), and a significant increase in the heterothermy index (HI; bottom panel) with the onset of winter.

including the ~ 360 -g laughing kookaburra *Dacelo novaeguineae* (Cooper et al. 2008) and ~ 500 -g tawny frogmouth *Podargus strigoides* (Körtner et al. 2000, 2001).

Although we found no evidence of torpor during our 3-month study period, we cannot rule out the possibility that *G. olivaceus* does indeed possess the physiological capacity for pronounced heterothermic responses. For instance, one limitation of the laboratory component of our study is that it involved only well-fed birds, and we did not use a restricted feeding protocol to elicit heterothermic responses. Nevertheless, among endotherms in general heterothermic responses are generally more frequent and pronounced in free-ranging individuals compared to captive individuals under

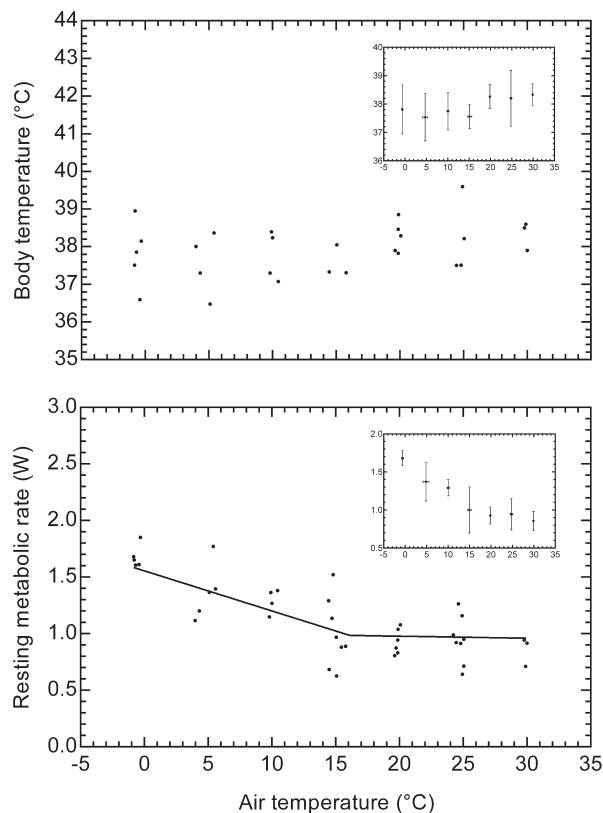


Figure 4. The relationships between body temperature (T_b ; top panel), resting metabolic rate (RMR; bottom panel) and air temperature (T_a) in ground woodpeckers *Geocolaptes olivaceus*. The inset graphs show the mean \pm SD values. The solid line in the lower panel is a segmented linear regression model fitted to the raw RMR data with lower critical limit at 16.1°C. The sample size for T_b varied between 3 and 6, whereas for RMR varied between 3 and 8.

laboratory conditions (Geiser et al. 2000), and so we think it is unlikely that including a restricted feeding protocol in the study would have altered our qualitative conclusions (but see Nowack et al. 2010).

There are two aspects of ground woodpecker behaviour that may be functionally linked to the absence of torpor in our study population. First, the woodpeckers always roosted in groups of 3–5 individuals. Communal roosting in birds can result in substantial rest-phase energy savings (Boix-Hinzen and Lovegrove 1998, McKechnie and Lovegrove 2001b, Wojciechowski et al. 2011, Chappell et al. 2016). However, communal roosting is by no means incompatible with torpor; Nowack and Geiser (2016) demonstrated that huddling in small mammals provides substantial energetic benefits when groups consist of torpid individuals or even a mix of torpid and normothermic individuals. Second, measurements of T_a in unoccupied roost burrows overnight suggested that the interiors of the holes were approximately 6°C warmer than outside T_a . It may thus be that energy savings associated with communal roosting in thermally buffered microsites obviate the need to conserve energy via heterothermy. Notwithstanding these behaviours, if *G. olivaceus* possesses the physiological capacity for torpor we would have expected to see at least some indication of deviations from

rigid endothermic homeothermy in the free-ranging birds we examined.

Thermoregulation in *G. olivaceus* appeared to conform closely to the classic Scholander-Irving model of endothermic homeothermy (Scholander et al. 1950), with an approximately constant T_b and clear thermoneutral zone, below which RMR increases linearly with decreasing T_a . Defence of a rest-phase T_b setpoint was relatively precise during laboratory measurements, with a range of mean T_b of just $\sim 1^\circ\text{C}$ over a 30°C range of T_a . This precise thermoregulation contrasts with that of some southern African species, such as the 220-g frugivorous columbid *Treron calvus* in which T_b varied by nearly 2°C over a similar range of T_a and was significantly correlated with T_a (Noakes et al. 2013), and moreover also contrasts with the torpor observed at similar T_a in taxa such as mousebirds and hummingbirds (Bartholomew and Trost 1970, Carpenter 1974, Withers 1977, Hoffmann and Prinzinger 1984, Hiebert 1990, Brigham 1992, Bech et al. 1997, McKechnie and Lovegrove 2001a, Smit et al. 2011). The BMR of *G. olivaceus* is equivalent to 139% of the value predicted for a 106-g species (0.615 W) by Londoño et al.'s (2015) equation for non-passerine orders other than Apodiformes.

Our data for free-ranging woodpeckers reveal seasonal acclimatisation in T_b , with a small but significant decrease in minimum rest-phase T_b over the course of the study period. This slightly lower T_b in mid-winter was manifested as significant increases in both R_T and HI. Seasonal acclimatisation of thermal physiology is common in birds (reviewed by McKechnie 2008, Swanson 2010), but few studies have investigated whether T_b varies between seasons (Maddocks and Geiser 2000). The $R_T = 4.2^\circ\text{C}$ we observed in *G. olivaceus* is equivalent to 211% of the value allometrically predicted for a 106-g non-passerine (Aschoff 1982), consistent with the greater than expected circadian amplitudes of T_b among southern African non-passerines (McKechnie and Smit 2010).

In conclusion, our data reveal that an Afrotropical high-altitude specialist woodpecker with a specialised diet of terrestrial insects does not use heterothermy during the coldest time of the year. These data reiterate that many birds do not use rest-phase heterothermy to conserve energy, despite ecological traits that make them likely candidates to do so. Moreover, our findings emphasise the evolutionary divergence between mammals and birds in terms of their overall propensity for daily torpor and hibernation. Whereas pronounced heterothermy is phylogenetically widespread among small mammals and strictly homeothermic species are increasingly seen as exceptions rather than the norm, the same does not appear to be the case among birds.

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Supplementary material (Appendix JAV-01453 at <www.avianbiology.org/appendix/jav-01453>). Appendix 1.