

## RESEARCH ARTICLE

# Avian torpor or alternative thermoregulatory strategies for overwintering?

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## ABSTRACT

It is unclear whether torpor really is uncommon amongst passerine birds. We therefore examined body temperature and thermoregulatory strategies of an Austral passerine, the white-browed babbler (*Pomatostomus superciliosus*), which has characteristics related to a high probability of torpor use; it is a sedentary, insectivorous, cooperative breeding species, which we studied during winter in a temperate habitat. Wild, free-living babblers maintained normothermy overnight, even at sub-zero ambient temperatures, with a mean minimum body temperature of  $38.5 \pm 0.04^\circ\text{C}$  that was independent of minimum black bulb temperature. Physiological variables measured in the laboratory revealed that babblers had a low basal metabolic rate and evaporative water loss, but their body temperature and thermal conductance were typical of those of other birds and they had a typical endothermic response to low ambient temperature. Huddling yielded significant energy savings at low temperatures and a roost nest created a microclimate that buffered against low temperatures. Low basal energy requirements, communal roosting and the insulation of a roost nest confer sufficient energetic benefits, allowing babblers to meet energy requirements without resorting to heterothermia, even in their depauperate, low-productivity landscape, suggesting that passerine birds use alternatives to torpor to balance their energy budgets when possible.

**KEY WORDS:** Temperature telemetry, Heterothermia, Body temperature, Respirometry, Metabolic rate, Evaporative water loss

## INTRODUCTION

Sedentary animals need to survive both the diurnal and seasonal energetic challenges of their environment. For endotherms, winter can be an energetic challenge, especially overnight when ambient temperatures ( $T_a$ ) are low, and this may be exacerbated by reduced food availability and limited foraging opportunities. For mammals, daily torpor or multiday hibernation are common strategies to overcome adverse environmental conditions (Withers et al., 2016). However, heterothermia appears much less common amongst birds (McKechnie and Mzilikazi, 2001; Withers et al., 2004; Ruf and Geiser, 2014), although it remains unclear whether this reflects less research effort devoted to describing avian thermoregulatory strategies compared with mammals (Astheimer and Buttemer, 2002; McKechnie and Lovegrove, 2002; Geiser et al., 2006).

Birds in Australian temperate woodlands may not experience winters as extreme as those of snow-bound northern hemisphere locations, but they must still contend with the energetic challenges of winter in a depauperate, low-productivity landscape (Chan et al., 1989; Geiser et al., 2006). For sedentary, insectivorous species, not only does winter present thermal challenges but also the increased energetic demand must be met when prey availability is reduced or unpredictable (Smit and McKechnie, 2010; Doucette et al., 2012). A small body size poses further energetic challenges. These factors are associated with widespread torpor use by Australia's small mammals (Geiser, 1998, 2004; Cooper and Geiser, 2008; Munn et al., 2010), but although torpor is a thermal strategy for some insectivorous non-passerines (Körtner et al., 2001; Cooper et al., 2008; Doucette et al., 2012; McKechnie et al., 2007; Smit and McKechnie, 2010), there is currently little quantitative evidence for torpor amongst southern hemisphere passerines. Other adaptations to a harsh and unpredictable climate such as aseasonal and cooperative breeding (Russell, 1989; Astheimer and Buttemer, 2002) suggest that torpor may be likely, together with the fact that many small Australian insectivorous birds are sedentary (Recher and Davis, 1997; Morris and Wooller, 2001). We therefore examined here the thermal biology and energetics of winter survival for a small, sedentary, insectivorous, cooperatively breeding passerine bird, the white-browed babbler [*Pomatostomus superciliosus* (Vigors and Horsfield 1827), ~45 g], that roosts communally overnight in domed nests (Higgins et al., 2006). The characteristics of this species make it a likely candidate for torpor use during winter, and it is therefore an excellent model to quantify whether torpor or hibernation has a thermoregulatory role for Austral passerines or whether other physiological or behavioural aspects of avian biology obviate the need for heterothermia.

## MATERIALS AND METHODS

All experiments were approved by the Curtin University Animal Ethics Committee (AEC\_2011\_41, AEC\_2012\_09), and were conducted under licence from the Department of Parks and Wildlife (SF008014 and SF008626). Field studies were undertaken at Dryandra Woodland ( $32^\circ45'S$ ,  $116^\circ55'E$ ), 170 km southwest of Perth, Western Australia. For laboratory studies, babblers were caught at Big Brook Dam, Pemberton ( $34^\circ38'S$ ,  $116^\circ03'E$ ), Western Australia, and were housed in outdoor aviaries at Curtin University.

## Field body temperature

Temperature-sensitive radio transmitters (BD-2TH; Holohil, ON, Canada) were implanted into the intraperitoneal cavity of eight babblers from three territories (six from two territories in winter 2012 and two from one territory in winter 2013) under general anaesthesia (isoflurane in  $O_2$ ) with analgesic (Meloxicam) administered subcutaneously. Prior to implantation, transmitters were calibrated at 14, 25, 35 and  $43^\circ\text{C}$ .

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**List of abbreviations**

BMR	basal metabolic rate
C	conductance
$E_{O_2}$	oxygen extraction
EWL	evaporative water loss
$f_R$	respiratory frequency
k	cooling constant
$M_b$	body mass
MR	metabolic rate
PRWE	point of relative water economy
RWE	relative water economy
$T_a$	ambient temperature
$T_{a,depart}$	$T_{bb}$ at time of roost departure
$T_b$	body temperature
$T_{b,arrive}$	$T_{b,field}$ at roost arrival
$T_{b,depart}$	$T_{b,field}$ at roost departure
$T_{b,field}$	field body temperature
$T_{bb}$	black bulb temperature
$T_{bb,depart}$	$T_{bb}$ at roost departure
$T_{bb,min}$	minimum $T_{bb}$
$T_{roost}$	roost nest temperature
$\dot{V}_{CO_2}$	carbon dioxide production
$V_I$	minute volume
$\dot{V}_{O_2}$	oxygen consumption
$V_T$	tidal volume

Field body temperature ( $T_{b,field}$ ) was monitored using an AR8000 or AR8200mk3 radio receiver (AOR, Torrance, CA, USA) and the audio output recorded with an audio recorder (Olympus LS-10 or VN-702PC or Sony ICD-PX333, Tokyo, Japan). Black bulb temperature ( $T_{bb}$ ) was recorded with a Hygrochron iButton (DS1923, Maxim, San Jose, CA, USA) placed inside a black table tennis ball, 0.5 m above ground level in an open location. Additional weather data were obtained from the Australian Bureau of Meteorology (for Wandering, ~30 km away), including  $T_a$ , rainfall, and wind direction, strength and maximum gust.

Cubase (Cubase LE4, Steinberg Media Technologies GmbH, Hamburg, Germany) was used to convert each radiotelemetry .mp3 sound file to .WAV format, which was analysed using custom-written Visual Basic software (P.C.W. and T.K.D.). Inter-pulse distances were calculated, then converted to  $T_{b,field}$  using the transmitter's temperature calibration curve. Roosting commencement time,  $T_{b,field}$  at roost arrival ( $T_{b,arrive}$ ), minimum  $T_{b,field}$ , time and  $T_a$  at minimum  $T_{b,field}$ ,  $T_{b,field}$  and  $T_{bb}$  at time of roost departure ( $T_{b,depart}$  and  $T_{a,depart}$ ), as well as roosting duration, were determined for each bird each night.

**Roost microclimate**

Roost nest temperature ( $T_{roost}$ ) was measured *in situ* every 10 min using iButton loggers. Two intact babbler nests were collected to measure nest thermal conductance; they were placed in a constant-temperature room ( $T_a=10^\circ\text{C}$ ) and a bag containing 190 ml of ~50°C water (equivalent mass of four babblers) was placed in the nest. Three iButtons recorded temperature at 10 s intervals in the nest as it cooled, one within the water, one in the bottom and one in the top of the nest. An iButton also logged temperature of another bag of hot water in the constant-temperature room, and another logged  $T_a$ . Cooling constants ( $k$ ) for the nest and the control bag were calculated following the methodology of Toolson (1987) and were converted to thermal conductance ( $C$ ;  $\text{J g}^{-1} \text{h}^{-1} \text{ }^\circ\text{C}^{-1}$ ) using the specific heat capacity of water ( $4.18 \text{ J g}^{-1}$ ) after Morrison and Tietz (1957) and de Vries and van Eerden (1995).

**Roost nest characteristics**

Characteristics of all babbler roost nests located in the study area were recorded. Location and elevation were recorded with a GPS 60 (Garmin, Kansas City, MS, USA) and tree characteristics of species, diameter at breast height over bark (DBHOB) and tree height, as well as distance to the two nearest neighbouring trees were noted. Nest entrance direction, height to the base of the nest and nest use were also recorded. Tree height and height to base of nest were measured with a Forestry 550 laser range finder (Nikon, Tokyo, Japan), calibrated against objects of known height.

**Laboratory respirometry**

Open flow-through respirometry was used to measure oxygen consumption ( $\dot{V}_{O_2}$ ), carbon dioxide production ( $\dot{V}_{CO_2}$ ) and evaporative water loss (EWL) of babblers in the laboratory at a range of  $T_a$  (10, 15, 20, 25, 30 and  $32.5^\circ\text{C}$ , in random order), after Withers (2001), using the methodology, calculations and calibration procedures of Barker et al. (2012). Birds were fasted during the preceding day and then measured overnight at a single  $T_a$  from approximately 18:00 h to 04:00 h in a 2 l clear Perspex chamber, with an air flow rate of  $900 \text{ ml min}^{-1}$  controlled by a mass-flow controller (32708-28, 0–5  $\text{l min}^{-1}$ , Cole Parmer, Vernon Hills, IL, USA; and GFC171 0–5  $\text{l min}^{-1}$ , Aalborg, Orangeburg, NY, USA).

Ventilatory data were obtained via whole-body plethysmography after Malan (1973) and Withers (1977), using the methodology, calculation and calibration techniques of Cooper and Withers (2010). Respiratory frequency ( $f_R$ , breaths  $\text{min}^{-1}$ ) and tidal volume ( $V_T$ , ml) were measured at the conclusion of the experiment when the babblers were resting, and minute volume ( $V_I$ , ml) and oxygen extraction ( $E_{O_2}$ , %) were calculated from these data. Body temperature ( $T_b$ ) was measured for each individual at the conclusion of each experiment with a Digi-Sense Thermometer (91100-20, Cole Parmer), using a plastic-tipped thermocouple inserted ~1.5 cm into the cloaca.

Physiological variables were also measured for babblers in pairs ( $N=8$  individuals,  $n=4$  measurements) and threes ( $N=9$ ,  $n=1-3$ ) at  $T_a$  of 10, 15 and  $20^\circ\text{C}$  at flow rates of  $1800 \text{ ml min}^{-1}$  for two and  $2500 \text{ ml min}^{-1}$  for three birds. It was not possible to measure larger groups as all birds were rarely resting simultaneously, and so physiological variables were overestimated at larger group sizes.  $T_b$  was only measured for the first bird removed from the chamber, as all birds awoke when the chamber was opened.

**Statistical analyses**

Values are presented as means $\pm$ s.e.m., with  $N$ =number of individuals and  $n$ =number of measurements. Statistical analyses were accomplished using R (R Core Team, 2013) and the R studio environment (Integrated Development Environment for R v0.98.501), StatistiXL (v1.10, www.statistiXL.com, Nedlands, WA, Australia) and SPSS (v22 IBM, North Castle, NY, USA).

General linear mixed models (GLMMs) were used to determine the relationship between fixed effects [e.g. environmental parameters such as minimum  $T_{bb}$  ( $T_{b,min}$ ),  $T_a$ ], random effects (e.g. individual, family group and date) and bird response variables (minimum  $T_{b,field}$ ,  $T_{b,depart}$ ,  $f_R$ , etc.) for  $T_{b,field}$ , roost microclimate and some laboratory-measured physiological variables (e.g.  $T_b$  and ventilation data). Models were built and tested with the *lmer* function of the *lmerTest* library (<http://cran.rproject.org/web/packages/lmerTest/index.html>) in R.  $P$ -values for the significance of fixed factors were calculated using the Kenward–Roger correction after Schaalje et al. (2002).

A  $\chi^2$  test was used to compare location preferences for roost nests. Tree density around roost nests was compared with mean tree

density for Dryandra Woodland (Luck, 2002) using a one-sample  $t$ -test; habitat, aspect and nest entrance direction were compared with a random distribution using circular goodness-of-fit tests; and nest height was compared by a test for uniformity after Zar (1999). Logarithmically transformed cooling constants ( $k$ ) of roost nests measured in the laboratory were compared against their paired logarithmic non-nest models by ANCOVA.

The effect of  $T_a$  on laboratory-measured physiological variables was analysed by multivariate repeated measures analysis of variance (MANOVA) with *a priori* contrasts (Withers and Cooper, 2011) unless the requirements for repeated measures could not be satisfied, in which case linear mixed effect models were used. Using  $T_a$  as a covariate, the fixed effects of both group size and  $T_a$  were compared using the Bonferroni adjustment for multiple pairwise comparisons, and for  $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$ , the slopes and intercepts of these relationships with  $T_a$  were compared with ANCOVA.

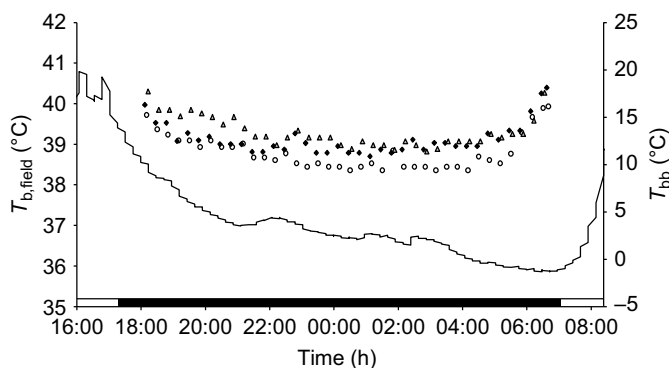
## RESULTS

### $T_{b,field}$

$T_{bb,min}$  during the study ranged from  $-2.6$  to  $14.5^\circ\text{C}$ .  $T_{b,field}$  data were recorded over 97 nights for eight babblers (body mass,  $M_b=48 \pm 0.6$  g), with data for individual birds ranging from 1 to 19 nights (Table S1). Babblers used roost nests on all measurement nights and arrived at and departed from roost nests as family groups (Fig. 1). Roost nest fidelity varied, e.g. one group roosted in the same nest for all measurement nights while another group used at least six different roost nests over a period of 27 nights.

Babblers commenced roosting  $0.60 \pm 1.52$  min after sunset, with a  $T_{b,arrive}$  of  $40.3 \pm 0.08^\circ\text{C}$  ( $N=4$ ,  $n=10$ ). The time of roost departure ( $N=8$ ,  $n=46$ ) was  $3.30 \pm 2.04$  min before sunrise and was not significantly influenced by  $T_{bb,min}$  ( $F_{1,31.4}=1.33$ ,  $P=0.274$ ; Fig. 2A) or weather variables. Babbler's  $T_{b,depart}$  of  $40.4 \pm 0.04^\circ\text{C}$  ( $N=8$ ,  $n=85$ ) did not differ from  $T_{b,arrive}$  (GLMM;  $t_{21}=0.320$ ,  $P=0.751$ ; Fig. 1). Neither  $T_{bb,min}$  nor  $T_{bb}$  at the time of roost departure ( $T_{bb,depart}$ ) had an effect on  $T_{b,depart}$  ( $F_{1,30.2}=0.70$ ,  $P=0.793$  and  $F_{1,29.0}=0.05$ ,  $P=0.819$ , respectively; Fig. 2A).

Mean minimum overnight  $T_{b,field}$  of  $38.5 \pm 0.04^\circ\text{C}$  did not vary with overnight  $T_{bb,min}$  (GLMM;  $F_{1,32}=2.66$ ,  $P=0.112$ ; Fig. 2). The mean difference between  $T_{b,depart}$  and minimum  $T_{b,field}$  of  $1.90 \pm 0.04^\circ\text{C}$  (85 nights) was independent of  $T_{bb,min}$  ( $F_{1,27.6}=0.031$ ,  $P=0.853$ ) and  $T_{bb,depart}$  ( $F_{1,25.0}=0.044$ ,  $P=0.835$ ). There was no evidence of torpor, defined as either  $T_{b,field} < 30^\circ\text{C}$  or  $T_{b,field} \leq 5^\circ\text{C}$  below normothermic  $T_{b,field}$  (e.g. Fig. 1).



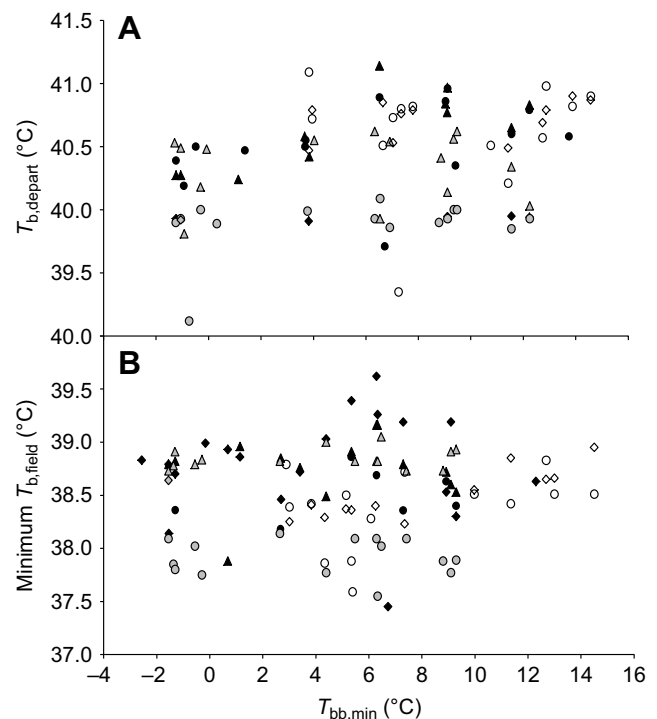
**Fig. 1. Typical overnight field body temperature ( $T_{b,field}$ ) for three white-browed babblers roosting in the same nest.** Black bulb temperature ( $T_{bb}$ , solid line) is shown on the secondary axis. The black bar indicates the period between sunset and sunrise.

### Roost microclimate

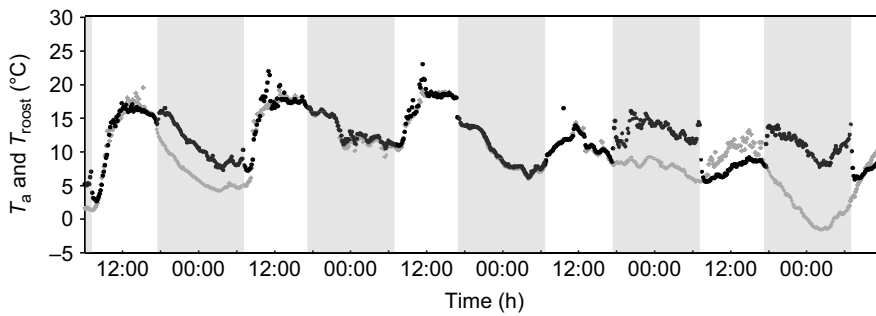
Three roost nests (of 9 total) provided thermal data for 40 occupied roost nest nights (Table S2). An internal  $T_{roost}$  equal to overnight ambient  $T_{bb}$  identified an unoccupied roost nest (Fig. 3). For occupied roosts,  $T_{roost}$  was approximately  $4.9 \pm 0.48^\circ\text{C}$  above  $T_{bb}$  for the duration of each measurement night. The  $T_{roost}-T_{bb}$  differential was greater on colder nights than on warmer nights and varied with overnight  $T_{bb,min}$  (GLMM;  $F_{1,37.9}=21.0$ ,  $P<0.001$ ;  $T_{roost}-T_{bb}=8.10 - 0.49T_{bb,min}$ ). There was no effect of individual nest. Roost nest thermal conductance ( $C$ ) measured in the laboratory was  $1.62 \text{ J h}^{-1} \text{ g}^{-1} \text{ }^\circ\text{C}^{-1}$ ; warm water inside the roost nest had a lower cooling constant ( $k_n=0.388 \text{ h}^{-1}$ ,  $N=2$ ) compared with water outside the nest ( $k_c=2.15 \text{ h}^{-1}$ ,  $N=2$ ;  $F_{3,5640}=2.04 \times 10^5$ ,  $P<0.001$ ).

### Roost nest characteristics

Of 59 roost nests within the study site (Table S3), 26 were intact, active nests, 22 were old disused nests, and the status of 11 was undetermined. Nests were in *Eucalyptus wandoo* or *E. accendens* overstorey, *Allocasuarina huegliana*, *Acacia acuminata* or *Banksia ilicifolia* mid-storey, *Corymbia callophylla* saplings, or *Gastrolobium crassifolia* understorey. There were similar ratios for canopy to mid-storey roost trees and habitat trees ( $\chi^2_1=0.429$ ,  $P=0.513$ ). Babblers did selectively roost in trees that formed stands; tree density surrounding roost trees of  $835 \pm 149$  trees  $\text{ha}^{-1}$  was higher than the mean for Dryandra Woodland (Luck, 2002) of  $246 \pm 11$  trees  $\text{ha}^{-1}$  ( $t_{58}=3.933$ ,  $P<0.001$ ). Roost nests were not uniformly distributed by height in host trees (test of uniformity;  $D_{59}=0.223$ ,  $P=0.005$ ), but were preferentially in the top third (nest height  $73.0 \pm 1.84\%$  of host height). Absolute height of nests above the ground was  $5.91 \pm 0.34$  m. There was no



**Fig. 2.  $T_{b,field}$  of white-browed babblers against  $T_{bb}$ .** (A)  $T_{b,field}$  of babblers as they depart their roost nests in the morning ( $T_{b,depart}$ ;  $N=8$  individuals,  $n=85$  measurements). (B) Minimum overnight  $T_{b,field}$  of babblers ( $N=8$ ,  $n=97$ ) as a function of ambient  $T_{bb}$ . Similarly shaded symbols indicate individuals from the same family group, with each group member represented by a different symbol.



**Fig. 3. Ambient and babler roost nest temperature for five consecutive nights, 13–18 August 2013.** Grey, ambient temperature ( $T_a$ ); black, roost nest temperature ( $T_{\text{roost}}$ ). Grey bars mark sunset to sunrise. Unoccupied roost nest nights (2 and 3) can be easily identified, as  $T_{\text{roost}}$  does not differ from  $T_a$ , while for occupied roost nests (nights 1, 4 and 5) there is a temperature differential between internal and external  $T_a$ .

preference for roost nest entrance direction (Rayleigh's  $Z_{26}=0.431$ ,  $P=0.200$ ,  $N=26$ ).

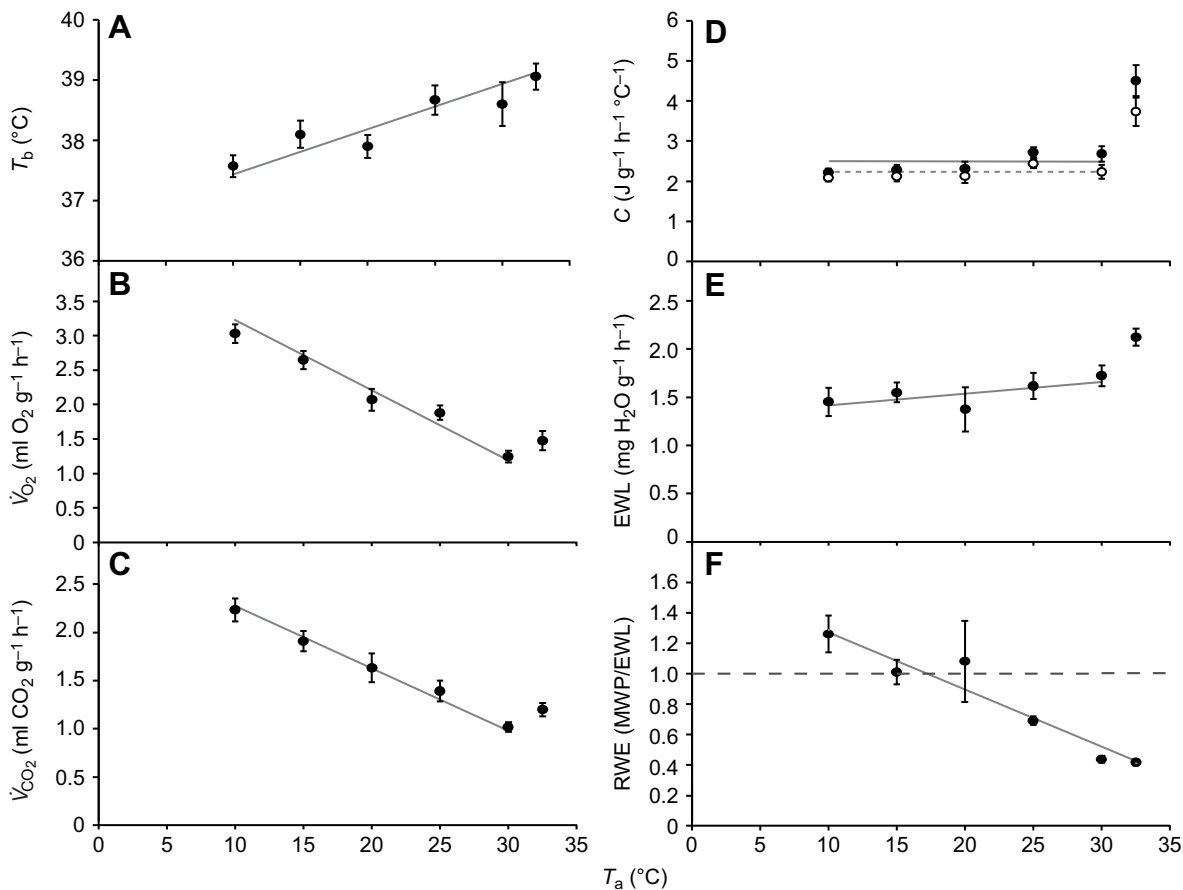
#### Laboratory respirometry and plethysmography

Laboratory-measured physiological variables are presented in Tables S4 and S5. Mean  $M_b$  was  $46.5 \pm 0.27$  g ( $N=9$ ,  $n=48$ ). In the laboratory, babler  $T_b$  varied with  $T_a$  (GLMM;  $F_{5,32.9}=7.13$ ,  $P<0.001$ ;  $N=7$ ,  $n=6-7$ ; Fig. 4A).  $T_b$  at thermoneutrality ( $T_a=30^\circ\text{C}$ ) of  $38.6^\circ\text{C}$  differed from  $T_b$  ( $t_{36}>2.20$ ,  $P<0.034$ ) at  $T_a=10^\circ\text{C}$  ( $37.6^\circ\text{C}$ ) and  $20^\circ\text{C}$  ( $37.9^\circ\text{C}$ ). The linear relationship between  $T_b$  and  $T_a$  was  $T_b=36.67+0.075T_a$ .

The  $\dot{V}_{\text{O}_2}$  of babblers differed between individuals (RMANOVA;  $F_{6,35}=866$ ,  $P<0.001$ ;  $N=7$ ) and was influenced by  $T_a$  ( $F_{5,2}=29.9$ ,  $P=0.033$ ), decreasing from  $3.03 \pm 0.134$  ml  $\text{O}_2$   $\text{g}^{-1}$   $\text{h}^{-1}$  at  $T_a=10^\circ\text{C}$  to  $1.24 \pm 0.084$  ml  $\text{O}_2$   $\text{g}^{-1}$   $\text{h}^{-1}$  at  $T_a=30^\circ\text{C}$ , before increasing again at

$32.5^\circ\text{C}$  (Fig. 4B). Linear, quadratic and cubic ( $P \leq 0.011$ ) polynomial *a priori* contrasts were significant when all six  $T_a$  were included in the model, but only the linear contrast remained significant ( $P<0.001$ ) when  $T_a=32.5^\circ\text{C}$  was removed from the model. The relationship between  $\dot{V}_{\text{O}_2}$  and  $T_a$  below thermoneutrality was  $\dot{V}_{\text{O}_2}=4.19-0.099T_a$ . We interpret the minimal value of  $\dot{V}_{\text{O}_2}$  at  $T_a=30^\circ\text{C}$  of  $1.24 \pm 0.084$  ml  $\text{O}_2$   $\text{g}^{-1}$   $\text{h}^{-1}$  as basal metabolic rate (BMR). Similar significant effects of  $T_a$  were apparent for  $\dot{V}_{\text{CO}_2}$  ( $F_{5,2}=19.9$ ,  $P=0.049$ ;  $N=7$ ; Fig. 4C); basal  $\dot{V}_{\text{CO}_2}$  at  $T_a=30^\circ\text{C}$  was  $1.02 \pm 0.050$  ml  $\text{CO}_2$   $\text{g}^{-1}$   $\text{h}^{-1}$ , with a respiratory exchange ratio of 0.82.

Wet ( $C_{\text{wet}}$ ) and dry ( $C_{\text{dry}}$ ) thermal conductance differed between individuals (RMANOVA;  $F_{6,35}=1217$ ,  $P<0.001$  and  $F_{6,35}=1209$ ,  $P<0.001$ , respectively;  $N=7$ ) but there was no overall effect of  $T_a$  ( $F_{5,2}=3.74$ ,  $P=0.224$  and  $F_{5,2}=3.74$ ,  $P=0.225$ , respectively). Reverse Helmert *a priori* contrasts confirmed the pattern (Fig. 4D)



**Fig. 4. Laboratory-measured physiological variables for white-browed babblers over a range of  $T_a$ .** (A) Body temperature ( $T_b$ ), (B) oxygen consumption ( $\dot{V}_{\text{O}_2}$ ), (C) carbon dioxide production ( $\dot{V}_{\text{CO}_2}$ ), (D) wet thermal conductance ( $C_{\text{wet}}$ ; black symbols, solid line) and dry thermal conductance ( $C_{\text{dry}}$ ; white symbols, dashed line), (E) evaporative water loss (EWL) and (F) relative water economy (RWE; MWP, metabolic water production). Symbols are means  $\pm$  s.e.m. and grey lines indicate linear relationships. Dashed grey line in F indicates  $\text{RWE}=1$ .  $N=8$  for  $T_b$  and  $N=7$  for other variables.

of constant  $C_{\text{wet}}$  and  $C_{\text{dry}}$  below thermoneutrality, increasing at  $T_a=32.5^\circ\text{C}$  ( $F_{1,6}=26.6$ ,  $P=0.002$  and  $F_{1,6}=17.3$ ,  $P=0.006$ , respectively). At thermoneutrality,  $C_{\text{wet}}$  was  $2.68\pm 0.192\text{ J g}^{-1}\text{ h}^{-1}\text{ }^\circ\text{C}^{-1}$  and  $C_{\text{dry}}$  was  $2.24\pm 0.171\text{ J g}^{-1}\text{ h}^{-1}\text{ }^\circ\text{C}^{-1}$ .

EWL differed significantly between individual babblers (RMANOVA;  $F_{6,35}=199$ ,  $P<0.001$ ) but although there was no overall effect of  $T_a$  ( $F_{5,2}=15.5$ ,  $P=0.062$ ;  $N=7$ ), polynomial *a priori* contrasts indicated a linear and quadratic ( $P\leq 0.032$ ) effect. Only a linear contrast ( $P=0.011$ ) remained when  $T_a=32.5^\circ\text{C}$  data were removed from the model, indicating EWL increased significantly at  $T_a=32.5^\circ\text{C}$  (Fig. 4E). Standard EWL at  $T_a=30^\circ\text{C}$  was  $1.59\pm 0.074\text{ mg H}_2\text{O g}^{-1}\text{ h}^{-1}$ . Relative water economy (RWE) varied with  $T_a$  ( $F_{5,2}=180$ ,  $P=0.006$ ), and polynomial *a priori* contrasts indicated a positive linear relationship ( $P<0.001$ );  $\text{RWE}=1.681-0.039T_a$  below thermoneutrality ( $r^2=0.515$ ). The point of relative water economy (PRWE) was calculated as  $17.5^\circ\text{C}$  (Fig. 4F).

For respiratory variables (Table S5),  $T_a$  influenced  $f_R$  (GLMM;  $F_{5,27.2}=12.9$ ,  $P<0.001$ ),  $V_T$  ( $F_{5,29.0}=4.71$ ,  $P=0.003$ ) and  $V_I$  ( $F_{5,28.4}=8.21$ ,  $P<0.001$ ) but not  $E_{\text{O}_2}$  ( $F_{5,28.7}=1.37$ ,  $P=0.265$ ; Fig. 5).  $f_R$  differed at thermoneutrality from that at all other  $T_a$  ( $t_{32}>2.18$ ,  $P<0.036$ ) while  $V_T$  and  $V_I$  differed from thermoneutrality at 10, 15 and  $20^\circ\text{C}$  ( $t_{39}>2.26$ ,  $P<0.03$  and  $t_{30}>3.40$ ,  $P<0.002$ , respectively).

### Huddling

All groups of huddling babblers (Fig. 6) maintained  $T_b$  independent of  $T_a$  (full-factorial ANOVA;  $F_{2,48}=1.40$ ,  $P=0.257$ ; Fig. 6A). Both group size ( $F_{2,49}=25.2$ ,  $P<0.001$ ) and  $T_a$  ( $F_{1,49}=114.7$ ,  $P<0.001$ ) influenced metabolic rate (MR; Fig. 6B) and  $\dot{V}_{\text{O}_2}$  was higher for solitary than for huddling babblers ( $F_{2,49}=25.2$ ,  $P<0.001$ ), but pairwise comparison (with a Bonferroni adjustment) indicated no difference in MR between pairs and groups of three birds ( $P\geq 0.999$ ). For huddling babblers,  $\dot{V}_{\text{O}_2}$  decreased with increasing  $T_a$ ; it was 71.8%, 64.6% and 74.1% of non-huddling MR at a  $T_a$  of 10, 15 and  $20^\circ\text{C}$ , respectively. Interpolation of the relationship between  $T_a$  and  $\dot{V}_{\text{O}_2}$  suggests that huddling babblers at 10, 15 and  $20^\circ\text{C}$  had the same MR as

individual babblers at 19.6, 25.0 and  $27.3^\circ\text{C}$ , respectively, a mean effective temperature buffer of  $8.98^\circ\text{C}$  above actual  $T_a$ . Huddling had no impact on EWL ( $F_{2,49}=1.26$ ,  $P=0.292$ ; Fig. 6F).

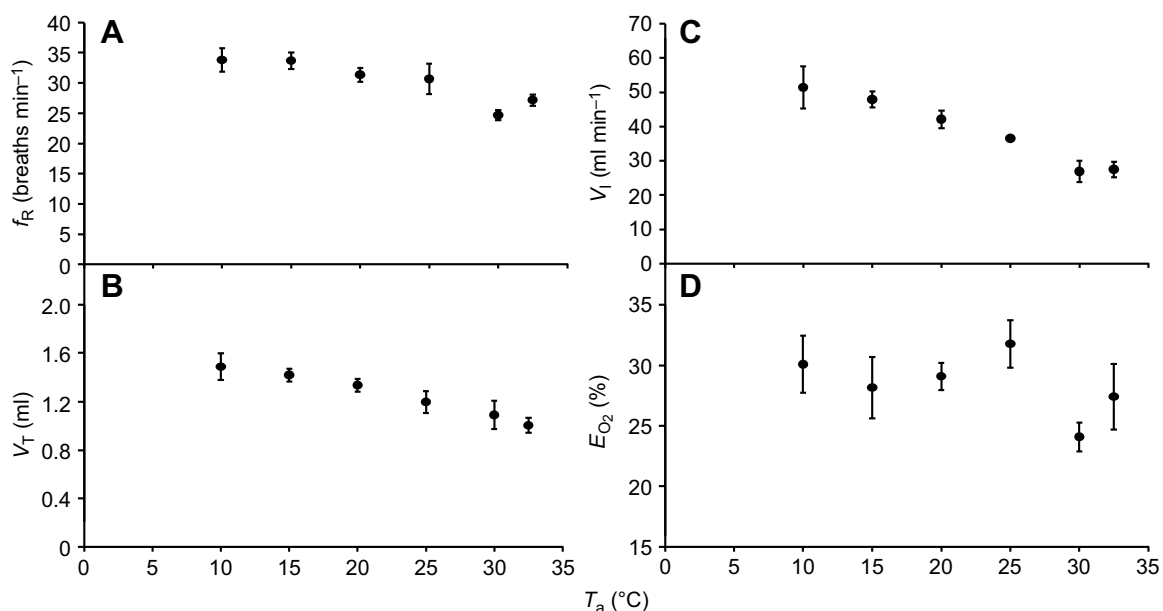
Overall, group size significantly influenced both  $C_{\text{wet}}$  ( $F_{3,49}=19.4$ ,  $P<0.001$ ; Fig. 6D) and  $C_{\text{dry}}$  ( $F_{3,49}=19.3$ ,  $P<0.001$ ; Fig. 6E); conductance was lower the larger the group size ( $C_{\text{wet}}$   $F_{2,49}=13.9$ ,  $P<0.001$ ;  $C_{\text{dry}}$   $F_{2,49}=19.9$ ,  $P<0.001$ ). There was no difference between pairs and groups of three babblers ( $C_{\text{wet}}$   $0.005\pm 0.189$ ,  $P=1.000$ ;  $C_{\text{dry}}$   $0.047\pm 0.174$ ,  $P=1.000$ ), but individuals had a higher conductance than huddling birds ( $C_{\text{wet}}>0.622\pm 0.133$ ,  $P<0.001$ ;  $C_{\text{dry}}>0.674\pm 0.122$ ,  $P<0.001$ ), for which  $C_{\text{wet}}$  and  $C_{\text{dry}}$  were 74.6% and 69.8% of solitary roosting values, respectively.

### DISCUSSION

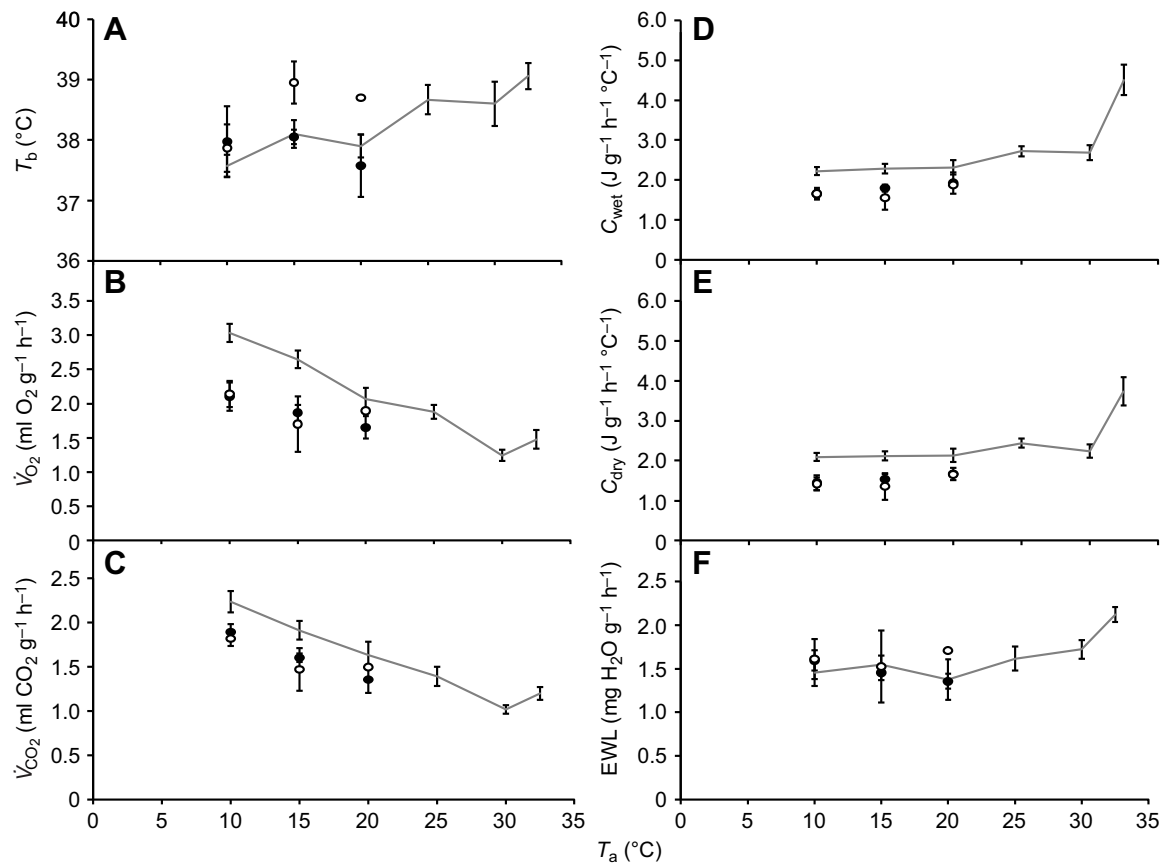
Our study used both field and laboratory data to examine how a small, insectivorous, sedentary, group-living passerine, a likely candidate for avian torpor, survives in an energetically challenging environment. Overnight measurement of  $T_b$  indicated that free-living white-browed babblers maintained normothermia over a wide range of  $T_a$  and did not use torpor or hibernation. Complementary laboratory experiments of individual and group-huddling physiology showed that roosting babblers derived energetic benefits from social thermoregulation, as well as the use of insulated roost nests. Our findings suggest that heterothermia may indeed be uncommon amongst Austral passerines, and that birds with a mostly typical avian physiology can offset the considerable energetic costs of endothermy with behavioural strategies to minimise heat loss and maintain a year-round existence in a variable environment.

### $T_b$

Free-ranging babblers maintained a near-constant  $T_b$  overnight, despite low, frequently sub-zero, overnight  $T_{\text{bb}}$ . The range of  $T_{b,\text{field}}$  for all individuals was  $<2.2^\circ\text{C}$  under all environmental conditions, and varied more between individuals than as a response to environmental conditions. Although torpor and hibernation have been observed only infrequently in a small number of avian families (Geiser et al., 2006), the capacity for nocturnal hypothermia is



**Fig. 5. Ventilatory parameters for white-browed babblers at a range of  $T_a$ .** (A) Respiratory frequency ( $f_R$ ), (B) tidal volume ( $V_T$ ), (C) minute volume ( $V_I$ ) and (D) oxygen extraction ( $E_{\text{O}_2}$ ). Symbols are means $\pm$ s.e.m.  $N=9$ .



**Fig. 6. Effect of huddling on physiological variables for white-browed babblers at a range of  $T_a$ .** (A)  $T_b$ , (B)  $\dot{V}_{O_2}$ , (C)  $\dot{V}_{CO_2}$ , (D)  $C_{wet}$ , (E)  $C_{dry}$  and (F) EWL of pairs (black symbols) and groups of three (white symbols) white-browed babblers. Grey lines are mean values for individuals (from Fig. 4), symbols are means  $\pm$  s.e.m.  $N=8$ ;  $n=4$  for pairs and  $n=1-3$  for groups of three.

generally considered to be widespread (McKechnie and Lovegrove, 2002). However, there was no evidence here that hypothermia was an important part of the babblers' energetic strategy, other than their typical homeothermic scotophase pattern (Schmidt-Nielsen, 1997; Fig. 1). Babblers warmed endogenously for roost departure at sunrise to a similar  $T_b$  to that at roost arrival. Both mean active-phase  $T_b$  ( $T_{b,depart}$ ; 40.4°C) and rest-phase  $T_b$  (minimum  $T_{b,field}$ ; 38.5°C) were similar to those for other normothermic passerines (41.6  $\pm$  1.13 and 38.9  $\pm$  0.87°C, respectively; Prinzinger et al., 1991). In the laboratory, individual babblers at  $T_a=10^\circ\text{C}$  maintained  $T_b$  only 1.0°C lower than at thermoneutrality (38.6°C at  $T_a=30^\circ\text{C}$ ), achieved by a 143% increase in MR (accommodated by increased ventilatory  $\dot{V}_I$ ) and a 15.7% decrease in  $C_{wet}$ ; a typical endothermic response.

Globally, non-passerines and particularly nocturnal species are more likely to be heterothermic, and much thermoregulatory research has focused on these species (e.g. Brigham, 1992; Körtner et al., 2001; Lane et al., 2004; McKechnie et al., 2007; Cooper et al., 2008; Smit and McKechnie, 2010; Doucette et al., 2011, 2012). However, only a handful of studies have documented the nocturnal energetic strategy of free-ranging passerines, and even fewer have measured core  $T_b$ . White-throated sparrows (*Zonotrichia albicollis*) have a rest-phase hypothermia, with a 3.4°C reduction in  $T_{skin}$  between active and rest phase (Dolby et al., 2004) and the diel variation in  $T_b$  of the arid-dwelling white-browed sparrow-weaver (*Plocepasser mahali*) is attributed to seasonal environmental conditions (Smit et al., 2013). The only comparable measurement of continuous, nocturnal  $T_b$  of an Australian passerine in the cold is for captive-raised juvenile dusky woodswallows (*Artamus*

*cyaneurus*; Maddocks and Geiser, 2007), measured in outdoor aviaries. These birds used heterothermy; overnight  $T_{b,min}$  decreased by  $>5^\circ\text{C}$  from resting  $T_b$ , which the authors classified as daily torpor. These data, based on skin temperature or for captive birds, suggest that heterothermia amongst passerines may be more common than currently recognised. As sedentary, insectivorous birds in a semi-arid habitat, white-browed babblers have characteristics that suggest they are likely candidates for torpor use, and indeed have other adaptations such as sociality and cooperative breeding associated with harsh and unpredictable environmental conditions; they therefore may be considered a good model for avian heterothermia. However, their lack of torpor, or indeed any significant heterothermy, suggests that avian torpor use may be rare, particularly compared with small mammals, if their general physiology is similar to other passerines, and indeed other birds. In this case, the paucity of data quantifying avian heterothermy may not just represent a lack of research in this area as is currently assumed (Astheimer and Buttemer, 2002; McKechnie and Lovegrove, 2002; Geiser et al., 2006).

#### Standard physiology

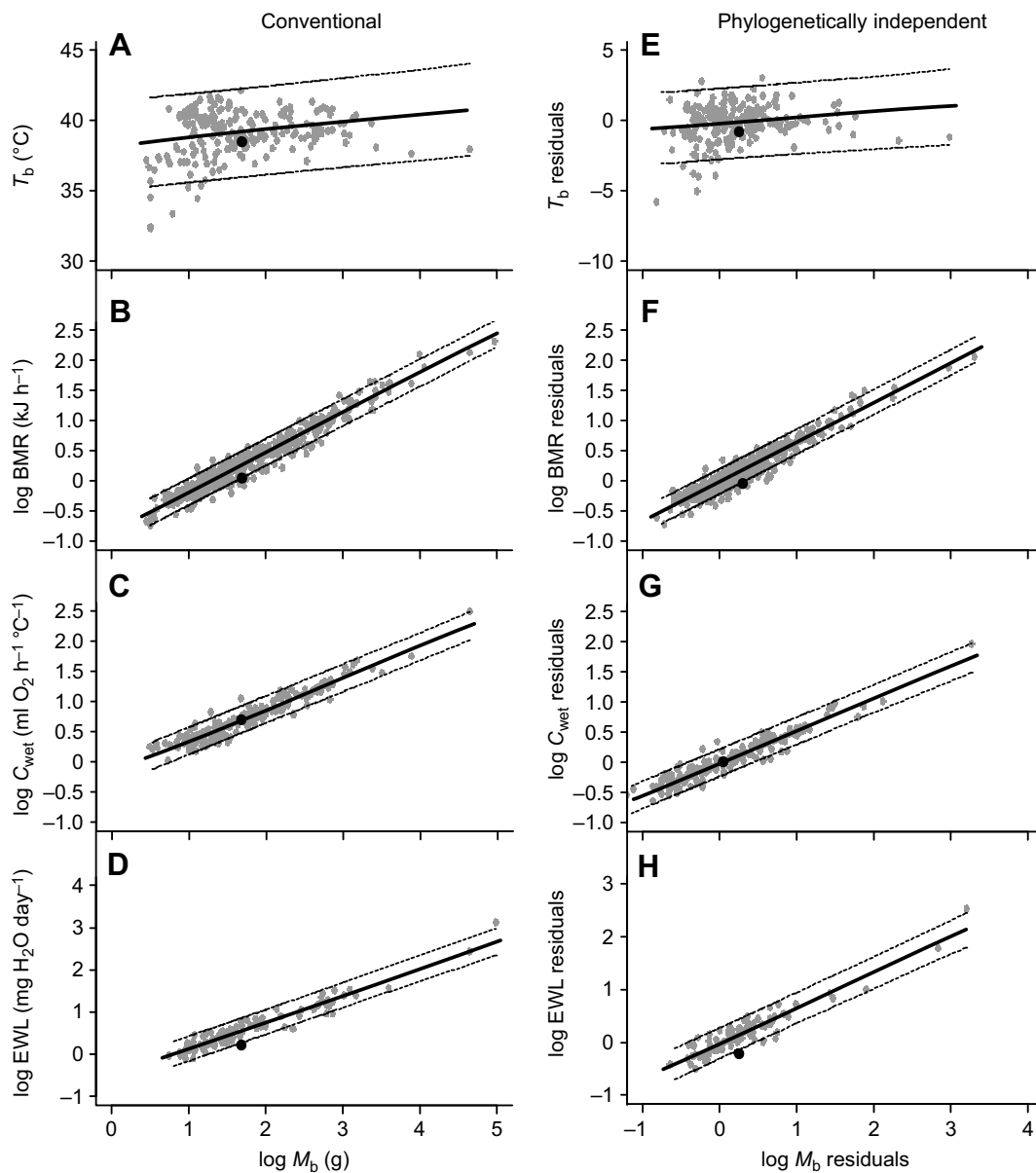
Babblers had a typical endothermic response to  $T_a$  above and below thermoneutrality in the laboratory. A near-constant  $T_b$  was maintained by an increase in metabolic heat production at low  $T_a$ . This increase in  $O_2$  demand was accommodated by an increase in  $\dot{f}_R$  and  $\dot{V}_T$  rather than  $E_{O_2}$ , which is typical of both birds and mammals (e.g. Larcombe et al., 2003; Cooper and Withers, 2004). Thermal conductance remained close to minimal below thermoneutrality, but

increased at higher  $T_a$ , as did EWL, as babblers increased their heat dissipation. The PRWE of 17.5°C was particularly high and presumably contributes to maintenance of water balance in the absence of free water, and is at least partly facilitated by homeothermy at low  $T_a$ .

To best interpret the physiological basis for our observations of nocturnal homeothermy for free-living babblers, it is necessary to examine their standard physiology in an allometric and phylogenetic context. For mammals, low  $T_b$  and low BMR correlate with the use of heterothermy and torpor (Geiser, 1998; Cooper and Geiser, 2008; Ruf and Geiser, 2014) and we assume a similarity in physiological drivers between convergently endothermic mammals and birds. We therefore compared here our standard physiological data for babblers with those of other birds (Table S6) using the 95% prediction limits (Cooper and Withers,

2006) for conventional and phylogenetically informed allometric regressions after Barker et al. (2016), using the phylogenetic tree from birdtree.org (Jetz et al., 2012, 2014) with the Hackett backbone (Hackett et al., 2008).

Standard  $T_b$  of babblers statistically conformed to that of other birds, both before and after correcting for phylogeny, as did their  $C_{wet}$ , suggesting there is nothing remarkable about babbler's insulation or heat balance (Fig. 7). Our value of BMR for solitary-roosting white-browed babblers ( $M_b$  46 g) of 1.24 ml  $O_2 g^{-1} h^{-1}$  was similar to, but lower than, the 1.51 ml  $O_2 g^{-1} h^{-1}$  measured by Chappell et al. (2016) for the chestnut-crowned babbler (*Pomatostomus ruficeps*;  $M_b$  50 g), despite our birds having a less arid habitat and slightly lower  $M_b$ , suggesting no stress response for solitary-roosting white-browed babblers. White-browed babblers had a BMR that was only 64.0% of that



**Fig. 7. Allometric and phylogenetic comparisons of physiological variables for white-browed babblers with those of other birds.**  $T_b$  (A), basal metabolic rate (BMR; B),  $C_{wet}$  (C) and EWL (D) for white-browed babblers (black symbols) compared with other birds (grey symbols; see Table S6).  $M_b$ , body mass. Phylogenetically independent residuals for the same parameters are shown in E–H. Solid lines indicate the least squares regression and dotted lines the 95% prediction intervals for each allometric relationship.

predicted by  $M_b$ . Although it was within the 95% prediction interval for the conventional allometric analysis, it was below the prediction limits after accounting for phylogeny (Fig. 7), indicating that babblers have a lower BMR than their nearest relatives. Low BMR is correlated with a propensity for torpor (Cooper and Geiser, 2008), presumably reflecting similar adaptation to a low-energy strategy. Despite this, we found no evidence of torpor for free-living babblers, suggesting their low BMR, together with strategies such as social thermoregulation and insulated roost nests, is sufficient to balance their energy budget.

Standard EWL was only 41.0% of the allometrically predicted value, and statistically lower than that for other birds, before and after accounting for phylogeny (Fig. 7). Low EWL (like low BMR) is associated with arid habitats (Williams and Tieleman, 2005) and contributes to their high PRWE. This, together with the preformed water of their insectivorous diet, may account for their apparent ability to maintain water balance without drinking, at least in winter (T.K.D., personal observation).

### Social thermoregulation

Many social endotherms roost communally (Gilbert et al., 2010), and huddling can play an important role in the maintenance of homeothermy. In extreme cases, communally roosting endotherms are obligate social thermoregulators, unable to regulate normal  $T_b$  at low  $T_a$  in the absence of conspecifics (e.g. McKechnie and Lovegrove, 2001). White-browed babblers always roosted communally in the field during the study, but even when held individually in the laboratory at  $T_a$  as low as  $10^\circ\text{C}$ , all babblers maintained  $T_b$  within  $1.15^\circ\text{C}$  of thermoneutral values. Therefore, babblers are facultative social thermoregulators and although they can survive roosting individually overnight in the wild (Chappell et al., 2016), they gain substantial energetic benefits by huddling.

The reduction in energy expenditure of huddling babblers, with a huddling MR 65–74% of individual MR at an equivalent  $T_a$ , is as expected for other huddling endotherms (see Gilbert et al., 2010, for review) and similar to that measured for two to three huddling chestnut-crowned babblers, and is likely to be even greater for more huddling individuals (Chappell et al., 2016). Presumably, the substantial reduction in MR of huddling babblers has a significant role in balancing their energy budget and partially negates the need for heterothermia. However, substantial variation in minimum  $T_{b,\text{field}}$  between individuals ( $\sim 2.1^\circ\text{C}$ ) was observed for free-living babblers (Fig. 2). Location within the roost nest probably impacts overnight  $T_b$ ; there may be a physiological cost associated with social status if social status determines position in a huddle. Thus, individual variation in  $T_{b,\text{field}}$  may indicate social status, as observed for vervet monkeys (*Chlorocebus pygerythrus*; McFarland et al., 2015).

### Roost nest characteristics

The energetic benefit of roosting in enclosed nests is a further aspect of babblers' nocturnal energy strategy. The  $T_{\text{roost}}$  of unoccupied babbler nests was the same as  $T_{\text{bb}}$ , unlike the nests of sociable weavers (*Philetairus socius*), which are sufficiently large and well-insulated to remain above ambient conditions overnight even when unoccupied (White et al., 1975). When occupied, the relationship of  $T_{\text{roost}}$  to  $T_{\text{bb}}$  for babbler nests is similar to that of solitary-roosting white-browed sparrow-weavers (*P. mahali*; Ferguson et al., 2002), with the  $T_{\text{roost}}-T_{\text{bb}}$  differential increasing as  $T_{\text{bb}}$  decreases. The thermal conductance of roost nests ( $C=1.62 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ ) was equivalent to the conductance of groups of two to three huddling babblers ( $C=1.61 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$  at  $10^\circ\text{C}$ ), so roost nests effectively

halve the rate of energy lost to the environment for small groups of huddling babblers. The insulative properties of sparrow-weaver roost nests are an important factor in allowing them to maintain homeothermy at low  $T_a$  (Ferguson et al., 2002) and presumably provide similar energetic advantages for white-browed babblers.

For some species, particularly nocturnal birds and bats, roost sites with favourable slope, aspect and entrance direction are selected to allow passive rewarming or to facilitate basking (e.g. Geiser et al., 2004; Turbill and Geiser, 2008). This was not a strategy used by babblers, as there was no preference in roost nest entrance direction, and babblers warmed endogenously prior to sunrise. While babbler roost nests are built preferentially in the top third of their host tree, the variation in host tree species and actual height of the host trees make it unlikely that microclimate considerations are important. A preference for building nests in dense stands of trees may have an energetic benefit, as dense foliage can deflect wind and mitigate radiative heat loss (Walsberg, 1986), but nest location might also be an anti-predator strategy.

### Thermoregulation

The combined use of social thermoregulation and communal roost nests allows substantive energy conservation for white-browed babblers. Minimum overnight babbler  $T_{\text{roost}}$  was calculated to range from  $6.8$  to  $15.4^\circ\text{C}$ , so the range of MRs for birds in these nests was calculated to be  $1.78$ – $2.44 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ . Extrapolating the linear relationship between  $T_a$  and  $\dot{V}_{\text{O}_2}$  below thermoneutrality for solitary birds outside roost nests to these  $T_a$ , huddling babblers in roost nests would have an energy expenditure only 55–65% of that of single, exposed birds under the same environmental conditions, and this would be even lower for larger groups (e.g. Chappell et al., 2016). In other words, small groups of communal roost-nesting babblers at a  $T_a$  of  $-3$  to  $+15^\circ\text{C}$  and a  $T_{\text{roost}}$  of  $6.8$  to  $15.4^\circ\text{C}$  would have a MR equivalent to that of a single, exposed bird at a  $T_a$  of  $17.6$  to  $24.3^\circ\text{C}$ . These substantial energy savings, together with the birds' intrinsically low BMR, would play an important role in babblers balancing their daily energy budget, and presumably negate any requirement for torpor in their energetically challenging environment. Therefore, despite a generally typical avian thermal physiology, the energetics and behaviour of the white-browed babbler allow maintenance of homeothermy, and suggest that heterothermy is not a preferred energetic tactic for avian species that can avoid it.

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### Competing interests

The authors declare no competing or financial interests.

### Author contributions

Conceptualisation, Methodology and Resources: T.K.D., C.E.C., P.C.W.; Software: T.D.K., P.C.W.; Investigation: T.K.D., C.E.C.; Data curation, Formal analysis and Writing – original draft: T.K.D.; Writing – revision and editing: C.E.C., P.C.W.; Visualisation: T.K.D., C.E.C.; Supervision: C.E.C., P.C.W.

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### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.154633.supplemental>



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