

School of Science
Department of Environment and Agriculture

Thermoregulatory responses of Australian birds to environmental
challenges

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Declaration

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgment has been made. This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. I was responsible for project design, procurement of additional funding, animal capture and husbandry, specimen preparation, collection of field and laboratory data, data screening, statistical analysis, and interpretation and preparation of subsequent manuscripts, under the guidance of my supervisors. Associate Professor Shane Maloney (School of Anatomy, Physiology and Human Biology, University of Western Australia) assisted with experimental methodology and data interpretation of the plumage study in Chapter 5.

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The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council Australian code for the care and use of animals for scientific purposes 8th edition (2013). The proposed research study received animal ethics approval from the Curtin University Animal Ethics Committee, (Animal Use Competency CU-AEC-0024; Project Approvals AEC-2011-41; AEC-2011-68; AEC-2012-09), the Western Australian Department of Parks and Wildlife (Regulation 23 BB002889; Regulation 17 SF008014, SF008625 and SF008626; and Regulation 4 CE003204, CE003534 and CE003535) and the Australian Bird and Bat Banding Scheme (Banding Authority #2824).

Signature: ...  Date: ...November 2017.....

For Jonathan Moon
who encouraged me to learn at least one new thing every day

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General Abstract

Relatively little is known about the physiological and behavioural thermoregulatory strategies used by Australian birds to meet their energetic demands. Sedentary animals in particular must be able to meet their environmental challenges on both daily and seasonal scales, including periods where low ambient temperature (T_a), reduced food availability and inclement weather lead to greater challenges associated with maintaining body temperature (T_b). Here the thermoregulatory physiology four sedentary, insectivorous passerines endemic to southern Australia; the White-browed Babbler, Rufous Treecreeper, Western Yellow Robin, and Australian Magpie, is presented for the first time to identify their thermoregulatory strategies, document heterothermia if it occurs and determine how they might balance their energy budgets.

I found no evidence that these species used torpor under either free-ranging or laboratory conditions. In temperate *Eucalyptus wandoo* woodland in winter, babblers, treecreepers and robins all maintained homeothermy, maintaining core T_b within 2.7 °C (treecreepers) and skin temperature within 4.1 °C (robins) of normothermia despite sub-zero conditions. Babblers maintained T_b independent of T_a at all T_a conditions experienced. Although T_b of treecreepers and skin temperature of robins decreased in small increments with T_a , these did not meet the criteria for nocturnal hypothermia (T_b drop of 5 °C) or torpor ($T_b < 30$ °C), and more likely represent the ‘gain’ of a physiological negative feedback system. In the laboratory all four species demonstrated a typical endothermic response to T_a , maintaining T_b only just below normothermia by increasing metabolic rate and decreasing thermal conductance. Standard metabolic and ventilatory physiological variables obtained for these birds were typical for their mass and phylogenetic history. Evaporative water loss was lower than predicted for all four species, but it is unclear if this represents an adaption to limited water availability or methodological effects resulting from stringent measurement conditions.

Nocturnal roosting behaviour differed between babblers, treecreepers, and robins. Although babblers roosted communally in a domed roost nest, reducing nocturnal energy

requirements by 35.2 – 45%, babblers were not obligate social thermoregulators, and were able to maintain homeothermy when roosting solitarily in the laboratory at T_a as low as 10 °C. Treecreepers roosted individually in tree hollows, and while some hollows had an internal temperature that would buffer treecreepers against extremely low T_a , they used hollows of varying quality, and were more often exposed to temperatures equal to sub-zero T_a . The robin, the smallest of the three species, showed the least specialised behaviour and roosted solitarily in exposed foliage, but still did not enter torpor even on the coldest nights. There were no diurnal activity and habitat use traits common to babblers, treecreepers, and robins that could be interpreted as compensation for increased energy demand at low T_a , or following nights of low minimum T_a .

The complex role of plumage in thermoregulation was demonstrated for the southwestern subspecies of Australian Magpie (*G. t. dorsalis*). Plumage thickness provided substantial insulation, and while different coloured plumages had similar resistance, solar heat gain varied with colour. While dark plumage gained heat at low windspeed and dissipated heat at high windspeeds, light-coloured plumage had more consistent solar heat gain at all the windspeeds tested. The thermoregulatory impact of these differences could drive sexual/developmental selection and geographic subspeciation in magpies.

In conclusion, while sympatric mammals use a broad range of physiological and behavioural thermoregulatory mechanisms, such as torpor, nocturnality, and use of insulated refuges to meet their energetic demands, birds studied here used alternative strategies to meet their winter energy requirements. While behavioural mechanisms provided some energetic benefit for free-ranging birds, they were not directly essential for homeothermy. Instead, a sedentary, group-living existence allowed these passerines to forage efficiently to meet daily energy requirements regardless of ambient temperature, with detailed, shared knowledge of their habitat, its resources and threats. The manner in which these four birds meet the energetic challenges of their environment suggests that homeothermy and capacity to cope with low ambient temperatures may be widespread amongst sedentary, Australian passerines.

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Abbreviations

ABBBS	Australian Bird and Bat Banding Scheme
AEC	(Curtin University) Animal Ethics Committee
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
BMR	Basal metabolic rate ($\text{mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$; kJ h^{-1})
BOM	(Australian Government) Bureau of Meteorology
BTPS	Body temperature and pressure saturated
C_{dry}	Dry thermal conductance ($\text{J g}^{-1} \text{ h}^{-1} \text{ }^{\circ}\text{C}^{-1}$)
C_{wet}	Wet thermal conductance ($\text{J g}^{-1} \text{ h}^{-1} \text{ }^{\circ}\text{C}^{-1}$; $\text{mL O}_2 \text{ h}^{-1} \text{ }^{\circ}\text{C}^{-1}$)
DBHOB	Diameter at breast height over bark (cm)
DPaW	(Western Australian Government) Department of Parks and Wildlife
ΔT	Differential between ambient and roost temperature ($= T_a - T_{\text{roost}}$; $^{\circ}\text{C}$)
ΔT_b	Change in body temperature ($^{\circ}\text{C min}^{-1}$)
EO_2	Oxygen extraction (%)
EWL	Evaporative water loss ($\text{mg H}_2\text{O g}^{-1} \text{ h}^{-1}$; $\text{mL H}_2\text{O day}^{-1}$)
$F_i\text{O}_2$	Fractional concentration of incurrent oxygen
$F_e\text{O}_2$	Fractional concentration of excurrent oxygen
f_R	Respiratory frequency (breaths min^{-1})
GAMMs	Generalised additive mixed models
k	Cooling constant (h^{-1})
m	Body mass (g)
MHP	Metabolic heat production ($\text{J g}^{-1} \text{ h}^{-1}$)
MR	Metabolic rate ($\text{mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$)
MWP	Metabolic water production ($\text{mL g}^{-1} \text{ h}^{-1}$)
N	Number of individuals
n	Number of measurements
pRWE	Point of relative water economy ($^{\circ}\text{C}$)
RER	Respiratory exchange ratio ($= V_{\text{CO}_2}/V_{\text{O}_2}$)
RH	Relative humidity (%)
RMANOVA	Multivariate repeated measures analysis of variance
RWE	Relative water economy
SE	Standard error
SH	Specific heat ($\text{J g}^{-1} \text{ }^{\circ}\text{C}^{-1}$)
STPD	Standard temperature and pressure dry
T_a	Ambient temperature ($^{\circ}\text{C}$)
T_b	Body temperature ($^{\circ}\text{C}$)
$T_{b,\text{arrive}}$	Body temperature at time of roost arrival ($^{\circ}\text{C}$)

$T_{b,depart}$	Body temperature at time of roost departure (°C)
$T_{b,field}$	Field body temperature (°C)
$T_{b,skin}$	Skin temperature (°C)
T_{bb}	Black bulb temperature (°C)
$T_{bb,arrive}$	Black bulb temperature at time of roost arrival (°C)
$T_{bb,depart}$	Black bulb temperature at time of roost departure (°C)
$T_{bb,min}$	Minimum black bulb temperature (°C)
T_{roost}	Temperature inside roost nests/hollows (°C)
TNZ	Thermoneutral zone
\dot{V}_I	Inlet flow rate (mL min ⁻¹)
V_I	Minute volume (mL min ⁻¹)
V_T	Tidal volume (mL)
$\dot{V}CO_2$	Rate of carbon dioxide production (mL CO ₂ g ⁻¹ h ⁻¹)
$\dot{V}O_2$	Rate of oxygen consumption (mL O ₂ g ⁻¹ h ⁻¹)
$\dot{V}O_{2,calc}$	Calculated rate of oxygen consumption (mL O ₂ g ⁻¹ h ⁻¹)
χ^2	Chi square

General Introduction

Although birds face significant energy challenges in the Australian environment, our understanding of the thermoregulatory strategies used by Australian birds is limited (Astheimer & Buttemer 2002; Geiser *et al.* 2006; Cooper 2017). Birds are generally small, so experience significant heat loss from a high surface area to volume ratio (Geiser *et al.* 2006) and are mostly diurnal, so cannot use exercise-related thermogenesis to maintain body temperature (T_b) when ambient temperature (T_a) is lowest (Dawson & O'Connor 1996). Furthermore they fly, and although flight is economic over great distances, it can be energetically expensive over short distances (Gill 2007). Yet birds generally maintain higher T_b (Prinzinger *et al.* 1991) and metabolic rate (MR) than mammals (McNab 2009), and so have higher energetic requirements than similar-sized mammals. While the physiological and behavioural thermoregulatory strategies used by a wide range of Australian mammals is quite well known (French 1993; Geiser 2004a; Gilbert *et al.* 2010), at present the diversity of physiological energy-saving tactics in birds is poorly understood (Geiser *et al.* 2006), and mostly limited to unusual, not common species (Astheimer & Buttemer 2002). Here the thermoregulatory strategies of four sympatric, endemic, sedentary passerines are examined for the first time, to determine how they meet their energy demands in an Australian climate.

Origins of endothermy and physiological strategies for energy balance in endotherms

The ability to regulate T_b independently of T_a has conferred a significant evolutionary advantage upon endotherms (Louw 1993; Lovegrove 2012). It has facilitated population of habitats that would otherwise be unviable and allowed exploitation of ecological niches otherwise unfilled (Sahney *et al.* 2010). Both phylogenetic and ontogenic evidence suggests that endothermy arose separately during the major radiations of birds and mammals (Geiser 2008). A capacity for heterothermy in a range of mammals and birds is evidence that heterothermy is the ancestral condition in both groups, and that

homeothermy is a derived state (Grigg *et al.* 2004; Geiser 2008; Lovegrove 2012; McKechnie 2014). Currently, heterothermy has been observed predominantly in modern avian lineages, but Geiser (2008) attributes this to a lack of broad sampling among more ancient lineages. Explanations of avian thermoregulatory evolution (Lovegrove 2012) are further complicated by inconsistencies between avian phylogenies constructed by phylogenomic (Hackett *et al.* 2008) versus palaeontological (Davis 2008) methods.

Body temperature of endotherms is generated primarily by proportional metabolic heat production, allowing for precise maintenance of T_b (Withers 1992). Where T_b is maintained at a constant level, the energetic cost of maintaining T_b increases as T_a falls. Repeatable and regulated circadian variation between active- and rest-phase setpoint T_b s allows for some energy conservation while inactive (Aschoff & Pohl 1970; Aschoff 1981), as mean rest-phase T_b for birds (38.54 ± 0.96 °C; Prinzinger *et al.* 1991) is 1.25 to 2.48 °C lower than mean active phase T_b (41.02 ± 1.29 °C). Rest-phase reduction in T_b is considered euthermia, a normal, post-absorptive resting condition, however even with these reductions the increased energy required to maintain T_b for small diurnal endotherms can still lead to significant loss in body mass over a single night, particularly at low overnight T_a (Maddocks & Geiser 1997). As a result, the evolutionary pressure for facultative, mitigating mechanisms that allow endotherms to survive at low T_a is significant (Tattersall *et al.* 2012). Controlled hypothermic departures from a euthermic rest-phase T_b have been identified and classified based on bout duration, depth and accompanying behavioural changes as rest-phase (nocturnal) hypothermia, daily torpor, and multi-day torpor or hibernation (Calder & King 1974; Prinzinger *et al.* 1991; Barclay *et al.* 2001; McKechnie & Lovegrove 2002; Geiser 2004b). The degree of heterothermic response varies between species, but can also vary within species between season, in direct response to T_a , food availability and/or breeding activity (Reinertsen 1996; McKechnie & Lovegrove 2002; Geiser *et al.* 2006; Munn *et al.* 2010; McKechnie & Mzilikazi 2011).

Rest-phase, or nocturnal, hypothermia is a phenomenon rarely reported for mammals but believed to be common in birds (McKechnie & Lovegrove 2002). It is classified as a small,

controlled lowering of resting T_b from a normothermic value accompanied by no detectable behavioural change (although, see Carr & Lima 2013). Defining smaller reductions in T_b can be challenging (Reinertsen 1996) as less pronounced fluctuations can be difficult to separate from normal, circadian oscillations (Prinzinger *et al.* 1991) or can even be seen as an artefact of methodology (Willis & Brigham 2003). However nocturnal hypothermia is generally differentiated from normothermic temperatures as a drop in active T_b of $> 3-5\text{ }^{\circ}\text{C}$ (Prinzinger *et al.* 1991; Cooper & Geiser 2008). As differences of $3-4\text{ }^{\circ}\text{C}$ can be mistaken for circadian fluctuation, in this study a more conservative definition of a T_b drop of $> 5\text{ }^{\circ}\text{C}$ below normothermic active phase T_b will be used to identify nocturnal hypothermia, following Maddocks & Geiser (1997).

Most definitions of torpor include both a physiological and a behavioural component (Merola-Zwartjes & Ligon 2000), although quantifying behavioural characteristics can be difficult (Barclay *et al.* 2001). Torpor bouts can last for several hours, during which MR and T_b are reduced from normothermic values and animals are non-responsive but able to re-warm to normothermic T_b using endogenous metabolic heat production. A raft of definitions exist for determining cut-off values when animals may be considered torpid, using metrics of T_b , MR, and/or behaviour, using both percentage reductions or discrete values (Barclay *et al.* 2001; Boyles *et al.* 2011b). However in the absence of a quantitative consensus definition (IUPS Thermal Commission 2003), $T_b < 30\text{ }^{\circ}\text{C}$ makes a conservative cut-off for detecting torpor in birds (Reinertsen 1996; Schleucher 2004), and will be used for this study. Multi-day torpor, or hibernation, is readily differentiated from single-day torpor by the longer duration ($>24\text{ h}$), and greater depth of torpor bouts (T_b and MR both significantly lower than single-day torpor values; Geiser & Ruf 1995).

Historically nocturnal hypothermia, torpor, and hibernation were treated as discrete responses (Prinzinger *et al.* 1991; Geiser & Ruf 1995). Although many authors now consider these states as part of a continuum (Reinertsen 1996; McKechnie & Lovegrove 2002; Schleucher 2004; Withers & Cooper 2010; Boyles *et al.* 2013). However, discussions on this topic remain lively (Brigham *et al.* 2011; Boyles *et al.* 2011b; Ruf &

Geiser 2014) and there is still no general consensus on how to consistently define nocturnal hypothermia, torpor, or hibernation.

At low T_a small reductions of endothermic T_b are often observed, as a consequence of T_b regulation being a negative feedback system (Withers 1992). Below thermoneutrality the ‘gain’ of the physiological system can result in actual T_b being below setpoint T_b , a differential that increases as T_a falls. Both the setpoint T_b and the gain vary between species, for example the mean thermolability for dasyurids is $0.064 \pm 0.018 \text{ } ^\circ\text{C } ^\circ\text{C}^{-1}$ (Withers & Cooper 2009) but for arboreal dasyurid *Phascogale calura* thermolability is $0.26 \pm 0.04 \text{ } ^\circ\text{C } ^\circ\text{C}^{-1}$ (Pusey *et al.* 2013). Thermolability is rarely reported for birds, even though the high resting T_b of birds means significant energy savings can still be made with small T_b reductions (Willis & Brigham 2003).

Methods to quantify thermoregulatory strategies

While various techniques exist for quantifying energetics of animals (Halsey 2011), a combination of laboratory and field techniques provides the most thorough approach. The full range of thermoregulatory responses is not always observed in a laboratory (Geiser *et al.* 2000), due to the impacts of captivity, stress, altered diet etc., however techniques like open-flow respirometry, measuring changing gas concentrations due to respiration (Withers 2001), have no direct field equivalent. Tracking fine-scale changes in metabolic rate of free-ranging animals over time is not possible by methods such as doubly-labelled water (Butler *et al.* 2004; Halsey 2011), however technological advances in biotelemetry allows collection of proxy data from free-ranging individuals under natural conditions (Cooke *et al.* 2004). Here, the extent by which free-living birds undergo periods of hypothermia was determined by monitoring T_b by radio-telemetry, (core T_b of two species, and skin temperature, T_{skin} , in the smallest of the study species). This is a standard technique for monitoring field T_b of mammals and birds (Körtner & Geiser 2000; Smit & McKechnie 2010). Laboratory measurements of conspecifics collected in the same, or nearby, locations were undertaken to see if metabolic, respiratory, and insulative characteristics of these sedentary, old-endemic species differed from values expected for

passerines generally, and could account for any observed patterns in field thermoregulation.

Thermoregulatory strategies of birds

Current knowledge of avian energetics does not match the diversity of avian taxonomy, ecology and distribution, even though this was recognised over forty years ago (Yarbrough 1971). Knowledge of standard physiological variables (such as BMR or T_b) exist for only small numbers of the world's extant bird species (for example, BMR data exists for less than < 6% of the world's 9865 bird species, see Appendices), concentrated for particular groups of birds (such as the hummingbird family Trochilidae; McKechnie & Lovegrove 2002), and studies that consider avian responses at a range of T_a are much rarer. At present torpor ($T_b < 30\text{ }^{\circ}\text{C}$) has been reported in birds from 15 families from nine orders (McKechnie & Lovegrove 2002; Ruf & Geiser 2014), with observational evidence of torpor in an additional four families (see below). Nocturnal hypothermia has been more variously defined, but McKechnie and Lovegrove (2002) report nocturnal hypothermia in at least 29 families from 11 orders, although the extent of hypothermia beyond those families is unknown.

While recent work has compiled BMR data for some Australian birds (Bech *et al.* 2016), very few studies have thoroughly investigated avian thermoregulatory physiology at a range of T_a (MacMillen 1984; Ambrose & Bradshaw 1988; Chan *et al.* 1989; Ambrose *et al.* 1996; Maddocks & Geiser 1997; Maddocks 2001; Astheimer & Buttemer 2002; Maddocks & Geiser 2007; Buttemer *et al.* 2009). In Australia, chance observational reports of passerine hypothermia account for almost equal knowledge as experimental studies, with anecdotal reports of winter torpor coming from arid-dwelling adult nectarivorous White-fronted Honeyeater (*Phylidonyris albifrons*; Ives 1973), insectivorous Banded Whiteface (*Aphelocephala nigrificincta*), Red-capped Robin (*Petroica goodenovii*), White-backed Swallow (*Cheramoeca leucosternus*; Serventy 1970b; Congreve 1972), and frugivorous, lerp- and manna-feeding Mistletoebird (*Dicaeum hirundinaceum*; Heumann 1926; Serventy 1970a). Consequently broad statements regarding the extent of

hypothermia in birds, for example that heterothermia is more prevalent in non-passerines, or that only passerines < 25 g are capable of torpor (McKechnie & Lovegrove 2002) presumably are a reflection of sampling bias rather than a true representation of thermoregulatory strategies of birds, particularly in Australia.

Behavioural strategies for energy balance

While physiological mechanisms such as nocturnal hypothermia or torpor are more extreme responses to energetic challenges, behavioural strategies are a less dramatic, but still beneficial, mechanism for facilitating energy balance. Sedentary diurnal birds are observed to use social behaviours such as huddling, and microclimate adjustments, such as basking or use of sheltered roost sites. But birds are highly gregarious animals and these behaviours perform multiple functions (Gill 2007). While the ecological and behavioural roles of these behaviours, such as increased predator vigilance, improved foraging efficiency (Glück 1987), strengthened pair and group bonds (Logue 2007), greater breeding success (Emlen 1994), reduced parasite loads have been studied, their thermoregulatory consequences have been largely ignored or assumed (Beauchamp 1999), with few exceptions (Boix-Hinzen & Lovegrove 1998; McKechnie & Lovegrove 2001b; McKechnie *et al.* 2006; Wojciechowski *et al.* 2011).

Communal roosting and huddling behaviour, known as social thermoregulation, can be an important mechanism for small, social endotherms, particularly when ambient environmental temperatures are low (Beauchamp 1999; Gilbert *et al.* 2010). While most often an inactive-phase behaviour, social thermoregulation is also observed during the active phase, when T_a is low or conditions unsuitable for foraging. Social thermoregulation is seen in small mammals such as gliders and pygmy possums, and in many species of bats, most of which huddle in roost hollows, rock crevices, nests etc. (Geiser *et al.* 2007; Boratyński *et al.* 2012; Nowack & Geiser 2016). Avian examples of social thermoregulation are varied – African mousebirds (Coliidae) roost by hanging in scrums of up to 25 birds (McKechnie & Lovegrove 2001b; McKechnie *et al.* 2006), Australian woodswallows (Artamidae), Varied Sittellas (Neosittidae) and Fairy-wrens (Maluridae)

roost on perches side-by-side (Rowley & Russell 1997; Noske 1998; Higgins *et al.* 2006) whereas Estrildid finches (Estrildidae) and Australo-Papuan babblers (Pomatostomidae) roost communally in purpose-built roost nests. Torpor is often recorded in endotherms that socially thermoregulate, and some species are unable to maintain homeothermy in the absence of conspecifics (such as White-backed Mousebirds *Colius colius*; McKechnie & Lovegrove 2001).

Roost sites that buffer against environmental extremes provide another behavioural mechanism to further reduce energy expenditure (Doucette *et al.* 2011). While even roosting in dense foliage can reduce nocturnal energetic costs (Walsberg 1986), some refuge sites can maintain a temperature independent of external T_a (White *et al.* 1975; Paclík & Weidinger 2007). Heterothermy is also frequently observed in endotherms that use arboreal and terrestrial refuges such as tree hollows and burrows (Hosken & Withers 1999; Körtner & Geiser 2000; Cooper & Withers 2004b). How roost site selection affects energy balance in free-ranging birds is understood only for a few species, such as the Australian Owlet-nightjar (*Aegotheles christatus*; Doucette *et al.* 2011).

Meeting energetic challenges in the Australian environment

The Australian environment presents significant energetic challenges to endotherms, as it is characterised by low primary productivity, low rainfall and high evaporation which affect both the immediate thermal environment and constrain resource acquisition (Geiser *et al.* 2006). Although conditions in Australia are less energetically extreme than a snow-bound northern hemisphere winter, the landscape still poses challenges for small endotherms. While many northern hemisphere species migrate to avoid unfavourable environmental conditions, migration and nomadism are far less common for Australian birds, particularly passerines (Allen & Saunders 2002; Withers *et al.* 2004). In arid Australia, avian nomadism is best predicted by body mass and diet, and insectivorous birds are more likely to be sedentary (Tischler *et al.* 2013), and large, nectarivorous birds are more likely to be nomadic (Allen & Saunders 2002). While endotherms can acclimatise to environmental changes on seasonal scales, coping with diurnal fluctuations, in

particular low T_{as} requires a wide thermal tolerance and a high thermogenic capacity (Maddocks & Geiser 1999), ability to use torpor and/or hypothermia, or behavioural strategies to mitigate their exposure to environmental extremes. As a result the distribution and abundance of Australian passerines may be constrained by their physiological and behavioural thermoregulatory attributes (Astheimer & Buttemer 2002; Geiser 2004a).

The Gondwanan origin of the passerines makes Australia's 'old endemic' passerines (*sensu* Geffen & Yom-Tov 2000; Bech *et al.* 2016) a good subject for thermoregulatory studies, as they have evolved *in situ* in the Australian environment. The low-productivity Australian environment has been attributed with driving avian characteristics such as small clutch sizes, high incidence of cooperative breeding, extended parental care that are markedly different to northern hemisphere counterparts (Russell 1989; Rowley & Russell 1991; Geffen & Yom-Tov 2000; Russell 2000; Cockburn 2006). Yet whether thermoregulatory or behavioural physiological responses of Australian passerines also differ under these environmental conditions is unknown.

In contrast with the paucity of physiological knowledge of Australian birds (Cooper 2017), Australian mammals are known to use a range of physiological mechanisms such as torpor and behavioural mechanisms such as huddling and basking to meet energy demands in the Australian environment (Withers *et al.* 2004; Geiser 2004a). Whether birds use the same mechanisms under the same environmental conditions and energetic constraints is unknown. However, in well-studied endotherm groups such as mammals, morphological, physiological, environmental and behavioural characteristics provide useful proxy evidence for likelihood of heterothermy and torpor (Geiser 1998; McKechnie & Lovegrove 2003; Schleucher 2004; Cooper & Geiser 2008). Characteristics such as small body size, arid distribution, sedentary habits and specialised roosting behaviour of many Australian passerines correlates with use of physiological thermoregulatory strategies of hypothermia and torpor in mammals and birds (Schleucher 2004). However at present we have limited understanding of the extent of heterothermy in Australian birds.

To address the paucity of thermoregulatory knowledge of Australian birds, the aim of this study is to investigate the thermoregulatory responses of native passerines to ambient temperature, particularly in winter. Four sedentary, insectivorous passerines were selected to examine the thermoregulatory strategies used by Australian passerines in response to environmental challenges (Table 1.1). All species are of Gondwanan origin (Geiser *et al.* 2006; Bech *et al.* 2016) and are found in the south west of Western Australia but have broader distributions. That they are resident throughout their range, even in the unpredictable seasons of the arid zone, implies that they are able to cope with all the conditions present in that environment. Prior to this study the thermoregulatory strategies of these species was unknown. Here I use a comprehensive methodology incorporating measurements of free-ranging and field-fresh birds at a range of natural and controlled conditions. These are supplemented by temperature measurements of roost sites, daily activity observations and plumage analyses.

Table 1.1: Species investigated in this study and reason for inclusion.

Species	Mass (g)	Reason for inclusion
<i>Pomatostomus superciliosus</i> White-browed Babbler	45	Sedentary, roosts communally in nests, broad distribution
<i>Climacteris rufus</i> Rufous Treecreeper	30	Small, sedentary, group-living, roosting habits unknown but likely roosts in hollows
<i>Eopsaltria griseogularis</i> Western Yellow Robin	18	Small, sedentary, group-living, roosting habits unknown, but likely roosts in open canopy
<i>Gymnorhina tibicen</i> Australian Magpie	308	Widespread but sedentary, geographic dimorphism with thermoregulatory implications

Winter thermoregulatory strategies of the White-browed Babbler *Pomatostomus superciliosus*: the energetic benefit of communal roosting¹

Abstract

White-browed Babblers (*Pomatostomus superciliosus*) are socially gregarious, ground-frequenting birds of central and southern Australia. Living in close-knit family groups, they construct domed nests in which they roost communally. In temperate *Eucalyptus wandoo* woodland, free-living babblers implanted with temperature-sensitive radio transmitters maintained strict homeothermy in winter, even at below-freezing ambient conditions. Field and laboratory measurements were used to examine the thermal and energetic strategies babblers use to maintain homeothermy including quantification of heat production and loss, social thermoregulation, roost nest temperature and diurnal behaviour. In the laboratory, standard open-flow respirometry was used to measure metabolic rate, evaporative water loss and body temperature for solitary and small groups (2 - 5 individuals) of captive babblers over a range of ambient temperatures (10 – 32.5 °C). Solitary babblers had a typical endothermic response to ambient temperature, with no evidence of torpor. Huddling yielded significant energy savings at low temperatures. At $T_a = 10\text{ °C}$, the energetic requirements of pairs of huddling babblers were 30% lower than solitary babblers at the same temperature. The thermal properties of roost nests provide a buffer against low temperatures. Diurnal observations of babblers provide no evidence they rely on specific thermoregulatory behaviours such as basking to buffer energetic costs on cold mornings. Both communal roosting behaviour and the insulation of roost nests are important in aiding nocturnal thermoregulation conferring energetic benefits that aid in meeting daily energy requirements without resorting to hypothermia even in habitats with extreme diurnal temperature fluctuations and/or very low overnight minima.

¹ This chapter contains material that has been published as a co-authored manuscript (Douglas, T.K., Cooper, C.E., and Withers, P.C. (2017) *Avian torpor or alternative thermoregulatory strategies for overwintering?* Journal of Experimental Biology **220**, 1341-1349; doi: 10.1242/jeb.154633). This chapter is my original contribution to the manuscript, which was subsequently edited by the co-authors to produce the final published manuscript.

Introduction

Animals that remain sedentary in environments with high diurnal and seasonal fluctuations in ambient temperature (T_a) and rainfall require tolerance of the entire range of conditions of their habitat. While birds in Australian temperate woodlands may not experience minimum T_a s during winter as extreme as for a snow-bound northern hemisphere winter, they still have to contend with energy shortage. Reduced food availability, sub-optimal foraging conditions (both reduction in daylight hours and increased proportion of inclement weather) and cold ambient conditions, particularly overnight, affect the ability of an endotherm to meet energy requirements in an already depauperate, low-productivity landscape (Chan *et al.* 1989; Geiser *et al.* 2006). Despite this, many Australian insectivorous birds are sedentary, even in semi-arid and arid climates (Recher & Davis 1997; Morris & Wooller 2001). While endotherms can acclimatise to environmental changes on seasonal scales, coping with diurnal fluctuations, in particular low T_a requires an increased thermogenic capacity to maintain body temperature (Maddocks & Geiser 1999), or use of hypothermia and/or possibly torpor in species where energy savings is a high priority, along with behavioural adjustments that ameliorate thermoregulatory costs.

Social thermoregulation

For social animals, group size can influence daily activity in terms of foraging efficiency, territorial defence, and predator vigilance (Bertram 1980; Glück 1987). But for group-living species that also roost communally, optimum group size may also have a thermal role (Beauchamp 1999). Group size fluctuates inversely with T_a for clustering social Bonin Flying Foxes (*Pteropus pselaphon* Sugita & Ueda 2013) and huddling House Sparrows (*Passer domesticus biblicus*; Burns *et al.* 2013). Whether environmental temperature can act as a driver in determining optimum group size of territorial species is unclear, although Buttemer *et al.* (2009) observed that the energy savings of a large group of Chestnut-crowned Babblers (*Pomatostomus ruficeps*) at low T_a was equivalent to a smaller group at higher T_a . Although social thermoregulation takes different forms (such as Varied Sittellas *Daphoenositta chrysoptera* perching side-by-side on branches, Noske 1998; aggregations

of Greater Mouse-eared Bats *Myotis myotis* suspended from cavern roofs, Boratyński *et al.* 2012; hanging clusters of White-backed Mousebirds *Colius colius*, McKechnie & Lovegrove 2001; and huddles of Sugar Gliders *Petaurus breviceps* in nests, Geiser *et al.* 2007) the physiological effects are similar. Huddling reduces the effects of wind chill and radiative heat loss to the surrounding environment, thereby reducing energetic requirements to maintain T_b (Vickery & Millar 1984; Buttemer 1985; Canals *et al.* 1997; Gilbert *et al.* 2010).

Roost nests

Sheltered roost sites minimise predation and confer significant energetic benefits (Doucette *et al.* 2011). Even simple roost sites in dense foliage or small nests can reduce the effects of wind chill, thereby significantly reducing energy expenditure (Walsberg 1986; Buttemer *et al.* 1987). Well-insulated roost sites such as tree hollows, rock crevices or elaborate aggregate nests can have a roost temperature (T_{roost}) nearly independent of T_a (White *et al.* 1975; Paclík & Weidinger 2007; Doucette *et al.* 2011). However smaller, more simple structures, such as roost nests of solitary-roosting White-browed Sparrow Weavers (*Plocepasser mahali*; Ferguson *et al.* 2002) and Bananaquits (*Coereba flaveola*; Merola-Zwartjes 1998), are not sufficiently insulated to maintain T_{roost} independent of T_a , but they do reduce the rate of heat loss of their occupants.

Use of both social thermoregulation and roost nests would be expected to have additive energetic benefits for birds, but few avian studies have quantified energy savings from huddling as well as taking into account roost temperature conditions. Huddling has been studied in controlled laboratory conditions (MacMillen 1984; Buttemer *et al.* 2009; Wojciechowski *et al.* 2011; Burns *et al.* 2013), and microclimate and biophysical properties of roost sites have been studied in the field (Merola-Zwartjes 1998; Ferguson *et al.* 2002; Paclík & Weidinger 2007). However the combination of the two approaches has only been investigated under captive conditions (du Plessis *et al.* 1994; du Plessis & Williams 1994; Chappell *et al.* 2016), not for free-ranging birds.

Diurnal behaviour

How animals partition time between different activities during their active phase influences the energy reserves available when inactive (Goldstein 1988). Many activity studies relate animal behaviour directly to daily energy requirements (Weathers *et al.* 1984; Williams & Nagy 1984; Duncan & Pillay 2013), but few consider the simultaneous impact of T_a on behaviour (Owen-Smith 1998; Gestich *et al.* 2014). Variables such as T_a vary with different locations and substrates in an animal's environment, so behavioural decisions that alter location and activity affect energy requirements. For example, the decision to bask (intercepting solar radiation to supplement metabolic heat production; Warnecke & Geiser 2010) instead of using exercise-related thermogenesis (Humphries & Careau 2011) may depend upon environmental conditions. The most beneficial behavioural thermoregulatory strategies would be expected at low T_a when potential energetic benefits are high.

Physiology in the laboratory and the field

Open-flow respirometry is considered the gold standard of techniques for gathering comparable, repeatable metabolic information in the laboratory (Halsey 2011). To date, there is no direct equivalent for studying diurnal fluctuations in metabolic rate (MR) in the field as isotopic methods of measuring field metabolic rates yield only mean MR values averaged over days or weeks (Butler *et al.* 2004). Heart rate and accelerometry can be used as short-term proxies for MR, but they require metabolic calibration and are better suited to quantifying active-phase energetics as opposed to rest-phase energetics (Williams *et al.* 2014). Instead, where short-term energetic responses to thermal conditions are of interest, body temperature (T_b) can be used to identify heterothermia of free-living animals in the field, due to the relationship between metabolic heat production and T_b at any particular T_a (Withers 1992). This is particularly true for measuring roosting diurnal birds, as activity, digestion and other energetic processes are at a minimum. Consequently a combination of laboratory and field experiments is important to correlate T_b with MR and other physiological variables such as thermal conductance (C) and evaporative water loss (EWL).

Study species

White-browed Babblers (*Pomatostomus superciliosus*; ~45 g, hereafter babbler) are sedentary throughout their range, living in gregarious family groups of 2-15 individuals (Cale 1999). They are the smallest of the Australo-Papuan babblers (family Pomatostomidae), a family of cooperatively-breeding, insectivorous passerines (Higgins *et al.* 2006). Babblers are widely distributed across southern Australia, inhabiting environments ranging from temperate tall wet forests to semi-arid and arid open woodlands and scrublands (Blakers *et al.* 1984). The reproductive strategy of babblers is to live as a cohesive social group and breed cooperatively (Chandler 1920; Cale 1999). Like the closely-related Grey-crowned Babbler (*Pomatostomus temporalis*), also an obligate cooperative breeder, White-browed Babblers rely on additional helpers at the nest to successfully raise young (Cale 1999; Eguchi *et al.* 2007). Like other pomatostomids, these babblers use domed nests for both communal roosting and breeding (Higgins *et al.* 2006). Each territorial group builds and maintains several roughly-spherical domed roost nests of sticks and grasses (external dimensions ~30cm diameter) within their territory. While the breeding biology and foraging ecology of babblers have been well studied (Cale 2003; Oppenheimer 2005; Taylor & Paul 2006), little is known of the thermoregulatory strategies that allow them to persist as sedentary birds throughout their range, particularly during cold ambient conditions, nor how their sociality might affect their thermoregulatory costs.

The aim of this study of White-browed babblers was to quantify the relationship between physiological and behavioural thermoregulatory strategies and T_a , and to examine the energetic strategy that enables these communally-roosting birds to sustain a sedentary existence in a variable environment. I measured core T_b of free-ranging babblers, examined their daily activity patterns, augmented these data with measurements of the thermal properties of roost nests in both the laboratory and field, and measured of standard physiological variables for individual and groups of huddling babblers in the laboratory.

Methods

Study site

Field body temperature ($T_{b,field}$), field behaviour, roost nest characteristics, and roost temperature data were collected for the White-browed Babbler at Dryandra Woodland (32° 45' S, 116° 55' E), 170 km southwest of Perth, Western Australia. Dryandra Woodland is a 28,066 ha conservation reserve consisting of several blocks of dry open woodland in an agricultural matrix (Luck 2002). It is largely dominated by a *Eucalyptus wandoo*, *E. accendens* and *E. astringens* canopy with open *Gastrolobium* spp. understorey, interspersed with *Dryandra* and *Banksia*-dominated lateritic outcrops and some granite complexes skirted by stands of *Allocasuarina huegliana*. The climate is Mediterranean, with hot, dry summers and cool, wet winters. Dryandra receives 500 – 600 mm rainfall per annum, and temperature ranges from minima of -6 °C in winter to maxima of 45 °C in summer. I studied seven babbler territories within the main woodland block (Figure 2.1).

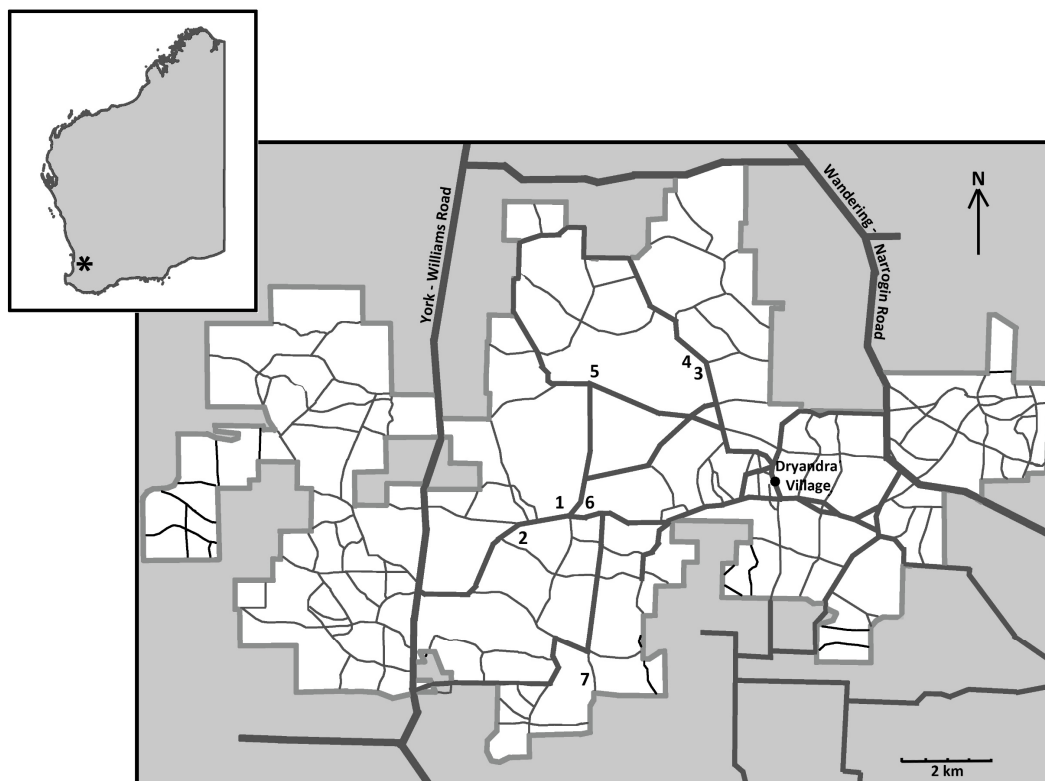


Figure 2.1: Map of main block of Dryandra Woodland, Western Australia (location marked with asterisk in inset). White-browed Babbler territories studied here are numbered 1 - 7. Body temperatures of free-living babblers were measured in territories 1 and 2 in winter 2012, and territory 3 in winter 2013. All territories were used for behavioural observations.

Free-ranging body temperature

Eight babblers from three territories (six from two territories in winter 2012 and two from a single territory in winter 2013; Figure 2.1) were captured with mistnets using audio playback (calls modified from BOCA 2007 and Stewart 2005). Temperature-sensitive radio transmitters (BD-2TH, 1.05 g; Holohil Systems Ltd) were surgically implanted into the intraperitoneal cavity of the birds under general anaesthesia (Isoflurane in O₂, 3% for induction, 1.5 - 2% for maintenance). A single dose of analgesic (Meloxicam; 0.2 mg kg⁻¹) was administered sub-cutaneously post-surgery. Birds were monitored post-surgery for a recovery period of several hours before they were released at the capture site. All implanted individuals, as well as any additional conspecifics caught, were marked with a unique colour combination of plastic leg bands for field identification. Prior to implantation, transmitters were calibrated in water baths at 14, 25, 35 and 43 °C, measured with a mercury thermometer traceable to a national standard, using a radio receiver (AOR AR8200) connected to a sound recorder (Olympus LS-10). A temperature calibration curve was produced for each transmitter by recording interpulse interval (time taken for 21 pulses to elapse ÷ 20) at each temperature using Cubase (Cbase LE4, Steinberg Media Technologies GmbH) and plotting a quadratic line of best fit to the data in Microsoft Excel.

Due to the limited range of the transmitters, implanted birds were initially followed to their evening roost site, until roost site fidelity could be confirmed. Once birds had gone to roost, field body temperature ($T_{b,field}$) was recorded overnight using a Yagi antenna connected to a wide-range radio receiver (AOR AR8200mk3 or AOR AR8000); the audio output recorded with a portable sound recorder (Olympus LS-10, Olympus VN-702PC or Sony ICD-PX333) and saved as a .MP3 file. When more than one babbler in the roost nest had a transmitter, the “scan” function of the radio receiver was used to alternate between the frequencies for all the birds in that roost nest. Each bird was recorded for 2 min, with 1 min of noise from an empty channel between each bird, then an empty channel was recorded for 2 min, before repeating the sequence. Recording equipment was

collected to download data and recharge batteries each morning after the birds had left the roost.

Black bulb temperature (T_{bb}) and relative humidity (RH) data were recorded simultaneously using a Hygrochron iButton (DS1923, Maxim Integrated Products) to log T_a (± 0.0625 °C) and RH ($\pm 0.04\%$) every 5 min. The iButton was placed inside a black table tennis ball, and affixed to a stake 0.5 m above ground level in an open location near the roost site. Data were downloaded periodically (OneWireViewer, v 0.3.15.50, Maxim Integrated Products). As T_{bb} combines air temperature, radiation, and wind speed in a single metric (Walsberg & Weathers 1986; IUPS Thermal Commission 2003), it provides a useful measure of the maximum environmental thermal load experienced by an animal in its habitat (Hetem *et al.* 2007; Mole *et al.* 2016). However, additional weather data were also obtained from the Bureau of Meteorology for the nearest weather station (Wandering; 32° 67' S, 116° 67' E; ~30 km away), including T_a , rainfall, wind direction, wind strength and maximum wind gust. Data were provided at 1 min intervals, but analyses compiled data for dusk (16:00 – 19:00 local time), dawn (05:00 – 08:00) and overnight (19:00 – 08:00) by calculating mean wind direction, mean wind strength, maximum wind gust and total rainfall for each of these three time periods. T_a data from the weather station were only used for one night when T_{bb} loggers failed. Times for dawn and dusk were obtained from Geoscience Australia (www.ga.gov.au/geodesy/astro/sunrise.jsp).

Two custom-written programs (Microsoft Visual Basic Express 2010; P. Withers & T. Douglas) were used to analyse the $T_{b,field}$ sound files. After the .MP3 file was converted to .WAV format using Cubase, the first VB program calculated interpulse distances for the entire sound file and saved the results as a .csv file. Where necessary, Microsoft Excel was used to separate the interpulse values into the two or three individual birds they corresponded to. The second program used the temperature calibration curve for the specific transmitter to convert these interpulse distances to $T_{b,field}$, which could then be plotted over time, along with the T_{bb} data recorded by the iButton. For sound files where

the signal to noise ratio was insufficient to unequivocally detect interpulse distance, the files were inspected manually, calculating interpulse distance (time elapsed for 21 pulses \div 20) using Cubase. For single bird sound files, interpulse distance was manually calculated at 10 min intervals. For multiple bird files, it was calculated for each bird every second scan cycle. These resulting interpulse distance files were then converted to $T_{b,field}$ and plotted over time with T_{bb} as above. Calculation of parameters such as roosting commencement time, minimum $T_{b,field}$, time and T_{bb} 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, using the second custom-written VB program.

Roost temperature

Occupancy and internal air temperature of eight babbler roost nests was measured *in situ* at Dryandra Woodland using iButton data loggers, placed against the internal, lower rear wall of the nests. To minimise eviction of data loggers from active nests by the babblers, iButtons were fastened to a length of wire and then inserted into intact nests. The data loggers recorded roost nest temperature (T_{roost}) and humidity (RH_{roost}) every ten minutes. Internal roost loggers were paired with external ambient loggers placed nearby at similar elevations to the nests. Where multiple nests of a similar height were in close proximity, they were matched against a single ambient logger. Data were downloaded periodically using the OneWireViewer program.

Two intact but currently unused babbler nests were collected from the study area to measure nest conductance under laboratory conditions (Merola-Zwartjes 1998). Nests were placed in a constant temperature (CT) room ($T_a = 10^\circ\text{C}$) and 190 mL of hot ($\sim 50^\circ\text{C}$) water (equivalent mass of four adult babblers) in a waterproof ziplock bag was placed in the nest. Three iButtons recorded temperature at 10 s intervals in the nest as it cooled, one within the water bag, one in the bottom of the nest and one in the nest ceiling. An additional 190 mL of hot water was placed in a bag and left to cool in the CT room, with one iButton logging temperature from inside the bag, and one logging CT room T_a . Cooling constants (k) for the nest and the control ziplock bag were calculated following

the methodology of Toolson (1987), where k (h^{-1}) is the slope obtained by plotting the natural logarithm of $(T_{\text{roost}} - T_a)/(T_0 - T_a)$ over time, T_{roost} is the temperature of the roost nest, T_a is ambient temperature and T_0 is T_{roost} at time = 0. Cooling constants were converted to conductance (C ; $\text{J } ^\circ\text{C}^{-1} \text{g}^{-1} \text{h}^{-1}$) using the specific heat capacity of water (4.18 J g^{-1}) where $C = k * 4.18$ (after Morrison & Tietz 1957 and de Vries & van Eerden 1995).

Roost nest characteristics

Roost nest characteristics were recorded for all babbler roost nests that could be located in the study area. Location and elevation were recorded (Garmin GPS 60), and characteristics of the nest tree including species, % alive, tree shape, tree health (on a scale from 1 dead to 5 healthy, after Ruthrof 1997), diameter at breast height (DBHOB; cm) and tree height were recorded. For the surrounding habitat I recorded vegetation type, slope, aspect, distance to, species and orientation of the two nearest neighbour trees and the % cover of leaf litter, coarse woody debris, herbs/grasses, understorey, midstorey and overstorey were estimated visually in a 5 x 5 m block surrounding the nest (after Newsome & Catling 1979 and Walker & Hopkins 1984). The vertical and horizontal location of the nest in the host tree, nest dimensions, nest shape, entrance direction and height to the base of the nest were all recorded. Tree height and height to base of nest were measured with a laser range finder (Nikon Forestry 550). The range finder was calibrated against objects of known height prior to use. Whether the nest was intact, known or believed to be active was also recorded.

Field behaviour

Interval sampling was used to gain a representative, unbiased perspective of bird behaviour (Altmann 1974). Bird behaviour was recorded at 15 s intervals, timed using a smart phone metronome app (Mobile Metronome for Android, v1.2.4F). The metronome was started at the beginning of each session and behaviour recording commenced at the first 15 s interval once a group of birds were sighted without causing alarm. A single individual was followed at a time, unless the individual was in a group, then the behaviour of the focal individual and all visible conspecifics was recorded. Recordings of a single individual were

made for a maximum of 20 minutes, although birds generally moved out of sight before that time had elapsed. At each interval, bird position and behaviour were noted as outlined in Table 2.1. Simultaneous T_{bb} data, collected for the free-ranging T_b study, were used in the analyses. From the resulting data, key questions could be addressed, including, a) does proportion of time dedicated to particular activities vary with environmental conditions? b) do environmental conditions affect substrate use by babblers? and c) do babblers use thermoregulatory behaviours (such as basking) when ambient temperatures are low?

Table 2.1: Babbler behaviour categories used to classify microclimate, habitat element, activity and posture. Position in habitat elements marked with an asterisk (*) were defined as being low, medium or high. Habitat elements marked with two asterisks (**) were noted as low, medium and high with additional descriptors of trunk, branch, twig, foliage or hollow. Whether or not the habitat element was dead or alive was noted. Posture was only recorded for stationary (resting alert or maintenance) behaviour.

Microclimate	Habitat element
Sun	Open ground
Shade	Rocks
Dappled light	Leaf litter
Overcast	Coarse woody debris
Twilight	Fallen log
Mist	Tree stump*
	Grass/herb/moss field
	Shrub*
Posture	Understorey tree**
Normal	Canopy tree**
Fluffed	In flight*
Lean	
Erect	
Hunched	Activity
Sitting	Roosting
One leg	Resting alert
Stretching	Foraging
Panting	Locomotion (including flying)
	Agonistic behaviour
	Maintenance (preening)
	Social behaviour (non-agonistic)
	Nest maintenance

Laboratory respirometry

Nine babblers were caught for laboratory studies, at Big Brook Dam, Pemberton (34° 38' S 116° 03' E), 300 km south of Perth, Western Australia, using mistnets and audio playback. Babblers were obtained at this alternative site, not the field study site, due to Department of Parks and Wildlife (DPaW) licencing restrictions. Six were caught in early spring 2012 and three in autumn 2013, all as non-breeding adults of unknown age. Babblers were transported to Curtin University's Bentley campus and housed in partially-covered outdoor aviaries as family groups. Food (crickets, wood roaches, termites, earthworms and mealworms) and water were available *ad libitum*, except for the 12 hours prior to experiments when the individuals to be measured were placed in a small fasting cage, with access to water but not food. All birds were allowed at least three days between successive measurements.

Open flow-through respirometry was used to measure basic physiological variables of oxygen consumption ($\dot{V}O_2$), carbon dioxide production ($\dot{V}CO_2$) and evaporative water loss (EWL) at a range of T_a (10, 15, 20, 25, 30 and 32.5 °C, in random order), after Withers (2001). Two separate open flow-through respirometry systems allowed concurrent measurement of two individuals each measurement night. Birds were measured overnight from approximately 18:00 to 04:00, before being released back into their aviary.

Experiments took place in a temperature-controlled cabinet (Arcus model 400E) into which birds were placed individually in 2L clear Perspex chambers, allowing visual monitoring of animals via a web camera (Swann Max-IP-Cam). Compressed air was dried using Drierite (~98% $CaSO_4$, ~ 2% $CoCl_2$, W.A. Hammond Drierite Co. Ltd) and airflow into each chamber was controlled at a constant rate of 900 mL min⁻¹ via mass-flow meters (Cole Parmer Mass Flow Controller 32708-28, 0 - 5 L min⁻¹ and Aalborg Mass Flow Controller GFC171, 0 - 5 L min⁻¹).

RH and T_a of excurrent air were measured using a thin-film capacitance RH and T_a probe (Vaisala MNP45A). A subsample of that air was then passed through a second small

Drierite column, into a carbon dioxide analyser (Qubit Systems S153) and finally a paramagnetic oxygen analyser (Servomex OA18). Data from the T_a /RH probe and the CO_2 and O_2 analysers were recorded at 20 second intervals by interfacing these devices with a series of Brymen multimeters (models BM202 for T_a /RH/ CO_2 and TBM859CF for O_2) via RS232 ports to a PC running a custom-written Visual Basic (version 6) data collection program (P. Withers). T_b was measured for each individual when it was removed from the chamber at the conclusion of each experiment, using a plastic-tipped thermocouple (connected to a Cole Parmer Digi-Sense Thermometer 91100-20) inserted ~1.5cm into the cloaca.

Ventilatory data were collected via whole-body plethysmography, by detecting pressure changes in the metabolic chamber caused by the warming and humidifying of inspired air (Malan 1973; Withers 1977a; Szewczak & Powell 2003). A custom-built pressure transducer (Motorola MPX2010) detected these pressure changes with voltage output recorded every 15 ms via a Pico Technology ADC-11 converter interfacing with a PC running PicoScope. Ventilatory frequency (f_R ; breaths min^{-1}) and tidal volume (V_T ; mL) were measured at the end of each night's experiment before the bird was removed from the chamber. Five to eight sets of 50 s samples were collected for each bird at each temperature, when metabolic traces and observation via the web camera indicated the babblers were resting.

Flowmeters were calibrated using a Gilibrator-2 air flow calibrator (Sensidyne), and the calibration of the RH probes was confirmed using a two-point calibration of 1% RH air (dried with Drierite) and 100% RH air (by breathing saturated air onto the probe). The Servomex oxygen analysers were two-point calibrated with compressed N_2 and dry ambient air. Oxygen drift due to changes in the room T_a and barometric pressure during experiments was accounted for by measuring a reference channel of dry ambient air and subtracting the O_2 of excurrent chamber air from this reference value continuously throughout the experiment. CO_2 analysers were calibrated with compressed N_2 and a compressed calibration gas (0.538% CO_2 , BOC Gas). The plethysmography system was

calibrated using the pressure decay corrections outlined by Szewczak & Powell (2003), with a 0.5 mL air injection into the system.

Metabolic, hygric and ventilatory variables were calculated using a custom-written analysis program (P. Withers; calculations after Malan 1973; Withers 2001; and Cooper & Withers 2004b), with oxygen consumption ($\text{mL O}_2 \text{ min}^{-1}$) calculated as $= (\dot{V}_I * F_{IO_2}) - ((\dot{V}_I * (1 - F_{IO_2}) / (1 - F_{EO_2} - F_{ECO_2})) * F_{EO_2})$, where \dot{V}_I is the inlet flow rate (mL min^{-1}), F_{IO_2} is the fractional concentration of incurrent O_2 (0.2095) and F_{EO_2} is the fractional concentration of O_2 leaving the chamber, and F_{ECO_2} is the fractional content of CO_2 leaving the chamber (Withers 2001). Carbon dioxide consumption ($\text{mL CO}_2 \text{ min}^{-1}$) is calculated as $= ((\dot{V}_I * (1 - F_{IO_2}) / (1 - F_{EO_2} - F_{ECO_2})) * F_{ECO_2}) - (\dot{V}_I * F_{ICO_2})$ where F_{ICO_2} is the fractional concentration of excurrent CO_2 . Evaporative water loss ($\text{mg H}_2\text{O min}^{-1}$) is calculated as $= \dot{V}_I * F_{EH_2O} * (1 - F_{IO_2}) / (1 - (F_{EO_2} * (1 - F_{EH_2O})) - (F_{ECO_2} * (1 - F_{EH_2O}))) - F_{EH_2O}$, where F_{EH_2O} is the fractional content of H_2O leaving the chamber. From each experiment \dot{V}_{O_2} ($\text{mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$), \dot{V}_{CO_2} ($\text{mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) and EWL ($\text{mg H}_2\text{O g}^{-1} \text{ h}^{-1}$) were averaged for a 20 min period when physiological variables were minimal and stable. Metabolic water production (MWP; $\text{mL g}^{-1} \text{ h}^{-1}$) and metabolic heat production (MHP; $\text{J g}^{-1} \text{ h}^{-1}$) were calculated from metabolic rate (\dot{V}_{O_2}) using the oxycalorific and hygric conversions to J interpolated from Withers (1992) using the measured respiratory exchange ratio ($\text{RER} = \dot{V}_{CO_2} / \dot{V}_{O_2}$) i.e. $19.5 \text{ J mL O}_2^{-1}$ and $0.566 \text{ mg H}_2\text{O mL O}_2^{-1}$ for $\text{RER} = 0.7$ and $21.4 \text{ J mL O}_2^{-1}$ and $0.663 \text{ mg H}_2\text{O mL O}_2^{-1}$ for $\text{RER} = 1$. Relative water economy (RWE) was calculated as MWP / EWL . The point of relative water economy (PRWE) was calculated as the T_a where $\text{RWE} = 1$ by plotting RWE against T_a by least squares regression. Wet (C_{wet} ; $\text{J g}^{-1} \text{ h}^{-1} \text{ } ^\circ\text{C}^{-1}$) and dry (C_{dry} ; $\text{J g}^{-1} \text{ h}^{-1} \text{ } ^\circ\text{C}^{-1}$) thermal conductance were calculated by $\text{MR} / (T_b - T_a)$ and $(\text{MHP} - \text{EHL}) / (T_b - T_a)$ respectively. Ventilatory values are expressed as body temperature and pressure saturated (BTPS) with the exception of oxygen extraction (EO_2) which was calculated using standard temperature and pressure dry (STPD) \dot{V}_{O_2} and minute volume (V_I). V_I was calculated as breathing frequency (f_R) x tidal volume (V_T) and EO_2 was calculated as $\text{MR} / (V_I * (F_{EO_2} + F_{IO_2} \div 2))$. The \dot{V}_{O_2} values used were from the time ventilatory data were collected, so were not

necessarily the overnight minimal values but were on average 116% of minimal values. Thermolability, the small fluctuations in core T_b with T_a below thermoneutrality (IUPS Thermal Commission 2003), were calculated as $\Delta T_b / \Delta T_a$ (Withers & Cooper 2009).

Huddling respirometry

To quantify the energetic benefit of huddling, the open-flow respirometry system described above was used to determine physiological variables for multiple babblers in the same chamber at T_a below thermoneutrality. Babblers were measured in pairs, threes and a group of five at a range of T_a (10, 15 and 20 °C) and sample sizes (Table 2.2), with the flow rate adjusted according to group size (1800 mL min⁻¹, 2500 mL min⁻¹ and 3500 mL min⁻¹ respectively). Further measurements of a group of five babblers were abandoned

Table 2.2: Sample sizes at each ambient temperature for each roosting group size in the huddling experiments.

Group size (N)	T_a (°C)	Sample size (n)
2	10	4
	15	4
	20	4
3	10	3
	15	2
	20	1
5	10	1

after an initial measurement at $T_a = 10$ °C, due to difficulty in obtaining data when all 5 birds were resting.

No ventilatory data were collected for multiple birds within a chamber as it is not possible to distinguish between the ventilation of individual birds in the same chamber. Whilst T_b was measured for all birds, only the T_b of the bird measured first upon removal from the chamber was used

in the analysis, as birds awoke immediately upon opening the chamber, so T_b of subsequent birds was always higher than the first bird measured and probably not representative of experimental T_b . Experimental interval, fasting procedures, system calibration and data collection were otherwise as for single birds.

Data handling and statistical analysis

Values are presented as mean \pm standard error (SE), with N = number of individuals and n = number of measurements unless otherwise indicated. Times were Western Australian

standard times (AWST; AWST = Greenwich Mean Time + 8 h). All statistical models were tested at $\alpha = 0.05$.

Free-ranging body temperature: Linear mixed models were used to determine the relationship between fixed effects (environmental parameters such as $T_{bb,min}$), random effects (individual, family group and date), and bird response variables (minimum $T_{b,field}$, $T_{b,field}$ at time of leaving the roost etc.). This allowed me to examine the relationship between environmental parameters and bird physiological response while accounting for the non-independence of repeat measures of nests and groups. Models were built and tested with the *lmer* function of the *lmerTest* library (Kuznetsova *et al.* 2013) in R (R Core Team 2013) using the R Studio platform (R Studio: Integrated Development Environment for R v0.98.501). *lmer* models also give P-values for the significance of fixed factors, calculated using the Kenward-Roger correction using the *lmerTest* library as advocated by Schaalje *et al.* (2002).

Roost temperature: The differential between T_{bb} and T_{roost} ($\Delta T = T_{roost} - T_{bb}$) was calculated for each occupied roost night (Ferguson *et al.* 2002). The relationship between ΔT and T_{bb} was investigated using the *lmerTest* (Kuznetsova *et al.* 2013) in R Studio, with T_a as a fixed effect and nest as a random effect in the model, to account for the non-independence of sequential measurements on the same nests. P-values for *lmer* models were calculated using the Kenward-Roger correction. Logarithmically-transformed cooling constants of roost nests measured in the laboratory were compared against their paired logarithmic non-nest models by ANCOVA using *StatistiXL* (www.statistiXL.com, v1.10).

Roost nest characteristics: A χ^2 test was used to compare preferences for roost nests in the midstorey versus the canopy. Tree density in the vicinity of roost nests was compared with tree density values for Dryandra (Luck 2002a) using Student's t-test, both using *StatistiXL*. Habitat aspect and nest entrance direction were compared with a random

distribution using circular goodness-of-fit tests in *StatistiXL*; and nest height by test for uniformity after Zar (1999) using SPSS (IBM, version 22).

Field behaviour: Generalised additive mixed models (GAMMs) were used to investigate whether babblers alter time allocated to particular activities under different environmental conditions (Wood 2006). GAMMs are a semi-parametric method appropriate for behavioural analysis, as they can be built using binomial response variables for example bird foraging (= 1) or not foraging (= 0), and can incorporate both linear and non-linear predictor variables. As with other mixed models, they allow the non-independence of sequential observations to be accounted for by incorporating observation session as a random effect in the model (Wood 2006). Data screening with Cleveland dot plots showed a suitable representation of observations for the range of the predictor variables, tests for correlation yielded values < 0.7 for all combinations, and tests for collinearity using variance inflation factors yielded corvif values < 3 in all instances, indicating that there were no outliers, and no variables were substantially correlated with another variable or group of variables (Zuur *et al.* 2009).

The full GAMM model was evaluated for each behaviour category separately. The model is expressed as:

$$\text{Logit}(p) = \beta_0 + f_1(T_a) + f_2(T_{bb,\min}) + f_3(\text{Time of day}) + f_4(\text{Day of year}) + \alpha_i$$

where the binomial link function (logit) for the probability (p) that a babbler will be displaying a particular behaviour can be explained by the predictor variables of black bulb temperature (as T_{bb} , °C), overnight minimum black bulb temperature ($T_{bb,\min}$, °C), time of day (expressed as a decimal with 0 and 1 being midnight and 0.5 being midday), day of year (an integer from January 1st being 1), each fitted with respective smoothing functions f_{1-4} , generated with cubic regression spline functions. The random effect of the observation session (α_i) was also incorporated into the model.

In each instance, the most parsimonious model was selected by first quantifying the significance of the random effect upon the full model, then determining the most

parsimonious combination of predictor variables using Akaike's Information Criterion (AIC) values. The predictor variables that lowered the AIC value were retained in the model. To test validity, AIC of each final model compared against the AIC of the null model ($\text{Logit}(p) = \beta_0 + \alpha_i$) for each behaviour.

To visualise these relationships, the response of each behaviour category to its significant predictor variables from the fitted GAMM was calculated using the predict function and a set of reference conditions (Wood 2006; Weltz *et al.* 2013). These reference conditions used the mean values of each predictor variable; $T_{bb} = 13^\circ\text{C}$, overnight minimum = 0°C , time of day = 0.5 (midday) and day of year = 215 (August 3rd). All analyses were run using the *gamm4* package (Wood & Scheipl 2014) in the R statistical platform (R Core Team 2013).

Roost arrival and departure times: Data for $T_{b, \text{field}}$, roost temperature and field behaviour components of this study were combined to determine roost arrival and departure times. These were plotted against times for first light, sunrise, sunset and full dark at Dryandra Woodland (Geoscience Australia 2013). To account for seasonal differences in day length, mean times were calculated as minutes after first light and minutes before full dark.

Laboratory respirometry: The effect of T_a on physiological variables of $\dot{V}O_2$, $\dot{V}CO_2$, EWL, RWE, C_{wet} and C_{dry} were analysed for 7 individuals by multivariate repeated measures analysis of variance (RMANOVA) using the Wilks-Lambda test in SPSS with polynomial ($\dot{V}O_2$, $\dot{V}CO_2$, RWE) and reverse Helmert (EWL, C_{wet} and C_{dry}) *a priori* contrasts (Withers & Cooper 2011). This allowed examination of specific hypotheses about the expected pattern of the variables (for polynomial contrasts, that the categories will follow linear, cubic, quadratic etc. relationship; for reverse Helmert contrasts, that a category differs from all previous categories pooled together) a more powerful approach than traditional ANOVA (that assumes all means are equal). Where variables had a significant linear contrast, the coefficients of the equation describing each relationship were calculated using a custom-written macro (Withers & Cooper 2011). When the requirements for repeated measures could not be satisfied (where there were missing values for some individuals due

to logistical issues, such as ventilatory data), the *lmerTest* package was used, with T_a as a fixed effect and individual as a random effect in the model, so that individual variation could still be accounted for. P-values for *lmer* models were calculated using the Kenward-Roger correction and significant differences between fixed effect levels were calculated using the Satterthwaite correction (Schaalje *et al.* 2002).

Huddling respirometry: The effect of group size on physiological variables ($\dot{V}O_2$, $\dot{V}CO_2$, EWL, C_{wet} , C_{dry} and T_b) was compared using general linear modelling in SPSS with *a priori* contrasts. Using T_a as a covariate, the fixed effects of both group size and T_a on the above variables were compared using the Bonferroni adjustment for multiple pairwise comparisons. For variables having a linear relationship with T_a , ($\dot{V}O_2$ and $\dot{V}CO_2$), the slopes and intercepts of these relationships were compared with ANCOVA using *StatistiXL*.

Results

Free-ranging body temperature

Ninety seven nights of $T_{b,field}$ data were collected for 8 babblers (mass at time of capture = $48 \text{ g} \pm 0.6 \text{ g}$) in August 2012 and July to August 2013. Sample sizes obtained for individual birds ranged from 1 to 19 nights. Babblers used roost nests on all measurement nights, and family groups of babblers roosted together in the same nest on all measurement nights. Roost nest fidelity did vary however; for example, one group roosted in the same nest for all measurement nights while another made use of at least six different roost nests over a period of 27 calendar nights. Babblers arrived at and departed roost nests as family groups (see Figure 2.2). Where evening roost arrival times were obtained ($N = 4$, $n = 10$), babbler groups went to roost $0.60 \pm 1.52 \text{ min}$ after sunset (range of -4 to 8 min after sunset), but there was a difference between years (Mann-Whitney $U_{7,3} = 21$, $P = 0.017$), where birds in territories 1 and 2, observed in 2012, roosted earlier (mean = $-2.29 \pm 0.57 \text{ min}$ after sunset; range -4 to 0 min after sunset, $n = 7$) than birds in territories 3 and 4, monitored in 2013 (mean $7.33 \pm 0.33 \text{ min}$ after sunset; range 7 to 8 min after sunset, $n = 3$).

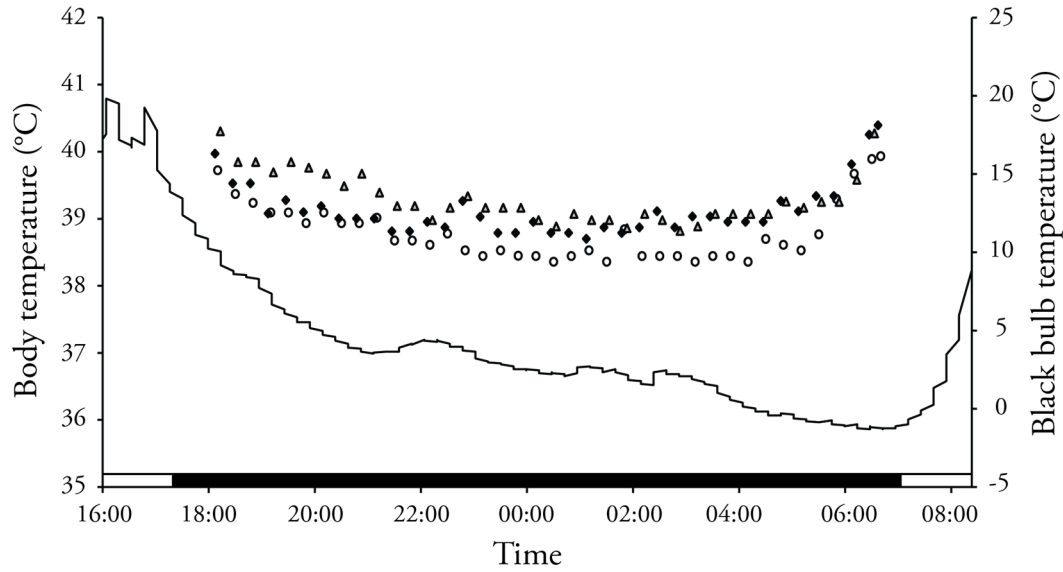


Figure 2.2: Typical overnight field body temperature (°C) trace for three babblers (triangles, diamonds and circles) in the same nest on 17th August 2012. Black bulb temperature (°C; solid line) is shown on the secondary axis. The dark bar indicates the period between sunset and sunrise.

Minimum T_{bb} for the measurement periods ranged by over 17 °C, from the coldest night of -2.6 °C to the warmest of 14.5 °C (Figure 2.3). Mean minimum overnight $T_{b,field}$ was $38.5 \text{ °C} \pm 0.04 \text{ °C}$ (range 37.4 – 39.6 °C), but did not vary with overnight minimum T_{bb} ($T_{bb,min}$; $F_{1,32} = 2.66$, $P = 0.112$). Random effects of individual (0.081) and date (0.005) accounted for 48.4% of the observed variance in the linear mixed model, with family group (0.000) not contributing (residual variance = 0.091).

Overnight conditions did influence the body temperature of babblers as they departed their roost nests ($T_{b,depart}$) in the morning. As T_b increased quickly prior to roost departure, only data from the last transmitter-carrying bird to leave from each nest each night was included ($n = 42$). While individual as a random effect (variance = 0.025) had some effect upon the model, day of year (0.000) and territory (0.000) did not (residual variance = 0.105). $T_{b,depart}$ decreased with decreasing $T_{bb,min}$ ($T_{bb,min}$; $F_{1,29.7} = 5.24$, $P = 0.029$; Figure 2.3B). Babbler $T_{b,depart}$ was predicted by the equation: $T_{b,depart} = 40.23 + 0.033 * T_{bb,min}$.

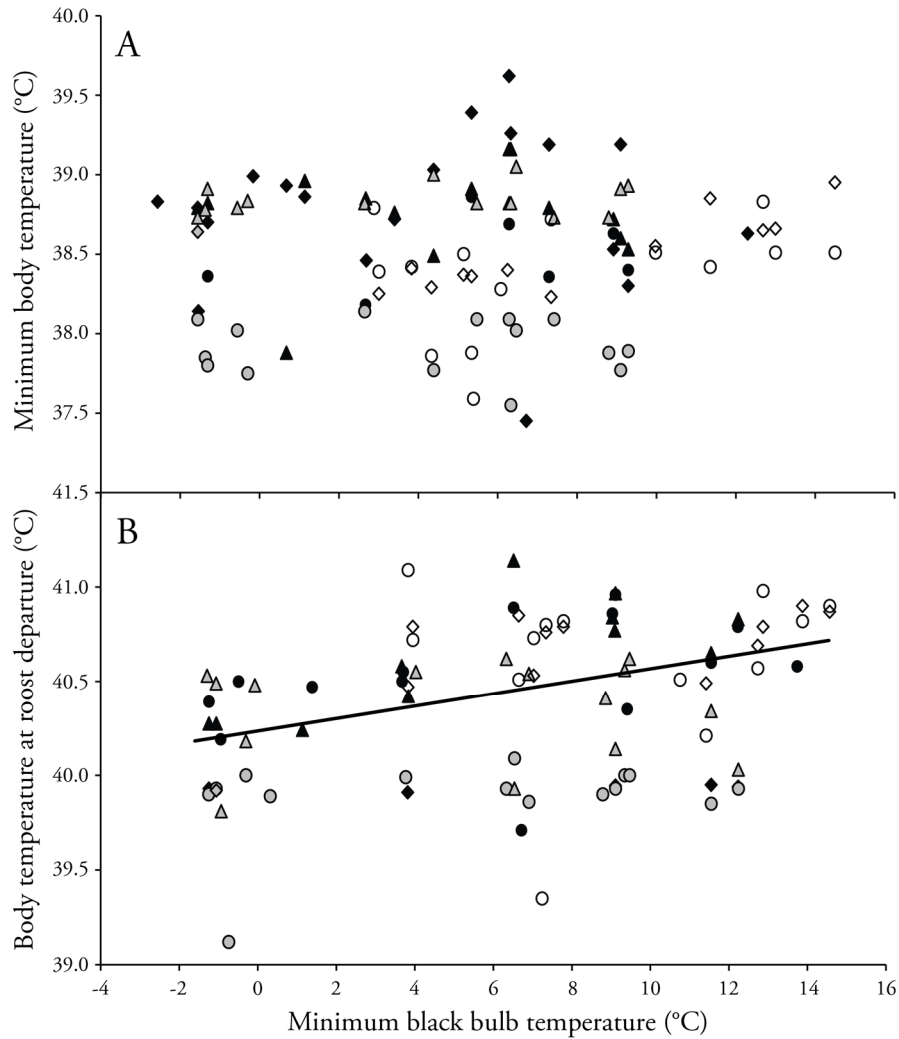


Figure 2.3: A) Minimum overnight field body temperature of babblers and minimum overnight black bulb temperature ($N = 8$, $n = 97$) and B) body temperature of babblers as they depart their roost nests in the morning against black bulb temperature at the time of departure ($N = 8$; $n = 85$). Similarly shaded symbols show individuals from the same family group (territory 1 = black; territory 2 = grey and territory 3 = white), with each group member a different symbol. The black line shows the relationship between body temperature at time of roost departure and overnight minimum black bulb temperature.

$T_{bb,min}$ did not affect roost departure time ($F_{1,31.9} = 0.000$, $P = 0.999$). Weather factors such as early morning rainfall, wind strength and wind direction, included as random effects, did not explain any variance in roost departure times (variance = 0.000 for each). Likewise variance of territory was 0.000, but time of year (6.01) and individual (4.59) both contributed (residual variance = 3.32; Figure 2.4).

For arrival body temperature ($T_{b,arrive}$), minimum $T_{b,field}$ and $T_{b,depart}$ data obtained for the same birds for the same measurement nights ($N = 4$, $n = 14$), a mixed linear model

indicated differences in these babbler $T_{b,field}$ values ($F_{2,31.01} = 346$, $P < 0.001$). $T_{b,arrive}$ and $T_{b,depart}$ were not different ($t_{21} = 0.320$, $P = 0.751$), but minimum $T_{b,field}$ was lower ($t_{21} = 23.3$, $P < 0.001$).

Where $T_{b,depart}$ data were recorded ($N = 8$, $n = 85$), factors contributing to the difference between minimum $T_{b,field}$ and $T_{b,depart}$ were analysed. Mean T_b difference was 1.90 ± 0.04 °C ($n = 85$ nights, range $1.03 - 2.85$ °C). Random effects of individual (31.4%), family group (23.9%) and date (14.9%) together accounted for 70.3% of the variance in the linear mixed model. Neither $T_{bb,min}$ nor $T_{bb,depart}$ had an effect on this T_b difference ($T_{bb,min}$ $F_{1,27.6} = 0.031$, $P = 0.853$; $T_{bb,depart}$ $F_{1,25.0} = 0.044$, $P = 0.835$).

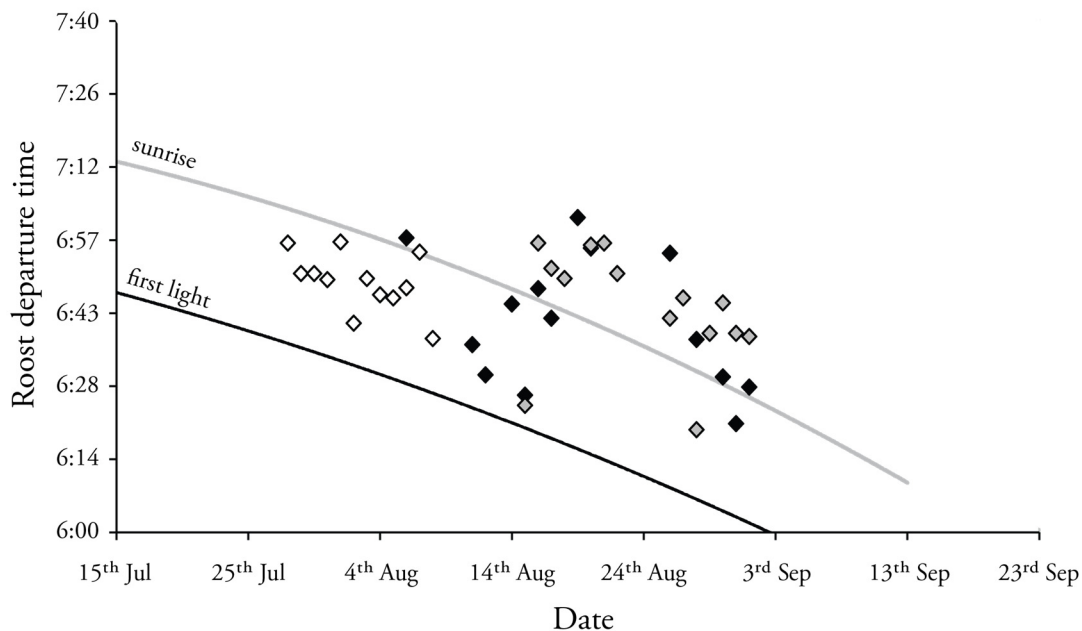


Figure 2.4: The timing of first light (black line) and sunrise (grey line) in relation to the roost departure time of different babbler groups in winter (each family group is a different symbol).

Roost temperature

Of the nine roosts with loggers, only three were occupied at any time during the measurement period. Thermal data were collected for a total of 40 occupied roost nest nights, from a total of 316 roost nest nights, between June and September 2013. Occupied versus unoccupied nights could easily be distinguished, as unoccupied roost nests were the same as ambient temperature (Figure 2.5).

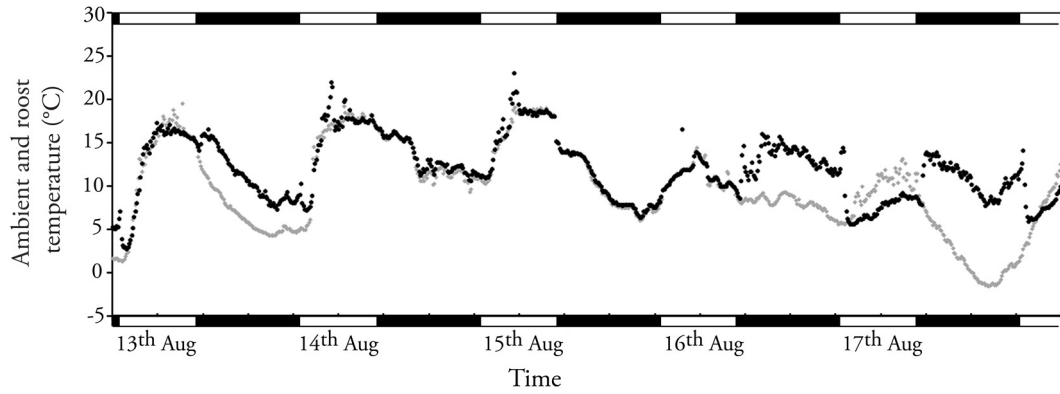


Figure 2.5: Typical black bulb temperature (T_{bb} ; °C; grey) and babbler roost nest temperature (°C; black) trace for five consecutive nights, August 13–18th, 2013. Grey bars mark sunset to sunrise. Unoccupied roost nest nights (2 and 3) can be easily identified, as roost nest temperature does not differ from ambient temperature. Occupied roost nests (1, 4 and 5) maintained a temperature differential between internal and external ambient temperature for the duration of the night.

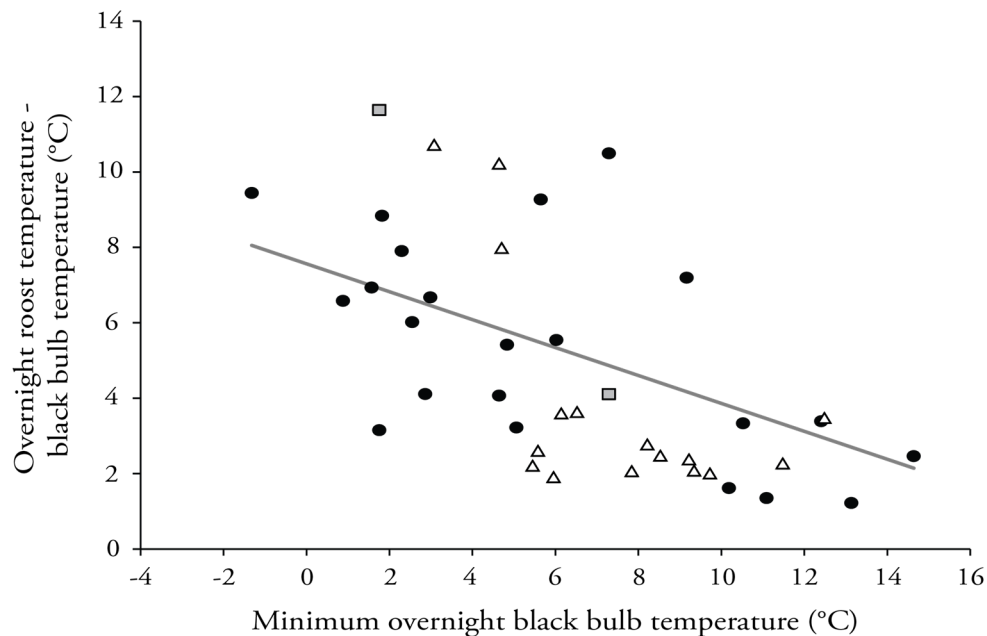


Figure 2.6: The relationship between minimum overnight black bulb temperature and the differential between mean overnight babbler roost nest temperature to black bulb temperature. The three different symbols represent the three different nests, and each point is a night's measurement. The least squares regression line (see text) is shown in grey.

The internal temperature of an occupied roost (T_{roost}) was maintained at a relatively constant increment above T_{bb} for the duration of each measurement night. This differential ($T_{roost} - T_{bb}$) did vary with overnight $T_{bb,min}$ ($F_{1,37.9} = 21.0$, $P < 0.001$), with a greater differential on colder nights than warmer nights (Figure 2.6). There was no variance between the differentials obtained from the three occupied nests, as the random

effect of nest in the linear mixed model contributed 0% to variance in the model. The relationship between mean overnight ($T_{\text{roost}} - T_{\text{bb}}$) and $T_{\text{bb,min}}$ ($F_{1,38} = 24.1$, $p < 0.001$, $r^2 = 0.388$) was: $\text{mean } (T_{\text{roost}} - T_{\text{bb}}) = 8.10 - 0.49 T_{\text{bb,min}}$.

Under controlled laboratory conditions, a roost nest had a lower cooling constant ($k_n = 0.388 \text{ h}^{-1}$, $n = 2$) compared to ambient conditions ($k_c = 2.15 \text{ h}^{-1}$, $n = 2$; $F_{3,5640} = 2.04 \times 10^5$; $P < 0.001$). The cooling constant equates to a mean roost nest thermal conductance of $1.62 \text{ J h}^{-1} \text{ g}^{-1} \text{ }^{\circ}\text{C}^{-1}$.

Roost nest characteristics

Of the 59 babbler roost nests found at Dryandra Woodland during the 2012 and 2013 winter seasons, 26 were known via observation and/or radio-tracking to be intact, active nests for either or both periods, 22 were old nests, and the status of the remaining 11 nests could not be determined. There was no preference for host plant selection, with ratio of canopy to midstorey trees used for nesting is similar to the ratio of occurrence of these trees in the babblers' habitat ($\chi^2_1 = 0.429$, $P = 0.513$). Babblers constructed roost nests in *Eucalyptus wandoo*, *E. accendens* (overstorey), *Allocasuarina huegliana*, *Acacia acuminata*, *Banksia ilicifolia* (midstorey), sapling *Corymbia callophylla*, and the understorey species *Gastrolobium crassifolia*. It is possible that understorey nests may be underrepresented due to reduced detectability. Babblers selectively nested in trees that formed part of stands rather than solitary trees, as mean tree density surrounding nest trees was $835 \pm 149 \text{ trees ha}^{-1}$, compared with habitat means for Dryandra of $246 \pm 11 \text{ trees ha}^{-1}$ (Luck 2002; $t_{58} = 3.933$ $P < 0.001$).

The aspect of the ground on which nest trees stood was not uniformly distributed ($Z_{53} = 15.1$, $P < 0.001$), being east northeast with a mean of $69.5 \pm 7.60^{\circ}$, but the slope of the ground surrounding roost nest trees was very gentle ($1.25 \pm 0.06^{\circ}$). Nests were not uniformly distributed by height in their host trees ($D_{59} = 0.223$; $P = 0.005$), but were built preferentially in the top third, with a mean nest height of $73.0 \pm 1.84\%$ of total host plant height. Mean height of nests above the ground was 5.91 m ($\pm 0.34 \text{ m}$, range $1.4 - 14.4$

m). For the 26 nests where entrance direction could be determined, there was no preference for roost nest entrance direction (Rayleigh's $Z_{26} = 0.431$, $P = 0.200$).

Field behaviour

A total of 161 observation sessions yielded 5526 single point behaviour records for White-browed Babblers (= 23.03 bird observation hours) over 40 days during winter of 2012 and 2013. Behaviour of individuals and groups of up to 10 babblers were recorded, lasting from a single point observation to 15 minutes of continuous records, at a range of T_{as} (-3.44 to 26.76 °C) and from pre-dawn until dusk. It is estimated that behaviour of at least 33 individual babblers from at least 7 different territories contributed to these observations.

Table 2.3: Effect of predictor variables on proportion of time babblers spent engaged in core activities, as determined by GAMMs, with test values derived from χ^2 -tests and corresponding effective degrees of freedom (edf) shown. Only variables that resulted in lower AIC values (listed in bold) were included in the final model for each activity.

	Model	χ^2 value	edf	p-value
Foraging				
T_{bb}	non-linear	14.2	6.79	0.043
$T_{bb,min}$	linear	0.02	1	0.88
Time of day	non-linear	60.6	8.04	<0.001
Day of Year	linear	0.43	1	0.51
Moving				
T_{bb}	non-linear	4.14	2.9	0.23
$T_{bb,min}$	linear	5.90	1	0.015
Time of day	linear	0.33	1	0.57
Day of Year	linear	1.53	1	0.22
Resting Alert				
T_{bb}	linear	0.28	1	0.59
$T_{bb,min}$	linear	0.02	1	0.88
Time of day	non-linear	87.3	8.5	<0.001
Day of Year	linear	1.78	1	0.18
Maintenance				
T_{bb}	non-linear	39.9	8.5	<0.001
$T_{bb,min}$	linear	5.59	1	0.018
Time of day	non-linear	7.48	3.1	0.047
Day of year	linear	0.047	1	0.828

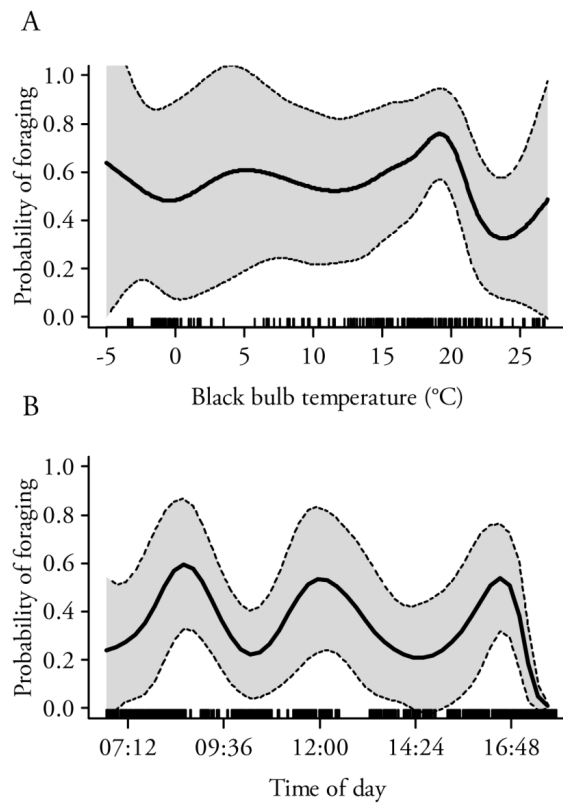


Figure 2.7: GAMM trend plots for effect of black bulb temperature (A) and time of day (B) on probability of a babbler foraging, using mean time of day (12:00pm); and mean black bulb temperature (13 °C). Plots include overall trend lines (solid lines) with 95% confidence intervals (dashed lines). Rug plots show distribution of observations.

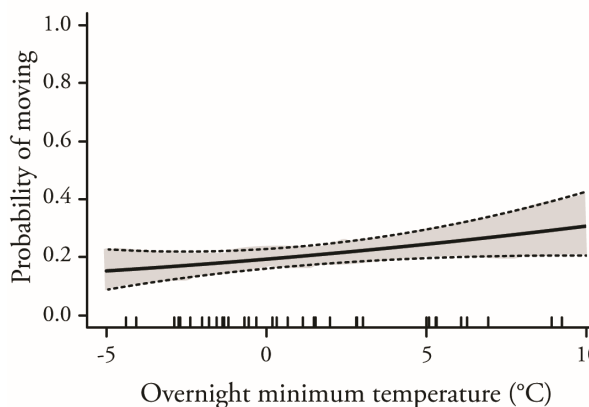


Figure 2.8: GAMM trend plot for effect of overnight minimum black bulb temperature on the probability of a babbler moving. Plot includes overall trend lines (solid line) with 95% confidence intervals (dashed lines), and rug plot shows distribution of observations.

Activity

The four most frequently observed babbler activities were foraging, locomotion, resting alert, and maintenance (such as bill stropping and preening), together accounting for over 91% of babbler day time. Other activities occurred in proportions too small to be suitable for analysis. Babblers were never observed drinking or bathing in standing water (puddles), but did routinely dust-bathe prior to going to roost (a technique to discourage ectoparasites; Poiani 1992; Clayton *et al.* 2010). The effects of time of day, day of year, T_{bb} and $T_{bb,min}$ on proportion of time that babblers dedicated to these four core activities observed were tested individually (Table 2.3).

Foraging accounted for 45.7% of babbler observations, and was influenced by T_{bb} and time of day. It was near constant for the typical ranges of T_{bb} (0 – 20 °C) experienced, but decreased at high T_{bb} (>20 °C; Figure 2.7A). Time of day had a trimodal effect, with distinct peaks in foraging

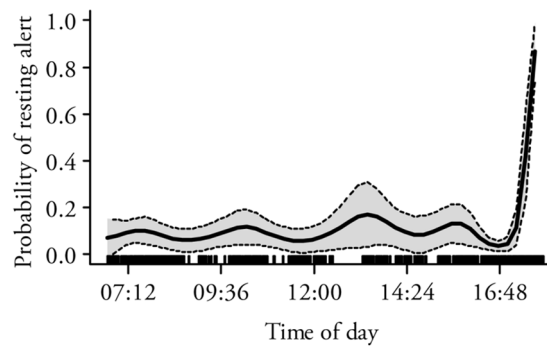


Figure 2.9: GAMM trend plot for effect of time of day on probability of babbler resting alert. Plot includes overall trend lines (solid line) with 95% confidence intervals (dashed lines), and rug plot shows distribution of observations.

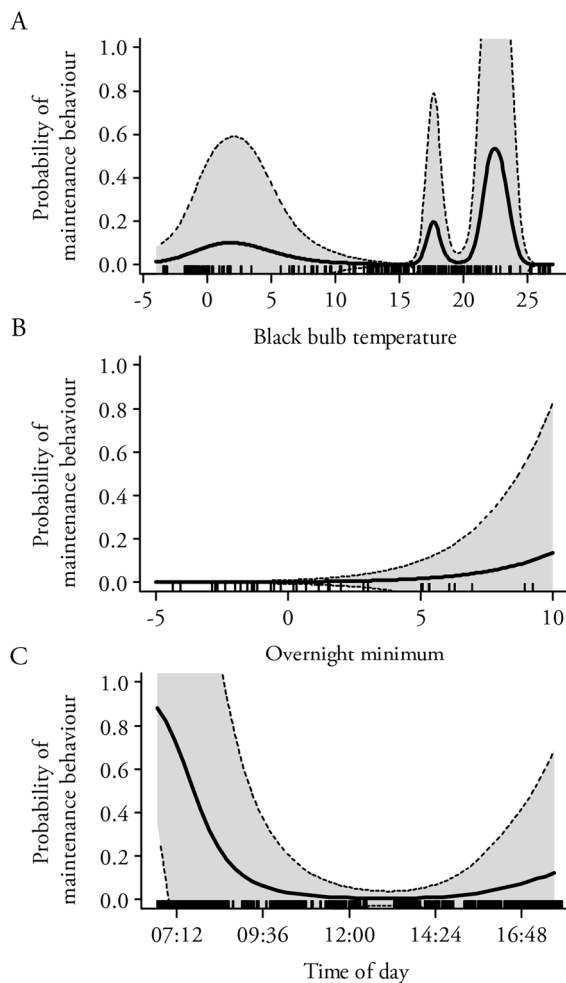


Figure 2.10: GAMM trend plots for effect of black bulb temperature (A), overnight minimum black bulb temperature (B) and time of day (C) on probability of a babbler engaging in maintenance behaviour. Generated using T_{bb} (5 °C), overnight minimum T_{bb} (8 °C) and time of day (9:36am). Plots include overall trend lines (solid lines) with 95% confidence intervals (dashed lines), and rug plots show distribution of observations.

activity at mid-morning, midday and late afternoon (Figure 2.7B). Time spent foraging reduced markedly near dusk.

On average, probability of babblers moving was 0.2 during the day, both in flight and hopping on the ground. This proportion of time did not vary with T_{bb} , time of day or day of year, but did show a positive linear increase with increasing $T_{bb,min}$ (Figure 2.8). Proportion of time spent in motion increased from ~0.18 when $T_{bb,min}$ was -5 °C to ~0.30 at 10 °C.

Babblers were resting alert during 13.4% of observations. Only time of day affected the proportion of time that babblers were resting alert (Figure 2.9). Proportion of time spent resting alert fluctuated around 0.20 throughout the day before increasing sharply prior to roosting.

On average, maintenance behaviours accounted for 12.6% of babbler daytime activities. Current T_{bb} , $T_{bb,min}$, and time of day all influenced babbler maintenance activity, with maintenance activities varying with T_{bb} (Figure 2.10A) but more likely at the beginning and end of the day (Figure 2.10B). Maintenance occurred at

slightly greater (and more variable) proportions after nights of higher $T_{bb,min}$ (Figure 2.10C).

Substrate

Use of the different height strata by babblers in their habitat varied with black bulb temperature, time of day and day of year (Table 2.4). While $T_{bb,min}$ was included in the initial models for all four height strata (ground, understorey, mid-canopy and upper canopy), it was not significant in any of the final models.

Babblers were on the ground (bare ground, herb fields or amongst coarse woody debris and leaf litter) during 44.5% of observations. Black bulb temperature and time of day both affected babbler time on ground but the pattern was complex (Figure 2.11). Babblers were observed on the ground throughout the range of T_{bb} conditions recorded and

Table 2.4: The effect of predictor variables on proportion of time babblers spent in different height strata of their habitat, as determined by GAMMs, with test values derived from χ^2 -tests, and corresponding effective degrees of freedom (edf) values shown. Only variables that resulted in lower AIC values (listed in bold) were included in the final model for each strata.

	Model	χ^2 value	edf	p-value
Ground				
T_{bb}	non-linear	86.7	12.0	<0.001
$T_{bb,min}$	non-linear	6.10	2.4	0.067
Time of day	non-linear	202	18.2	<0.001
Day of year	non-linear	2.65	2.2	0.29
Understorey				
T_{bb}	non-linear	8.02	5.2	0.173
$T_{bb,min}$	non-linear	2.12	1.8	0.298
Time of day	non-linear	17.7	6.0	0.006
Day of year	linear	5.17	1	0.023
Mid-canopy				
T_{bb}	linear	5.36	1	0.021
$T_{bb,min}$	linear	0.084	1	0.772
Time of day	linear	10.8	1	0.001
Day of year	linear	1.01	1	0.315
Upper-canopy				
T_{bb}	non-linear	31	6.2	<0.001
$T_{bb,min}$	linear	1.12	1	0.289
Time of day	non-linear	286	16.7	<0.001
Day of year	non-linear	15.0	2.8	0.002

throughout the day, but appear to move discretely between being on the ground and being in other strata.

Babblers used understorey habitat elements (logs, stumps, understorey shrubs, low trunks/branches of canopy trees) only 5.4% of the time. Babblers were more likely to be using low vegetation strata in the afternoon. Day of year also influenced time spent in the understorey with the proportion dropping later in the year.

Babblers were observed in medium-height habitat elements (mid-storey vegetation and mid-storey elements of canopy trees) in 34.2% of observations. Black bulb temperature and time of day had opposing influences on babbler mid-storey use, with observations in

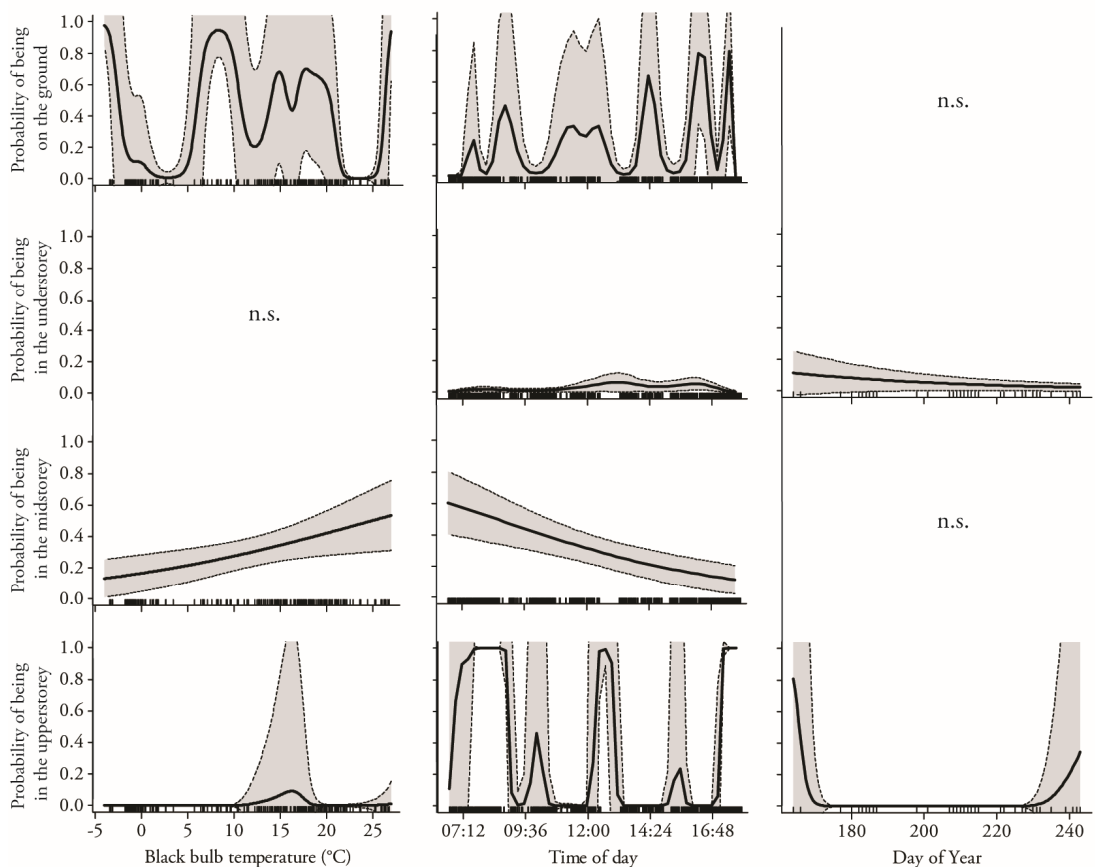


Figure 2.11: GAMM trend plots for effect of black bulb temperature (°C), time of day and day of year on probability of a babbler being in different vegetation height strata. Each row presents the output from a different model; plots could not be generated for non-significant variables, so these are omitted. Plots were generated using mean black bulb temperature (13 °C), mean time of day (12:00pm) and mean day of year (215; August 3rd). Plots include overall trend lines (solid lines) with 95% confidence intervals (dashed lines). Rug plots show distribution of observations.

the midstorey decreasing with increasing T_{bb} , but increasing throughout the course of the day (Figure 2.11).

Lastly, babblers were observed in the upper canopy 15.9% of the time. Black bulb temperature, time of day, and day of year all influenced when babblers were in the upper canopy. Babblers were observed in the upper canopy in the early morning and prior to roosting in the evening. Day of year data suggests that time spent in the canopy is greater in early winter and early spring than in mid- and late winter (Figure 2.11).

Location

The potential for babblers to save energy by increasing their exposure to solar radiation was examined by measuring how time spent in the sun, shade or patchy light varied with the predictor variables of T_{bb} , time of day, and day of year (Table 2.5). Observations made at twilight or when it was misty or overcast were excluded from this dataset (to only examine periods when babblers had access to all three potential light levels), yielding 2887 observations (12.0 bird hours). Babblers divided their time evenly between sun, patchy and fully-shaded locations, with mean proportions of 28.5%, 38.5% and 32.9% respectively.

Table 2.5: The effect of predictor variables on proportion of time babblers spent exposed to varying levels of solar radiation as determined by GAMMs, with test values derived from χ^2 -tests, and corresponding effective degrees of freedom (edf) values shown. Only variables that resulted in lower AIC values (listed in bold) were included in the final model for each location.

	Model	χ^2 value	edf	p-value
Sun				
T_{bb}	non-linear	3.83	2.7	0.228
Time of day	non-linear	19.7	4.7	0.001
Day of year	non-linear	6.91	3.1	0.024
Patchy light				
T_{bb}	linear	6.24	1	0.012
Time of day	non-linear	87.5	8.4	<0.001
Day of year	linear	6.53	1	0.011
Shade				
T_{bb}	linear	11.5	1	<0.001
Time of day	non-linear	128	8.6	<0.001
Day of year	linear	1.13	1	0.289

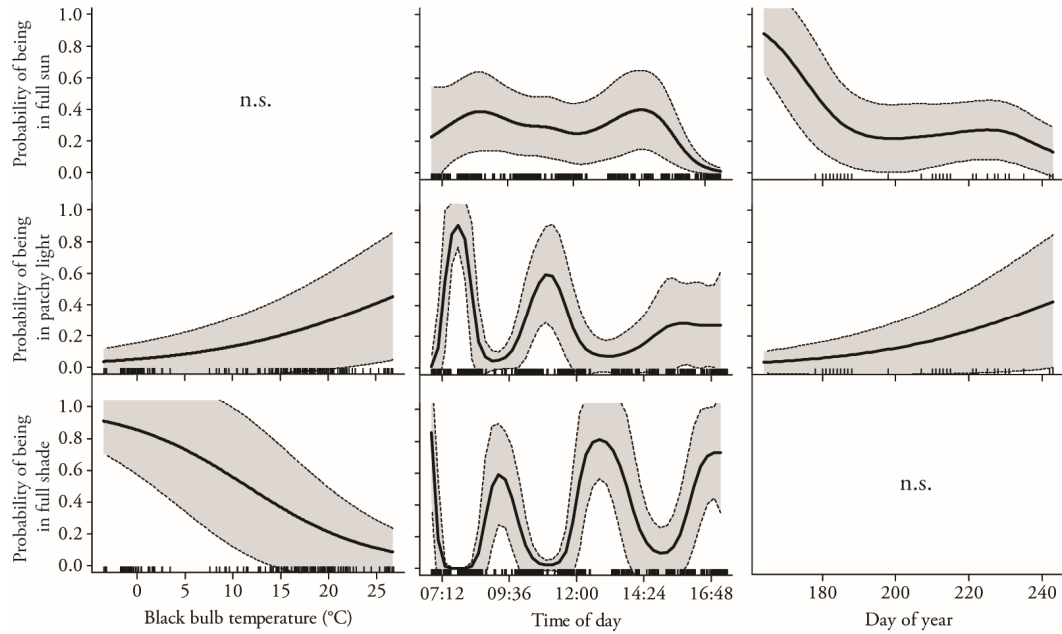


Figure 2.12: GAMM trend plots for effect of black bulb temperature on probability of a babbler being in full sun, patchy light and in full shade in response to black bulb temperature (°C), Time of day and day of year. Each row presents the output from a different model; plots could not be generated for non-significant variables, so these are omitted. Plots were generated using mean black bulb temperature (13 °C), mean time of day (12:00pm), and mean day of year (215; August 3rd). Plots include overall trend lines (solid lines) with 95% confidence intervals (dashed lines). Rug plots show distribution of observations.

Both time of day and day of year influenced the proportion of time babblers were observed in full sun, but not T_{bb} . Babblers were observed in sunlit locations at or near a constant level throughout the day until late afternoon, when proportions decreased (Figure 2.12). The seasonal effect shows sunlit locations more in early winter, with proportions dropping to a low, constant level for mid- to late winter and into spring.

Time in dappled light locations varied with T_{bb} , time of day and day of year. Babblers were in patchy light more as T_{bb} increased (Figure 2.12). The temporal pattern was more complex, with proportions fluctuating in the morning, but steadying at an intermediate level from early afternoon onwards (Figure 2.12). Proportion of time spent in patchy light increased steadily throughout the measurement period.

Time babblers spent in fully-shaded locations varied with both T_{bb} and time of day. Probability of babblers being in the shade dropped as T_{bb} increased (Figure 2.12). The

effect of time of day on time in shade was complex, with proportions fluctuating throughout the day however the peaks of time in shade match well with the troughs of time in patchy light, and vice versa (Figure 2.12).

Laboratory respirometry

In the laboratory, babbler T_b varied with T_a (GLMM; $F_{5,32.9} = 7.13$, $P < 0.001$; Figure 2.13A). At thermoneutrality ($T_a = 30^\circ\text{C}$) T_b was 38.6°C , different from T_b at $T_a = 10^\circ\text{C}$ (37.6°C) and 20°C (37.9°C ; $t_{36} > -2.20$; $P < 0.034$). Thermolability of babblers was $0.05 \pm 0.02^\circ\text{C } ^\circ\text{C}^{-1}$, and the relationship between T_b and T_a is described by the linear function $T_b = 36.67 + 0.075(T_a)$. Individual as a random effect (variance = 0.004) only accounted for a small percentage (0.91%) of the observed variation in the linear mixed model (residual variance = 0.418).

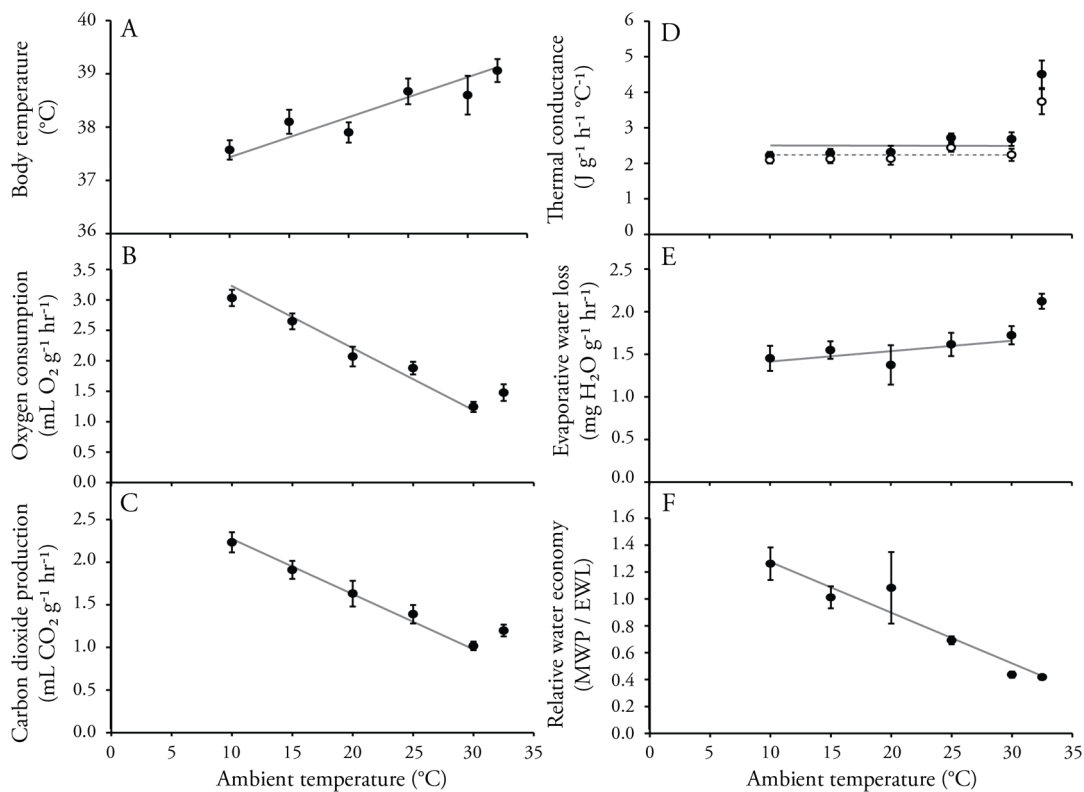


Figure 2.13: A) Body temperature, B) oxygen consumption, C) carbon dioxide production, D) wet (black symbols) and dry (white symbols) thermal conductance, E) evaporative water loss and F) relative water economy of babblers at a range of ambient temperatures. Symbols show mean \pm 1 standard error, grey lines show linear relationships. Body temperature is for $N = 8$ individual per temperature, and $N = 7$ birds for the other variables.

Repeated Measures ANOVA indicated that $\dot{V}O_2$ differed between individual babblers ($F_{6,35} = 866$, $P < 0.001$) and was influenced by T_a ($F_{5,2} = 29.9$, $P = 0.033$), decreasing from $3.03 \pm 0.134 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $T_a = 10^\circ \text{C}$ to a minimum value of $1.24 \pm 0.084 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $T_a = 30^\circ \text{C}$, before rising again at 32.5°C (Figure 2.13B). Polynomial *a priori* contrasts support this pattern, with linear ($P < 0.001$), quadratic ($P = 0.007$) and cubic polynomials ($P = 0.011$) significant when all six T_a s are included in the model, but only the linear contrast remains ($P < 0.001$) when $T_a = 32.5^\circ \text{C}$ is removed. The relationship between $\dot{V}O_2$ and T_a below thermoneutrality was $\dot{V}O_2 = 4.19 - 0.099 T_a$. I interpret the minimal value of $\dot{V}O_2$ at $T_a = 30^\circ \text{C}$ of $1.24 \pm 0.084 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ as basal MR (BMR).

$\dot{V}CO_2$ also differed between babblers ($F_{6,35} = 623$, $P < 0.001$), as well as with T_a ($F_{5,2} = 19.9$, $P = 0.049$). It was highest at $T_a = 10^\circ \text{C}$ ($2.23 \pm 0.118 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$), decreasing to a minimum when $T_a = 30^\circ \text{C}$ ($1.02 \pm 0.050 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$), before rising at $T_a = 32.5^\circ \text{C}$ ($1.20 \pm 0.069 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$). Polynomial *a priori* contrasts indicate both linear ($P < 0.001$) and cubic relationships ($P = 0.012$) when $T_a = 32.5^\circ \text{C}$ data are included, but only the linear contrast remains ($P < 0.001$) when $T_a = 32.5^\circ \text{C}$ is removed from the model. The relationship between $\dot{V}CO_2$ and T_a below thermoneutrality was $\dot{V}CO_2 = 2.89 - 0.063 T_a$. At thermoneutrality, $\dot{V}CO_2$ is $1.02 \pm 0.050 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ and the RER is 0.82.

Wet and dry thermal conductance differed between individual babblers ($F_{6,35} = 1217$, $P < 0.001$ and $F_{6,35} = 1209$, $P < 0.001$ respectively). Repeated measures ANOVA suggested no overall effect of T_a on C_{wet} or C_{dry} ($F_{5,2} = 3.74$, $P = 0.224$ and $F_{5,2} = 3.74$, $P = 0.225$ respectively). However reverse Helmert *a priori* contrasts confirm the visual pattern (Figure 2.13D) of C_{wet} and C_{dry} varying little below thermoneutrality, before 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). C_{wet} at thermoneutrality was $2.68 \pm 0.192 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ \text{C}^{-1}$ and C_{dry} was $2.24 \pm 0.171 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ \text{C}^{-1}$.

EWL differed significantly between individual birds ($F_{6,35} = 199$, $P < 0.001$). EWL increased slightly with increasing T_a below thermoneutrality, before increasing more rapidly at $T_a = 32.5^\circ \text{C}$ (Figure 2.13E). Repeated measures ANOVA indicated no overall

effect of T_a on EWL ($F_{5,2} = 15.5$, $P = 0.062$) but polynomial *a priori* contrasts indicate a linear ($P = 0.005$) and quadratic pattern ($P = 0.032$) when $T_a = 32.5$ °C data were included in the model, and only a linear contrast ($P = 0.011$) when $T_a = 32.5$ °C was removed. This indicated that EWL does increase slightly with T_a , then increases markedly at $T_a = 32.5$ °C.

Relative water economy differed between individual birds ($F_{6,35} = 115$, $P < 0.001$) and also varied with T_a ($F_{5,2} = 180$, $P = 0.006$), decreasing with increasing ambient T_a . Polynomial *a priori* contrasts show a linear relationship ($P < 0.001$). The linear relationship ($r^2 = 0.515$) between RWE and T_a below thermoneutrality is described by the equation $RWE = 1.681 - 0.039(T_a)$. The point of relative water economy (pRWE) is calculated to be 17.5°C.

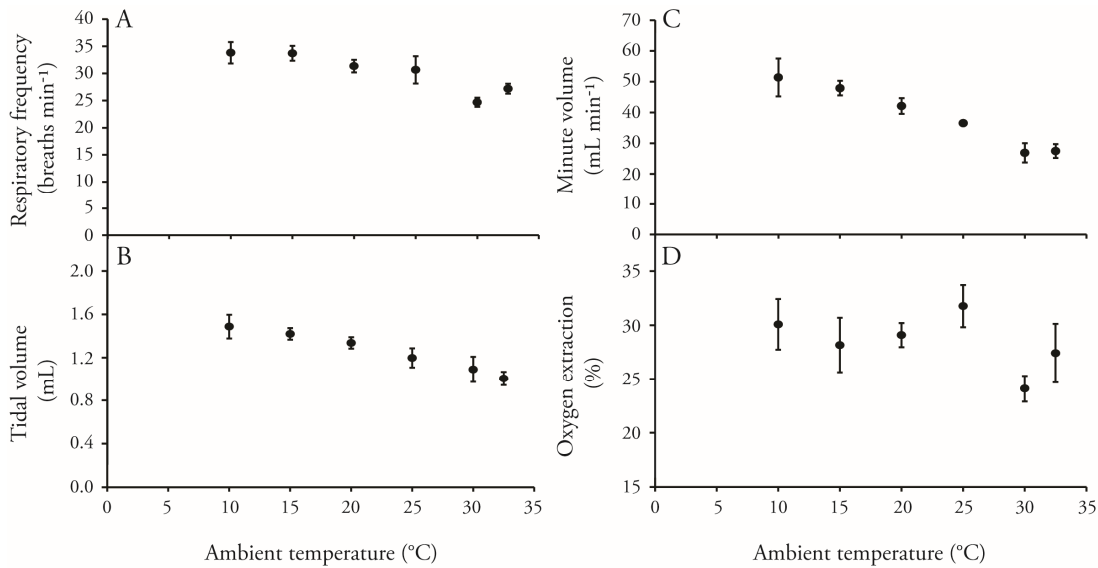


Figure 2.14: A) Respiratory frequency, B) tidal volume, C) minute volume and D) oxygen extraction for babblers at a range of ambient temperatures. Symbols show mean \pm standard error.

GLMM indicated that ambient temperature influenced f_R ($F_{5, 27.2} = 12.9$, $P < 0.001$), 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 EO_2 ($F_{5, 28.7} = 1.37$, $P = 0.265$; Figure 2.14). The f_R at thermoneutrality differed from all other T_a s ($t_{32} > 2.18$; $P < 0.036$). V_T and V_I were both different from thermoneutrality only at 10, 15 and 20 °C ($t_{39} > 2.26$; $P < 0.03$ and $t_{30} > 3.40$; $P < 0.002$ respectively). As a random effect, individual contributed substantially as a component of variance for f_R (4.95, residual =

6.51), but in much smaller proportions for V_T (0.000, residual = 0.048), V_I (7.80, residual = 80.07) and EO_2 (1.23, residual = 24.03) models.

Huddling respirometry

There was no statistical support for T_a having an impact on T_b of huddling babblers ($F_{2,48} = 1.40$, $P = 0.257$). However ANOVA with T_a as a covariate indicated both group size ($F_{2,49} = 25.2$, $P < 0.001$) and T_a ($F_{1,49} = 114.7$, $P < 0.001$) influenced babbler metabolic rate (Figure 2.15). Simple *a priori* contrasts indicated $\dot{V}O_2$ for solitary birds was 0.781 ± 0.125 mL O_2 g^{-1} h^{-1} higher than that for huddling birds ($F_{2,49} = 25.2$; $P < 0.001$), but pairwise comparison shows no difference between pairs and groups of three birds at these sample sizes ($P \geq 0.999$). Mean $\dot{V}O_2$ decreases with increasing T_a , with mean $\dot{V}O_2$ for huddling pairs of birds at 20 °C of 1.48 ± 0.195 mL O_2 g^{-1} h^{-1} , 1.71 ± 0.237 mL O_2 g^{-1} h^{-1} at $T_a = 15$ °C, and 2.25 ± 0.176 mL O_2 g^{-1} h^{-1} at $T_a = 10$ °C. This equates to mean huddling MRs of 71.8%, 64.6% and 74.1% of non-huddling MRs at those temperatures respectively. There was no statistical support for huddling having an impact on EWL ($F_{2,49} = 1.26$, $P = 0.292$).

Analysis of covariance indicated the intercept ($F_{1,43} = 42.9$; $P < 0.001$) but not the slope ($F_{1,43} = 0.171$; $P = 0.681$) between $\dot{V}O_2$ and T_a below thermoneutrality differed between pairs and solitary roosting birds. The linear relationship between $\dot{V}O_2$ and T_a for pairs of huddling babblers can be described by the equation: $\dot{V}O_2 = 2.96 - 0.076 (T_a)$. At 10, 15 and 20 °C, huddling babblers had the same MR as individual babblers at 19.6, 25.0 and 27.3 °C respectively, a mean effective temperature buffer of 8.98 °C above actual T_a .

As expected, similar effects of huddling were observed for $\dot{V}CO_2$ as for $\dot{V}O_2$. There was a relationship between roosting group size, T_a and $\dot{V}CO_2$ ($F_{3,49} = 33.3$, $P < 0.001$). Both group size and T_a had an effect (group size $F_{2,49} = 9.70$, $P < 0.001$; T_a $F_{1,49} = 99.6$, $P < 0.001$), and simple *a priori* contrasts indicate huddling birds have lower $\dot{V}CO_2$ than solitary birds (contrast estimate for pairs 0.351 ± 0.093 mL CO_2 g^{-1} h^{-1} less than solitary birds, $P < 0.001$; threes 0.401 ± 0.124 mL CO_2 g^{-1} h^{-1} , $P = 0.002$), but pairwise comparisons find

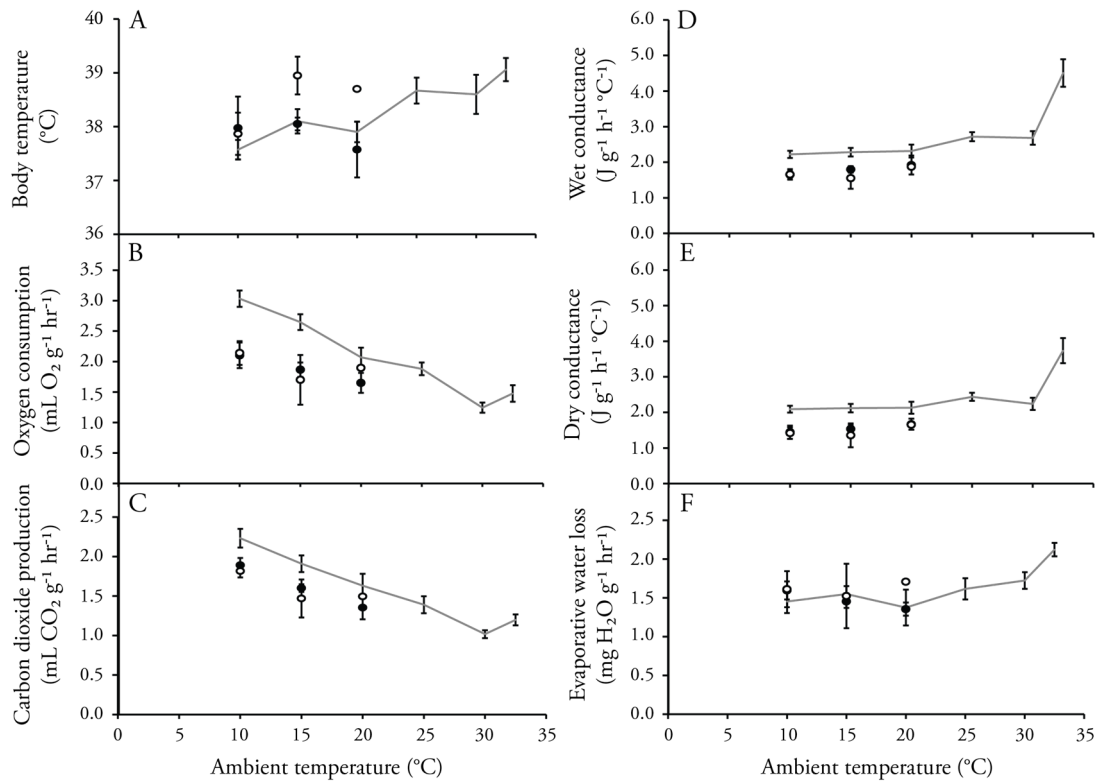


Figure 2.15: A) Body temperature, B) oxygen consumption, C) carbon dioxide production, D) wet thermal conductance, E) dry thermal conductance and F) evaporative water loss of pairs (black symbols) and groups of three (white symbols) huddling babblers. For comparison, grey lines show mean values obtained for individuals (from Figure 2.13). Data are presented as mean \pm standard error.

no difference between pairs and groups of three birds ($P = 1.000$). Mean $\dot{V}\text{CO}_2$ for huddling pairs of birds at 20 °C was $1.28 \pm 0.119 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$, $1.49 \pm 0.097 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $T_a = 15^\circ\text{C}$ and $1.96 \pm 0.081 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $T_a = 10^\circ\text{C}$. This equates to huddling MRs 78.4%, 78.3% and 87.8% of non-huddling MRs at those temperatures respectively.

With T_a as a covariate, ANOVA indicates differences in thermal conductance with roosting group size for both C_{wet} ($F_{3,49} = 19.4$, $P < 0.001$) and C_{dry} ($F_{3,49} = 19.3$, $P < 0.001$). In both instances conductance was lower the larger roosting group size (C_{wet} $F_{2,49} = 13.9$, $P < 0.001$; C_{dry} $F_{2,49} = 19.9$, $P < 0.001$). Simple *a priori* contrasts indicate individual birds have a higher conductance than huddling birds ($C_{\text{wet}} > 0.622 \pm 0.133$, $P < 0.001$; $C_{\text{dry}} > 0.674 \pm 0.122$, $P < 0.001$). There was no difference in conductance between pairs and groups of three babblers (C_{wet} 0.005 ± 0.189 , $P = 1.000$; C_{dry} 0.047 ± 0.174 , $P = 1.000$). Mean C_{wet} for pairs of huddling birds was $1.69 \pm 0.100 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ and mean C_{dry} $1.47 \pm$

$0.093 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^{\circ}\text{C}^{-1}$. This equates to a huddling C_{wet} and C_{dry} of 74.6% and 69.8% of solitary roosting values respectively. Group size only varied with T_a for C_{wet} ($F_{1,49} = 9.13$, $P = 0.004$), not C_{dry} ($F_{1,49} = 2.08$, $P = 0.156$).

Discussion

This study demonstrates how group-living reduces roosting costs of a sedentary species living in an energetically-challenging environment. The White-browed Babblers studied here showed no tendency for substantial heterothermy, instead benefitting from roosting behaviour and nest temperature to facilitate energy balance. Energetic benefits were derived from both social thermoregulation during communal roosting, as well as use of insulated roost nests. Patterns in diurnal behaviour and habitat use played a limited role in thermoregulatory energetic savings.

Here the importance of a comprehensive methodology comprising both laboratory and field techniques is illustrated. While to date few studies have quantified the interplay between individual, group and roost temperature upon nocturnal energetics for socially-roosting endotherms in this way (du Plessis & Williams 1994; Willis & Brigham 2007; Wojciechowski *et al.* 2011; Chappell *et al.* 2016), the benefits of a combined approach are obvious. To understand the additive benefits of roosting behaviour and roost temperature upon individual physiology, the responses of birds in the field must be viewed alongside controlled, laboratory experiments that can consider these aspects of individual physiology, huddling and roost temperature separately. Such an approach is necessary to fully understand the energetic parameters acting on free-living birds in an energetically-challenging habitat.

Body temperatures of free-ranging babblers

Free-ranging babblers maintained near constant overnight T_b , regardless of low, frequently sub-zero, overnight temperatures. The range of minimum $T_{b,\text{field}}$ for all individuals was $< 2.2 \text{ }^{\circ}\text{C}$, at all environmental conditions during the study, and was better explained by variation between individuals rather than response to environmental

conditions. Although torpor and hibernation have been observed only infrequently in a small number of avian families (Geiser *et al.* 2006), capacity for more limited nocturnal hypothermia is generally considered quite widespread (McKechnie & Lovegrove 2002). However, there was no evidence here that hypothermia formed a part of babblers' energetic strategy.

Babblers instead exhibited a typical homeothermic scotophase pattern (Schmidt-Nielsen 1997), cooling from an active T_b upon arrival at the roost nest to an overnight resting T_b which remained constant for the remainder of the night (Figure 2.2). Babblers then warmed endogenously before roost departure at sunrise to a similar T_b as prior to roost arrival the previous evening. Both mean active-phase ($T_{b,depart}$; 40.4 °C) and rest-phase T_b s (minimum $T_{b,field}$; 38.5 °C) recorded for babblers in the field were not dissimilar to those recorded for other normothermic passerines (41.6 ± 1.13 °C and 38.9 ± 0.87 °C respectively; Prinzinger *et al.* 1991). In the laboratory, individual babblers maintained T_b at $T_a = 10$ °C only 1.0 °C lower than at thermoneutrality (38.6 °C at $T_a = 30$ °C), achieved by a 143% increase in metabolic rate and a 15.7% decrease in thermal conductance. The pattern in these physiological parameters with varying T_a is also a typical endothermic response to low T_a (Withers 1992). Patterns in hygric and ventilatory physiology also showed similarly typical endothermic responses to T_a .

Babblers' strategy of homeothermy is different to energetic strategies of some other free-ranging Australian birds. Australian Owlet-nightjars (*Aegotheles cristatus*; 50 g; Brigham *et al.* 2000) regularly use torpor under cold ambient conditions, Tawny Frogmouths (*Podargus strigoides*; 453 g; Körtner *et al.* 2001) use shallow torpor during their active and inactive phases, and Laughing Kookaburras (*Dacelo novaeguineae*; 348 g; Cooper *et al.* 2008) are heterothermic, with overnight minimum T_b up to 9.1 °C below arrival T_b . While evidence of heterothermy has only been gathered from a relatively small proportion of Australian taxa, globally the evidence suggests that non-passerines and nocturnal species are more likely to be heterothermic. The only comparable measurement of continuous, nocturnal T_b of an Australian passerine under ambient conditions is for the Dusky

Woodswallow (*Artamus cyaneurus*; 30 g; Maddocks & Geiser 2007), captive-raised juveniles measured in outdoor aviaries. These Dusky Woodswallows were heterothermic, their overnight minimum T_b decreased with both low T_a and in response to season. The authors classified this as torpor, as T_b decreased by $> 5\text{ }^{\circ}\text{C}$ from resting T_b levels. So while the energetic strategy observed here for babblers seems unusual compared to strategies documented for other Australian species, thermoregulatory physiology of the breadth of Australian avian diversity has by no means been extensively investigated.

Allometric and phylogenetic comparisons

To better understand the physiological data collected for babblers it is necessary to place them in allometric and phylogenetic contexts. For many mammals, low T_b and low BMR correlate with heterothermy and incidence of torpor use (Geiser 1998; Cooper & Geiser 2008). Conversely, high and constant T_b combined with a high BMR is indicative of species with a high energy strategy. Despite limited data for birds, if the physiological drivers between endothermic groups are similar, then relationship between T_b and BMR should indicate frugal and high energy strategies for birds too.

Babbler nocturnal T_b measured at thermoneutrality under controlled, laboratory conditions ($T_b = 38.6\text{ }^{\circ}\text{C}$) conforms to T_b s of other birds under similar conditions, both before and after correcting for phylogeny (Figure 2.16A). Babbler T_b was only $0.5\text{ }^{\circ}\text{C}$ below that predicted, well within the 95% prediction limits. Therefore there is no evidence of a low T_b that might be associated with a propensity for heterothermia.

White-browed Babbler BMR was only 64.0% of that predicted by body mass, but is within the 95% prediction interval for the avian dataset. However after correcting for phylogeny, the babbler's phylogenetically-independent BMR fell below the 95% prediction interval (61% of predicted; Figure 2.16B, F). Lower-than-expected BMR is frequently observed for arid-dwelling marsupials and birds (Williams *et al.* 1991; Withers *et al.* 2006), and for endotherms with a propensity for torpor. Presumably a low energy use is advantageous for balancing the energy budget and therefore serves a similar function

to heterothermia, responding to similar environmental pressures. However, despite their low BMR, babblers were homeothermic, suggesting that their BMR could be maintained without resorting to lowering T_b by torpor. Presumably this is explained in part by their huddling behaviour and use of roost nests.

Thermal conductance of solitary babblers was 98.2% that predicted by mass (Figure 2.16C), and both conventional and phylogenetically-independent values were well within the 95% prediction limits for the conventional and phylogenetically-independent data for avian species. This suggests there is nothing remarkable about babbler insulation compared to other birds that might account for their homeothermy.

Evaporative water loss of babblers was 41.0% of that predicted by body mass alone (Figure 2.16D), below the 95% prediction limits. Accounting for phylogeny did not account for this discrepancy, with phylogenetically-independent EWL still below the 95% prediction intervals of (Figure 2.16H). Low EWL is another attribute associated with arid-dwelling endotherms (Withers *et al.* 2006). This, together with a high preformed water content in their insectivorous diet, and their ability to maintain water balance without drinking free water (pers. obs.) presumably contribute to the babbler's wide distribution, well into the arid zone (Higgins & Peter 2002). The low minimal EWL value may instead relate to the long measurement duration used here, as measurement duration directly affects EWL values obtained from respirometry for a range of species (Cooper & Withers 2009; Page *et al.* 2011; Connolly & Cooper 2014).

I also examined ventilatory variables in an allometric and phylogenetic context, to determine if babblers accommodated their O_2 demand in a manner consistent with other birds of a similar size. Minimal f_R , as well as V_T and EO_2 data from the T_a when f_R was minimal were compiled from the literature (Appendix 1). Minimal respiratory frequency (measured at $T_a = 30\text{ }^{\circ}\text{C}$) was only 49% of that predicted by body mass (Figure 2.17A), but both conventional and phylogenetically-independent values fell within 95%

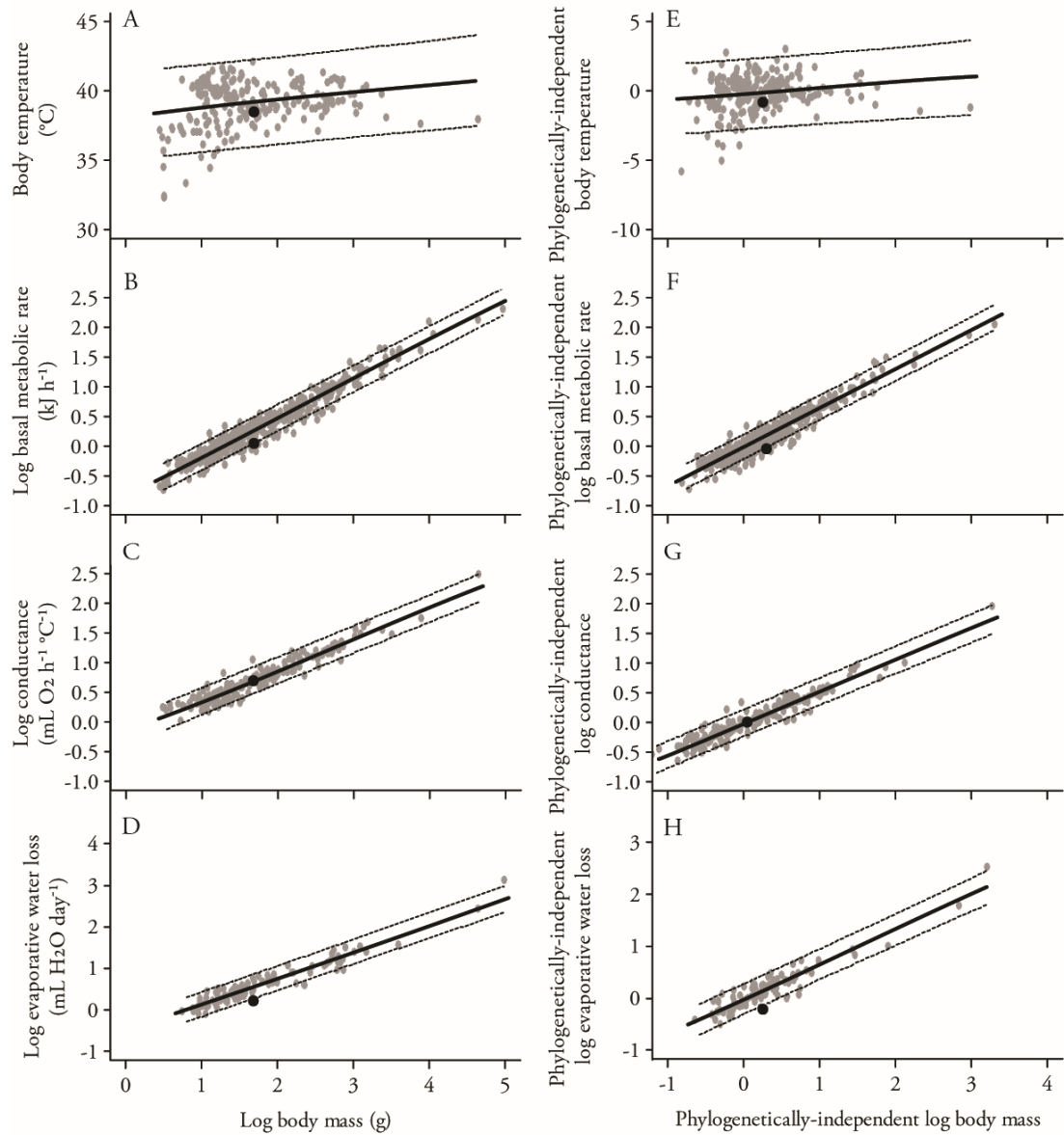


Figure 2.16: Conventional allometric comparison of body temperature (A), basal metabolic rate (B), conductance (C) and evaporative water loss (D) values obtained for babblers (black symbols) compared with other birds (grey symbols). Phylogenetically-independent residuals for the same parameters are displayed in E-H respectively. All values are presented as \log_{10} values, with the exception of body temperature. Where a linear relationship exists, the solid line marks the linear least squares regression line, and the dotted lines 95% prediction intervals. Methodology is described in Chapter 6 and datasets are presented in the Appendices.

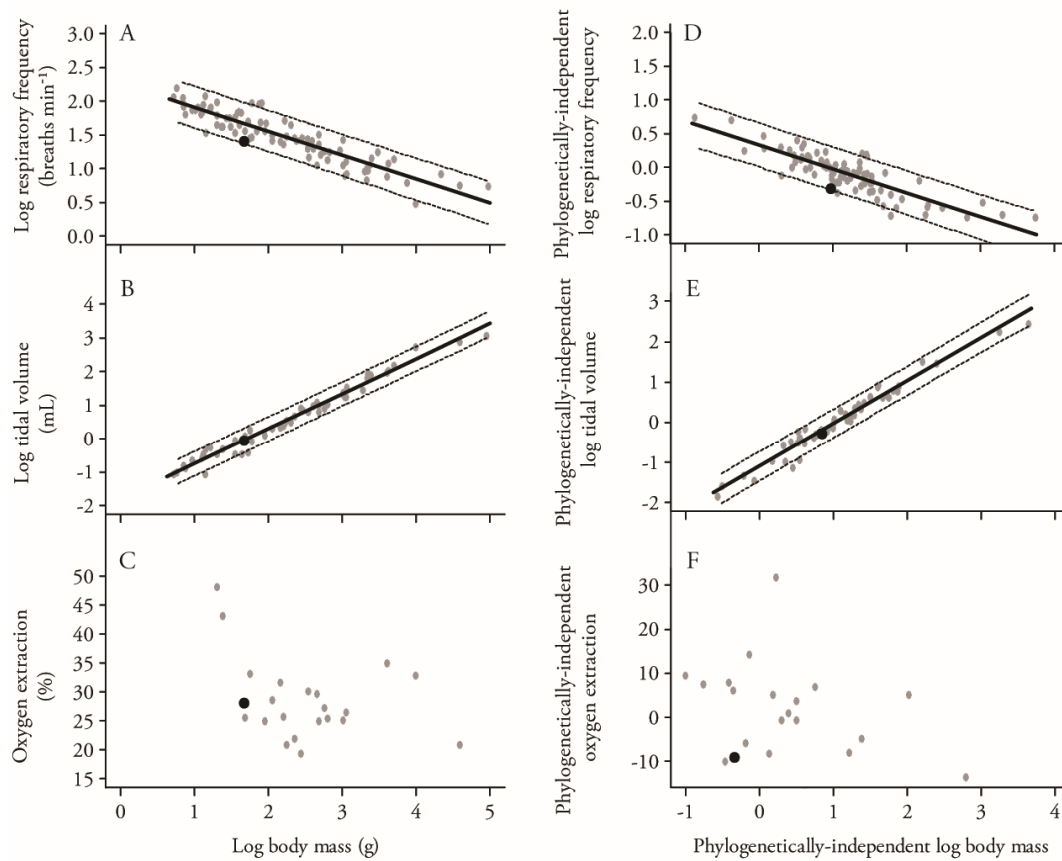


Figure 2.17: Conventional allometric comparison of ventilatory parameters respiratory frequency (A), tidal volume (B), and oxygen extraction (C) values obtained for babblers (black symbols) compared with other birds (grey symbols). Phylogenetically-independent residuals for the same parameters are displayed in D - F respectively. All values are presented as log₁₀ values, with the exception of EO₂. Where a linear relationship exists, the solid line marks the linear least squares regression line, and the dotted lines 95% prediction intervals. Methodology is described in Chapter 6 and datasets are presented in the Appendices.

prediction estimates. Tidal volume, measured at minimal f_R , was 100% of that predicted, and applying a phylogenetic correction did not alter this. Oxygen extraction did not scale with log body mass before or after accounting for phylogeny ($p = 0.393$; $p = 0.08$ respectively), but babbler EO_2 at minimum f_R (28.4%) was well within the range recorded for other birds (Figure 2.17C; F).

Social thermoregulation

Communal roosting occurs in many groups of social endotherms (Gilbert *et al.* 2010), and for many species is used to maintain homeothermy. T_b of individually-roosting animals is more variable than huddling individuals. 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 (such as White-backed Mousebird *Colius colius*; McKechnie & Lovegrove 2001). Although White-browed Babblers roosted communally in the field and laboratory, there was no evidence for nocturnal hypothermia or torpor under any conditions, even when measured individually in the lab all individuals maintained T_b to within 1.15°C of thermoneutral laboratory values. Therefore babblers are facultative social thermoregulators, as they can most likely survive roosting individually overnight in the wild, but gain substantial energetic and presumably social benefits by roosting communally.

The reduction in energy expenditure of babblers achieved by huddling, where huddling MR is 64.6 – 74.1% of individual MR, is well within the range of values recorded for other huddling birds and mammals (see Gilbert *et al.* 2010 for review). I found no relationship between the magnitude of energetic savings and T_a ; instead the savings achieved were constant between 10 – 20°C, evidenced by the difference in intercept, but not in slope between the VO_2 and T_a relationship of individual and huddling babblers. This response is not uniform, as huddling Chesnut-crowned Babblers (*Pomatostomus ruficeps*, Chappell *et al.* 2016), Green Woodhoopoes (*Phoeniculus purpureus*, du Plessis and Williams 1994), and Speckled Mousebirds (*Colius striatus*; Brown and Foster 1992) both have increased energy savings with decreasing T_a , whereas energy savings decreased with decreasing T_a for Common Bushtits (*Psaltiriparus minimus*; Chaplin 1982). Kendeigh *et al.* (1977) infer that differences in energy saving may be attributed to differing structures of the huddle, but while plausible this has not been rigorously tested. Common Bushtits row-huddle, sitting side by side on a roost perch, whereas species that huddle in three dimensions (like babblers) may have a better capacity for optimising the huddle dimensions (becoming more spherical) in response to environmental conditions. Hanging

aggregations of mousebirds would likely be most efficient at minimising surface area to volume ratio, as they are not hindered by filling a predetermined roosting space such as a hollow or nest and can arrange themselves to suit environmental conditions, thereby maximising energetic savings.

Increasing group size from 2 to 3 individuals had no effect on energy saved by an individual at any of the T_a s investigated. This finding is consistent with some other studies (du Plessis & Williams 1994; McKechnie & Lovegrove 2001b), but not with others (Chappell *et al.* 2016). For Acorn Woodpeckers (*Melanerpes formicivorus*), this was attributed to the observation that while birds roost as family groups in the same tree hollow, they don't huddle (du Plessis *et al.* 1994). This was not the case here, as video of the babblers in the metabolic chambers confirmed they consistently huddled and the limited internal space in babbler roost nests would make it impossible for free-living babblers to use the same nest and not huddle. Under laboratory conditions, respirometry might underestimate the energy savings achieved by large groups of huddling endotherms. As group size increases it becomes less likely that all individuals are resting simultaneously, so the single data trace obtained for all birds would overestimate minimum physiological variables. This has been acknowledged as influencing the values achieved for huddling in stripe-faced dunnarts (*Sminthopsis macroura*; Tomlinson 2011). It is possible that group size does affect energetic savings in agreement with Brown & Foster's (1992) conclusion, but this could not be determined here.

Substantial variation in T_{bmin} between individuals measured under similar T_{bb} conditions (~ 2.1 °C at $T_a = 6$ °C) was observed for free-living, huddled babblers, and individual differences seem quite consistent over the range of T_{bb} experienced (Figure 2.3A). While individual differences in rho-phase setpoint T_b may occur between individuals, differences in roosting position may also play a role. Not all positions within a huddle of roosting babblers would experience identical environmental conditions, as factors such as proximity to the nest entrance and distance from the centre of the huddle would affect heat loss. Therefore location within the roost nest probably impacts on overnight T_b and

can account for this variation. For Varied Sittellas (*Daphoenositta chrysoptera*), adult males consistently roost on the ends of huddles (Noske 1985a), despite being similar in size to females and subadults (de Rebeira 2006). This physiological cost of social status is also likely in babblers, as field observations of babbler roosting behaviour suggest some social rules. At dusk, babblers would approach the nest singly and cryptically to roost. On occasion individual babblers were observed evicting already roosting group members from the nest, with the evicted birds then waiting until the evictor was in the nest before entering again themselves. Thus observed individual variation in T_b here is possibly a proxy indicator of social status, although the precise dynamics of this are unknown. Long-term studies of other cooperatively-breeding birds record differences in longevity between males (shorter) and females (longer), and between breeding birds (shorter) and helpers (longer), attributing differences to breeding pressures (Brown *et al.* 1990), but the energetics of roosting behaviour might also be a contributing mechanism.

In summary, White-browed Babblers gain similar energetic advantages from communal roosting as do other socially-thermoregulating endotherms. However, unlike some communal roosting species, babblers are not obligate social thermoregulators, as they can maintain homeothermy even when roosting solitarily. Consistent individual differences in overnight T_b of free-living babblers suggest social rules and provide proxy evidence that energetic savings are not experienced equally in the huddling group.

Roost nest characteristics

The energetic benefit of roosting in enclosed nests is a further element of babbler's nocturnal energy strategy. Unlike the nests of Sociable Weavers (*Philetairus socius*), which are sufficiently large and well-insulated that even when unoccupied they remain above nocturnal ambient temperatures (White *et al.* 1975), here the T_{roost} of unoccupied babbler nests were the same as T_{bb} . When occupied, the relationship of T_{roost} to T_a inside White-browed Babbler roost nests is similar to that inside roost nests of solitary-roosting White-browed sparrow-weavers (*Plocepasser mahali*; Ferguson *et al.* 2002) where the $T_{\text{roost}} - T_a$ differential increases as T_a falls. The insulative properties of sparrow-weaver roost nests

are believed to be an important factor in allowing them to maintain homeothermy at low T_a (Ferguson *et al.* 2002). While evidence supports babblers are facultative social thermoregulators, the insulative properties of their roost nests would still provide favourable energetic savings.

When measured in the laboratory, the conductance of roost nests ($C = 1.62 \text{ J h}^{-1} \text{ g}^{-1} \text{ }^{\circ}\text{C}^{-1}$) was equivalent to the conductance of groups of 2-3 huddling babblers ($C = 1.61 \text{ J h}^{-1} \text{ g}^{-1} \text{ }^{\circ}\text{C}^{-1}$ at $10 \text{ }^{\circ}\text{C}$), so roost nests effectively halve the rate of energy lost to the environment for huddling babblers. While babbler roost nests did not provide as effective insulation as some nests of another Dryandra woodland inhabitant, the Numbat (*Myrmecobius fasciatus*; $C = 1.2 \text{ J h}^{-1} \text{ g}^{-1} \text{ }^{\circ}\text{C}^{-1}$; Cooper & Withers 2005), the lower thermal conductance of bird plumage and the use of huddling already confers a significant energetic advantage (Aschoff 1981). Under windy conditions, nests also act to mitigate the effects of convective cooling, as quantified for winter roost nests of Verdins (*Auriparus flaviceps*; Buttemer *et al.* 1987).

In 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 (Geiser *et al.* 2004). 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, departing roost nests within a few minutes of sunrise. However, there were still some patterns in babbler nest characteristics. Some, such as the prevalence of roost nest trees situated with an ENE aspect, reflect broad characteristics of the study sites used, where ENE slopes dominated, rather than being indicative of roost nest preferences. The varying locations of babbler roost nests provide further evidence that external temperature is not a significant driver of general nest characteristics and nest site selection in winter. While nests are built preferentially in the top third of their host tree, the variation in tree species and actual height of the host trees make it unlikely that microclimate considerations are important. While the disproportionate 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), nest location decisions might also be an anti-predator strategy. Where babbler groups used more than one nest, there appeared to be little correlation between weather conditions and nest selection; that is, babblers frequently roosted in tall, exposed trees rather than selecting low, protected nests on windy nights (pers. obs.).

Combined energy savings of social thermoregulation in roost nests

The combined use of social thermoregulation and communal roost nests allows substantive energy conservation for White-browed Babblers under cold ambient conditions. The results of the laboratory and free-living components of my study can be used to calculate the overall energy savings achieved by free-living babblers as a result of both social thermoregulation and use of roost nests. Given the range of $T_{a,min}$ recorded at the study site (-2.57 to 14.5 °C) and using the relationship between $T_{a,min}$ and T_{roost} , minimum overnight babbler roost nest temperatures range can be calculated as being between 6.8 and 15.4 °C. Together with the equation for the relationship between T_a and $\dot{V}O_2$ for huddling birds, the range of MRs experienced by huddling birds at these T_{roost} range from 1.78 to 2.44 mL O_2 g⁻¹ h⁻¹. Extrapolating the linear relationship between T_a and $\dot{V}O_2$ below thermoneutrality for solitary birds outside of roost nests (2.75 to 4.44 mL O_2 g⁻¹ h⁻¹), the huddling babblers in roost nests have an energy expenditure 55.0 to 64.8% of those of single, exposed birds at the same environmental conditions. Communal roost-nesting birds at a T_a of 6.8 – 15.4 °C have a metabolic rate equivalent to a single, exposed bird at T_a of 17.6 – 24.3 °C. These energy savings are similar to those reported for the closely-related Chestnut-crowned Babbler (*Pomatostomus superciliosus*, Chappell *et al.* 2016) and presumably play an important role for sedentary, communal roosting passerines (Vickery & Millar 1984) in balancing their daily energy budget and may be important in allowing them to maintain homeothermy in an energetically-challenging environment.

Effect of diurnal behaviour

Intensity of foraging behaviour is often viewed as a proxy for a bird's energy expenditure (Bednekoff & Houston 1994). Diurnal birds are typically reported as having a bimodal

foraging pattern, with an intensive foraging peak early in the morning to redress overnight energy depletion, and a less intensive foraging peak in the afternoon, to maximise energy stores prior to their inactive nocturnal phase (Bednekoff & Houston 1994; McNamara *et al.* 2004). In winter, low T_a s mean energetic requirements are higher but fewer daylight hours and increased proportion of inclement weather result in reduced foraging opportunities and reduced prey activity (Speakman & Thomas 2003; Geiser 2004a). Under these restrictive conditions, compensatory behaviours should be maximised. However Taylor & Paul (2006) report a positive linear increase in time spent foraging throughout the day for babblers in northeastern Victoria. In contrast, babblers studied here had a trimodal foraging pattern, with peaks in mid-morning, midday, and then mid-afternoon. If this were simply an adjustment of the bimodal strategy, with the addition of an extra, midday foraging bout, it would be expected that the first foraging peak would occur directly after leaving roost nests, and the third foraging peak would occur immediately prior to roosting. This was not the case; babblers departed their roost nests in the morning before or just after dawn (roost departure times 06:20 - 07:02, Figure 2.4), yet the first bout of foraging activity did not peak until just before 09:00 (Figure 2.7). Again, in the evening, babblers were observed entering roost nests 15 – 20 minutes after sunset (17:42 – 17:52), yet the previous foraging bout peaked at ~16:30, after which time spent foraging dropped off markedly. Instead of foraging, at the beginning and end of the day, the major activity of babblers was maintenance and resting alert behaviour respectively. This supports the hypothesis that even at low T_a , with reduced daily foraging potential, babbler behaviour is not driven solely by energetic demands and babblers have excess time to meet their daily energy requirements. Time taken to meet daily energy needs is not prohibitive for Forest Red-Tailed Black-cockatoos (*Calyptorhynchus banksii naso*) either, as even with the time taken to extract seeds from woody *Corymbia callophylla* fruit, they can fulfil their daily energy requirements in as little as 81 minutes (Cooper *et al.* 2002), leaving plenty of time for other activities.

Babblers did not supplement metabolic heat production by actively basking at low T_a , providing further evidence that they were not energy-limited. Field observations of

babblers indicated T_{bb} did not influence time spent in full sun (Table 2.5). Neither were babblers more likely to be in sun early in the morning, when both T_a and energy reserves are minimal (Figure 2.12). Rather, babblers were observed in sunlit locations in almost equal proportions throughout the day. On average, when the sun was shining, babblers were still observed in full sun only half as frequently as not. Dedicated basking behaviour incurs costs, as time spent actively basking cannot be spent foraging, defending territory, or sometimes being alert for predators. For dark-eyed juncos (*Junco hyemalis*), heat conservation behaviour increased response time to simulated predation events (Carr & Lima 2012), indicating that there was an increased predation risk with this form of thermoregulation. That babblers did not regularly bask infers that either the trade-off costs were too high, or that babblers adequately mitigated their energetic costs in other ways. Given the calculated energy savings from their nocturnal roosting strategies and daily foraging patterns, the latter explanation seems most likely.

Trend plots from GAMMs indicated that babblers had clear, consistent, if complex, patterns in use of substrate and location within their habitat. These patterns varied with temporal and thermal conditions, but not in a manner that suggested babblers were directly avoiding or preferring particular microclimates in their habitat. As foraging was the activity that occurred most frequently and consistently throughout the day, it is the most likely explanation for these patterns. Some bird species remain inactive because their prey is inactive. Aerial hawkers such as Dusky Woodswallows (*Artamus cyanopterus*) and Tree Martins (*Petrochelidon nigricans*) will huddle and sometimes bask at low T_a when their insect prey is not active (Higgins *et al.* 2006; pers. obs.). This was obviously not the case for babblers as they foraged under all conditions. Other animals that eat more stationary food, such as large herbivores, do not alter foraging patterns in response to low T_a (Belovsky & Jordan 1978; Iwamoto & Dunbar 1983). While babblers foraged consistently throughout the day, and at low T_a , mostly by gleaning and probing (Miller & Cale 2000; pers. obs.), they did shift their foraging substrate and location with regularity, moving to different height strata in the woodland, and between sun and shade. Meliphagid honeyeaters maintain foraging activity levels throughout the day, but alter

foraging location and behaviour in response to changing food availability (Timewell & McNally 2004), and this may also be what influences the substrate shifts of babblers. For Chestnut-crowned Babblers (*Pomatostomus ruficeps*) predation risk and predator encounters alter foraging behaviour, leading to an increase in time spent in sentinel behaviour (recorded as resting alert here) and using various substrates (Sorato *et al.* 2012). While babblers are not as closely tied to the activity levels of their prey, their complex pattern in habitat use may be in response to switching between different prey types over the course of the day.

Implications

Thermoregulatory strategies can have behavioural implications, as seen for hypothermic Mourning Doves (*Zenaida macroura*), which were slower to take flight after a simulated nocturnal predator attack than normothermic doves (Carr & Lima 2013). Therefore thermoregulatory strategies can potentially involve a trade-off between energy conservation and predation risk (Geiser *et al.* 2004). Babblers negate this trade-off to some extent, as social thermoregulation and use of roost nests provide the energetic benefits to allow babblers to maintain nocturnal normothermia during winter, despite the challenges of being a sedentary insectivore in a variable environment, and may have additional social and predator-avoidance advantages.

Superficially, White-browed Babblers appear to experience limited thermoregulatory challenge despite their often harsh habitat. They show no evidence of torpor use during cold conditions and benefit energetically from social thermoregulation. The combination of laboratory and field techniques used here enabled the T_b of free-ranging babblers to be understood not just in terms of response to T_a , but in the context of their individual thermoregulatory physiology, communal roosting behaviour, roost nests characteristics, and diurnal behaviour. Babblers appear to be facultative rather than obligate social thermoregulators, maintaining a finely-controlled system in which they balance physiology with behavioural strategies that act to cement social cohesion and mitigate

predation threats, exerting a very fine control over their energy expenditure to persist in a temperate winter environment.

The hollow promise: variable energetic benefits of roosting in tree hollows for the Rufous Treecreeper *Climacteris rufa*

Abstract

Rufous Treecreepers (*Climacteris rufa*) are small (30 g), insectivorous, cooperatively-breeding passerines endemic to southern Australia. In temperate Wandoo (*Eucalyptus wandoo*) woodland they are ground-frequenting and despite below-freezing overnight temperatures in winter, they roost singly in tree hollows. I examined the role that roosting in tree hollows plays in the thermoregulatory strategy of treecreepers in winter, in the context of other behavioural and physiological attributes. The thermal and physical characteristics of roost hollows varied; some were similar to ambient conditions, but others created more favourable microclimates that were 3 - 9 °C warmer than ambient overnight temperatures. Body temperatures of wild, free-living treecreepers, measured using implanted temperature-sensitive radio transmitters, did not drop below 37 °C even when ambient temperatures were below 0 °C, regardless of tree hollow quality. Behavioural observations suggest that treecreepers do not alter their daily activity patterns to incorporate thermal behaviour, with no evidence of basking during the day or social thermoregulation at night. Complementary laboratory work using open-flow respirometry at a range of ambient temperatures (10 °C to 30 °C) showed that treecreepers had typical endothermic responses to low ambient temperature, with no evidence of torpor. Mean body temperature in the laboratory at ambient temperature of 10 °C was only 1°C lower than thermoneutral body temperature (39.4 °C, n = 6), achieved by a 40% increase in metabolic rate and a 20% decrease in thermal conductance. Despite tree hollows being an abundant resource in the habitat studied here, there was little evidence that treecreepers selected roost sites on the basis of thermal characteristics. Instead, a low energy foraging strategy is likely more important in helping these small birds maintain a sedentary lifestyle in an energetically-challenging environment.

Introduction

Birds in general have an energetically-expensive lifestyle. They maintain a high or higher body temperature (T_b) with a high or higher metabolic rate (MR) than the other major endothermic lineage, mammals (Withers 1992). However birds are mostly diurnal, and so have limited potential for substituting activity-generated heat for metabolic thermoregulation before sunrise, when T_a s are lowest (Humphries & Careau 2011). Although flight is an energetically-expensive (hence heat-producing) form of locomotion over short distances (Blem 2000; Butler & Bishop 2000; Gill 2007), it is only of benefit during the active phase. Feathers mitigate heat losses and gains across the skin surface, and avian plumage provides better insulation than mammalian fur (Aschoff 1981), but as birds are generally small with a high surface area to volume ratio, their relative heat loss is high (Aschoff 1981; Schleucher & Withers 2001). Despite these challenges, birds are a dominant component of many ecosystems, even those where environmental conditions pose considerable thermal challenges (Withers *et al.* 2004; Gill 2007).

Many Australian landscapes, including *Eucalypt* woodlands, are characterised by little or no standing water, low nutrient levels, poor soil and low productivity (Geiser *et al.* 2006; Cousin & Phillips 2008). During winter, sedentary woodland species are faced with low, often below-freezing ambient temperatures (T_a s; Bureau of Meteorology 2014), as well as reduced daylight hours and sub-optimal foraging conditions (Dawson *et al.* 1983). Yet sedentary birds are often abundant in temperate woodland systems (Recher & Davis 1998; Recher *et al.* 2010; Moore 2013). Being sedentary requires the capacity to survive variation in ambient environmental conditions over both seasonal and diurnal scales, so the physiological and behavioural attributes that allow sedentary species to persist year-round in these environments are of particular interest.

Tree hollows, as well as providing temporary refuge from predators and nesting sites, can also provide an important resting and roosting location, as hollows not only shelter occupants from predators (French 1993), but buffer against environmental extremes, particularly T_a (du Plessis & Williams 1994; Rose 1996; Cooper & Withers 2005; Paclík

& Weidinger 2007; Doucette *et al.* 2011). In the *Eucalyptus wandoo* woodlands of temperate southwestern Australia, tree and log hollows are abundant (Rose 1993; Gibbons & Lindenmayer 2002). Consequently, fauna communities of these woodlands include many hollow-dependent species (Mawson & Long 1994; Gibbons & Lindenmayer 2002).

Endotherms that roost in tree cavities under conditions of low T_a sometimes use nocturnal hypothermia or torpor to further reduce energy expenditure. This has been observed for hollow-roosting bats (Hosken & Withers 1999; Lumsden *et al.* 2002; Willis & Brigham 2003), nocturnal birds (Brigham *et al.* 2000), various marsupials (Körtner & Geiser 2000; Cooper & Withers 2004b) and small primates (Nowack *et al.* 2013). While nocturnal hypothermia can increase predation risk by reducing response times (Laurila & Hohtola 2005; Carr & Lima 2013), roosting in inaccessible and cryptic locations like tree hollows presumably reduces predation rate, akin to how nesting in tree hollows minimises nest predation (Newton 1994; Fisher & Weibe 2006).

The Rufous Treecreeper *Climacteris rufus* is a medium-sized (~30g), sedentary insectivorous passerine of Eucalypt woodlands (Higgins *et al.* 2001). Although the breeding, foraging and habitat requirements of Rufous Treecreepers (hereafter ‘treecreeper’) have been well-studied (Rose 1996; Recher & Davis 1998; Luck 1999, 2001; Craig 2002; Luck 2002a, 2002b; Craig 2007), there is currently no information concerning the thermoregulatory strategies that enable them to persist as sedentary birds throughout their range. Like other members of the Climacteridae, *C. rufus* breeds cooperatively (Higgins *et al.* 2001). All Climacteridae nest in tree hollows, but roosting behaviour varies between species. White-throated Treecreepers (*Cormobates leucophaeus*) roost mostly in partially-exposed tree fork crevices or under bark, while Brown (*Climacteris picumnus*) and Red-browed Treecreepers (*Climacteris erythrops*) roost in a tree crevices as well as open-topped stumps, enclosed trunk hollows and branch hollows (Noske 1977, 1985b). Prior to this study the roosting behaviour of Rufous Treecreepers was unknown, but data gathered here suggest this may be the only member of the genus

to be an obligate hollow-roosting species. Whether this roosting behaviour occurred in conjunction with torpor, like other hollow using species, was unknown.

Here I investigate the physiological and behavioural thermoregulatory strategies of Rufous Treecreepers in temperate woodland in winter. A comprehensive methodology incorporating field T_b telemetry, roost temperature measurement and daily activity observations with standard laboratory respirometry was used to examine the role that roosting in tree hollows plays in the thermoregulatory strategy of treecreepers in winter, in the context of other behavioural and physiological attributes..

Methods

Study site

Field body temperature ($T_{b,field}$), field behaviour, roost temperature and laboratory respirometry were quantified for Rufous Treecreepers inhabiting the main block of Dryandra Woodland (32°45'S, 116°55'E; Figure 3.1), the same site used to study White-browed Babblers in Chapter 2. Treecreepers are common throughout the woodland (Recher & Davis 1998; Moore *et al.* 2013b), but were primarily studied at the sites marked in Figure 3.1. Work was conducted during the Austral winter; June – September 2012 and June – August 2013.

Free-ranging body temperature

Six treecreepers (30g), two in winter 2012 and four in winter 2013, were captured with mistnets using audio playback (calls modified from Stewart 2005 and BOCA 2007). Temperature-sensitive radio transmitters (BD-2TH, 1.05g; Holohil Systems Ltd) were calibrated and surgically implanted into the intraperitoneal cavity under anaesthesia, following the same protocol as for White-browed Babblers (Chapter 2). Implanted birds were initially followed to their evening roost sites using visual and audible cues until roost hollow fidelity could be confirmed. An identical protocol was used for overnight $T_{b,field}$ recording and data analysis as for Babblers (Chapter 2), using a Yagi antenna, radio receiver (AOR AR8200mk3 or AOR AR8000), and portable sound recorder (Olympus

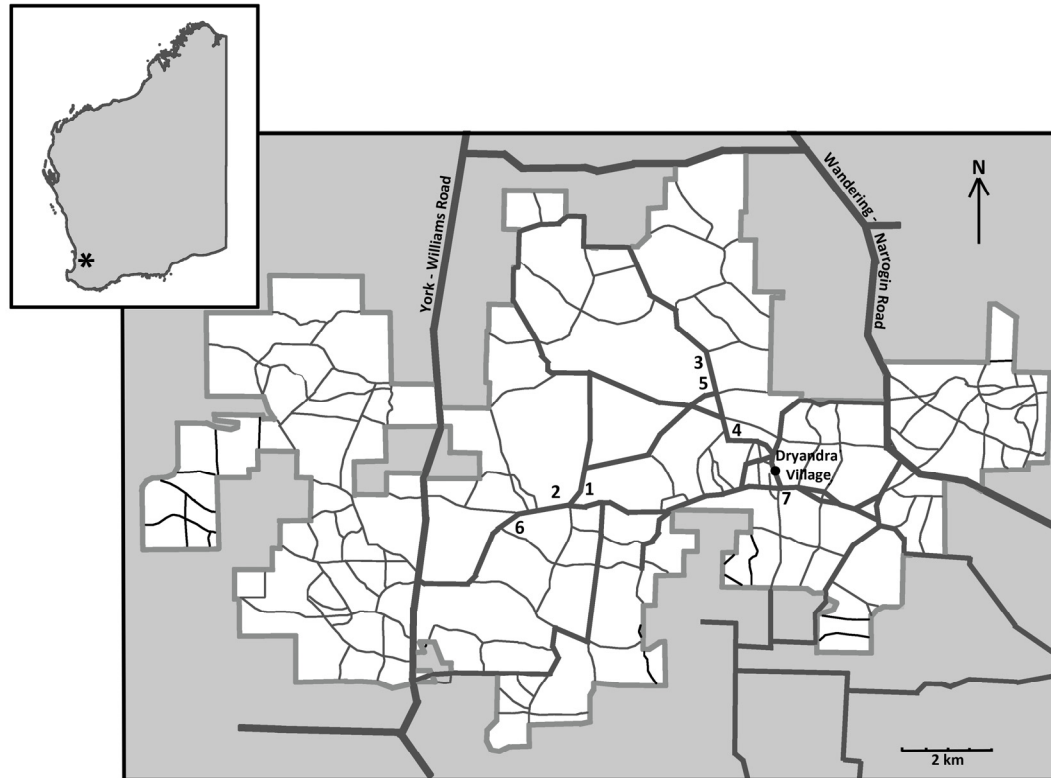


Figure 3.1: Map of main block of Dryandra Woodland, Western Australia (location marked with an asterisk in inset). Rufous Treecreeper capture sites are numbered. $T_{b,field}$ data was for treecreepers in sites 1, 2 and 3 in winter 2012 and 2013, and all other sites were used for capture of individuals for overnight respirometry experiments in winter 2013. All sites were utilised for behavioural observations.

LS-10, Olympus VN-702PC or Sony ICD-PX333). Analyses of treecreeper $T_{b,field}$ data and environmental data (recorded as black bulb temperature, T_{bb} , and relative humidity; RH) from Hygrochron iButton data loggers, together with BOM weather station data were measured as for White-browed Babblers (Chapter 2), with the exception that implanted treecreepers never roosted in close enough proximity to detect multiple birds with the same antenna, so each overnight sound file was always for one individual.

Roost temperature

Internal temperature of treecreeper roost hollows was measured *in situ* at Dryandra Woodland using iButton (DS1923, Maxim Integrated Products) data loggers. Roost hollows were located by following the treecreepers carrying radio transmitters as they went to their evening roosts. For roost hollows that could be accessed using an extendable ladder (≤ 5.5 m above ground level), iButtons were fastened to a length of wire inserted as far into

the roost hollow as possible. Each wire had two loggers, one at the end of the wire to measure conditions at the bottom of the roost cavity, and one partway along to measure central cavity temperature. The data loggers recorded roost temperature (T_{roost}) and RH (RH_{roost}) every ten minutes. External ambient loggers were paired with the internal roost loggers, placed nearby in foliage at similar elevations to the hollows. Where multiple hollows were in close proximity, they were matched against a single ambient logger. Data were downloaded using the OneWireViewer program (v0.3.15.50, Maxim Integrated Products).

Roost site characteristics

Physical characteristics were recorded for all roost hollows that could be located in the study area. Location and elevation were recorded (Garmin GPS 60) and characteristics of the roost tree and surrounding habitat were determined as for babblers (Chapter 2). Characteristics of roost hollows included height of hollow entrance above the ground, entrance dimensions, entrance direction, and where possible, cavity depth. Tree height and height of hollow entrance were measured with a Nikon Forestry 550 laser range finder. The range finder was calibrated against objects of known height prior to use.

Field behaviour

Behaviour of free-ranging treecreepers was quantified using the same protocols and categories as for babblers (Chapter 2). Individuals and groups of treecreepers were observed at all 7 sites (Figure 3.1).

Laboratory respirometry

Non-breeding, adult treecreepers (30.3 ± 0.4 g, $N = 25$) of unknown age were caught at several sites at Dryandra Woodland (see Figure 3.1), using mistnets and audio playback (calls modified from Stewart 2005 and BOCA 2007). Treecreepers were netted in the morning and held for the day in a small fasting cage, with free access to water but not food. Birds were measured overnight from approximately 18:00 to 04:00, then released back at the capture site after sunrise the following day. All individuals were marked with

a unique combination of coloured plastic leg bands for identification. Nineteen treecreepers were measured once, five treecreepers were measured twice, and one was measured three times, with a minimum of four days between captures.

Open flow-through respirometry was used to measure basic physiological variables of oxygen consumption ($\dot{V}O_2$), carbon dioxide production ($\dot{V}CO_2$) and evaporative water loss (EWL) at a range of T_a (10°C, 15°C, 20°C, 25°C and 30°C), after Withers (2001). Two complete respirometry systems were used simultaneously, each measuring a single treecreeper at one T_a each night. Treecreepers were measured at different T_a s in random order. Experiments took place in a darkened temperature-controlled cabinet (Arcus model 400E) with each treecreeper placed in a 65 mm internal diameter (volume ~620.5 mL) clear Perspex chamber. Each system used a FoxBox-C Field Gas Analysis System (Sable Systems International to regulate flowrate and quantify excurrent gas concentration. Outside air was drawn through canisters of Drierite (~98% $CaSO_4$, ~ 2% $CoCl_2$, W. A. Hammond Drierite Co. Ltd) and subsequent dry air was pushed through the metabolic chamber at a constant rate of 800 mL min⁻¹. RH and T_a of excurrent air were measured using a thin film capacitance RH and T_a probe (Vaisala MNP45A), interfaced with the FoxBox auxiliary ports. A subsample of excurrent air was then passed through a second small Drierite column, then through the CO_2 and O_2 analysers of the FoxBox. Data from the T_a /RH probe, and the CO_2 and the O_2 analysers, were recorded at 10 second intervals by a PC running a custom-written data collection program (Microsoft Visual Basic, P. Withers). T_b was measured for the treecreeper when it was removed from the chamber at the conclusion of each experiment, using a plastic-tipped thermocouple (connected to a Cole Parmer Digi-Sense Thermometer 91100-20) inserted ~1.5cm into the cloaca. Ventilatory data were collected via whole-body plethysmography, as for babblers (Chapter 2).

Flowrates of the FoxBoxes were calibrated using a Gilibrator-2 air flow calibrator (Sensidyne), and the gas analysers of the FoxBoxes were two-point calibrated with compressed N_2 and dry ambient air for O_2 and compressed N_2 and a compressed

calibration gas (0.538% CO₂, BOC Gas) for CO₂. The calibration of the RH probes was routinely confirmed using a two-point calibration of 1% RH air (dried with Drierite) and 100% RH air (by breathing saturated air onto the probe). The plethysmography data were corrected for pressure decay and the tidal volume (V_T) determined from calibration injections of 0.3 mL air during each experiment (Szewczak & Powell 2003). Metabolic, hygric and ventilatory variables were calculated as for Babbler (Chapter 2). Oxygen extraction (EO_2) was calculated using $\dot{V}O_2$ at the time of ventilatory measurement, not necessarily the minimal $\dot{V}O_2$ for the experiment. These were on average 130% of minimal values.

Data handling and statistical analysis

Values are presented as mean \pm standard error (SE), with N = number of individuals and n = number of experiments unless otherwise indicated. Values are presented at standard temperature and pressure, dry (STPD), except V_T and V_I which are presented at body temperature and pressure, saturated (BTPS). Times are given as Western Australian standard times (AWST; AWST = GMT + 8 h). All statistical models were tested at $\alpha = 0.05$. All analyses were conducted with the same protocol as for Babbler (Chapter 2), with the following exceptions.

Free-ranging body temperature: As treecreepers did not roost together, family group was not included as a random effect in the linear mixed model.

Roost temperature: Differences between minimum overnight T_{bb} and minimum overnight T_{roost} were compared with linear regression function (*lm*) in R.

Roost hollow characteristics: Age (years) of *E. wandoo* trees used by roosting treecreepers was calculated from diameter at breast height over bark (DBHOB; mm) using the DBHOB-age data collected at Dryandra by Rose (1993). In response to the growth and senescence patterns of the trees, three different equations were used. Age for trees with DBHOB < 300 mm were calculated as $\text{age} = 8.06 + 3.28 * \text{DBHOB}$ ($r^2 = 0.998$), trees

with DBHOB 300 – 630 mm as $\text{age} = 16.69 + 3.01 * \text{DBHOB}$ ($r^2 = 0.995$) and trees with a DBHOB > 630 mm as $\text{age} = 308 + 1.64 * \text{DBHOB}$ ($r^2 = 0.991$).

Roost arrival and departure times: roost arrival and departure times were collated from $T_{b,\text{field}}$ data and field behavioural observations. Linear mixed models were used to test for factors influencing arrival and departure times, using T_{roost} and environmental variables, using the *lmerTest* package in R.

Laboratory respirometry: As birds were only held and measured for a single night before being released not all individuals were measured at all T_a , precluding traditional multivariate repeated measures analysis of variance (RMANOVA) analyses (Withers & Cooper 2011). Therefore the effect of T_a on physiological and ventilatory variables were analysed by a generalised linear mixed model (GLMM) using the *lmerTest* package in R, with T_a as a fixed factor and individual as a random effect, to account for multiple measurements of some individuals. Differences were assessed by comparing values obtained at the T_a that gave the lowest value for that parameter against those at other T_a s (for example differences in $\dot{V}O_2$ were assessed by comparing $T_a = 20^\circ\text{C}$ (*sensu* BMR) against other T_a s). P-values were calculated using the Kenward-Roger correction and significant differences between fixed effect levels were calculated using the Satterthwaite correction (Schaalje *et al.* 2002).

Results

Roost site characteristics

Poor light at roost time, cryptic behaviour and abundance of potential roost sites made roost site identification difficult. Nevertheless, 11 Rufous Treecreeper roost hollows were identified during the 2012 and 2013 winter seasons. These roost hollows were in upright trees of both dominant canopy species, *E. wandoo* (N = 10) and *E. accendens* (N = 1). Hollow branches, spouts and trunk cavities were used, in both live and dead trees. Treecreepers showed no preference for roosting in trees that either formed part of dense stands or were solitary, as mean tree density surrounding roost trees (305.4 ± 96.6 trees

ha⁻¹) was not different from the mean, with habitat eucalypt density for *Dryandra* of 246.9 ± 11.38 trees ha⁻¹ (Luck 2002; $t_{10} = 0.605$ $P = 0.559$).

Using DBHOB, mean age of live *E. wandoo* used by roosting treecreepers was calculated as approximately 199 ± 40 years ($n = 7$; range 74 – 382 years; Rose 1993) and mean age of dead *E. wandoo* trees was at least 162 ± 35 years ($n = 3$; range 98 – 219 years). *E. wandoo* trees shed the outer layer of living tissue when they die, so DBHOB measurements are likely an underestimation of age at death. The four roost cavities that could be measured had depths of 31 – 106 cm, and included both simple, single-entrance, and complex, multi-entrance cavities. Where the hollow opening could be seen from the ground, treecreepers roosted preferentially in north-facing hollows ($10.3 \pm 14.9^\circ$; $Z_7 = 4.08$, $P = 0.011$, $n = 7$). Mean height of hollow entrances above the ground was 6.81 m (± 1.48 m, range 3.2 – 14.4 m, $n = 7$). The mean aspect of roost tree habitat was 38.5° (\sim NE; $\pm 15.0^\circ$, $Z_{11} = 4.24$, $P = 0.011$, $n = 11$), but the slope was minimal ($1.15 \pm 0.18^\circ$).

Roost temperature

Thermal data were collected for 261 roost nights from 5 known treecreeper roost hollows between June and September 2013. These roost hollows were in use for at least some proportion of the winter 2012 and 2013 seasons. Occupancy rate could not be calculated, as not every roost could be observed each night and roost occupation could not be determined from hollow temperature alone.

There was a significant linear relationship between minimum T_{roost} and minimum T_{bb} ($T_{\text{bb,min}}$) for all hollows (Figure 3.2; $F_{1,46} > 170$; $P < 0.001$). Individual hollows had different thermal characteristics, with all but two hollows ($P > 0.983$) differing significantly in intercept ($P < 0.001$). Two patterns in thermal response in the slope of T_{roost} against $T_{\text{bb,min}}$ could be identified by ANCOVA ($F_{4,251} = 5.96$; $P < 0.001$). Three of the hollows had similar slope, ≈ 1.27 ($P > 0.984$), with overnight T_{roost} several °C above

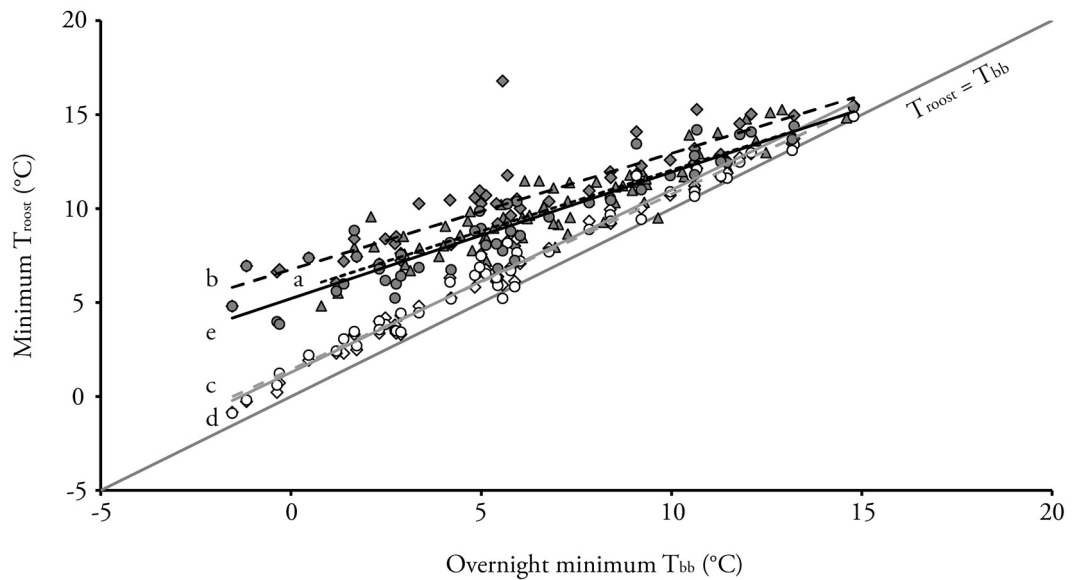


Figure 3.2: The relationship between minimum roost temperature and minimum black bulb temperature of treecreeper roost hollows. White symbols indicate the two poorly-insulated hollows (c, d), and the dark symbols the three well-insulated hollows (a, b, e), with their respective linear relationships shown by the different thin lines. The equations for these lines are given in Table 3.1.

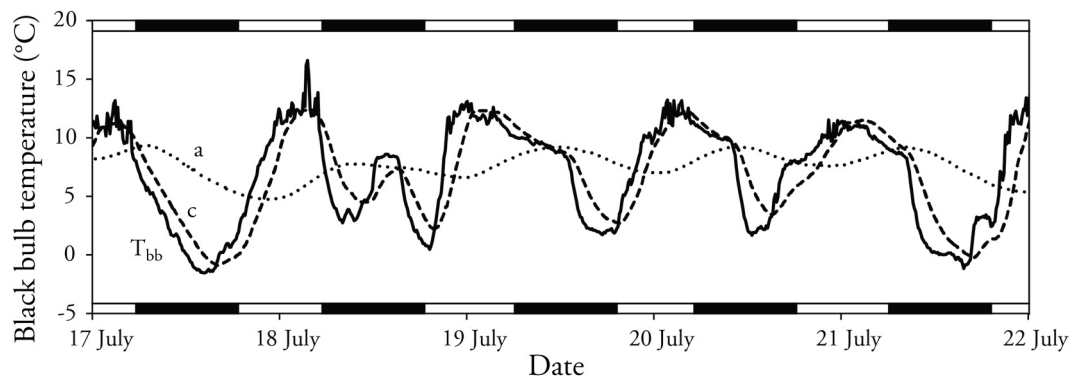


Figure 3.3: Black bulb temperature (°C; black line), and treecreeper roost hollow temperatures in a poorly-insulated (c; dashed line) and a well-insulated hollow (a; dotted line) for five consecutive nights in Dryandra Woodland. Black and white bars show nighttime and daytime respectively.

Table 3.1: Thermal and physical characteristics of treecreeper roost hollows, with thermal classification. ID, symbols and line styles are given for each hollow, as used in Figure 3.2.

ID	Hollow occupant	Sex	Cavity type	Hollow depth (cm)	DBHOB (cm)	Intercept	Slope	r ²	Thermal buffering	Symbol	Line style
a	RuTr05	♂	simple	u/k	465	-5.57	1.24	0.807	good	▲	-----
b	RuTr14	♀	simple	78	936	-7.39	1.27	0.788	good	◆	-----
c	RuTr16	♂	simple	62	251	-1.34	1.04	0.974	poor	○	———
d	RuTr17	♀	complex	106	602	-1.16	1.01	0.978	poor	◇
e	unknown	-	simple	31	280	-6.03	1.30	0.873	good	●	———

T_{bb} , and a differential that varied with $T_{bb,min}$. T_{roost} for these hollows did not immediately respond to changes in T_{bb} , so these were classified as having good thermal buffering capacity. The overnight T_{roost} in the remaining two hollows was never more than 1 °C above ambient with only a small lag between T_{roost} and T_{bb} (Figure 3.3), and slope ≈ 1 ; these hollows were classified as having a poor thermal buffering capacity. The thermal characteristics of the two hollows that were not well-insulated did not differ in slope ($P = 0.984$), and one differed in slope from the well-insulated hollows ($P < 0.045$), and the other differed from all but one ($P = 0.140$). The equations to predict T_{roost} for each of these hollows are given in Table 3.1.

Both male and female treecreepers occupied well- and poorly-insulated hollows. There was no pattern with roost hollow fidelity of individual treecreepers and hollow insulation. However the hollows that were well-insulated were all in live trees, with trunk hollows or hollows that extended back into the trunk, and all had DBHOB > 280 mm (calculated age $> \sim 82$ years). Poorly-insulated hollows were in both dead and live trees and were in both branches or the main trunk, although the live tree (with trunk hollow) had a DBHOB of only 251 mm (calculated age = 74 years).

Free-ranging body temperature

A total of 148 nights of $T_{b,field}$ data were collected from 6 treecreepers (2 female, 4 male) in June and August 2012 and June - July 2013. Sample sizes for individual birds ranged from 14 to 40 nights. Treecreepers roosted in tree hollows on all measurement nights, and although family groups would go to roost within several minutes of each other, treecreepers always roosted individually. Roost hollow fidelity varied; one treecreeper used hollows in at least three different trees, three used two different sites each, and two treecreepers only made use of a single site. Roost hollow selection may have varied with weather conditions and level of disturbance prior to roosting, and there may be an influence of sex and/or social status, as the two treecreepers that used only a single hollow were both male, and the treecreeper that used three different hollows was female, but the sample sizes were too small for formal analyses. Where multiple individuals from the same

family group each had a transmitter, they did not use the same roost hollows used by other group members.

Treecreepers commenced roosting at 12.04 ± 1.01 min after sunset ($N = 4$; $n = 24$, range: -3 to 19 min; Figure 3.4). Treecreeper roost arrival time was not influenced by T_{bb} nor atmospheric conditions (rainfall, mean wind strength or maximum wind gust) recorded at dusk (16:00 – 19:00), either individually or in combination (GLMM; $F_{1,14.3} < 2.96$; $P > 0.107$).

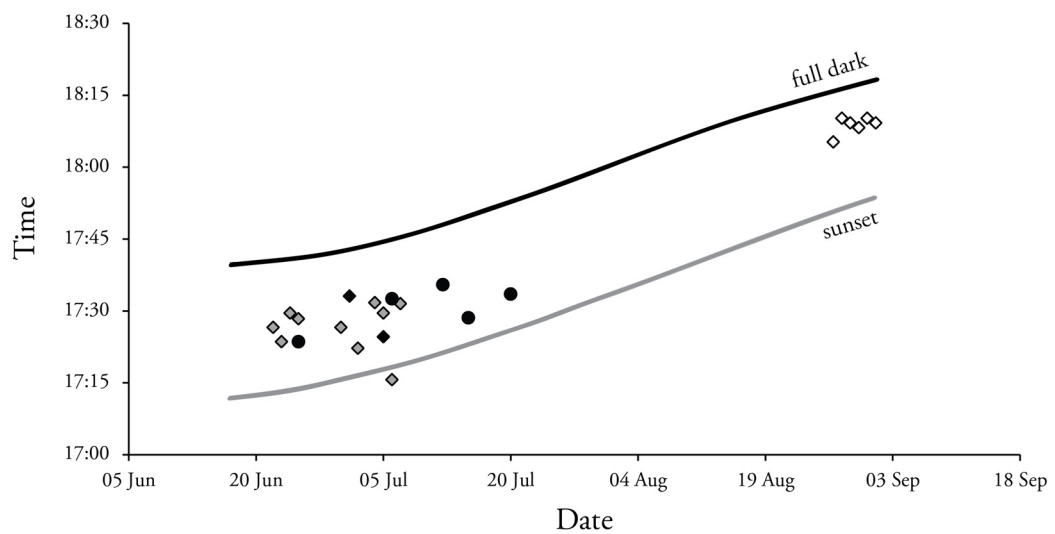


Figure 3.4: Evening roost arrival times of free-living treecreepers. Sunset is marked by the grey line, full dark by the solid line. The white diamonds identify one of the treecreepers measured in winter 2012, and the grey and black symbols are individuals measured the following year. The circles correspond to female treecreepers and the diamonds to males.

Rufous treecreepers departed their roost hollows 13.8 ± 1.7 min after first light (Figure 3.5; $n = 93$; $N = 6$; range -3 – 69 minutes). $T_{bb,min}$ was not a good predictor of roost departure time ($F_{1,30.1} = 0.208$, $P = 0.652$). None of the random factors of sex, date, day length, dawn wind speed, dawn wind direction or accumulated rainfall at dawn accounted for any of the variation in the model. Of the random factors, individual accounted for the most variance in the model (8.39), with the others all much less ($< 3.62 \times 10^{-5}$), but the majority of the variance arose from the fixed effect of $T_{bb,min}$ and residual error (255.2).

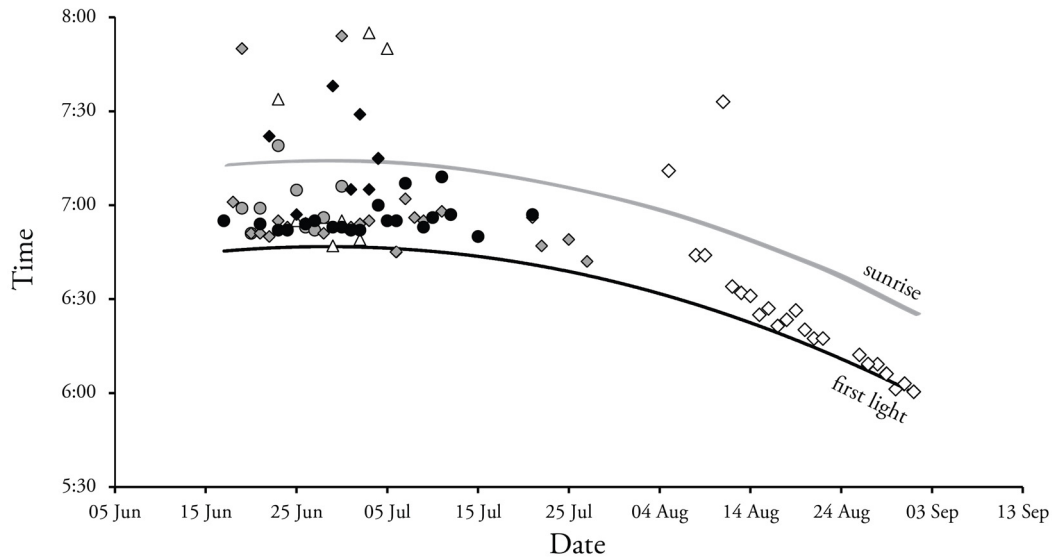


Figure 3.5: Treecreeper morning roost departure times, with time of first light marked with the solid line and sunrise marked by the grey line. The white symbols indicate the two treecreepers measured in winter 2012, and the grey and black symbols the individuals measured the following year. The circles correspond to the two female treecreepers, and the diamonds and triangles to the four males.

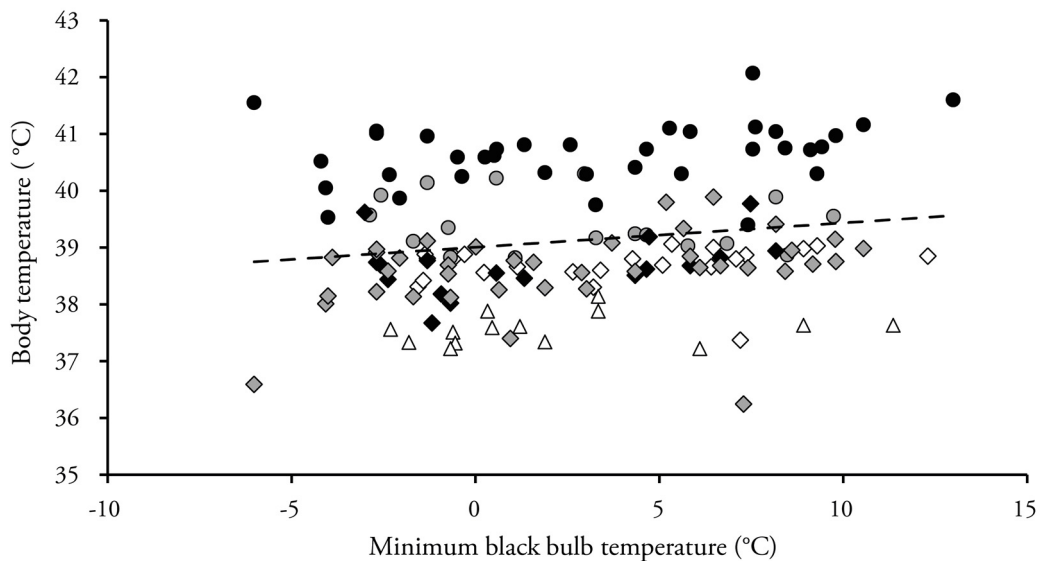


Figure 3.6: Minimum overnight field body temperature of treecreepers plotted against minimum overnight black bulb temperature ($N = 6$, $n = 148$). Each point represents a single night's minimum T_b for an individual, with the overall relationship marked by the dashed line. The white symbols show the two treecreepers measured in winter 2012, and the grey and black symbols show the individuals measured the following year. The circles correspond to the two female treecreepers, and the diamonds and triangles the four males.

Minimum T_{bb} for the measurement periods spanned a 19 °C range, with the coldest night -6.02 °C, and the warmest 12.9 °C (Figure 3.6). Mean minimum overnight $T_{b,field}$ was 39.3 ± 0.10 °C (range 37.1 – 42.1 °C). There was a small, but significant, effect of $T_{bb,min}$ on minimum overnight $T_{b,field}$ ($F_{1,63.8} = 8.07$, $P = 0.006$), with $T_{b,field}$ dropping by 0.033 °C with every 1 °C decrease in $T_{bb,min}$, as described by the equation: minimum $T_{b,field} = 0.033 * T_{bb,min} + 39.0$. Individual as a random effect accounted for the majority of the variance in the model (0.846; date 0.006; residual error 0.352).

Treecreeper $T_{b,depart}$ was 41.76 ± 0.17 °C (range 38.6 – 45.1 °C, $N = 6$, $n = 96$). Black bulb temperature at time of roost departure was not a good predictor of treecreeper $T_{b,field}$ at departure time ($F_{1,42.1} = 0.386$, $P = 0.538$). Of the random factors, individual (1.17) and sex (0.643) accounted for most of the variance in the model, with date (0.014) and early morning rainfall (0.007) contributing smaller amounts and leave time, early morning wind strength and wind direction not impacting $T_{b,depart}$ at all (<0.001 ; residual variance 0.795). Where active treecreepers returned to within range of the radio receiver during the morning, mean active T_b was 43.5 ± 0.30 °C ($N = 2$, $n = 4$).

Field behaviour

A total of 3923 field observations of treecreepers, for 16.4 bird observation hours, were made during the winter seasons of 2012 and 2013. Observations were made at a range of T_{as} (-3.31 – 27.2 °C) from pre-dawn until dusk. It is estimated that behaviour of at least 42 individuals from at least 15 different territories contributed to these observations. Including sampling session as a random effect in the GAMM always lowered the Akaike Information Criterion (AIC) value, so was it was included in each model.

Activity

Foraging, resting alert, and locomotion accounted for 95.8% of treecreeper daytime activity. Other activities included preening/maintenance behaviour and social behaviour, but these occurred at frequencies too low to be included in the analysis. The effect of T_{bb} , previous overnight $T_{bb,min}$, time of day and day of year on time spent on these three core

activities was examined individually, but only $T_{bb,min}$ and time of day had any significant effect ($\chi^2 > 7.38$, $P < 0.014$; Table 3.2).

Table 3.2: Effect of predictor variables on proportion of time that treecreepers engaged in particular activities, as determined by GAMMs, using χ^2 -tests and corresponding effective degrees of freedom (edf). Only variables that resulted in lower AIC values (listed in bold) were included in each final model.

	Model	χ^2 value	edf	p-value
Foraging				
T_{bb}	linear	1.01	1	0.314
$T_{bb,min}$	non-linear	81.8	8.1	<0.001
Time of day	non-linear	0.66	1.7	0.656
Day of Year	linear	0.801	1	0.371
Moving				
T_{bb}	linear	0.003	1	0.958
$T_{bb,min}$	non-linear	13.3	4.4	0.014
Time of day	linear	7.38	1	0.007
Day of Year	linear	0.59	1	0.441
Resting Alert				
T_{bb}	non-linear	2.90	2.2	0.258
$T_{bb,min}$	non-linear	87.3	7.8	<0.001
Time of day	linear	2.67	1	0.10
Day of Year	linear	0.003	1	0.853

Treecreepers spent 46.9% of their day foraging, mostly probing and gleaning in leaf litter, coarse woody debris, logs, and under bark. Proportion of time spent foraging varied with previous overnight minimum T_{bb} (Table 3.2); time spent foraging was highest after low overnight temperatures, decreasing to a minimum at 3 °C, before increasing again with increasing overnight temperatures (Figure 3.7).

Treecreepers spent 26.1% of time moving through their habitat, hopping along horizontal surfaces, creeping up vertical surfaces, or in flight. Proportion of time spent moving varied with overnight minimum temperature, being mostly constant but falling slightly at both low and high $T_{bb,min}$ s. Proportion of time spent moving also increased slightly, but significantly, throughout the day.

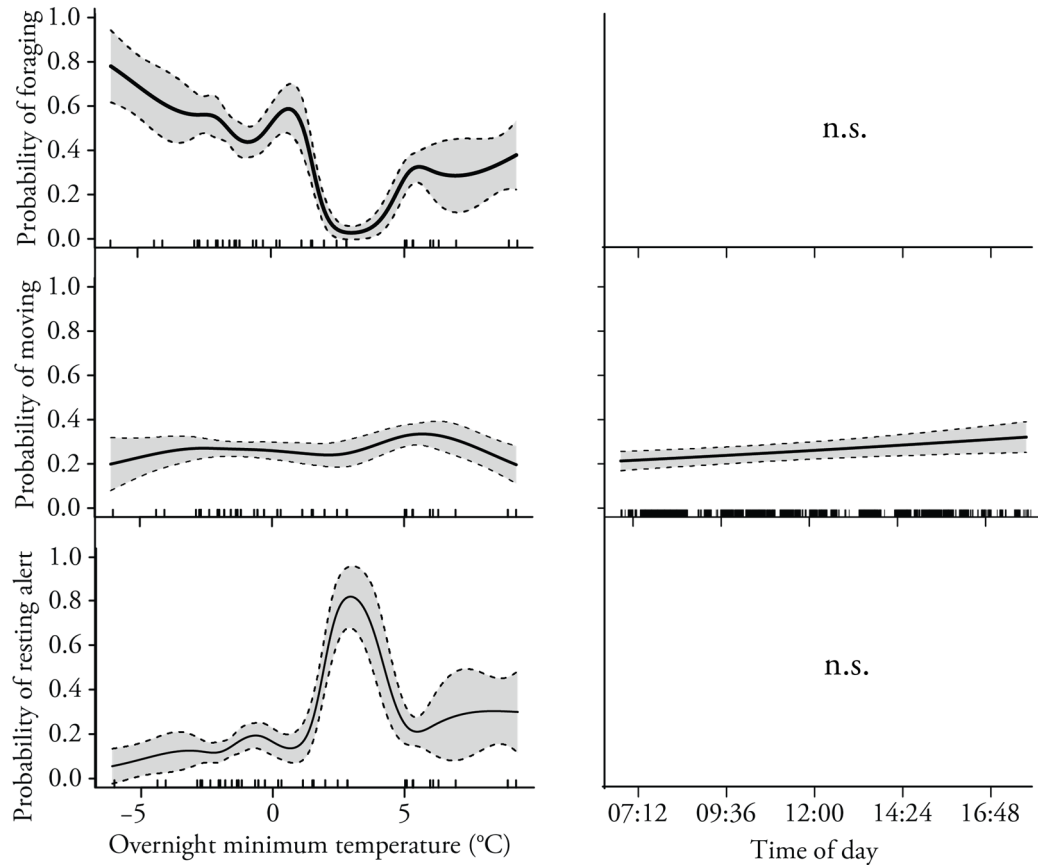


Figure 3.7: GAMM trend plots for effect of overnight minimum black bulb temperature on probability of a treecreeper being engaged in particular activities. Each row presents the output for different activities (foraging, moving, resting alert), and each column for mean overnight minimum T_{bb} (0 °C, right column) and mean time of day (12:00pm, left column). Plots include overall trend lines (solid line) with 95% confidence intervals (dashed lines). Rug plots show distribution of observations.

Treecreepers were observed resting alert in 22.8% of observations. Treecreepers became vigilant for brief periods in the middle of foraging bouts, or when perched on exposed, open locations in their habitat, such as dead branches or logs. Proportion of time spent resting alert generally increased with increasing $T_{bb,min}$, but with a large increase at $T_{bb,min} = 3$ °C.

Substrate

Treecreepers' use of different height substrate varied with current T_{bb} , $T_{bb,min}$, time of day and day of year (Table 3.3). Treecreepers were recorded on the ground (open ground, herbfields, grassland, leaf litter and coarse woody debris) in 58.9% of observations.

Treecreepers were less likely to be on the ground at low T_{bb} than when it was warmer, but were on the ground more frequently if $T_{bb,min}$ had been low (Figure 3.8).

Table 3.3: Effect of predictor variables on proportion of timetreecreepers spent in different height strata of their habitat, as determined by GAMMs, with χ^2 values and corresponding effective degrees of freedom (edf). Only variables that resulted in lower AIC values (bold) were included in the final model for each strata.

	Model	χ^2 value	edf	p-value
Ground				
T_{bb}	non-linear	24.9	6.5	<0.001
$T_{bb,min}$	non-linear	42.3	5.1	<0.001
Time of day	linear	1.03	1	0.309
Day of year	linear	1.18	1	0.278
Low				
T_{bb}	non-linear	34.1	7.2	<0.001
$T_{bb,min}$	linear	10.7	1	0.001
Time of day	non-linear	4.71	2.4	0.133
Day of year	non-linear	10.8	3.5	0.020
Mid-canopy				
T_{bb}	linear	4.94	1	0.026
$T_{bb,min}$	non-linear	17.9	4.5	0.002
Time of day	linear	10.4	1	0.001
Day of year	linear	3.16	1	0.076
High				
T_{bb}	linear	0.57	1	0.45
$T_{bb,min}$	non-linear	2.76	2.5	0.341
Time of day	linear	0.013	1	0.911
Day of year	linear	0.421	1	0.516

Treecreepers used various understorey habitat elements (logs, tree stumps, understorey shrubs and lower parts of both mid-storey and canopy trees) in 21.2% of observations. T_{bb} , $T_{bb,min}$ and day of year all affected understorey use by treecreepers. Proportions fluctuated in small peaks and troughs with changing T_{bb} (Figure 3.8). There was a linear pattern with overnight minimum temperature with time spent in understorey increasing with increasing overnight minimum and also a slight, but significant fluctuation in habitat use with day of year.

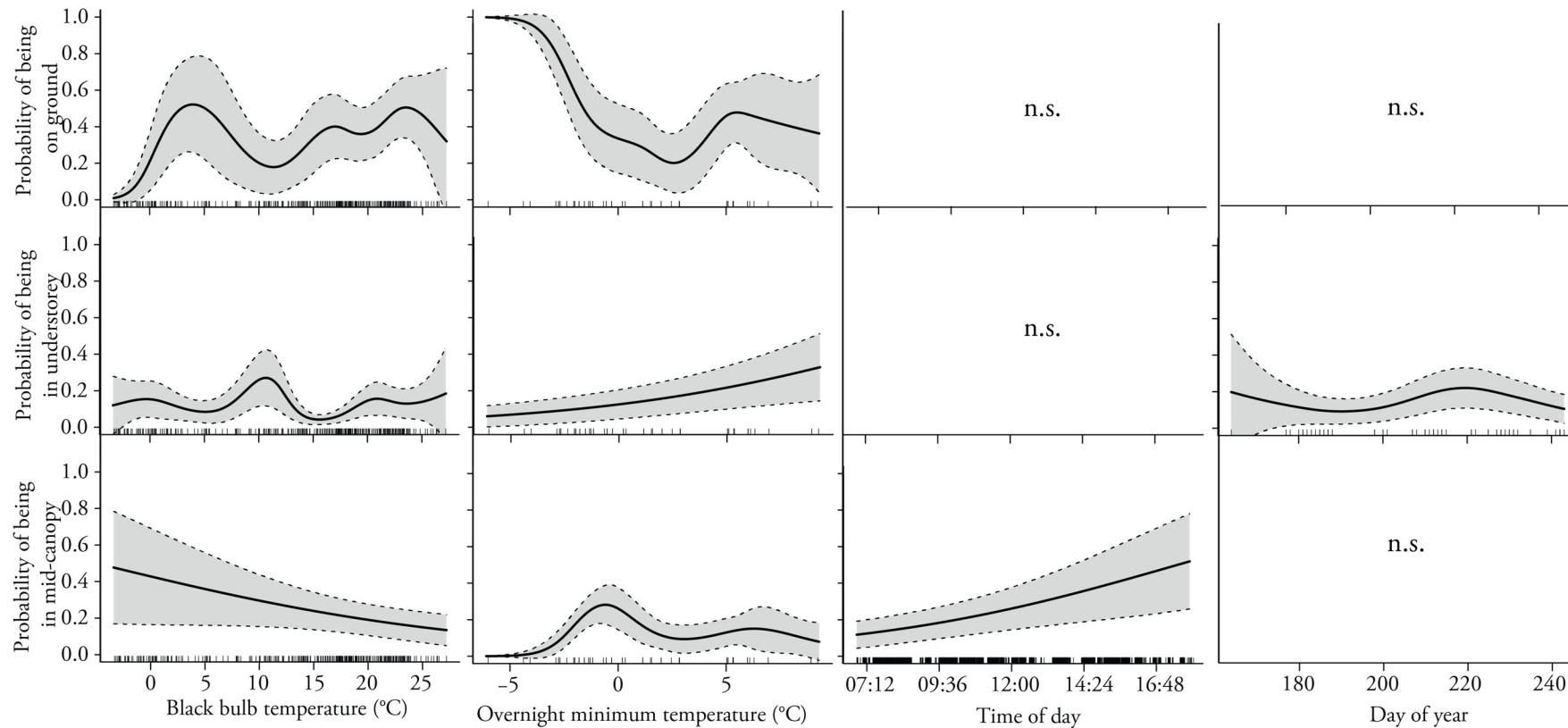


Figure 3.8: GAMM trend plots of the probability of treecreepers being on the ground, in the understorey or in the mid-storey in response to black bulb temperature (°C), overnight minimum black bulb temperature (°C), time of day and day of year. Each row is for a different model (ground, understorey, midstorey), and each column a different variable (black bulb temperature (°C), overnight minimum temperature (°C), time of day, and day of year). Plots were generated using mid-range black bulb temperatures (15 °C), mean overnight black bulb temperature (0 °C), mean time of day (12:00) and mean day of year (= 213 ; August 3rd). Plots include overall trend lines (solid lines), 95% confidence intervals (dashed lines), and rug plots showing distribution of observations. Plots could not be generated for non-significant variables, marked 'n.s.'.

Treecreepers spent 16.0% of their daytime in midstorey, in smaller trees, or in mid-storey height trunks and branches of canopy trees. Midstorey substrate use varied with three of the predictor variables. Time spent in the midstorey decreased linearly with increasing T_{bb} . Treecreepers did not use the middle canopy when $T_{bb,min}$ was minimal, but values fluctuated around an increased value as $T_{bb,min}$ increased. Time of day also affected midstorey use, with treecreepers observed more frequently in the midstorey as the day progressed.

Treecreepers were only observed in the upper canopy on 3.9% of records. At this low proportion, none of the predictors influenced time spent in the upper canopy (Table 3.3), and the null model better explained the deviance in the observations than any of the variables.

Location

To examine treecreeper preference for sunlit, patchy or shaded locations, observations made during overcast, twilight, or misty conditions (when sunlit, patchy and shaded locations were not all available to the treecreepers) were discarded, leaving a dataset of 2553 observations (10.6 bird observation hours). Minimum overnight temperature was included in all three base models, but had no effect, so it was removed in each instance (Table 3.4). Treecreepers split their time almost evenly between sunlit, patchy and shaded locations, accounting for 36.6%, 26.4% and 36.9% of observations respectively.

When the sun was out, proportion of time treecreepers were recorded in the sun varied with T_{bb} , time of day and day of year. Treecreepers were in full sun at the lowest proportions when T_{bb} was lowest, but proportions increased linearly with increasing T_{bb} (Figure 3.9). Time of day also had a linear effect on proportion of time spent in sunlit locations, with proportions decreasing as the day progressed. Time spent in sunlight was minimal earlier in the measurement period, increasing to a maximum around August 8th, and then falling again.

Table 3.4: Effect of predictor variables on proportion of time that treecreepers spent exposed to varying levels of solar radiation, as determined by GAMMs, with χ^2 values and corresponding effective degrees of freedom (edf). Only variables that resulted in lower AIC values (bold) were included in the final model for each location.

	Model	χ^2 value	edf	p-value
Sun				
T_{bb}	linear	10.3	1	0.001
T _{bb,min}	linear	0.40	1	0.529
Time of day	linear	8.83	1	0.002
Day of year	non-linear	9.54	2.35	0.013
Patchy light				
T_{bb}	linear	9.87	1	0.001
T _{bb,min}	linear	0.48	1	0.487
Time of day	linear	4.42	1	0.035
Day of year	linear	0.53	1	0.467
Shade				
T_{bb}	linear	4.7	1	0.030
T _{bb,min}	linear	0.211	1	0.646
Time of day	non-linear	19.63	2.34	<0.001
Day of year	linear	9.88	1	0.001

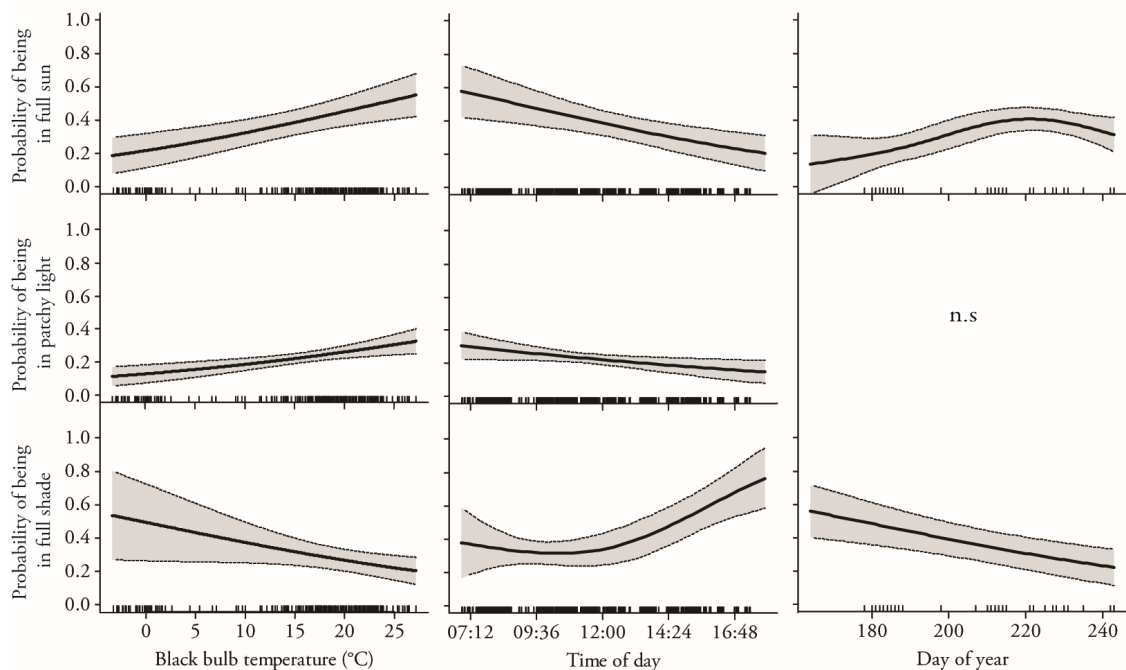


Figure 3.9: GAMM trend plots of probability of treecreepers being in full sun, patchy or completely shaded locations in response to black bulb temperature (°C), time of day and day of year. Each row is for a different model (full sun, patchy light, full shade), and each column for the different variables (black bulb temperature (°C), time of day, and day of year). Plots were generated using mean black bulb temperatures (15 °C), mean time of day (12:00) and mean day of year (= 213 ; August 3rd). Plots include overall trend lines (solid lines), 95% confidence intervals (dashed lines), and rug plots showing distribution of observations. Plots could not be generated for non-significant variables, marked 'n.s.'.

Both T_{bb} and time of day influenced time treecreepers spent in patchy light. The trends for these two variables were similar to the trends for time spent in full sun, with proportions increasing with increasing T_{bb} , and decreasing with time of day.

The response of treecreepers to T_{bb} and time of day on the proportion of time spent in shaded locations was the inverse of the patterns for time spent in full sun and patchy locations. Time spent in the shade decreased with increasing T_{bb} . Time spent in shade was consistent prior to midday, but increased throughout the afternoon. Day of year also influenced the proportion of time treecreepers spent in the shade, decreasing as the year progressed.

Laboratory respirometry

There was a significant effect of T_a on treecreeper T_b (GLMM, $F_{4,22.6} = 5.96$, $P = 0.002$; Figure 3.10A). At $T_a = 10\text{ }^{\circ}\text{C}$, T_b was $38.8 \pm 0.28\text{ }^{\circ}\text{C}$, lower than at $T_a = 30\text{ }^{\circ}\text{C}$ ($T_b = 40.7\text{ }^{\circ}\text{C}$; $t_{30} = 4.87$; $P < 0.001$) but not different from T_{bs} at the other T_a s measured ($t_{30} > 1.54$; $P > 0.134$). Individual as a random effect (0.00) did not account for any of the variance observed in the model (residual variance = 0.46).

Individual as a random effect (0.229) accounted for a significant proportion of the variance in the model for $\dot{V}O_2$ (residual variance = 0.006). Treecreeper $\dot{V}O_2$ changed with changing T_a ($F_{4,6.68} = 8.59$, $P = 0.009$, Figure 3.10B). Minimal $\dot{V}O_2$ occurred at $T_a = 20\text{ }^{\circ}\text{C}$ ($2.154 \pm 0.076\text{ mL O}_2\text{ g}^{-1}\text{ h}^{-1}$), and differed from $\dot{V}O_2$ both at $T_a = 10\text{ }^{\circ}\text{C}$ and $30\text{ }^{\circ}\text{C}$ ($3.00 \pm 0.292\text{ mL O}_2\text{ g}^{-1}\text{ h}^{-1}$; $t_{24} = 4.11$; $P < 0.001$ and $2.52 \pm 0.236\text{ mL O}_2\text{ g}^{-1}\text{ h}^{-1}$; $t_{7.4} = 7.44$; $P < 0.001$ respectively). I interpret the minimal $\dot{V}O_2$ value at $T_a = 20\text{ }^{\circ}\text{C}$ as BMR. Below thermoneutrality the relationship between T_a and $\dot{V}O_2$ can be described by the equation $\dot{V}O_2 = 3.791 - 0.085 * T_a$.

Individual as a random effect (0.036) accounted for a large proportion of the variance in the model for $\dot{V}CO_2$ (residual variance = 0.01). $\dot{V}CO_2$ of treecreepers also differed with T_a (GLMM; $F_{4,13.1} = 5.93$, $P = 0.006$; Figure 3.10C). Treecreeper $\dot{V}CO_2$ at $T_a = 20\text{ }^{\circ}\text{C}$ was

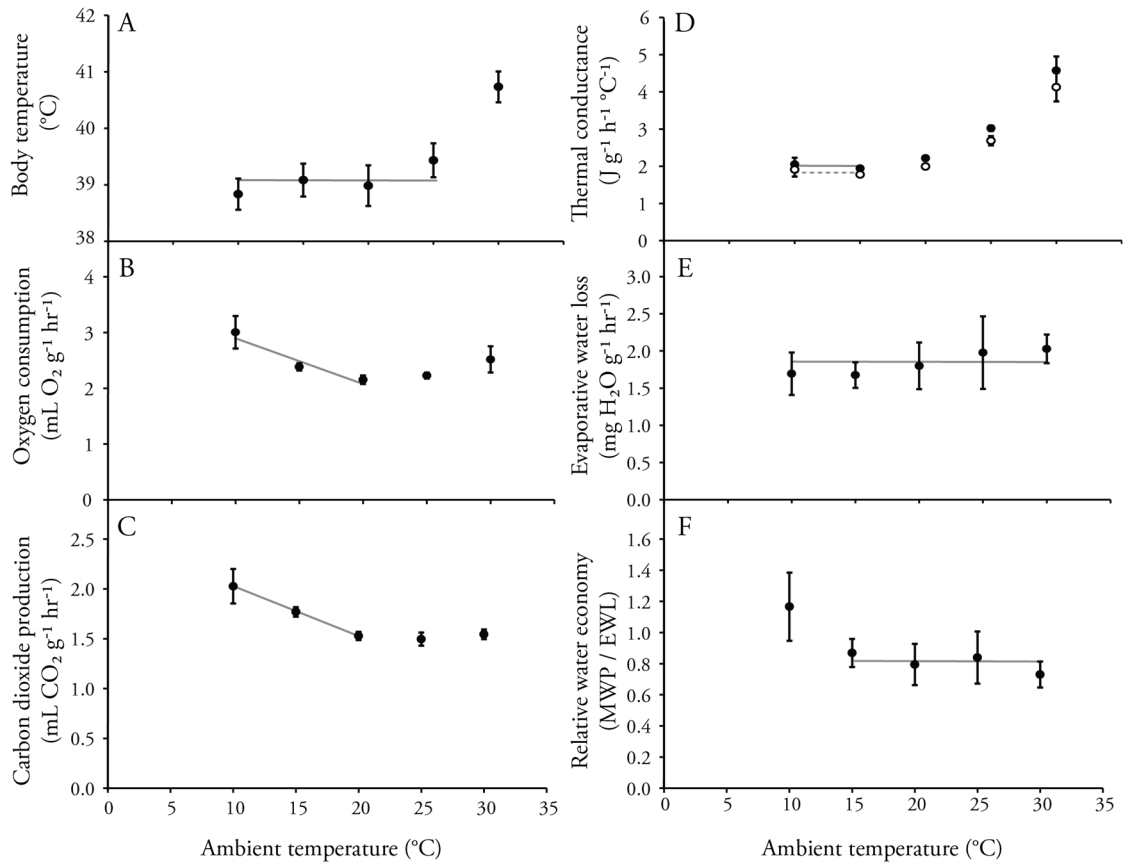


Figure 3.10: A) Body temperature, B) oxygen consumption, C) carbon dioxide production, D) wet (black symbols) and dry (white symbols) thermal conductance, E) evaporative water loss and F) relative water economy of treecreepers at a range of ambient temperatures. Symbols show mean values and error bars ± 1 standard error (N = 23, n = 30).

lower than $\dot{V}\text{CO}_2$ values measured at lower T_a s ($2.03 \pm 0.17 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $T_a = 10 \text{ }^\circ\text{C}$; $t_{28} = 4.24$; $P < 0.001$ and $1.77 \pm 0.05 \text{ mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $T_a = 15 \text{ }^\circ\text{C}$; $t_{9.5} = 2.40$; $P = 0.04$). Above $T_a = 20 \text{ }^\circ\text{C}$, there was no difference ($t_8 < -0.350$; $P > 0.736$). Below thermoneutrality the relationship between T_a and $\dot{V}\text{CO}_2$ can be described by the equation $\dot{V}\text{CO}_2 = 2.523 - 0.050 * T_a$.

As a random effect, individual was a source of substantial variation in both C_{wet} (0.272) and C_{dry} (0.270) models (residual variance = 0.007 and 0.013 respectively). T_a had a significant impact upon both C_{wet} and C_{dry} ($F_{4,6.7} = 138$, $P < 0.001$ and $F_{4,7.5} = 63.8$, $P < 0.001$ respectively; Figure 3.10D). For C_{wet} and C_{dry} , values obtained at $T_a = 15 \text{ }^\circ\text{C}$ differed from values at all other T_a s, with the exception of $T_a = 10 \text{ }^\circ\text{C}$ ($P < 0.001$ and $P < 0.01$ respectively). At $T_a = 15 \text{ }^\circ\text{C}$, C_{wet} and C_{dry} were minimal ($1.94 \pm 0.03 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ and $1.78 \pm 0.04 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$) respectively.

Individual as a random effect (0.365) was a large source of variation in the EWL model (residual variance = 0.124). There was no evidence of a T_a effect for EWL ($F_{4,12.7} = 0.685$, $P = 0.615$; Figure 3.10E). Mean EWL was $1.84 \pm 0.33 \text{ mL H}_2\text{O g}^{-1} \text{ h}^{-1}$. In modelling RWE, individual variance (0.098) was a substantial component of total variance (residual variance = 0.018). There was no overall change in RWE with T_a ($F_{4,10.4} = 1.45$, $P = 0.286$; Figure 3.10F), however comparison between the fixed effect levels demonstrated that RWE at $T_a = 10^\circ\text{C}$ was different from RWE at $T_a > 20^\circ\text{C}$ ($t_{28} > -2.175$; $P < 0.038$).

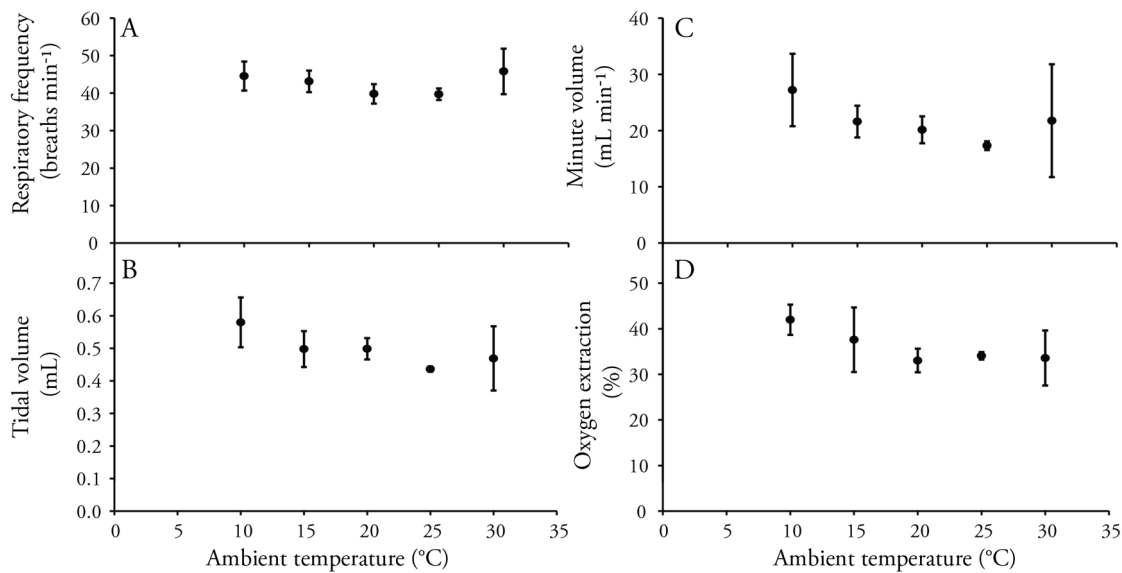


Figure 3.11: A) Respiratory frequency, B) tidal volume, C) minute volume and D) oxygen extraction for treecreepers at a range of ambient temperatures. Symbols show mean and error bars are \pm standard error.

There was no overall effect of T_a on treecreeper breathing rate (f_R ; $F_{4,11.6} = 1.52$, $P = 0.260$; Figure 3.11A), however f_R at $T_a = 30^\circ\text{C}$ ($51.7 \pm 6.06 \text{ breaths min}^{-1}$) was higher than that at $T_a < 25^\circ\text{C}$ ($< 39.7 \pm 1.68 \text{ breaths min}^{-1}$; $t_{15} = 3.02$, $P = 0.008$). There was no overall effect on V_T ($F_{4,9.121} = 0.952$, $P = 0.477$) or V_I ($F_{4,7.1} = 1.39$, $P = 0.345$) with changing T_a , but minute volume (V_I) at $T_a = 30^\circ\text{C}$ ($38.67 \pm 12.40 \text{ mL min}^{-1}$) was higher than at $T_a < 25^\circ\text{C}$ ($T_a = 25^\circ\text{C}$, $21.33 \pm 1.10 \text{ mL min}^{-1}$; $t_{9.2} = 2.85$, $P = 0.019$). There was no overall effect of T_a on treecreeper EO_2 ($F_{4,10.5} = 0.61$, $P = 0.670$). As a random effect, individual fluctuated as a component of variance for f_R (59.82, residual = 16.59), V_T (0.032, residual = 0.004), V_I (294.19, residual = 13.51) and EO_2 (96.41, residual = 16.18) in the models.

Discussion

My study is the first to examine the roosting habits and thermal biology of free-ranging Rufous Treecreepers. Treecreepers examined here used tree hollows as cryptic roost sites, but were never heterothermic and did not enter torpor. Instead they maintained homeothermy, with T_b only falling by 0.033°C with every 1°C drop in T_{bb} , even as T_{bb} fell below 0°C . While tree hollows were abundant in their habitat, the treecreepers studied here used hollows of varying quality, both well- and poorly-insulated, with no apparent preference. Furthermore, they always roosted solitarily. By not roosting communally, not selecting roosts on the basis of internal roost temperature, and not being heterothermic, the thermoregulatory strategy of the Rufous Treecreeper differs from many other endotherms.

Communal roosting is considered a trait common to many avian lineages (Beauchamp 1999). It is advantageous as it conserves energy by slowing the rate of heat lost to the environment (decreasing C_{wet} of the group), reinforces group cohesion (which is particularly important for breeding systems where extra-pair paternity is high, and improves the group's predator detection (Beauchamp 1999; Gilbert *et al.* 2010). However, these treecreepers were never observed roosting communally, and furthermore no tree hollows were used by multiple birds, even on different nights. Resource availability is unlikely to be driving this behaviour, as 29% of *E. wandoo* at Dryandra have hollows (74 hollow stems hectare⁻¹; Rose 1993). At this high density there is likely availability of large enough hollows to allow communal roosting, but it was never observed. It may be that roosting individually is advantageous, allowing treecreepers to use small tree hollows with less competition from larger animals, such as Brush-tailed Possums *Trichosurus vulpecula*. Although communal roosting can facilitate significant energy savings (30% by row-huddling Blackcaps *Sylvia atricapilla*, Wojciechowski *et al.* 2011; 30% by huddling White-browed Babbblers *Pomatostomus superciliosus*, Chapter 2), treecreepers maintain homeothermy without it. Roosting solitarily is a consistent trait within the Climacteridae (Noske 1977, 1985b; Higgins *et al.* 2001), even with interspecific differences in preferred

roost sites. So despite communal roosting being an ancestral trait, I provide here evidence for a basal passerine group (Ames 1987; Ericson *et al.* 2002) that has secondarily lost this behavioural trait.

Many birds and mammals act to minimise exposure to low T_a during their inactive phase by selecting a roost site with a favourable microclimate (House Sparrow *Passer domesticus*, Kendeigh 1961; Western Long-eared Bat *Myotis evotis*, Chruszcz & Barclay 2002; Big Brown Bats *Eptesicus fuscus*, Lausen & Barclay 2006; and Australian Owlet-nightjar *Aegotheles cristatus*, Doucette *et al.* 2011). At the high density of 74 hollow stems hectare⁻¹ (Rose 1993), there would also be potential for treecreepers to select roost sites on the basis of internal roost temperature. The hollows measured here fell into two distinct categories on the basis of their thermal characteristics, well-insulated hollows, that maintained a temperature separate from T_{bb} conditions, and poorly-insulated hollows, that mirrored T_{bb} closely. The hollows that could buffer the occupant against the extremes of ambient environmental conditions were primarily in large-diameter, live trees, in agreement with observations of tree cavities in the northern hemisphere (Wiebe 2001; Paclík & Weidinger 2007).

Despite the energetic savings possible from careful roost site selection, there was no evidence that well-insulated hollows were used preferentially by treecreepers. Neither was there a pattern between roost hollow fidelity and thermal characteristics of hollows. For Australian Owlet Nightjars (*Aegotheles cristatus*) that also use roost sites of varying thermal characteristics, use of poorly-buffered roost sites correlated with increased incidence and duration of torpor (Doucette *et al.* 2011), but there was no evidence of a relationship between hollow choice and $T_{b,field}$ for treecreepers. Roost temperature was not a key driver of treecreeper roost site selection, as treecreepers did not use them preferentially even in a habitat where thermally-buffered roost sites may be abundant (Rose 1993). This supports the hypothesis that treecreepers can physiologically balance their energy expenditure without such an energy-saving behaviour.

There is some overlap between treecreeper roost and nest hollow characteristics. In my study treecreepers preferred nocturnal roost hollows on the north and eastern sides of trees, in agreement with Craig's (2007) observations of nest hollow preference of treecreepers in jarrah (*E. marginata*) forest. Several northern hemisphere species select nest hollows facing specific directions that confer significant energy savings, through the amount of daytime solar radiation the tree trunk intercepts (Paclík & Weidinger 2007). For spring-breeding treecreepers, similar thermal benefits would be expected to drive nest hollow selection, as eggs are incubated during the daytime, but this would have little benefit for roost hollows that are vacant during the day. In 87% of instances, treecreepers departed roost hollows before sunrise, so they receive no energetic advantage in the form of passive rewarming from solar radiation in the mornings.

I found no evidence of unusual treecreeper physiology. Some hollow-using endotherms select cryptic refuges that provide no thermal benefit, but reduce the likelihood of predation while hypothermic or torpid (as seen in Lesser Long-eared Bat *Nyctophilus geoffroyi* and Gould's Wattled Bat, *Chalinolobus gouldii*, Lumsden *et al.* 2002; Australian Owlet-nightjar *Aegotheles cristatus* Brigham *et al.* 2000; Sugar Gliders *Petaurus breviceps*, Körtner & Geiser 2000; and Numbat, *Myrmecobius fasciatus*, Cooper & Withers 2004). But here the physiological response of treecreepers to T_a was typical of a general homeotherm (Withers 1992), with no evidence of torpor. Below thermoneutrality ($T_a < 20\text{ }^{\circ}\text{C}$), treecreepers maintained T_b with a 40% increase in metabolic rate and a 20% decrease in wet thermal conductance. The transition between active- and rest-phase states for treecreepers was also similar to that recorded elsewhere for non-torpid, non-hypothermic birds (for example Red-billed woodhoopoes *Phoeniculus purpureus* Boix-Hinsen & Lovegrove 1998), and typical for endotherms (Refinetti & Menaker 1992; Schmidt-Nielsen 1997). That is, they arrived at evening roost sites with an active-level T_b , before T_b dropped to a rest-phase T_b that was maintained at a near constant level for the rest of the night. Treecreepers warmed endogenously before departing from their roost site, and had achieved a similar T_b as active-level T_b before sunrise and any potential for passive rewarming.

Geiser *et al.* (2000) suggest that studies of animals in captivity can underestimate the capacity for hypothermia and torpor. Here a comprehensive methodology using both free-ranging animals as well as measuring field-fresh individuals under laboratory conditions demonstrated consistency in both T_b values and patterns of change. Measurements of $T_{b,field}$ were consistent with T_b laboratory respirometry experiments, where T_b (38.85 °C at $T_a = 10$ °C) was maintained only 0.15 °C lower than thermoneutral body temperature (39.0 °C at $T_a = 20$ °C). The extent of interindividual variation in T_b at each T_a was also consistent with my laboratory study. I am confident data obtained here are an accurate representation of the range of thermoregulatory mechanisms used by treecreepers in this habitat in winter, and they do not use heterothermy, including torpor, for energy savings.

When comparative physiological values obtained for a single species are placed in an allometric and phylogenetic context, disproportionately high or low values give evidence of a high or low energy strategy respectively, and may be used to identify a potential predisposition for torpor (Geiser 1998). Body temperature, BMR, C, EWL, f_R , V_T and EO_2 values obtained here for Rufous Treecreepers under standard conditions were compared with those of other species. The methodology for data collection and analysis is outlined in Chapter 6, and the comparative datasets are presented in Appendix 1. There was limited evidence from these physiological variables that treecreepers are physiologically unusual in comparison with other birds.

Free-living treecreepers maintained a near-constant typical avian T_b overnight in sometimes sub-zero conditions. Both the mean active-phase ($T_{b,depart}$) and rest-phase T_b (minimum $T_{b,field}$) values observed here for free-ranging treecreepers were all well within the range of T_b s recorded for other passerines (41.6 ± 1.13 °C and 38.9 ± 0.87 °C respectively; Prinzinger *et al.* 1991). The T_b s measured in the laboratory were also comparable to other birds of equivalent mass, with T_b conforming closely to allometric predictions before and after accounting for phylogeny (Figure 3.12A). Treecreeper BMR and C_{wet} were 88% and 68.5% respectively of allometric predictions, but both fall within

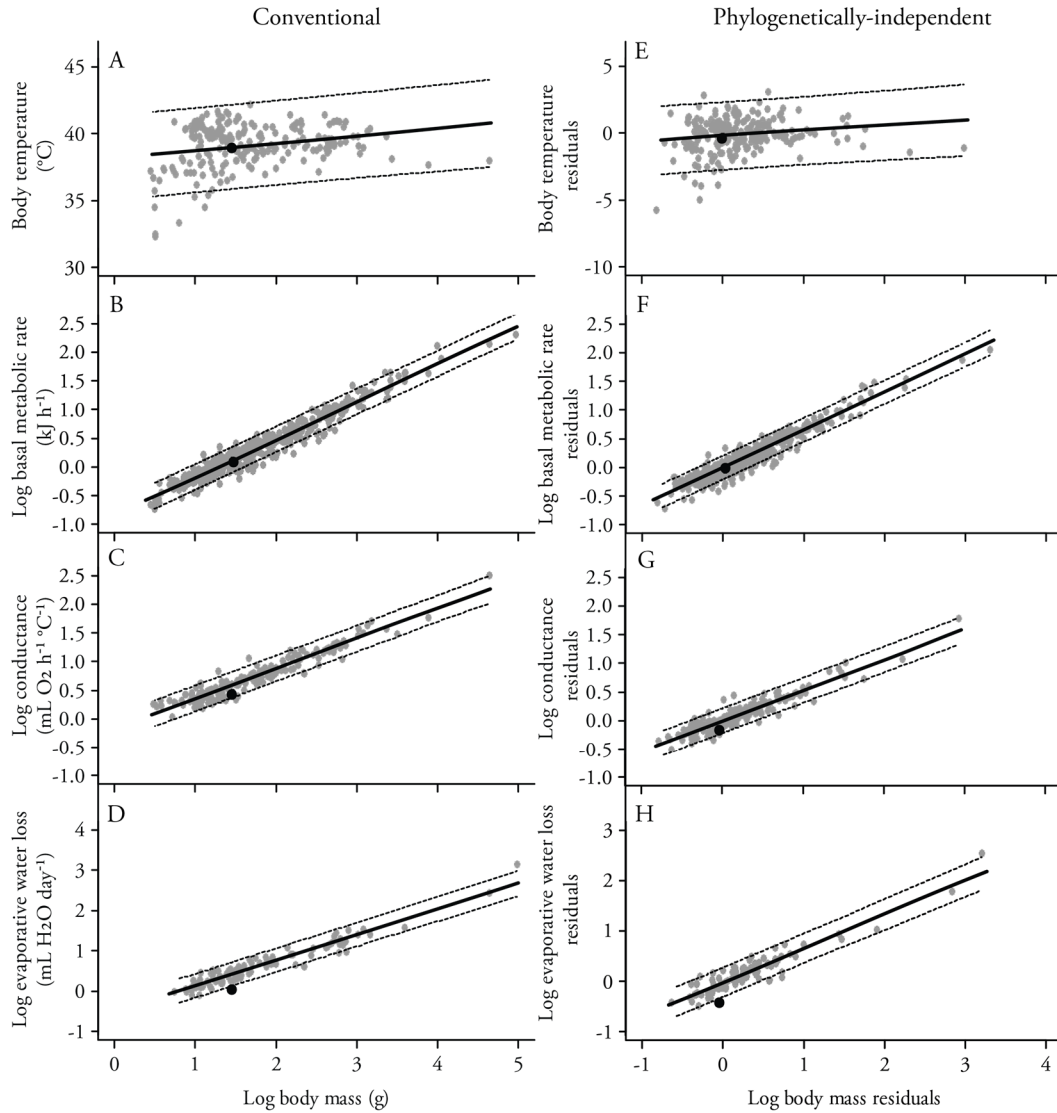


Figure 3.12: Allometric comparison of body temperature (A), basal metabolic rate (B), conductance (C), and evaporative water loss (D) for treecreepers (black symbols) compared with other birds (grey symbols). Phylogenetically-independent residuals are shown in E – H respectively. All values are \log_{10} values, with the exception of body temperature, which is untransformed. Solid lines are the least squares regression lines and the dotted lines are 95% prediction intervals. Methodology is described in Chapter 6 and datasets are presented in the Appendices.

the 95% prediction interval for birds before and after accounting for phylogenetic history. Treecreeper ventilatory variables of f_R and V_T were within the 95% prediction intervals (66.5% and 82.3% respectively; Figure 3.13A; B), which did not alter after correcting for phylogeny. While there was no significant allometric relationship between EO_2 and body mass, treecreeper EO_2 was also within the cluster of values recorded for other species.

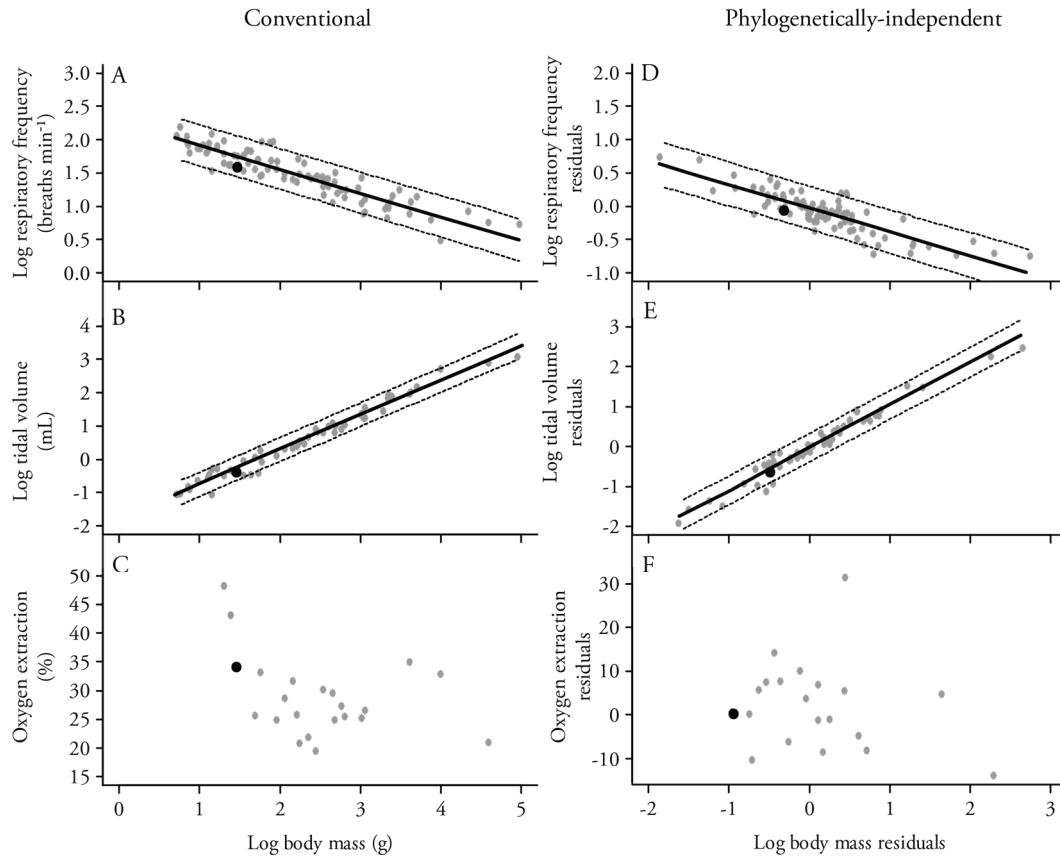


Figure 3.13: Allometric comparison of respiratory frequency (A), tidal volume (B), and oxygen extraction (C) for treecreepers (black symbols) compared with other birds (grey symbols). Phylogenetically-independent residuals for the same parameters are displayed in D – F respectively. All values are represented as \log_{10} values, with the exception of oxygen extraction, which is untransformed. Where a linear relationship exists, solid lines mark the least squares regression lines and the dotted lines 95% prediction intervals. Methodology is described in Chapter 6 and datasets are presented in the Appendices.

The minimal EWL of treecreepers was only 66.2% of that predicted from body mass, which fell below the 95% prediction limits for both conventional and phylogenetically-independent allometric relationships. Low minimal evaporative water loss is often considered an adaptation to arid environments, as frugality is a necessity where water availability is low (Williams 1996). For a sedentary, insectivorous bird living in a habitat with substantial variation in T_a and only seasonal access to standing water, this is unsurprising. However, methodological differences in EWL measurement may impact on comparisons (Cooper & Withers 2009; Page *et al.* 2011; Connolly & Cooper 2014). The low minimal EWL measured here may be related to my using a long measurement duration to obtain a true minimal EWL value, compared to other studies that measured

birds for shorter durations. A more comprehensive dataset of truly minimal, standard EWL variables for birds would be useful to better interpret divergence from predictions.

When considered together, comparative physiological variables suggest little unusual in the physiology of treecreepers. With the exception of EWL, despite a small tendency for frugality, all other variables are well within the 95% prediction limits both before and after accounting for phylogeny. This suggests the thermal biology of treecreepers is consistent with that of other birds and that a specialised physiology is not required by them to maintain homeothermia overnight in the cold environment examined here.

Even small reductions in MR can result in significant energy savings for small passerines (Willis & Brigham 2003). This can be quantified for treecreepers by calculating metabolic rate from field T_b measurements (Withers *et al.* 1990; Cooper & Withers 2004b) using the equation $\Delta T_{b,field} = 20.1 * [\dot{V}O_{2,calc} - C * (T_{b,field} - T_{bb})] / (m * SH)$, where ΔT_b is the change in body temperature ($^{\circ}C \text{ min}^{-1}$; calculated from a running average of $T_{b,field}$ values at 10 min intervals), $\dot{V}O_{2,calc}$ is calculated rate of oxygen consumption ($\text{mL O}_2 \text{ min}^{-1}$), C is thermal conductance ($\text{ml O}_2 \text{ }^{\circ}C^{-1} \text{ min}^{-1}$; minimal treecreeper conductance was $1.94 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^{\circ}C^{-1} = 0.047 \text{ ml O}_2 \text{ }^{\circ}C^{-1} \text{ min}^{-1}$), m is body mass (g ; 28.95 g), SH is the specific heat of tissues ($3.47 \text{ J g}^{-1} \text{ }^{\circ}C^{-1}$) and 1 ml O_2 is assumed to be equivalent to 20.1 J. For an individually-roosting treecreeper where ambient conditions dropped to below $0^{\circ}C$, MR calculated from actual $T_{b,field}$ is slightly, but consistently lower than if $T_{b,field}$ had remained normothermic ($39.825^{\circ}C$; Figure 3.14). Excluding the endogenous rewarming phase, this equates to an average energy saving of $0.205 \text{ mL O}_2 \text{ g}^{-1} \text{ hr}^{-1}$, or 1.19 kJ over 10 hours. Values closely approximate those calculated from laboratory data. At 01:00, when $T_a = 0.956$, $\dot{V}O_2$ calculated from T_a is $3.71 \text{ mL O}_2 \text{ g}^{-1} \text{ hr}^{-1}$, where calculation based upon T_b gave a $\dot{V}O_{2,calc}$ of $3.68 \text{ mL O}_2 \text{ g}^{-1} \text{ hr}^{-1}$. Using Majer *et al.*'s (2003) trunk invertebrate capture data from *E. wandoo* trees in Dryandra in June to calculate mean invertebrate mass (0.760 mg), and Withers *et al.*'s (2016) values for digestibility and energy content of arthropods (21.7 kJ g^{-1}), this is equivalent to requiring 73 fewer prey items per day (0.055 g).

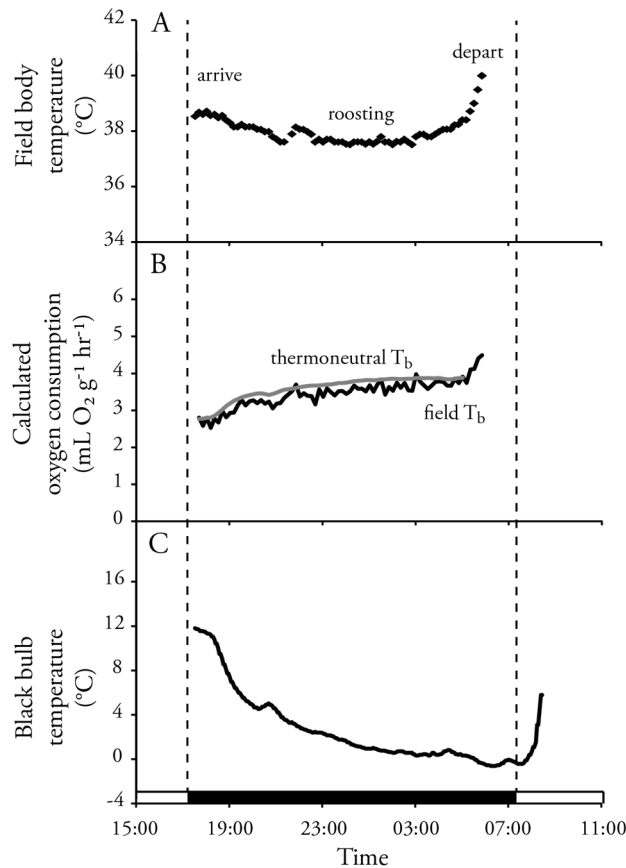


Figure 3.14: Field body temperature (A) and calculated metabolic rate (as oxygen consumption; B) of a single, free-ranging treecreeper under black bulb temperature conditions (C) for a single night, June 28th, 2012. B shows both the calculated metabolic rate based on the measured body temperature (black line), as well as the predicted metabolic rate if body temperature had been kept at thermoneutral (grey line). The black bar and the dotted lines mark the period from sunset to sunrise.

Models of avian daily activity patterns link the intensity of foraging behaviour with the degree of energy shortage (Bednekoff & Houston 1994). Here, while exhibiting only limited physiological responses to low T_{bb} , treecreepers used a substantial behavioural strategy to meet their energetic requirements, spending a greater proportion of time foraging after nights of low minimum T_{bb} . While increased time spent foraging does not necessarily equate to increased food intake, treecreepers glean and probe under bark and in leaf litter for invertebrates (Recher & Davis 1998; Moore *et al.* 2013b), so the activity levels of their ectothermic prey are not as important for foraging success, and birds can likely obtain food at a range of ambient conditions. Contrary to many northern hemisphere studies where diurnal birds exhibit a bimodal foraging pattern with time of

day (Aschoff 1966; Bednekoff & Houston 1994), here time of day had no influence on time spent foraging. However, this may be indicative of treecreepers in general, as both foraging substrate and proportion of time spent foraging was similar to that of Rufous Treecreepers studied elsewhere (Recher & Davis 1998; Craig 2002, 2007) as well as other Climacteridae, such as Brown Treecreepers (Antos & Bennett 2006).

Treecreepers spent a greater proportion of time in sunny locations early in the day, but this was not necessarily evidence of basking. Treecreepers were more likely to be in sunlit locations first thing in the morning regardless of ambient conditions, with the proportion of time spent in the sun decreased with decreasing T_{bb} , contrary to what would be expected if birds were making use of solar radiation to passively maintain body temperature. Some species, such as honeyeaters (Meliphagidae) show significant diurnal shifts in foraging substrate and food type (Timewell & McNally 2004). Here, treecreepers may also be switching between prey types in different locations in response to changes in the activity patterns of prey, in the process passively intercepting solar radiation.

In summary there is no evidence that extreme behavioural or physiological strategies are necessary for treecreepers to survive the energetic challenges of their winter environment. They maintain homeothermy while roosting alone in refuges of varying quality, meeting energy requirements with a slight increase in time spent foraging after nights of low T_{bb} . This suggests that distribution of Rufous Treecreepers is unlikely to be driven by thermal environmental variables, only the availability of tree hollows. While studies suggest treecreepers are sensitive to habitat quality, particularly post-fire age, vegetation maturity and tree cover (Craig 2007; Fox *et al.* 2016), these are factors that all relate to tree hollow availability, not thermal characteristics of tree hollows. In habitats where density of tree hollows is low, or competition for hollows is great, roosting individually in tree hollows may limit the density of Rufous Treecreepers, as seen in other hollow-dependent species (Newton 1994; Lohmus & Remm 2005; Lutermann *et al.* 2010). But this is unlikely to be the case in the mature wandoo woodland studied here, where both Rufous Treecreepers and roost hollows are common (Recher & Davis 1998; Moore *et al.* 2013b).

Going it alone: Thermoregulatory strategies of the Western Yellow Robin *Eopsaltria griseogularis*, a small, solitary roosting insectivore

Abstract

Rates of heat exchange with the environment vary inversely with body size, so small endotherms gain substantial energetic benefits from undergoing controlled hypothermia or torpor when exposed to cold conditions. At 18.5g, the small, territorial Western Yellow Robin is in the size range of passerines predicted to use torpor (<20g). Here I examine the physiological and behavioural responses of robins in the context of the consequences of meeting the increased energy demands of winter. Despite experiencing below-freezing overnight winter temperatures in their temperate woodland habitat, robins roosted alone in foliage, and did not use social thermoregulation or roost site selection to facilitate energy balance. There was limited evidence for nocturnal hypothermia or torpor for wild, free-living robins, as at ambient temperatures as low as -3.95 °C mean skin temperature ($T_{b,skin}$) was maintained at 35.0 °C. In the laboratory, open-flow respirometry measurements of metabolic rate, evaporative water loss and body temperature at a range of ambient temperatures (10 °C – 32.5 °C) showed that robins had a typical endothermic response to low ambient temperature of elevated metabolic rate, with no evidence of torpor. Mean body temperature of birds in the laboratory at 10 °C was only 1.9 °C lower than that at thermoneutrality (38.6 °C, $n = 7$), maintained by an 51% increase in metabolic rate and an 23% decrease in thermal conductance. Diurnal behavioural observations of wild robins suggest that a low energy foraging strategy and a long active phase likely assist in helping these small passerines meet their energy demands during winter.

Introduction

For small sedentary passerines in cold conditions, the energetic incentives for thermoregulatory mechanisms that limit heat loss to the environment should be great. In an environment with large daily and seasonal temperature variation, these endotherms may modify behaviour to avoid sub-optimal environmental conditions and/or have physiological responses that provide for meeting the energetic demands of cold exposure, particularly in winter. Australian environments, characterised by low primary productivity, low rainfall, high evaporation and periodic drought (Geiser *et al.* 2006), present sedentary endotherms with both challenging thermal environments and constraints on resource acquisition. While much is known about how small Australian mammals address these challenges (Geiser 1994; Withers *et al.* 2004; Geiser 2004a), relatively little is known regarding the corresponding physiological and behavioural mechanisms used by sympatric birds (Astheimer & Buttemer 2002; Geiser *et al.* 2006).

In the northern hemisphere, faced with a snow-bound winter, many passerines use a behavioural mechanism to avoid cold conditions – migration (Geiser *et al.* 2006). However neither migration nor nomadism are common strategies for Australian passerines (Allen & Saunders 2002; Withers *et al.* 2004). In Australia's arid interior avian nomadism is best predicted by body mass and diet, as insectivorous birds are more likely to be sedentary (Tischler *et al.* 2013), and large nectarivorous birds nomadic (Allen & Saunders 2002).

A sedentary organism must survive the potentially wide range of seasonal conditions in their habitat (Reinertsen 1983; Geiser *et al.* 2006). The foraging routines of insectivores and other visual predators rely on the activity patterns and abundance of their prey. In winter, low T_a reduces invertebrate activity, shorter daylight hours reduce foraging time (Reinertsen 1983), and increased chance of inclement weather further reduces foraging opportunities. Under these circumstances (Timewell & McNally 2004), there is an increased probability of food shortage and hence energetic stress. Geiser *et al.* (2006) argue that Australian sedentary insectivorous birds, will be exposed to energy shortages both in

predictable seasonal cycles and during less predictable weather events, so appropriate physiological response mechanisms are necessary for their long-term survival. These should be most evident when environmental conditions are the harshest, as in winter when T_a s are low and nights are long. Indeed, endotherms that rely on a food source that is unpredictable (e.g. Fat-tailed Dunnart *Sminthopsis crassicaudata*; Munn *et al.* 2010) or that experience predictable or periodic conditions of food shortage are more likely to be heterothermic (McKechnie & Lovegrove 2002; Geiser 2004a), and specific food shortage events are triggers for reductions of T_b and metabolic rate in heterothermic endotherms.

Physiological strategies such as the controlled reduction of metabolism and body temperature during hibernation, daily torpor or nocturnal hypothermia have been extensively studied amongst some endotherm groups, particularly mammals (Grigg *et al.* 2004; McKechnie & Mzilikazi 2011; Tattersall *et al.* 2012; Ruf & Geiser 2014).

Although globally only one bird species has been observed to hibernate (Common Poorwill, *Phalaenoptilus nuttallii*, Jaeger 1949), less severe forms of heterothermy are slightly more widespread. Hypothermic responses have been documented in 11 bird orders (McKechnie & Lovegrove 2002), and torpor has been reported in 7 bird orders, three of them in Australia – Caprimulgiformes, Apodiformes and Passeriformes (Geiser *et al.* 2006). While many taxa yet to be thoroughly investigated, Australian passerines that have been reported to use torpor are mostly small, feed on active prey, with varied roosting habits, such as Dusky Woodswallow (*Artamus cyanopterus*, ~36g; Maddocks & Geiser 2007), White-backed Swallow (*Cheramoeca leucosternus*, ~15.6 g; Serventy 1970), Mistletoebird (*Dicaeum hirundinaceum*, ~8.5 g Heumann 1926), and Welcome Swallow (*Hirundo neoxena*, ~17.5 g; Dove 1923).

For a small, sedentary insectivore that such as the Western Yellow Robin (*Eopsaltria griseogularis*, 18.5g) that feeds on active prey, and presumably roosts in the open canopy, heterothermy may be predicted to be a beneficial energy-conservation trait during winter. Here I quantify the thermal physiology of the Western Yellow Robin (hereafter robin),

using a comprehensive methodology incorporating standard laboratory respirometry and field skin temperature ($T_{b,skin}$) telemetry, roost temperature measurement and daily activity observations. These methodologies were used to quantify the physiological and behavioural thermoregulatory strategies of this species to identify the mechanisms used by this small, sedentary endotherm in response to environmental challenges.

Methods

Study site

Robins were studied in main block of Dryandra Woodland (32°45'S, 116°55'E), the same location used for White-browed Babblers (Chapter 2) and Rufous Treecreepers (Chapter 3). Robins are common at Dryandra (Recher & Davis 1998), and the free ranging telemetry work took place at different sites to the capture work for laboratory respirometry (Figure 4.1).

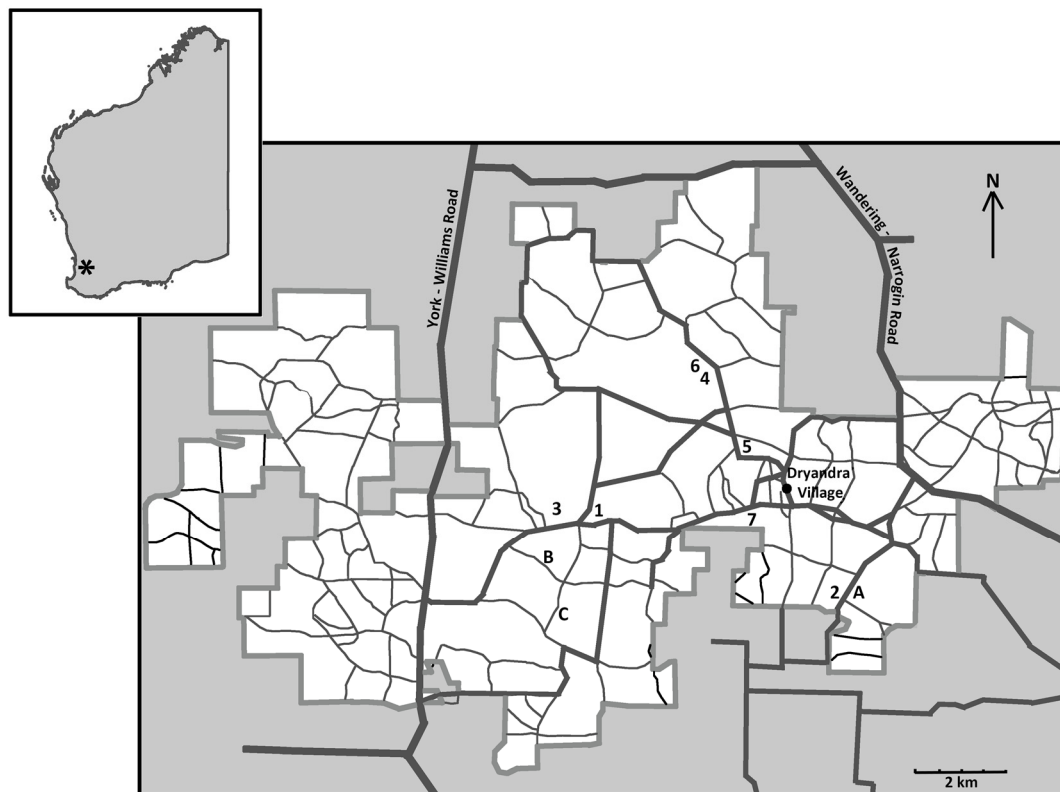


Figure 4.1: Map of main block of Dryandra Woodland, Western Australia. Sites marked A, B and C were used for capture of Western Yellow Robins for respirometry experiments. Sites 1 to 5 were used for collection of $T_{b,skin}$ data in winter 2012 and 2013. All sites were utilised for collection of behavioural observations.

Free-ranging body temperature

Seven robins (18.5g), three in winter 2012 and four in winter 2013, were captured with mistnets using audio playback (calls modified from BOCA 2007 and Stewart 2005). All individuals, as well as any additional conspecifics caught, were marked with a unique colour combination of plastic leg bands to aid field identification. In winter 2012, robins were fitted with temperature-sensitive radio transmitters (BD-2NT 0.55 g; Holohil Systems Ltd) glued to the skin in the interscapular region. Glued-on transmitters became loose within several days of attachment however, and robins were difficult to recapture for reattachment. So, in winter 2013, the same model transmitter was instead fitted to the robins with a small backpack harness, consisting of the radio transmitter glued to a rubber band (total mass ~0.7 g; Figure 2.2). The loops of the band went over the robin's wings and held the temperature-sensitive component of the transmitter against its dorsal skin surface. After preening, the transmitter was completely covered by the plumage. Both methods yielded equivalent skin temperature ($T_{b,skin}$) data, so data from both years were pooled.

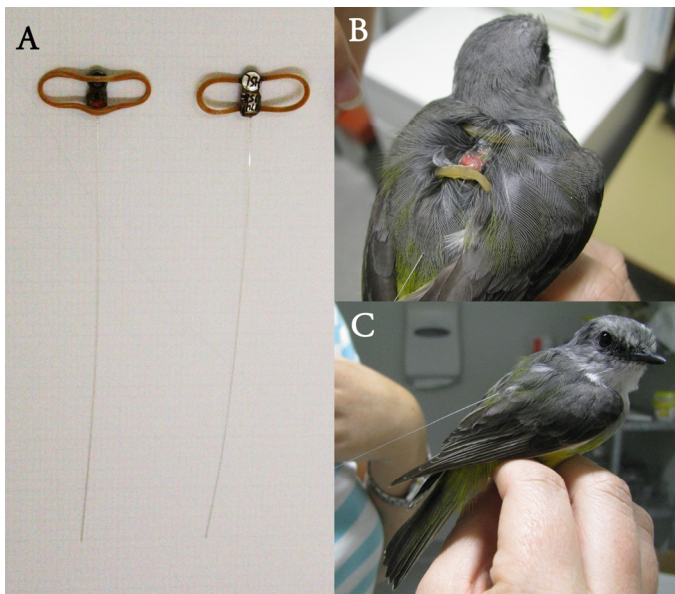


Figure 4.2: Transmitter backpack harnesses used to measure skin temperature of free-living robins: A) The backpack harness, with Holohil BD-2NT temperature sensitive transmitter attached to a rubber band, from above (left) and below (right); B) Robin with freshly-fitted transmitter, with feathers smoothed back to show dorsal placement of transmitter and wing loops; C) Robin with fitted harness, showing plumage completely covering transmitter.

In both years, transmitters were calibrated as for those used on White-browed babblers (Chapter 2). Robins were followed at a distance by their calls and/or by tracking their transmitter to evening roost sites, until lack of further movement indicated birds had roosted for the night. Skin temperature and environmental data were collected, screened and translated as for White-browed Babbler (Chapter 2).

Robins never roosted close enough to detect multiple birds with the same antenna, so each sound file was only ever recording one bird per night. Final parameters included in the analysis included minimum $T_{b,skin}$, time and T_{bb} at minimum $T_{b,skin}$, minimum T_{bb} and $T_{b,skin}$ and T_{bb} at time of roost departure (Figure 4.3). Thermolability was approximated for free-ranging robins as $\Delta T_{b,skin} / \Delta T_{bb}$ (Withers & Cooper 2009).

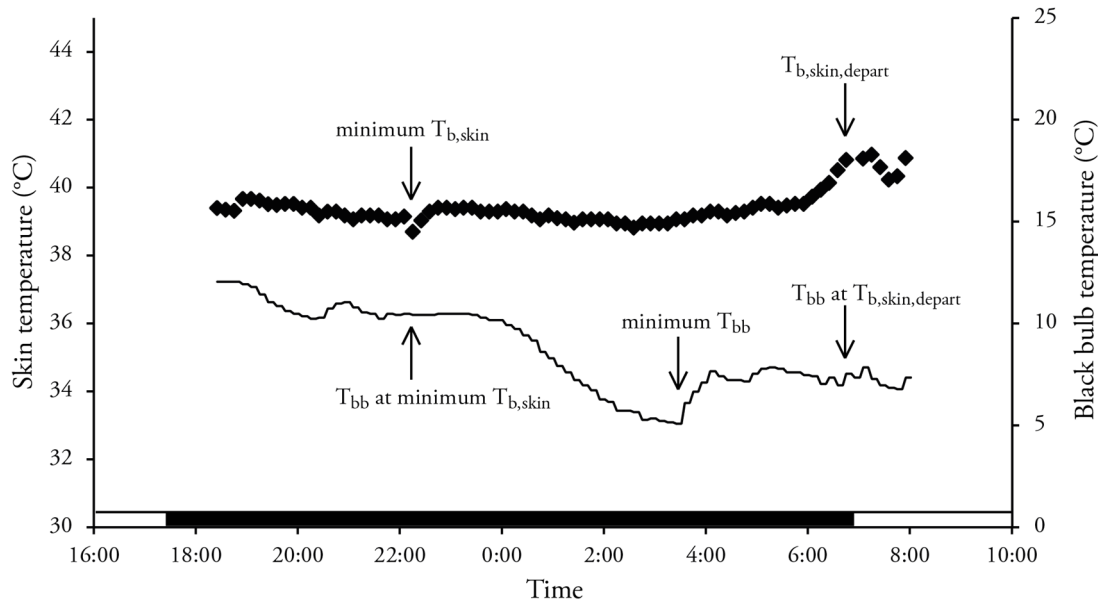


Figure 4.3: Typical overnight skin temperature (°C) of a Western Yellow Robin (black symbols), measured on the 29th July 2013, with likely roost departure time indicated. Black bulb temperature (°C; solid line) is shown on the secondary axis. The dark bar indicates the period between sunset and sunrise.

Field behaviour

Behavioural observations of free-living robins were collected opportunistically at various locations throughout Dryandra woodland (Figure 4.1), using methodology as for White-browed Babblers (Chapter 2).

Laboratory respirometry

Eight non-breeding adult Western Yellow Robins (18.5 g) of unknown age and sex were caught at several sites at Dryandra Woodland (see Figure 4.1) in autumn 2012 (N = 3), spring 2012 (N = 2) and autumn 2013 (N = 3), using mistnets and audio playback. Robins were transported to Curtin University's Bentley campus and housed in densely-vegetated outdoor aviaries as family groups. A mix of live food (crickets, wood roaches, termites,

earthworms, moths and mealworms) and an artificial diet (insectivore mix, ground dog biscuits, boiled egg and grated cheese) and water, were available *ad libitum*, except for the 12 hours prior to experiments when the individuals to be measured were placed in a fasting cage, with access to water but no food. All birds were allowed at least three days between successive measurements.

To measure robin metabolic, hygric and ventilatory variables, two complete, separate open flow-through respirometry systems allowed concurrent measurement of two individuals each measurement night. Robins were measured at a range of T_a (10, 15, 20, 25, 30 and 32.5 °C in random order), as for individual White-browed Babblers (Chapter 2), with several amendments. To account for their smaller size, robins were placed individually in 65 mm internal diameter (volume ~620.5 mL) clear glass tubes, sealed with rubber stoppers held in place with F clamps. Incurrent airflow was controlled at a constant rate of 500 mL min⁻¹ via mass-flow meters (Cole Parmer Mass Flow Controller 32708-28, 0-5 L min⁻¹ and Aalborg Mass Flow Controller GFC171, 0-5 L min⁻¹), and flow rates were regularly calibrated from 300 – 1500 mL min⁻¹ (Sensidyne Gilibrator-2 air flow calibrator). Calibration of the respirometry and plethysmography systems was also as outlined for White-browed Babblers in Chapter 2, but 0.3 mL of air was used as injection volume for the robin plethysmography calibration.

Data handling and statistical analysis

Values are presented as mean \pm standard error (SE), N = number of individuals and n = number of measurements. Times are Western Australian standard times (AWST; AWST = Greenwich Mean Time + 8 h). Analyses were all conducted as for Chapter 2, with the following exceptions: Analyses of free-ranging body temperature, models used $T_{b,skin}$ instead of $T_{b,field}$ (including $T_{b,skin,depart}$ in place of $T_{b,depart}$ etc), and family group was not included as a random effect in any of the field studies analyses as robins did not roost together.

To allow for comparison between body temperature data collected by different methodologies, the linear regressions obtained from free-ranging ($T_{b,skin}$) and captive robins (T_b) were compared by ANCOVA using *StatistiXL* (www.statistiXL.com, v1.10).

Results

Free-ranging body temperature

53 nights of $T_{b,skin}$ data from 7 robins were collected during June and July 2012 and July and August 2013, with sample sizes for individual birds ranging between 1 and 12 nights. Robins roosted individually amongst twigs in the sub-canopy of mid- and upper-storey trees, although precise locations could not be determined without disturbance to the birds. When multiple robins in the same family group were simultaneously fitted with transmitters, robins roosted ~100 m from each other. Individual robins roosted in the same place each night during the experiments. The exact time of roosting could not be determined due to low light.

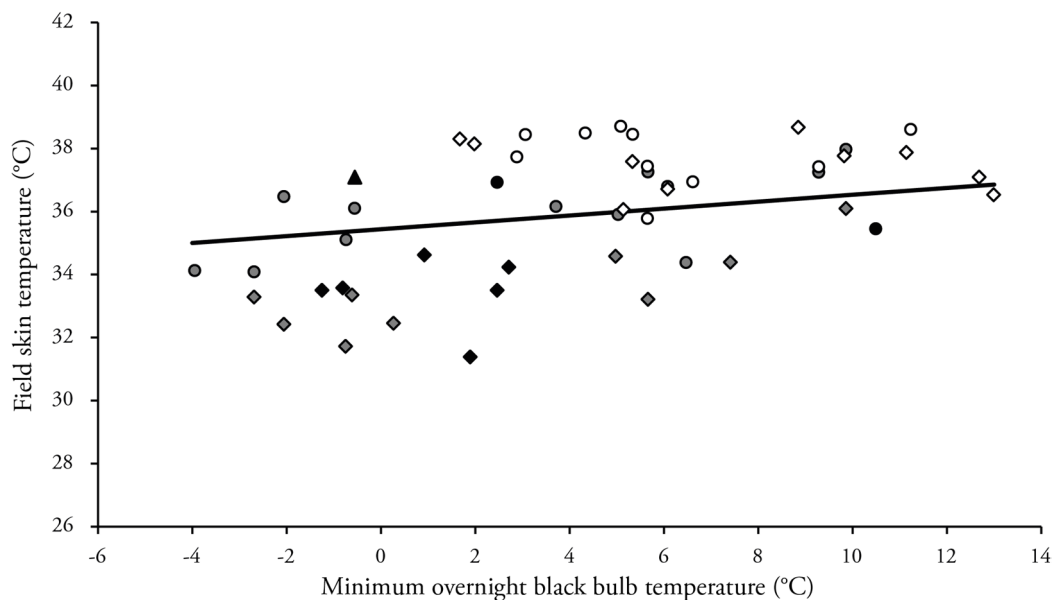


Figure 4.4: The relationship between minimum overnight skin temperature of robins and mean minimum overnight black bulb temperature ($N = 7$; $n = 53$). Each symbol/colour combination represents a different individual, with similarly coloured symbols showing individuals measured at the same time. The black symbols are from robins measured in winter 2012, and the grey and white symbols are robins measured in winter 2013.

Minimum T_{bb} ($T_{bb,min}$) for the measurement periods ranged by 16.9 °C, with the coldest night dropping to -3.9 °C, and the warmest to 13.0 °C (Figure 4.4). Overnight minimum $T_{b,skin}$ of robins under these conditions ranged from 31.4 °C to 38.7 °C. Linear mixed effect modelling showed that robin $T_{b,skin}$ fell approximately 0.11 °C with every 1 °C drop in $T_{bb,min}$ ($F_{1,44.4} = 6.96$, $P = 0.011$); however there was a substantial difference between individuals, with individual as a random effect (variance = 1.899) contributing greater variance to the model than any residual error did (residual variance = 1.086). The relationship between robin $T_{b,skin}$ and $T_{bb,min}$ can be described by the equation: $T_{b,skin} = 35.44 + 0.11*(T_{bb,min})$. The thermolability of free-ranging robins was 0.360 ± 0.010 °C⁻¹.

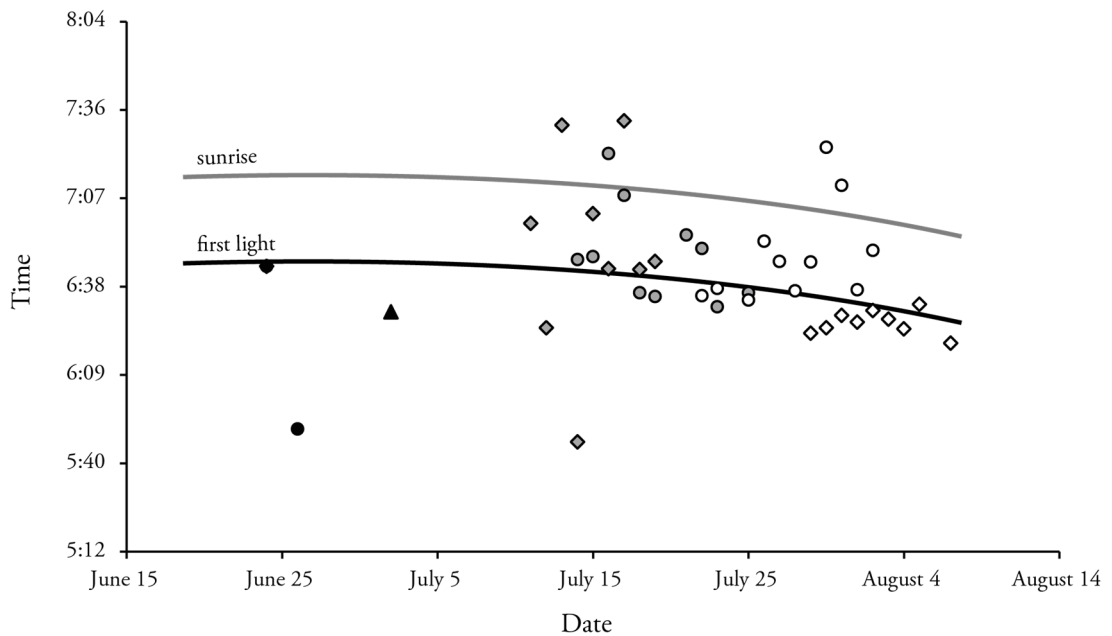


Figure 4.5: Time of roost departure for robins (symbols as for Figure 4.4) at Dryandra woodland in winter. The black line marks the time of first light, and the grey line shows dawn.

Roost site departure time could not be confirmed visually, but could be inferred from the $T_{b,skin}$ data. $T_{b,skin}$ increases prior to sunrise. Although the signal was sometimes lost immediately as the bird left the range of the radio receiver, other times the bird remained or returned within range of the radio receiver after first light, evidenced by high and fluctuating $T_{b,skin}$ values in response to movement and preening (Figure 4.3). The onset of these high and variable $T_{b,skin}$ values is considered a conservative roost departure time and the start of the robins' active phase. Robins departed roost sites on average 24.3 minutes

before sunrise, around first light (range 84 minutes before to 22 minutes after sunrise; Figure 4.5). Mean skin temperature of robins at the start of their active phase ($T_{b,skin,depart}$) was 39.8 ± 0.15 °C ($N = 7$; $n = 43$ nights, range 36.7 – 41.6 °C). $T_{b,skin,depart}$ did not vary with either $T_{bb,min}$ or T_{bb} at roost departure time ($F_{1,36.3} = 1.753$, $P = 0.194$; and $F_{1,37.9} = 1.715$, $P = 0.198$ respectively).

Laboratory respirometry

There were significant individual differences for all physiological variables (RMANOVA; $F_{6,35} \geq 1001$, $P < 0.001$). T_b of robins varied in response to T_a ($F_{5,2} = 20.8$, $P = 0.047$; Figure 4.6). Polynomial *a priori* contrasts indicated a linear relationship ($P = 0.006$), with a mean T_b of 39.7 °C at $T_a = 32.5$ °C, decreasing to 36.7 °C at $T_a = 10$ °C. This relationship is described by the equation $T_b = 34.3 + 0.166(T_a)$, and this equates to a thermolability of 0.143 ± 0.021 °C °C⁻¹.

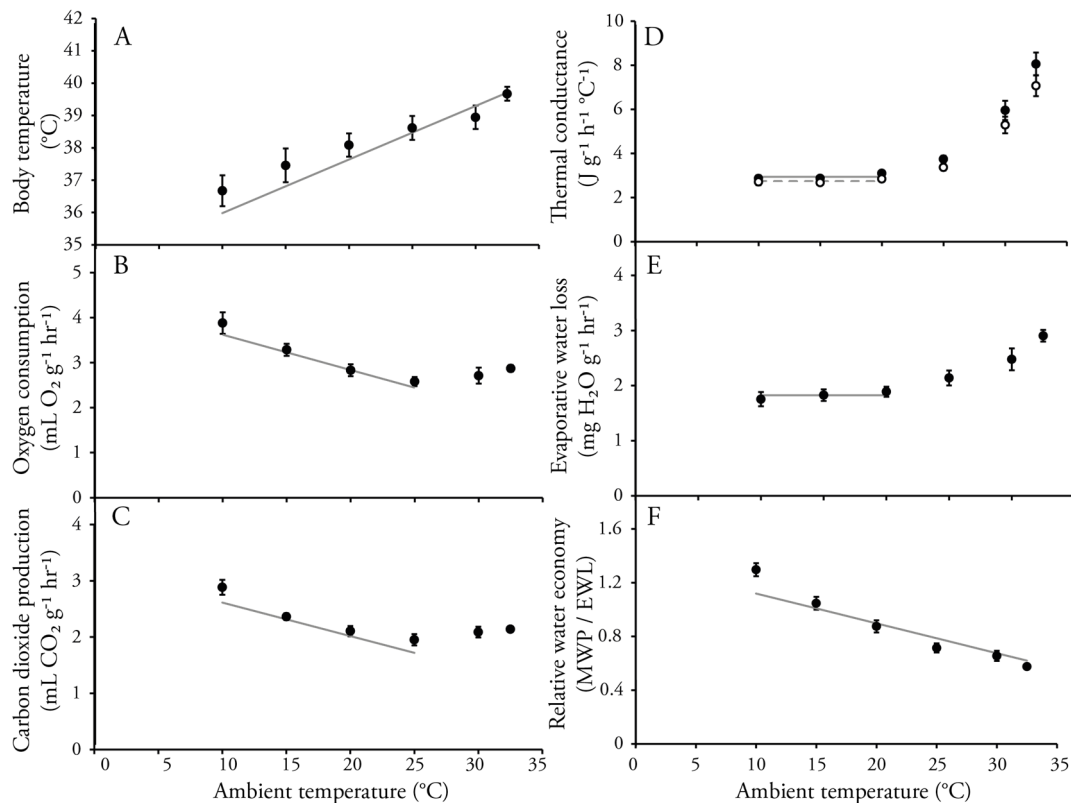


Figure 4.6: Body temperature, oxygen consumption, carbon dioxide production, wet (black symbols) and dry (white symbols) thermal conductance, evaporative water loss and relative water economy of robins at a range of ambient temperatures. Values are mean \pm 1 standard error ($N = 7$).

Robin $\dot{V}O_2$ and $\dot{V}CO_2$ both varied with T_a ($F_{5,2} = 29.9$, $P = 0.033$ and $F_{5,2} = 19.4$, $P = 0.0496$ respectively). $\dot{V}O_2$ decreased from $3.88 \pm 0.238 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $T_a = 10^\circ\text{C}$ to a minimum of $2.58 \pm 0.102 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ at $T_a = 25^\circ\text{C}$, before rising again at 30°C and 32.5°C (Figure 4.6), with $\dot{V}CO_2$ showing a similar pattern. Significant linear ($P = 0.001$) and quadratic ($P = 0.001$) polynomial relations were apparent when all six T_a s were included in the $\dot{V}O_2$ model, but only the linear contrast remained significant ($P < 0.001$) when $T_a = 30^\circ\text{C}$ and $T_a = 32.5^\circ\text{C}$ were removed. Likewise for $\dot{V}CO_2$, linear ($P < 0.001$) and cubic relationships ($P < 0.001$) were significant with all T_a data in the model, but the relationship was only linear at $T_a \leq 25^\circ\text{C}$ ($P < 0.001$). I interpret the minimal values at $T_a = 25^\circ\text{C}$ as basal MR (BMR). The relationship between $\dot{V}O_2$ and T_a below thermoneutrality was $\dot{V}O_2 = 4.41 - 0.079(T_a)$, and for $\dot{V}CO_2$ and T_a below thermoneutrality, the equation was $\dot{V}CO_2 = 3.21 - 0.060(T_a)$.

C_{wet} and C_{dry} varied with T_a ($F_{5,2} = 61.4$, $P = 0.016$ and $F_{5,2} = 51.6$, $P = 0.019$ respectively). Reverse Helmert *a priori* contrasts confirmed the pattern (Figure 4.5) of C_{wet} and C_{dry} varying little at low T_a , before increasing at $T_a \geq 25^\circ\text{C}$ ($F_{1,6} > 26.0$, $P < 0.002$ and $F_{1,6} > 20.1$, $P < 0.004$ respectively). Mean C_{wet} was $3.74 \pm 0.152 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ and C_{dry} was $3.37 \pm 0.133 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ at $T_a = 25^\circ\text{C}$.

The pattern of EWL suggested a slight increase in EWL with increasing T_a below thermoneutrality, before increasing more sharply above. Repeated measures ANOVA showed no overall effect of T_a on EWL ($F_{5,2} = 11.2$, $P = 0.084$) but reverse Helmert *a priori* contrasts statistically confirm the observed pattern, with EWL at $T_a = 25$, 30 and 32.5°C each differing from cumulative lower T_a s ($F_{6,35} > 7.57$, $P < 0.033$). Relative water economy of robins varied with T_a ($F_{5,2} = 46.3$, $P = 0.021$), decreasing with increasing ambient T_a . Polynomial *a priori* contrasts showed a linear relationship ($P < 0.001$) between RWE and T_a ; $\text{RWE} = 1.34 - 0.022(T_a)$. The point of relative water economy (pRWE; $\text{RWE} = 1$) was $T_a = 15.4^\circ\text{C}$.

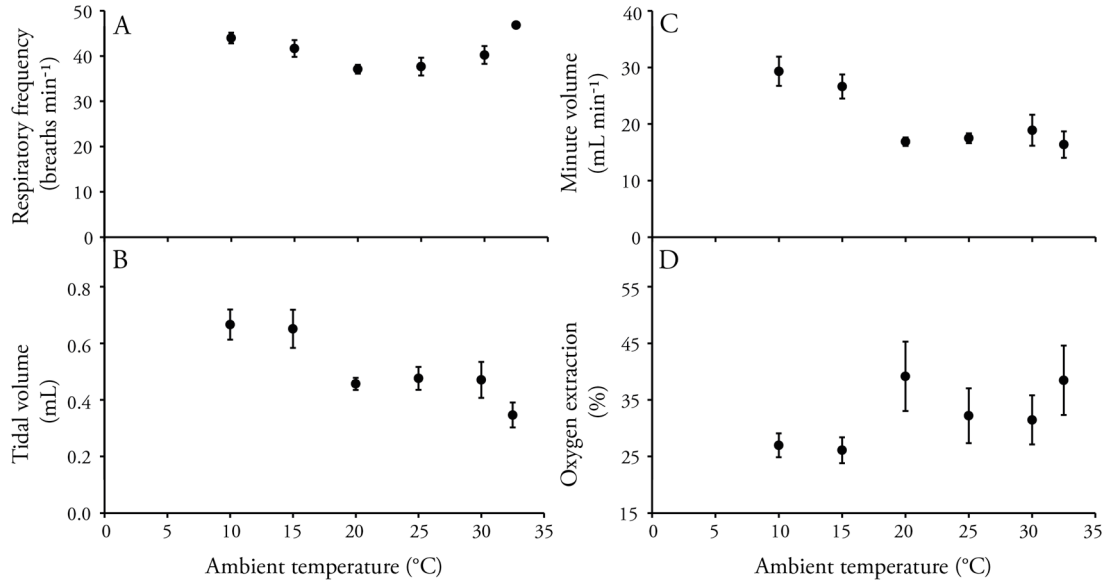


Figure 4.7: Respiratory frequency, tidal volume, minute volume and oxygen extraction for robins at a range of ambient temperatures. Values are mean \pm 1 standard error.

Individual as a random effect accounted for some of the variance in the ventilatory models for breathing rate (f_R , variance = 8.437, residual variance = 9.496) and tidal volume (V_T , variance = 0.001, residual variance = 0.016) but explained none of the variance for minute volume (V_I , variance = 0.000, residual variance = 28.37) and oxygen extraction (EO_2 , variance = 0.000, residual variance = 98.03) models. f_R was minimal at $T_a = 20$ °C (37.1 breaths min⁻¹), and there was an effect of T_a on f_R ($F_{5, 29.4} = 9.13$, $P < 0.001$), with f_R substantially higher at $T_{as} < 15$ °C and $T_a = 32.5$ °C ($t_{34.1} > 2.74$, $P < 0.010$ and $t_{34.7} = 6.28$, $P < 0.001$ respectively). V_T also varied with T_a ($F_{5, 30.2} = 6.07$, $P < 0.001$), with V_T at $T_a < 15$ °C significantly higher ($t_{35.8} > 4.58$, $P < 0.001$) than the minimal value recorded at $T_a = 32.5$ °C (0.346 mL). Likewise V_I also varied with T_a ($F_{5, 30.5} = 6.75$, $P < 0.001$), with minimal values recorded at $T_a = 32.5$ °C (16.4 mL min⁻¹) significantly lower than those recorded at $T_{as} > 15$ °C ($t_{42} > 3.60$, $P < 0.001$). Although there was no overall T_a effect on EO_2 ($F_{5, 30.5} = 1.26$, $P = 0.306$; Figure 4.6), EO_2 was substantially higher at $T_a = 32.5$ °C (38.5%; $t_{42} = 2.34$, $P = 0.024$) compared with minimal EO_2 at $T_a = 15$ °C (26.1%).

Comparison of field and laboratory body temperature

In the absence of direct calibrations between $T_{b,skin}$ from free-ranging birds and core T_b from captive birds, comparison by ANCOVA of the linear regressions quantified the

relationship between $T_{b,skin}$ and T_{bb} , and T_b and T_a respectively. Field and laboratory collected data were similar in both slope ($F_{1,89} = 1.69$, $P = 0.197$) and intercept ($F_{1,90} = 0.027$, $P = 0.871$). The common relationship between T_b and T_a for free-ranging and captive robins was $T_b = 35.1 + 0.14 (T_a)$.

Field behaviour

I made 2278 field observations of Western Yellow Robins, totalling 9.5 bird observation hours during winter of 2012 and 2013. Observations were made at a range of T_{bbs} (-2.1 to 27.9 °C) and times (from pre-dawn until dusk). It is estimated that behaviour of at least 32 individuals from at least 12 different territories contributed to these observations. Including observation session as a random effect in the model always lowered the Akaike Information Criterion (AIC), so it was included in each model.

Activity

Foraging, resting alert, and locomotion together accounted for 91.8% of robins' daily activity. Other activities included preening/maintenance behaviour (4%) and social

Table 4.1: Effect of predictor variables on proportion of time Western Yellow Robins spent engaged in particular activities, as determined by GAMMs, with test values derived from χ^2 -tests, and corresponding effective degrees of freedom (edf) shown. Only variables that resulted in minimum AIC values (listed in bold) were included in the final model for each activity.

	Model	χ^2 value	edf	p-value
Resting Alert				
T_{bb}	linear	1.31	1	0.253
$T_{bb,min}$	linear	0.26	1	0.608
Time of day	non-linear	2.71	1.86	0.228
Day of Year	linear	3.87	1	0.049
Foraging				
T_{bb}	linear	0.48	1	0.486
$T_{bb,min}$	linear	0.42	1	0.516
Time of day	linear	0.60	1	0.437
Day of Year	non-linear	27.6	4.4	<0.001
Moving				
T_{bb}	linear	0.22	1	0.638
$T_{bb,min}$	linear	0.72	1	0.397
Time of day	non-linear	7.26	2.77	0.054
Day of Year	linear	0.08	1	0.781

behaviour (4%), but these occurred at frequencies too low to be analysed. The effect of T_{bb} , $T_{bb,min}$, time of day and day of year on time spent engaged in these three core activities was tested individually, but only day of year and time of day had any effect (Table 4.1).

Robins were observed resting alert during 73.0% of observations. Robins forage primarily by pouncing, so spend long periods of time perched on low trunks and branches watching for food. Time spent resting alert varied only with day of year, decreasing linearly as the year progressed, from 80% in late June down to 70% by late August (Figure 4.8). With their pouncing foraging strategy, robins spent only 11.7% of their daylight time actively engaged in foraging manoeuvres, pouncing on small invertebrate prey in leaf litter and coarse woody debris and manipulating or ingesting prey items. Proportion of time spent foraging also varied with time of year, increasing to 20% of the time in August (Figure

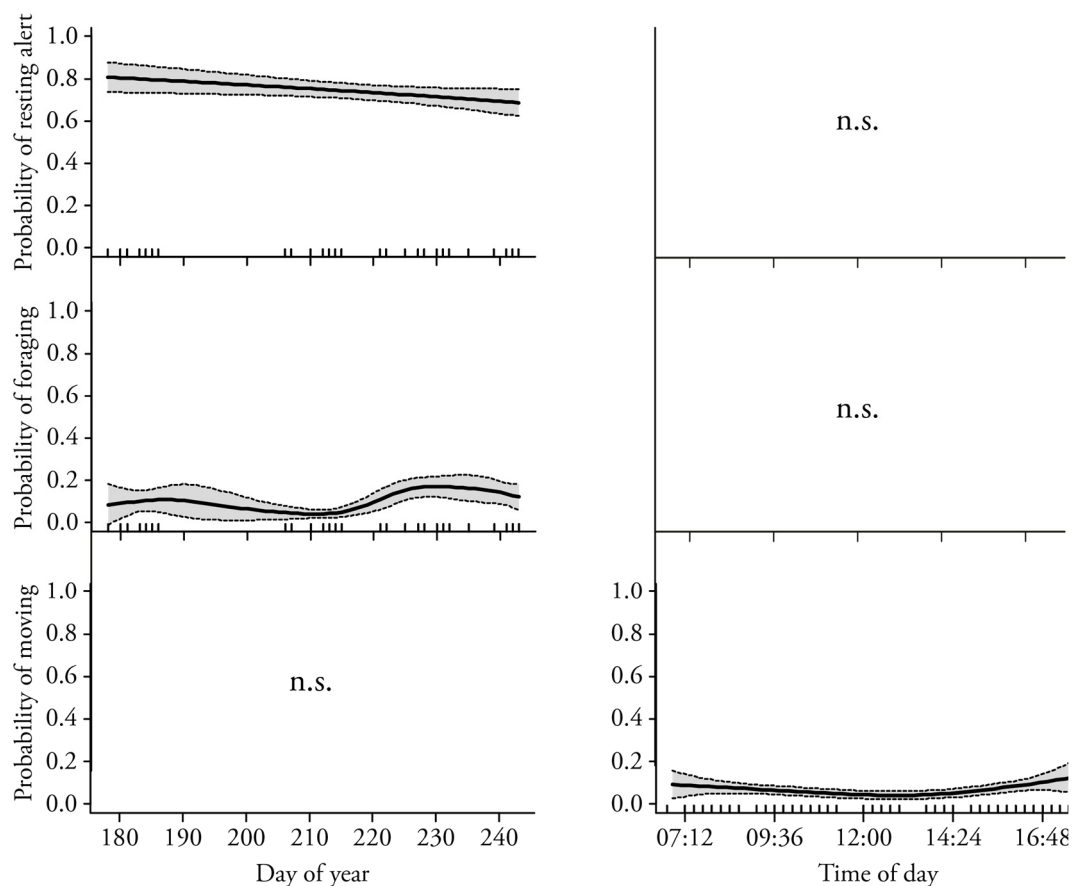


Figure 4.8: GAMM trend plots for effect of day of year and time of day on probability of a robin being observed resting alert, foraging, or moving. Each row presents the output from a different model. Plots include overall trend lines (solid line) with 95% confidence intervals (dashed lines). Rug plots show distribution of observations.

4.8). Robins spent only 7.1% of time moving through their habitat, mostly in flight or hopping along the ground. Time of day was the only variable that influenced proportion of time robins spent moving, with a bimodal response; they moved around their habitat more early in the morning and late in the afternoon (Figure 4.8).

Substrate

Robins' use of particular substrate heights varied with concurrent T_{bb} , overnight minimum T_{bb} , time of day and day of year (Table 4.2). Robins used 'ground' substrates (incorporating open ground, mossfields, grassland, leaf litter, and coarse woody debris) in 18.3% of observations. The proportion of time robins spent on the ground was influenced by both $T_{bb,min}$ and day of year. As $T_{bb,min}$ increased, robins were less likely to be observed on the ground (Figure 4.9) and time spent on the ground increased linearly from June to August.

Table 4.2: Effect of predictor variables on proportion of time Western Yellow Robins spent using different height strata, as determined by GAMMs, with test values derived from χ^2 tests and corresponding effective degrees of freedom (edf) shown. Only variables that resulted in minimum AIC values (listed in bold) were included in the final model for each strata.

	Model	χ^2 value	edf	p-value
Ground				
T_{bb}	non-linear	3.36	1.5	0.111
$T_{bb,min}$	linear	2.44	1	0.118
Time of day	linear	0.03	1	0.861
Day of year	linear	4.89	1	0.027
Understorey				
T_{bb}	non-linear	31.1	4.2	<0.001
$T_{bb,min}$	linear	0.59	1	0.443
Time of day	linear	0.57	1	0.449
Day of year	non-linear	23.9	4.7	<0.001
Mid-canopy				
T_{bb}	non-linear	33.2	4.8	<0.001
$T_{bb,min}$	linear	0.87	1	0.350
Time of day	linear	0.19	1	0.665
Day of year	non-linear	17.1	2.3	<0.001
High				
T_{bb}	non-linear	17.8	3.46	<0.001
$T_{bb,min}$	linear	0.000	1	0.990
Time of day	linear	0.007	1	0.932
Day of year	linear	0.001	1	0.971

Robins were observed using understorey habitat elements (logs, tree stumps, understorey shrubs and lower parts of both mid-storey and canopy trees) during 51.3% of observations. This varied with both T_{bb} and day of year. Proportion of time spent in the understorey was largely constant for all ambient conditions, but increased markedly at high T_{bb} . Proportion of time in the understorey fluctuated with day of year, but the pattern was complex, as shown in Figure 4.9. Robins spent 27.0% of their daytime in the middle canopy, in smaller trees, or on mid-storey height trunks and branches of canopy trees. Midstorey substrate use varied with black-bulb temperature and day of year (Table 4.2). Mid-canopy use was most frequently recorded at mid-range T_{bb} s, and was largely constant in June-July, but fell in late winter (Figure 4.9). Robins were only observed in the upper canopy during 3.5% of records, although this was in combination with sitting fluffed up and resting alert in sunny positions – basking behaviour (pers. obs.). Black bulb

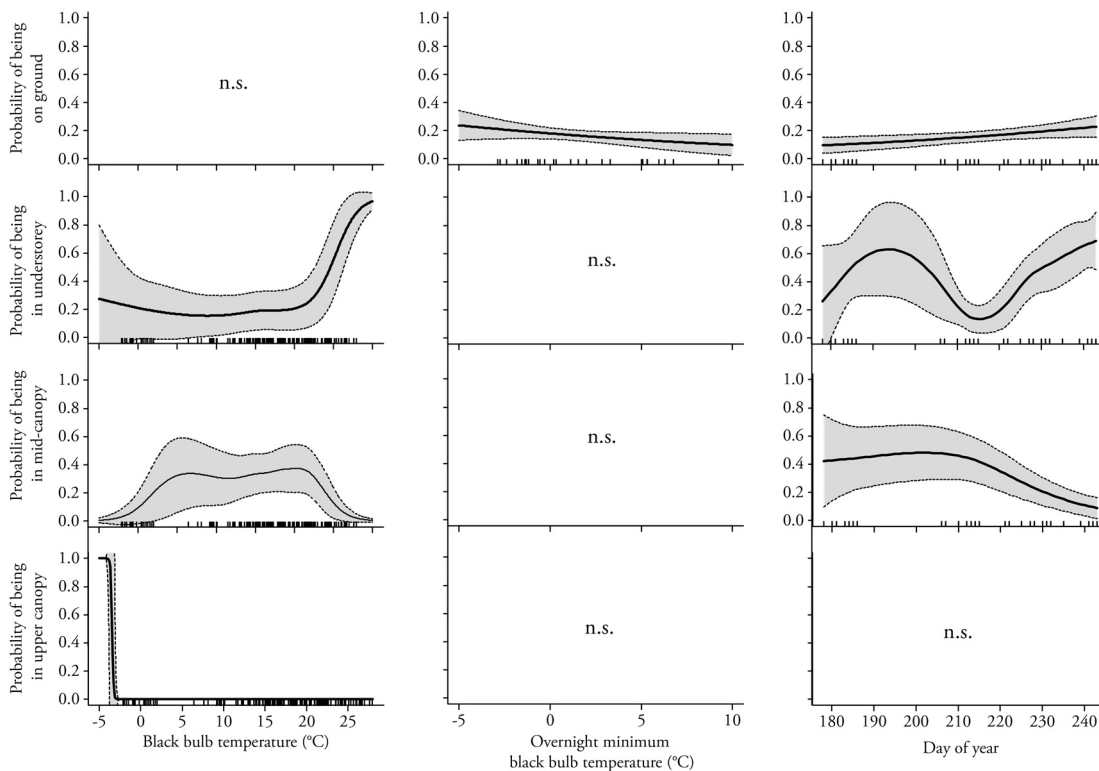


Figure 4.9: GAMM trend plots of probability of robins being on the ground, in the understorey, mid- and upper canopy in response to black bulb temperature (°C), overnight minimum black bulb temperature (°C), and day of year. Each row presents the output from different model. Plots could not be generated for non-significant variables, marked 'n.s.'. Plots were generated using mid-range black bulb temperatures (15 °C), mean overnight black bulb temperature (0 °C), and mean day of year (= 213 ; August 3rd). Plots include overall trend lines (solid lines), 95% confidence intervals (dashed lines), and rug plots showing distribution of observations.

temperature was the only variable that influenced presence in the upper canopy (Table 4.2), with robins only recorded using these substrates at the lowest T_{bb} s (Figure 4.9).

Location

To determine under what conditions robins moved between sunlit, patchy or shaded locations, observations made during overcast, twilight, or misty conditions were discarded, leaving a dataset of 1705 observations (7.1 bird observation hours). Robins were recorded in sunlit, patchy and shaded locations on 32.5%, 22.5% and 45.0% of observations respectively. Black bulb temperature and time of day were the only variables that influenced location choice (Table 4.3).

Table 4.3: Effect of predictor variables on proportion of time Western Yellow Robins spent exposed to varying levels of solar radiation, as determined by GAMMs, with test values derived from χ^2 tests and corresponding effective degrees of freedom (edf) shown. Only variables that resulted in minimum AIC values (listed in bold) were included in the final model for each location.

	Model	χ^2 value	edf	p-value
Sun				
T_{bb}	non-linear	66.7	5.8	<0.001
$T_{bb,min}$	linear	0.06	1	0.803
Time of day	linear	2.44	1	0.119
Day of year	linear	2.09	1	0.508
Patchy light				
T_{bb}	non-linear	45.2	5.37	<0.001
$T_{bb,min}$	linear	0.21	1	0.644
Time of day	linear	0.02	1	0.883
Day of year	linear	1.28	1	0.259
Shade				
T_{bb}	linear	5.52	1	0.019
$T_{bb,min}$	linear	0.391	1	0.532
Time of day	linear	3.48	1	0.062
Day of year	linear	1.25	1	0.265

Robins had a trimodal response to T_{bb} , being more likely to be in sunny positions at the lowest, the highest T_{bb} s, and mid-range T_{bb} s, but were rarely observed in the sun at moderately low or moderately high T_{bb} (Figure 4.10). Conversely, robins only used patchily lit locations in small proportions at mid-range temperatures. Both T_{bb} and time of day had linear effects upon proportion of time robins were observed in fully shaded

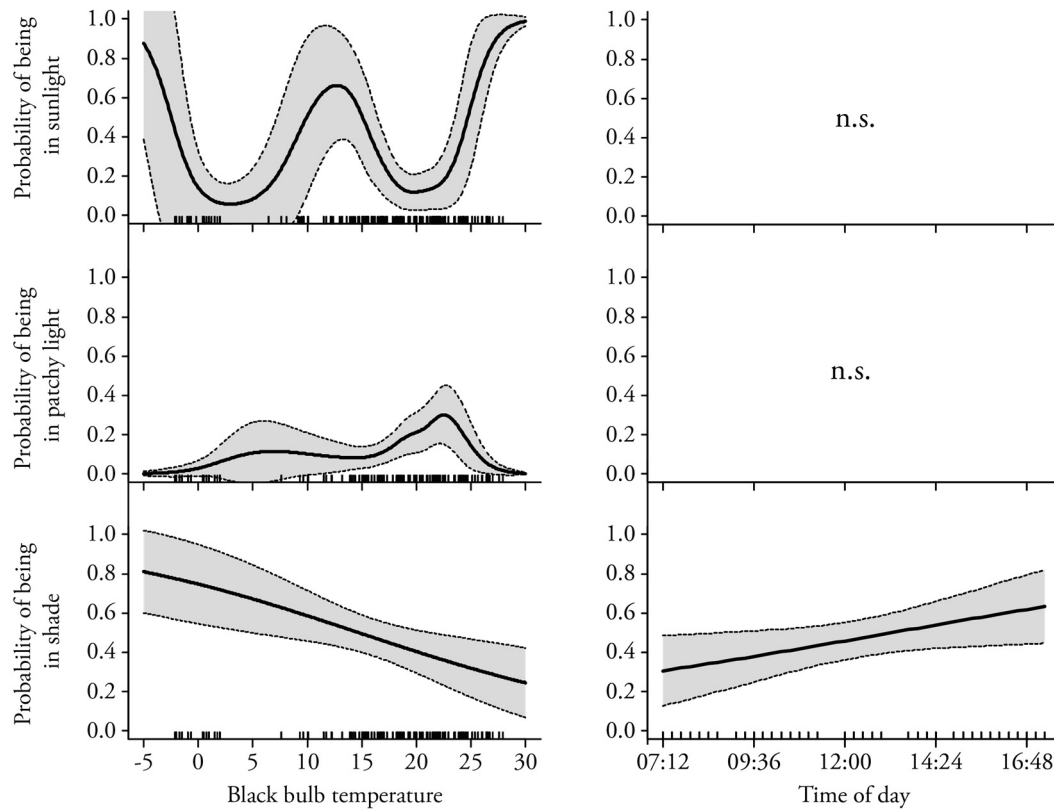


Figure 4.10: GAMM trend plots of probability of robins being in full sun, patchy or completely shaded locations in response to black bulb temperature ($^{\circ}\text{C}$), time of day and day of year. Each row presents the output from different model. Plots could not be generated for non-significant variables, marked ‘n.s.’. Plots were generated using mean black bulb temperature and mean time of day (12:00). Plots include overall trend lines (solid lines), 95% confidence intervals (dashed lines), and rug plots showing distribution of observations.

locations. When time of day was held constant, robins were more likely to be observed in shaded locations at colder T_{bb} s than high, but when T_{bb} was held constant, robins were less likely to be in shaded locations earlier in the day than later.

Discussion

Despite the potential energetic challenges faced by small endotherms in winter, this study outlines how a small, sedentary passerine persists in a temperate habitat without employing thermoregulatory mechanisms used by some of the co-occurring endotherms (such as communal roosting, use of insulated roost sites, or torpor). Despite a smaller mass than the other group-living birds studied at this site (White-browed Babblers, Chapter 2;

Rufous Treecreepers, Chapter 3), robins did not use social thermoregulation or enclosed roost sites to facilitate energy balance, instead roosting individually in the open. While robin T_b did decrease in response to decreasing T_a , the decrease was only small (mean $T_{b,skin}$ at $T_{bb} = -3.95$ °C was 3.6 °C below thermoneutrality), and they were never cold enough to be considered torpid. Studies elsewhere have recorded torpor in avian species that share this environment such as Dusky Woodswallows (*Artamus cyanopterus*; Maddocks & Geiser 2007), Mistletoebirds (*Dicaeum hirundinaceum*; Heumann 1926) and Australian Owlet-nightjars (*Aegotheles cristatus*; Brigham *et al.* 2000), as well as in co-occurring small mammals such as Numbats (*Myrmecobius fasciatus*; Cooper & Withers 2004), Lesser Long-eared Bats (*Nyctophilus geoffroyi*; Hosken & Withers 1999), and Red-tailed Phascogales (*Phascogale calura*; Pusey *et al.* 2013). I argue instead that with a small rest-phase decrease in nocturnal T_b , as well as a low-energy, pouncing, foraging strategy, a long active phase, and some early morning basking robins negate the necessity for torpor or deep nocturnal hypothermia.

Measuring small, vagile animals in the wild can be problematic, as their small mass limits the size of devices that can be used to monitor them and so also the signal range and battery life of transmitters and loggers used. Using the 5% guideline of transmitter mass to body mass, robins (18.5g) were deemed too small to carry implanted transmitters (minimum mass of Holohil Systems Ltd BD-2TH is 1.05g), so instead I used smaller transmitters attached with a backpack harness (total mass ~0.7g) to measure $T_{b,skin}$ instead of core T_b . $T_{b,skin}$ transmitters used on Australian Owlet-nightjars (*Aegotheles cristatus*; Brigham *et al.* 2000) and Big Brown Bats (*Eptesicus fuscus*; Barclay *et al.* 1996, Willis & Brigham 2003) give a reliable estimate of core T_b , although temperature differentials between $T_{b,skin}$ and core T_b can occur, particularly at low T_a (Brigham *et al.* 2000). Here the linear relationships between robin $T_{b,skin}$ and T_{bb} (field) and T_b and T_a (laboratory) were similar, suggesting $T_{b,skin}$ provides a useful approximation of cloacal T_b in these small passerines.

Many small, sedentary, cooperatively-breeding birds such as Fairy-wrens (*Malurus* spp.; Rowley & Russell 1997), Varied Sittellas (*Daphoenositta chrysoptera*; Noske 1985), and Redthroats (*Pyrholaemus brunneus*; pers. obs.) roost together, generally by row-huddling in foliage. Row huddling reduces the surface area exposed to the cold, thereby reducing conductance and so reducing energy requirements (Gilbert *et al.* 2010). Work on Blackcaps (*Sylvia atricapilla*; Wojciechowski *et al.* 2011) found row huddling reduced overnight energy expenditure at low T_a by 30%. Robins in this study were unusual amongst small, group-living endotherms in that they roosted individually and did not make use of hollows or roost nests. Family groups did not roost together and individuals roosted on open branches and in foliage in the mid-canopy. Robins in captivity for the laboratory component of this study behaved similarly, roosting mid-height in the aviary on open branches (pers. obs.). Robins are therefore clearly able to meet their thermoregulatory energy requirements without modification of their thermal conductance from either conspecifics or shelter.

Robins had the longest active period of the three species studied here, roosting later (pers. obs.) and departing roost sites earlier (24.27 ± 3.26 minutes before sunrise) than treecreepers (14.78 ± 1.63 minutes before sunrise) and babblers (3.30 ± 2.04 minutes before sunrise). In other bird communities the species that left roost sites earliest were small, insectivorous or nectarivorous, and roosting solitarily (Stokes 1979), all characteristics of robins. Stokes (1979) attributed early roost departures as being driven by energetic demands, but did not measure it specifically. For robins, with no insulated roost site or conspecifics to huddle with on winter mornings, there is no thermal incentive to remain still beyond first light, if there is the potential for exercise-related thermogenesis or foraging (Humphries & Careau 2011). Although robins were observed basking in the upper canopy at low T_{bb} – sitting still in the sun, with feathers erect (Figure 4.9), they cannot do this until after sunrise, so this does not explain the early roost departure time. Departing exposed roost sites early would minimise predation risk however, and increase available time to eat the quantities of food necessary to satisfy their energy needs.

Classifying small reductions in T_b to the various definitions of heterothermy is problematic. It can be difficult to differentiate heterothermic responses to environmental conditions from normal, circadian oscillations (Prinzinger *et al.* 1991) and nocturnal hypothermia, torpor, and hibernation may be viewed as a continuum rather than discrete states (Withers & Cooper 2010). Studies with differing methodology (Prinzinger *et al.* 1991; McKechnie & Lovegrove 2002; Willis & Brigham 2003), and fundamental differences between taxa makes the use of consistent criteria problematic (Barclay *et al.* 2001). In torpor and hibernation, T_b and MR reductions are generally accompanied by specific behaviours (Barclay *et al.* 2001; Geiser 2004b), however this is not always observed for nocturnal, or rest-phase, hypothermia (although see Carr & Lima 2013). Generally, nocturnal hypothermia is differentiated from homeothermy as a small reduction ($<10\text{ }^{\circ}\text{C}$) in T_b below normothermia (Prinzinger *et al.* 1991), however, definitions of both normothermic T_b as well as the amount of the T_b reduction vary. Normothermic T_b is described both as rest-phase T_b at thermoneutrality in laboratory studies, but also as pre- or post-activity active-phase T_b s in field telemetry studies (Barclay *et al.* 2001). The amount of the T_b reduction necessary to differentiate nocturnal hypothermia from normal circadian oscillation has also been variously defined, usually $3 - 5\text{ }^{\circ}\text{C}$ (Barclay *et al.* 2001; McKechnie & Lovegrove 2002). However, regardless of the definition, while robin T_b and $T_{b,skin}$ varied with T_a and T_{bb} , it did not meet the criteria for nocturnal hypothermia.

Robins were thermolabile under both controlled, laboratory conditions ($0.143 \pm 0.021\text{ }^{\circ}\text{C }^{\circ}\text{C}^{-1}$) and in the field ($0.360 \pm 0.010\text{ }^{\circ}\text{C }^{\circ}\text{C}^{-1}$). In the laboratory, the difference between normothermic robin T_b ($T_b = 38.6\text{ }^{\circ}\text{C}$ at $T_a = 25\text{ }^{\circ}\text{C}$) and mean minimum T_b ($T_b = 36.7\text{ }^{\circ}\text{C}$ at $T_a = 10\text{ }^{\circ}\text{C}$) was $<3\text{ }^{\circ}\text{C}$. For free-ranging birds, in the absence of rho-phase normothermic values, heterothermia is often described by the T_b reduction below resting, alpha-phase temperatures (Barclay *et al.* 2001), in this instance $T_{b,skin,depart}$. For free-ranging robins, the difference between minimum $T_{b,skin}$ and $T_{b,skin,depart}$ was only $1 - 4\text{ }^{\circ}\text{C}$ for most individuals, not far removed from normal (normothermic) alpha- and rho- phase values (Prinzinger *et al.* 1991). While one individual showed variation in $T_{b,skin}$ and $T_{b,skin,depart}$ of

5 – 7 °C, when compared with other individuals, it appears likely that this may be a result of the transmitter not being flush against the skin. Even though robins cannot be classified as using nocturnal hypothermia, even small reductions in T_b can result in significant overnight energy savings for small endotherms (Willis & Brigham 2003).

Assuming that $T_{b,skin}$ is an approximation of core T_b , the energy savings resulting from a reduction in $T_{b,skin}$ can be estimated (as for Rufous Treecreepers; Chapter 3). Data from a single rest-phase of a wild, individually-roosting robin, on a night when T_{bb} dropped to a minimum of 5.0 °C (16th July 2013) shows MR calculated from actual $T_{b,skin}$ is consistently lower than if the bird had maintained a consistent normothermic T_b of 40.0 °C (at start of active-phase; Figure 4.11). Excluding the endogenous rewarming phase, this equates to an average energy saving of 3.22 mL O₂ g⁻¹ hr⁻¹, or 11.90 kJ over 10 hours. Assuming the digestibility and energy content of arthropods is 21.7 kJ g⁻¹ (Withers *et al.* 2016), this T_b reduction reduces the robin's arthropod intake by 0.55g. This may explain why robins here showed little change in activity in response to either current (T_{bb}) or recent (overnight minimum T_{bb}) environmental conditions. Although many birds exhibit peaks in foraging intensity in response to energy shortages, such as diurnal birds feeding heavily in early mornings to compensate for overnight accrued energy shortages (Bednekoff & Houston 1994), robins did not. Instead robin foraging time varied only with day of year, suggesting a seasonal change in food availability or a shift in foraging efficiency, rather than a response to a short-term energy shortage. Although temporal patterns in robin foraging behaviour haven't been investigated before, habitat use (preference for open understorey) and foraging methods (pouncing onto leaf litter) are consistent with those observed elsewhere (Recher & Davis 1998; Recher *et al.* 2002; Cousin 2004).

A number of characteristics can be used as predictors for use of nocturnal hypothermia, torpor, and hibernation by endotherms. These include a small body mass (Cooper & Geiser 2008), sedentary lifestyle (Geiser *et al.* 2006) and fluctuations in food availability (Geiser *et al.* 2006). In addition to these biological and ecological traits, physiological attributes such as low T_b and low BMR (Cooper & Geiser 2008) have also been

acknowledged as predictors of heterothermy. Being a small, sedentary insectivore, robins exhibit many of the ecological traits associated with heterothermy. Using the same methodology as for White-browed Babblers (Chapter 2) and Rufous Treecreepers (Chapter 3), I found that robins had typical values for standard physiological variables (T_b , BMR, minimal EWL, C_{wet} , f_R , EO_2 and V_T) compared to other birds.

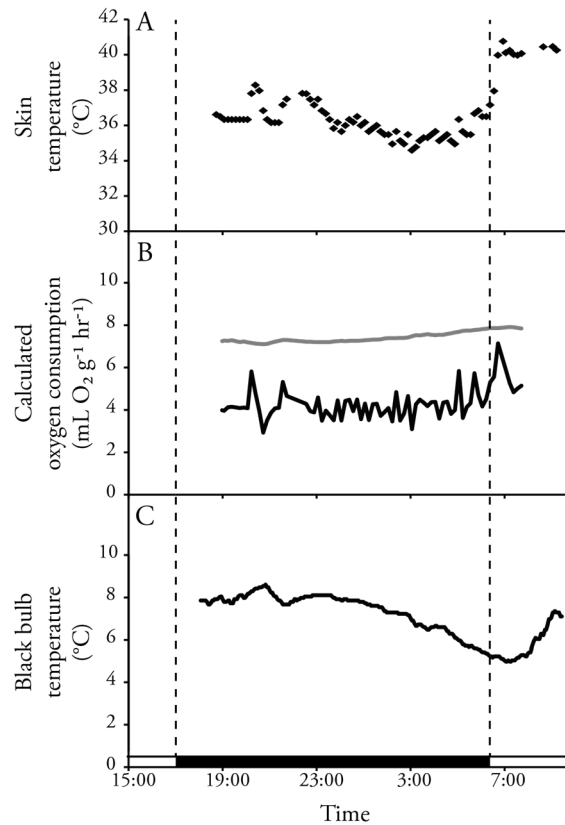


Figure 4.11: Skin temperature (A) and calculated metabolic rate (displayed as oxygen consumption; B) of a single, free-ranging Western Yellow Robin under black bulb temperature conditions (C) for a single night, July 16th, 2013. B shows both the calculated metabolic rate based upon the measured skin temperature (black line), as well as the predicted metabolic rate if skin temperature had been kept at normothermic T_b levels (grey line). The black bar and the dotted lines mark the period from sunset to sunrise.

In itself, a low normothermic T_b can be a predictor of potential for heterothermy (Cooper & Geiser 2008). Robin T_b was only 0.68 °C below that predicted by body mass alone, well within the 95% prediction limits for the avian allometric relationship both before and after accounting for phylogenetic history (Figure 4.12). $T_{b,skin}$ and T_b measured here in both the field and laboratory were comparable to active and rest phase values for

passerines reported elsewhere (41.6 ± 1.13 °C and 38.9 ± 0.87 °C respectively; Prinzinger *et al.* 1991), providing no expectation that robins would be heterothermic.

Although the relationship between BMR and body mass has been used as a predictor for both endothermy and heterothermy in birds and mammals (see Cooper & Geiser 2008 for review), this concept is problematic for birds. McNab (1983) used the relationship between BMR, body mass and heterothermy to calculate a ‘boundary curve’ to identify the BMR and body mass characteristics where heterothermy would be necessary. While

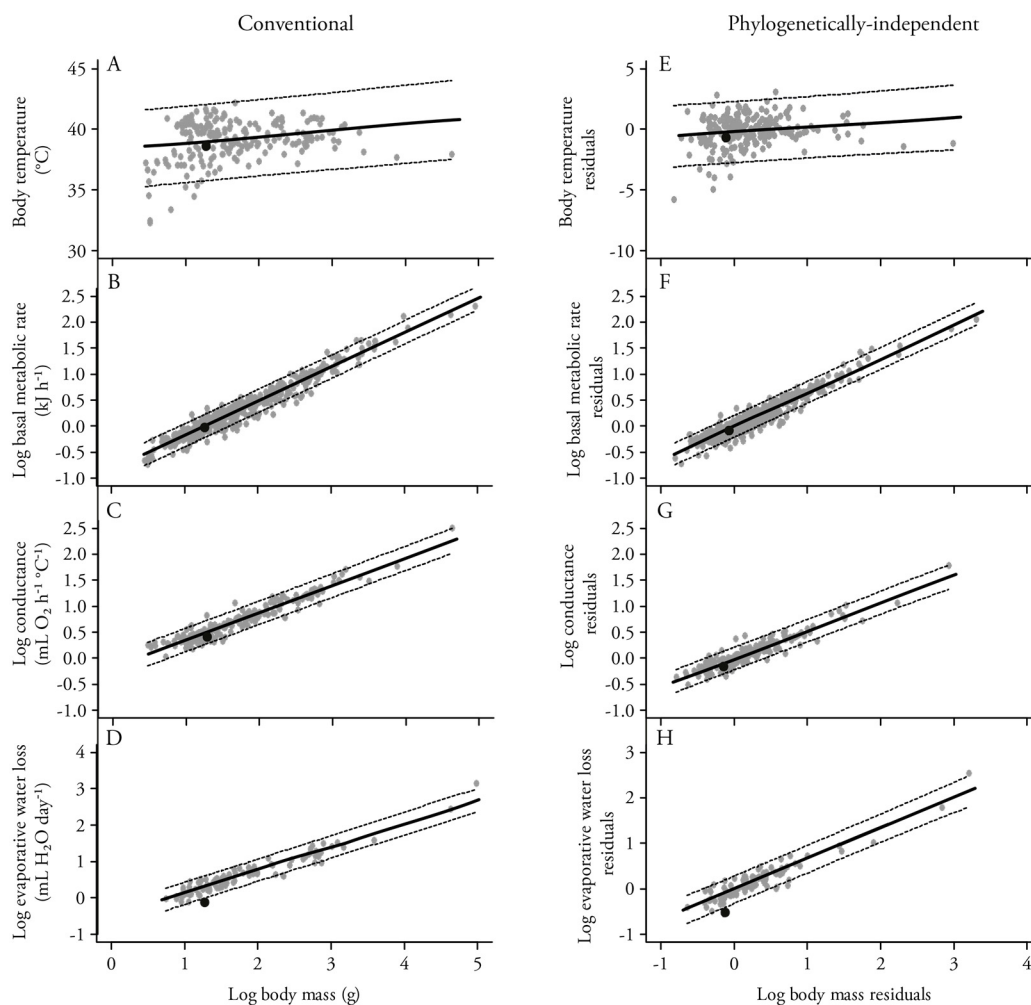


Figure 4.12: Allometric comparison of body temperature (A), basal metabolic rate (B), thermal conductance (C), and evaporative water loss (D) for robins (black symbols) compared with other birds (grey symbols). Phylogenetically-independent residuals are displayed in E – H respectively. All values are \log_{10} values, with the exception of body temperature, which is untransformed. Solid lines mark the least squares regression lines and the dotted lines show 95% prediction intervals. Methodology is described in Chapter 6 and datasets are presented in the Appendices.

this curve correctly predicts torpor for many marsupials, bats and rodents (Cooper & Geiser 2008), birds both above and below the boundary curve exhibit heterothermy. Interpretation of this relationship is made more difficult as there is a bias towards reporting only birds that exhibit ‘interesting’ thermoregulatory responses, so evidence of homeothermy is likely under-reported. Using McNab’s curve, described by the equation $\text{BMR (mL O}_2 \text{ h}^{-1}) = 15.56 \text{ m(g)}^{0.33}$, only a robin-sized bird (18.5g) with a BMR of less than 40.8 mL O₂ h⁻¹ would be expected to use torpor (or be heterothermic, according to Cooper & Geiser’s supposition). Robin BMR measured here had a BMR of 47.7 mL O₂ h⁻¹, well above the boundary curve. In an allometric context, robin BMR was 90.9% of that predicted by body mass alone, and well within the prediction limits (Figure 4.12). Accounting for phylogeny did not alter this pattern.

It would be expected that a bird that roosts in an open location may have sufficiently insulating plumage to significantly reduce total thermal conductance, minimising heat loss. While robin conductance was only 81.8% of that predicted by body mass, this was not remarkable, as it still fell within the 95% prediction limits for the avian dataset (Figure 4.12), and accounting for phylogeny did not alter this. Most birds appear well-insulated due to the effectiveness of plumage and at low T_a postural adjustments to reduce heat loss appear almost universally amongst birds (Gill 2007). Fluffing up feathers, sitting on feet and tucking in extremities are well recorded (Stokes 1979; Reinertsen 1983; Reeb 1986). The benefits of these behaviours vary. Fluffing of feathers alone reduced heat loss by over 26% in Chaffinches at 0 °C, but wind has a significant effect upon the effectiveness of this strategy (Gavrilov, Dol’nik, Keskpaik & Yu 1970, Kendeigh et al. 1977).

The EWL of robins was only 37.2% of that predicted by allometry, below the 95% prediction limits (Figure 4.12). Taking phylogenetic relationships into account did not alter this. For a sedentary insectivore in a dry habitat with only seasonal access to standing water, a low minimal evaporative water loss is unsurprising, as it is a trait often associated with arid dwelling animals (Williams 1996). As discussed in Chapters 2 and 3 however, differences in measurement protocol may account for these differences, with low minimal

EWL obtained here a product of the long measurement duration and high chamber washout rates, used to obtain a true minimal value, compared to values obtained from studies that measured birds for shorter periods (Page *et al.* 2011).

There was no evidence that robin ventilatory parameters differed from what could be predicted from allometry. f_R and V_T were 53.3% and 112% respectively of predicted values, both within the 95% prediction intervals and not altered before and after accounting for phylogeny (Figure 4.13). Likewise robin EO_2 fell within the cluster of values recorded for other species. Ventilatory physiology provided little evidence that robins do anything unusual compared to other birds; they accommodate their $\dot{V}O_2$ demand as expected for other small birds.

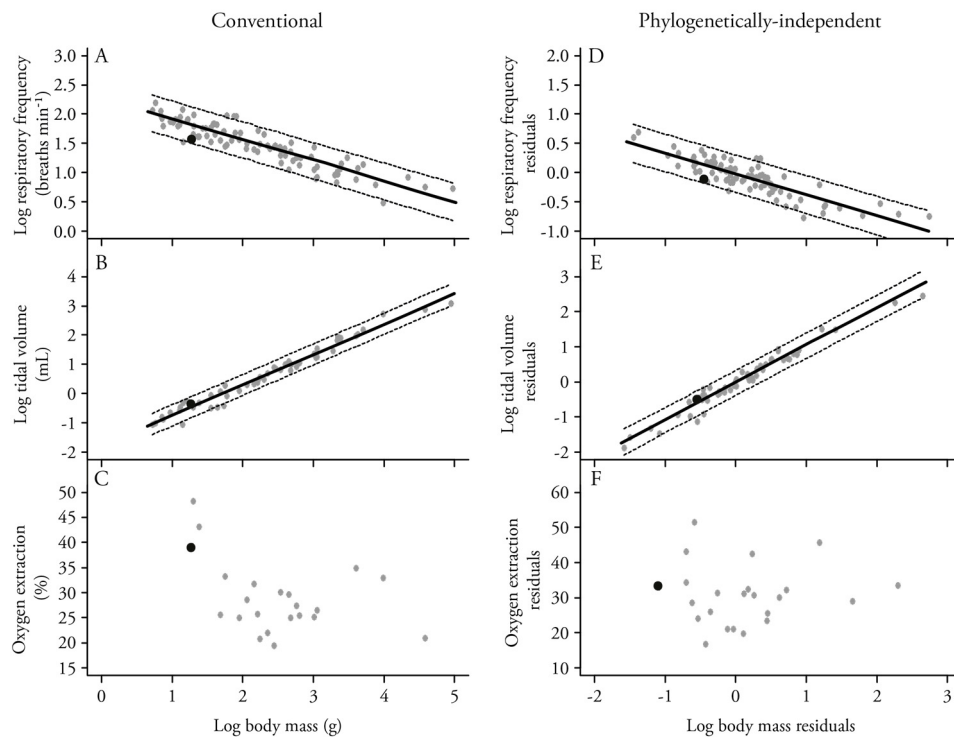


Figure 4.13: Allometric comparison of respiratory frequency (A), tidal volume (B), and oxygen extraction (C) for robins (black symbols) compared with other birds (grey symbols). Phylogenetically-independent residuals are displayed in D – F respectively. All values are \log_{10} values, with the exception of oxygen extraction, which is untransformed. Where a linear relationship exists, solid lines mark the least squares regression lines and the dotted lines show 95% prediction intervals. Methodology is described in Chapter 6 and datasets are presented in the Appendices.

Robins maintained near homeothermy at below-freezing conditions, even though they exhibit several ecological characteristics often considered predictors of nocturnal hypothermia, torpor, and hibernation in other endotherms. Their response to low T_a was a typical endothermic response (Dawson & Whittow 2000), with no evidence of torpor and comparative physiological variables (T_b , BMR, minimal EWL, C_{wet} , f_R , EO_2 and V_T) indicate that they achieve this without any particular physiological specialisation. At $T_a = 10\text{ }^{\circ}\text{C}$, T_b was maintained only $1.9\text{ }^{\circ}\text{C}$ below T_b thermoneutral by a 51% increase in metabolic rate and a 23% decrease in C_{wet} at low T_a . Although McKechnie and Lovegrove (2002) predicted that avian facultative responses, in particular rest-phase hypothermia, may be more common in birds than previously considered, there was no evidence for it here in this small passerine, as reduction in T_b was well within normal circadian fluctuations (Prinzinger *et al.* 1991).

Thermal physiology of a dichromatic passerine, the Western Magpie *Gymnorhina tibicen dorsalis*

Abstract

The Australian Magpie (*Gymnorhina tibicen*) is a large, sedentary passerine (300 g), common in open habitats throughout a range of Australian climates. Despite being a common and widespread species, there are currently no basic physiological data for magpies, so it is not known how magpies balance their energy budgets at low ambient temperatures (T_a) in their varied habitats. I measured standard physiological variables for the southwestern magpie subspecies (*G. t. dorsalis*) using open-flow respirometry at T_a from 5 to 32.5 °C. Magpies had a typical homeothermic response to low T_a , maintaining T_b at $T_a = 5$ °C only 0.6 °C below that at thermoneutrality ($T_a = 25$ °C). They achieved this with a 38% increase in metabolic rate and a 40% decrease in conductance. There was no evidence of torpor. Observations of free-living magpies basking suggests they may use solar heat gain to reduce thermoregulatory costs. In southwest Australia the magpie is sexually dimorphic; males have white dorsal plumage while it is black for juveniles, females, and sub-adults. Magpies of different age and sex may subsequently experience different radiant heat loads. I measured insulative plumage characteristics at wind speeds of 1 to 6 m sec⁻¹ and quantified solar heat gain at the level of the skin. Plumage of males, females and sub-adults showed similar patterns in thermal resistance, decreasing with increasing wind speed from 536 s m⁻¹ at windspeeds of 1 m sec⁻¹ to 190 s m⁻¹ at 6 m sec⁻¹. As expected, the reflectivity of the male's white dorsal plumage was greater than that of the dark females and sub-adults. There was substantially less variation in solar heat gain with increasing wind speed for males (6.63% at 1 m sec⁻¹ to 5.33% at 6 m sec⁻¹), compared with females and sub-adults from (8.13% to 2.20%). The high thermal resistance and variable solar heat gain of magpies means that their plumage may play a considerable role in balancing their energy budget and facilitating the maintenance of homeothermia in winter.

Introduction

Colour variation in bird plumage has both an ecological and a thermoregulatory role. Between species, plumage colour can variously enhance visibility or encourage crypsis, and within species variation in colour can also advertise breeding condition or signal social status of individuals (Ward *et al.* 2002; Caro 2005; Gill 2007). The effectiveness of avian plumage as an insulating body covering is reasonably well understood (Aschoff 1981; Bakken 1991; Schleucher & Withers 2001), yet the interaction between plumage/pelt colour, solar heat loads, and thermoregulation is more complex (Lustick *et al.* 1980; Walsberg 1983; Caro 2005). As variation in plumage and coat colour incur different thermoregulatory costs, so the variation in plumage colour between subspecies or closely-related species may aid in thermoregulation in their different thermal environments (Margalida *et al.* 2008). However the relationship between pelage/plumage colour and its thermoregulatory consequences has only been investigated in a few species (see Walsberg 1983; Hetem *et al.* 2009).

The Australian Magpie, *Gymnorhina tibicen*, in particular the southwestern subspecies, the Western Magpie *G. t. dorsalis*, is a useful model for investigating the thermoregulatory cost of plumage colour variation. Of all the Australian Magpie subspecies, the Western Magpie shows the most marked sexual dichromatism, so is an ideal choice for exploring the effect of plumage colour in the energy budget of the species. The Australian Magpie is one of the most common and widely-distributed Australian birds (Higgins *et al.* 2006). This large (300g), omnivorous, sedentary, group-living passerine is found in arid, tropical, temperate and alpine climates, in natural, rural and suburban habitats of Australia and New Guinea.

Throughout their distribution Australian Magpies are birds of open habitats, foraging primarily on the ground. Their typical horizontal posture when foraging and 45° inclined posture when resting alert means the majority of an magpie's intercepted solar radiation falls on its dorsal surface. There are clear geographic differences in magpie dorsal plumage colour, with southern subspecies characterised by greater white dorsal areas, particularly

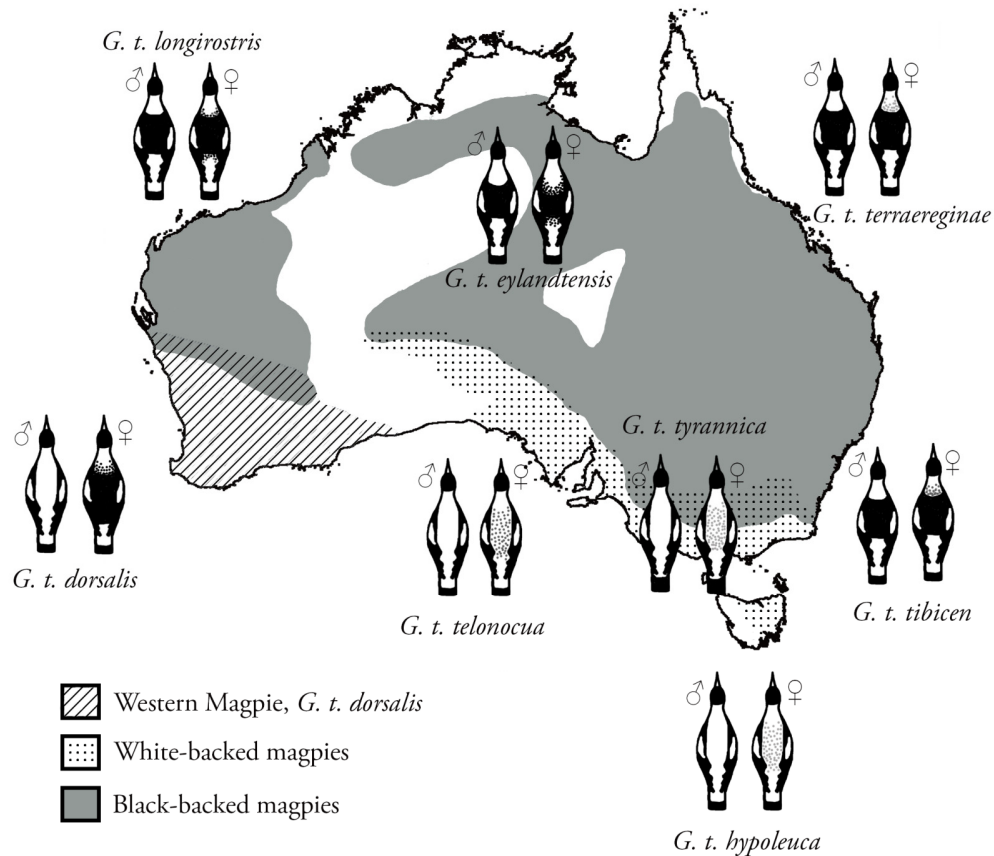


Figure 5.1: Plumage differences and distribution of the subspecies of the Australian Magpie *Gymnorhina tibicen*, after Schodde & Mason 1999 and Kaplan 2004.

for males (Figure 5.1). Of the eight currently recognised subspecies of Australian Magpie (Schodde & Mason 1999; Kaplan 2004), the southwestern subspecies, the Western Magpie (*C. t. dorsalis*) shows the most marked sexual variation. Adult male *C. t. dorsalis* have white dorsal plumage, while the backs of females, sub-adults and juveniles are black with white scalloping in new feathers, wearing away to nearly solid black as feathers age (Figure 5.2).

The Australian Magpie has been the subject of studies of breeding behaviour and group structure (Robinson 1956; Schmidt 1987; Durrant 2004), juvenile learning, foraging (Edwards *et al.* 2015), and genetics and subspeciation (Black 1986; Toon *et al.* 2003; Toon 2006). But despite this body of work, there is nothing known about the physiology of the Australian Magpie and how it maintains energy balance and thermoregulates to be successful in these varied habitats.

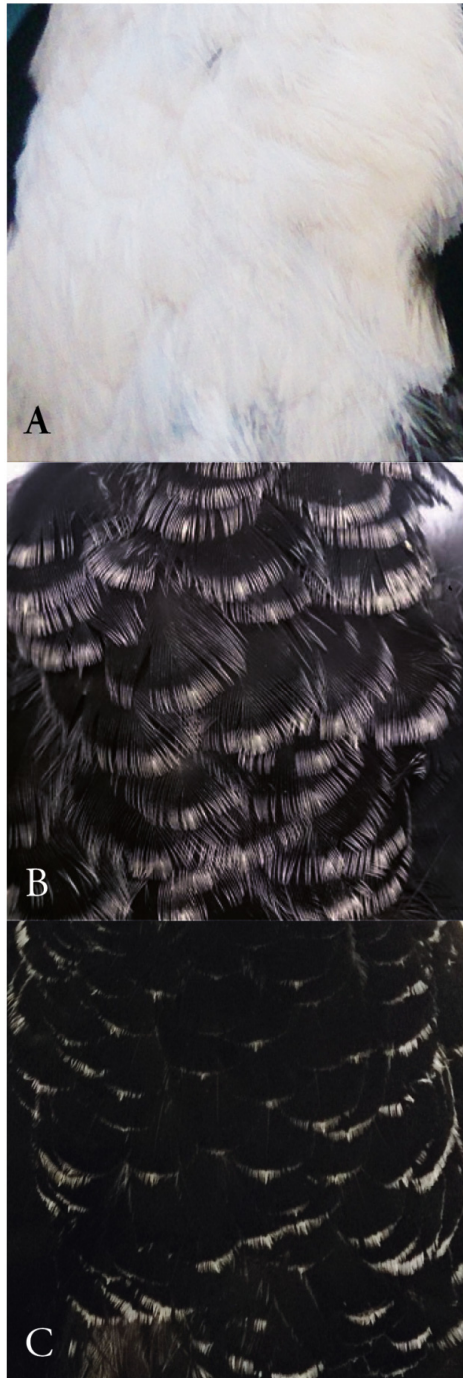


Figure 5.2: Variation in dorsal plumage of the Western Magpie *Gymnorhina tibicen dorsalis*, with white adult male plumage (A), and fresh (B) and worn (C) black dorsal plumage of adult females and sub-adult magpies.

Here I investigate the physiological and potential behavioural thermoregulatory strategies available to Australian Magpies in southwest Australia. I use standard respirometry to measure live birds under controlled laboratory conditions, and a wind tunnel to calculate the biophysical properties of sexually dimorphic magpie plumage.

Methods

Laboratory respirometry

Two adult female, two adult male and four sub-adult (1.5 – 2.5 year old) Western Magpies *Gymnorhina tibicen* (308 g, range 260 – 338 g), were captured at various locations in Perth, Western Australia in September 2013 using cage traps baited with grated cheese and kangaroo mince. They were housed in adjoining outdoor aviaries at Curtin University's Bentley campus, and fed a combination of insectivore mix, grated cheese, kangaroo mince and cat biscuits, supplemented with fruit and live food including cockroaches, crickets, earthworms and mealworms. Birds were isolated and fasted for the 12 hours prior to each experiment, but water was always available *ad libitum*. Each magpie had at least three days between successive measurements.

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) at a range of T_a (5, 10, 15, 20, 25, 30 and 32.5 °C, in random order), after Withers (2001). Birds were measured overnight from approximately 18:00 to 04:00, before being released back into their aviary. Two complete systems allowed concurrent measurement of two birds each night. The experimental set-up, calibration, measurement and analyses were identical to those used for White-browed Babblers (Chapter 2), with several minor amendments to account for the greater mass of magpies. Here 32L clear Perspex chambers were used to measure individual magpies, with air flow rates of 2500 mL min⁻¹. Injections of 2 mL air were used to calibrate the whole-body plethysmography system used to measure ventilatory properties. Ventilatory calculations used $\dot{V}O_2$ values from the time ventilatory data were collected, so were not necessarily the overnight minimal values used in the other calculations, but were on average 108% of minimal values.

Plumage properties

Magpie specimens were obtained from several sources, including euthanised birds from Kanyana Wildlife Rehabilitation Centre in Martin, Perth and opportunistically-collected specimens donated by the public; 4 adult males, 4 adult females and 4 sub-adults were measured. All samples were collected on the Swan Coastal Plain and Perth hills areas. Most samples were from birds that were victims of car strike, but only those with intact dorsal plumage were used. Each specimen was prepared by removing the skin containing the spinal feather tract from nape to preen gland, widening at the scapulars to include the humeral tract and at the pelvis to include the upper crural tract. Skins were pinned out until dry and then any small amounts of residual subcutaneous fat were removed. Mean depth of plumage samples was 22.5 ± 1.7 mm.

The biophysical properties of the plumage samples were measured using a similar methodology to that of Maloney & Dawson (1995) for Emu (*Dromaius novaehollandiae*) plumage, with adjustments for the smaller size of the plumage samples (Figure 5.3).

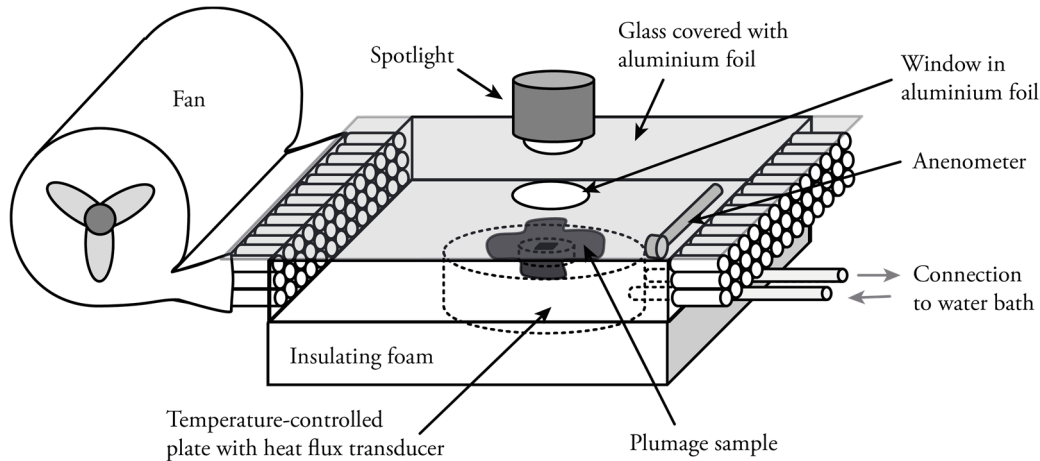


Figure 5.3: Wind-tunnel setup.

Samples were mounted on the upper surface of a temperature-controlled stage consisting of a heat flux transducer (greenTEG; gSKIN-XE 23 8C; 8.5 x 8.5mm) set into a metal block (38 x 54 mm), heated from below by a large, water-filled metal plate (255mm diameter, 58mm thick). The surface of the upper block was maintained at 41°C (body temperature of active Passeriformes of this size; Prinzinger *et al.* 1991) by circulating water between the plate and a water bath (Isotemp, Fisher Scientific Inc) maintained at a constant temperature. The stage surrounding the upper block was insulated by Styrofoam, covered with a Perspex sheet with a cut-out so the transducer and block were flush with the surface. Each plumage sample was taped flat so it covered the block, with the transducer directly under the spinal plumage tract. The stage was placed in a wind tunnel, and an anemometer (Schiltknecht 39400, Technical & Scientific Equipment Co., Melbourne, Australia) positioned behind the sample, fully exposed to the wind, measured wind speed, adjustable by varying the power supplied to a fan (TD Preece Pty Ltd, Manly, Australia). Laminar flow was maintained by parallel baffles at the front and end of the tunnel. In addition to measuring T_a , thermocouples measured temperature on top of the block (T_{block}), at the surface of the skin (T_{skin}), and on the surface of the plumage (T_{surface}), as well as measuring waterbath temperature to control for datalogger drift. All thermocouples were calibrated in a water bath (20 – 50°C, at 5°C increments) against a mercury thermometer traceable to a national standard. The heat flux transducer was

calibrated using an insulative blanket (National Institute of Standards and Technology, USA) of known conductivity ($1.610 \text{ W m}^{-2} \text{ }^{\circ}\text{C}^{-1}$) at 30, 35 and 40 °C.

Each sample was measured at four wind speeds (1, 2, 4 and 6 ms^{-1}), with and without solar radiation (simulated by an ARRI Daylight 575W spotlight, Maloney & Dawson 1995). During each experiment, the thermocouples, heat flux transducer and anemometer were connected to an analog/digital converter (DataTaker 500 Series 2 Data Logger, Data Electronics Australia) then to a laptop running DataTaker software to record each channel simultaneously at 10 sec intervals.

Total thermal conductance (C ; $\text{W m}^{-2} \text{ }^{\circ}\text{C}^{-1}$) of the plumage samples was calculated as $C = Q/(T_{\text{block}} - T_{\text{a}})$, where Q is heat flow through the sample (W m^{-2}). Thermal conductance was then converted to total thermal resistance, (r_t ; s m^{-1}) using the volumetric specific heat of air at 20°C ($1200 \text{ J m}^{-3} \text{ K}^{-1}$; $r_t = 1200/C$; Cooper *et al.* 2003). Similarly, the partial contributions of skin, plumage and air boundary layers were calculated using differences between T_{block} , T_{skin} , T_{surface} , and T_{a} , and modifying the above equations accordingly. Solar heat gain (SHG) was calculated for each sample at each wind speed as the net heat flux with solar radiation minus the net heat flux without (Walsberg 1990).

To measure reflectance of the samples under the ARRI spotlight, samples were placed on a horizontal surface, with the spotlight directed on them at an angle 25° from vertical. Incident light reflected by the samples was measured by a radiometer (Model 6-1.8, Eppley Inc, Newport, Rhode Island), also angled at 25° from vertical. A 20 cm long, black tube was placed between the sample and the radiometer, to minimise light diffusion and external light interference. Reflectivity of samples was calibrated against reference boards of solid black and solid white. with calculated reflectivity of 9.1 and 85.5% respectively, after Moore (2015). Solar absorption efficiency (SAE) of the samples was then calculated as $(\% \text{ irradiation})/(1 - \text{reflectivity}/100)$.

Data handling and statistical analysis

Values are presented as mean \pm standard error (SE), with N = number of individuals and n = number of measurements unless otherwise indicated. Times are Western Australian standard times (AWST; AWST = Greenwich Mean Time + 8 h). All statistical models were tested at $\alpha = 0.05$. The effect of T_a on physiological variables of $\dot{V}O_2$, $\dot{V}CO_2$, EWL, RWE, C_{wet} , C_{dry} , f_R , V_T , V_I , and EO_2 were analysed for 8 individual magpies by multivariate repeated measures analysis of variance (RMANOVA) using the Wilks-Lambda test in SPSS with polynomial ($\dot{V}O_2$, $\dot{V}CO_2$, RWE, f_R , V_T , V_I , and EO_2) and reverse Helmert (EWL, C_{wet} and C_{dry}) *a priori* contrasts (Withers & Cooper 2011). The effect of windspeed and simulated sunlight on the thermal resistance of magpie plumage was also calculated using RMANOVA, but with age/sex as a between-subject factor. Where variables had a significant linear contrast, the coefficients of the equation describing each relationship were calculated using a custom-written macro (Withers & Cooper 2011).

Results

Laboratory respirometry

Average T_b ranged from 40.0 °C at $T_a = 32.5$ °C to 37.87 °C at $T_a = 10$ °C, before increasing to 38.67 °C at $T_a = 5$ °C, but T_a had no statistical effect on magpie T_b (RMANOVA, $F_{6,2} = 7.78$, $P = 0.118$). However polynomial *a priori* contrasts supported linear ($P = 0.001$), quadratic ($P = 0.003$) and cubic relationships ($P = 0.042$) between T_b and T_a (Figure 5.4A). When T_b at $T_a = 5$ °C was excluded from the model, only a linear pattern for T_b with T_a remained ($P = 0.001$), indicating that T_b at $T_a = 5$ °C deviated significantly from the general linear pattern, described by the equation $T_b = 36.9 + 0.09 \cdot T_a$. T_b differed between individual magpies ($F_{1,7} = 59919$, $P < 0.001$).

Mean $\dot{V}O_2$ decreased from 1.33 ± 0.12 mL $O_2 g^{-1} h^{-1}$ at $T_a = 5$ °C to 0.96 ± 0.05 mL $O_2 g^{-1} h^{-1}$ at $T_a = 25$ °C before rising again slightly to 1.02 ± 0.03 mL $O_2 g^{-1} h^{-1}$ at $T_a = 32.5$ °C. There was no overall effect of T_a on $\dot{V}O_2$ (RMANOVA, $F_{6,2} = 5.28$, $P = 0.168$), however polynomial *a priori* contrasts indicated both a linear ($P = 0.037$) and quadratic relationship ($P < 0.001$) between T_a s of 5 °C and 32.5 °C (Figure 5.4B). With the

exclusion of data at 30 °C and 32.5 °C from the model only a linear pattern of $\dot{V}O_2$ with T_a remained ($P = 0.004$). I interpret the minimum $\dot{V}O_2$ at $T_a = 25$ °C to be BMR; the relationship between $\dot{V}O_2$ and T_a below thermoneutrality can be described by the equation $\dot{V}O_2 = 1.23 - 0.01 \cdot T_a$. $\dot{V}O_2$ differed between individual magpies ($F_{1,7} = 596$, $P < 0.001$).

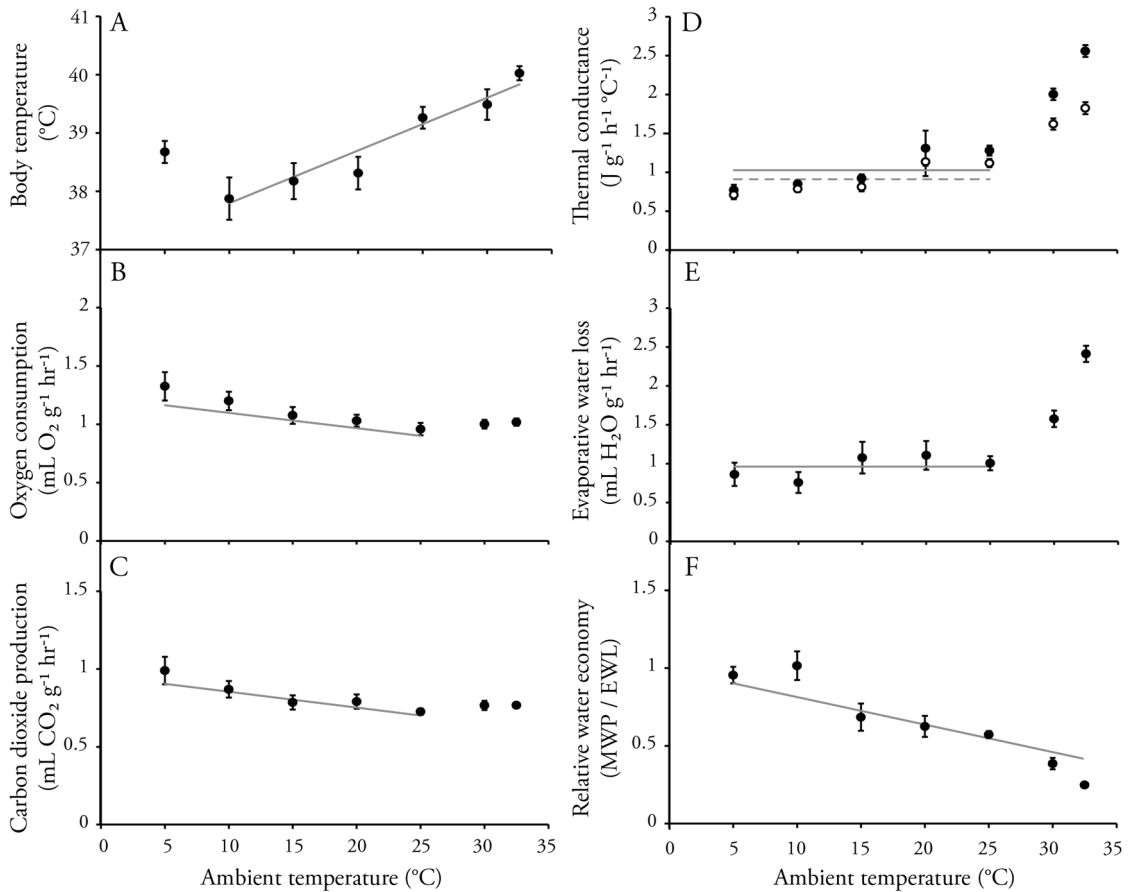


Figure 5.4: Body temperature (A), oxygen consumption (B), carbon dioxide production (C), wet (black symbols) and dry (white symbols) thermal conductance (D), evaporative water loss (E) and relative water economy (F) of magpies at a range of ambient temperatures. Symbols show mean values and error bars ± 1 standard error ($N = 8$).

Mean $\dot{V}CO_2$ decreased from a maximum of 0.99 ± 0.09 mL CO_2 g $^{-1}$ h $^{-1}$ at $T_a = 5$ °C to 0.73 ± 0.02 mL CO_2 g $^{-1}$ h $^{-1}$ at $T_a = 25$ °C before rising again slightly to 0.77 ± 0.01 mL CO_2 g $^{-1}$ h $^{-1}$ at $T_a = 32.5$ °C. Analysis of $\dot{V}CO_2$ data also indicated no overall effect of T_a on $\dot{V}CO_2$ ($F_{6,2} = 5.36$, $P = 0.166$), however polynomial *a priori* contrasts again supported the visual pattern (Figure 5.4C) of both linear ($P = 0.027$) and quadratic relationships ($P = 0.012$) between $\dot{V}CO_2$ and T_a . With the exclusion of data at 30 °C and 32.5 °C only a

linear pattern remained ($P = 0.009$). Here magpie $\dot{V}\text{CO}_2$ also differed between individuals ($F_{1,7} = 677$, $P < 0.001$). The equation $\dot{V}\text{CO}_2 = 0.96 - 0.01 \cdot T_a$ describes the relationship between $\dot{V}\text{CO}_2$ and T_a below thermoneutrality.

Wet thermal conductance at thermoneutrality was $1.28 \pm 0.06 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ and C_{dry} was $1.12 \pm 0.05 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$. Repeated measures ANOVA showed both C_{wet} and C_{dry} varied with T_a ($F_{6,2} = 385$, $P = 0.003$ and $F_{6,2} = 56.06$, $P = 0.018$ respectively), and while reverse Helmert *a priori* contrasts confirmed (Figure 5.4D) C_{wet} and C_{dry} varied little below thermoneutrality, as T_a exceeded 25°C , both C_{wet} and C_{dry} increased ($F_{6,2} = 45.0$, $P < 0.001$ and $F_{6,2} = 30.7$, $P = 0.01$ respectively). C_{wet} and C_{dry} values differed between individual magpies ($F_{1,7} = 839$, $P < 0.001$ and $F_{1,7} = 864$, $P < 0.001$ respectively).

Minimal EWL ($0.76 \pm 0.13 \text{ mL H}_2\text{O g}^{-1} \text{ h}^{-1}$) occurred at $T_a = 10^\circ\text{C}$, although EWL varied both with T_a ($F_{6,2} = 122$, $P = 0.008$) and between individuals ($F_{1,7} = 129$, $P < 0.001$). Reverse Helmert *a priori* contrasts showed EWL at $T_a = 20^\circ\text{C}$, 30°C and 32.5°C were higher than those recorded at lower T_a ($P = 0.046$, $P = 0.001$, and $P < 0.001$ respectively). While RWE also differed between individual magpies ($F_{1,7} = 270$, $P < 0.001$) and although there was no overall effect of T_a upon RWE ($F_{6,2} = 12.0$, $P = 0.079$), polynomial *a priori* contrasts showed a linear relationship ($P < 0.001$). RWE decreased with increasing T_a (Figure 5.4F), and the linear relationship between RWE and T_a below thermoneutrality is described by the equation $\text{RWE} = 0.99 - 0.02(T_a)$. The point of relative water economy (pRWE) is calculated to be -0.7°C .

Ventilatory data were collected for magpies at T_a s of 5, 10, 15, 20, 25 and 30°C . Over this range, there was no overall effect of T_a on f_R ($F_{5,3} = 0.689$, $P = 0.667$). Mean f_R was $15.0 \text{ breaths min}^{-1}$, and polynomial *a priori* contrasts did not indicate a linear ($P = 0.149$) or any other pattern (Figure 5.5A). T_a had no overall effect on V_T , V_I nor EO_2 by RMANOVA ($F_{5,3} = 3.20$, $P = 0.184$; $F_{5,3} = 5.41$ $P = 0.098$; and $F_{5,3} = 5.58$ $P = 0.094$ respectively; Figure 5.5), although a cubic relationship was identified for all three by polynomial *a priori* contrasts ($P = 0.045$, $P = 0.023$, and $P = 0.003$ respectively). There

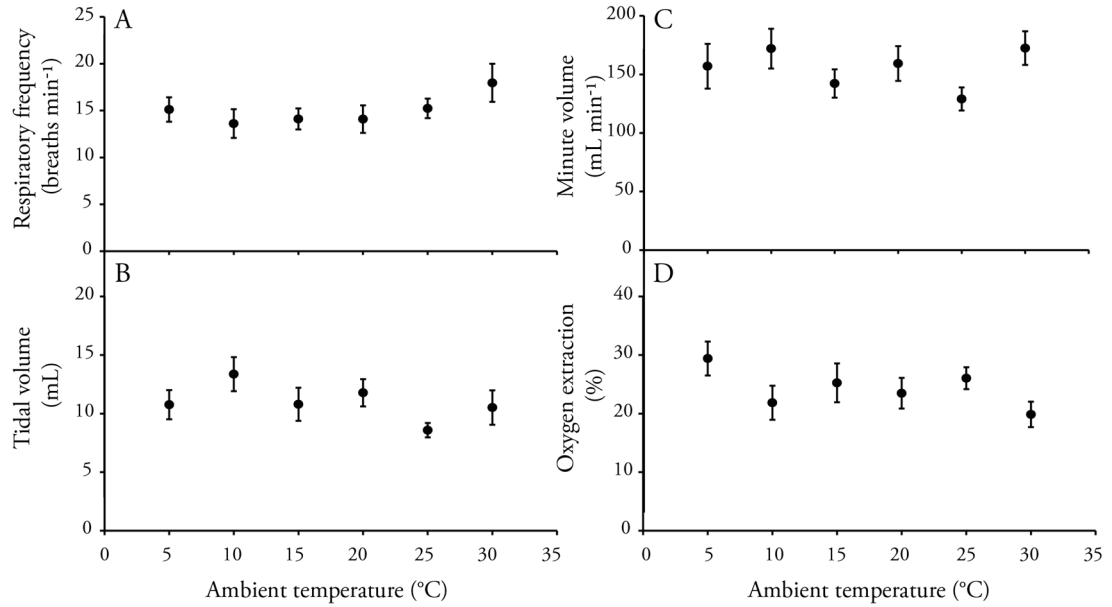


Figure 5.5: Respiratory frequency (A), tidal volume (B), minute volume (C) and oxygen extraction (D) for magpies at a range of ambient temperatures. Values are mean \pm standard error (N = 8).

was significant individual variation between magpies for f_R ($F_{1,7} = 174$, $P < 0.001$), V_T ($F_{1,7} = 151$, $P < 0.001$), V_I ($F_{1,7} = 226$, $P < 0.001$), and EO_2 ($F_{1,7} = 240$, $P < 0.001$).

Thermal resistance and solar heat gain

Total resistance of magpie plumage was not constant at the different windspeeds ($F_{3,7} = 50.09$, $P < 0.001$), but fell from $536 \pm 30 \text{ s m}^{-1}$ at 1 m sec^{-1} to $190 \pm 23 \text{ s m}^{-1}$ at 6 m sec^{-1} (Figure 5.6). Polynomial *a priori* contrasts showed the reduction in resistance with increasing windspeed was linear ($F_{1,9} = 150.6$, $P < 0.001$). Although resistance differed between individual magpies ($F_{1,9} = 142$, $P < 0.001$), there was no difference in resistance between sub-adult, adult female and adult male plumage ($F_{2,9} = 0.088$, $P = 0.916$).

Breaking total resistance into its component parts, at 1 m sec^{-1} the heat loss through the depth of the plumage accounted for 80.6% of total resistance, resistance over the skin surface accounted for 11.7%, and resistance of the boundary layer of air surrounding the plumage accounted for the remaining 7.7% of total resistance. There was no interaction effect between age-sex class and windspeed (skin $F_{6,14} = 0.577$, $P = 0.743$; plumage $F_{6,14} =$

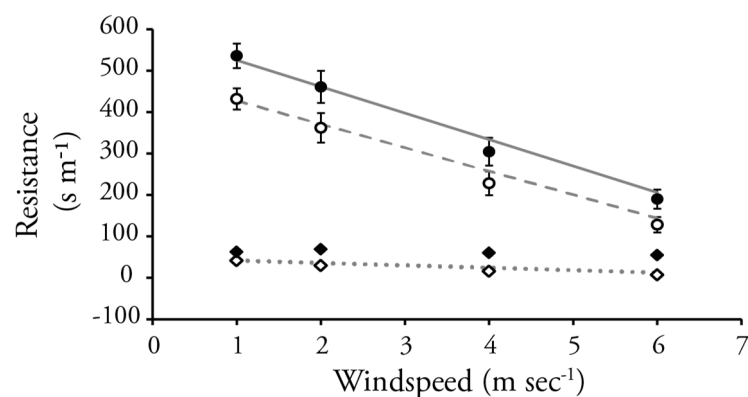


Figure 5.6: Variation in resistance (s m⁻¹) of magpie plumage with wind speed (m sec⁻¹). Components of total resistance (black circles, solid grey line) include plumage resistance (white symbols, dashed line), boundary resistance (white diamonds, dotted line), and skin resistance (black diamonds). Symbols show mean \pm standard error (N = 12).

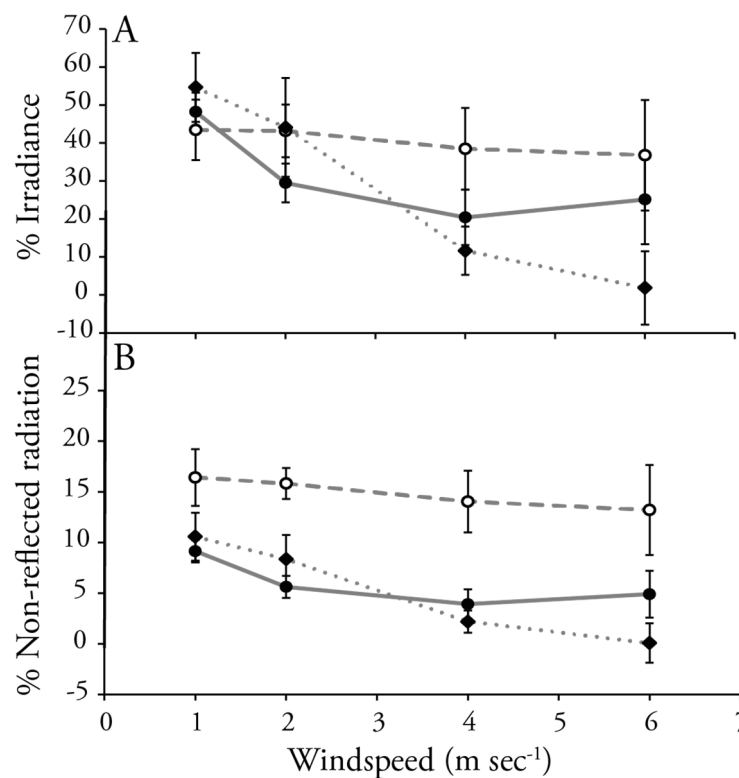


Figure 5.7: Solar heat gain (SHG; % irradiance; A) and solar absorption efficiency (SAE; % non-reflected radiation; B) of plumage of adult male (white circles; dashed lines), adult female (black circles; solid lines) and sub-adult (black diamonds; dotted lines) magpies, with changing wind speed (m sec⁻¹). Values are mean \pm standard error (N = 4).

1.870, $P = 0.157$; boundary $F_{6,14} = 1.263$, $P = 0.334$) and neither did patterns in boundary, plumage and skin resistance vary between adult male, female or sub-adults (skin $F_{2,9} = 0.126$, $P = 0.883$; plumage $F_{2,9} = 0.211$, $P = 0.814$; boundary $F_{2,9} = 1.216$, $P = 0.341$). However, skin, plumage and boundary resistance did all vary with wind speed (skin $F_{2,7} = 4.993$, $P = 0.037$; plumage $F_{3,7} = 72.39$, $P < 0.001$; boundary $F_{3,7} = 36.37$, $P < 0.001$). Polynomial *a priori* contrasts showed only resistance in the plumage and boundary layers both decreased linearly with increasing wind speed (skin $F_{1,9} = 2.603$, $P = 0.141$; plumage $F_{1,9} = 170.08$, $P < 0.001$; boundary $F_{1,9} = 115$, $P < 0.001$), plumage resistance falling by 70.3% between 1 and 4 m sec⁻¹, and boundary resistance falling by 83.0%. There were differences between individual magpies were consistent for skin, plumage and boundary layer resistance (skin $F_{1,9} = 139.43$, $P < 0.001$; plumage $F_{1,9} = 118.25$, $P < 0.001$; boundary $F_{1,9} = 105.64$, $P < 0.001$).

Reflectance of adult male magpie plumage was $59.4 \pm 3.6\%$, and was $15.3 \pm 0.72\%$ and $17.0 \pm 2.05\%$ for adult females and sub-adults respectively. Solar heat gain varied with windspeed and age ($F_{3,7} = 5.071$, $P = 0.036$), with a significant linear relationship ($F_{3,7} = 5.071$, $P = 0.036$; Figure 5.7). This was most evident for sub-adult magpie plumage, which fell from $54.6 \pm 9.1\%$ irradiance at 1 m sec⁻¹ to $1.84 \pm 9.7\%$ at 6 m sec⁻¹, while adult male plumage only varied from $43.4 \pm 7.9\%$ to $36.8 \pm 14.6\%$ over the same range of windspeeds. While there was no overall multivariate effect of windspeed and age/sex class on SAE ($F_{3,7} = 2.737$, $P = 0.123$), the percentage of non-reflected radiation acting as SHG on the skin, did differ between adult male, female and sub-adult plumage ($F_{2,9} = 20.799$, $P < 0.001$), with % non-reflected radiation consistently greater for adult males at all the windspeeds tested. Polynomial *a priori* contrasts indicated that SAE decreased linearly with increasing windspeed ($F_{1,9} = 6.068$, $P = 0.036$), and sub-adult magpie plumage again had the greatest change, falling from $10.6 \pm 2.4\%$ of non-reflected radiation at 1 m sec⁻¹ to $0.08 \pm 1.9\%$ at 6 m sec⁻¹. Over these windspeeds the change in SAE for adult male plumage was much less, $16.4 \pm 2.8\%$ to $13.2 \pm 4.4\%$ respectively.

Discussion

Despite being one of Australia's most widespread, common and iconic passerines, this study presents the first data concerning the thermoregulatory physiology of the Australian Magpie, *Gymnorhina tibicen*. Magpies had a typical homeothermic response to low T_a , increasing MR and lowering conductance while maintaining T_b , with no evidence of torpor. In the wind tunnel, magpie plumage also had a typical response, with insulation falling as windspeed increased. The plumage accounted for the majority of total thermal resistance, rather than the skin or the boundary layer. Under simulated sunlight, SHG and SAE of adult male (white) plumage was relatively constant as windspeed increased, however adult female and sub-adult (black) plumage varied substantially, absorbing much less heat as windspeed increased. The Western Magpie (*G. t. dorsalis*) can be used as a model to explain how plumage variation in this widespread passerine assists the differing subspecies manage the thermal loads of their environments.

Physiological knowledge of common, widespread species is important to understand the attributes that enable species to persist under a broad range of environmental conditions. The thermoregulatory physiology of many species varies between subspecies or habitat, as seen in Rufous-collared Sparrows *Zonotrichia capensis* (Cavieres & Sabat 2008) or White-browed Scrubwrens *Sericornis frontalis* (Ambrose 1985). Australian Magpies are known to vary at a subspecies level in their biology, ecology, and genetics. While all magpie subspecies are observed to favour open habitats, be sedentary and defend and maintain territories in family groups, there are marked differences in genetics, plumage, and breeding mode between subspecies (Toon *et al.* 2003; Kaplan 2004). How this relates to their physiology is unknown.

For their size and phylogenetic position, with the exception of EWL, the standard thermoregulatory variables (T_b , BMR, thermal conductance, EWL, f_R , V_T , and EO_2) of magpies agree with values predicted from other studies (Figure 5.8; 5.9). Placing these variables in an allometric and phylogenetic context is necessary to understand whether magpies display any unusual adaptations to their temperate environment (as per White-

browed Babblers, Rufous Treecreepers and Western Yellow Robins; Chapters 2 – 4 respectively). At thermoneutrality actual magpie T_b was only 0.2 °C below that predicted by body mass alone, and BMR was 86.4% of that predicted, well within the 95% prediction limits both before and after accounting for phylogenetic history (Figure 5.8).

Magpie thermal conductance measured by respirometry was 83.7% of that predicted by body mass alone, but well within the 95% prediction limits (Figure 5.9). Magpie

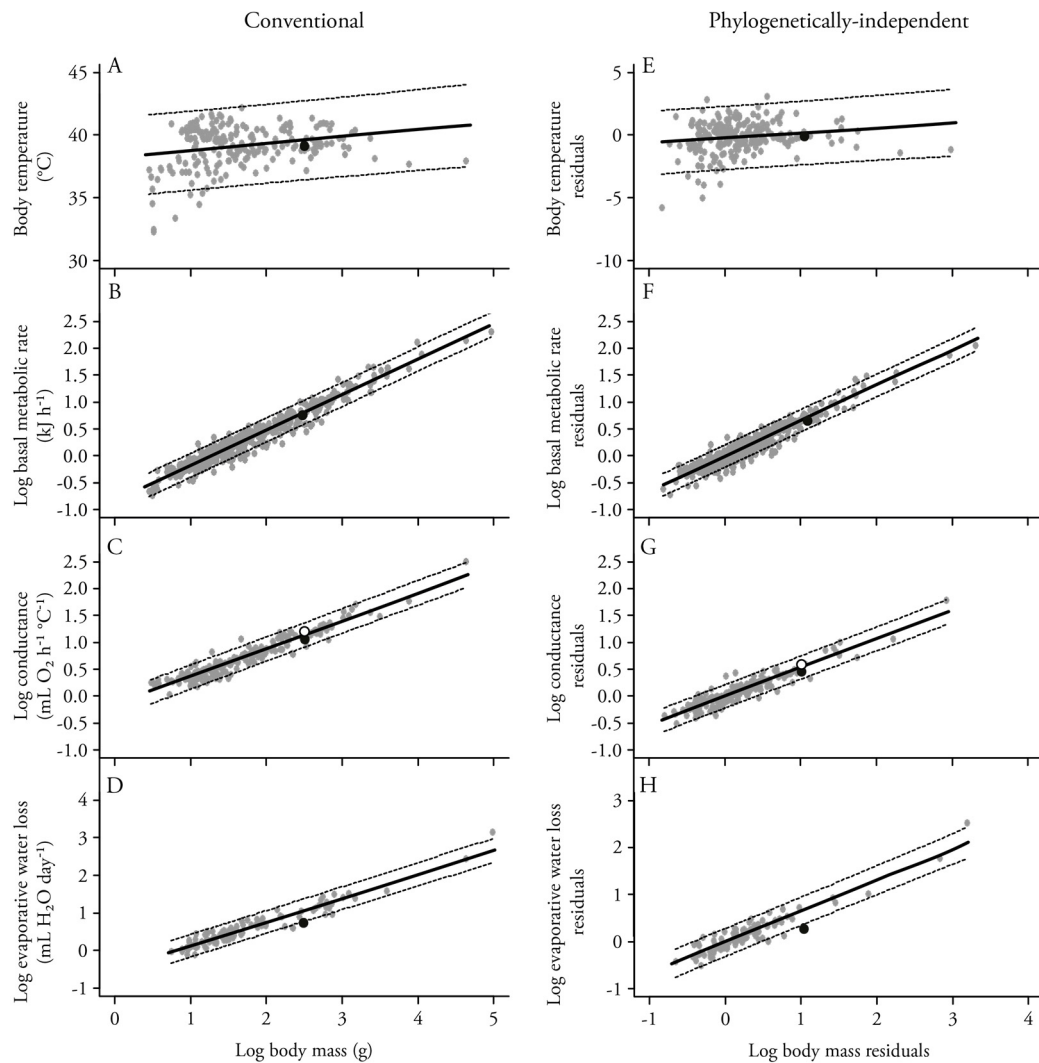


Figure 5.8: Allometric comparison of body temperature (A), basal metabolic rate (B), conductance (C), and evaporative water loss (D) values obtained for magpies (black symbols) compared with other birds (grey symbols). White symbols show the plumage conductance in the wind tunnel at 1 m s⁻¹. Phylogenetically-independent residuals for the same parameters are displayed in E – H respectively. All values are represented as log₁₀ values, with the exception of body temperature, which is untransformed. Solid lines mark the least squares regression lines and the dotted lines 95% confidence intervals. Methodology is described in Chapter 6 and datasets are presented in the Appendices.

conductance calculated from a dorsal plumage sample was 108% that predicted by body mass, also well within the 95% prediction limits. There was no evidence to suggest that magpie plumage differed structurally between age/sex classes, as thermal resistance values obtained from adult female, adult male and sub-adult magpie plumage measured in the wind tunnel were statistically indistinguishable. This is consistent with data from plumages of different colour Rock Doves (*Columba livia*; Walsberg *et al.* 1978).

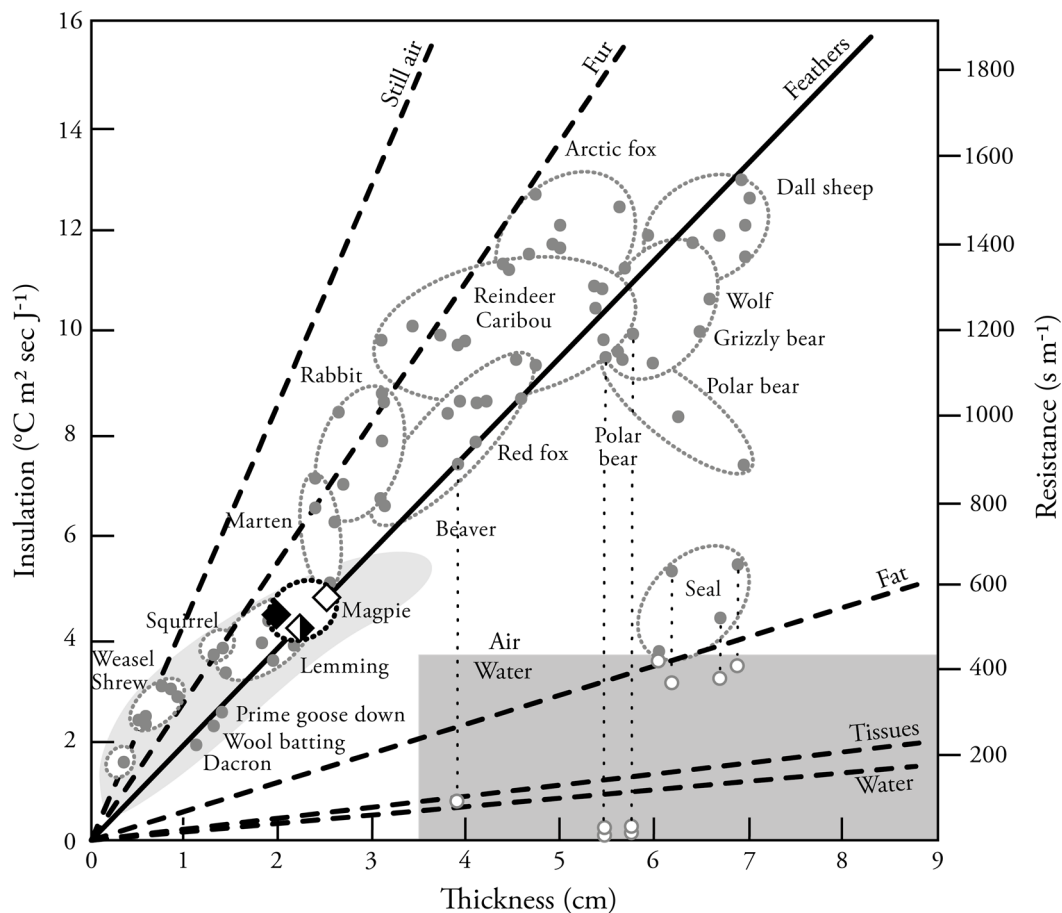


Figure 5.9: Comparison of endotherm fur and feather insulation ($^{\circ}\text{C m}^2 \text{ sec J}^{-1}$) and resistance (s m^{-1}) plotted by pelt and plumage thickness (cm). Figure is drawn from Withers (1992), incorporating arctic mammal data from Scholander *et al.* (1950), artificial substances Kaufman, Bothe and Mayer (1982) as well as this study. Grey and white circles are data from these earlier studies, and the pale grey polygon shows the distribution of tropical insulation values (see Figure 5.10 for details). Diamonds are values for adult male (white), adult female (black) and sub-adult (black and white) magpies. Thick solid and dashed lines are predicted insulation patterns for substances of different thickness.

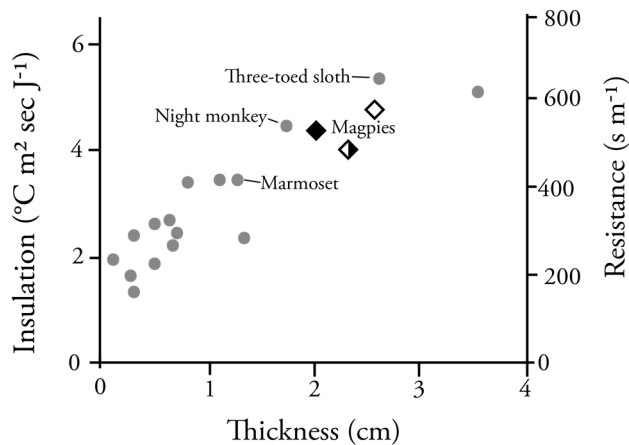


Figure 5.10: Comparison of insulation ($^{\circ}\text{C m}^2 \text{ sec J}^{-1}$) and resistance (s m^{-1}) of tropical endotherm fur (grey circles; Scholander *et al.* 1950) and plumage of adult male (white diamond), adult female (black diamond), and sub-adult (black and white diamond) magpies plotted by pelt and plumage thickness (cm).

Plumage thermal resistance was exactly as predicted for feathers of that thickness (Figure 5.9; Withers 1992). Birds generally have lower conductance than mammals of similar mass (Aschoff 1981; Schleucher & Withers 2001), but here temperate magpies have equivalent plumage thickness to Arctic mammals of similar mass (Figure 5.9; Northern Collared

Lemming, *Dicrostonyx*

groenlandicus; 30 – 122 g; and American Marten, *Martes americana*; 280 – 1300 g; Scholander *et al.* 1950; body mass data from ADW Online 2016). However, when placed alongside tropical animals (Scholander *et al.* 1950), plumage thickness is equivalent to much larger tropical mammals (Figure 5.10; Northern Night Monkey, *Aotus trivirgatus*; 800 g; Brown-throated Three-toed Sloth, *Bradypus variegatus*; 3490 – 5190 g), and temperate magpies have greater insulation and plumage thickness than equivalent size mammals (Geoffroy's Marmoset, *Callithrix geoffroyi*, 190 – 350 g). Increasing the depth of the fur or feathers yields substantial increases to total resistance and SAE by increasing the contribution of the pelt/plumage in insulation, for Vervet Monkeys (*Chlorocebus pygerythrus*; McFarland *et al.* 2016), and Numbats (*Myrmecobius fasciatus*; Cooper *et al.* 2003). This suggests that not only is piloerection an important mechanism for retaining body heat, but also that if birds like magpies have deeper plumage than the pelts of mammals of equivalent mass, then plumage provides significant energetic benefit in helping small endotherms retain body heat under low T_a .

The effect of increasing windspeed decreasing resistance of magpie plumage was similar to the pelts and plumages of other species measured (Walsberg *et al.* 1978; Maloney &

Dawson 1995). The relative contribution of the boundary layer of air at 1 ms^{-1} was similar for magpies (7.7%), as for Emus (8.8%; Maloney & Dawson 1995), despite their difference in size (magpie total resistance was 50.2% of Emu resistance 1067 s m^{-1} , and magpie feathers were half as thick as 44.75mm Emu plumage). As expected, the decrease in the resistance and effectiveness of the boundary layer occurred at a greater rate than the decrease in plumage resistance (Wolf & Walsberg 2000; Wolf *et al.* 2000).

Plumage provides birds with a substantial capacity for heat retention (Aschoff 1981; Schleucher & Withers 2001), but also minimises SHG by intercepting a substantial proportion of incident solar radiation before it reaches the body (Walsberg & Wolf 1995). Despite substantial variation observed between species, SHG reported here for magpies is within the range for that reported for other birds (Wolf & Walsberg 1996, 2000; Wolf *et al.* 2000).

For the dichromatic magpie, how plumage interacted with solar radiation varied with coat colour, in agreement with observations of black and white Rock Doves (Walsberg *et al.* 1978; Walsberg 1983). The light plumage of adult male magpies reflected solar radiation directly at the outer feather layer, so SHG and SAE were more constant at the windspeeds tested, with percentage of non-reflected radiation that acted as SHG at the level of the skin falling only from $16.4 \pm 2.8\%$ at 1 m sec^{-1} to $13.2 \pm 4.4\%$ at 6 m sec^{-1} . Conversely, although dark plumage absorbs solar radiation at the outer feather surface and results in high SHG at low windspeeds (Walsberg 1983), at higher windspeed turbulence at the boundary layer provides potential for heat dissipation. At windspeeds of 6 m sec^{-1} , plumage of sub-adult magpies provided near complete protection from solar radiation ($\text{SHG} = 1.84 \pm 9.7\%$, $\text{SAE} = 0.08 \pm 1.9\%$). How dichromatic Western Magpie populations respond to this difference between sex/age cohorts is unknown. Although field behaviour studies of the Western Magpie have recorded changes in magpie behaviour with T_{a} , windspeed was not measured, so it is unsurprising that no behavioural difference between black- and white-backed birds was detected (Edwards *et al.* 2015).

The impact of plumage colour can be seen in the geographic subspecies variation of magpies. Black-backed magpie subspecies are all present in the lower latitudes (Higgins *et al.* 2006), in the habitats where T_a and incident radiation are greatest. This suggests that under these environmental conditions a plumage that absorbs solar radiation at the outer surface, creating a heat shield that facilitates rapid heat dissipation at high windspeeds may be an important mechanism for meeting energetic demands (Figure 5.1). Many dark-plumaged birds, such as Emus (*Dromaius novaehollandiae*; Maloney & Dawson 1995), are successful in environments with high T_a and high incident radiation (Cloudsley-Thompson 1999), where plumage depth and colour reduces solar heat loads and allows them to maintain activity when other diurnal animals, such as kangaroos, must adjust behaviour and use behavioural mechanisms to compensate (Dawson & Maloney 2004, 2016). Conversely white-backed magpie subspecies are found in the higher latitudes (Higgins *et al.* 2006), areas of lower T_a and lower incident solar radiation. White plumage absorbs more solar radiation through the depth of the plumage, regardless of windspeed. This consistent solar heat load may be advantageous under the conditions in these habitats.

Capacity for frugal water consumption is important for birds in high T_a , exposed environments (Williams & Tieleman 2000; Tieleman & Williams 2002; Tieleman *et al.* 2002). Here, magpie EWL was only 45.5% that predicted for a bird of their mass, just inside the 95% prediction limits, but outside after accounting for phylogeny. As discussed previously for the other species (Chapters 2 – 4) however, low EWL recorded here may be a true adaption to a water-scarce environment (Withers *et al.* 2006), or may simply be an artefact of the longer measurement duration used, allowing for truly ‘basal’ EWL measurements (Cooper & Withers 2009; Page *et al.* 2011; Connolly & Cooper 2014). Magpie pRWE (-0.7 °C) demonstrates that these temperate magpies are dependent upon additional water intake under the T_a conditions measured, obtained via either preformed water in their diet, or standing water if available. Western Magpies in an arid habitat, Wanjarri Nature Reserve (27° 25’ S, 120° 40’ E), were heard in the vicinity of waterholes, but were never observed to drink (Davies 1972). However in urban and rural areas in

temperate eastern Australia, magpies (*G. t. tibicen* and *G. t. tyrannica*) are common and are regular visitors to bird baths and watersources (Cleary *et al.* 2016). The omnivorous diet of magpies likely assists them to meet their water requirements where water is scarce (Barker & Vestjens 1990; Kaplan 2004).

Comparison of ventilatory variables demonstrates how magpies meet their oxygen demand both at thermoneutral and low T_a . Although $\dot{V}O_2$ doesn't scale allometrically, at thermoneutrality magpie $\dot{V}O_2$ was at a similar efficiency to other birds measured. Magpies met their oxygen demands at thermoneutrality with a lower breathing rate and higher tidal volume than predicted by body mass (51.9% and 170% respectively), although both were within the 95% prediction limits both before and after accounting for phylogeny (Figure 5.11). Below thermoneutrality the relative contribution of f_R and V_T to meeting

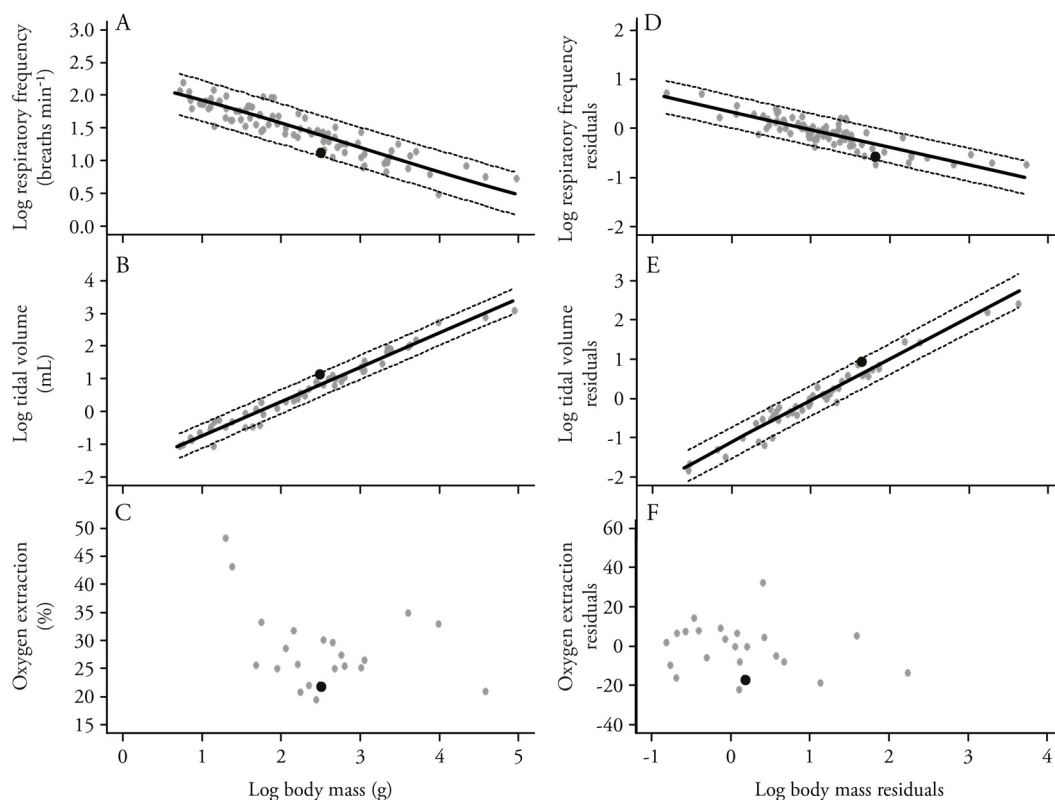


Figure 5.11: Allometric comparison of respiratory frequency (A), tidal volume (B), and oxygen extraction (C) for magpies (black symbols) compared with other birds (grey symbols). Phylogenetically-independent residuals for the same parameters are displayed in D – F respectively. All values are represented as \log_{10} values, with the exception of oxygen extraction, which is untransformed. Where a linear relationship exists, solid lines mark the least squares regression lines and the dotted lines 95% confidence intervals. Methodology is described in Chapter 6 and datasets are presented in the Appendices.

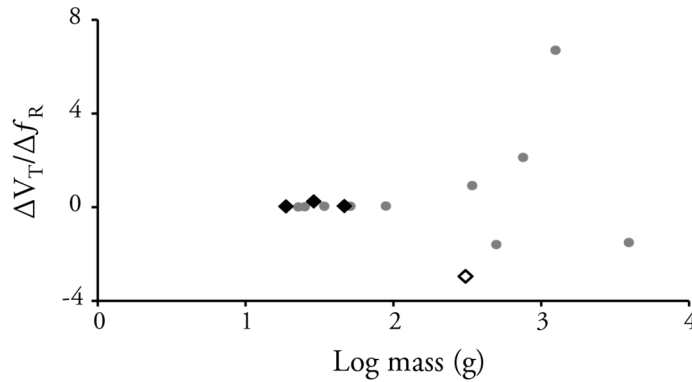


Figure 5.12: Patterns of accommodating increased oxygen demand below thermoneutrality (measured by the ratio of change in tidal volume to change in breathing rate) with changing body mass for magpies (white diamond), other birds from this study (black diamonds) and other birds (grey circles). Additional data is from Bucher 1985; Kaiser & Bucher 1985; Clemens 1988; Prinzinger 1988; Bucher & Morgan 1990; Withers & Williams 1990; and Morgan *et al.* 1992.

oxygen demands can be compared by calculating $\Delta V_T/\Delta f_R$ using the methodology outlined by Cooper & Withers (2004a; Schmidt *et al.* 2009). Smaller birds (including the babbler, robin and treecreeper, Chapters 2 - 4) increased breathing rate to accommodate increased energy demands below thermoneutrality, while maintaining near constant tidal volume, so $\Delta V_T/\Delta f_R \approx 0$ (Figure 5.12), in a manner similar to small mammals (Cooper & Withers 2004a). Larger birds, including magpies, had more diverse responses. Some had large $\Delta V_T/\Delta f_R$, like large mammals do (Cooper & Withers 2004a), but the magpie ($\Delta V_T/\Delta f_R = -2.96$), male Prairie Falcon (*Falco mexicanus*; Kaiser & Bucher 1985) and Giant Petrel (*Macronectes giganteus*; Morgan *et al.* 1992) had negative $\Delta V_T/\Delta f_R$ values, as result of f_R at thermoneutral that was above f_R at low T_a . Although these birds had minimal f_R below thermoneutrality, all still met their increased oxygen demands by increasing V_T with at low T_a , in agreement with other large endotherms.

In conclusion, the thermoregulatory physiology of the Western Magpie demonstrated a typical, homeothermic response to low T_a . The role of plumage in thermoregulation was more complex, but provided insight into avian strategies for meeting energetic challenges. While magpie plumage had typical avian resistance for both its thickness and for magpie

mass, comparisons with mammal pelts show magpie plumage is substantially thicker than that of equivalent sized mammals. If this greater plumage loft is characteristic of other birds it may help explain the relative scarcity of extreme physiological thermoregulatory strategies like torpor in birds, in comparison with mammals of similar mass. Plumage structure aids avian thermoregulation at both low T_a and when exposed to solar radiation. Dark and light plumage respond differently to increasing windspeed, and the thermoregulatory impact of these differences could drive sexual/developmental selection and geographic sub-speciation in magpies.

General discussion

Here I examined the thermoregulatory physiology of four sedentary, endemic, Australian passerines to identify the physiological and behavioural strategies they used to meet the energetic challenges of their environment. There was no evidence that these birds used substantial heterothermy or torpor during cold ambient conditions when either free-ranging or in the laboratory. Instead all four species demonstrated a typical endothermic response to low ambient temperature (T_a), maintaining body temperature (T_b) only just below normothermia by increasing metabolic rate and decreasing thermal conductance (C). Nocturnal roosting behaviour differed between babblers, treecreepers, and robins. Although babblers saved substantial energy by roosting communally in a domed roost nest, they were not obligate social thermoregulators, and were able to maintain homeothermy when roosting solitarily in the laboratory. Treecreepers roosted individually in tree hollows, and while some hollows had an internal temperature that would buffer treecreepers against extremely low T_a , some hollows used were little different to ambient conditions. The robin, the smallest of the three, showed the least specialised behaviour and roosted solitarily in exposed foliage. Despite these differences, all three species were able to maintain homeothermy despite below freezing T_a . Likewise there were no common diurnal behavioural traits between species at low T_a , or following nights of low T_a . Investigation of magpie plumage revealed that the depth and structure of plumage benefits both heat retention at low T_a as well as being a mechanism to minimise overheating under solar radiation. These characteristics of plumage may play a considerable role in balancing avian energy budgets and allowing the maintenance of homeothermia at low T_a .

Thermoregulatory physiology of Australian passerines

There was no evidence for nocturnal hypothermia in these four ‘old endemic’ Australian passerines (*sensu* Geffen & Yom-Tov 2000; Bech *et al.* 2016), despite an *a priori* expectation that nocturnal hypothermia is more common in passerines than supported by the current limited data (McKechnie & Lovegrove 2002). None of my study species exhibited a nocturnal T_b drop fitting the generally accepted definition of T_b more than 5 °C below rest-phase thermoneutral T_b in

Table 6.1: Compiled laboratory data for babblers, treecreepers, robins, and magpies, listing body mass (g), normothermic body temperature (°C), thermolability (°C °C⁻¹), basal metabolic rate (mL O₂ g⁻¹ hr⁻¹), minimal thermal conductance (J g⁻¹ h⁻¹ °C⁻¹), minimal evaporative water loss (mg H₂O g⁻¹ h⁻¹), breathing rate (breaths min⁻¹), tidal volume (mL) and oxygen extraction (%).

Species	Mass (g)	Body temperature (°C)	Thermolability in laboratory (°C °C ⁻¹)	Basal metabolic rate (mL O ₂ g ⁻¹ hr ⁻¹)	Minimal thermal conductance (J g ⁻¹ h ⁻¹ °C ⁻¹)	Minimal evaporative water loss (mg H ₂ O g ⁻¹ h ⁻¹)	Breathing rate (breaths min ⁻¹)	Tidal volume (mL)	Oxygen extraction (%)
<i>Pomatostomus superciliosus</i>									
White-browed Babbler	46.6	38.6 ± 0.4	0.05 ± 0.02	1.24 ± 0.08	2.22 ± 0.10	1.37 ± 0.23	24.7 ± 0.8	1.09 ± 0.19	24.1 ± 1.2
<i>Climacteris rufus</i>									
Rufous Treecreeper	28.8	39.0 ± 0.9	0.02	2.15 ± 0.08	1.94 ± 0.03	2.65 ± 0.76	39.7 ± 1.5	0.54 ± 0.01	34.1 ± 0.8
<i>Eopsaltria griseogularis</i>									
Western Yellow Robin	18.5	38.6 ± 0.4	0.14 ± 0.02	2.58 ± 0.10	2.87 ± 0.15	1.75 ± 0.13	37.1 ± 1.0	0.46 ± 0.02	39.2 ± 6.1
<i>Gymnorhina tibicen</i>									
Australian Magpie	310	39.3 ± 0.2	0.03 ± 0.01	0.96 ± 0.05	0.77 ± 0.07	0.76 ± 0.13	13.6 ± 1.5	13.4 ± 1.5	21.9 ± 2.9

Table 6.2: Compiled field data for babblers, treecreepers, and robins, listing mean active body temperature (°C), mean overnight resting body temperature (°C), thermolability (°C °C⁻¹), roost site details and roosting behaviour.

Species	Active body temperature (°C)	Resting body temperature (°C)	Thermolability in the field (°C °C ⁻¹)	Roost site	Roosting behaviour
<i>Pomatostomus superciliosus</i>					
White-browed Babbler	40.4 ± 0.1	38.5 ± 0.0	n/a	Domed roost nest	Communal
<i>Climacteris rufus</i>					
Rufous Treecreeper	41.7 ± 0.2	39.3 ± 0.1	0.02 ± 0.01	Tree and branch hollows	Solitary
<i>Eopsaltria griseogularis</i>					
Western Yellow Robin	39.8 ± 0.1	35.8 ± 0.3	0.36 ± 0.01	On branches or in foliage	Solitary

laboratory studies (Table 6.1), or more than 5 °C below active-phase T_b in field-studies (Table 6.2; Barclay *et al.* 2001). However, as T_a fell, all of my species (with the exception of babblers in the field) did show the small, but significant linear decrease in T_b that is expected from the ‘gain’ in the temperature regulation negative feedback system. But even at $T_a = 0$ °C, the drop in mean T_b was only 2.7 °C below active temperature for treecreepers, and 4.1 °C for skin temperature ($T_{b,skin}$) of robins.

The robin, the smallest of the study species, had the highest thermolability (0.14 ± 0.02 °C °C⁻¹ in the laboratory, 0.36 ± 0.00 °C °C⁻¹ in the field), but otherwise values did not track with body mass and the $\Delta T_b/\Delta T_a$ values for other species were all lower, but similar (Table 6.1; 6.2). Even though the T_b decrease was small, it still provided appreciable energy savings, as on a typical winter night a treecreeper saved 1.19 kJ, equivalent to metabolic input required for 41 minutes at $T_a = 10$ °C. Although interspecific differences in thermolability have been reported (Pusey *et al.* 2013), how variations in the ‘gain’ of the thermoregulatory physiology system and hence thermolability fit in as part of broader thermoregulatory strategies is not understood. The construction of metrics such as Thermoregulatory Scope and Heterothermy Index (Boyles *et al.* 2011a; Boyles *et al.* 2013) have helped describe the continuum of thermoregulatory responses and facilitate broadscale comparison that is inclusive of smaller $\Delta T_b/\Delta T_a$ changes, but recognition and understanding of the adaptive mechanisms driving these small responses is still lacking.

Comparison of standard physiological variables

It is not just the pattern of physiological variables under changing environmental conditions that can provide source of energy savings for endotherms, but also how low or high baseline values such as basal metabolic rate (BMR) are compared to other species. But standard physiological variables obtained from different species do not represent truly independent data, as greater similarities in physiology and morphology would be expected amongst the more closely-related species (Ricklefs & Starck 1996). As many physiological variables scale with body mass, so comparisons of traditional regression relationships between parameters against body mass, presented side-by-side with values derived from

phylogenetically-independent contrasts allows the influence of phylogeny to be better understood (Cooper & Withers 2006).

Values of normothermic T_b , BMR, thermal conductance (C), evaporative water loss (EWL), respiratory frequency (f_R), tidal volume (V_T), and oxygen extraction (EO_2) obtained for species studied here were compared to the literature (using the data screening rationale outlined in Appendix 1), using both conventional and phylogenetically-independent allometric regression. For each parameter, 1000 trees were generated on the BirdTree project online platform (birdtree.org; Jetz *et al.* 2012; Jetz *et al.* 2014) constructing the phylogenetic relationships between the species contributing to the dataset (including data collected here), using the Hackett backbone (Hackett *et al.* 2008) of 10 000 trees with 9993 OTUs each. 1000 trees is considered a suitable number to minimise coefficients of variation (Rubolini *et al.* 2015). Trees were then condensed to a single consensus tree based upon maximum clade credibility using Monte Carlo Markov Chain analysis in BEAST's TreeAnnotator program (v1.8.0; Drummond *et al.* 2012). The resulting consensus tree was saved as a nexus file (*.nex) and converted to a distance matrix using the *ape* (Paradis *et al.* 2004) and *phangorn* (Schliep 2011) packages in R (R Core Team 2013). Comparative analyses were made of both conventional values using conventional linear regression and phylogenetically-independent residuals using autoregression for each parameter plotted on body mass (Cheverud & Dow 1985; Rohlf 2001) with a custom-written Visual Basic program (P. Withers; v217; after Barker *et al.* 2016). Both conventional and phylogenetically-independent datasets (minus the values obtained from this study) were plotted in R and 95% prediction intervals were generated for linear relationships. To better understand patterns of homeothermy and heterothermy alongside standard physiological variables, birds recorded to use torpor ($T_b < 30$ °C) and nocturnal hypothermia (T_b drop of > 5 °C) were also identified. Data obtained in this study could then be examined relative to the 95% prediction limits for each parameter (Cooper & Withers 2006), with meaningful conclusions made from the log-transformed conventional regression by correcting antilog predicted values using the minimum

variance unbiased estimator (MVUE; Hayes & Shonkwiler 2006; 2007) in a custom-written Excel macro (P. Withers; v9).

For the four species that I studied, with the exception of EWL, the majority of the variables were within the range predicted by body mass, before and after accounting for phylogeny. While the resting T_{bs} of heterothermic birds were dispersed throughout the

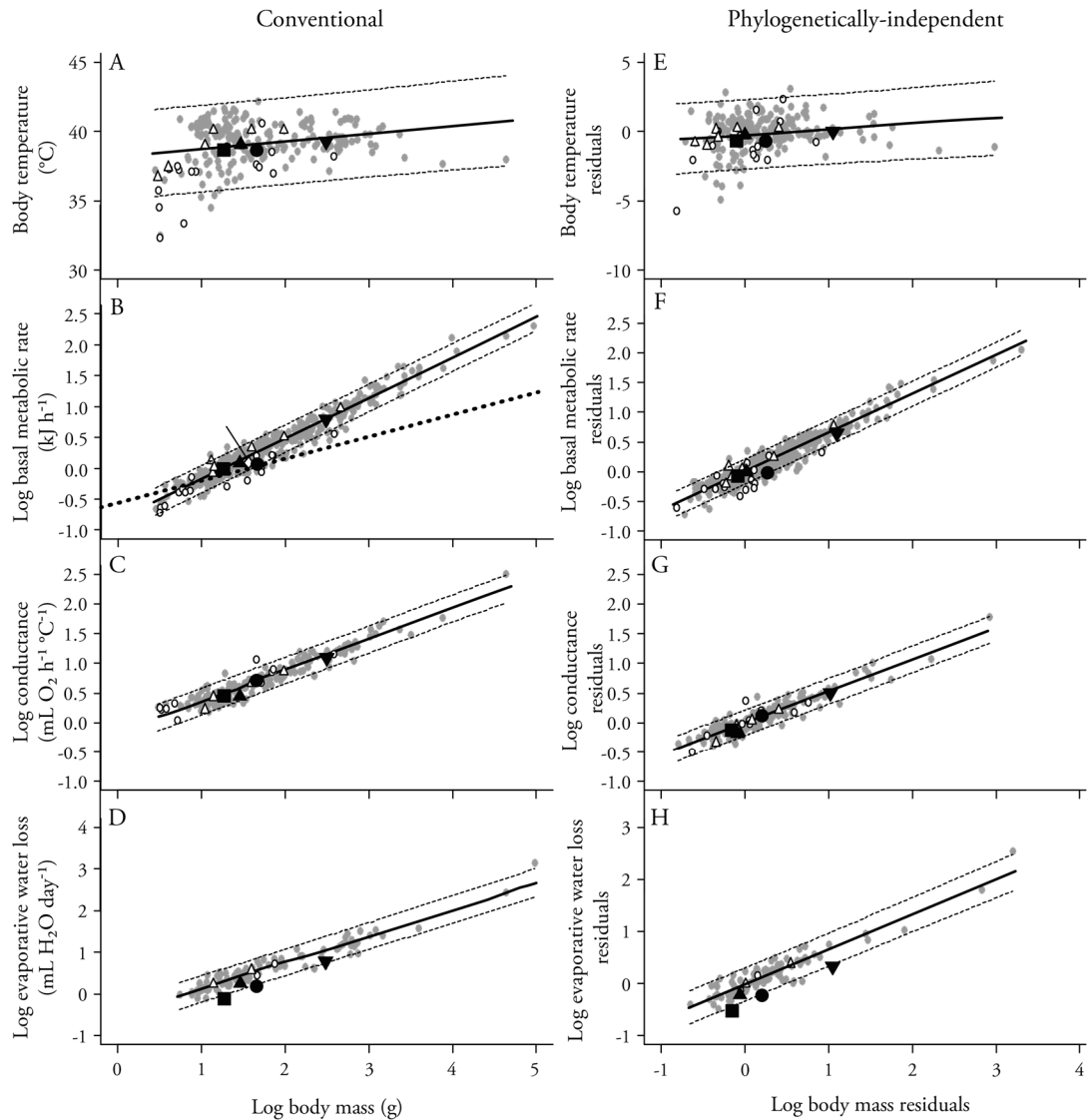


Figure 6.1: Allometric comparison of body temperature (A), basal metabolic rate (B), thermal conductance (C), and evaporative water loss (D) values obtained for White-browed Babblers (black circles), Rufous Treecreepers (black diamonds), Western Yellow Robins (black squares), and Australian Magpies (black inverted triangles), compared with birds known to use torpor (white circles), birds known to use nocturnal hypothermia (white triangles), and other birds (grey symbols). Phylogenetically-independent residuals for the same parameters are displayed in E – H respectively. All values are represented as \log_{10} values, with the exception of body temperature, which is untransformed. Solid lines mark the least squares regression lines and the dotted lines 95% confidence intervals. On figure B, the thick dotted line is McNab's (1983) minimal boundary line for endothermy, and the white diamond marks the BMR for babblers reported by Bech *et al.* (2016). Datasets are in Appendix 1.

dataset, and the resting T_{bs} of my four study species in the laboratory at thermoneutral was less than 0.5 °C different from those predicted for birds of their respective sizes (Figure 6.1A; E). Including McNab's (1983) minimal boundary curve for endothermy on the conventional BMR plot reinforces that McNab's boundary line does not predict avian heterothermy well (Cooper & Geiser 2008), with examples of homeothermic and heterothermic species on both sides of the line. BMR closely fitted values predicted from body mass for babblers (61.1%), treecreepers (89.9%) robins (92.4%), and magpies (90.0%). 'Low' BMR was also observed (although not tested, *sensu* Cooper & Withers 2006) for the smaller, eastern subspecies, *Pomatostomus superciliosus gilgandra* (Bech *et al.* 2016), but falls well within the 95% prediction limits when viewed here (Figure 6.1B). There was likewise no obvious pattern between heterothermia and thermal conductance, and values for my study species were also within the 95% prediction limits (Figure 6.1C; G), 66.8 to 99.1% of that predicted by body mass.

The only comparative variable where these species differed significantly from other birds was EWL. There was no visible pattern in EWL in heterothermic species, despite a limited dataset. Conversely, all four study species had below average EWL for their mass, and while treecreeper EWL was still within the 95% prediction limits (66.4% of that predicted), water loss for babblers, robins, and magpies were all outside the 95% prediction limits (37.2 – 44.7%, Figure 6.1). Accounting for phylogeny did not alter this. Although low EWL provides a frugality suitable to surviving arid environments (Williams *et al.* 1991; Withers *et al.* 2006), methodology is likely to be a confounding factor here. Short measurement duration overestimates EWL (Cooper & Withers 2009; Page *et al.* 2011; Connolly & Cooper 2014), so although data compiled from the literature had a minimum measurement duration of 3 hours, it is likely that the measurement period for many values was too short and EWL was overestimated.

There was no stark evidence from a conventional or phylogenetically-independent regression that either heterothermic or homeothermic birds used differing mechanisms to meet their oxygen demands (Figure 6.2). Ventilatory variables for the study species were

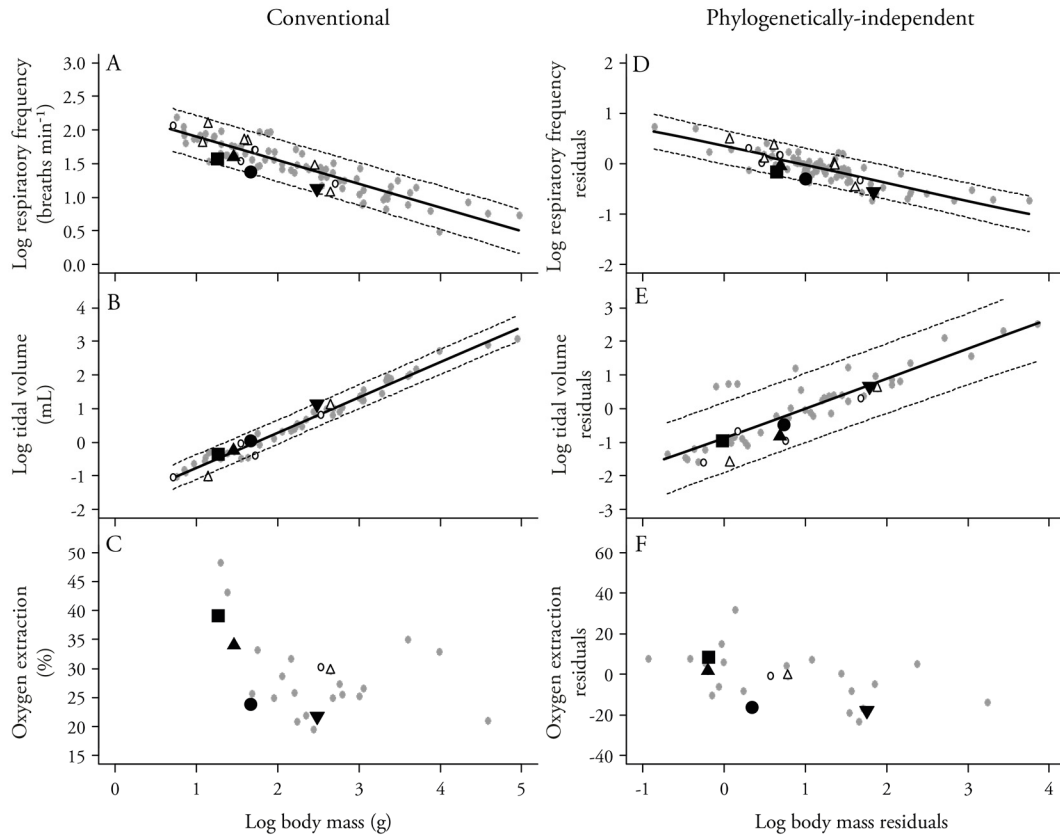


Figure 6.2: Allometric comparison of respiratory frequency (A), tidal volume (B), and oxygen extraction (C) values obtained for hite-browed Babblers (black circles), Rufous Treecreepers (black diamonds), Western Yellow Robins (black squares), and Australian Magpies (black inverted triangles), compared with birds known to use torpor (white circles), birds known to use nocturnal hypothermia (white triangles), and other birds (grey symbols). Phylogenetically-independent residuals for the same parameters are displayed in D - F respectively. All values are represented as \log_{10} values, with the exception of body temperature, which is untransformed. Solid lines mark the least squares regression lines and the dotted lines 95% confidence intervals. Datasets are in Appendix 1.

all within the 95% prediction limits for all four species (respiratory frequency, f_R range 50.0 – 67.6%; tidal volume, V_T range 89.1 – 190%) or within the ‘cloud’ for oxygen extraction (EO_2), which doesn’t plot linearly with body mass either before or after accounting for phylogeny.

The role of plumage in energy conservation

The depth and structural properties of plumage contribute to birds’ ability to meet energetic demands at low T_a . The thickness of magpie plumage is much greater than is generally seen in pelts of equivalent-sized mammals (Scholander *et al.* 1950). As increases in depth of plumage and pelts increases insulation (Cooper *et al.* 2003; McFarland *et al.*

2016), having a disproportionately thicker body covering increases insulation relative to mass, resulting in lower thermal conductance for magpies and other birds compared with mammals of similar mass (Aschoff 1981; Schleucher & Withers 2001). At low T_a birds use the thickness of plumage together with posture to substantially modify their total surface area, thermal conductance, and as a result their energy expenditure (Reebs 1986; Tickle *et al.* 2012).

The structure of feathers also aids heat retention during shivering thermogenesis (Hohtola 2004). The independent origins of endothermy in mammals and birds (Geiser 2008; Lovegrove 2012) means that although shivering is the thermogenic mechanism common to birds and mammals (Hohtola 2004), its expression and alternative mechanisms such as capacity for, and location of, non-shivering thermogenesis patterns differ from mammals (Hohtola 1981; Saarela *et al.* 1989). Functionally, the effect of these differences is that shivering-related tremors in birds that are smoother and less visible than those of mammals (Hohtola 2004). By disturbing the plumage less, the boundary layer of the plumage is kept intact, reducing heat loss to the environment at low T_a . It is argued that together with thick plumage covering their compact form, the absence of shivering tremors makes them more cold tolerant than equal-sized mammals (Withers *et al.* 2016), and thus better adapted to use exposed nocturnal roost sites.

For comparison, the absence of significant heterothermy in free-ranging babblers, treecreepers and robins is in direct contrast to mammals in the same habitat. Although they experience the same environmental conditions and are reliant on the same foraging resources, heterothermy is much more prevalent in mammals at Dryandra Woodland. Echidna (*Tachyglossus aculeata*; Nowack *et al.* 2016) and Numbat (*Myrmecobius fasciatus*; Cooper & Withers 2004) studied at Dryandra have all readily using torpor at low T_a . Co-occurring mammals (Moore 2013; Moore *et al.* 2013a; Moore *et al.* 2014) studied elsewhere, such as Lesser Long-eared Bats (*Nyctophilus geoffroyi*; Hosken & Withers 1999), Yellow-footed Antechinus (*Antechinus flavipes*; Geiser 1988), Western Quoll (*Dasyurus geoffroyi*; Arnold 1976), Red-tailed Phascogale (*Phascogale calura*; Pusey *et al.* 2013), and

Western Pygmy Possum (*Cercartetus concinnus*; Geiser 1987) also readily use torpor. Yet the three small (< 50 g) birds studied here are adapted to the same environments but showed no evidence of torpor and exhibit only small changes in T_b .

Behavioural mechanisms for temperature regulation

In the absence of specialised physiology mechanisms, behavioural mechanisms would be expected to be critical in mitigating energy expenditure for small endotherms at low T_a . All three birds investigated in the field were cooperatively-breeding species (Higgins *et al.* 2001; Higgins & Peter 2002), so had potential to roost communally and use social thermoregulation to lower thermal conductance and minimise nocturnal energy expenditure (Beauchamp 1999). However, only the largest of the three species, the babbler (46.6 g), roosted communally, despite huddling MR reducing individual metabolic requirements by 25.9 – 35.4 %, consistent with other species (Gilbert *et al.* 2010). Despite social thermoregulation being considered an ancestral state (Beauchamp 1999), here was evidence for secondary loss, as there was no evidence that treecreepers or robins roosted communally under any circumstances, and all three species could maintain homeothermy alone.

Tree hollows can provide an important rest-phase refuge, with potential for substantial thermal buffering capacity. The high density of tree hollows in the field site here (estimated at 74 hollow stems ha⁻¹; Rose 1993), in theory provided plentiful options for babblers, treecreepers and robins to conserve energy by careful roost site selection. However, only one of the three species, the treecreeper, used tree hollows as nocturnal refuges. Babblers made their own domed nest refuges that didn't differ from ambient thermal conditions, but did halve their thermal conductance. By roosting communally in them, babblers reduced overnight energy requirements by 45%. While the ~30 g treecreeper did use tree and branch hollows as nocturnal roosts, they roosted individually in them and did not appear to select them on the basis of temperature. It would be expected that the smaller birds, with the greatest surface area to volume ratio hence greater relative capacity for heat loss (Tattersall *et al.* 2012), would use the greatest energy-saving

strategies, here my smallest study species, the ~18 g robin, used neither social thermoregulation or protected roost sites, instead maintained homeothermy while roosting alone in exposed sites in foliage. Despite prevalence of communal roosting and use of protected roost sites being associated with heterothermia in endotherms (McKechnie & Lovegrove 2001b; McKechnie *et al.* 2006; Doucette *et al.* 2011), there was no evidence for that here. This suggests that for these birds the primary role driving their roosting behaviour is not thermoregulation, but something else, such as group cohesion or predator avoidance (Beauchamp 1999).

Diurnal behaviour of birds is often interpreted as providing alternative mechanisms for meeting energy requirements, compared to nocturnal methods. Bimodal foraging - peaks in feeding activity both in the early morning and the late afternoon - is often considered a key avian behavioural response to energetic shortage, to compensate and prepare for nocturnal energy loss (Bednekoff & Houston 1994). This link is assumed more often than tested, and is derived mostly from Northern Hemisphere studies (such as Hutto 1981), and is not always corroborated in Australian environments (Taylor & Paul 2006). Although bimodal foraging has been observed on a crude timescale for the magpie (Edwards *et al.* 2015), the other three species that I studied in the field showed no consistent pattern in change of foraging effort or height strata used under different temporal or thermal conditions, although there were some species-specific interactions. Group-living species are better able to improve foraging efficiency over solitary animals, both through information sharing and shared predator vigilance (Ward & Zahavi 1973; Beauchamp 1998; Sorato *et al.* 2012). The lack of consistent patterns between temperature and time spent foraging suggest that these sedentary passerines may achieve higher foraging efficiency, mitigating the need for an increased proportion of time spent foraging.

Costs of heterothermy and the benefits of a sedentary lifestyle

Heterothermy has been suggested as a likely strategy by which sedentary Australian birds survive the energetic bottlenecks of harsh Australian environments (Geiser *et al.* 2006),

based upon anecdotal reports of Australian passerines using torpor, such as nectarivorous White-fronted Honeyeater (*Phylidonyris albifrons*; Ives 1973; insectivorous Banded Whiteface, *Aphelocephala nigricincta*, Red-capped Robin, *Petroica goodenovii*, and White-backed Swallow, *Cheramoeca leucosternus* (Serventy 1970b; Congreve 1972); and frugivorous, lerp- and manna-feeding Mistletoebird (*Dicaeum hirundinaceum*; Heumann 1926; Serventy 1970a). However, my study found no evidence of heterothermy for four species of sedentary, insectivorous passerines in winter, with a comprehensive methodology of laboratory and field techniques. The species for which there is anecdotal evidence of torpor are of a similar and smaller mass than the birds studied here (de Rebeira 2006), but unlike my sedentary species here, all show some nomadic tendencies throughout part, if not all, of their range (Higgins *et al.* 2001; Higgins & Peter 2002; Higgins *et al.* 2006). While the role of mass and diet in predicting nomadism in Australian birds has been investigated (Allen & Saunders 2002), how these interact with homeothermy is unknown. Instead of heterothermy facilitating a sedentary lifestyle (Geiser *et al.* 2006), data from this study suggests instead that sedentary insectivorous passerines are able to meet their energetic requirements and still maintain homeothermy under Australian environmental conditions. Only a small proportion of Australian passerines migrate (Allen & Saunders 2002), and if being resident does correlate with homeothermy, it might explain the lack of evidence for it in my study species.

Remaining sedentary confers significant advantages that may not be fully realised by nomadic species that are less familiar with their surroundings (Pérez-Tris & Tellería 2002). Being a permanent resident in a particular location allows for accumulation of specific knowledge of locations and abundance of food resources (Eguchi *et al.* 2008); presence, identity and habits of local predators (Parejo & Avilés 2011); as well as routes and refuges to escape them. It is also argued that by being capable of flight, sedentary birds have greater mobility to exploit food resources in a habitat than co-occurring sedentary mammals (Withers *et al.* 2004), using flight to cover larger distances in a shorter time, and to make use of all height strata in the habitat. Studies of Australian honeyeaters have demonstrated that food availability and prey activity determine both foraging substrate

and foraging effort (Timewell & McNally 2004). Sedentary passerines may be better able to meet energy demands in times of low resource availability in comparison with less vagile mammals in the same habitat.

The behavioural traits that accompany torpor and hibernation can increase risk of predation, even shallow torpor can increase response time to potential predators (Laurila & Hohtola 2005; Carr & Lima 2013). Many heterothermic endotherms use behavioural adjustments to minimise predation risk by selecting sheltered roost sites (Hosken & Withers 1999; Brigham *et al.* 2000), or selecting sites that allow for passive rewarming (Geiser *et al.* 2004; Currie *et al.* 2014). Given the absence of heterothermy for the passerines in this study, it may be that predation-related costs of heterothermy are too great for solitary-roosting species or babblers in roost nests with a single entrance.

Conclusion

My study documented the thermoregulatory physiology of four sympatric, endemic, sedentary, insectivorous Australian passerines for the first time. Despite differences in body mass, all four species demonstrated a similar physiological response to low T_a , maintaining near homeothermy with a typical increase in MR, reduction in thermal conductance, and small $\Delta T_b / \Delta T_a$. My comprehensive methodology that incorporated both laboratory and field components was critical in confirming the absence of torpor in three of these species under natural conditions, and in quantifying the energy savings of nocturnal roosting behaviours. Although roosting behaviour had the potential to provide significant energy savings, these behaviours were not common to all three species. With seemingly small adjustments to diurnal behaviour, these species were able to maintain near homeothermy in winter. The structure of avian plumage, together with their compact form, and the absence of shivering tremors improves their tolerance to cold. Even though there are many potential behavioural and physiological strategies these sedentary, Australian passerines could be using to meet energy requirements, they did not need to use extreme mechanisms in order to persist in their environment. A sedentary and communal lifestyle presumably benefits these passerines through local knowledge and

information sharing. This study raises again the importance of having a consistent vocabulary for defining small changes in T_b , as well as encouraging the communication of thermoregulatory studies of Australian birds, regardless of findings. A better understanding of the capacity of avian thermoregulatory strategies will allow more confident predictions of avian responses to changing climate, enabling knowledge of thermoregulatory physiology to complement existing modelling, conservation action and environmental management (Barnagaud *et al.* 2012).

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Appendix 1 – Methodology for phylogenetic comparisons

Data compilation and screening

Standard physiological data was collated from the literature for 582 bird species into separate datasets for T_b ($n = 207$; Table A2.1), BMR ($n = 546$), EWL ($n = 96$), C_{wet} ($n = 184$), f_R ($n = 88$), V_T ($n = 52$), and EO_2 ($n = 22$). For meaningful analysis of truly representative parameters (McKechnie & Wolf 2004), only data obtained under controlled laboratory conditions of $n \geq 3$ post-adsorptive adults in their inactive phase were used. Only data where measurement duration was greater than 1 h were included (≥ 3 h for EWL). Where multiple values exist for the same species, e.g. from comparisons between different populations, mean values were used.

Data were excluded where methods were not obvious in the paper, or where they were predicted from daytime values. As per the comparative EWL analysis of Williams (1996), values of EWL collected during water-deprivation were not included in the dataset, however other methodologies incorporating seasonal acclimation, time of measurement, chamber illumination, absorptive state were all included. EWL data was ideally at 25 °C, but included some exceptions, as long as they were within the TNZ. Thermal conductance values were only included where calculated from respirometry data, not estimated from skin surface area. Minimal C_{wet} values were used. Minimal f_R data were used, as well as V_T and EO_2 data from the T_a when f_R was minimal. V_T is expressed as body temperature and pressure saturated (BTPS). All parameters, with the exception of T_b and EO_2 were \log_{10} transformed. Datasets were kept in the same units as the majority of the data were presented in.

Data analysis

Values obtained for species studied here were compared to the literature, using both conventional and phylogenetically-independent allometric regression. For each parameter, 1000 trees were generated on the BirdTree project online platform (birdtree.org; Jetz *et al.* 2012; Jetz *et al.* 2014) constructing the phylogenetic

relationships between the species contributing to the dataset (including data collected here), using the Hackett backbone (Hackett *et al.* 2008) of 10 000 trees with 9993 OTUs each. 1000 trees is considered a suitable number to minimise coefficients of variation, as suggested by Rubolini and colleagues (2015). These trees were then condensed to a single consensus tree based upon maximum clade credibility using Monte Carlo Markov Chain analysis in BEAST's TreeAnnotator program (v1.8.0; Drummond *et al.* 2012). The resulting consensus tree was saved as a nexus file (*.nex) and converted to a distance matrix using the *ape* (Paradis *et al.* 2004) and *phangorn* (Schliep 2011) packages in R (R Core Team 2013). Comparative analyses were made of both conventional values using conventional linear regression and phylogenetically-independent residuals using autoregression for each parameter plotted on body mass (Cheverud & Dow 1985; Rohlf 2001) with a custom-written Visual Basic program (P. Withers; v217; after Barker *et al.* 2016). Both conventional and phylogenetically-independent datasets (minus the values obtained from this study) were plotted in R and 95% prediction intervals were generated for linear relationships. Data obtained in this study could then be examined relative to the 95% prediction limits for each parameter (Cooper & Withers 2006), with meaningful conclusions made from the log-transformed conventional regression by correcting antilog predicted values using the minimum variance unbiased estimator (MVUE; Hayes & Shonkwiler 2006; 2007) in a custom-written Excel macro (P. Withers; v9).

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Appendix 2: Comparative dataset

Table A1.1: Compiled dataset for comparative phylogenetic analyses, listing species, body mass (g), resting body temperature (T_b ; °C) at thermoneutral, basal metabolic rate (BMR: kJ h⁻¹), minimal thermal conductance (C; mL O₂ h⁻¹ °C⁻¹), evaporative water loss (EWL; mL H₂O day⁻¹) at thermoneutral, minimal breathing frequency (f_R ; breaths min⁻¹), tidal volume (V_T ; mL) at minimal f_R , oxygen extraction (E_{O_2} ; %) at minimal f_R , and data source for each. * indicates species reported to use nocturnal hypothermia, ** indicates species reported to use torpor, and ‡ indicates the species reported to hibernate.

Family <i>Scientific name</i>	Description <i>Common name</i>	g	°C	kJ h ⁻¹	mL O ₂ h ⁻¹ °C ⁻¹	mL H ₂ O	breaths min ⁻¹	mL	%	References
STRUTHIONIFORMES										
Struthionidae	Ostriches									
<i>Struthio camelus</i>	Ostrich	92400	40.0	208.8		1420.0	5.5	1200.0		Crawford & Schmidt-Nielsen 1967; Schmidt-Nielsen <i>et al.</i> 1969; Withers 1983
RHEIFORMES										
Rheidae	Rheas									
<i>Rhea americana</i>	Greater Rhea	21700					8.5			Crawford & Lasiewski 1968
CASUARIIFORMES										
Dromaiidae	Emus									
<i>Dromatius novaehollandiae</i>	Emu	43050	38.0	140.3	324.0	276.0	5.8	783.1	21.0	Crawford & Lasiewski 1968; Maloney & Dawson 1994
APTERYGIFORMES										
Apterygidae	Kiwis									
<i>Apteryx australis</i>	Southern Brown Kiwi	2443.5	38.2	15.7	30.7					King & Farner 1961; McNab 1996
GALLIFORMES										
Odontophoridae	New World quails									
<i>Colinus virginianus</i>	Northern Bobwhite	258.0		4.8			45.0	3.1		Boggs & Kilgore 1983; Londoño <i>et al.</i> 2014
Phasianidae	Grouse, pheasants and partridges									
<i>Alectoris chukar</i>	Chukar	525.7	40.4	4.4			23.3	6.5	25.0	Chappell & Bucher 1987; Londoño <i>et al.</i> 2014
<i>Alectoris graeca</i>	Rock Partridge	626.5	39.3	9.7	17.3	19.8				Kendeigh <i>et al.</i> 1977; Gavrilov 2014
<i>Pardipendix</i>	Grey Partridge	486.0	39.6	8.6	16.4	16.0				Gavrilov 2014
<i>Coturnix coturnix</i> *	Common Quail	97.0	40.1	3.2	7.2	5.2				Kendeigh <i>et al.</i> 1977; Gavrilov 2014; Hohtola <i>et al.</i> 1991*
<i>Coturnix japonica</i>	Japanese Quail	140.5	40.7	4.4						Prinzinger & Hänsler 1980; Ben-Hamo <i>et al.</i> 2010
<i>Coturnix chinensis</i>	Blue Quail	45.7	42.2	1.9			68.0	0.4		Lasiewski <i>et al.</i> 1966; Bernstein 1970 in Lasiewski & Calder 1971; Prinzinger & Hänsler 1980; Pis 2010; Londoño <i>et al.</i> 2014
<i>Gallus gallus</i>	Red Junglefowl	1196.0		10.9			18.0	29.3		Calder 1968; Kassim & Sykes 1982; Gleeson 1985; Londoño <i>et al.</i> 2014
<i>Phasianus colchicus</i>	Common Pheasant	1133.0					8.4	35.8		Boggs & Birchard 1983
<i>Lagopus lagopus</i>	Willow Ptarmigan	524.0	40.4	11.2	17.1	18.0				King & Farner 1961; Kendeigh <i>et al.</i> 1977; Gavrilov 2014
<i>Tetrao urogallus</i>	Western Capercaillie	3900.0		42.9						Kendeigh <i>et al.</i> 1977
ANSERIFORMES										
Anatidae	Ducks, geese and swans									
<i>Cygnus olor</i>	Mute Swan	9700.0	39.3	131.5			3.1	533.5	33.0	Bech & Johansen 1980
<i>Anser anser</i>	Greylag Goose	3250.0		39.0			14.0	157.0		Kendeigh <i>et al.</i> 1977; Scheid <i>et al.</i> 1989
<i>Anser indicus</i>	Bar-headed Goose	2360.0					11.8	66.7		Fedde <i>et al.</i> 1989
<i>Chen canagica</i>	Emperor Goose	2609.0		32.3						Gavrilov & Dol'nik 1985
<i>Branta canadensis</i>	Canada Goose	3800.0	41.1				12.0	109.2		King & Farner 1961; Funk <i>et al.</i> 1989
<i>Branta bernicla</i>	Brent Goose	1253.0		21.8						Daan <i>et al.</i> 1990
<i>Hymenolaimus malacorhynchus</i>	Blue Duck	717.1	40.9	11.3	19.4					McNab 2003
<i>Cairina moschata</i>	Muscovy Duck	2160.0					10.5	69.0		Jones & Hooton 1972
<i>Aix sponsa</i>	Wood Duck	448.0	39.6	8.1	17.5	14.0				Kendeigh <i>et al.</i> 1977; Gavrilov 2014
<i>Anas penelope</i>	Eurasian Wigeon	720.5	39.4	10.2	19.4	17.6				Kendeigh <i>et al.</i> 1977; Gavrilov 2014
<i>Anas rubripes</i>	American Black Duck	1018.0		21.7			27.2	24.0		Berger <i>et al.</i> 1970
<i>Anas platyrhynchos</i>	Mallard	880.5	40.5	26.9	28.4	26.4	14.6	79.3		King & Farner 1961; Calder 1968; Jones & Hooton 1972; Colacino <i>et al.</i> 1977; Kendeigh <i>et al.</i> 1977; Black & Tenney 1980; Kiley <i>et al.</i> 1985; Daan <i>et al.</i> 1990; Gavrilov 2014
<i>Anas rhynchos</i>	Australasian Shoveler	508.0	40.9	9.5	14.7					McNab 2003
<i>Aythya collaris</i>	Ring-necked Duck	681.5	40.5	11.8	23.2					McNab 2003
<i>Aythya fuligula</i>	Tufted Duck	611.0		10.5						Daan <i>et al.</i> 1990
<i>Aythya affinis</i>	Lesser Scaup	561.5	41.2	10.3	21.9					King & Farner 1961; McNab 2003
<i>Anas gracilis</i>	Grey Teal	393.7	41.4	12.0	15.7					McNab 2003
SPHENISCIFORMES										
Spheniscidae	Penguins									
<i>Apelodytes patagonicus</i>	King Penguin	11080		78.7						Gavrilov 1977
<i>Pygoscelis adeliae</i>	Adelie Penguin	3970.0	38.9	44.0			7.8	96.3	35.0	Kooyman <i>et al.</i> 1976; Chappell & Souza 1988
<i>Eudyptes chrysocome</i>	Southern Rockhopper Penguin	2330.0		21.0						Gavrilov 1977; Brown 1984
<i>Eudyptes pachyrhynchus</i>	Fiordland Penguin	2600.0		24.9						Drent & Stonehouse 1971
<i>Eudyptes chrysolophus</i>	Macaroni Penguin	3870.0		31.1						Gavrilov 1977; Brown 1984
<i>Eudyptula minor</i>	Little Penguin	1091.0	38.4	12.2			7.9	17.7	55.0	Baudinette <i>et al.</i> 1986; Stadel & Nicol 1988
<i>Spheniscus humboldti</i>	Humboldt Penguin	3870.0		34.1		39.0				Drent & Stonehouse 1971
GAVIIFORMES										
Gaviidae	Loons or divers									
<i>Gavia immer</i>	Common Loon	2123.0					6.8			Calder 1968
PROCELLARIIFORMES										
Procellariidae	Petrels and shearwaters									
<i>Fulmarus glacialis</i>	Northern Fulmar	728.0		13.8						Bryant & Furness 1994
<i>Puffinus puffinus</i>	Manx Shearwater	367.0		8.4						Bryant & Furness 1994
PHOENICOPTERIFORMES										
Phoenicopteridae	Flamingos									
<i>Phoenicopterus ruber</i>	American Flamingo	2210.0	39.5	45.5			9.6	89.3		Bech <i>et al.</i> 1979
PELECANIFORMES										
Pelecanidae	Pelicans									
<i>Pelecanus erythrorhynchos</i>	American White Pelican	7500.0					6.3			Calder 1968
SULIFORMES										
Sulidae	Gannets and boobies									
<i>Morus bassanus</i>	Northern Gannet	2574.0	41.4	45.0						King & Farner 1961; Bryant & Furness 1994
Phalacrocoracidae	Cormorants									
<i>Phalacrocorax auritus</i>	Double-crested Cormorant	1330.0	41.2	19.7	42.6					Henneman 1983
<i>Phalacrocorax aristotelis</i>	European Shag	1619.0		30.8						Bryant & Furness 1994
Anhingidae	Anhingas									
<i>Anhinga anhinga</i>	Anhinga	1040.0	39.9	11.4	37.9					Henneman 1983

ORDER	Family	Description	Mass g	T _b °C	BMR kJ h ⁻¹	C mL O ₂ h ⁻¹ °C ⁻¹	EWL mL H ₂ O	f _R breaths min ⁻¹	V _T mL	Eo ₂ %	References
	Scientific name	Common name									
ACCIPITRIFORMES											
	Cathartidae	New World vultures									
	<i>Cathartes aura</i>	Turkey Vulture	2000.0					9.2			Calder 1968
FALCONIFORMES											
	Falconidae	Falcons and caracaras									
	<i>Caracara plancus</i>	Southern Caracara	350.0					15.0			Groebbels 1932
	<i>Falco tinnunculus</i>	Common Kestrel	178.5	41.0	3.1						Gavrilov & Dol'nik 1985; Daan <i>et al.</i> 1989
	<i>Falco sparverius</i>	American Kestrel	113.8		3.2	7.2		31.9	2.1	28.7	Wasser 1986; Souza 1988 in Maloney & Dawson 1994; Londoño <i>et al.</i> 2014
	<i>Falco subbuteo</i>	Eurasian Hobby	208.0		4.7						Kendeigh <i>et al.</i> 1977
	<i>Falco mexicanus</i>	Prairie Falcon	626.5					13.7	11.4	25.5	Kaiser & Bucher 1985
ACCIPITRIFORMES											
	Accipitridae	Osprey, kites, hawks and eagles									
	<i>Pandion haliaetus</i>	Osprey	1495.0		19.9	51.1					Wasser 1986
	<i>Pernis ptilorhynchus</i>	European Honey-buzzard	652.0		8.4						Kendeigh <i>et al.</i> 1977
	<i>Gyps fulvus</i>	Griffon Vulture	7600.0	38.9	42.6	58.5					Prinzinger <i>et al.</i> 2002
	<i>Accipiter nisus</i>	Eurasian Sparrowhawk	135.0		3.4						Kendeigh <i>et al.</i> 1977
	<i>Buteo lineatus</i>	Red-shouldered Hawk	633.5		8.8	11.3		18.2	8.4	27.4	Wasser 1986; Souza 1988 in Maloney & Dawson 1994; Londoño <i>et al.</i> 2014
	<i>Buteo jamaicensis</i>	Red-tailed Hawk	1140.9		15.6			12.9	18.2	26.6	Souza 1988 in Maloney & Dawson 1994; Londoño <i>et al.</i> 2014
	<i>Buteo buteo</i>	Common Buzzard	1012.0		13.5			18.0			Groebbels 1932; Prinzinger & Hänsler 1980
OTIDIFORMES											
	Otididae	Bustards									
	<i>Chlamydotis undulata</i>	Houbara Bustard	1462.0				25.8				Tiedeman <i>et al.</i> 2002
GRUIFORMES											
	Rallidae	Rails, cranes and allies									
	<i>Gallirallus ovstoni</i>	Guam Rail	198.8	40.2	3.3	11.3					McNab & Ellis 2006
	<i>Crex crex</i>	Corncrake	96.0		2.8						Kendeigh <i>et al.</i> 1977
	<i>Gallinula tenebrosa</i>	Dusky Moorhen	512.4	39.4	8.4	20.5					McNab & Ellis 2006
	<i>Fulica atra</i>	Common Coot	412.0	38.9	7.4	16.2	12.3	20.0	10.0		Kendeigh <i>et al.</i> 1977; Brent <i>et al.</i> 1984; Gavrilov 2014
CHARADRIIFORMES											
	Haematopodidae	Oystercatchers									
	<i>Haematopus ostralegus</i>	Eurasian Oystercatcher	449.0		9.4						Daan <i>et al.</i> 1990
	Charadriidae	Plovers									
	<i>Pluvialis squatarola</i>	Grey Plover	226.0		6.4						Kersten & Piersma 1987
	<i>Charadrius dubius</i>	Little Ringed Plover	36.0	39.2	1.5	4.5	2.2				Kendeigh <i>et al.</i> 1977; Gavrilov 2014
	Thinocoridae	Seedsnipes									
	<i>Thinocorus rumicivorus</i>	Least Seedsnipe	55.5		1.1		6.7				Ehlers & Morton 1982
	Scolopacidae	Sandpipers and allies									
	<i>Scolopax rusticola</i>	Eurasian Woodcock	430.0		7.8						Kendeigh <i>et al.</i> 1977
	<i>Limosa lapponica</i>	Bar-tailed Godwit	240.0		5.5						Daan <i>et al.</i> 1990
	<i>Arenaria interpres</i>	Ruddy Turnstone	90.0		3.3						Kersten & Piersma 1987
	<i>Calidris tenuirostris</i>	Great Knot	198.2		7.2						Battley <i>et al.</i> 2001
	Laridae	Gulls and terns									
	<i>Larus canus</i>	Mew Gull	429.5	38.6	8.2	16.4	13.1	26.0			Groebbels 1932; Kendeigh <i>et al.</i> 1977; Gavrilov 2014
	<i>Larus argentatus</i>	Herring Gull	875.5		14.1			19.0			Calder 1968; Daan <i>et al.</i> 1990; Bryant & Furness 1995
	<i>Larus ridibundus</i>	Black-headed Gull	280.0	38.8	6.9	13.1	11.6				Kendeigh <i>et al.</i> 1977; Gavrilov 2014; Daan <i>et al.</i> 1990
	<i>Rhodostethia rosea</i>	Ross's Gull	155.0		3.8						Gavrilov 1996
	<i>Rissa tridactyla</i>	Black-legged Kittiwake	305.0	41.5	9.9						King & Farner 1961; Bryant & Furness 1995
	Stercorariidae	Skuas and jaegers									
	<i>Stercorarius parasiticus</i>	Parasitic Jaeger	351.0		8.3						Bryant & Furness 1995
	<i>Catharacta skua</i>	Great Skua	1159.0	41.2	22.4						King & Farner 1961; Bryant & Furness 1995
	Alcidae	Auks									
	<i>Uria aalge</i>	Common Guillemot	771.0		16.3						Bryant & Furness 1995
	<i>Fratercula arctica</i>	Atlantic Puffin	329.0		9.3						Bryant & Furness 1995
COLUMBIFORMES											
	Columbidae	Doves and pigeons									
	<i>Columba livia</i>	Rock Pigeon	342.2	40.7	6.8			27.9	7.2		Groebbels 1932; Hart & Roy 1966; Calder & Schmidt-Nielsen 1967; Bouverot <i>et al.</i> 1976; Gavrilov & Dol'nik 1985; Williams <i>et al.</i> 1995; Londoño <i>et al.</i> 2014
	<i>Columba palumbus</i>	Common Wood-pigeon	493.0		7.2						Gavrilov & Dol'nik 1985
	<i>Columba leucomela</i>	White-headed Pigeon	456.0		8.8						Schleucher & Withers 2002
	<i>Streptopelia turtur</i>	European Turtle-dove	154.0		4.1						Kendeigh <i>et al.</i> 1977
	<i>Streptopelia senegalensis</i>	Laughing Dove	100.3		2.9						Kendeigh <i>et al.</i> 1977; McKechnie <i>et al.</i> 2007
	<i>Streptopelia capicola</i>	Ring-necked Dove	151.9		3.3						Londoño <i>et al.</i> 2014
	<i>Streptopelia decaocto</i>	Eurasian Collared-dove	178.5	39.4	4.0	8.9					Daan <i>et al.</i> 1990; Schleucher & Withers 2002
	<i>Oena capensis</i>	Namaqua Dove	36.0	40.9	0.9						Schleucher 2001
	<i>Chalcophaps indica</i>	Emerald Dove	124.0	39.3	2.9	9.3					Schleucher & Withers 2002
	<i>Phaps chalcoptera</i>	Common Bronzewing	304.0		5.5						Schleucher & Withers 2002
	<i>Phaps elegans</i>	Brush Bronzewing	207.0	40.7	4.2	13.0	4.1	29.0	4.9	22.0	Schleucher & Withers 2002; Larcombe <i>et al.</i> 2003
	<i>Phaps histrionica</i>	Flock Bronzewing	257.0		4.7						Schleucher & Withers 2002
	<i>Ocyphaps lophotes</i>	Crested Pigeon	180.5	40.9	3.2	12.3	4.5	31.0	3.7	20.9	Schleucher & Withers 2002; Larcombe <i>et al.</i> 2003
	<i>Geophaps plumifera</i>	Spinifex Pigeon	89.0	40.5	1.5	5.8	7.3	37.0	1.3	25.0	Withers & Williams 1990
	<i>Geophaps smithii</i>	Partridge Pigeon	198.0		3.1						Schleucher & Withers 2002
	<i>Geopelia cuneata</i>	Diamond Dove	37.2	39.8	1.1	5.4	2.5	59.5	0.3		Schleucher <i>et al.</i> 1991; Schleucher & Withers 2002; Londoño <i>et al.</i> 2014
	<i>Geopelia placida</i>	Peaceful Dove	52.0	38.9	1.3	6.4					Schleucher & Withers 2002
	<i>Leucosarcia melanoleuca</i>	Wonga Pigeon	445.0	38.7	6.1	16.9					Schleucher & Withers 2002
	<i>Zenaidura macroura</i>	Mourning Dove	121.7		2.8						Wiersma <i>et al.</i> 2007
	<i>Columbina inca</i> **	Inca Dove	44.2	40.9	1.0	4.4					MacMillen & Trost 1967**
	<i>Columbina talpacoti</i>	Ruddy Ground-dove	45.7		1.5						Wiersma <i>et al.</i> 2007
	<i>Leptotila rufaxilla</i>	Grey-fronted Dove	150.6		2.5						Londoño <i>et al.</i> 2014
	<i>Geotrygon montana</i>	Ruddy Quail-dove	117.9		3.0						Londoño <i>et al.</i> 2014
	<i>Caloenas nicobarica</i>	Nicobar Pigeon	613.0	40.9	6.5	20.2					McNab 2000
	<i>Treron calvus</i>	African Green-pigeon	218.2	38.0	3.0	6.4	4.3				Noakes <i>et al.</i> 2013
	<i>Ptilinopus superbus</i>	Superb Fruit-dove	120.4	39.6	2.8	10.5					Schleucher 1999
	<i>Ptilinopus melanospilus</i>	Black-naped Fruit-dove	94.0	41.1	1.8	6.0					Schleucher 2002
	<i>Ducula pacifica</i>	Pacific Imperial-pigeon	333.4	39.8	2.9	11.7					McNab 2000
	<i>Ducula pistrinaria</i>	Island Imperial-pigeon	394.2	39.7	3.9	15.4					McNab 2000
	<i>Ducula spilorrhoa</i>	Torresian Imperial-pigeon	453.6	40.7	4.9	16.3					McNab 2000

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	<i>Scientific name</i>	<i>Common name</i>									
	<i>Hemiphaea novaeseelandiae</i>	New Zealand Pigeon	435.6	39.3		17.0					McNab 2000
	<i>Gymnophaps albertisi</i>	Papuan Mountain-pigeon	241.6	39.2	3.4	13.3					McNab 2000
	<i>Goura cristata</i>	Western Crowned-pigeon	2313.4	39.8	15.4	37.0					McNab 2000
CUCULIFORMES											
	Cuculidae	Cuckoos									
	<i>Cuculus canorus</i>	Common Cuckoo	111.6		3.0						Kendeigh <i>et al.</i> 1977
	<i>Geococcyx californianus</i> *	Greater Roadrunner	284.7					28.9			Calder & Schmidt-Nielsen 1967; Ohmart & Lasiewski 1971
PSITTACIFORMES											
	Psittacidae	Parrots									
	<i>Calyptrorhynchus baudinii</i>	Baudin's Black-Cockatoo	597.0		9.7		9.3				Cooper <i>et al.</i> 2002
	<i>Calyptrorhynchus latirostris</i>	Carnaby's Black-Cockatoo	665.0		11.4		14.2				Cooper <i>et al.</i> 2002
	<i>Calyptrorhynchus banksii</i>	Red-tailed Black-cockatoo	608.4		10.9		14.6				Williams <i>et al.</i> 1991; Cooper <i>et al.</i> 2002
	<i>Cacatua roseicapilla</i>	Galah	268.7		4.5		8.0				Williams <i>et al.</i> 1991
	<i>Cacatua galerita</i>	Sulphur-crested Cockatoo	776.1		12.3		32.7				Williams <i>et al.</i> 1991
	<i>Cacatua pastinator</i>	Western Corella	733.5		12.1		9.5				Cooper <i>et al.</i> 2002
	<i>Cacatua tenuirostris</i>	Long-billed Corella	549.9		11.4		28.0				Williams <i>et al.</i> 1991
	<i>Nymphicus hollandicus</i>	Cockatiel	91.2	39.2	2.4	8.5	4.8				Kendeigh <i>et al.</i> 1977; Gavrilov 2014; Londoño <i>et al.</i> 2014
	<i>Trichoglossus haemotodus</i>	Rainbow Lorikeet	137.1		4.3		12.5				Williams <i>et al.</i> 1991
	<i>Psittacula krameri</i>	Brahm's Tiger-parrot	99.8	37.4	2.8	7.9					McNab 2013
	<i>Barnardius zonarius</i>	Ringneck Parrot	131.8		2.9						Williams <i>et al.</i> 1991
	<i>Cyanoramphus novaeseelandiae</i>	Red-fronted Parakeet	56.1	38.2	2.2	5.8					McNab & Salisbury 1995
	<i>Cyanoramphus auriceps</i>	Yellow-crowned Parakeet	52.9	38.1	1.8	5.4					McNab & Salisbury 1995
	<i>Neopsittacus bourkii</i>	Bourke's Parrot	41.4		1.8						Prinzinger & Hänsler 1980; Burton <i>et al.</i> 2008
	<i>Neophema elegans</i>	Elegant Parrot	42.1		2.2						Burton <i>et al.</i> 2008
	<i>Neophema pulchella</i>	Turquoise Parrot	41.0		2.1						Prinzinger & Hänsler 1980; Burton <i>et al.</i> 2008
	<i>Neophema splendida</i>	Scarlet-chested Parrot	40.9		1.9						Burton <i>et al.</i> 2008
	<i>Melospiza undulata</i>	Budgerigar	35.2	39.1	1.5	3.8	1.9	69.0			Calder 1968
	<i>Coracopsis vasa</i>	Vasa Parrot	454.3	39.1	10.6	15.1					Lovegrove <i>et al.</i> 2011
	<i>Agapornis roseicollis</i>	Rosy-faced Lovebird	50.0	39.0	1.7	5.9	3.1	36.2	1.2	25.7	Bucher & Morgan 1989; Burton <i>et al.</i> 2008; Gavrilov 2014; Londoño <i>et al.</i> 2014
	<i>Agapornis fischeri</i>	Fischer's Lovebird	53.2		2.0						Gavrilov & Dol'nik 1985; Burton <i>et al.</i> 2008
	<i>Agapornis personatus</i>	Yellow-collared Lovebird	46.7		1.8						Burton <i>et al.</i> 2008
	<i>Agapornis nigrigenis</i>	Black-cheeked Lovebird	41.4		1.8						Burton <i>et al.</i> 2008
	<i>Loriculus galgulus</i>	Blue-crowned Hanging-parrot	27.0		1.9						Prinzinger & Hänsler 1980
	<i>Bolborhynchus lineola</i>	Barred Parakeet	56.0					28.7	1.9	33.3	Bucher 1981
	<i>Bolborhynchus orbygniesii</i>	Andean Parakeet	46.4		1.4						Londoño <i>et al.</i> 2014
STRIGIFORMES											
	Tytonidae	Barn owls									
	<i>Tyto alba</i> *	Barn Owl	456.1		9.4			11.5	12.6	29.7	Souza 1988 in Maloney & Dawson 1994; Thouzeau <i>et al.</i> 1999; Londoño <i>et al.</i> 2014
	Strigidae	Owls									
	<i>Otus scops</i>	Common Scops-owl	78.9		1.7						Gavrilov & Dol'nik 1985
	<i>Megascops kennicottii</i>	Western Screech-owl	147.3		4.6			25.5	2.2	31.8	Souza 1988 in Maloney & Dawson 1994; Londoño <i>et al.</i> 2014
	<i>Megascops trichopsis</i>	Whiskered Screech-owl	99.8		1.5						Ligon 1969
	<i>Bubo virginianus</i>	Great Horned Owl	1195.4	40.8	15.8			11.3	21.6	25.2	King & Farner 1961; Souza 1988 in Maloney & Dawson 1994; Londoño <i>et al.</i> 2014
	<i>Strix aluco</i>	Tawny Owl	350.0					24.0			Groebels 1932
	<i>Glucidium gnoma</i>	Northern Pygmy-owl	52.0		1.7						Ligon 1969
	<i>Glucidium jandini</i>	Andean Pygmy-owl	60.6		2.4						Londoño <i>et al.</i> 2014
	<i>Micrathene whitneyi</i>	Elf Owl	45.0		0.9						Ligon 1969
	<i>Athene cunicularia</i>	Burrowing Owl	159.7		3.7			23.4	2.5	25.8	Souza 1988 in Maloney & Dawson 1994; Londoño <i>et al.</i> 2014
	<i>Aegolius funereus</i>	Boreal Owl	130.0	39.7	4.1	7.1					Hohtola <i>et al.</i> 1994
	<i>Ptilopsis granti</i>	Southern White-faced Owl	221.1		2.7	6.2					Smit <i>et al.</i> 2011
CAPRIMULGIFORMES											
	Podargidae	Frogmouths									
	<i>Podargus strigoides</i> **	Tawny Frogmouth	380.5	38.2	3.6	14.1		16.1	6.6	30.2	Lasiewski & Bartholomew 1966; McNab & Bonaccorso 1995; Bech & Nichol 1999
	<i>Podargus papuensis</i>	Papuan Frogmouth	314.6	38.8	3.8	16.5					McNab & Bonaccorso 1995
	Caprimulgidae	Nightjars									
	<i>Eurostoedus mystacalis</i>	White-throated Eared-nightjar	162.0	40.1	1.7	7.6					McNab & Bonaccorso 1995
	<i>Chordeiles minor</i> **	Common Nighthawk	72.0		1.6	7.9	5.4				Lasiewski & Dawson 1964
	<i>Phalaenoptilus nuttallii</i> ‡	Common Poorwill	35.0					34.0	0.9		Withers 1977; Brigham 1992‡
	<i>Caprimulgus macrurus</i>	Large-tailed Nightjar	68.6		1.1	4.4					McNab & Bonaccorso 1995
APODIFORMES											
	Aegothelidae	Owlet-nightjars									
	<i>Aegothales cristatus</i> **	Australian Owlet-nightjar	45.6	37.7	1.2	11.6					Brigham <i>et al.</i> 2000**; Douchette & Geiser 2008**
	Apodidae	Swifts									
	<i>Collocalia esculenta</i>	Glossy Swiftlet	6.8	38.2	0.3	2.2					McNab & Bonaccorso 1995
	<i>Collocalia vanikorensis</i>	Uniform Swiftlet	11.6		0.4	2.8					McNab & Bonaccorso 1995
	<i>Apus apus</i> **	Common Swift	44.9		1.6						Koskimies 1948**, in McKechnie & Lovegrove 2002; Kendeigh <i>et al.</i> 1977
	Trochilidae	Hummingbirds									
	<i>Phaethornis guy</i> **	Green Hermit	5.9		0.5						Schuchmann & Prinzinger 1988**; Londoño <i>et al.</i> 2014
	<i>Phaethornis superciliosus</i>	Long-tailed Hermit	5.2		0.5						Londoño <i>et al.</i> 2014
	<i>Phaethornis hispidus</i>	White-bearded Hermit	4.9		0.5						Londoño <i>et al.</i> 2014
	<i>Eutoxeres condensini</i>	Buff-tailed Sicklebill	10.0		0.8						Londoño <i>et al.</i> 2014
	<i>Doryfera ludovicae</i>	Green-fronted Lancebill	5.9		0.6						Londoño <i>et al.</i> 2014
	<i>Eupetomena macroura</i> **	Swallow-tailed Hummingbird	8.6	37.1							Bech <i>et al.</i> 1997**
	<i>Florisuga fusca</i> **	Black Jacobin	7.7	37.1							Bech <i>et al.</i> 1997**
	<i>Colibri coruscans</i>	Sparkling Violet-ear	8.4		0.5						Londoño <i>et al.</i> 2014
	<i>Chloerestes notata</i> **	Blue-chinned Sapphire	3.0	36.7							Morrison, 1962**
	<i>Hylocharis cyanus</i>	White-chinned Sapphire	3.0	38.8							Morrison, 1962
	<i>Tuphropilus hypostictus</i>	Many-spotted Hummingbird	7.5		0.5						Londoño <i>et al.</i> 2014
	<i>Amazilia versicolor</i> **	Versicoloured Emerald	4.1	37.3							Bech <i>et al.</i> 1997**
	<i>Amazilia leucogaster</i> *	Plain-bellied Emerald	4.0	39.4							Morrison 1962*
	<i>Adelomyia melanogenys</i>	Speckled Hummingbird	3.5		0.3						Londoño <i>et al.</i> 2014
	<i>Heliodoxa leadbeateri</i>	Violet-fronted Brilliant	7.5		0.7						Londoño <i>et al.</i> 2014
	<i>Aglaeactis cupripennis</i> **	Shining Sunbeam	7.2		0.4						Krüger <i>et al.</i> 1982**; Londoño <i>et al.</i> 2014
	<i>Coeligena coeligena</i>	Bronzy Inca	7.1		0.7						Londoño <i>et al.</i> 2014
	<i>Coeligena violifer</i>	Violet-throated Starfrontlet	7.8		0.5						Londoño <i>et al.</i> 2014

ORDER	Family	Description	Mass g	T _b °C	BMR kJ h ⁻¹	C mL O ₂ h ⁻¹ °C ⁻¹	EWL mL H ₂ O	f _R breaths min ⁻¹	V _T mL	E _{O₂} %	References
COLIIFORMES	Trogonidae	<i>Boissonneaua matthewsii</i> **									Krüger et al. 1982**; Londoño et al. 2014
		<i>Helangelus amethysticollis</i>									Londoño et al. 2014
		<i>Haplophastria aureliae</i>									Londoño et al. 2014
		<i>Metallura tyrianthina</i>									Londoño et al. 2014
		<i>Chalcostigma ruficeps</i>									Londoño et al. 2014
		<i>Schistes geoffroyi</i>									Londoño et al. 2014
		<i>Archilochus colubris</i>									Lasiewski 1963
		<i>Archilochus alexandri</i> **									Lasiewski 1963; Krüger et al. 1982**
		<i>Calypte anna</i> **									Lasiewski 1963**
		<i>Calypte costae</i> **									Lasiewski 1963**
		<i>Stellula calliope</i>									Lasiewski 1963
		<i>Selasphorus rufus</i> **									Lasiewski 1963; Hiebert 1993**
		<i>Selasphorus sasin</i>									Lasiewski 1963
		<i>Threnetes leucurus</i>									Londoño et al. 2014
	Coliidae	Mousebirds									
		<i>Colius striatus</i> **									Bartholomew & Trost 1970; Brown & Foster 1992; McKechnie & Lovegrove 2001a**
		<i>Colius castanotus</i> **									Prinzinger et al. 1981**
		<i>Colius colius</i> **									McKechnie & Lovegrove 2001b**
	<i>Urocolius macrourus</i> **	Blue-naped Mousebird									Prinzinger 1988; Prinzinger et al. 1992**
CORACIIFORMES	Alcedinidae	Kingfishers									
		<i>Alcedo atthis</i>									Kendeigh et al. 1977
		<i>Alcedo azurea</i>									McNab 2013
		<i>Ceyx lepidus</i>									McNab 2013
		<i>Dacelo novaezguineae</i>									Buttemer et al. 2003
		<i>Todiramphus sanctus</i>									McNab 2013
	Todidae	Todies									
		<i>Todus mexicanus</i> **									Merola-Zwartjes & Ligon 2000**
	Motmotidae	Motmots									
		<i>Barphothengus martii</i>									Londoño et al. 2014
		<i>Momotus momota</i>									Wiersma et al. 2007
	Meropidae	Bee-eaters									
		<i>Merops viridis</i>									Bryant et al. 1984
BUCEROTIFORMES	Phoeniculidae	Woodhoopoes									
		<i>Phoeniculus purpureus</i>									Williams et al. 1991
PICIFORMES	Ramphastidae	Toucans and barbets									
		<i>Selenidera maculirostris</i>									McNab 2001
	Picidae	Woodpeckers									
		<i>Jynx torquilla</i>									Kendeigh et al. 1977
		<i>Dendrocopos major</i>									Kendeigh et al. 1977; Gavrilov 2014
		<i>Picoides pubescens</i>									Liknes & Swanson 1996
		<i>Veniliornis nigriceps</i>									Londoño et al. 2014
		<i>Colaptes rivoli</i>									Londoño et al. 2014
		<i>Colaptes auratus</i>									Lewis 1967
		<i>Bucconidae</i>									
		<i>Monasa nigrifrons</i>									Londoño et al. 2014
PASSERIFORMES	Pipridae	Manakins									
		<i>Pipra fasciata</i>									Londoño et al. 2014
		<i>Pipra mentalis</i>									Bartholomew et al. 1983
		<i>Pipra chloromeros</i>									Londoño et al. 2014
		<i>Lepidothrix coronata</i>									Londoño et al. 2014
		<i>Lepidothrix coerulescapilla</i>									Londoño et al. 2014
		<i>Chirotophia boliviana</i>									Londoño et al. 2014
		<i>Manacus vitellinus</i>									Vleck & Vleck 1979; Bartholomew et al. 1983
	Cotingidae	Cotingas									
		<i>Rupicola peruvianus</i>									Londoño et al. 2014
	Tyrannidae	Tyrant-flycatchers									
		<i>Mionectes striaticollis</i>									Londoño et al. 2014
		<i>Mionectes olivaceus</i>									Londoño et al. 2014
		<i>Mionectes olegineus</i>									Londoño et al. 2014
		<i>Mionectes macconnelli</i>									Londoño et al. 2014
		<i>Leptopogon amaurocephalus</i>									Londoño et al. 2014
		<i>Leptopogon superciliosus</i>									Londoño et al. 2014
		<i>Todirostrum cinereum</i>									Wiersma et al. 2007
		<i>Corythopis torquatus</i>									Londoño et al. 2014
		<i>Elaenia albiceps</i>									Londoño et al. 2014
		<i>Elaenia pallatangae</i>									Londoño et al. 2014
		<i>Mecocerculus leucophrys</i>									Londoño et al. 2014
		<i>Rhyncobrychus fulvipes</i>									Londoño et al. 2014
		<i>Pyrrhomyias cinnamomeus</i>									Londoño et al. 2014
		<i>Contopus virens</i>									Yarborough 1971; Dutenhoffer & Swanson 1996
		<i>Empidonax flaviventris</i>									King & Farner 1961; Lewis 1967
		<i>Empidonax virens</i>									Yarborough 1971
		<i>Sayornis phoebe</i>									Yarborough 1971; Ro & Williams 2010
		<i>Ochthoeca pulchella</i>									Londoño et al. 2014
		<i>Ochthoeca rufipectoralis</i>									Londoño et al. 2014
		<i>Myiarchus cinerascens</i>									Yarborough 1971
		<i>Myiodynastes maculatus</i>									Wiersma et al. 2007
	Thamnophilidae	Antbirds									
		<i>Thamnophilus doliatus</i>									Wiersma et al. 2007
		<i>Thamnophilus atrinucha</i>									Wiersma et al. 2007
		<i>Thamnomanes ardesiacus</i>									Londoño et al. 2014
		<i>Thamnomanes schistogynus</i>									Londoño et al. 2014
		<i>Myrmotherula baucowelli</i>									Londoño et al. 2014
		<i>Epinecrophylla leucophthalma</i>									Londoño et al. 2014
		<i>Myrmotherula axillaris</i>									Londoño et al. 2014
		<i>Cercomacra tyrannina</i>									Wiersma et al. 2007
		<i>Pyrgilena leuconota</i>									Londoño et al. 2014
		<i>Myrmoborus myotherinus</i>									Londoño et al. 2014
		<i>Pernostola lophotes</i>									Londoño et al. 2014
		<i>Myrmeciza esul</i>									Wiersma et al. 2007
		<i>Myrmeciza hemimelaena</i>									Londoño et al. 2014

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	<i>Scientific name</i>	<i>Common name</i>									
	<i>Myrmeciza esul</i>	Chestnut-backed Antbird	28.3		1.0						Wiersma <i>et al.</i> 2007
	<i>Myrmeciza hemimelaena</i>	Chestnut-tailed Antbird	18.0		0.9						Londoño <i>et al.</i> 2014
	<i>Myrmeciza goeldii</i>	Goeldi's Antbird	42.4		1.5						Londoño <i>et al.</i> 2014
	<i>Gymnophithys leucaspis</i>	Bicoloured Antbird	27.7		1.2						Wiersma <i>et al.</i> 2007
	<i>Gymnophithys salvini</i>	White-throated Antbird	27.1		1.2						Londoño <i>et al.</i> 2014
	<i>Hylaphylax naevioides</i>	Spotted Antbird	16.1		0.9						Wiersma <i>et al.</i> 2007
	<i>Willisornis poecilinotus</i>	Scale-backed Antbird	22.3		1.4						Londoño <i>et al.</i> 2014
	<i>Hypocnemis subflava</i>	Yellow-breasted Warbling-antbird	15.6		0.9						Londoño <i>et al.</i> 2014
	Conopophagidae	Gnateaters									
	<i>Conopophaga peruviana</i>	Ash-throated Gnateater	24.5		1.2						Londoño <i>et al.</i> 2014
	<i>Conopophaga ardesiaca</i>	Slaty Gnateater	27.5		1.4						Londoño <i>et al.</i> 2014
	Rhinocryptidae	Tapaculos									
	<i>Scytalopus parvirostris</i>	Trilling Tapaculo	17.0		1.3						Londoño <i>et al.</i> 2014
	<i>Scytalopus atratus</i>	White-crowned Tapaculo	21.5		1.4						Londoño <i>et al.</i> 2014
	Formicariidae	Antthrushes and antpittas									
	<i>Formicarius analis</i>	Black-faced Anthrush	54.9		2.2						Londoño <i>et al.</i> 2014
	Furnariidae	Ovenbirds									
	<i>Shizoeaca belleri</i>	Puna Thistletail	15.0		0.7						Londoño <i>et al.</i> 2014
	<i>Synallaxis azarae</i>	Azara's Spinetail	13.6		0.8						Londoño <i>et al.</i> 2014
	<i>Synallaxis cabanisi</i>	Cabanis's Spinetail	19.3		1.1						Londoño <i>et al.</i> 2014
	<i>Cranioleuca maccapatae</i>	Marcapata Spinetail	19.0		1.0						Londoño <i>et al.</i> 2014
	<i>Premnoplex brunescens</i>	Spotted Barbtail	15.7		1.2						Londoño <i>et al.</i> 2014
	<i>Margarornis squamiger</i>	Pearled Treerunner	16.7		1.0						Londoño <i>et al.</i> 2014
	<i>Lochmias nematura</i>	Sharp-tailed Streamcreeper	30.5		1.2						Londoño <i>et al.</i> 2014
	<i>Anabacerthia striatocollis</i>	Montane Foliage-gleaner	24.2		1.3						Londoño <i>et al.</i> 2014
	<i>Thripadectes melanorhynchus</i>	Black-billed Treehunter	47.5		1.9						Londoño <i>et al.</i> 2014
	<i>Thripadectes holostictus</i>	Striped Treehunter	42.5		1.4						Londoño <i>et al.</i> 2014
	<i>Automolus rufipileatus</i>	Chestnut-crowned Foliage-gleaner	36.2		1.7						Londoño <i>et al.</i> 2014
	<i>Sclerurus mexicanus</i>	Tawny-throated Leafosser	28.8		1.6						Londoño <i>et al.</i> 2014
	<i>Sclerurus caudatus</i>	Black-tailed Leafosser	36.2		1.7						Londoño <i>et al.</i> 2014
	Dendrocolaptidae	Woodcreepers									
	<i>Dendrocincla fuliginosa</i>	Plain-brown Woodcreeper	36.1		1.6						Wiersma <i>et al.</i> 2007; Londoño <i>et al.</i> 2014
	<i>Dendrocincla merula</i>	White-chinned Woodcreeper	52.8		2.2						Londoño <i>et al.</i> 2014
	<i>Glyphorhynchus spirurus</i>	Wedge-billed Woodcreeper	15.5		0.9						Londoño <i>et al.</i> 2014
	<i>Xiphorhynchus guttatus</i>	Buff-throated Woodcreeper	60.1		1.9						Londoño <i>et al.</i> 2014
	<i>Xiphorhynchus triangularis</i>	Olive-backed Woodcreeper	44.1		2.2						Londoño <i>et al.</i> 2014
	<i>Xiphorhynchus elegans</i>	Elegant Woodcreeper	41.4		1.8						Londoño <i>et al.</i> 2014
	Climacteridae	Australian treecreepers									
	<i>Climacteris rufus</i>	Rufous Treecreeper	29.0	38.6	1.2	39.0	1.8	39.7	0.5	33.0	This study
	Meliphagidae	Honeyeaters									
	<i>Lichmera indistincta</i>	Brown Honeyeater	9.6	40.4	0.8						Collins <i>et al.</i> 1980; Vitali <i>et al.</i> 1999
	<i>Lichenostomus virescens</i>	Singing Honeyeater	25.0		1.1						Collins <i>et al.</i> 1980
	<i>Melithreptus lunatus</i>	White-naped Honeyeater	14.3	40.2	0.9						Vitali <i>et al.</i> 1999
	<i>Ptiloprora guisei</i>	Rufous-backed Honeyeater	20.2	36.4	1.0	2.6					McNab 2013
	<i>Ptiloprora perstriata</i>	Black-backed Honeyeater	24.7	36.5	1.2	2.5					McNab 2013
	<i>Melidectes belfordi</i>	Belford's Melidectes	66.6	38.8	2.7	7.2					McNab 2013
	<i>Melidectes ruficristalis</i>	Yellow-browed Melidectes	63.9	40.0	2.8	5.2					McNab 2013
	<i>Melipotes fumigatus</i>	Smoky Honeyeater	57.4	38.6	2.5	4.0					McNab 2013
	<i>Phylidonyris novaehollandiae</i>	New Holland Honeyeater	17.3		1.1						Weathers <i>et al.</i> 1996
	<i>Phylidonyris melanops</i>	Tawny-crowned Honeyeater	18.8	40.2	1.1						Vitali <i>et al.</i> 1999
	<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill	9.7		0.9						Weathers <i>et al.</i> 1996
	Acanthizidae	Thornbills and gerygones									
	<i>Craterocercus robusta</i>	Mountain Mouse-warbler	17.3	37.0	0.9	2.0					McNab 2013
	<i>Sericornis frontalis</i>	White-browed Scrubwren	11.0		0.7						Ambrose & Bradshaw 1988
	<i>Sericornis nouhuysi</i>	Large Scrubwren	16.1	37.4	0.9	1.9					McNab 2013
	<i>Sericornis perspicillatus</i>	Buff-faced Scrubwren	8.5	37.8	0.6	2.1					McNab 2013
	<i>Sericornis papuensis</i>	Papuan Scrubwren	9.8	35.3	0.6	1.6					McNab 2013
	Pomatostomidae	Australasian babblers									
	<i>Pomatostomus superciliosus</i>	White-browed Babbler	46.6	38.6	1.2	5.2	1.5	24.7	1.1	28.5	This study
	Orthonychidae	Logrunners									
	<i>Ifrita kowaldi</i>	Ifrit	28.9	36.8	1.2	2.9					McNab 2013
	Cnemophilidae	Satin birds									
	<i>Cnemophilus macgregorii</i>	Crested Bird-of-paradise	87.1	39.2	2.7	5.2					McNab 2013
	<i>Cnemophilus lorae</i>	Loria's Bird-of-paradise	77.7	38.8	2.4	5.5					McNab 2005; 2013
	Melanochartidae	Berrypeckers									
	<i>Melanocharis versteri</i>	Fan-tailed Berrypecker	14.3	35.4	0.9	1.9					McNab 2013
	<i>Toxarhamphus poliopterus</i>	Grey-winged Longbill	12.2	36.9	0.6	1.6					McNab 2013
	Cracticidae	Butcherbirds									
	<i>Gymnorhina tibicen</i>	Australian Magpie	310.3	39.3	5.9	12.0	5.6	13.6	13.4	21.9	This study
	Artamidae	Woodswallows									
	<i>Artamus maximus</i>	Great Woodswallow	61.2	39.9	2.2	4.5					McNab 2013
	Pachycephalidae	Whistlers									
	<i>Aleadryas rufinucha</i>	Rufous-naped Whistler	40.0		1.6	3.2					McNab 2013
	<i>Pachycephala soror</i>	Sclater's Whistler	23.4	38.5	1.3	2.3					McNab 2013
	<i>Pachycephala schlegelii</i>	Regent Whistler	22.0	37.6	1.0	2.2					McNab 2013
	Laniidae	Shrikes									
	<i>Lanius collurio</i>	Red-backed Shrike	26.6		1.3						Kendeigh <i>et al.</i> 1977; Lindström & Kvist 1995
	<i>Lanius excubitor</i>	Great Grey Shrike	72.4		3.7						Kendeigh <i>et al.</i> 1977
	<i>Lanius collaris</i>	Common Fiscal	48.9	40.8	2.8		5.0				Soobramoney <i>et al.</i> 2003
	Vireonidae	Vireos and allies									
	<i>Vireo olivaceus</i>	Red-eyed Vireo	16.2		0.9		2.8				Wiersma <i>et al.</i> 2007; Ro & Williams 2010
	<i>Vireo flavoviridis</i>	Yellow-green Vireo	15.9		1.0						Wiersma <i>et al.</i> 2007
	Oriolidae	Orioles and figbirds									
	<i>Oriolus oriolus</i>	Eurasian Golden Oriole	64.9		2.3						Kendeigh <i>et al.</i> 1977
	Rhipiduridae	Fantails									
	<i>Rhipidura atra</i>	Black Fantail	11.0	38.3	0.9	2.0					McNab 2013
	<i>Rhipidura albolimbata</i>	Friendly Fantail	10.3	36.2	0.6	2.4					McNab 2013
	Corvidae	Crows and jays									
	<i>Cyanocitta cristata</i>	Blue Jay	77.1					49.0			Lewis 1967
	<i>Garrulus glandarius</i>	Eurasian Jay	153.0		5.0						Kendeigh <i>et al.</i> 1977
	<i>Pica pica</i>	Black-billed Magpie	180.5		5.2	9.4	8.1	52.4	3.0		Prinzinger 1976; Kendeigh <i>et al.</i> 1977; Hayworth & Weathers 1984; Boggs <i>et al.</i> 1997
	<i>Pica nuttalli</i>	Yellow-billed Magpie	151.9		5.3	7.5	8.3				Hayworth & Weathers 1984
	<i>Nucifraga caryocatactes</i>	Spotted Nutcracker	147.0		4.9						Kendeigh <i>et al.</i> 1977
	<i>Pyrrhocorax graculus</i>	Yellow-billed Chough	206.4		6.2						Kendeigh <i>et al.</i> 1977
	<i>Corvus monedula</i>	Eurasian Jackdaw	188.0		6.2			26.0			Groebbels 1932; Daan <i>et al.</i> 1990
	<i>Corvus frugilegus</i>	Rook	390.0		9.4			25.0			Groebbels 1932; Kendeigh <i>et al.</i> 1977
	<i>Corvus ossifragus</i>	Fish Crow	274.0		10.1			27.3	8.2	19.5	Bernstein & Schmidt-Nielsen 1974

Appendix 2: Comparative dataset

ORDER	Family	Description	Mass g	T _b °C	BMR kJ h ⁻¹	C mL O ₂ h ⁻¹ °C ⁻¹	EWL mL H ₂ O	f _R breaths min ⁻¹	V _T mL	Eo ₂ %	References
	<i>Scientific name</i>	<i>Common name</i>									
	<i>Corvus cryptoleucus</i>	Chihuahuan Raven	480.0					32.5	10.5		Hudson & Bernstein 1981; 1983
	<i>Corvus ruficollis</i>	Brown-necked Raven	660.0		12.2						Kendeigh <i>et al.</i> 1977
	<i>Corvus corax</i>	Common Raven	1203.0	39.0	19.8	32.0	34.2				Gavrilov 2014
Paradisaeidae		Birds of paradise									
	<i>Manucodia keraudrenii</i>	Trumpet Manucode	170.7	40.4	4.3	14.5					McNab 2005
	<i>Epimachus meyeri</i>	Brown Sicklebill	202.7	41.0	6.6	16.4					McNab 2005
	<i>Lophorina superba</i>	Superb Bird-of-paradise	74.6	40.5	2.6	6.6					McNab 2005
	<i>Astrapia stephaniae</i>	Stephanie's Astrapia	148.2	41.4	5.8	15.7					McNab 2005
	<i>Paradisaea raggiana</i>	Raggiana Bird-of-paradise	215.7	39.7	6.8	15.7					McNab 2005
	<i>Paradisaea rudolphi</i>	Blue Bird-of-paradise	156.1	40.5	5.5	11.7					McNab 2005
Petroicidae		Australasian robins									
	<i>Microeca papuana</i>	Canary Flyrobin	12.9	34.5	0.7	2.5					McNab 2013
	<i>Eopsaltria griseogularis</i>	Western Yellow Robin	18.5	38.6	1.0	2.7	0.8	37.1	0.5	39.2	This study
	<i>Pencothello sigillatus</i>	White-winged Robin	21.1	37.1	1.1	2.2					McNab 2013
	<i>Pencothello cyanus</i>	Blue-grey Robin	23.8	37.8	1.3	2.1					McNab 2013
Bombycillidae		Waxwings									
	<i>Bombycilla garrulus</i>	Bohemian Waxwing	72.5		3.4						Kendeigh <i>et al.</i> 1977
Paridae		Tits and chickadees									
	<i>Parus montanus</i> *	Willow Tit	11.0	41.4		1.7					Reinertsen & Haftorn 1983*
	<i>Parus atricapillus</i> *	Black-capped Chickadee	13.1		1.3			64.0			Odum 1941; Chaplin 1976; Dutenhoffer & Swanson 1996
	<i>Parus ater</i>	Coal Tit	10.4	40.5	0.8	2.3	1.4				Gavrilov 1974; 2014; Gavrilov & Morgunova 2014
	<i>Parus major</i>	Great Tit	17.5	39.8	1.2	3.2	2.1				Gavrilov 1974; Broggi <i>et al.</i> 2004; Gavrilov 2014
Hirundinidae		Swallows and martins									
	<i>Tachycineta bicolor</i>	Tree Swallow	16.4		1.0		3.4				Wiersma <i>et al.</i> 2007; Ro & Williams 2010
	<i>Progne chalybea</i>	Grey-breasted Martin	34.9		1.7						Wiersma <i>et al.</i> 2007
	<i>Riparia riparia</i> *	Sand Martin	13.6	41.4	0.8			121.8	0.1		King & Farner 1961; Keskpaik 1972* (in McKechnie & Lovegrove 2002); Kendeigh <i>et al.</i> 1977; Colby <i>et al.</i> 1987;
	<i>Hirundo rustica</i>	Barn Swallow	18.4	40.8	1.1			79.5	0.6		Gavrilov & Dol'nik 1985; Williams <i>et al.</i> 1995
	<i>Hirundo tahitica</i>	Pacific Swallow	14.1		0.6						Bryant <i>et al.</i> 1984
	<i>Delichon urbicum</i> **	Northern House-martin	20.0	41.1	0.5						Prinzinger & Siedle 1988**
Aegithalidae		Long-tailed Tits									
	<i>Aegithalos caudatus</i>	Long-tailed Tit	8.9	40.6	0.7	2.2	1.2				Gavrilov & Dol'nik 1985; Gavrilov 2014
Alaudidae		Larks									
	<i>Certhilauda erythrochlamys</i>	Dune Lark	27.3		1.5		1.9				Williams 1999
	<i>Chersomanes albofasciata</i>	Spike-heeled Lark	25.7		1.2		3.2				Tielemans <i>et al.</i> 2003
	<i>Eremopterix nigriceps</i>	Black-crowned Sparrow-lark	15.2		0.7		1.3				Tielemans <i>et al.</i> 2003
	<i>Ammomanes deserti</i>	Desert Lark	21.5		0.8		1.6				Tielemans <i>et al.</i> 2003
	<i>Alaemon alaudipes</i>	Greater Hoopoe-lark	74.3	40.8	2.9		2.6				Williams & Tielemans 2000; Tielemans <i>et al.</i> 2002; 2003a; 2003b
	<i>Melanocorypha calandra</i>	Calandra Lark	50.6		2.1						Tielemans <i>et al.</i> 2003
	<i>Calandrella brachydactyla</i>	Greater Short-toed Lark	24.0		1.5						Tielemans <i>et al.</i> 2003
	<i>Calandrella rufescens</i>	Lesser Short-toed Lark	23.6		1.3						Tielemans <i>et al.</i> 2003
	<i>Eremalauda dunni</i>	Dunn's Lark	20.6	40.5	1.0		1.6				Tielemans <i>et al.</i> 2002; 2003a; 2003b
	<i>Galerida cristata</i>	Crested Lark	31.2		1.3		2.4				Tielemans <i>et al.</i> 2003
	<i>Lullula arborea</i>	Wood Lark	29.4	41.5	1.9		2.3				Kendeigh <i>et al.</i> 1977; Tielemans <i>et al.</i> 2002; 2003a; 2003b
	<i>Alauda arvensis</i>	Eurasian Skylark	31.7	41.0	2.6		3.5				Tielemans <i>et al.</i> 2002; 2003a; 2003b
	<i>Eremophila alpestris</i>	Horned Lark	29.0	41.5	1.5	4.0	2.1				Trost 1972; Tielemans <i>et al.</i> 2003
Pycnonotidae		Bulbuls									
	<i>Pycnonotus barbatus</i>	Common Bulbul	40.3	40.3	1.7	5.2					Seavy & McNab 2007
	<i>Pycnonotus finlaysoni</i>	Stripe-throated Bulbul	26.3		0.8						Hails 1983
	<i>Pycnonotus goiavier</i>	Yellow-vented Bulbul	28.6		0.9						Hails 1983
	<i>Andropadus virens</i>	Little Greenbul	24.2	39.6	1.2	3.6					Seavy & McNab 2007
	<i>Andropadus latirostris</i>	Yellow-whiskered Greenbul	26.6	39.5	1.3	3.7					Seavy & McNab 2007
Sylviidae		Old World warblers									
	<i>Acrocephalus schoenobaenus</i>	Sedge Warbler	11.0		0.8						Kendeigh <i>et al.</i> 1977; Lindström & Kvist 1995
	<i>Acrocephalus palustris</i>	Marsh Warbler	10.8		0.7						Kendeigh <i>et al.</i> 1977
	<i>Acrocephalus arundinaceus</i>	Great Reed-warbler	21.9		0.9						Hails 1983
	<i>Hippolais icterina</i>	Icterine Warbler	12.5		1.7						Kendeigh <i>et al.</i> 1977
	<i>Phylloscopus trochilus</i>	Willow Warbler	10.7		0.8						Kendeigh <i>et al.</i> 1977
	<i>Phylloscopus collybita</i>	Common Chiffchaff	7.5		0.6						Kendeigh <i>et al.</i> 1977; Lindström & Kvist 1995
	<i>Phylloscopus sibilatrix</i>	Wood Warbler	9.2		0.6						Kendeigh <i>et al.</i> 1977
	<i>Eremiornis carteri</i>	Spinifexbird	11.6	39.1	0.7	3.9	2.9				Ambrose <i>et al.</i> 1996
	<i>Sylvia atricapilla</i>	Blackcap	19.4	42.5	1.2						Kendeigh <i>et al.</i> 1977; Lindström & Kvist 1995; Wojciechowski & Pinshow 2009
	<i>Sylvia borin</i>	Garden Warbler	24.8		1.5						Kendeigh <i>et al.</i> 1977
	<i>Sylvia curruca</i>	Lesser Whitethroat	10.6		0.7						Kendeigh <i>et al.</i> 1977
	<i>Sylvia nisoria</i>	Barred Warbler	21.3		1.4						Kendeigh <i>et al.</i> 1977
Troglodytidae		Wrens									
	<i>Cinnycteria fulva</i>	Fulvous Wren	16.3		0.7						Londoño <i>et al.</i> 2014
	<i>Thryothorus ludovicianus</i>	Carolina Wren	20.1		2.3						Wiersma <i>et al.</i> 2007
	<i>Thryothorus rufalbus</i>	Rufous-and-white Wren	22.6		1.1						Wiersma <i>et al.</i> 2007
	<i>Thryothorus leucotis</i>	Buff-breasted Wren	18.0		0.8						Wiersma <i>et al.</i> 2007
	<i>Troglodytes troglodytes</i>	Winter Wren	9.0	40.2	0.8	2.5	1.3				Gavrilov 1974; 2014
	<i>Troglodytes aedon</i>	House Wren	10.0		0.7		1.9	83.0			Odum 1941; Dutenhoffer & Swanson 1996; Wiersma <i>et al.</i> 2007; Ro & Williams 2010
	<i>Troglodytes cobbi</i>	Cobb's Wren	13.3		0.8						Wiersma <i>et al.</i> 2007
	<i>Henicorhina leucophrys</i>	Grey-breasted Wood-wren	15.3		1.1						Londoño <i>et al.</i> 2014
	<i>Microcerculus marginatus</i>	Southern Nightingale-wren	19.4		1.2						Londoño <i>et al.</i> 2014
	<i>Cypothorus thoracicus</i>	Chestnut-breasted Wren	34.4		1.5						Londoño <i>et al.</i> 2014
Timaliidae		Babblers and parrotbills									
	<i>Garrulax canorus</i>	Chinese Hwamei	57.6		3.6	8.6					Xia <i>et al.</i> 2013
Zosteropidae		White-eyes									
	<i>Zosterops lateralis</i>	Silvereye	11.5	40.3	0.5	4.1					Maddocks & Geiser 1997; 2000
Reguliidae		Goldcrests and kinglets									
	<i>Regulus regulus</i>	Goldcrest	5.5	40.9	0.6	2.0	1.0				Kendeigh <i>et al.</i> 1977; Gavrilov 2014
Muscicapidae		Chats and Old World flycatchers									
	<i>Muscicapa striata</i>	Spotted Flycatcher	14.4		0.9						Kendeigh <i>et al.</i> 1977
	<i>Ficedula hypoleuca</i>	European Pied Flycatcher	11.7		0.8						Kendeigh <i>et al.</i> 1977
	<i>Erithacus rubecula</i>	European Robin	17.1	39.8	1.0	3.6	1.8	97.0			Groebels 1932; Kendeigh <i>et al.</i> 1977; Lindström & Kvist 1995; Gavrilov 2014
	<i>Luscinia svecica</i>	Bluethroat	18.2		1.1						Kendeigh <i>et al.</i> 1977; Lindström & Kvist 1995
	<i>Luscinia cyane</i>	Siberian Blue Robin	13.4		0.6						Hails 1983

ORDER	Family	Description	Mass g	T _b °C	BMR kJ h ⁻¹	C mL O ₂ h ⁻¹ °C ⁻¹	EWL mL H ₂ O	f _R breaths min ⁻¹	V _T mL	Eo ₂ %	References
	<i>Scientific name</i>	<i>Common name</i>									
	<i>Luscinia svecica</i>	Bluethroat	18.2			1.1					Kendeigh <i>et al.</i> 1977; Lindstrom & Kvist 1995
	<i>Luscinia cyane</i>	Siberian Blue Robin	13.4			0.6					Hails 1983
	<i>Turdus cyanurus</i>	Orange-flanked Bush-robin	14.8			0.9					Gavrilov & Dol'nik 1985
	<i>Copsychus saularis</i>	Oriental Magpie-robin	33.5			0.8					Hails 1983
	<i>Phoenicurus phoenicurus</i>	Common Redstart	13.0			0.8					Kendeigh <i>et al.</i> 1977
	<i>Saxicola rubetra</i>	Whinchat	14.3			0.9					Kendeigh <i>et al.</i> 1977
	<i>Saxicola torquatus</i>	Common Stonechat	15.9			0.9		1.2			Tielemans 2007
Nectariniidae		Sunbirds									
	<i>Anthreptes orientalis</i>	Kenya Violet-backed Sunbird	11.8			0.6					Prinzinger & Jackel 1986
	<i>Anthreptes collaris</i>	Collared Sunbird	8.5			0.6					Prinzinger & Jackel 1986
	<i>Nectarinia olivacea</i>	Olive Sunbird	11.2	39.8		0.7	2.8				Seavy 2006
	<i>Nectarinia veronii</i>	Mouse-coloured Sunbird	8.4			0.7					Prinzinger & Jackel 1986
	<i>Nectarinia verticalis</i>	Green-headed Sunbird	14.1	39.9		0.9	3.1				Seavy 2006
	<i>Nectarinia cyanolaema</i>	Blue-throated Brown Sunbird	15.8	40.3		1.0	3.3				Seavy 2006
	<i>Nectarinia amethystina</i>	Amethyst Sunbird	12.5			0.8					Prinzinger & Jackel 1986; Lindsay <i>et al.</i> 2009
	<i>Nectarinia senegalensis</i>	Scarlet-chested Sunbird	13.2	40.2		0.9	2.9		68.0	0.3	Prinzinger & Jackel 1986; Seavy 2006
	<i>Nectarinia adelberti</i>	Buff-throated Sunbird	9.3			1.0			75.5	0.2	Prinzinger & Jackel 1986
	<i>Nectarinia venusta</i>	Variable Sunbird	7.1			0.6			85.0	0.2	Prinzinger & Jackel 1986
	<i>Nectarinia cuprea</i>	Copper Sunbird	8.2	40.2		0.5	2.2		64.0	0.1	Prinzinger & Jackel 1986; Seavy 2006
	<i>Nectarinia tacazeae</i>	Tacaze Sunbird	13.7			0.7					Prinzinger & Jackel 1986
	<i>Nectarinia kilimensis</i>	Bronze Sunbird	15.2	39.7		0.8	3.1		34.0	0.5	Prinzinger & Jackel 1986; Seavy 2006
	<i>Aethopyga christinae</i> **	Fork-tailed Sunbird	5.2	37.5			1.1		117.0	0.1	Prinzinger <i>et al.</i> 1992**
	<i>Aethopyga siparaja</i>	Crimson Sunbird	6.8			0.5					Prinzinger & Jackel 1986
Estrildidae		Waxbills, grass finches, munias and allies									
	<i>Uraeginthus bengalus</i>	Red-cheeked Cordonbleu	9.2			0.6	2.9	1.1			Kendeigh <i>et al.</i> 1977; Gavrilov 2014
	<i>Estrilda melpoda</i>	Orange-cheeked Waxbill	6.9						113.0		Calder 1968
	<i>Estrilda troglodytes</i>	Black-rumped Waxbill	7.5	40.3		0.5	2.7	1.0	95.0		Calder 1968; Kendeigh <i>et al.</i> 1977; Gavrilov 2014
	<i>Oreoscoptes fuliginosus</i>	Mountain Firetail	16.2	35.8		0.7	2.2				McNab 2013
	<i>Taeniopygia guttata</i>	Zebra Finch	12.9			0.6	4.3	1.3	89.8	0.4	Williams & Kilgore 1992; Gavrilov 2014; Londoño <i>et al.</i> 2014
	<i>Lonchura cucullata</i>	Bronze Munia	10.6			0.4					Lovegrove & Smith 2003
	<i>Lonchura fringilloides</i>	Maggie Munia	19.8			0.8					Londoño <i>et al.</i> 2014
	<i>Lonchura striata</i>	White-rumped Munia	10.2	39.8		0.7	3.6	1.3			Kendeigh <i>et al.</i> 1977; Gavrilov 2014
	<i>Lonchura fuscans</i>	Dusky Munia	9.5	37.1		0.4		1.8			Weathers 1977
	<i>Lonchura punctulata</i>	Scaly-breasted Munia	14.5			0.7					Londoño <i>et al.</i> 2014
	<i>Lonchura malacca</i>	Tricoloured Munia	11.8			0.5					Hails 1983
	<i>Lonchura maja</i>	White-headed Munia	12.8			0.6					Hails 1983
	<i>Amadina fasciata</i>	Cut-throat	18.2			0.8					Londoño <i>et al.</i> 2014
	<i>Amadina erythrocephala</i>	Red-headed Finch	21.7	39.6		0.8	3.3				McKechnie & Lovegrove 2003
Motacillidae		Wagtails and pipits									
	<i>Motacilla alba</i>	White Wagtail	18.0	40.1		1.1	3.2	1.9			Gavrilov 1974; Gavrilov & Dol'nik 1985; Gavrilov 2014
	<i>Motacilla flava</i>	Yellow Wagtail	14.7			0.9					Kendeigh <i>et al.</i> 1977
	<i>Anthus campestris</i>	Tawny Pipit	21.8			1.4					Kendeigh <i>et al.</i> 1977
	<i>Anthus trivialis</i>	Tree Pipit	19.7			1.2					Kendeigh <i>et al.</i> 1977
	<i>Anthus pratensis</i>	Meadow Pipit	18.9			1.1					Kendeigh <i>et al.</i> 1977
Parulidae		New World warblers									
	<i>Parula americana</i>	Northern Parula	7.0	38.0		0.4	1.8				Yarbrough 1971
	<i>Dendroica petechia</i>	Yellow Warbler	10.0			0.6					Dutenhoffer & Swanson 1996; Wiersma <i>et al.</i> 2007
	<i>Dendroica coronata</i>	Yellow-rumped Warbler	11.5	40.5		0.7	2.0				Yarbrough 1971
	<i>Dendroica dominica</i>	Yellow-throated Warbler	9.8	39.7		0.6	2.0				Yarbrough 1971
	<i>Dendroica palmarum</i>	Palm Warbler	9.8	40.9		0.6	1.6				Yarbrough 1971
	<i>Protonotaria citrea</i>	Prothonotary Warbler	12.8	40.3		0.7	2.6				Yarbrough 1971
	<i>Seiurus aurocapilla</i>	Ovenbird	19.0	41.5		0.9	2.3				Yarbrough 1971
	<i>Seiurus noveboracensis</i>	Northern Waterthrush	18.7	41.7		1.0	3.0				Yarbrough 1971
	<i>Geothlypis trichas</i>	Common Yellowthroat	10.6			0.6	1.8				Yarbrough 1971
	<i>Wilsonia citrina</i>	Hooded Warbler	12.0	41.2		0.8	2.3				Yarbrough 1971
	<i>Myioborus miniatus</i>	Slate-throated Redstart	9.8			0.7					Londoño <i>et al.</i> 2014
	<i>Myioborus melanocephalus</i>	Spectacled Redstart	11.7			0.8					Londoño <i>et al.</i> 2014
	<i>Basileuterus bivitatus</i>	Two-banded Warbler	15.5			1.1					Londoño <i>et al.</i> 2014
	<i>Basileuterus luteoviridis</i>	Citrine Warbler	14.7			0.9					Londoño <i>et al.</i> 2014
	<i>Basileuterus coronatus</i>	Russet-crowned Warbler	17.4			1.2					Londoño <i>et al.</i> 2014
	<i>Basileuterus tristriatus</i>	Three-striped Warbler	12.6			0.9					Londoño <i>et al.</i> 2014
Sittidae		Nuthatches and Wallcreepers									
	<i>Sitta canadensis</i>	Red-breasted Nuthatch	11.2			0.8		0.8			Mugaas & Templeton 1970
	<i>Sitta carolinensis</i>	White-breasted Nuthatch	18.3			1.0					Liknes & Swanson 1996
Mimidae		Mockingbirds and thrashers									
	<i>Dumetella carolinensis</i>	Grey Catbird	32.2			1.8		57.0			Lewis 1967; Dutenhoffer & Swanson 1996
	<i>Mimus polyglottos</i>	Northern Mockingbird	44.2	42.7		2.4		6.2			King & Farner 1961; Wiersma <i>et al.</i> 2007; Ro & Williams 2010
	<i>Mimus gilvus</i>	Tropical Mockingbird	68.9			2.7					Wiersma <i>et al.</i> 2007
	<i>Toxostoma rufum</i>	Brown Thrasher	59.2					30.0			Lewis 1967
Sturnidae		Starlings									
	<i>Onychognathus morio</i>	Red-winged Starling	127.5	39.2		4.6					Chamane & Downs 2009
	<i>Sturnus vulgaris</i>	Common Starling	75.0			3.2		92.0			Groebels 1932; Kendeigh <i>et al.</i> 1977
Turdidae		Thrushes									
	<i>Myadestes ralloides</i>	Andean Solitaire	28.8			1.4					Londoño <i>et al.</i> 2014
	<i>Catharus dryas</i>	Spotted Nightingale-thrush	35.9			1.7					Londoño <i>et al.</i> 2014
	<i>Catharus ustulatus</i>	Swainson's Thrush	28.2			1.5					Londoño <i>et al.</i> 2014
	<i>Hylocichla mustelina</i>	Wood Thrush	30.5					43.0			Lewis 1967
	<i>Turdus merula</i>	Eurasian Blackbird	82.6	39.1		3.3	7.2	5.5	48.0		Groebels 1932; Gavrilov 1974; 2014
	<i>Turdus poliocephalus</i>	Island Thrush	66.1	39.7		2.7	5.4				McNab 2013
	<i>Turdus philomelos</i>	Song Thrush	62.7	39.2		2.6	6.8	5.0	94.0		Groebels 1932; Gavrilov 1974; Gavrilov & Dol'nik 1985; Lindstrom & Kvist 1995; Gavrilov 2014
	<i>Turdus viscivorus</i>	Mistle Thrush	108.2			4.0					Kendeigh <i>et al.</i> 1977
	<i>Turdus chiguanco</i>	Chiguanco Thrush	87.0			1.9					Londoño <i>et al.</i> 2014
	<i>Turdus serranus</i>	Glossy-black Thrush	81.2			3.5					Londoño <i>et al.</i> 2014
	<i>Turdus nigricaps</i>	Slaty Thrush	51.1			1.9					Londoño <i>et al.</i> 2014
	<i>Turdus hawswellii</i>	Hawswell's Thrush	63.3			1.8					Londoño <i>et al.</i> 2014
	<i>Turdus grayi</i>	Clay-coloured Thrush	77.9			2.4					Wiersma <i>et al.</i> 2007
	<i>Turdus albicollis</i>	White-necked Thrush	51.3			1.7					Londoño <i>et al.</i> 2014
	<i>Turdus migratorius</i>	American Robin	62.4	43.2		2.7		7.1	36.5		King & Farner 1961; Lewis 1967; Wiersma <i>et al.</i> 2007; Ro & Williams 2010
Passeridae		Sparrows, snowfinches and allies									

Appendix 2: Comparative dataset

ORDER	Family	Description	Mass g	T _b °C	BMR kJ h ⁻¹	C mL O ₂ h ⁻¹ °C ⁻¹	EWL mL H ₂ O	f _R breaths min ⁻¹	V _T mL	Eo ₂ %	References
	<i>Scientific name</i>	<i>Common name</i>									
Passeridae		Sparrows, snowfinches and allies									
	<i>Passer domesticus</i>	House Sparrow	24.6	40.8	1.5	3.9	2.8	58.0			Kendeigh 1944; King & Farner 1961; Calder 1968; Gavrilov 1974; Dutenhoffer & Swanson 1996; Arens & Cooper 2005; Gavrilov 2014; Londoño <i>et al.</i> 2014
	<i>Passer montanus</i>	Eurasian Tree Sparrow	17.5		0.7						Hails 1983
	<i>Plocepasser mahali</i>	White-browed Sparrow-weaver	40.0	40.7							Ferguson <i>et al.</i> 2002
Ploceidae		Weavers and allies									
	<i>Ploceus aurantius</i>	Orange Weaver	18.7		0.8						Londoño <i>et al.</i> 2014
	<i>Euplectes orix</i>	Red Bishop	23.0		1.2						van de Ven <i>et al.</i> 2013
Prunellidae		Accentors									
	<i>Prunella modularis</i>	Hedge Accentor	17.7		1.2						Kendeigh <i>et al.</i> 1977; Lindstrom & Kvist 1995
Fringillidae		Finches and Hawaiian honeycreepers									
	<i>Fringilla coelebs</i>	Eurasian Chaffinch	21.0	39.6	1.3	3.8	2.2				Gavrilov 1974; Gavrilov & Dol'nik 1985; Gavrilov 2014
	<i>Fringilla montifringilla</i>	Brambling	21.2		1.3						Kendeigh <i>et al.</i> 1977; Lindstrom & Kvist 1995
	<i>Serinus canaria</i>	Island Canary	13.3		0.8			82.5			Groebbels 1932; Odum 1941; Kendeigh <i>et al.</i> 1977
	<i>Carduelis chloris</i>	European Greenfinch	28.2	39.6	1.7	4.1	3.2				Kendeigh <i>et al.</i> 1977; Gavrilov 2014
	<i>Carduelis spinus</i>	Eurasian Siskin	14.0		1.0	2.7	1.8				Gavrilov 2014
	<i>Carduelis pinus</i>	Pine Siskin	14.0		1.0						Gavrilov 1974
	<i>Carduelis tristis</i>	American Goldfinch	11.4				2.0				Ro & Williams 2010
	<i>Carduelis carduelis</i>	European Goldfinch	16.5		1.3						Kendeigh <i>et al.</i> 1977
	<i>Carduelis flammea</i> *	Common Redpoll	14.0	40.1	1.0	2.7	1.7				Gavrilov 1974; Reinertsen & Haftorn 1986*; Gavrilov 2014
	<i>Carduelis cannabina</i>	Eurasian Linnet	16.9		1.2						Kendeigh <i>et al.</i> 1977
	<i>Leucosticte arctica</i>	Asian Rosy-finch	24.0	41.7	1.4	3.5		42.2	0.5	43.2	Clemens 1988
	<i>Carpodacus erythrinus</i>	Common Rosefinch	21.2	39.8	1.3	4.5	2.0				Gavrilov 1974; 2014
	<i>Carpodacus mexicanus</i>	House Finch	19.9	40.5	1.1	3.0		45.2	0.3	48.3	Clemens 1988
	<i>Pinicola enucleator</i>	Pine Grosbeak	78.4		3.9						Gavrilov & Dol'nik 1985
	<i>Loxia pytyopsittacus</i>	Parrot Crossbill	53.7		2.9						Kendeigh <i>et al.</i> 1977
	<i>Loxia curvirostra</i> *	Red Crossbill	39.4	40.1	2.2	4.7	3.7	70.0			Groebbels 1932; Gavrilov 1974; 2014; Prinzing <i>et al.</i> 1991*
	<i>Pyrrhula pyrrhula</i>	Eurasian Bullfinch	30.4		2.0			42.0			Groebbels 1932; Kendeigh <i>et al.</i> 1977
	<i>Coccothraustes coccothraustes</i>	Hawfinch	48.3		2.5						Kendeigh <i>et al.</i> 1977
	<i>Coccothraustes vespertinus</i>	Evening Grosbeak	59.0		2.9			95.0	0.9		Berger <i>et al.</i> 1970
	<i>Hemignathus virens</i>	Common Amakihi	21.6		1.5	4.1	1.8				MacMillen 1974
	<i>Hemignathus parvus</i>	Anianiau	9.0		0.7	2.7	0.8				MacMillen 1974
Icteridae		New World blackbirds									
	<i>Amblycercus holosericeus</i>	Yellow-billed Caticque	50.4		2.1						Londoño <i>et al.</i> 2014
	<i>Icterus galbula</i>	Baltimore Oriole	34.0	40.0	1.6		3.1				Rising 1969
	<i>Icterus bullockii</i>	Bullock's Oriole	34.0	39.8	1.6		4.2				Rising 1969
	<i>Agelaius phoeniceus</i>	Red-winged Blackbird	58.4		2.5						Lewies & Dyer 1969
	<i>Sturnella militaris</i>	Red-breasted Blackbird	38.2		1.6						Wiersma <i>et al.</i> 2007
	<i>Quiscalus mexicanus</i>	Great-tailed Grackle	137.3		4.1						Wiersma <i>et al.</i> 2007
	<i>Quiscalus quiscula</i>	Common Grackle	92.2		3.6						Wiersma <i>et al.</i> 2007
Coerebidae		Bananaquit									
	<i>Coereba flaveola</i>	Bananaquit	10.5	40.7	0.9						Merola-Zwartjes 1998; Londoño <i>et al.</i> 2014
Emberizidae		Buntings, American sparrows and allies									
	<i>Emberiza citrinella</i>	Yellowhammer	26.8	39.9	1.6	4.0	3.1				Gavrilov 1974; Gavrilov & Dol'nik 1985; Gavrilov 2014
	<i>Emberiza hortulana</i>	Oortolan Bunting	24.3	39.4	1.4	4.5	2.7				Gavrilov 1974; Gavrilov & Dol'nik 1985; Gavrilov 2014
	<i>Emberiza schoeniclus</i>	Reed Bunting	17.6		1.1						Kendeigh <i>et al.</i> 1977
	<i>Melospiza melodia</i>	Song Sparrow	19.1	40.9	1.0	2.8	3.3	63.0			Odum 1941; Yarbrough 1971; Wiersma <i>et al.</i> 2007; Ro & Williams 2010
	<i>Melospiza georgiana</i>	Swamp Sparrow	14.9	39.7	0.8	2.4					Yarbrough 1971
	<i>Zonotrichia capensis</i>	Rufous-collared Sparrow	21.1	40.2	1.3	6.9	2.4				Sabat <i>et al.</i> 2006; Maldonado <i>et al.</i> 2009; Londoño <i>et al.</i> 2014
	<i>Zonotrichia querula</i>	Harris's Sparrow	33.3	41.3	1.6	4.0					Yarbrough 1971
	<i>Zonotrichia albicollis</i>	White-throated Sparrow	20.2	40.5	1.0	2.9					Yarbrough 1971
	<i>Zonotrichia leucophrys</i>	White-crowned Sparrow	26.1	40.9	1.2	3.1					Yarbrough 1971
	<i>Junco hyemalis</i>	Dark-eyed Junco	19.9	42.9	1.7						King & Farner 1961; Dutenhoffer & Swanson 1996
	<i>Passerculus sandwichensis</i>	Savannah Sparrow	15.9	39.8	0.8	2.4					Yarbrough 1971
	<i>Ammodramus savannarum</i>	Grasshopper Sparrow	13.8	38.6	0.6	2.4					Yarbrough 1971
	<i>Spizella arborea</i>	American Tree Sparrow	17.5		1.5						Dutenhoffer & Swanson 1996
	<i>Spizella passerina</i>	Chipping Sparrow	11.9		0.7	2.1	1.3				Yarbrough 1971; Dawson <i>et al.</i> 1979; Ro & Williams 2010
	<i>Spizella breweri</i>	Brewer's Sparrow	12.2				1.3				Dawson <i>et al.</i> 1979
	<i>Spizella pusilla</i>	Field Sparrow	11.9		0.9						Dutenhoffer & Swanson 1996
	<i>Poocetes gramineus</i>	Vesper Sparrow	21.5	39.5	1.0	2.9					Yarbrough 1971
	<i>Arremon taciturnus</i>	Pectoral Sparrow	27.7		1.5						Londoño <i>et al.</i> 2014
	<i>Arremonops conirostris</i>	Black-striped Sparrow	39.7		1.6						Wiersma <i>et al.</i> 2007
	<i>Arremon torquatus</i>	Stripe-headed Brush-finch	42.8		1.7						Londoño <i>et al.</i> 2014
	<i>Sporophila americana</i>	Wing-banded Seedeater	10.2		0.7						Wiersma <i>et al.</i> 2007
	<i>Sporophila castaneiventris</i>	Chestnut-bellied Seedeater	8.5		0.7						Londoño <i>et al.</i> 2014
	<i>Oryzoborus angolensis</i>	Lesser Seed-finch	12.3		0.7						Wiersma <i>et al.</i> 2007
	<i>Tiaris canorus</i>	Cuban Grassquit	7.3	40.4	0.6	2.7	1.1				Kendeigh <i>et al.</i> 1977; Gavrilov 2014
	<i>Atlappetes melanolaemus</i>	Black-faced Brush-finch	25.5		1.2						Londoño <i>et al.</i> 2014
Thraupidae		Tanagers									
	<i>Chlorornis riefferii</i>	Grass-green Tanager	49.8		1.8						Londoño <i>et al.</i> 2014
	<i>Chlorospingus parvirostris</i>	Yellow-whiskered Bush-tanager	23.1		1.2						Londoño <i>et al.</i> 2014
	<i>Chlorospingus flavigularis</i>	Yellow-throated Bush-tanager	26.5		1.2						Londoño <i>et al.</i> 2014
	<i>Hemispingus atropileus</i>	Black-capped Hemispingus	20.4		1.4						Londoño <i>et al.</i> 2014
	<i>Hemispingus superciliaris</i>	Superciliaried Hemispingus	14.6		1.2						Londoño <i>et al.</i> 2014
	<i>Hemispingus melanotis</i>	Black-eared Hemispingus	17.3		1.2						Londoño <i>et al.</i> 2014
	<i>Hemispingus xanthophthalmus</i>	Drab Hemispingus	13.0		0.7						Londoño <i>et al.</i> 2014
	<i>Thlypopsis ruficeps</i>	Rust-and-yellow Tanager	11.9		0.8						Londoño <i>et al.</i> 2014
	<i>Eucometis penicillata</i>	Grey-headed Tanager	30.7		1.4						Wiersma <i>et al.</i> 2007
	<i>Trichothraupis melanops</i>	Black-goggled Tanager	24.9		1.6						Londoño <i>et al.</i> 2014
	<i>Ramphocelus dimidiatus</i>	Crimson-backed Tanager	26.4		1.3						Wiersma <i>et al.</i> 2007
	<i>Ramphocelus carbo</i>	Silver-beaked Tanager	26.5		1.0						Londoño <i>et al.</i> 2014
	<i>Thraupis episcopus</i>	Blue-grey Tanager	30.4		1.4						Wiersma <i>et al.</i> 2007
	<i>Thraupis cyanocephala</i>	Blue-capped Tanager	38.2		1.7						Londoño <i>et al.</i> 2014
	<i>Thraupis bonariensis</i>	Blue-and-yellow Tanager	34.8		2.0						Londoño <i>et al.</i> 2014
	<i>Buthraupis montana</i>	Hooded Mountain-tanager	89.7		3.7						Londoño <i>et al.</i> 2014
	<i>Anisognathus igniventris</i>	Scarlet-bellied Mountain-tanager	35.0		1.6						Londoño <i>et al.</i> 2014

ORDER		Mass	T _b	BMR	C	EWL	f _R	V _T	Eo ₂	References
Family	Description	g	°C	kJ h ⁻¹	mL O ₂ h ⁻¹ °C ⁻¹	mL H ₂ O	breaths min ⁻¹	mL	%	
Scientific name	Common name									
<i>Iridosornis analis</i>	Yellow-throated Tanager	27.1			1.7					Londoño <i>et al.</i> 2014
<i>Iridosornis jelskii</i>	Golden-collared Tanager	20.6			1.4					Londoño <i>et al.</i> 2014
<i>Pipraeidea melanonota</i>	Fawn-breasted Tanager	20.3			1.4					Londoño <i>et al.</i> 2014
<i>Euphonia xanthogaster</i>	Orange-bellied Euphonia	12.9			0.8					Londoño <i>et al.</i> 2014
<i>Chlorochrysa calliparaca</i>	Orange-eared Tanager	16.9			0.9					Londoño <i>et al.</i> 2014
<i>Tangara arthus</i>	Golden Tanager	22.4			1.3					Londoño <i>et al.</i> 2014
<i>Tangara vasorii</i>	Blue-and-black Tanager	18.5			0.8					Londoño <i>et al.</i> 2014
<i>Catamblyrhynchus diadema</i>	Plushcap	17.0			0.9					Londoño <i>et al.</i> 2014
<i>Diglossa mystacalis</i>	Moustached Flowerpiercer	15.4			1.0					Londoño <i>et al.</i> 2014
<i>Diglossa brunneiventris</i>	Black-throated Flowerpiercer	10.6			0.9					Londoño <i>et al.</i> 2014
<i>Diglossa cyanea</i>	Masked Flowerpiercer	19.1			1.2					Londoño <i>et al.</i> 2014
Cardinalidae	Grosbeaks, saltators and allies									
<i>Piranga olivacea</i>	Scarlet Tanager	27.3				3.6				Ro & Williams 2010
<i>Phreugicus ludovicianus</i>	Rose-breasted Grosbeak	38.8		1.9						Dutenhoffer & Swanson 1996
<i>Cardinalis cardinalis</i>	Northern Cardinal	41.3	38.9	1.8		4.5	45.0			Odum 1941; Hinds & Calder 1973; Ro & Williams 2010
<i>Cardinalis sinuatus</i>	Pyrrhuloxia	32.0	40.3	1.4		3.4				Hinds & Calder 1973
<i>Saltator maximus</i>	Buff-throated Saltator	44.8		2.0						Wiersma <i>et al.</i> 2007
<i>Saltator coerulescens</i>	Greyish Saltator	47.0	39.4	1.4	5.5					Bosque <i>et al.</i> 1999
<i>Saltator aeneocensis</i>	Orinoco Saltator	32.7	38.8	1.1	4.7					Bosque <i>et al.</i> 1999
<i>Cyanocampa cyanooides</i>	Blue-black Grosbeak	26.5		1.4						Wiersma <i>et al.</i> 2007; Londoño <i>et al.</i> 2014

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Publications arising from this research

Peer-reviewed papers arising from this research

Douglas, T.K., Cooper, C.E., and Withers, P.C. (2017) *Avian torpor or alternative thermoregulatory strategies for overwintering?* Journal of Experimental Biology **220**, 1341-1349.

Conference presentations arising from this research

Douglas, T.K., Cooper, C.E., and Withers, P.C. (2017) *It's not black and white: How dichromatic plumage affects heat load for the Western Magpie* *Gymnorhina tibicen dorsalis*. Australasian Ornithological Congress, Geelong, Australia.

Hamilton, N., Burbidge, A.H., Comer, S. and Douglas, T.K. (2017) *Safe radio-tracking harnesses for a variety of birds using elastic rubber bands*. Australasian Ornithological Congress, Geelong, Australia.

Douglas, T.K., Cooper, C.E., Withers, P.C. and Davies, S.J.J.F (2015) *The biophysical properties of plumage for the Western Magpie* *Gymnorhina tibicen dorsalis*. Australian and New Zealand Society for Comparative Physiology and Biochemistry, Fowler's Gap, Australia.

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