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1 **Energetics of communal roosting in Chestnut-crowned Babblers:**
2 **Implications for group dynamics and breeding phenology**

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21 Running title: Energetics of communal roosting in babblers

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24 **Key-words:** cooperative breeding; energy expenditure; group size; metabolic rate; oxygen
25 consumption; thermoregulatory costs

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28 **Summary statement:** Cooperatively breeding chestnut-crowned babblers save considerable
29 energy by group roosting within enclosed nests; this economy helps explain the species' social
30 dynamics and breeding phenology.

33

SUMMARY

34 For many endotherms, communal roosting saves energy in cold conditions, but how this might
35 affect social dynamics or breeding phenology is not well understood. Using chestnut-crowned
36 babblers (*Pomatostomus ruficeps*), we studied effects of nest use and group size on roosting
37 energy costs. These 50 g cooperatively breeding passerine birds of outback Australia breed
38 from late winter to early summer and roost in huddles of up to 20 in single-chambered nests.
39 We measured babbler metabolism at three ecologically relevant temperatures: 5 °C (similar to
40 minimum nighttime temperatures during early breeding), 15 °C (similar to nighttime
41 temperatures during late-breeding) and 28 °C (thermal neutrality). Nest use alone had modest
42 effects: even for solitary babblers at 5 °C, it reduced nighttime energy expenditures by <15%.
43 However, group-size effects were substantial, with saving of up to 60% in large groups at low
44 temperatures. Babblers roosting in groups of 7 or more at 5 °C, and 5 or more at 15 °C, did not
45 need to elevate metabolic rates above basal levels. Furthermore, even at 28 °C (thermoneutral
46 for solitary babblers), individuals in groups of 4 or more had 15% lower BMR than single birds,
47 hinting that roosting in small groups is stressful. We suggest that the substantial energy savings
48 of communal roosting at low temperatures help explain why early breeding is initiated in large
49 groups and why breeding females, which roost alone and consequently expend 120% more
50 energy overnight than other group members, suffer relatively higher mortality than communally
51 roosting group mates.

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INTRODUCTION

55 Group living is widespread in the animal kingdom and has consequences for phenotypic traits,
56 mating systems and population dynamics (Courchamp et al. 1999; Cockburn 2004; Sussman
57 and Chapman 2004; Dunbar 2009; Aplin et al. 2015). The ‘choice’ of joining a group versus
58 living alone should reflect an integrated balance of costs and benefits: individuals are expected
59 to join groups whenever their net fitness is enhanced by doing so (Krause and Ruxton 2002).
60 This fitness balance is affected by individual attributes (e.g. relatedness to other group
61 members, sex, age, condition; Russell and Hatchwell 2001; Clutton-Brock et al. 2002; Silk et al.
62 2014) and by a range of ecological factors including resource availability and competition
63 (Koenig et al. 1992; Russell 2004), predation intensity (Elgar 1989; Beauchamp 2008), disease

64 risk (Nunn et al. 2015) and climate (Jetz and Rubenstein 2010; Cockburn and Russell 2011).
65 However, testing the effects of ecological factors on levels of sociality is often challenging
66 because many are both difficult to quantify and common to the population under study.
67 Studying social species living in temporally heterogeneous environments offer a way around the
68 latter problem: an ecological 'driver' of group size that varies over time should produce
69 predictable concomitant fluctuations of group size (Aureli et al. 2008).

70 One salient ecological parameter that often varies temporally is environmental
71 temperature. Temperature affects nearly all biological systems, both directly (e.g., Q10 effects
72 on physiological rate processes) or indirectly (e.g., habitat productivity; resource availability).
73 In endotherms, particularly small species in cool climates, a primary impact is on energy
74 budgets: the regulatory cost of maintaining core body temperature increases as ambient
75 temperature declines below the zone of thermoneutrality. Compensatory physiological
76 responses (adjusted insulation and peripheral blood flow; torpor or hibernation) are well known,
77 but in social species group behaviour may also be an important component of thermal biology.
78 Huddling or communal roosting occurs in a variety of birds and mammals and has been shown
79 to conserve energy by reducing each individual's resting metabolic rate (extensively reviewed
80 in Du Plessis 2004, Gilbert et al. 2010). For some species from extreme climates (e.g., emperor
81 penguins, *Aptenodytes forsteri*; Le Maho et al. 1976, Pinshow et al. 1976; Ancel et al. 1997),
82 survival or reproduction would be difficult or impossible without the energy savings provided
83 by clustering. Even in less challenging habitats, regulatory heat production can comprise a
84 large fraction of avian daily energy expenditures (Weathers and Sullivan 1993), so savings
85 derived from clustering may have considerable fitness value. For example, in small (<100 g)
86 temperate or subtropical bird species, the overnight energy savings from communal roosting can
87 be as much as 50%, depending on ambient conditions and group size (Du Plessis et al. 1994;
88 Boix-Hinzen and Lovegrove 1998; McKechnie and Lovegrove 2001; Du Plessis and Williams
89 1994). The use of an insulated nest or cavity with protection from wind may further enhance
90 savings (Buttemer et al. 1987; Du Plessis and Williams 1994; Du Plessis et al. 1994).

91 Despite the demonstrated potential for clustering behaviour to ameliorate the energy
92 demands of low environmental temperatures, relatively little work has explored the potential
93 association between temperature, energetics, and group dynamics. Temperature varies
94 seasonally in many ecosystems, so if the benefits of communal roosting are ecologically
95 relevant and driven by thermal biology, we might expect group size to vary in synchrony with
96 ambient temperature cycles. One approach is to quantify energy expenditure during roosting
97 over a variety of group sizes at ecologically relevant temperatures (Du Plessis 2004) and

98 evaluate the findings in the context of thermal seasonality in natural habitats. Doing so may
99 provide important insights not only into fission-fusion dynamics and group size, but also
100 breeding phenology (Visser et al. 2015).

101 In this study, we quantified the effects of temperature, nest use, and group size on the
102 nighttime energetics of a highly social 50 g passerine bird, the cooperatively breeding chestnut-
103 crowned babbler (*Pomatostomus ruficeps*, Hartlaub 1852). Chestnut-crowned babblers are
104 residents of semi-arid and arid regions of inland southeastern Australia, living in groups of up to
105 20 or more individuals. There is considerable genetic relatedness among many group members
106 and cooperative behaviour, at least during breeding, seems to be based largely on kin selection:
107 helping at the nest is strongly directed towards close relatives (Browning et al. 2012a). Several
108 aspects of babbler behaviour, ecology, and natural history make them an interesting system for
109 exploring the possible social repercussions of communal roosting at seasonally variable
110 temperatures. First, groups construct numerous enclosed stick nests (Fig. 1) in tall shrubs and
111 trees within their home range; these are used for both roosting and breeding. Nearly all
112 individuals roost communally throughout the year, with up to 22 birds sharing a nest. The key
113 exception is the single breeding female at each nest, who roosts alone with her eggs and chicks
114 from the onset of incubation. Second, there is strong selection favouring early-season
115 reproduction because it allows time for multiple breeding events within an annual temperature
116 cycle that precludes breeding for much of the year (Russell et al. 2010). Nesting usually begins
117 in winter (July) and continues until early summer (October-November) when minimum
118 nighttime temperatures average ≈ 5 and 15 °C, respectively (Fig. 2; Russell 2016). Thus,
119 breeding babblers routinely experience nighttime temperatures well below the expected lower
120 critical temperature of 50 g birds (~ 25 °C; Aschoff 1981; Schleucher and Withers 2001;
121 McKechnie and Wolf 2004). Although nights are warmer later in the summer, breeding at that
122 time is likely precluded by the risk of daytime temperatures and solar heat loads that can raise
123 nest temperatures to levels presumably fatal for eggs or nestlings (above 50 °C; unpublished
124 data). Third, although babblers are obligatorily social, their group sizes vary seasonally, with
125 up to 4 (mode = 1-2) smaller breeding units splitting from the larger social group to initiate
126 separate nests as the season progresses (Russell 2016). The selective forces driving this
127 fragmentation (or perhaps more interestingly, why smaller breeding groups do not form at the
128 start of the reproductive season) are not fully understood.

129 The present study had three major aims. First, we evaluated the energetic benefits of
130 roosting inside versus outside of a nest for lone birds. The rationale was to estimate the benefits
131 of nest use, and, for breeding females, the energy budget repercussions resulting from solitary

132 roosting. Second, we measured metabolic rates of babblers roosting in groups of up to 9 birds
133 to assess the thermal benefits of communal roosting and how these are affected by group size.
134 In both conditions (with or without nests), we subjected roosting birds to three ecologically
135 relevant temperatures, with 5 °C typical for early reproduction, 15 °C typical for late
136 reproduction, and 28 °C representing thermoneutral conditions. Finally, we discuss our findings
137 in light of studies of other communally roosting birds and then assess the relevance of roosting
138 costs for babbler social dynamics.

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141 **MATERIALS AND METHODS**

142 **Field site and climate**

143 The study was conducted at the University of New South Wales Arid Zone Research Station,
144 Fowlers Gap, located in arid scrubland 110 km north of Broken Hill, New South Wales,
145 Australia (141° 39' E, 31° 09' S). The local population of chestnut-crowned babblers has been
146 intensively studied for over a decade (Russell 2016) and previous work has described their
147 habitat, foraging ecology (Portelli et al. 2009, Sorato et al. 2012), and cooperative breeding
148 system (Browning et al. 2012a, 2012b; Nomano et al. 2014). Seasonality at Fowlers Gap is
149 substantial, with average nighttime temperatures ranging from around 5 °C in July to above 20
150 °C in January, with midsummer daytime maxima well above 40 °C (Australian Bureau of
151 Meteorology; Fig. 2).

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154 **Capture and housing**

154 Over two weeks in September 2009, we mist-netted 67 babblers from 15 social groups. Two to
155 nine individuals were removed from groups that averaged 11 birds (range = 6-18). To minimize
156 ecological and behavioural impacts, we restricted captures to groups that were non-breeding at
157 the time, and always left at least 4 resident babblers (mean = 7) within each group's home range.
158 Captured babblers were transported by vehicle in bird bags to onsite aviaries (2 x 2.5 x 2 m) a
159 few kilometres away and housed with members of the same group (up to 3 birds per
160 compartment, with vocal contact between adjacent compartments). Captives experienced
161 ambient photoperiods and temperatures and were provided with natural perches and foraging
162 substrate, as well as water and 20 mealworms per bird every 2 h (for further details see Engesser
163 et al. 2015). Food was withheld after 16:30 h local time. Babblers were never held captive for
164 more than 48 h. All birds used in the study appeared healthy following measurements and were
165 released into their home range, where they were immediately accepted into their social group

166 without exception (e.g. Nomano et al. 2015).

167 For tests in which several birds were measured simultaneously in one metabolic
168 chamber (see below), all individuals came from the same social group and therefore were
169 familiar with each other.

170 The work was conducted under the approval of UNSW Animal Care and Ethics
171 Committee (license no. 06/40A) and the authority of NSW National Parks and Wildlife Service
172 and the Australian Bird and Bat Banding Scheme. Respirometry methods were also approved
173 by the University of California, Riverside Institutional Animal Care and Use Committee.

174

175 **Respirometry**

176 We used open-system respirometry to measure metabolic rates as oxygen consumption ($\dot{V}O_2$;
177 ml O_2 /min). Air was supplied at positive pressure by a pump and dried with silica gel. Flow
178 rates to the metabolic chambers (up to 4, depending on the experiment; see below) were
179 regulated $\pm 1\%$ by upstream mass flow controllers (MFCs, 1 per chamber, capacity 0-3 or 0-20
180 litres min^{-1} ; Tylan; Torrance, California). The MFCs were calibrated with a bubble meter
181 (Giliblator 2; Sensidyne, Clearwater, Florida). Flow rates varied according to group size and
182 chamber volume, from 800 ml min^{-1} for single birds in small chambers to 1800 ml min^{-1} for
183 single birds in nests to 5500 ml min^{-1} for the largest group sizes (7-9 birds). Air exiting
184 chambers was sub-sampled at 80 to 100 ml min^{-1} , dried (Drierite), scrubbed of CO_2 (soda lime),
185 redried, and pulled through a two-channel oxygen analyser (Sable Systems Oxzilla II; Sable
186 Systems, Las Vegas, Nevada). A computer-driven multiplexer (Sable Systems RM8) obtained
187 2.5 min reference readings every 30 min. The system could measure 1 or 2 chambers
188 continually (exclusive of references) or 3 or 4 chambers in alternating 30-min cycles. Duty
189 factors (the percentage of time each chamber was monitored) were about 92% for 1 or 2
190 chambers (55 min per hour) and 46% for 3 or 4 chambers (27.5 min per hour). Chambers were
191 placed in an environmental cabinet that controlled ambient temperature (T_a) ± 1 °C.

192 Temperatures in each chamber were monitored with a thermocouple attached to a Sable
193 Systems TC-2000. Temperature typically varied by 1-1.5 °C among chambers, but this
194 difference had no detectable effect on metabolic rates ($P = 0.87$) and was not included in final
195 analyses.

196 Oxygen concentrations, flow rates and T_a were recorded every 2 sec by a Macintosh
197 laptop computer interfaced to an A-D converter (Sable Systems UI-2) with Warthog LabHelper
198 software (www.warthog.ucr.edu). Oxygen consumption was computed using the Mode 1

199 equation in Warthog LabAnalyst:

$$200 \quad \dot{V}O_2 \text{ (ml min}^{-1}\text{)} = \dot{V} \cdot (\text{FiO}_2 - \text{FeO}_2) / (1 - \text{FeO}_2)$$

201 where \dot{V} = flow rate of dry air in ml min⁻¹ (corrected to standard temperature and pressure) and
202 FiO₂ and FeO₂ are the fractional incurrent and excurrent O₂ concentrations, respectively.

203

204

Metabolic trials

205 Birds temporarily held in aviaries were captured an hour after dark (\approx 19:00 h) using red light,
206 and taken to the lab in cloth bird bags. Each bird was weighed \pm 0.5 g with a spring scale (100
207 g capacity; Pesola, Switzerland). The metabolic chambers were metal paint cans painted flat
208 black on the inside and equipped with input and output ports for air flow. For trials without
209 nests ($n = 8$), we placed single birds into one of four 2-litre cans fitted with a wooden perch. In
210 all other trials ($n = 21$), babblers were inserted into a nest collected from natural habitat and
211 fitted inside 22-litre paint cans (35 cm tall, 29 cm diameter). We selected three nests known to
212 be in current use; these were mounted in separate cans in their naturally vertical orientation and
213 retained their structure and dimensions (Fig. 1), although a few peripheral twigs required
214 trimming. Measurements with nests included 6 single birds, 3 pairs, 2 trios, 3 quartets, 3
215 quintets, 2 sextets, 1 septet and a group of 9. All babblers were used once, except for 14
216 individuals used in single-bird trials that were also used in a communal trial the next day. Birds
217 were inserted into cans or nests in a quiet room in dim red light. For trials with nests, birds
218 were slid into the nest chamber sequentially through a PVC pipe extending to the nest opening
219 and then secured inside by blocking the nest opening with a small cloth bag.

220 Trials began around 20:00 h and continued until the following morning. We subjected
221 babblers to low T_a initially (mean = 4.7 ± 0.89 °C; hereafter 5°C) for \approx 4 h. Subsequently T_a
222 was raised to 14.9 °C (hereafter 15 °C) and held there for \approx 3 h. For the remainder of the night
223 (\approx 2.5 h), T_a was raised to \sim 28 °C (large groups) or to 28-30 °C (single birds and small groups;
224 mean = 28.7 ± 1.5 °C; hereafter 28 °C). We used the slightly lower temperature for large
225 groups out of concern that overheating might occur within the insulated nest; preliminary tests
226 indicated that for single babblers, the minimal $\dot{V}O_2$ of single babblers held at 28 °C did not
227 differ from that at 32 °C (Bech et al. 2016). The temperature sequence (cold to warm) was
228 chosen in order to expose birds to the most severe cold stress early in the experiment, and also
229 to minimise the potential for digestion-related elevations in metabolic rate, which mainly occur
230 in warm conditions where regulatory thermogenesis is minimal (Baudinette et al. 1986;

231 Chappell et al. 1997; Bech et al. 2004). All data obtained at 28 °C involved birds that had
232 fasted for at least 11 h and were presumably postabsorptive (e.g., Dykstra and Krasov 1992),
233 thus permitting valid measurements of basal metabolic rate (BMR).

234 Following a short period of activity after being placed in the chambers, babblers usually
235 were largely quiescent for the remainder of the night (as judged from vocalizations and $\dot{V}O_2$
236 records). When episodes of activity occurred, they were typically brief and $\dot{V}O_2$ returned to
237 stable and low values fairly quickly. In most tests there was a small, gradual rise in $\dot{V}O_2$
238 beginning about an hour before dawn (\approx 05:30). Babblers lost an average of 2.8 g (SD = \pm 1.0)
239 overnight, equating to 5.7% (SD = \pm 2%) of the mean initial mass of 49.8 g. The effects of
240 specific temperatures on mass loss could not be analysed, since all birds experienced at least
241 two temperatures and most experienced three temperatures during a trial. Also, we did not
242 investigate the effects of nest occupancy (for single birds) or group size on mass loss, since over
243 a single night the majority of mass loss is likely from excreta and evaporative water loss, and
244 we could not quantify the amount of food in the gut at the start of trials. For all T_a , we defined
245 the resting metabolic rate as the lowest stable 10 min of $\dot{V}O_2$ at each temperature (see below).
246 Shortly after dawn, babblers were removed from the chambers, weighed, and either released
247 into their home range or, for single-bird trials, returned to the aviary, fed, and held for use in a
248 group trial the following night.

249

250

Statistics

251 Analyses were performed in Genstat v 17 (VSN International) and JMP Pro 11 (SAS Institute,
252 Cary, North Carolina, USA). Data are shown as mean \pm SD unless otherwise noted; the
253 significance level was 0.05.

254 The effect of T_a and nest use on the $\dot{V}O_2$ of single birds was analysed using a General
255 Analysis of Variance (gANOVA), in which $\dot{V}O_2$ was the response term fitted to a normal error
256 structure and temperature (3-level factor) and the presence/absence of a nest were fitted as
257 interacting categorical terms. Body mass (50.3 ± 2.6 g) was initially included as a covariate, but
258 was non-significant and was dropped from the final model ($F_{1,11} = 0.73$, $P = 0.41$, estimate (\pm
259 SE) = -0.024 ± 0.028). Trial identity was fitted as a blocking function to account for repeated
260 measures from the same individuals across the three test temperatures. The distribution of
261 residuals did not deviate from normality (Shapiro-Wilks test, $P = 0.72$).

262 All communal roosting data were obtained from birds in nests. Since we could not
263 differentiate the metabolic contributions of individual birds, we computed and analysed a mean

264 value (total $\dot{V}O_2/N$). As for single birds, average body mass (49.2 ± 2.6 g), initially included as
265 a covariate, did not have a significant effect and was dropped from the final model ($F_{1,18} = 1.11$,
266 $P = 0.30$, estimate (\pm SE) = 0.02 ± 0.02). The effects of temperature (3-level factor) and group
267 size on $\dot{V}O_2$ were analysed using a Residual Linear Mixed effect Model (REML); $\dot{V}O_2$ was
268 natural log-transformed to ensure normal distribution of residuals (Shapiro-Wilks test, $P =$
269 0.27). Temperature and group size were fitted as interacting explanatory terms, while trial
270 identity was fitted as a random term. Models with group size fitted as an interacting linear,
271 quadratic, or natural logarithmic function revealed a superior fit of the latter (AIC = -113, -102,
272 and -134, respectively). Accordingly, analysis was conducted on log group size, indicating that
273 the energy saving with increasing group size follows a diminishing, rather than linear, function.

274 **RESULTS**

275 **Single birds**

276
277 As expected, the primary determinant of $\dot{V}O_2$ for single birds was ambient temperature
278 (gANOVA; $F_{2,24} = 337.8$, $P < 0.001$; Fig. 3), which explained 85% of the variance. Energy
279 costs followed the typical pattern of temperature effects on endotherms (Scholander et al. 1950):
280 metabolic rates at 5 °C were 112% higher than at 28 °C and 34% higher than at 15 °C; rates at
281 15 °C were 59% higher than at 28 °C. There was a small but significant effect of occupying a
282 nest ($F_{2,12} = 6.32$, $P = 0.027$), which explained 4% of the variation in $\dot{V}O_2$ and resulted in a 13%
283 reduction in energy expenditure overall. As expected, the benefit of nest use was temperature
284 dependent, although the interaction between nest use and T_a explained only 1% of the variation
285 in $\dot{V}O_2$ ($F_{2,24} = 3.76$, $P = 0.038$). At 5 °C, babblers reduced their metabolic rate by 15% by
286 roosting in a nest ($T_{12} = 2.89$, $P = 0.014$), while at 15 °C and 28 °C the savings from nest use
287 (11% and 8%, respectively) were not significantly different from values when roosting without
288 a nest (15 °C: $T_{12} = 1.82$, $P = 0.12$; 28 °C: $T_{12} = 1.16$, $P = 0.27$). Finally, there was significant
289 among-individual variation in metabolic rates, with individual identity explaining 7% of the
290 variation (component = 0.035 ± 0.018 SE).

291 **Communal roosting**

292
293 The $\dot{V}O_2$ of babbler groups roosting in nests was largely determined by T_a and group size, and
294 the interaction between the two (Fig. 4). Unsurprisingly, roosting babblers expended less
295 energy in warm than in cold temperatures (temperature main effect: $F_{2,38} = 76.3$, $P < 0.001$,
296 42% variance) and benefited from increasing group size (log group size main effect: $F_{1,18} =$

297 57.4, $P < 0.001$, 22% variance). Also, a significant interaction between T_a and log group size
298 on $\dot{V}O_2$ ($F_{2,36} = 20.6$, $P < 0.001$, 13% variance) indicated that babblers gained disproportionate
299 energy savings from communal roosting at the lowest T_a . Compared to roosting alone in a nest
300 at 5°C, communally roosting birds reduced nighttime energy expenditures by $\approx 20\%$ in pairs
301 and trios and 60% in groups of 7 or more (estimate = -0.40 ± 0.05 SE). At 15°C, savings were
302 only slightly less dramatic, with savings of $\approx 20\%$ in pairs or trios and up to 50% in groups of 5
303 or more (estimate = -0.36 ± 0.05 SE). The effect of group size on energy expenditure was much
304 lower at 28 °C, (estimate = -0.10 ± 0.05 SE). Nevertheless, there was a slight but significant
305 reduction in $\dot{V}O_2$ in groups of 4 or more. That was unexpected, because there was no difference
306 between the minimal $\dot{V}O_2$ of solitary birds tested at 28 °C versus 32 °C, suggesting that both
307 temperatures are thermoneutral (see Discussion). Finally, as was the case for single birds, we
308 found a significant effect of the random term on explanatory power, indicating inter-group
309 variation in metabolic rates that were neither explained by T_a or group size (component = 0.015
310 ± 0.0065 SE; 12% of variance).

311

312

DISCUSSION

313 In general, our findings for chestnut-crowned babblers are similar in many respects to previous
314 reports of energy savings from communal roosting in birds: both roosting in groups and, to a
315 lesser extent, use of an enclosed nest, help reduce nighttime energy costs in cold conditions.
316 However, babblers achieved considerably greater energy savings than two other cavity nesting
317 species tested at roughly similar temperatures and group sizes: acorn woodpeckers (*Melanerpes*
318 *formicivorus*; Du Plessis et al. 1994) and green woodhoopoes (*Phoeniculus purpureus*; Du
319 Plessis and Williams 1994; Boix-Hinzen and Lovegrove 1998). In large groups (7 or more
320 birds), roosting babblers expended 50-60% less energy than solitary birds at 5 °C; the
321 corresponding savings for green woodhoopoes was about 30%, and for acorn woodpeckers
322 about 17%. The difference may be partially due to their smaller body size (~ 50 g versus ~ 80 g)
323 and/or the slightly larger group sizes we tested in babblers (up to 9 individuals, versus 4-6),
324 although we did not detect additional benefits from group sizes above 6 birds. The modest
325 energy savings observed in acorn woodpeckers is probably due to the fact that they roosted
326 separately inside cavities (i.e., not touching each other) and hence did not benefit from the
327 reductions in total surface area and heat loss made possible by close-contact huddling. Another
328 highly social species, the ≈ 50 g white-backed mousebird (*Colius colius*), attained group-
329 roosting benefits similar to those of chestnut-crowned babblers: an energy savings of $\approx 50\%$ in

330 groups of six compared to solitary birds at a T_a of 15 °C. However, roosting mousebirds do not
331 use a nest, instead huddling together on a branch, and much of their energy savings is due to
332 unusually large reductions of nighttime body temperature (in fact, group roosting may be
333 necessary to maintain stable nocturnal body temperature in this species; McKechnie and
334 Lovegrove 2001).

335 Unsurprisingly, in all of these birds the energetic benefits of communal roosting were
336 strongly temperature-dependent, being maximal at low T_a and declining in conditions closer to
337 thermal neutrality. Interestingly, at warm T_a (30 °C), woodhoopoes roosting communally had
338 higher metabolic rates than those roosting alone, perhaps because the higher overall insulation
339 or nest temperatures achieved during group roosting prevented adaptive torpor (Boix-Hinzen
340 and Lovegrove 1998). No such increase occurred in chestnut crowned babblers (Fig. 4): their
341 metabolic rates at 28-30 °C were similar (1-3 birds) or slightly lower (4 or more birds) than
342 those of solitary babblers tested at 32 °C (Bech et al. 2016).

343 While clustering is clearly beneficial to the energy economy of chestnut-crowned
344 babblers, especially at low T_a , we found substantial variation in energy expenditures among
345 individuals and groups (Fig. 4). Resting metabolic rates (RMR) of solitary birds in nests varied
346 by \approx 50% at both 5 °C and 15 °C, and even at thermoneutral temperatures RMR varied by \approx
347 25% among individuals. During communal roosting the among-group variation in mean RMR
348 averaged 40%, 28% and 18% at 5, 15 and 28 °C, respectively, after accounting for group-size
349 differences. These effects are not explained by body mass, which was never a significant
350 predictor of $\dot{V}O_2$ in any analysis. Some RMR variation may have stemmed from differences in
351 plumage insulation, posture, position within nest cavities, or, for groups, the degree to which
352 individuals huddled within the nest. Additionally, individual variation in metabolic rate was
353 probably partially responsible, especially at thermoneutral T_a . Differences in metabolic
354 intensity among individuals are of increasing interest to physiologists and evolutionary
355 biologists and may derive from a variety of factors, including feedbacks with energy or activity
356 budgets, developmental conditions, acclimatory history, and genetic differences among
357 individuals (Careau and Garland 2012; Metcalfe et al. 2016). One possible physiological
358 mechanism is individual differences in levels of activation of the hypothalamic-pituitary-adrenal
359 axis in response to environmental or experimental conditions (Hennessy et al. 2009).

360 This ‘stress hypothesis’ might help explain our surprising finding of group size effects
361 on metabolic rates of chestnut-crowned babblers roosting at T_a that fit the standard definition of
362 thermoneutrality. Our ‘basal’ $\dot{V}O_2$ for single birds at 28-30 °C (1.26 ml O₂ min⁻¹) does not
363 differ from the $\dot{V}O_2$ of solitary chestnut-crowned babblers tested at 32 °C (1.31 ml O₂ min⁻¹;

364 Bech et al. 2016), indicating that 28-32 °C is within the species' thermal neutral zone.
365 However, babblers roosting in groups of 4 or more had significantly lower $\dot{V}O_2$ at ~28 °C (1.05
366 ml O₂ min⁻¹; Figs. 4a, 4b). This was probably not due to facultative hypothermia, which would
367 be unexpected at warm T_a and, moreover, was not recorded during group roosting in captive or
368 free-living congeneric white-browed babblers (*P. superciliosus*; T.K. Douglas, pers. comm.).
369 Perhaps the most likely explanation is that chestnut-crowned babblers roosting alone or in small
370 groups are socially stressed and have increased sympathetic output as a consequence (Taylor et
371 al. 2014). Isolated individuals of several social species are known to exhibit symptoms of stress
372 (Young et al. 2006; Hennessy et al. 2009) and this can affect energy metabolism. For example,
373 roosting RMR of solitary pallid bats (*Antrozous pallidus*) were greater than in communal
374 huddles at all temperatures tested, including thermoneutral conditions (Trune and Slobodchikoff
375 1976). In white mice (*Mus musculus*) and Mongolian gerbils (*Meriones unguiculatus*),
376 metabolic rate increased more slowly in response to decreasing T_a below thermoneutrality in
377 trios than in solitary individuals, even if communal huddling (contact) was prevented (Martin et
378 al. 1980). These studies indicate that improved thermoregulation is not the only factor that
379 generates energy savings during communal roosting. For chestnut-crowned babblers we
380 estimate that across all tested T_a , most (~ 85%), but not all, of the energy saving from
381 communal roosting is achieved through reduced requirements for heat production (assuming no
382 interaction between T_a and 'stress' levels of lone individuals); the remainder may result at least
383 in part from reduced 'stress'. In terms of thermoregulatory physiology, the salient point is that
384 solitary babblers (or groups of less than 4 birds) apparently cannot attain 'true' basal metabolic
385 rates, even at thermoneutral T_a . While defining BMR in this context is something of a semantic
386 argument, if BMR is stipulated to be the minimum possible normothermic metabolic rate, then
387 in chestnut-crowned babblers it is only realized when roosting with several conspecifics.
388 Accordingly, we used the mean thermoneutral large-group BMR value (1.05 ml O₂ min⁻¹) as the
389 index for minimal achievable metabolic rate when comparing energy savings across
390 temperatures and group sizes (Fig. 4b).

391 These caveats notwithstanding, the energy savings chestnut-crowned babblers achieve
392 by roosting communally are impressive. At 5 °C birds in groups of seven or more, and at 15 °C
393 groups of five or more, do not need to increase $\dot{V}O_2$ above basal rates (Fig. 4). These findings
394 are particularly noteworthy in comparison to most solitary-roosting small birds from cool
395 climates, which probably rarely encounter thermoneutral conditions, and so rarely attain BMR.
396 Hence, direct selection on BMR in such species seems unlikely. In contrast, chestnut-crowned
397 babblers appear to routinely attain BMR during communal roosting, making BMR a viable
398 'target' for selection because a change in BMR – such as the ≈ 15-20% decrease in

399 thermoneutral metabolic rates we observed in large roosting groups – can engender energy costs
400 or savings that are potentially ecologically relevant. At 5 °C over a typical 14-h winter night,
401 groups of seven or more babblers roosting communally expend about 20.9 kJ per bird, a savings
402 of 24.7 kJ compared to costs for single birds roosting in nests (\approx 45.6 kJ, 2.2 times higher). The
403 potential importance of such savings is probably best evaluated in the context of daily energy
404 expenditures (DEE), which includes expenditures for activity and maintenance as well as
405 thermoregulation and BMR, and specifies how much energy birds must obtain by foraging. A
406 doubly labelled water study of chestnut-crowned babblers encompassing a range of group sizes
407 during breeding shows an average DEE of 76 ± 12 kJ (N=20; A.F. Russell et al. unpublished
408 data), relatively low for a 50 g bird (Nagy 1995). Thus a roosting energy savings of 24.7 kJ is
409 34% of DEE, which should decrease foraging requirements by a roughly proportionate amount.

410
411 This economy might help account for two puzzling aspects of chestnut-crowned babbler
412 socio-ecology. In previous studies we have struggled to understand the causality and
413 interactions between fission-fusion dynamics and breeding phenology. During non-breeding
414 periods and up to the onset of the reproductive season, babblers at our study site live in large
415 groups averaging 11 nutritionally independent individuals (3-23; Russell 2016) that roost
416 together. Breeding is initiated when ambient temperatures are near their annual minimum (July-
417 August; Fig. 1) and usually involves a single mating pair plus nest helpers; with all group
418 members (except for the breeding female, see below) continuing to roost communally
419 regardless of whether they are male breeders, helpers or non-participants in the breeding event.
420 Several weeks later, on average, smaller groups of 2-6 birds (mean = 3.5) cleave from the initial
421 social group and initiate separate nests; at this time nighttime T_a average approximately 10 °C,
422 rising to about 15 °C as the nesting cycle progresses (Fig. 2). The cause of the transition from
423 singular to plural breeding has been difficult to explain: if other factors were equal, the
424 initiation of multiple nesting from the start of the breeding season should maximize both the
425 breeders' reproductive success and the inclusive fitness of related group members. The
426 transition is not attributable to seasonal increases in food availability or the presence of avian
427 predators (the dominant predators on adult babblers at this site), neither of which vary across the
428 breeding season (Sorato et al. 2012; Sorato et al. 2016). Instead, our metabolic data suggest that
429 the energy costs of roosting in cold winter conditions at least partially explain fission dynamics
430 and breeding phenology. Specifically, at the T_a of 5-10 °C prevailing during early breeding, a
431 roosting group of 10-11 babblers would easily achieve BMR, but comparable costs would be
432 70-90% above BMR for secondary breeding units of 3-4 birds (Fig. 4). During later breeding

433 events when nighttime T_a are close to 15 °C, roosting costs for secondary units of 3-4 would be
434 considerably lower (roughly 30% above BMR; Figs. 2, 4). In other words, early-season
435 breeding by small secondary units may be compromised by high energy costs of
436 thermoregulation and the concomitant reduction in the fraction of foraging effort that can be
437 devoted to the provisioning of offspring (or the breeding female; see below).

438 The second puzzle is that while the annual survival rate of male breeders and helpers
439 combined is $\approx 55\%$, breeding females have a significantly lower annual survival rate of $\approx 45\%$
440 (Sorato et al. 2016), despite the males averaging twice the nestling provisioning contribution of
441 breeding females (Browning et al. 2012b). Our roosting cost data provide a potential
442 explanation. While most group members roost communally throughout the year, breeding
443 females roost alone while incubating eggs or brooding nestlings, possibly because this reduces
444 the risk of egg breakage or injury to nestlings. However, solitary roosting carries a considerable
445 energy penalty: our data indicate that during early-season nesting when T_a is low (Fig. 4),
446 breeding females must expend at least twice as much energy overnight as birds roosting
447 communally in large groups – and potentially even more than that if there are additive costs
448 from heating eggs or nestlings (e.g., Haftorn and Reinertsen 1985; Weathers 1985). We have
449 no evidence that females either disappear suddenly during breeding (suggesting predation is not
450 the causal factor) or that they disperse once they attain breeding status. There are other costs
451 specific to reproductive females (particularly egg production), and to some extent a female's
452 high thermoregulatory expenditures during early-season reproduction are probably partially
453 offset (especially in large groups) by the numerous helpers that feed her during incubation and
454 brooding and allow her to considerably reduce her contributions to nestling provisioning
455 (Russell et al. 2010; Browning et al. 2012b; Russell 2016). Nevertheless, the high energy costs
456 of solitary roosting may partly explain the higher mortality of females, with follow-on effects
457 including heavily male-biased population sex ratios and levels of philopatry (Rollins et al.
458 2009).

459 Many vertebrate societies undergo cycles of dissociation into subgroups followed by re-
460 aggregation. These events may help resolve conflicts of interest between individuals (Jacobs
461 2010; Magrath et al. 2004), or accommodate differences in food availability, predation risk or
462 disease dynamics (Beauchamp 2008; Conradt and Roper 2005; Elgar 1989; Nunn et al. 2015).
463 Our results for chestnut-crowned babblers indicate that in this obligate cooperative breeder, the
464 energy savings provided by communal roosting may be an important selective force shaping
465 social dynamics and breeding phenology. A similar situation may occur in long-tailed tits
466 (*Aegithlos caudatus*) which, like chestnut-crowned babblers, are cooperative breeders that

467 benefit from communal roosting (they huddle in linear clusters and this reduces rates of
468 overnight mass loss compared to solitary individuals; Hatchwell et al. 2009). Like babblers,
469 they show seasonal fission-fusion social dynamics. Compared to chestnut-crowned babblers,
470 long-tailed tit flocks fragment more synchronously into breeding pairs, but as we have
471 suggested for babblers, the timing of fragmentation and breeding phenology are strongly
472 temperature-dependent (Gullett et al. 2013). More broadly, the concept that energy costs of
473 solitary roosting might act as a significant selection pressure on social dynamics and breeding
474 phenology may be relevant to many social species. For example, climate models predict that
475 the availability of many prey types may shift temporally in response to rising temperatures, but
476 also that short-term weather variability may increase (e.g. Thomas et al. 2001; Visser et al.
477 2015). Even for species that obtain considerable thermal "buffering" from communal roosting,
478 this variability might be a barrier to advancing reproductive phenology to synchronize with
479 changing food availability: if breeding females roost solitarily, there may be increased risk of
480 early-season cold snaps that put her or her brood at risk. Accordingly, we suggest that studies
481 of small social endotherms should consider the potential repercussions of thermal benefits of
482 communal roosting on social dynamics and breeding phenology, as well as on thermoregulatory
483 costs.

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491

492

AUTHOR CONTRIBUTIONS

493 All authors planned the work and all contributed extensively to writing the paper. The field
494 experiments and analyses were conducted by MAC and AFR, with considerable assistance in
495 equipment setup and logistics by WAB.

496

497

COMPETING INTERESTS

498 No competing interests declared.

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504 DATA ACCESSIBILITY

505 All data used in this manuscript are in the text or the Appendix.

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738 **Table 1:** Effects of group size on nighttime resting rates of oxygen consumption ($\dot{V}O_2$, ml
739 O_2/min). The first row is for single birds without nests and temperature had a highly significant
740 effect ($F_{2,29} = 274$, $P < 0.001$). The remaining data are for birds roosting inside nests and F
741 statistics and significance tests (P) for group size effects are shown at the bottom of the table.
742 Values show predicted means \pm SE. For groups (>1 bird), $\dot{V}O_2$ was calculated as the mean $\dot{V}O_2$
743 per bird.

744

Group size	nest	5 °C $\dot{V}O_2$ (N trials)	15 °C $\dot{V}O_2$ (N trials)	28 °C $\dot{V}O_2$ (N trials)
1	no	3.16 \pm .09 (8)	2.28 \pm .09 (8)	1.39 \pm .09 (8)
1	yes	2.66 \pm 0.16 (6)	1.99 \pm 0.12 (6)	1.26 \pm 0.08 (6)
2	yes	1.99 \pm 0.17 (3)	1.56 \pm 0.13 (3)	1.30 \pm 0.11 (3)
3	yes	2.20 \pm 0.23 (2)	1.49 \pm 0.16 (2)	1.23 \pm 0.17 (1)
4	yes	1.64 \pm 0.14 (3)	1.31 \pm 0.11 (3)	1.05 \pm 0.09 (3)
5	yes	1.16 \pm 0.10 (3)	0.91 \pm 0.08 (3)	0.99 \pm 0.08 (3)
6	yes	1.70 \pm 0.18 (2)	1.30 \pm 0.13 (2)	1.09 \pm 0.15 (1)
7	yes	1.06 \pm 0.16 (1)	0.88 \pm 0.13 (1)	1.07 \pm 0.16 (1)
9	yes	1.06 \pm 0.16 (1)	0.94 \pm 0.14 (1)	1.08 \pm 0.16 (1)
F, P		$F_{1,19} = 41.9$ $P < 0.001$	$F_{1,19} = 49.3$ $P < 0.001$	$F_{1,17} = 17.8$ $P < 0.001$
Estimate \pm SE		-0.40 \pm 0.06	-0.36 \pm 0.05	-0.12 \pm 0.027

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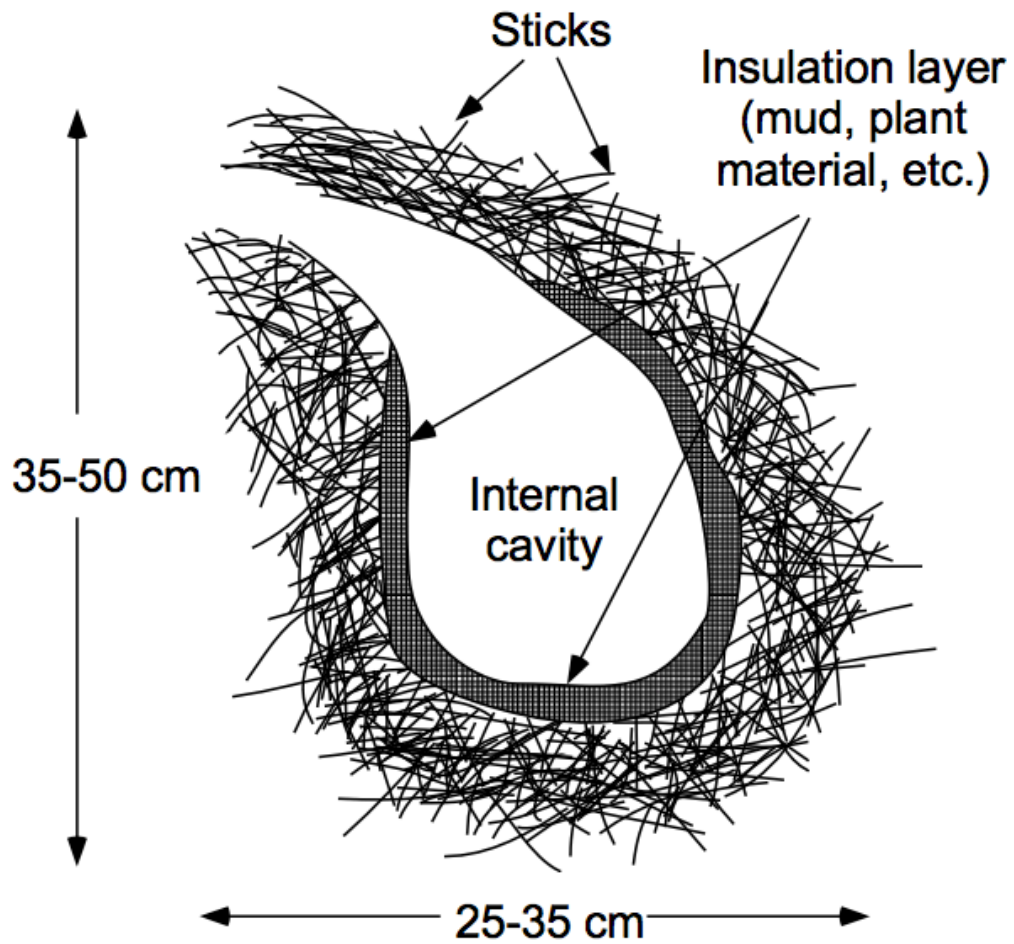
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750 **Figure legends**

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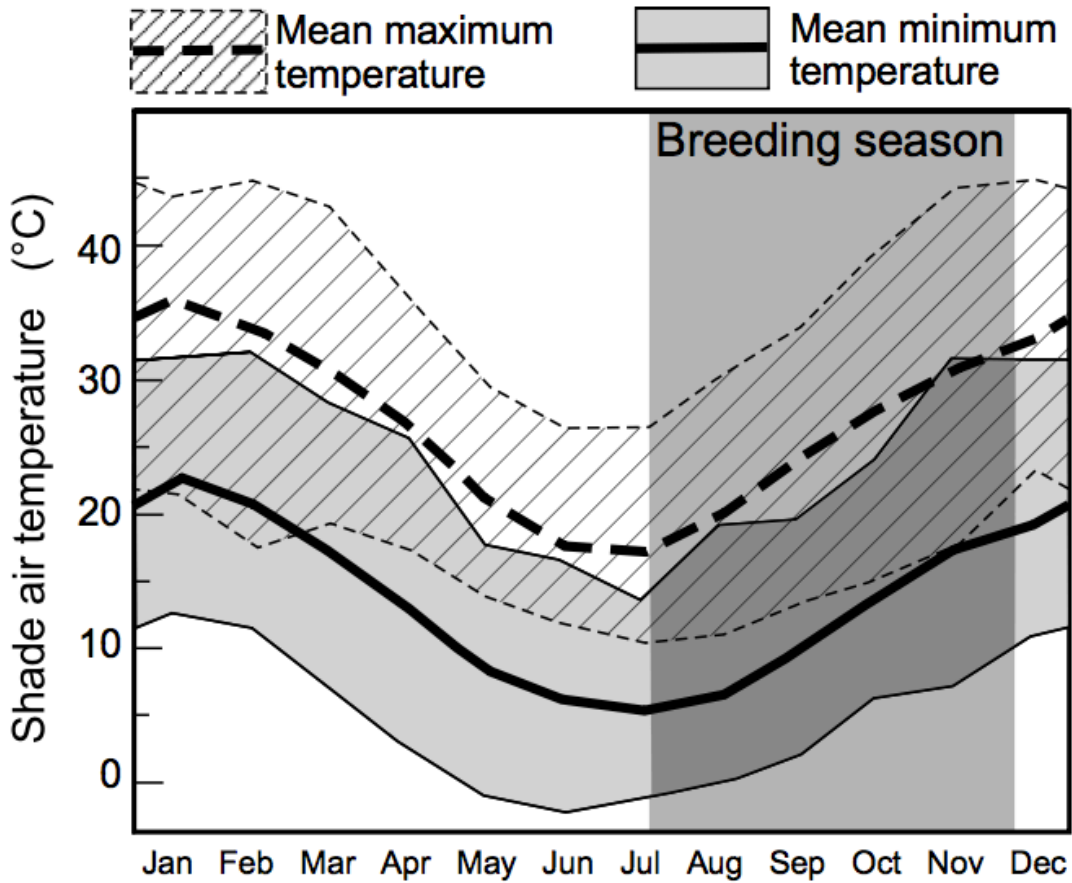
752 **Figure 1:** Diagram of a typical nest of chestnut-crowned babblers used for breeding and
753 communal roosting.



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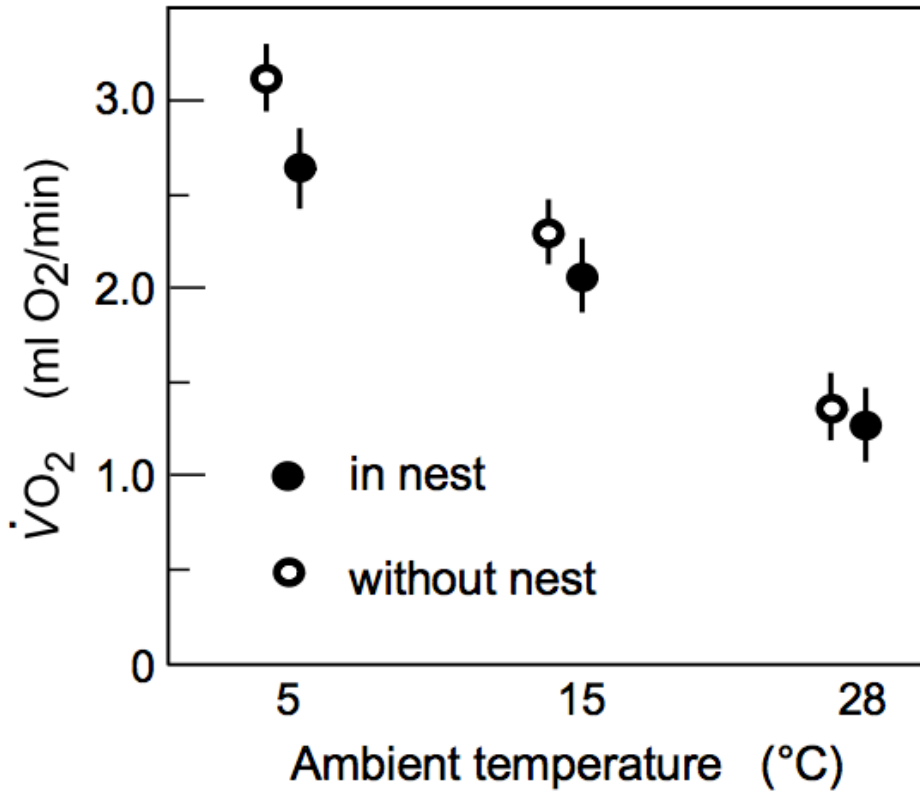
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756 **Figure 2:** Long-term monthly mean minimum and maximum temperatures recorded at Fowlers
 757 Gap from 2004 through 2016. The breeding period for chestnut-crowned babbblers is shown by
 758 the vertical shaded bar (starting with laying of initial broods and ending with fledging of last
 759 broods). Long-term averages are shown as heavy lines and the highest and lowest recorded
 760 monthly means are shown as thin lines. (Australian Government Bureau of Meteorology;
 761 www.bom.gov.au/climate/averages/tables/cw_046128.shtml).



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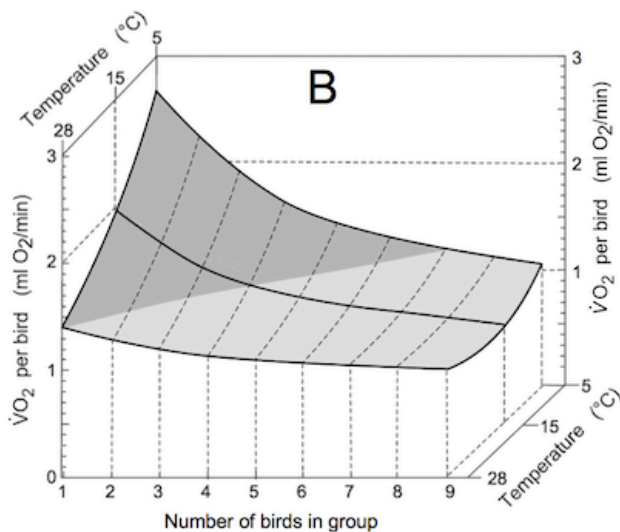
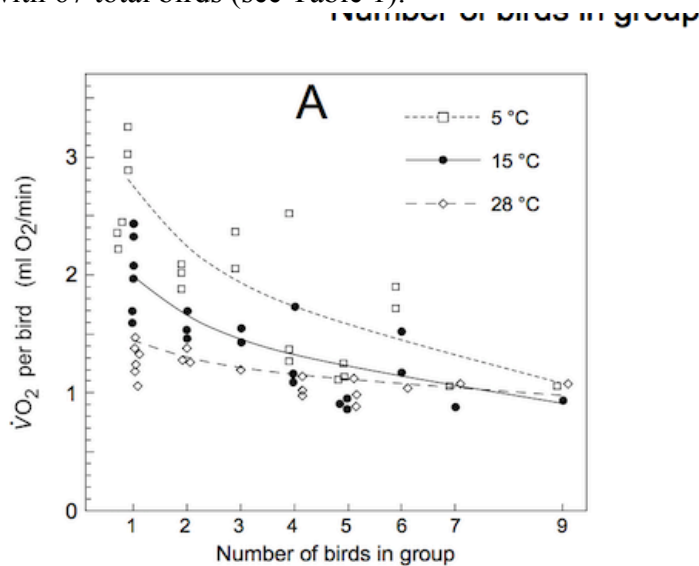
764 **Figure 3.** Metabolic rate (measured as oxygen consumption ($\dot{V}O_2$, ml O₂ min⁻¹) of solitary
765 chestnut-crowned babbblers roosting with or without nests. Dots display predicted means and
766 bars show ± 1 s.e.m. N = 14 birds (6 with nests and 8 without). There was a small but
767 significant effect of using a nest ($F_{2,12} = 6.32$, $P = 0.027$)



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770 **Figure 4:** (A) Metabolic rate (measured as oxygen consumption, $\dot{V}O_2$) of chestnut-crowned
771 babblers roosting in nests as a function of ambient temperature (5, 15, and 28 °C) and group
772 size. Note that for single birds, data points represent individuals, while for groups data points
773 reflect average $\dot{V}O_2$ per bird; (B) Graphical representation of $\dot{V}O_2$ of roosting chestnut-crowned
774 babblers as a function of group size and ambient temperature (T_a). The range of T_a includes
775 most of the nighttime environmental temperatures experienced in natural habitats (see
776 Introduction and Fig. 2). Dark shading indicates $\dot{V}O_2$ greater than the basal metabolic rate
777 (BMR) of single birds (about 1.34 ml O₂ min⁻¹); light shading indicates $\dot{V}O_2$ equal to, or lower
778 than, the BMR of single birds (see text). Groups of seven or more experience no energy cost of
779 regulatory thermogenesis at any tested T_a , and even at thermoneutral temperatures (28 °C), birds
780 in large groups have slightly lower $\dot{V}O_2$ than the BMR of solitary individuals. N = 21 trials
781 with 67 total birds (see Table 1).

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