Energetics of communal roosting in chestnut-crowned babblers: implications for group dynamics and breeding phenology

Mark A. Chappell[1],*, William A. Buttemer[2,3] and Andrew F. Russell[4,5]

ABSTRACT

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

KEY WORDS: Cooperative breeding, Energy expenditure, Group size, Metabolic rate, Oxygen consumption, Thermoregulatory costs

INTRODUCTION

Group living is widespread in the animal kingdom and has consequences for phenotypic traits, mating systems and population dynamics (Courchamp et al., 1999; Cockburn, 2004; Sussman and Chapman, 2004; Dunbar, 2009; Aplin et al., 2015). The 'choice' of joining a group versus living alone should reflect an integrated balance of costs and benefits: individuals are expected to join groups whenever their net fitness is enhanced by doing so (Krause and Ruxton, 2002). This fitness balance is affected by

individual attributes (e.g. relatedness to other group members, sex, age, condition; Russell and Hatchwell, 2001; Clutton-Brock et al., 2002; Silk et al., 2014) and by a range of ecological factors including resource availability and competition (Koenig et al., 1992; Russell, 2004), predation intensity (Elgar, 1989; Beauchamp, 2008), disease risk (Nunn et al., 2015) and climate (Jetz and Rubenstein, 2011; Cockburn and Russell, 2011). However, testing the effects of ecological factors on levels of sociality is often challenging because many are both difficult to quantify and common to the population under study. Studying social species living in temporally heterogeneous environments offers a way around the latter problem: an ecological 'driver' of group size that varies over time should produce predictable concomitant fluctuations of group size (Aureli et al., 2008).

One salient ecological parameter that often varies temporally is environmental temperature. Temperature affects nearly all biological systems, both directly (e.g. Q_{10} effects on physiological rate processes) and indirectly (e.g. habitat productivity, resource availability). In endotherms, particularly small species in cool climates, a primary impact is on energy budgets: the regulatory cost of maintaining core body temperature increases as ambient temperature declines below the zone of thermoneutrality. Compensatory physiological responses (adjusted insulation and peripheral blood flow; torpor or hibernation) are well known, but in social species, group behaviour may also be an important component of thermal biology. Huddling or communal roosting occurs in a variety of birds and mammals and has been shown to conserve energy by reducing each individual's resting metabolic rate (extensively reviewed in Du Plessis, 2004; Gilbert et al., 2010). For some species from extreme climates (e.g. emperor penguins, *Aptenodytes forsteri*; Le Maho et al., 1976; Pinshow et al., 1976; Ancel et al., 1997), survival or reproduction would be difficult or impossible without the energy savings provided by clustering. Even in less challenging habitats, regulatory heat production can comprise a large fraction of avian daily energy expenditures (Weathers and Sullivan, 1993), so savings derived from clustering may have considerable fitness value. For example, in small (<100 g) temperate or subtropical bird species, the overnight energy savings from communal roosting can be as much as 50%, depending on ambient conditions and group size (Du Plessis et al., 1994; Boix-Hinzen and Lovegrove, 1998; McKechnie and Lovegrove, 2001; Du Plessis and Williams, 1994). The use of an insulated nest or cavity with protection from wind may further enhance savings (Buttemer et al., 1987; Du Plessis and Williams, 1994; Du Plessis et al., 1994).

Despite the demonstrated potential for clustering behaviour to ameliorate the energy demands of low environmental temperatures, relatively little work has explored the potential association between temperature, energetics and group dynamics. Temperature varies seasonally in many ecosystems, so if the benefits of communal roosting are ecologically relevant and driven

[1]Department of Biology, University of California, Riverside, Riverside, CA 92521, USA. [2]School of Biological Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia. [3]Centre for Integrative Ecology, Deakin University, Geelong, Victoria 3217, Australia. [4]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn, Cornwall TR10 9FE, UK. [5]Fowlers Gap Arid Zone Research Station, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia.

*Author for correspondence (chappell@ucr.edu)

M.A.C., 0000-0002-3776-5088

by thermal biology, we might expect group size to vary in synchrony with ambient temperature cycles. One approach is to quantify energy expenditure during roosting over a variety of group sizes at ecologically relevant temperatures (Du Plessis, 2004) and evaluate the findings in the context of thermal seasonality in natural habitats. Doing so may provide important insights into not only fission–fusion dynamics and group size, but also breeding phenology (Visser et al., 2015).

In this study, we quantified the effects of temperature, nest use and group size on the nighttime energetics of a highly social 50 g passerine bird, the cooperatively breeding chestnut-crowned babbler [*Pomatostomus ruficeps* (Hartlaub 1852)]. Chestnut-crowned babblers are residents of semi-arid and arid regions of inland southeastern Australia, living in groups of up to 20 or more individuals. There is considerable genetic relatedness among many group members, and cooperative behaviour, at least during breeding, seems to be based largely on kin selection: helping at the nest is strongly directed towards close relatives (Browning et al., 2012a). Several aspects of babbler behaviour, ecology and natural history make them an interesting system for exploring the possible social repercussions of communal roosting at seasonally variable temperatures. First, groups construct numerous enclosed stick nests (Fig. 1) in tall shrubs and trees within their home range; these are used for both roosting and breeding. Nearly all individuals roost communally throughout the year, with up to 22 birds sharing a nest. The key exception is the single breeding female at each nest, who roosts alone with her eggs and chicks from the onset of incubation. Second, there is strong selection favouring early-season reproduction because it allows time for multiple breeding events within an annual temperature cycle that precludes breeding for much of the year (Russell et al., 2010). Nesting usually begins in winter (July) and continues until early summer (October–November), when minimum nighttime temperatures average ~5 and ~15°C, respectively (Fig. 2; Russell, 2016). Thus, breeding babblers routinely experience nighttime temperatures well below the expected lower critical temperature of 50 g birds (~25°C; Aschoff, 1981; Schleucher and Withers, 2001; McKechnie and Wolf, 2004). Although nights are warmer later in the summer, breeding at that time is likely precluded by the risk of daytime temperatures and solar heat loads that can raise nest temperatures to levels presumably fatal for eggs or nestlings (above 50°C;
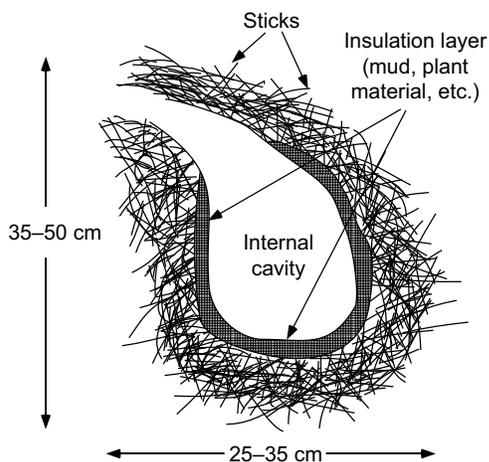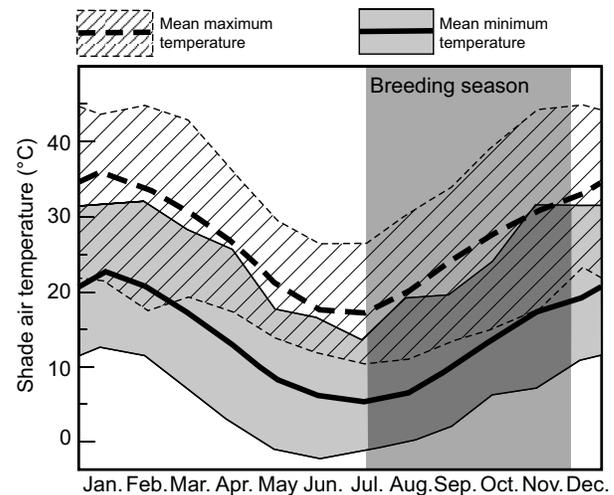

Fig. 2. Long-term monthly mean minimum and maximum temperatures recorded at Fowlers Gap from 2004 through 2016. The breeding period for chestnut-crowned babblers is shown by the vertical shaded bar (starting with laying of initial broods and ending with fledging of last broods). Long-term averages are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

A.F.R., unpublished data). Third, although babblers are obligatorily social, their group sizes vary seasonally, with up to four (mode=1–2) smaller breeding units splitting from the larger social group to initiate separate nests as the season progresses (Russell, 2016). The selective forces driving this fragmentation (or perhaps more interestingly, why smaller breeding groups do not form at the start of the reproductive season) are not fully understood.

The present study had three major aims. First, we evaluated the energetic benefits of roosting inside versus outside of a nest for lone birds. The rationale was to estimate the benefits of nest use, and, for breeding females, the energy budget repercussions resulting from solitary roosting. Second, we measured metabolic rates of babblers roosting in groups of up to nine birds to assess the thermal benefits of communal roosting and how these are affected by group size. In both conditions (with or without nests), we subjected roosting birds to three ecologically relevant temperatures, with 5°C typical for early reproduction, 15°C typical for late reproduction and 28°C representing thermoneutral conditions. Finally, we discuss our findings in light of studies of other communally roosting birds and then assess the relevance of roosting costs for babbler social dynamics.

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

Fig. 1. Diagram of a typical nest of chestnut-crowned babblers used for breeding and communal roosting.

Capture and housing

Over 2 weeks in September 2009, we mist-netted 67 babblers from 15 social groups. Two to nine individuals were removed from groups that averaged 11 birds (range=6–18). To minimize ecological and behavioural impacts, we restricted captures to groups that were non-breeding at the time, and always left at least four resident babblers (mean=7) within each group's home range. Captured babblers were transported by vehicle in bird bags to onsite aviaries (2×2.5×2 m) a few kilometres away and housed with members of the same group (up to three birds per compartment, with vocal contact between adjacent compartments). Captives experienced ambient photoperiods and temperatures and were provided with natural perches and foraging substrate, as well as water and 20 mealworms per bird every 2 h (for further details, see Engesser et al., 2015). Food was withheld after 16:30 h local time. Babblers were never held captive for more than 48 h. All birds used in the study appeared healthy following measurements and were released into their home range, where they were immediately accepted into their social group without exception.

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

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

Respirometry

We used open-system respirometry to measure metabolic rates as oxygen consumption ($\dot{V}_{O_2}$; ml O_2 min^{-1}). Air was supplied at positive pressure by a pump and dried with silica gel. Flow rates to the metabolic chambers (up to four, depending on the experiment; see below) were regulated ±1% by upstream mass flow controllers (MFCs; one per chamber, capacity 0–3 or 0–20 l min^{-1}; Tylan, Torrance, CA, USA). The MFCs were calibrated with a bubble meter (Gilibrator 2; Sensidyne, Clearwater, FL, USA). Flow rates varied according to group size and chamber volume, from 800 ml min^{-1} for single birds in small chambers to 1800 ml min^{-1} for single birds in nests to 5500 ml min^{-1} for the largest group sizes (7–9 birds). Air exiting chambers was sub-sampled at 80 to 100 ml min^{-1}, dried (Drierite), scrubbed of CO_2 (soda lime), redried and pulled through a two-channel oxygen analyser (Sable Systems Oxzilla II; Sable Systems, Las Vegas, NV, USA). A computer-driven multiplexer (Sable Systems RM8) obtained 2.5 min reference readings every 30 min. The system could measure one or two chambers continually (exclusive of references) or three or four chambers in alternating 30-min cycles. Duty factors (the percentage of time each chamber was monitored) were approximately 92% for one or two chambers (55 min h^{-1}) and 46% for three or four chambers (27.5 min h^{-1}). Chambers were placed in an environmental cabinet that controlled ambient temperature (T_a) ±1°C. Temperatures in each chamber were monitored with a thermocouple attached to a Sable Systems TC-2000. Temperature typically varied by 1–1.5°C among chambers, but this difference had no detectable effect on metabolic rates (P=0.87) and was not included in final analyses.

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

$$\dot{V}_{O_2} = \dot{V} \, (F_{I_{O_2}} - F_{E_{O_2}})/(1 - F_{E_{O_2}}), \tag{1}$$

where $\dot{V}$ is the flow rate of dry air in ml min^{-1} (corrected to standard temperature and pressure) and $F_{I_{O_2}}$ and $F_{E_{O_2}}$ are the fractional incurrent and excurrent O_2 concentrations, respectively.

Metabolic trials

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

Trials began around 20:00 h and continued until the following morning. We subjected babblers to low T_a initially (mean=4.7± 0.89°C; hereafter 5°C) for ~4 h. Subsequently, T_a was raised to 14.9°C (hereafter 15°C) and held there for ~3 h. For the remainder of the night (~2.5 h), T_a was raised to ~28°C (large groups) or to 28–30°C (single birds and small groups; mean=28.7±1.5°C; hereafter 28°C). We used the slightly lower temperature for large groups out of concern that overheating might occur within the insulated nest; preliminary tests indicated that for single babblers, the minimal $\dot{V}_{O_2}$ of single babblers held at 28°C did not differ from that at 32°C (Bech et al., 2016). The temperature sequence (cold to warm) was chosen in order to expose birds to the most severe cold stress early in the experiment, and also to minimize the potential for digestion-related elevations in metabolic rate, which mainly occur in warm conditions where regulatory thermogenesis is minimal (Baudinette et al., 1986; Chappell et al., 1997; Bech and Praesteng, 2004). All data obtained at 28°C involved birds that had fasted for at least 11 h and were presumably post-absorptive (e.g. Dykstra and Karasov, 1992), thus permitting valid measurements of basal metabolic rate (BMR).

Following a short period of activity after being placed in the chambers, babblers usually were largely quiescent for the remainder of the night (as judged from vocalizations and $\dot{V}_{O_2}$ records). When episodes of activity occurred, they were typically brief and $\dot{V}_{O_2}$ returned to stable and low values fairly quickly. In most tests there was a small, gradual rise in $\dot{V}_{O_2}$ beginning about an hour before dawn (~05:30 h). Babblers lost an average of 2.8 g (s.d.=±1.0) overnight, equating to 5.7% (s.d.=±2%) of the mean initial mass of 49.8 g. The effects of specific temperatures on mass loss could not be analysed, as all birds experienced at least two temperatures and most experienced three temperatures during a trial. Also, we did not

investigate the effects of nest occupancy (for single birds) or group size on mass loss, as over a single night the majority of mass loss is likely from excreta and evaporative water loss, and we could not quantify the amount of food in the gut at the start of trials. For all T_a, we defined the resting metabolic rate as the lowest stable 10 min of $\dot{V}_{O_2}$ at each temperature (see below). Shortly after dawn, babblers were removed from the chambers, weighed and either released into their home range or, for single-bird trials, returned to the aviary, fed and held for use in a group trial the following night.

Statistics

Analyses were performed in Genstat v. 17 (VSN International) and JMP Pro 11 (SAS Institute, Cary, NC, USA). Data are shown as means±s.d. unless otherwise noted; the significance level was 0.05.

The effect of T_a and nest use on the $\dot{V}_{O_2}$ of single birds was analysed using a general ANOVA (gANOVA), in which $\dot{V}_{O_2}$ was the response term fitted to a normal error structure and temperature (three-level factor) and the presence/absence of a nest were fitted as interacting categorical terms. Body mass (50.3±2.6 g) was initially included as a covariate, but was non-significant and was dropped from the final model [$F_{1,11}$=0.73, P=0.41, estimate (±s.e.)=−0.024± 0.028]. Trial identity was fitted as a blocking function to account for repeated measures from the same individuals across the three test temperatures. The distribution of residuals did not deviate from normality (Shapiro–Wilk test, P=0.72).

All communal roosting data were obtained from birds in nests. Because we could not differentiate the metabolic contributions of individual birds, we computed and analysed a mean value (total $\dot{V}_{O_2}/N$). As for single birds, average body mass (49.2±2.6 g), initially included as a covariate, did not have a significant effect and was dropped from the final model [$F_{1,18}$=1.11, P=0.30, estimate (±s.e.)=0.02±0.02]. The effects of temperature (three-level factor) and group size on $\dot{V}_{O_2}$ were analysed using a residual linear mixed-effects model (REML); $\dot{V}_{O_2}$ was natural log-transformed to ensure normal distribution of residuals (Shapiro–Wilk test, P=0.27). Temperature and group size were fitted as interacting explanatory terms, while trial identity was fitted as a random term. Models with group size fitted as an interacting linear, quadratic or natural logarithmic function revealed a superior fit of the latter (AIC=−113, −102 and −134, respectively). Accordingly, analysis was conducted on log group size, indicating that the energy savings with increasing group size follows a diminishing, rather than linear, function.

RESULTS
Single birds

As expected, the primary determinant of $\dot{V}_{O_2}$ for single birds was ambient temperature (gANOVA; $F_{2,24}$=337.8, P<0.001; Fig. 3; Table S1), which explained 85% of the variance. Energy costs followed the typical pattern of temperature effects on endotherms (Scholander et al., 1950): metabolic rates at 5°C were 112% higher than at 28°C and 34% higher than at 15°C; rates at 15°C were 59% higher than at 28°C. There was a small but significant effect of occupying a 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% reduction in energy expenditure overall. As expected, the benefit of nest use was temperature dependent, although the interaction between nest use and T_a explained only 1% of the variation in $\dot{V}_{O_2}$ ($F_{2,24}$=3.76, P=0.038). At 5°C, babblers reduced their metabolic rate by 15% by roosting in a nest (T_{12}=2.89, P=0.014), while at 15 and 28°C the savings from nest use (11 and 8%, respectively) were not significant roosting without a nest (15°C: T_{12}=1.82, P=0.12; 28°C: T_{12}=1.16,
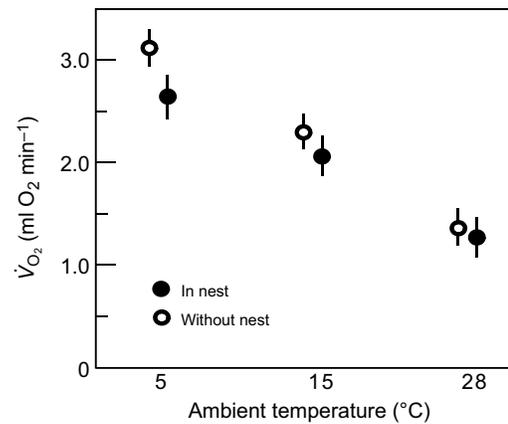

Fig. 3. Metabolic rate (measured as oxygen consumption, $\dot{V}_{O_2}$, ml O$_2$ min^{-1}) of solitary chestnut-crowned babblers roosting with or without nests. Circles display predicted means and bars show ±1 s.e.m. N=14 birds (6 with nests and 8 without). There was a small but significant effect of using a nest ($F_{2,12}$=6.32, P=0.027).

P=0.27). Finally, there was significant among-individual variation in metabolic rates, with individual identity explaining 7% of the variation (component=0.035±0.018 s.e.).

Communal roosting

The $\dot{V}_{O_2}$ of babbler groups roosting in nests was largely determined by T_a, group size and the interaction between the two (Fig. 4; Table S1). Unsurprisingly, roosting babblers expended less energy in warm than in cold temperatures (temperature main effect: $F_{2,38}$=76.3, P<0.001, 42% variance) and benefited from increasing group size (log group size main effect: $F_{1,18}$=57.4, P<0.001, 22% variance). Also, a significant interaction between T_a and log group size on $\dot{V}_{O_2}$ ($F_{2,36}$=20.6, P<0.001, 13% variance) indicated that babblers gained disproportionate energy savings from communal roosting at the lowest T_a. Compared with roosting alone in a nest at 5°C, communally roosting birds reduced nighttime energy expenditures by ∼20% in pairs and trios and 60% in groups of seven or more (estimate=−0.40±0.05 s.e.). At 15°C, savings were only slightly less dramatic, with savings of ∼20% in pairs or trios and up to 50% in groups of five or more (estimate=−0.36±0.05 s.e.). The effect of group size on energy expenditure was much lower at 28°C (estimate=−0.10±0.05 s.e.). Nevertheless, there was a slight but significant reduction in $\dot{V}_{O_2}$ in groups of four or more. That was unexpected, because there was no difference between the minimal $\dot{V}_{O_2}$ of solitary birds tested at 28°C versus 32°C, suggesting that both temperatures are thermoneutral (see Discussion). Finally, as was the case for single birds, we found a significant effect of the random term on explanatory power, indicating inter-group variation in metabolic rates that were explained by neither T_a nor group size (component=0.015±0.0065 s.e.; 12% of variance).

DISCUSSION

In general, our findings for chestnut-crowned babblers are similar in many respects to previous reports of energy savings from communal roosting in birds: both roosting in groups and, to a lesser extent, use of an enclosed nest, help reduce nighttime energy costs in cold conditions. However, babblers achieved considerably greater energy savings than two other cavity nesting species tested at roughly similar temperatures and group sizes: acorn woodpeckers (*Melanerpes formicivorus*; Du Plessis et al., 1994) and green woodhoopoes (*Phoeniculus purpureus*; Du Plessis and Williams,
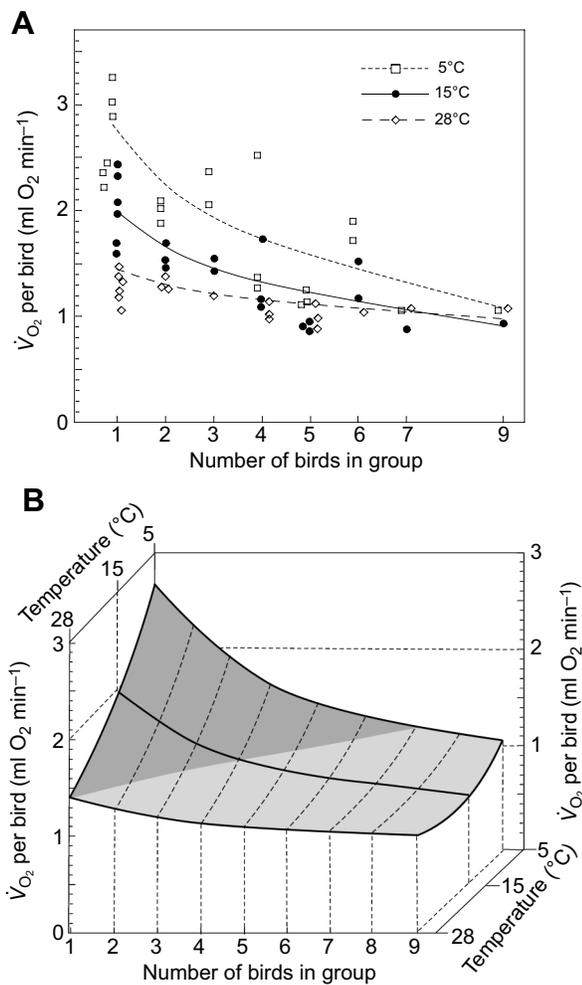
Fig. 4. Effects of group size and temperature on roosting energy costs.
(A) Metabolic rate (measured as oxygen consumption, $\dot{V}_{O_2}$) of chestnut-crowned babblers roosting in nests as a function of ambient temperature (5, 15 and 28°C) and group size. Note that for single birds, data points represent individuals, while for groups, data points reflect average $\dot{V}_{O_2}$ per bird. (B) Graphical representation of $\dot{V}_{O_2}$ of roosting chestnut-crowned babblers as a function of group size and ambient temperature (T_a). The range of T_a includes most of the nighttime environmental temperatures experienced in natural habitats (see Introduction and Fig. 2). Dark shading indicates $\dot{V}_{O_2}$ greater than the basal metabolic rate (BMR) of single birds (~1.34 ml O_2 min^{-1}); light shading indicates $\dot{V}_{O_2}$ equal to, or lower than, the BMR of single birds (see Results). Groups of seven or more experience no energy cost of regulatory thermogenesis at any tested T_a, and even at thermoneutral temperatures (28°C), birds in large groups have slightly lower $\dot{V}_{O_2}$ than the BMR of solitary individuals. N=21 trials with 67 total birds (see Table 1).

1994; Boix-Hinzen and Lovegrove, 1998). In large groups (seven or more birds), roosting babblers expended 50–60% less energy than solitary birds at 5°C; the corresponding savings for green woodhoopoes was approximately 30%, and for acorn woodpeckers approximately 17%. The difference may be partially due to their smaller body size (~50 g versus ~80 g) and/or the slightly larger group sizes we tested in babblers (up to nine individuals, versus four to six), although we did not detect additional benefits from group sizes above six birds. The modest energy savings observed in acorn woodpeckers is probably due to the fact that they roosted separately inside cavities (i.e. not touching each other) and hence did not benefit from the reductions in total surface area and heat loss made possible by close-contact huddling.

Another highly social species, the ~50 g white-backed mousebird (*Colius colius*), attained group-roosting benefits similar to those of chestnut-crowned babblers: an energy savings of ~50% in groups of six compared with solitary birds at a T_a of 15°C. However, roosting mousebirds do not use a nest, instead huddling together on a branch, and much of their energy savings is due to unusually large reductions of nighttime body temperature (in fact, group roosting may be necessary to maintain stable nocturnal body temperature in this species; McKechnie and Lovegrove, 2001).

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

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

This 'stress hypothesis' might help explain our surprising finding of group-size effects on metabolic rates of chestnut-crowned babblers roosting at T_a that fit the standard definition of thermoneutrality. Our 'basal' $\dot{V}_{O_2}$ for single birds at 28–30°C (1.26 ml O_2 min^{-1}) does not differ from the $\dot{V}_{O_2}$ of solitary chestnut-crowned babblers tested at 32°C (1.31 ml O_2 min^{-1}; Bech et al., 2016), indicating that 28–32°C is within the species' thermal neutral zone. However, babblers roosting in groups of four or more had significantly lower $\dot{V}_{O_2}$ at ~28°C (1.05 ml O_2 min^{-1}; Fig. 4). This was probably not due to facultative hypothermia, which would be unexpected at warm T_a and, moreover, was not recorded during group roosting in captive or free-living congeneric white-browed babblers (*P. superciliosus*; T. K. Douglas, personal communication). Perhaps the most likely explanation is that chestnut-crowned babblers roosting alone or in small groups are socially stressed and have increased sympathetic output as a consequence (Taylor et al., 2014). Isolated individuals of several

Table 1. Effects of group size on nighttime resting rates of oxygen consumption ($\dot{V}_{O_2}$) in chestnut-crowned babblers at three different ambient temperatures (5, 15 and 28°C)

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

The first row is for single birds without nests, and temperature had a highly significant effect ($F_{2,29}=274$, $P<0.001$). The remaining data are for birds roosting inside nests, and F-statistics and significance tests (P) for group size effects are shown at the bottom of the table. Values show predicted means±s.e., with number of trials in parentheses. For groups (>1 bird), $\dot{V}_{O_2}$ was calculated as the mean $\dot{V}_{O_2}$ per bird.

social species are known to exhibit symptoms of stress (Young et al., 2006; Hennessy et al., 2009), and this can affect energy metabolism. For example, roosting RMR of solitary pallid bats (*Antrozous pallidus*) were greater than in communal huddles at all temperatures tested, including thermoneutral conditions (Trune and Slobodchikoff, 1976). In white mice (*Mus musculus*) and Mongolian gerbils (*Meriones unguiculatus*), metabolic rate increased more slowly in response to decreasing T_a below thermoneutrality in trios than in solitary individuals, even if communal huddling (contact) was prevented (Martin et al., 1980). These studies indicate that improved thermoregulation is not the only factor that generates energy savings during communal roosting. For chestnut-crowned babblers, we estimate that across all tested T_a, most (∼85%), but not all, of the energy savings from communal roosting is achieved through reduced requirements for heat production (assuming no interaction between T_a and 'stress' levels of lone individuals); the remainder may result at least in part from reduced 'stress'. In terms of thermoregulatory physiology, the salient point is that solitary babblers (or groups of less than four birds) apparently cannot attain 'true' BMR, even at thermoneutral T_a. Although defining BMR in this context is something of a semantic argument, if BMR is stipulated to be the minimum possible normothermic metabolic rate, then in chestnut-crowned babblers it is only realized when roosting with several conspecifics. Accordingly, we used the mean thermoneutral large-group BMR value (1.05 ml O_2 min^{-1}) as the index for minimal achievable metabolic rate when comparing energy savings across temperatures and group sizes (Fig. 4B).

These caveats notwithstanding, the energy savings chestnut-crowned babblers achieve by roosting communally are impressive. At 5°C, birds in groups of seven or more, and at 15°C, birds in groups of five or more do not need to increase $\dot{V}_{O_2}$ above basal rates (Fig. 4). These findings are particularly noteworthy in comparison to most solitary-roosting small birds from cool climates, which probably rarely encounter thermoneutral conditions, and so rarely attain BMR. Hence, direct selection on BMR in such species seems unlikely. In contrast, chestnut-crowned babblers appear to routinely attain BMR during communal roosting, making BMR a viable 'target' for selection because a change in BMR – such as the ∼15–20% decrease in thermoneutral metabolic rates we observed in large roosting groups – can engender energy costs or savings that are potentially ecologically relevant. At 5°C over a typical 14-h winter

night, groups of seven or more babblers roosting communally expend approximately 20.9 kJ per bird, a savings of 24.7 kJ compared with costs for single birds roosting in nests (∼45.6 kJ, 2.2 times higher). The potential importance of such savings is probably best evaluated in the context of daily energy expenditure (DEE), which includes expenditure for activity and maintenance as well as thermoregulation and BMR, and specifies how much energy birds must obtain by foraging. A doubly labelled water study of chestnut-crowned babblers encompassing a range of group sizes during breeding showed an average DEE of 76±12 kJ (N=20; A.F.R., unpublished data), relatively low for a 50 g bird (Nagy, 2005). Thus a roosting energy savings of 24.7 kJ is 34% of DEE, which should decrease foraging requirements by a roughly proportionate amount.

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

babblers would easily achieve BMR, but comparable costs would be 70–90% above BMR for secondary breeding units of three to four birds (Fig. 4). During later breeding events when nighttime T_a is close to 15°C, roosting costs for secondary units of three to four would be considerably lower (roughly 30% above BMR; Figs 2, 4). In other words, early-season breeding by small secondary units may be compromised by high energy costs of thermoregulation and the concomitant reduction in the fraction of foraging effort that can be devoted to the provisioning of offspring (or the breeding female; see below).

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

Many vertebrate societies undergo cycles of dissociation into subgroups followed by re-aggregation. These events may help resolve conflicts of interest between individuals (Jacobs, 2010; Magrath et al., 2004), or accommodate differences in food availability, predation risk or disease dynamics (Beauchamp, 2008; Conradt and Roper, 2005; Elgar, 1989; Nunn et al., 2015). Our results for chestnut-crowned babblers indicate that in this obligate cooperative breeder, the energy savings provided by communal roosting may be an important selective force shaping social dynamics and breeding phenology. A similar situation may occur in long-tailed tits (*Aegithlos caudatus*), which, like chestnut-crowned babblers, are cooperative breeders that benefit from communal roosting (they huddle in linear clusters and this reduces rates of overnight mass loss compared with solitary individuals; Hatchwell et al., 2009). Like babblers, they show seasonal fission–fusion social dynamics. Compared with chestnut-crowned babblers, long-tailed tit flocks fragment more synchronously into breeding pairs, but as we have suggested for babblers, the timing of fragmentation and breeding phenology are strongly temperature dependent (Gullett et al., 2013). More broadly, the concept that energy costs of solitary roosting might act as a significant selection pressure on social dynamics and breeding phenology may be relevant to many social species. For example, climate models

predict that the availability of many prey types may shift temporally in response to rising temperatures, but also that short-term weather variability may increase (e.g. Thomas et al., 2001; Visser et al., 2015). Even for species that obtain considerable thermal 'buffering' from communal roosting, this variability might be a barrier to advancing reproductive phenology to synchronize with changing food availability: if breeding females roost solitarily, there may be increased risk of early-season cold snaps that put her or her brood at risk. Accordingly, we suggest that studies of small social endotherms should consider the potential repercussions of thermal benefits of communal roosting on social dynamics and breeding phenology, as well as on thermoregulatory costs.

Supplementary information
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References
Ancel, A., Visser, H., Hendrich, Y., Masman, D. and Le Maho, Y. (1997). Energy saving in huddling penguins. *Nature* **385**, 304-305.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A. and Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538-541.

Aschoff, J. (1981). Thermal conductance in mammals and birds: its dependence on body size and circadian phase. *Comp. Biochem. Physiol.* **69A**, 611-619.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Di Fiore, A., Dunbar, R. I. M., Henzi, S. P. et al. (2008). Fission-fusion dynamics: new research frameworks. *Curr. Anthropol.* **49**, 627-654.

Baudinette, R. V., Gill, P. and O'Driscoll, M. (1986). Energetics of the little penguin, *Eudyptula minor*: temperature regulation, the calorigenic effect of food and moulting. *Aust. J. Zool.* **34**, 35-45.

Beauchamp, G. (2008). What is the magnitude of group-size effect on vigilance? *Behav. Ecol.* **19**, 1361-1368.

Bech, C. and Praesteng, K. E. (2004). Thermoregulatory use of heat increment of feeding in the tawny owl (*Strix aluco*). *J. Therm. Biol.* **29**, 649-654.

Bech, C., Chappell, M. A., Astheimer, L. B., Londoño, G. A. and Buttemer, W. A. (2016). A 'slow pace of life' in Australian old-endemic passerine birds is not accompanied by low basal metabolic rates. *J. Comp. Physiol. B* **186**, 503-512.

Boix-Hinzen, C. and Lovegrove, B. G. (1998). Circadian metabolic and thermoregulatory patterns of red-billed woodhoopoes (*Phoeniculus purpureus*): the influence of huddling. *J. Zool. Lond.* **244**, 33-41.

Browning, L. E., Patrick, S. C., Rollins, L. A., Griffith, S. C. and Russell, A. F. (2012a). Kin selection, not group augmentation, predicts helping in an obligate cooperatively breeding bird. *Proc. R. Soc. Lond. Biol. Sci.* **279**, 3861-3869.

Browning, L. E., Young, C. M., Savage, J. L., Russell, D. J. F., Barclay, H., Griffith, S. C. and Russell, A. F. (2012b). Carer provisioning rules in an obligate cooperative breeder: prey type, size and delivery rate. *Behav. Ecol. Sociobiol.* **66**, 1639-1649.

Buttemer, W. A., Astheimer, L. B., Weathers, W. W. and Hayworth, A. M. (1987). Energy savings attending winter-nest use by verdins (*Auriparus flaviceps*). *Auk* **104**, 531-535.

Careau, V. and Garland, T. (2012). Performance, personality, and energetics: correlation, causation, and mechanism. *Physiol. Biochem. Zool.* **85**, 543-571.

Chappell, M. A., Bachman, G. C. and Hammond, K. A. (1997). The heat increment of feeding in house wren chicks: magnitude, duration and substitution for thermostatic costs. *J. Comp. Physiol. B* **167**, 313-318.

Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Young, A. J., Balmforth, Z. and McIlrath, G. M. (2002). Evolution and development of sex differences in cooperative behavior in meerkats. *Science* **297**, 253-256.

Cockburn, A. (2004). Mating systems and sexual conflict. In *Ecology and Evolution of Cooperative Breeding in Birds* (ed. W. D. Koenig and J. L. Dickinson), pp. 81-101. Cambridge: Cambridge University Press.

Cockburn, A. and Russell, A. F. (2011). Cooperative breeding: a question of climate? *Curr. Biol.* **21**, R195-R197.

Conradt, L. and Roper, T. J. (2005). Consensus decision making in animals. *Trends Ecol. Evol.* **20**, 449-456.

Courchamp, F., Clutton-Brock, T. and Grenfell, B. (1999). Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* **14**, 405-410.

Dunbar, R. I. M. (2009). The social brain hypothesis and its implications for social evolution. *Ann. Hum. Biol.* **36**, 562-572.

Du Plessis, M. A. (2004). Physiological ecology. In *Ecology and Evolution of Cooperative Breeding in Birds* (ed. W. D. Koenig and J. L. Dickinson), pp. 117-127. Cambridge: Cambridge University Press.

Du Plessis, M. A. and Williams, J. B. (1994). Communal cavity roosting in green woodhoopoes: consequences for energy expenditure and the seasonal pattern of mortality. *Auk* **111**, 292-299.

Du Plessis, M. A., Weathers, W. W. and Koenig, W. D. (1994). Energetic benefits of communal roosting by acorn woodpeckers during the non-breeding season. *Condor* **96**, 631-637.

Dykstra, C. R. and Karasov, W. H. (1992). Changes in gut structure and function of house wrens (*Troglodytes aedon*) in response to increased energy demands. *Physiol. Zool.* **65**, 422-442.

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* **64**, 13-33.

Engesser, S., Crane, J. M. S., Crane, J. M. S., Savage, J. L., Russell, A. F. and Townsend, S. W. (2015). Experimental evidence for phonemic contrasts in a nonhuman vocal system. *PLoS Biol.* **13**, e1002171.

Gilbert, C., McCafferty, D., Le Maho, Y., Martrette, J. M., Giroud, S., Blanc, S. and Ancel, A. (2010). One for all and all for one: the energetic benefits of huddling in endotherms. *Biol. Rev.* **85**, 545-569.

Gullett, P., Hatchwell, B. J., Robinson, R. A. and Evans, K. L. (2013). Phenological indices of avian reproduction: cryptic shifts and prediction across large spatial and temporal scales. *Ecol. Evol.* **3**, 1864-1877.

Haftorn, S. and Reinertsen, R. E. (1985). The effect of temperature and clutch size on the energetic cost of incubation in a free-living blue tit (*Parus caeruleus*). *Auk* **102**, 470-478.

Hatchwell, B. J., Sharp, S. P., Simeoni, M. and McGowan, A. (2009). Factors influencing overnight loss of body mass in the communal roosts of a social bird. *Funct. Ecol.* **23**, 367-372.

Hennessy, M. B., Kaiser, S. and Sachser, N. (2009). Social buffering of the stress response: diversity, mechanisms and functions. *Front. Neuroendicrinol.* **30**, 470-482.

Jacobs, A. (2010). Group cohesiveness during collective movements: travelling apart together. *Behav. Processes* **84**, 678-680.

Jetz, W. and Rubenstein, D. R. (2011). Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.* **21**, 72-78.

Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L. and Stanback, M. T. (1992). The evolution of delayed dispersal in cooperative breeders. *Q. Rev. Biol.* **67**, 111-150.

Krause, J. and Ruxton, G. D. (2002). *Living in Groups*. Oxford: Oxford University Press.

Le Maho, Y., Delclitte, P. and Chatonnet, J. (1976). Thermoregulation in fasting emperor penguins under natural conditions. *Am. J. Physiol.* **231**, 913-922.

Magrath, R. D., Heinsohn, R. G. and Johnstone, R. A. (2004). Reproductive skew. In *Ecology and Evolution of Cooperative Breeding in Birds* (ed. W. D. Koenig and J. L. Dickinson), pp. 157-176. Cambridge: Cambridge University Press.

Martin, R. A., Fiorentini, M. and Connors, F. (1980). Social facilitation of reduced oxygen consumption in *Mus musculus* and *Meriones unguiculatus*. *Comp. Biochem. Physiol.* **65**, 519-522.

McKechnie, A. E. and Lovegrove, B. G. (2001). Thermoregulation and the energetic significance of clustering behavior in the white-backed mousebird (*Colius colius*). *Physiol. Biochem. Zool.* **74**, 238-249.

McKechnie, A. E. and Wolf, B. O. (2004). The allometry of avian basal metabolic rate: good predictions need good data. *Physiol. Biochem. Zool.* **77**, 502-521.

Metcalfe, N. B., Val Leeuwen, T. E. and Killen, S. S. (2016). Does individual variation in metabolic phenotype predict fish behaviour and performance? *J. Fish Biol.* **88**, 298-321.

Nagy, K. A. (2005). Field metabolic rate and body size. *J. Exp. Biol.* **208**, 1621-1625.

Nomano, F. Y., Browning, L. E., Nakagawa, S., Griffith, S. C. and Russell, A. F. (2014). Validation of an automated data collection method for quantifying social networks in collective behaviours. *Behav. Ecol. Sociobiol.* **68**, 1379-1391.

Nunn, C. L., Jordan, F., McCabe, C. M., Verdolin, J. L. and Fewell, J. H. (2015). Infectious disease and group size: more than just a numbers game. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **370**, 20140111.

Pinshow, B., Fedak, M. A., Battles, D. R. and Schmidt-Nielsen, K. (1976). Energy expenditure for thermoregulation and locomotion in emperor penguins. *Am. J. Physiol.* **231**, 903-912.

Portelli, D. J., Barclay, H., Russell, D. J. F., Griffith, S. C. and Russell, A. F. (2009). Social organisation and foraging ecology of the cooperatively breeding chestnut-crowned babbler (*Pomatostomus ruficeps*). *Emu* **109**, 153-162.

Rollins, L. A., Browning, L. E., Holleley, C. E., Savage, J. L., Russell, A. F. and Griffith, S. C. (2012). Building genetic networks using relatedness information: a novel approach for the estimation of dispersal and characterization of group structure in social animals. *Mol. Ecol.* **21**, 1727-1740.

Russell, A. F. (2004). Mammals: comparisons and contrasts. In *Ecology of Cooperative Breeding in Birds*, Vol. 2 (ed. W. D. Koenig and J. L. Dickinson), pp. 210-227. Cambridge: Cambridge University Press.

Russell, A. F. (2016). Chestnut-crowned babblers: dealing with climatic adversity and uncertainty in the Australian arid zone. In *Cooperative Breeding in Vertebrates: Studies in Ecology, Evolution and Behavior* (ed. W. D. Koenig and J. L. Dickinson), pp. 150-164. Cambridge: Cambridge University Press.

Russell, A. F. and Hatchwell, B. J. (2001). Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. *Proc. R. Soc. B Biol. Sci.* **268**, 2169-2174.

Russell, A. F., Portelli, D. J., Russell, D. J. F. and Barclay, H. (2010). Breeding ecology of the chestnut-crowned babbler: a cooperative breeder in the desert. *Emu* **110**, 324-331.

Schleucher, E. and Withers, P. C. (2001). Re-evaluation of the allometry of wet thermal conductance for birds. *Comp. Biochem. Physiol. A Mol. Intergr. Physiol.* **129**, 821-827.

Scholander, P. F., Hock, R., Walters, V., Johnson, F. and Irving, L. (1950). Heat regulation in some arctic and tropical mammals and birds. *Biol. Bull.* **99**, 237-258.

Silk, M. J., Croft, D. P., Tregenza, T. and Bearhop, S. (2014). The importance of fission-fusion social group dynamics in birds. *Ibis* **156**, 701-715.

Sorato, E., Gullett, P. R., Griffith, S. C. and Russell, A. F. (2012). Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. *Anim. Behav.* **84**, 823-834.

Sorato, E., Griffith, S. C. and Russell, A. F. (2016). The price of associating with breeders in the cooperatively breeding chestnut-crowned babbler: foraging constraints, survival and sociality. *J. Anim. Ecol.* **85**, 1340-1351.

Sussman, R. W. and Chapman, A. R. (2004). *The Origins and Nature of Sociality*. New York: Aldine de Gruytner.

Taylor, E. W., Leite, C. A. C., Sartori, M. R., Wang, T., Abe, A. S. and Crossley, D. A. (2014). The phylogeny and ontogeny of autonomic control of the heart and cardiorespiratory interactions in vertebrates. *J. Exp. Biol.* **217**, 690-703.

Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M. and Speakman, J. R. (2001). Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* **291**, 2598-2600.

Trune, D. R. and Slobodchikoff, C. N. (1976). Social effects of roosting on the metabolism of the pallid bat (*Antrozous pallidus*). *J. Mammal.* **57**, 656-663.

Visser, M. E., Gienapp, P., Husby, A., Morrisey, M., de la Hera, I., Pulido, F. and Both, C. (2015). Effects of spring temperatures on the strength of selection on timing of reproduction in a long-distance migratory bird. *PLoS Biol.* **13**, e1002120.

Weathers, W. W. (1985). Energy cost of incubation in the canary. *Comp. Biochm. Physiol. A* **81**, 411-413.

Weathers, W. W. and Sullivan, K. A. (1993). Seasonal patterns of time and energy allocation by birds. *Physiol. Zool.* **66**, 511-536.

Young, A., Carlson, A. A., Monfort, S. L., Russell, A. F., Bennett, N. C. and Clutton-Brock, T. H. (2006). Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proc. Natl. Acad. Sci. USA* **103**, 12005-12010.