

The energetic significance of communal roosting and insulated roost nests in a small arid-zone passerine

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Abstract

Small endotherms have evolved behavioural mechanisms for reducing rest-phase energy expenditure, which reduce the likelihood of mismatches between energy supply and demand during periods of cold weather and/or food scarcity. Although the energetic consequences of communal roosting and the use of insulated roosts have been the subject of numerous studies, less is known about the energy savings achieved by species that use these two behaviours simultaneously. We hypothesized that communal roosting in insulated roost nests by a small arid-zone passerine, the Scaly-feathered Weaver *Sporopipes squamifrons*, results in additive energetic benefits that reduce nocturnal energy requirements far below those of individual birds roosting in the open. We measured metabolic rates in weavers over air temperatures (T_a) between $-5\text{ }^{\circ}\text{C}$ and $20\text{ }^{\circ}\text{C}$ using flow-through respirometry. Measurements were taken from single weavers and groups varying in size from two to 12 individuals, with or without a roost nest. Consistent with our predictions, rest-phase resting metabolic rate (RMR) of weavers decreased when the birds roosted communally and decreased further when groups were roosting in a nest. In the absence of a nest, groups of 8 or 12 birds reduced RMR by $> 30\%$ compared with single birds. These energy savings increased further when groups roosted in nests; at $T_a = 0\text{ }^{\circ}\text{C}$, groups of 8 or 12 weavers approximately halved their RMR compared to groups without nests. Our data confirm that Scaly-feathered Weavers save considerable energy by roosting communally in roost nests, and these behaviours likely are a key reason why this small species from subtropical latitudes can occur in areas with winter night-time temperatures as low as $-10\text{ }^{\circ}\text{C}$.

L'importance énergétique des dortoirs collectifs et les nids-gîtes isolés chez un petit passereau des zones arides

Résumé

Les petites endothermes ont développé des mécanismes comportementaux pour réduire les dépenses énergétiques en phase de repos, ce qui réduit le risque de déséquilibre entre l'offre et la demande en énergie pendant les périodes de froid et / ou de pénurie alimentaire. Bien que les conséquences énergétiques des dortoirs collectifs et de l'utilisation de nids-gîtes isolés aient fait l'objet de nombreuses études, on en sait moins sur les économies d'énergie réalisées par les espèces qui utilisent simultanément ces deux comportements. Nous avons émis l'hypothèse que les dortoirs

collectifs dans les nids-gîtes isolés par un petit passereau de la zone aride, le Sporopipe squameux *Sporopipes squamifrons*, entraîne des avantages énergétiques supplémentaires qui réduisent les besoins énergétiques nocturnes bien inférieurs à ceux des oiseaux individuels dormant à l'air libre. Nous avons mesuré les taux métaboliques chez ces tisserins à des températures de l'air (T_a) comprises entre $-5\text{ }^{\circ}\text{C}$ et $20\text{ }^{\circ}\text{C}$ en utilisant une respirométrie à flux continu. Les mesures ont été prises à partir d'oiseaux isolés et d'oiseaux groupés de taille variable allant de 2 à 12 individus, avec ou sans gîte. Conformément à nos prévisions, le taux métabolique de repos (TMR) des Sporopipe au repos (phase de repos) a diminué lorsque les oiseaux se sont rassemblés en groupe et a encore diminué lorsque des groupes dormaient dans un nid. En l'absence de nid, des groupes de 8 ou 12 oiseaux ont réduit le TMR de $> 30\%$ par rapport aux oiseaux isolés. Ces économies d'énergie ont encore augmenté lorsque des groupes gîtent dans des nids; à $T_a = 0\text{ }^{\circ}\text{C}$, les groupes de 8 ou 12 Sporopipe ont approximativement réduit de moitié leur TMR par rapport aux groupes sans nids. Nos données confirment que les Sporopipe squameux économisent une énergie considérable en dormant ensemble dans des nids-gîtes, et que ces comportements sont probablement une des principales raisons pour lesquelles cette petite espèce de latitudes subtropicales peut être présente dans des zones où les températures nocturnes sont aussi basses que $-10\text{ }^{\circ}\text{C}$.

Keywords: energetics, huddling, nest, *Sporopipes squamifrons*, thermoregulation, Scaly-feathered Finch

Introduction

Endothermic homeothermy in birds and mammals arises from metabolic heat production in concert with insulation effective enough to facilitate the defence of a set point body temperature (T_b) over a wide range of environmental temperatures (Hayes and Garland 1995, Ruben 1995). The evolution of endothermy, which occurred independently in birds and mammals (Grigg et al. 2004), involved increases in maintenance metabolism to facilitate substantial increases in endogenous heat production (Stevens 1973). The benefits of endothermic thermoregulation are offset by substantial costs, primarily related to energy requirements being $10\text{-}20\times$ higher than those of comparatively-sized ectotherms (Nagy 2005), and the associated increases in food requirements (Koteja 2000). The energetic costs of endothermic homeothermy are particularly

pronounced in small endotherms, especially during cold exposure and/or periods of food shortage (Geiser 2008).

Endotherms have evolved several morphological, physiological, and behavioural mechanisms to reduce heat loss, particularly during the rest phase of their circadian cycle (Bennett and Ruben 1979, Gilbert et al. 2010, Ruf and Geiser 2015). Morphological mechanisms include the insulation provided by fur or feathers (Hart 1956, Wolf and Walsberg 2000), and physiological mechanisms include heterothermic responses such as torpor and hibernation (pronounced reductions in metabolic rate and T_b over time scales varying from hours to months, (Ruf and Geiser 2015). Behavioural mechanisms include social thermoregulation via roosting communally (Gilbert et al. 2010), and roosting in thermally-buffered microsites such as nests and cavities (Hatchwell et al. 2009).

Social thermoregulation occurs in many bird orders and families and increases thermoregulatory efficiency, reducing the individual energy requirements of communally roosting individuals (Beauchamp 1999, Hatchwell et al. 2009, Farquhar et al. 2018). The adaptive significance of communal roosting is not limited to temperate latitudes with severe winters (e.g., Emperor Penguins *Aptenodytes forsteri*; Gilbert et al. 2008) and this behaviour is widespread in species occupying more moderate subtropical and tropical climates (Boix-Hinzen and Lovegrove 1998, Chappell et al. 2016, Gilbert et al. 2010, McKechnie and Lovegrove 2001, Paquet et al. 2016). In the Afrotropics, Green Woodhoopoes *Phoeniculus purpureus* reduce energy expenditure by up to ~30% when roosting communally with conspecifics at air temperatures (T_a) below 20 °C (Boix-Hinzen and Lovegrove 1998), and White-backed Mousebirds *Colius colius* can halve energy requirements by roosting in a group of six individuals at $T_a = 15^\circ\text{C}$ (McKechnie and Lovegrove 2001).

Another widespread behavioural avenue whereby birds and mammals offset the energetic costs of endothermic homeothermy is by roosting in thermally-buffered microsites where temperatures may remain well above outside T_a (Weathers et al. 1990, White et al. 1975). Although the energetic benefits of communal roosting are not limited to very low temperatures (du Plessis & Williams 1994, McKechnie & Lovegrove 2001), it may be particularly important in small bird species during prolonged periods of cold exposure (Mainwaring 2011). In the Kalahari Desert during winter, the thermoregulatory benefits of communal roosting and insulated nest use by Sociable Weavers *Philetairus socius* are substantial and occupied nest temperatures

can be up to 23°C higher than outside air temperature (White et al. 1975). Although it is well established that these activities can considerably decrease the rest-phase energy demands of birds, few studies have investigated the additive benefits of both behaviours simultaneously (Chappell et al. 2016). In the Australian arid zone, Chestnut-crowned Babblers *Pomatostomus ruficeps* roosting in groups of seven or more in insulated nests at T_{as} as low as 5 °C did not increase metabolic rate above basal levels, which translated to maximum energy savings of 60% (Chappell et al. 2016). These observations reiterate the adaptive value of behavioural mechanisms of energy conservation for birds living in unpredictable, arid environments.

In the current study, we quantified the energetic and thermoregulatory benefits of communal roosting and the use of insulated nests in a very small (~10 g) Afrotropical passerine, the Scaly-feathered Weaver (Finch) *Sporopipes squamifrons*. The species roosts in groups ranging in size from 6-12 individuals in hollow ball-type nests approximately 200 mm long and 110 mm wide constructed primarily from dry twigs and grass, with feathers often lining the inside (Dean 2005). This species is widespread and abundant in arid and semi-arid parts of southern Africa, including the Kalahari Desert where night-time temperatures can approach -10°C during winter. As such, it is a good study species to answer questions about the additive effects of communal roosting and insulated nests on energy requirements. We hypothesised that group size and nest insulation would influence rest-phase energy expenditure. Specifically, we predicted that individuals' rest-phase energy expenditures would decrease with increasing group size and would be lower when birds were roosting in a nest compared to when they were not. We also predicted that the energy savings of communal roosting and insulated nest use would be additive in nature, and that a combination of communal roosting and nest use would result in overnight energy requirements equivalent to a fraction of what it would be in the absence of these behaviours (Figure 1).

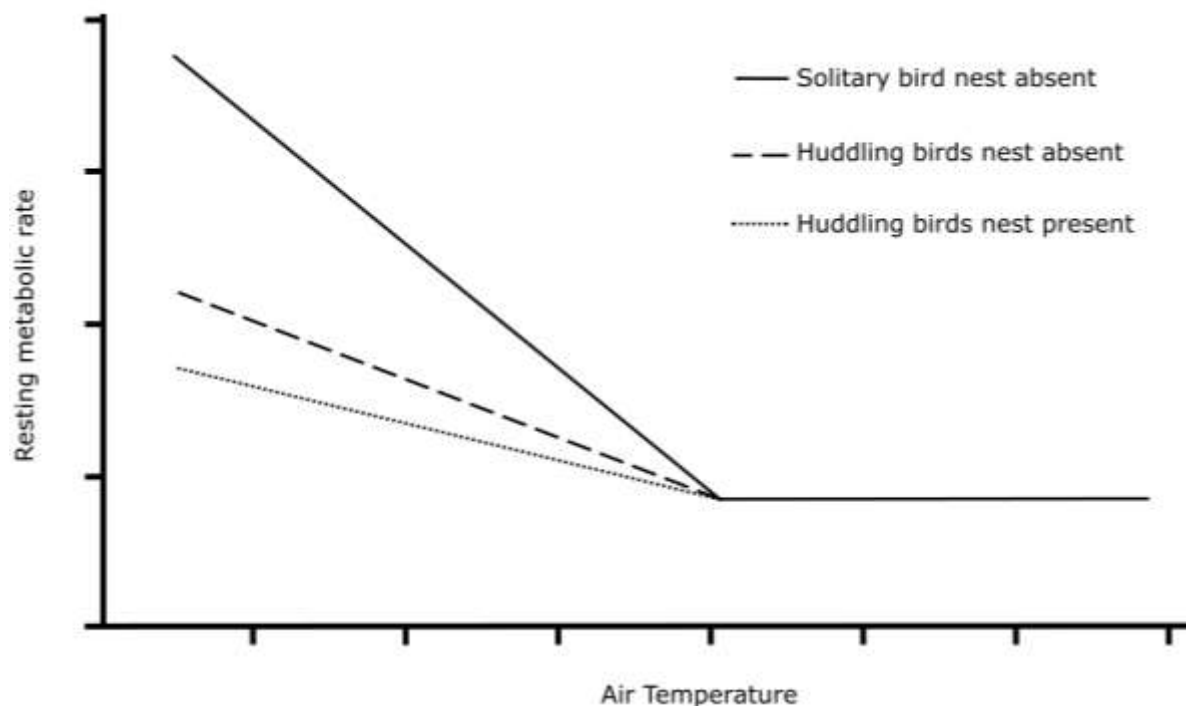


Figure 1: Predicted relationships between resting metabolic rates and air temperatures (T_a) for solitary Scaly-feathered Weavers without a nest (solid line), huddling birds without a nest (dashed line) and huddling birds with a nest (dotted line). Communal roosting should result in a shallower increase in RMR with decreasing T_a compared to single individuals, and the additional use of a thermally-insulated nest should result in additive energy savings manifested as further reductions in the slope of RMR as a function of T_a .

Methods and Materials

Capture and housing

Wild Scaly-feathered Weavers ($n = 37$) were captured using mist-nets over a one-week period near Askham in the Northern Cape Province of Southern Africa (29.9833° S, 20.7833° E) during April 2017 (mid-autumn). There is substantial seasonal variation in temperature at this site, with daily minima as low as -9.1°C during winter (mean: $-1.2 \pm 3.8^\circ\text{C}$), and daily maxima as high as 44.4°C during summer (mean: $35 \pm 3.5^\circ\text{C}$; M.L. Thompson, M.J. Noakes and A.E. McKechnie *unpublished data*). The mean daily minimum and maximum temperatures for April were $12.6 \pm 2.8^\circ\text{C}$ and $30.8 \pm 3.9^\circ\text{C}$ respectively at the closest South African Weather Service station to our study site, at Twee Rivieren (~ 62 km; $26^\circ 28'$ S, $20^\circ 36'$ E). The study site near Askham consists of sparse grassland interspersed with *Vachellia erioloba* and *Senegalia mellifera* on red

sand dunes. Following capture, birds were transported back to the field site in cloth bags and housed in outdoor aviaries (4 x 2.5 x 2.5 m) with members of the same aviary group for two nights. The aviaries were equipped with natural perches, roost sites, and sufficient shade (approximately a third of the roof surface area was covered in shade cloth). Captured individuals had *ad libitum* access to water and food, which consisted of wild bird mix and mealworms. The mean body mass (M_b) of captured individuals was 11.67 ± 0.1 g ($n = 37$).

The birds were transported by road to the University of Pretoria (UP) Small Animal Physiological Research Facility (25.7472° S, 28.2588° E) where all experiments were performed. The Small Animal Physiological Research Facility is approximately 870 km from the field site and birds were transported in pet carrier crates modified with perches and *ad libitum* access to food and water. The birds spent ~6 hours in transit each day over the course of two days. Upon arrival in Pretoria, the birds were placed into two separate indoor aviaries (3 m x 2 m x 1.8 m) constructed in two rooms at the Small Animal Physiological Research Facility. Photoperiods were set to simulate day-time from 7:00 to 19:00 and night-time from 19:00 to 7:00 h. The T_a and relative humidity in both rooms was kept constant at 25 °C and 35 %. Each aviary was equipped with natural perches, roost sites, and red sand. The birds had *ad libitum* access to water and food, consisting of wild bird seed mix and five mealworms per bird per day.

Birds were acclimated to captive conditions for about 30 days before the onset of experiments. To minimize stress, individuals were only disturbed when feeding or when captured for metabolic measurements. For trials in which several birds were measured simultaneously in one metabolic chamber, all individuals came from the same aviary. For measurements that included the presence of a nest, we used Scaly-feathered Weaver nests obtained from the capture site. Birds were allowed adequate time (four days) between trials to recover and avoid cumulative stress effects. Nearly all measurements took place during June – August 2017.

Gas exchange and air temperature measurements

Metabolic rates were measured indirectly as the rates of oxygen consumption (V_{O_2} ; ml min⁻¹) and CO₂ production (V_{CO_2} ; ml min⁻¹) using an open flow-through respirometry system. Atmospheric air was supplied to the system by a compressor and passed through two columns of silica gel and drierite connected in series. Incurrent air was then split between the baseline and experimental channels. Chambers were placed in a darkened, soundproof, temperature-controlled

cabinet (Model KMF 720, Binder, Tuttlingen, Germany). Air temperatures in each chamber were recorded with a thermistor probe (Sable Systems International, Las Vegas, Nevada, USA) inserted into the chamber through a hole sealed with a rubber grommet. Flow rates to the metabolic chambers (up to three used simultaneously) were regulated using mass flow controllers (MFC; one per chamber, Model FMA5520, Omega Engineering, Bridgeport, New Jersey, USA), regularly calibrated against a soap bubble flow meter (Baker and Pouchot 1983). Flow rates varied with group size, the volume of the chamber (1.3 – 5.2 L), and the presence or absence of a nest. Flow rates for birds without a nest varied from 800 ml min⁻¹ for individuals and small groups to 3500 ml min⁻¹ for group size =12, while flow rates for birds in nests varied from 1000 ml min⁻¹ to 3000 ml min⁻¹. Flow rates were adjusted to maintain O₂ depletion between incurrent and excurrent air of < 0.5%. Air mixing within the chamber was maximised by positioning the air inlet near the top of the chamber and the air outlet near the bottom. Excurrent air from the chambers and incurrent air from the baseline channel entered a respirometry multiplexor (RM-8, Sable Systems International, Las Vegas, Nevada, USA). During measurements where nests were used, excurrent air passed through filters to remove debris. The multiplexor was used to sequentially subsample baseline air and excurrent air from the chambers. A subsampler (SS-3, Sable Systems International, Las Vegas, Nevada USA) pulled air through an FC-10a O₂ analyser and CA-10a CO₂ analyser (Sable Systems International, Las Vegas, Nevada, USA) at a flow rate of ~ 200 ml min⁻¹. Subsampled air passed through a column of drierite to remove H₂O before reaching the analysers. Each cycle of readings lasted for 80 minutes, measuring baseline air for the first 10 minutes, then each chamber for 30 minutes respectively if there were two chambers and 20 minutes respectively if three chambers were connected, switching back to baseline for the last 10 minutes of every cycle. These cycles were repeated overnight, with the birds spending about 12 hours in the chambers per trial. Data were recorded in ExpeData 1.3.10 (Sable Systems International, Las Vegas, Nevada, USA) using an analog-digital converter (UI-2, Sable Systems International, Las Vegas, Nevada, USA). The V_{O2} and V_{CO2} values were obtained by calculating the difference in O₂ and CO₂ concentration between the excurrent chamber and baseline air.

Experimental protocol

Birds were caught in the aviaries approximately an hour before the start of measurements which typically commenced at 18:00-18:30 h using a butterfly net with padded edges. Each bird was weighed with an electronic balance (Model ALC-810.2, ACCULAB Sartorius Group, Arvada, Colorado, USA) and placed into a metabolic chamber. The birds were transported in metabolic chambers covered with a dark cloth from the UP Small Animal Physiological Research Facility to the Zoology Building on the UP Hatfield Campus (a 5-minute drive), where the metabolic measurements took place.

For measurements, birds were placed in clear plastic chambers that varied in volume according to group size and the presence or absence of a nest. For measurements without nests, individual birds and groups of two were placed into chambers with a volume of 1.3 L, and groups of four, eight and 12 placed into 4-L chambers. A plastic mesh platform was positioned to elevate birds ~10 cm from the bottom of the chamber. In trials where a nest was present, weavers were placed inside the nest (*sensu* Chappell et al. 2016; active roost nests were obtained from the capture site) and the nest positioned in a plastic mesh tube inside a 5.2-L chamber. The tubes were custom-made to be slightly bigger than the nest itself and ensured the nests were at a vertical orientation throughout the night with the nest entrance facing upwards, while also helping to maintain the structural integrity of the nest. The entrance of the nest was covered with shade cloth fastened with rubber bands to ensure individuals would remain in the nest throughout the night, while still allowing for natural airflow throughout the night.

For trials with and without nests, we used group sizes of one, two, four, eight and 12, which represents the range of group sizes found in this species in the wild (Dean 2005). All individuals were used multiple times during this study, but no individual was used more than 12 times for all measurements combined. Trials began around 19:00-19:30 h and continued until the following morning. The number of measurements taken for each experimental treatment (i.e., group size and nest use) varied based on the number of groups we could form from the same aviary without individuals being measured more than once for a specific treatment (Table 1).

Weavers experienced two T_a values per night, ranging from -5 °C to 20 °C in 5 °C increments. The T_a values chosen for the study are within the normal range of T_a experienced by individuals in the Kalahari Desert at night during winter. We selected combinations of group size and T_a to avoid exposing solitary individuals and small groups to conditions more challenging

Table 1: Mean \pm SD resting metabolic rate (RMR) of Scaly-feathered Weavers over a range of air temperatures and group sizes. For each combination of air temperature and group size, the upper value in normal font refers to RMR in the absence of a nest, and the lower value in bold font refers to RMR when the weavers were roosting in a nest. Values in parentheses are sample sizes (i.e., numbers of groups at each air temperature / group size combination).

Group size	Air temperature					
	-5 °C	0 °C	5 °C	10 °C	15 °C	20 °C
Solitary				0.498 \pm 0.163 (12)	0.569 \pm 0.159 (9)	0.370 \pm 0.144 (9)
				0.478 \pm 0.279 (7)	0.616 \pm 0.338 (8)	0.403 \pm 0.221 (8)
2			-----	0.452 \pm 0.110 (7)	0.372 \pm 0.067 (7)	0.288 \pm 0.061 (8)
			0.435 \pm 0.061 (4)	0.219 \pm 0.126 (4)	0.261 \pm 0.105 (4)	0.157 \pm 0.049 (5)
4	-----	-----	0.485 \pm 0.173 (6)	0.379 \pm 0.072 (9)	0.480 \pm 0.216 (6)	0.300 \pm 0.134 (8)
	0.483 \pm 0.349 (4)	0.571 (2)	0.199 \pm 0.107 (4)	0.346 \pm 0.063 (3)	0.225 \pm 0.118 (5)	0.154 \pm 0.065 (7)
8	-----	0.391 \pm 0.134 (4)	0.392 \pm 0.161 (6)	0.320 \pm 0.029 (4)	0.232 \pm 0.043 (3)	0.229 \pm 0.037 (3)
	0.240 \pm 0.125 (4)	0.193 \pm 0.092 (4)	0.243 (2)	0.278 \pm 0.080 (4)	0.281 \pm 0.066 (5)	0.228 \pm 0.078 (5)
12	-----	0.699 \pm 0.052 (3)	0.369 (2)	0.337 \pm 0.028 (4)	0.343 (2)	0.351 \pm 0.103 (3)
	0.453 (2)	0.381 (2)	0.345 (2)	0.292 (1)	0.218 (2)	0.189 (2)

than they are likely to experience naturally, with only larger groups exposed to $T_a \leq 5$ °C (Table 1). During measurements, weavers were at each T_a for at least five hours per night, with the temperature decreasing from a higher T_a to a lower T_a over about half an hour at 00:30 h. To control for the possibility of habituation to experimental procedures, the order that birds were measured at different T_a and experimental treatments were randomized. Following a short period of activity of about an hour after being placed into the temperature cabinet, individuals settled down and were calm for the remainder of the night. The weavers were removed from the chambers around 07:45 h each morning, transported back to UP Small Animal Physiological Research Facility in the chambers, weighed and released into the aviaries.

Data analysis

Outputs from the analysers were recorded using an analog-digital convertor (UI-2 Universal Interface, Sable Systems) and ExpeData software (Sable Systems). For each metabolic trial, we identified a stable period representative of the lowest resting metabolic rate at each T_a . The mean fractional concentrations of O_2 and CO_2 in excurrent air from each of the chambers were calculated from the lowest stable 5-min interval within this period, and were used to calculate V_{O_2} and V_{CO_2} . Metabolic rates (Watts) were estimated by multiplying V_{O_2} by a conversion factor calculated from respiratory exchange ratio ($RER = V_{CO_2} / V_{O_2}$) and joule equivalence data obtained from Table 4.2 of Withers (1992). An RER of 0.71, which is indicative of lipid metabolism in post-absorptive birds, was assumed if RER was outside the range for which thermal equivalence data is available ($0.71 < RER < 1.00$, (Withers 1992)). We are confident that birds were post-absorptive as data from the first 90 minutes of measurements were excluded from analyses, and the gut retention time for a 10-g bird is approximately 48.2 minutes (Karasov 1990). Individuals' metabolic rates could not be calculated when using groups of birds, and thus overall metabolic values were divided by the group size of respective trials to estimate the mean metabolic contribution of each individual. Analyses were performed using R 3.4.2 (R Core Team 2017). All values are represented as mean \pm SD.

A general linear model (GLM) was fitted to determine the effect of T_a , nest use and group size (predictor variables) on the RMR of individual birds (response variable). Interaction effects were tested in the initial model. However, no interactions among T_a , nest use and group size were significant and excluding these interactions improved or maintained model fits (lowered or

did not change Akaike Information Criterion values), so interaction effects were excluded from the final models. The assumptions of all models (normality, homogeneity of variance and multicollinearity), as well as model fit (residuals, leverage and Cook's D values), were checked using the appropriate tests described by Logan (2011). Our experiment involved a repeated measures design (i.e., multiple measurements from the same individuals at various T_a and experimental categories). However, we could not use mixed effects models to analyse our data as it was not possible to calculate the actual individual metabolic contributions of weavers measured in groups. The lack of a random effect (i.e., number of individuals) introduces a level of pseudoreplication in our models and increases the chance of type I error due to inter-related data points and unconstrained degrees of freedom. However, as each group measured had unique combinations of individuals at different T_a values, we considered them to be separate entities. Regardless, the results of our models are not as conservative as would be ideal.

To establish specific energy savings of individuals in different group sizes, we ran separate GLMs to determine the relationship between RMR and T_a in each experimental category (i.e., group size with nest absent/ present). If a clear inflection point was observed (such as for group size of 12 without a nest), we used the segmented package (Muggeo 2009) to estimate the inflection point and fit a broken-stick linear regression.

Results

The rest-phase RMR of Scaly-feathered Weavers was predicted by T_a , group size, and the presence or absence of a nest (Figure 2). Overall, RMR increased significantly with decreasing T_a ($F_{1,209} = 20.680$, $p < 0.001$). RMR also decreased significantly with increasing group size ($F_{1,209} = 18.804$, $p < 0.001$) and was significantly lower when a nest was present ($F_{1,209} = 17.139$, $p < 0.001$), confirming that communal roosting and nest use confer significant energetic advantages.

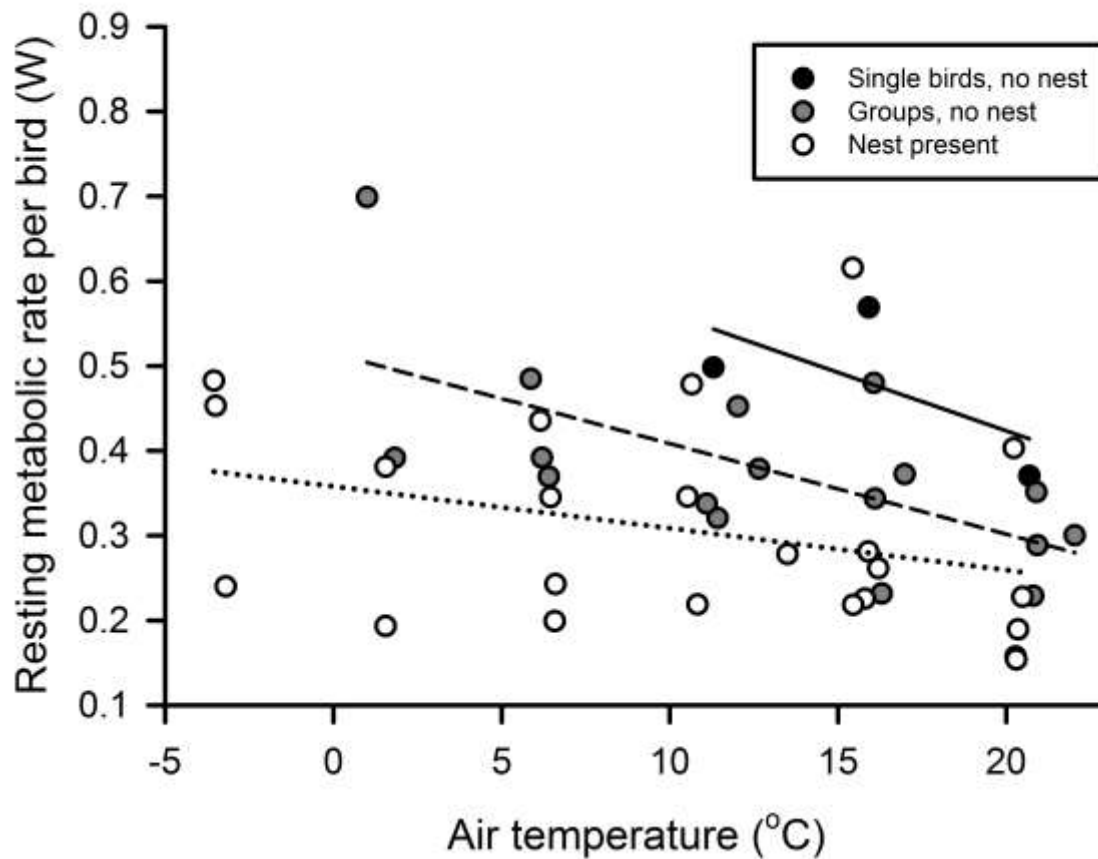


Figure 2: Resting metabolic rates as a function of air temperature in Scaly-feathered Weavers roosting either solitarily without a nest, in groups of 2-12 individuals without a nest, or in groups of 2-12 individuals roosting in a nest. The lines, which are plotted purely for illustrative purposes, represent linear regression models for solitary birds with no nest (solid line), groups of 2-12 individuals with no nest (dashed line) or solitary birds and groups roosting in a nest (dotted line).

Effect of group size without a nest

In the absence of a nest, T_a significantly influenced RMR for group sizes of two or more weavers (Table 2). The rate of increasing RMR with decreasing T_a decreased as group size increased from two to eight birds, with the RMR of an individual in a group of eight being about half that of an individual in a group of two. The relationship between RMR and T_a for a group size of 12 in the absence of a nest differed from that of other treatments as they maintained a stable RMR with decreasing T_a until an inflection point at $T_a = 7.3$ °C, below which RMR increased significantly with decreasing T_a .

Table 2: Results of general linear models fitted to resting metabolic rate (RMR) of Scaly-feathered Weavers in different experimental treatments (group size of 1-12, and presence / absence of nest) as a function of air temperature. For a group size of 12 in the absence of a nest, a clear inflection point was present, and a broken stick linear regression was fitted. Slopes and y-intercepts (y-int.) of the lines for the relationship between T_a and RMR are also provided for each experimental category.

Group size	Nest	t-value	d.f.	p-value	Inflection point	Slope	y-int.
1	N	-1.68	28	0.102		-0.013	0.68
2	N	-3.79	20	< 0.001		-0.017	0.66
4	N	-2.49	27	0.019		-0.011	0.56
8	N	-2.67	18	0.015		-0.009	0.43
12	N	-6.03	10	< 0.001	$T_a < 7.3^\circ\text{C}$	-0.060	0.75
		0.51	10	< 0.001	$T_a > 7.3^\circ\text{C}$	0.002	0.31
1	Y	-0.54	21	0.598		-0.008	0.63
2	Y	-3.51	15	< 0.001		-0.016	0.48
4	Y	-2.94	21	< 0.001		-0.012	0.4
8	Y	0.73	22	0.471		0.001	0.23
12	Y	-6.04	9	< 0.001		-0.011	0.401

In the absence of a nest, energy savings associated with increasing group size depended on temperature. At higher T_a treatments there was no obvious pattern of energy savings as a function of group size (Table 1). The influence of group size became more apparent at low T_a and, at 10°C for instance, each weaver in a group of two spent approximately 9% less energy compared to single birds, groups of four spent 24% less, groups of eight 36% less and groups of twelve 32% less energy.

Effect of nest use and group size

In the presence of a nest, there was no significant relationship between RMR and T_a for solitary birds (Table 2). However, T_a did significantly influence the RMR of individuals in groups, except for a group size of eight. The slopes of RMR *versus* T_a decreased with increasing group size, with no change in RMR with decreasing T_a in groups of eight. However, RMR did increase significantly with decreasing T_a in groups of 12.

For the majority of combinations of group sizes and T_a values, RMR was considerably lower when nests were present compared to when nests were absent (Table 1). Overall, the use of a nest enhanced energy savings at lower temperatures, with savings dependent on group size and T_a (Table 3). The additive effect of communal roosting and nest use was particularly evident at lower T_a (Table 3). For solitary birds, there was no substantial difference in energy expenditure when a nest was present at $T_a = 10-20$ °C and potential benefits of a nest at lower temperatures were not explored.

Table 3: Energy expenditure of groups of Scaly-feathered Weavers roosting in the presence of nests calculated as percentage (%) of that in groups roosting in the absence of nests at various air temperatures (T_a).

Group size	Air temperature (°C)				
	0	5	10	15	20
1			96	119	109
2			48	70	55
4		41	91	47	51
8	49	62	83	121	100
12	54	93	87	64	54

Discussion

In support of our hypothesis that group size and nest insulation influence rest-phase energy expenditure in Scaly-feathered Weavers, we found that roosting with conspecifics and roosting in a nest increased energy savings at low T_a . Our data reveal that the RMR of weavers was lower when roosting in a nest, and that the RMR of birds in groups, regardless of whether they were in a nest, was affected by T_a . As we predicted, energy savings increased with increasing group size, and the benefits of communal roosting and nest use were additive when used simultaneously. Our results confirm that huddling within an insulated roost is an important thermoregulatory behaviour for Scaly-feathered Weavers.

Communal roosting

Huddling within a communal roost confers thermoregulatory benefits to individuals by lowering their energy demands (Beauchamp 1999). By minimizing the surface area exposed to ambient

conditions, huddling individuals can defend T_b without drastically increasing their metabolic heat production (Gilbert et al. 2010). In Common Starlings *Sturnus vulgaris*, roosting with conspecifics contributed to energy savings and their metabolic rates were significantly higher when they roosted alone compared to larger groups (Brenner 1965). Gilbert et al. (2008) estimated that, of the 38% reduction in metabolic rates achieved by free-ranging penguins roosting communally, two-thirds could be attributed directly to huddling with conspecifics and the remainder to warming of the surrounding environment. The heat lost by each individual in the roost reduces the gradient between T_b and the environment resulting in decreased heat loss from individuals and increased energy savings (Beauchamp 1999, Gilbert et al. 2010). Scaly-feathered Weavers tended to huddle for the duration of the metabolic trials, and the thermoregulatory advantages conferred by huddling explain the higher energy expenditure of individual birds both in the presence and absence of nests.

At low T_a , energy savings generally increase with group size (Gilbert et al. 2010). Consistent with our prediction, the slope of RMR as a function of T_a was steeper for huddling birds without a nest, and shallower for birds huddling in a nest. Groups saved significantly more energy when compared to birds roosting individually. Moreover, we found that as group size increased, there was a reduction in the slope of the negative relationship between RMR and T_a , and these energy savings were similar to those previously reported for similarly-sized birds (Chaplin 1982). At 20°C, Scaly-feathered Weavers roosting in pairs each spent ~78% of the energy of a solitary individual, similar to the 21% energy savings achieved by a pair of Common Bushtits *Psaltriparus minimus* (Chaplin 1982). When compared to solitary birds, larger groups of weavers achieved energy savings (~60%) similar to those of groups of six White-backed Mousebirds (50%; McKechnie and Lovegrove 2001). The energy savings achieved by the mousebirds (which do not use roost nests) resulted from both huddling and reductions in their rest-phase T_b (McKechnie and Lovegrove 2001).

The absence of a significant relationship between RMR and T_a in single weavers with or without a nest can, in our opinion, be attributed to the small range of T_a values at which we collected data compared to the ranges for larger group sizes. An additional factor may have been the absence of conspecifics; for a small species that almost always roosts in groups, one might expect that roosting alone, particularly at T_a below thermoneutrality, would act as a stressor and thereby lead to elevated RMR. This notion is supported by the observations of Chappell et al.

(2016) that the basal metabolic rates of single Chestnut-crowned Babblers, and those of individuals in small groups, were higher than values measured in larger groups similar to those observed for babblers under natural conditions.

Insulated nest use

Roosting in insulated sites can provide individuals with a thermal buffer from outside conditions (Kendeigh 1961). Even when the difference in T_a between the inside and outside of a nest is relatively small, the thermoregulatory benefits conferred may nevertheless be substantial (Du Plessis and Williams 1994, Paquet et al. 2016, van Dijk et al. 2013). In the Kalahari Desert, the huge nests of Sociable Weavers, which sometimes consist of hundreds of individual chambers (Spottiswoode 2005), provide an excellent buffer from winter night-time temperatures that can approach -10°C , thereby conferring energy savings to their occupants (van Dijk et al. 2013). For Scaly-feathered Weavers in groups, individuals in a nest had lower RMR, resulting in increased energy savings. Interestingly, there seemed to be no energetic benefits for solitary individuals that roosted in nests. Energy expenditure was equivalent to 96 - 119 % of that of solitary individuals without nests across the range of T_a we investigated, suggesting that although nests confer energy savings to groups, roosting communally is a better energy conservation mechanism for an individual weaver.

In the presence of a nest, the slope of the relationship between RMR and T_a decreased as group size increased from two to eight birds. Moreover, groups of eight used 38% less energy at $T_a = 5^{\circ}\text{C}$ compared to the same-sized group in the absence of a nest, savings quantitatively similar to those achieved by other nest- or cavity-using species (Chappell et al. 2016, Du Plessis et al. 1994, Du Plessis and Williams 1994). Interestingly, for groups of eight in a nest, there was no significant relationship between RMR and T_a , suggesting that in these groups the effective thermoneutral zone achieved through a combination of communal roosting and insulated nest use may include the coldest T_a (i.e., as low as -5°C) to which they were exposed in the present study.

Although energy savings increased with group size, this pattern did not hold for groups of 12. For groups of 12, we expected no increase of RMR with decreasing T_a as we observed in groups of eight; unexpectedly, RMR increased with decreasing T_a in a manner similar to smaller groups. One potential explanation may be overcrowding, as there may have been more individuals roosting together than would be the case under natural conditions, possibly resulting

in higher metabolic rates due to elevated stress levels. Scaly-feathered Weavers roosting in the wild can form groups of 12 individuals in a nest during cold periods (Dean 2005); however, the conditions in which they do so might differ to those in our experimental setup in terms of factors such as T_a , nest size, and social structures. We used random individuals to form each group and this, especially at large group sizes, might not have been conducive to forming cohesive social groups similar to those that characterize wild populations.

Conclusions

Communal roosting is an important mechanism used by small endotherms to reduce energy expenditure during periods of high energy demand and/or low energy supply. Our results suggest that communal roosting in Scaly-feathered Weavers allows these birds to save substantial amounts of energy and is likely important for their survival during cold winter nights in the Kalahari Desert. Individually roosting weavers did not appear to gain energetic benefits from nest use, an observation potentially attributable to stress effects as this species almost never roosts alone in the wild. The use of a nest while simultaneously roosting communally was most beneficial at low T_a , although the amount of energy saved by the birds was also dependent on T_a and group size. Overall, communal roosting and to a greater extent, communal roosting combined with insulated nest use, did result in large energy savings for Scaly-feathered Weavers as predicted. These energy savings were maximal for a group size of eight roosting in a nest even at T_a as low as ~ -5 °C. Determining the energetic significance of communal behaviours in avian species can greatly contribute to understanding the fitness benefits associated with sociality.

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