



The thermoregulatory benefits of the communal nest of sociable weavers *Philetairus socius* are spatially structured within nests

René E. van Dijk, Jennifer C. Kaden, Araceli Argüelles-Ticó, L. Marcela Beltran, Matthieu Paquet, Rita Covas, Claire Doutrelant and Ben J. Hatchwell

R. E. van Dijk (r.van.dijk@sheffield.ac.uk), J. C. Kaden, A. Argüelles-Ticó, L. M. Beltran and B. J. Hatchwell, Dept of Animal and Plant Sciences, Univ. of Sheffield, Western Bank, Sheffield S10 2TN, UK. – M. Paquet and C. Doutrelant, CEFE-CNRS, 1919 Route de Mende, FR-34293, Cedex 5, Montpellier, France. – R. Covas, CIBIO, Research Centre in Biodiversity and Genetic Resources, PT-4485-661 Vairão, Portugal. RC also at: Biology Dept, Science Faculty, Univ. of Porto, Porto, Portugal, and Percy FitzPatrick Inst. of African Ornithology, DST/NRF Centre of Excellence, Univ. of Cape Town, Rondebosch 7701, South Africa.

Structures built by animals, such as nests, mounds and burrows, are often the product of cooperative investment by more than one individual. Such structures may be viewed as a public good, since all individuals that occupy them share the benefits they provide. However, access to the benefits generated by the structure may vary among individuals and is likely to be an important determinant of social organisation. Here we use the massive, communal nests of sociable weavers *Philetairus socius*, to investigate whether their thermoregulatory function varies in relation to the size of communal nests, and the position of individual nest chambers within the communal structure. We then examine whether this spatial variation in thermoregulatory function predicts the social organisation of colonies. First, we show that the sociable weavers' communal nests buffer variation in ambient temperature, and reduce temperature variability within nest chambers. The extent of this buffering effect depends significantly on the position of nest chambers within the communal structure, and on the depth to which chambers are embedded within the nest mass. We detected no effect of nest volume on thermoregulatory benefits, suggesting that there are likely to be additional, non-thermoregulatory benefits leading to communal nests. Finally, our results indicate that there may be competition for access to the benefits of the public good, since older birds occupied the chambers with the highest thermoregulatory benefits, where breeding activity was also more common. We discuss how the spatial structure of the benefits of the public good might influence social organisation in the unique communal lifestyle of sociable weavers.

The function of physical structures built by animals to control their environment is often poorly understood and the extent to which such structures approach their adaptive optima is rarely investigated (Hansell 2005). Nests, burrows or mounds may provide thermoregulatory benefits (Reid et al. 2002), reduce the risk of predation for adults (Jackson 2000, Hözl et al. 2009) or their offspring (Siedelmann 1999, Kleindorfer 2007, Prokop and Trnka 2011), or, in the case of bowers, they may act as signals to conspecifics (Humphries and Ruxton 1999, Olsson et al. 2009). In birds, parents and offspring benefit from well-insulated nests, slowing egg-cooling rates when the parents are not attending the clutch and thus reducing the parents' energetic costs of reheating the eggs to incubation temperatures (Drent 1975, Collias and Collias 1984, Reid et al. 2000). Nestling growth rates and offspring survival may also be influenced by nest microclimate (Martin and Schwabl 2008, Nord and Nilsson 2011). However, the extent to which animals may build nest structures to enhance thermoregulatory benefits is likely to be influenced by the time and energy costs of nest construction (McGowan et al. 2004, Mainwaring and

Hartley 2009, Olsson et al. 2009, Moreno et al. 2010), as well as various interacting environmental factors, such as climate and predation risk (Spottiswoode 2007, Edelman 2011, Prokop and Trnka 2011).

An interesting characteristic of many of these physical structures built by animals is that they may be viewed as a public good. The benefits that are derived from the nest are shared among all of a nest's occupants, whereas the costs of construction of nests or burrows are borne only by the individuals that contribute to it. Therefore, when multiple individuals contribute to the construction of a communal nest, as in mound-building mice *Mus spicilegus* (Garza et al. 1997) or monk parakeets *Myiopsitta monachus* (Navarro et al. 1995; see also Manning et al. 1992, Ford and Johnson 2007, Bollazzi and Rocas 2010), each individual would obtain the highest overall payoffs by not paying the costs of construction, but gaining the benefits of the communal structure. This type of conflict between individuals over investment in a public good is rife in nature (Hardin 1968, Arnqvist and Rowe 2005, MacLean and Gudelj 2006, McGowan et al. 2006, West et al. 2006,

Gutierrez et al. 2011), and may eventually lead to the breakdown of cooperation in a process described by the tragedy of the commons (Hardin 1968). How such conflicts between individuals over investment in the communal good are resolved, depends on the costs and benefits of the public good, their spatial and temporal distribution, as well as on the social structure and dominance hierarchies within the community (Rankin et al. 2007).

Here, we examine spatial variation in the benefits of the massive communal nest of the sociable weaver *Philetairus socius* and the effects of this variation on social organisation. The nests of the sociable weavers are one of the largest nests known among birds, and both sexes invest in its building and maintenance (Collias and Collias 1978). The nest structure consists of nest chambers embedded within a communal thatch overarching the nest chambers. The nest chambers are used not only for breeding, but also for roosting throughout the year, which means that the potential thermoregulatory benefits extend beyond the breeding phase. Once constructed, the nest may exist for many decades and be used by many generations (Collias and Collias 1964). This communal structure provides an excellent model system to address questions concerning the function of the nest as a public good and the variation in the benefits that individuals derive from that public good. Two previous studies directly addressed the potential benefits of the sociable weaver's nest, showing that it buffers against low temperatures at night, especially during winter, and against high temperatures during the day, especially in the summer (White et al. 1975, Bartholomew et al. 1976). Although these studies revealed the heat retaining capacities of the thatch and the nest chambers, their focus was on how the ecology of the sociable weaver may be affected by the ameliorating effects of their communal nests. Furthermore, birds were allowed to enter the nest chambers in which temperature was recorded, and temperature was measured in very few chambers in one or two nests. In order to understand the social organisation of sociable weaver colonies and the benefits of contributing to the communal structure it is necessary to determine whether the thermoregulatory benefits of a communal nest vary between colonies of different sizes and between nest chambers at different positions within colonies. Measurements of such benefits should be recorded without birds present in the nest.

The objective of this study was to measure the temperature inside multiple nest chambers within colonies of different volumes to investigate whether: 1) the volume of the nest predicts its thermoregulatory properties, 2) the thermoregulatory properties vary within colonies depending on the position of the nest chamber, and 3) the thermoregulatory benefits of nest chambers predict social organisation at colonies. We expected: 1) the benefits to increase with increasing volume of the thatch, and 2) towards the centre of the nest where the size of the thatch is likely to be largest; and 3) that the chambers that provide the largest buffer against the ambient temperatures would be occupied by better competitors and would have a higher probability of breeding activity. Here we use the age of an individual as a proxy for its competitive abilities, the rationale being that male sociable weavers are philopatric to their natal colonies (Brown et al. 2003, Doutrelant et al. 2004) and older birds

are therefore likely to be better able to obtain the best nest chambers due to their experience and prior occupancy at a given colony.

Methods

Study species and field site

The sociable weaver is a colonial, cooperatively breeding passerine endemic to the semi-arid *Acacia* savannahs of southern Africa that are associated with the Kalahari ecosystem (Spottiswoode 2005). These weavers live in colonies varying in size from five to over 300 individuals that are built communally by the colony members. The colony structure consists of thatched *Stipagrostis* grasses forming a large structure into which the individual nest chambers are embedded. In addition to being used for breeding, the nest chambers are used for roosting throughout the year by family groups or, more rarely, by single individuals (Maclean 1973; RC, CD and MP unpubl.). The colonies are typically built on *Acacia* trees, although other tree species and man-made structures, such as telephone poles, can also be used (Maclean 1973).

The study was conducted between 8 September and 5 December 2010 and between 23 September and 22 December 2011 at Benfontein Game Farm, Kimberley, South Africa (28°52'S, 24°50'E). This study area, containing approximately 30 colonies of sociable weavers, covers about 15 km² of Kalahari sandveld, consisting of open savannah dominated by *Stipagrostis* grasses and camelthorn trees, *Acacia erioloba*. In this study we included data from 20 colonies.

Temperature logging

We logged the ambient temperature and the temperature inside the nest chambers at 20 colonies using a flexible thermistor PB-5006-3M probe, which was inserted into the nest chamber to a constant depth (to the centre of the nest chamber) and was connected to a TinyTag Plus 2 TGP-4510 data logger (Gemini Data Loggers, Chichester, UK) recording data every 30 s. The temperature probe was inserted into nest chambers at three different positions at each colony: T1 – a nest chamber near the edge of the communal nest (mean distance to nearest edge \pm SD: 12.8 \pm 3.8 cm, n = 18 colonies), T2 – a nest chamber at intermediate distance from the edge of the communal nest (26.5 \pm 8.5 cm, n = 13), and T3 – a nest chamber near the centre of the communal nest (55.5 \pm 14.7 cm, n = 20).

After inserting the temperature probe, we sealed off the entrance to the nest chamber using chicken wire and a single layer of mosquito netting. This allowed the normal airflow in and out of the chambers, but prevented birds from entering the chambers, which would disturb our measurements of the physical thermoregulatory conditions inside the chamber. The ambient temperature was logged near the thatch on the branch supporting the communal nest in the shade and at a similar height from the ground as the communal nest. The temperature inside the three chambers and the ambient temperature were measured

simultaneously for a continuous period of 78 h 14 min 32 s \pm 14 h 7 min 18 s per nest (mean \pm SD). All temperature measurements were conducted before and during the early phase of the breeding season when the sociable weavers may regularly switch between nest chambers for roosting (REvD and MP unpubl.). None of the monitored chambers contained eggs or nestlings. Thus, disturbance to roosting or breeding activity was likely to be minimal. The depth of the nest chamber where we inserted the temperature probe was measured as a straight line from the outer rim of the entrance tunnel alongside the lip at the base of the nest chamber to the ceiling of the nest chamber using a ruler.

Communal nest volume

A digital photograph was taken from each of four sides of the nest, each at a 90° angle to each other, at a fixed distance (10 m) using a Panasonic Lumix TZ-7 camera. A 1 m ruler with 10 cm markings was held against the nest side that was photographed. The digital images were then imported into Adobe Photoshop (ver. 7.0) to estimate the length, width and height of the nest, using our ruler to calibrate our measurements and the 'measure tool' in Adobe Photoshop to take the measurements. The length (or width) and height were taken across the centre of the visible side of the thatch on the photograph. To account for the irregularity of the nest shape to some extent, we estimated height of the thatch as the mean of the height measured on each of the four photographs (percentage of variation in measurements relative to the largest measurement per nest: 23.2 \pm 14.1% (mean \pm SD)), length as the mean of the length measured on the two photographs of the two longest sides of the thatch (9.5 \pm 9.8%), and width as the mean of the length of the two shortest sides (13.6 \pm 9.6%). The volume (in m³) of the communal nest was then estimated as length \times width \times height.

Nest chamber assignment

The birds of the 20 colonies that we monitored were trapped using mist nets positioned around the nests at dawn, and were ringed with one numbered, metal ring and three colour rings (Covas et al. 2011). We labelled all nest chambers with an individually numbered tag. Individuals were assigned to nest chambers when they were seen building or roosting inside nest chambers at 15 colonies in 2010 and at 14 colonies in 2011 in observations conducted throughout the day (between 06:16 and 18:50 SAST). These observations were performed from a hide positioned beneath the nest for an average of 33 h 53 min \pm 24 h 56 min per nest. The hide was placed initially at about 10 m from the colony to accustom the birds to the hide and avoid disturbance. After at least 12 h the hide was moved closer to the nest so that the nest chambers could be observed. When an individual used multiple nest chambers ($n = 175$ individuals out of a total of $n = 432$ individuals used 2.9 \pm 1.2 (mean \pm SD) nest chambers), we included the chamber that was used most frequently in the analyses concerning how age is related to the position of the nest chamber in the nest. For each individual we had 4.7 \pm 7.9 (mean \pm SD) observations.

Using a long-term dataset on the population of sociable weavers we studied (which has been regularly ringed since 1993), we then searched for birds whose exact age was known, i.e. sociable weavers in the database that were first ringed as nestlings. When two individuals of known age used the same chamber at equal frequency, we randomly selected an individual to include in the analyses ($n = 6$ nest chambers; at four out of these six chambers the individuals had the same age). For each individual of known age we had 2.7 \pm 2.1 observations.

We used photographs taken from the underside of the communal nest, so that a 1 m ruler, the labelled nest chambers and their position were visible to measure the distance between the nest chambers and the nearest edge of the communal nest. For the nests where we assigned individuals to nest chambers in 2010, we also determined in which chambers, and at which position, a breeding attempt was observed ($n = 75$ nest chambers in 13 communal nests) between 9 September 2010 and 6 April 2011. A 'breeding attempt' was defined as eggs were laid. All nest chambers of 14 nests were checked for breeding activity approximately every three days during this period. For graphical purposes in Fig. 2 and 4 and for the analysis concerning likelihood of breeding activity we classified the position of the nest chambers following the criteria described above (T1 < 16.6 cm, 16.6 cm \leq T2 < 35.0 cm, and T3 \geq 35.0 cm).

Statistical analyses

The volume of the communal nest (m³) (or nest segment if a colony consisted of two or three separate nest structures) and the number of birds in each colony (or nest structure) were highly correlated ($r = 0.880$, DF = 19, $p < 0.001$). We therefore include only the volume in the models we present.

We used linear mixed models (LMM) with restricted maximum likelihood implemented using the package nlme in R (R Development Core Team) to account for the pseudoreplication introduced by the statistical non-independence of multiple temperature measurements at a given position of a nest chamber (i.e. near the edge, in the centre or in between those positions) and of nest chambers within colonies. Position (where appropriate) and colony ID were entered as random factors with position nested within colony.

To determine whether communal nest volume or nest chamber position has thermoregulatory consequences, we used the temperature buffer ΔT , defined as the absolute difference between the ambient temperature and the temperature measured inside the nest chambers, as a response variable. We used the distance between the nest chamber and the nearest edge of the communal nest as the independent variable representing nest chamber position. Ambient temperature (°C) and nest volume (m³) were entered as additional covariates. ΔT was square-root-transformed prior to the analyses concerning the spatial variation in temperature benefits to achieve a normal distribution of the errors. In order to accommodate the serial autocorrelation in our data due to diurnal effects, we used the mean values per hour for ΔT and for the ambient temperature in our LMMs and applied a moving average model as the class of

autocorrelation structure (AIC = 2707.12, likelihood ratio = 3822.60, $p < 0.001$).

To test whether temperature variability changed towards the centre of the nest, we ran a separate LMM with the standard deviation of chamber temperature (T_{SD}) per position (i.e. T1, T2, and T3) per colony as the response variable. T_{SD} was log-transformed to achieve a normal error structure prior to analyses. To investigate whether the change in temperature buffer or variability may depend on the depth of the nest chambers, we ran an LMM with depth of the nest chambers in response to the distance to the nearest edge of the nest chamber and to communal nest volume, including colony ID as a random effect. In order to analyse how the depth of a nest chamber predicts its thermoregulatory capacities, in a separate LMM we used the means of ΔT per nest chamber as the response variable with the depth of the nest chamber, the communal nest volume and the ambient temperature as covariates, while colony ID was entered as a random effect.

To investigate whether the position of the nest chamber predicted the age of its occupants, we used a LMM with maximum likelihood and occupant's age as the response variable, the nest chamber's distance from the nearest edge and volume of the communal nest as covariates, and colony ID as a random factor. If an individual of known age used more than one nest chamber ($n = 12$ individuals using 3.0 ± 1.3 nest chambers) we used the average distance between the nest chambers and the nearest edge of the nest in the analysis. Five out of these 12 individuals used 3.2 ± 1.3 nest chambers that were of the same distance category (i.e. T1, T2 or T3). Age was log-transformed prior to analysis. To investigate whether the position of the nest chamber predicted the likelihood of a breeding attempt we calculated the proportion of nest chambers per position (i.e. T1, T2 and T3, using the criteria mentioned above) where a breeding attempt had been observed. This proportion of nest chambers was then square-root transformed and

included as the response variable in an LMM with restricted maximum likelihood with position of the nest chamber as the fixed effect, and colony ID as the random factor.

Results

Nest size

The ambient temperature at the colonies during observations ranged from 1.4°C at night to 42.4°C during the day (median = 20.8°C), while the temperature inside nest chambers ranged from 4.4 to 36.2°C (median = 22.3°C). ΔT ranged from 0.0 to 13.1°C (median = 2.6°C). Temperature was logged inside 51 nest chambers (18 at T1, 13 at T2, and 20 at T3) at 20 colonies, ranging in size from 0.7 m^3 to 10.0 m^3 and from 7 to 65 active nest chambers.

The thermoregulatory capacity of the sociable weaver's nest was not associated with the volume of the communal nest (Fig. 1, Table 1a), although ΔT was smallest at the nest with the smallest volume.

Spatial variation of temperature buffer

ΔT increased significantly towards the centre of the colony (Fig. 2a, Table 1a), so that ΔT increased on average by 0.47°C from position T1 to position T2 and by 0.57°C from T1 to T3. These results remained unchanged when T3 or T1 were excluded from these analyses: ΔT increased significantly with the distance from the nearest edge from T1 to T2 (0.013 ± 0.005 , $DF = 11$, $t = 2.447$, $p = 0.032$) and from T2 to T3 (0.005 ± 0.002 , $DF = 12$, $t = 2.633$, $p = 0.022$). Not only did ΔT increase towards the centre of the colony, but the temperature inside the chambers also became less variable (Fig. 2b, Table 1b), so that standard deviation of ΔT decreased on average by 0.73°C from position T1 to position T2 and by 0.59°C from T1 to T3.

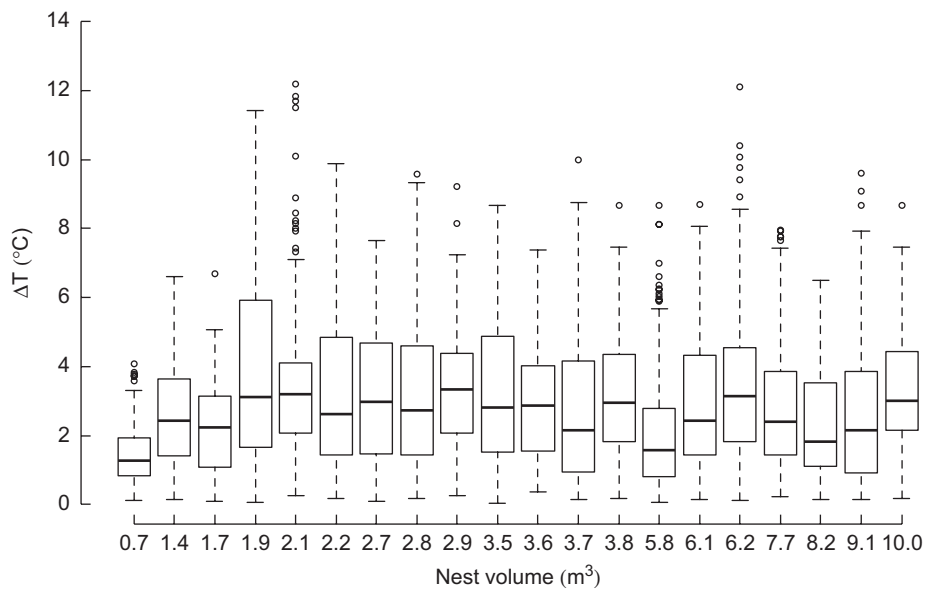


Figure 1. Temperature buffer, ΔT ($^\circ\text{C}$), as a function of the volume of the communal nest of sociable weavers. Boxplots indicate the median, the interquartile range, the maximum and minimum values excluding outliers, and outliers; $n = 20$ colonies.

Table 1. (a) ΔT ($^{\circ}\text{C}$), (b) T_{SD} , and (c) the depth of sociable weaver nest chambers in relation to the volume of the communal nest and the distance between the nest chamber and the nearest edge of the communal nest. The random terms ‘Colony’ and ‘Position’ had a significant effect in model (a) (likelihood ratio ‘Colony’: 191.90, $p < 0.001$; likelihood ratio ‘Position’: 111.92, $p < 0.001$), while the random effects in the models (b) and (c) were non-significant ($p > 0.113$); $n = 20$ colonies.

Fixed effects	Model effect estimate \pm SE	DF	t	p
(a) ΔT				
Distance from edge	0.007 \pm 0.002	30	4.733	<0.001
Volume	-0.004 \pm 0.015	18	-0.299	0.769
Ambient temperature	-0.010 \pm 0.002	4098	-5.459	<0.001
(b) T_{SD}				
Distance from edge	-0.004 \pm 0.001	29	-3.562	0.001
Volume	$< 1.0 \times 10^{-7} \pm 1.0 \times 10^{-7}$	18	1.518	0.146
Ambient temperature	-0.041 \pm 0.013	29	-3.160	0.004
(c) Nest chamber depth				
Distance from edge	0.438 \pm 0.197	31	2.220	0.034
Volume	$1.0 \times 10^{-6} \pm 2.0 \times 10^{-6}$	18	1.413	0.175

The low effect estimates of these results are probably a consequence of the relatively large spread of the data surrounding the observed increase in ΔT towards the centre of the colony.

The depth of the nest chambers was not predicted by the volume of the communal nest (Table 1c), but increased significantly towards the centre of the communal nest (Fig. 2c; Table 1c). Accordingly, ΔT increased (Fig. 3;

Table 2a), and T_{SD} decreased with the depth of the chamber (Table 2b). Volume appeared to be negatively associated with ΔT in this model, but the effect estimate of this result is extremely low. We did not find a significant interaction between depth of the chamber and the distance from nearest edge (DF = 25, $t = -0.148$, $p = 0.884$; random effect ‘Colony’: $p = 0.999$).

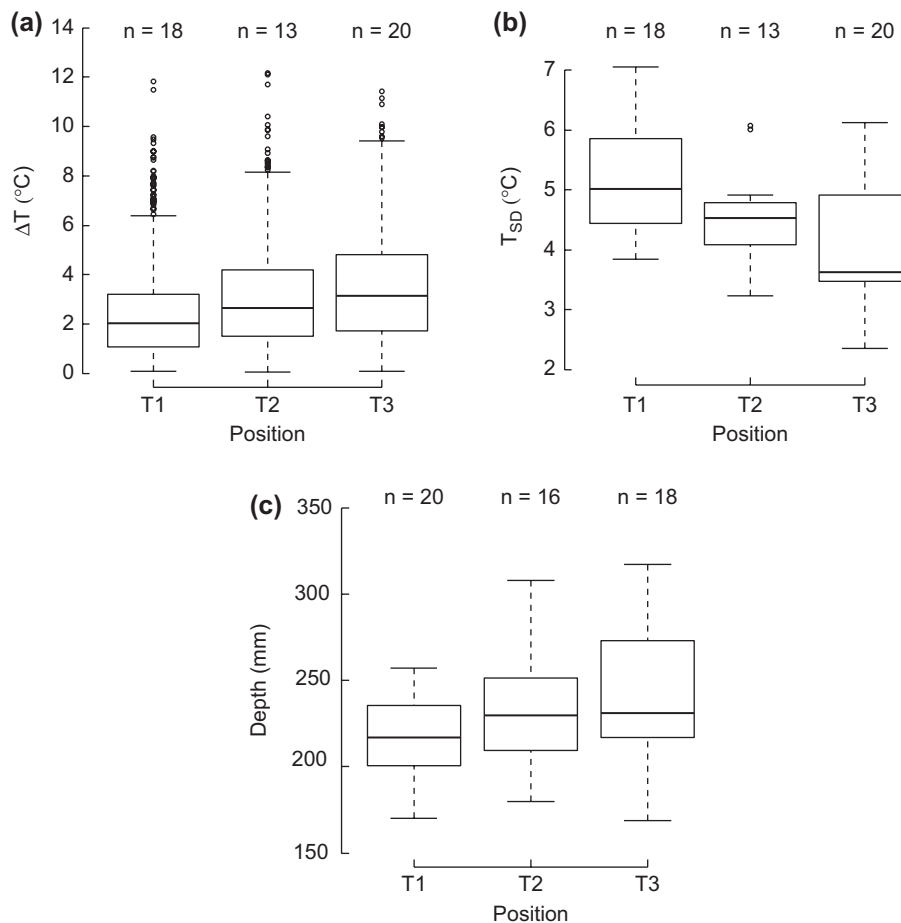


Figure 2. (a) The temperature buffer, ΔT ($^{\circ}\text{C}$); (b) standard deviation of ΔT , T_{SD} ($^{\circ}\text{C}$); and (c) the depth of the nest chamber as a function of the chambers’ position in the communal nests of sociable weavers. T1, T2 and T3 correspond to positions near the edge of the communal nest (T1), near the centre of the communal nest (T3), and in between those two positions (T2; see text for mean \pm SD distance from the nearest edge for each position) and are used here for graphical purposes; n is the number of colonies.

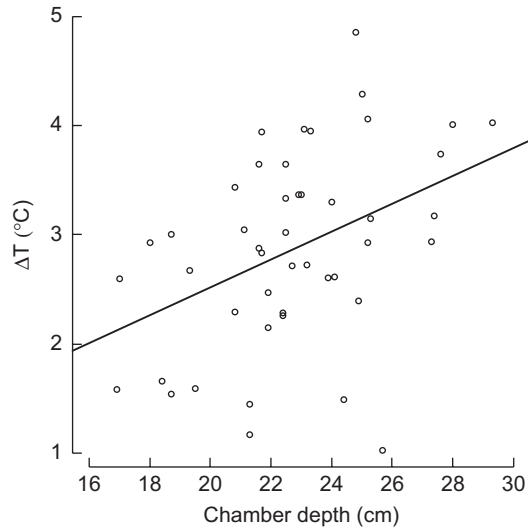


Figure 3. Temperature buffer, ΔT ($^{\circ}\text{C}$), inside sociable weaver nest chambers as a function of their depth.

Social organisation and spatially structured benefits

We knew the exact age (1–12 yr (range), 4.1 ± 2.7 (mean \pm SD) yr) for 46 individuals with an identified nest chamber. Older individuals occupied nest chambers near the centre of the colony, while nest chambers near the colony edge were occupied by younger birds (Fig. 4a, Table 3a). Using our observations of breeding attempts between September 2010 and April 2011, we found that breeding was more likely to take place in nest chambers near the centre of the communal nest (Table 3b; Fig. 4b).

Discussion

Our study shows that the sociable weaver's unique communal nest is an effective temperature buffer. The communal

Table 2. Temperature inside sociable weaver nest chambers as a function of the depth of the nest chamber. (a) ΔT ($^{\circ}\text{C}$) and (b) T_{SD} ($^{\circ}\text{C}$). The random term 'Colony' was not significant in model (a) ($p = 0.999$), but had a significant effect in (b) (likelihood ratio: 4.77, $p = 0.029$).

	Model effect estimate \pm SE	DF	t	p
(a) ΔT				
Depth	0.153 ± 0.032	27	4.758	<0.001
Volume	$-1.0 \times 10^{-7} \pm <1.0 \times 10^{-7}$	18	-2.720	0.014
Ambient temperature	0.136 ± 0.043	27	3.184	0.004
(b) T_{SD}				
Depth	-0.124 ± 0.036	27	-3.398	0.002
Volume	$<1.0 \times 10^{-7} \pm 1.0 \times 10^{-7}$	18	1.819	0.086
Ambient temperature	-0.205 ± 0.066	27	-3.120	0.004

structure acts as a buffer against the cold temperatures at night (this is likely to be especially important during winter when temperatures may drop well below 0°C at night with temperatures of -5°C or lower being relatively common) and against high temperatures during the day (during the summer temperatures regularly reach more than 40°C ; <www.climate-charts.com>). Developing sociable weaver offspring may benefit from higher temperatures inside chambers at night during the breeding period between September and March. Although relatively little is known about the effect of temperature on the development of eggs and nestlings, stable temperatures inside the nest chambers are likely to be beneficial (Martin and Schwabl 2008, Nord and Nilsson 2011). The temperature buffer may also mitigate the energetic demand on parents to maintain a stable temperature during the incubation and nestling phase (Drent 1975, Collias and Collias 1984, Reid et al. 2000, Kosztolányi et al. 2009, Dawson et al. 2011).

Interestingly, our study also shows spatial variation in the thermoregulatory benefits of the nest. These benefits increased towards the centre of the communal nest and with the depth to which the nest chamber is embedded into the thatch. Our data further suggest that this variation has

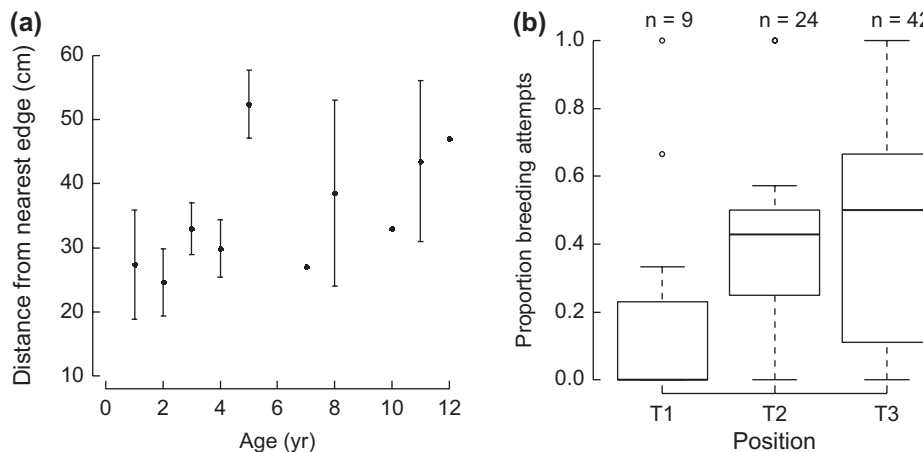


Figure 4. (a) The age of the individuals versus the distance between their nest chamber and the nearest edge of the communal nest (mean \pm SE; $n = 46$ individuals) and (b) the proportion of nest chambers where a breeding attempt was observed as a function of the position of the nest chamber. T1, T2 and T3 correspond to positions near the edge of the communal nest (T1), near the centre of the communal nest (T3), and in between those two positions (T2; see text for mean \pm SD distance from the nearest edge for each position) and are used here for graphical purposes; n is the number of nest chambers.

Table 3. (a) Age and (b) the proportion of nest chambers where a breeding attempt was observed as a function of the position of the nest chamber in the communal nest of sociable weavers. The random term 'Colony' was not significant in models (a) and (b) ($p = 0.999$). Position T1 is used as the reference category (intercept) in (b).

	Model effect estimate \pm SE	DF	t	p
(a)				
Distance from edge	0.016 \pm 0.006	27	2.577	0.016
Volume	$< 1.0 \times 10^{-7} \pm 0.5 \times 10^{-7}$	27	-0.740	0.465
(b)				
Intercept	0.122 \pm 0.140	24	0.871	0.392
T2	0.376 \pm 0.135	24	2.796	0.010
T3	0.313 \pm 0.135	24	2.330	0.029
Volume	0.019 \pm 0.019	11	0.968	0.354

consequences for the social organisation within colonies: we showed that the position of the nest chamber within the communal nest predicted the age of the occupant, and that breeding was more likely to take place towards the centre of the colony. We also found that ΔT did not increase with increasing communal nest volume overall, although there did appear to be some decrease in thermoregulatory benefits for the smallest nests.

Any absolute thermoregulatory benefit of nesting in a communal nest appears to be small, given that there was a median difference of only 2.6°C in recorded nest chamber temperature compared to ambient temperature. Nonetheless, a small difference in temperature is likely to be significant for a small bird like the sociable weaver (mean body mass = 26.9 g) that not only breeds but also roosts in the nest chambers throughout the year (Ferguson et al. 2002). In contrast to White et al. (1975), who concluded that the insulative effectiveness (and heat input of the occupants) of the communal nest increases with size, our results suggests that there is no general thermoregulatory benefit of larger colony size. The proportion of high quality nest chambers away from edges of nests is higher in larger colonies, which could provide a benefit of communal living, but against that benefit are likely to be increasing costs of nest predation, parasite infection and brood reduction (Spottiswoode 2007). Furthermore, the risk of the nest becoming too heavy for the supporting tree (eventually resulting in branches breaking and the nest falling out of the tree) increases with nest size (REvD unpubl., White et al. 1975).

Given minimal thermoregulatory benefits of larger colonies, there may be benefits other than thermoregulation from living in larger communities. Larger groups are potentially more successful at finding food (Ward and Zahavi 1973, Alonzo and Sheldon 2010, King et al. 2011) or reducing predation risk through enhanced vigilance (Harrison and Whitehouse 2011, Hirsch 2011). In addition, there is significant kin structure among males between communal nests of sociable weavers and they are facultative cooperative breeders in which helpers are generally related to the breeders they assist (Covas et al. 2006). Thus, thatch building may be a kin-selected behaviour (Hamilton 1964) if investment in the communal nest benefits relatives living within the same colony.

For example, contributions to building may depend on an individual's relatedness to other colony members and the spatial arrangement of any relatives in the communal structure.

Alternatively, the benefits of investing in nest construction may be selfish, rather than altruistic, with thatch building acting as a handicap signal (Zahavi 1995). For example, if thatch-building behaviour is costly, it may indicate the dominance status or parental quality of individuals and hence be used in mate choice (Zahavi 1995, Soler et al. 1998, Szentirmai et al. 2005, Berg et al. 2006, Schaedelin and Taborsky 2010, Sanz and Garcia-Navas 2011). A role of individual quality in the social organisation of sociable weaver nests is suggested by our findings that older birds occupied better quality nest chambers, and that breeding was more likely to take place in these chambers. We note that the fact that breeding was more likely in central chambers could be due to either the individual quality of the occupants or a direct consequence of the thermoregulatory characteristics of these chambers, or both. Further analyses are required to tease apart these effects.

Our observation that older individuals occupied the best quality nest chambers suggests competition for access to the best positions within the communal nest. Predation risk is unlikely to provide a satisfactory explanation for such competition for central chambers. Nest predators, mostly snakes (Cape cobras *Naja nivea* and boomslangs *Dispholidus typus*), cause an average of 75% of offspring mortality (Covas 2002). Snakes typically take all offspring present at a colony during a single foraging bout, although some nests do survive such events (Spottiswoode 2007). Whether offspring in central nest chambers, or in chambers that are more deeply embedded into the thatch, are more likely to survive such predation events remains to be investigated. Nevertheless, the relationship between nest chamber position and occupants' age and probability of breeding suggests that spatially structured benefits of the public good could strongly influence social organisation of sociable weavers. Similarly, in a study of long-tailed tits *Aegithalos caudatus* the benefits of roosting communally vary with position within the roost (Hatchwell et al. 2009) and access to the best positions is related to an individual's dominance status within the flock (McGowan et al. 2006).

It would be interesting to determine whether thatch building is costly and to investigate which individuals contribute to the public good most in order to substantiate the above propositions that thatch building may be a selfish behaviour associated with gaining access to breeding opportunities or that it may be a kin-selected behaviour. Addressing the costs of communal investment and the question of who should bear these costs will help us to explain how cooperation may be maintained in sociable weavers.

Acknowledgements – C. Spottiswoode, E. Herrmann, M. Anderson, D. J. Schaeffer and many volunteers contributed to the regular captures that allowed us to estimate the weavers' age. We are grateful to L. Malm for her help with the fieldwork, to De Beers Consolidated Mines for the opportunity to work at Benfontein Game Farm, and to Robert Magrath for his constructive comments on an earlier draft of this manuscript. This project conformed to the legal requirements of South Africa and has received a research

permit from the Northern Cape Province's department of Tourism, and Environment and Conservation (permit numbers FAUNA 480/2010, FAUNA 481/2010) and an ethics approval from the Univ. of Cape Town, South Africa (2010/RV14/RC). Our research has received funding from the Natural Environment Research Council (UK) to BJH, from the French ministry of research and CNRS to MP and CD, and from the Science and Technology Foundation (Portugal) and the Percy FitzPatrick Inst. of African Ornithology (DST/NRF Centre of Excellence) at the Univ. of Cape Town (South Africa) to RC.

References

- Alonzo, S. H. and Sheldon, B. C. 2010. Population density, social behaviour and sex allocation. – In: Székely, T., Moore, A. J. and Komdeur J. (eds), *Social behaviour: genes, ecology and evolution*. Cambridge Univ. Press, pp. 474–488.
- Arnqvist, G. and Rowe, L. 2005. *Sexual conflict*. – Princeton Univ. Press.
- Bartholomew, G. A., White, F. N. and Howell, T. R. 1976. The thermal significance of the nest of the sociable weaver *Philetairus socius*: summer observations. – *Ibis* 118: 402–410.
- Berg, M. L., Beintema, N. H., Welbergen, J. A. and Komdeur, J. 2006. The functional significance of multiple nest-building in the Australian reed warbler *Acrocephalus australis*. – *Ibis* 148: 395–404.
- Bollazzi, M. and Rocas, F. 2010. The thermoregulatory function of thatched nests in the South American grass-cutting ant, *Acromyrmex heyeri*. – *J. Insect Sci.* 10: 137.
- Brown, C. R., Covas, R., Anderson, M. D. and Bomberger Brown, M. 2003. Multistate estimates of survival and movement in relation to colony size in the sociable weaver. – *Behav. Ecol.* 14: 463–471.
- Collias, E. C. and Collias, N. E. 1978. Nest building and nesting behaviour of the sociable weaver *Philetairus socius*. – *Ibis* 120: 1–15.
- Collias, N. E. and Collias, E. C. 1964. Evolution of nest-building in the weaverbirds (Ploceidae). – *Univ. Calif. Publ. Zool.* 43: 1–239.
- Collias, N. E. and Collias, E. C. 1984. *Nest building and bird behaviour*. – Princeton Univ. Press.
- Covas, R. 2002. *Life-history evolution and cooperative breeding in the sociable weaver*. – PhD thesis, Univ. of Cape Town, South Africa.
- Covas, R., Dalecky, A., Caizergues, A. and Doutrelant, C. 2006. Kin associations and direct versus indirect benefits in colonial cooperatively breeding sociable weavers *Philetairus socius*. – *Behav. Ecol. Sociobiol.* 60: 323–331.
- Covas, R., Deville, A.-S., Doutrelant, C., Spottiswoode, C. N. and Grégoire, A. 2011. The effect of helpers on the post-fledging period in a cooperatively breeding bird, the sociable weaver. – *Anim. Behav.* 81: 121–126.
- Dawson, R. D., O'Brien, E. L. and Mlynowski, T. J. 2011. The price of insulation: costs and benefits of feather delivery to nests for male tree swallows *Tachycineta bicolor*. – *J. Avian Biol.* 42: 93–102.
- Doutrelant, C., Covas, R., Caizergues, A. and du Plessis, M. 2004. Unexpected sex ratio adjustment in a colonial cooperative bird: pairs with helpers produce more of the helping sex whereas pairs without helpers do not. – *Behav. Ecol. Sociobiol.* 56: 149–154.
- Drent, R. H. 1975. Incubation. – In: Farner, D. S. and King, J. R. (eds), *Avian biology*. Academic Press, pp. 333–420.
- Edelman, A. J. 2011. Kangaroo rats remodel burrows in response to seasonal changes in environmental conditions. – *Ethology* 117: 430–439.
- Ferguson, J. W. H., Nijland, M. J. M. and Bennett, N. C. 2002. Simple roost nests confer large energetic savings for sparrowweavers. – *J. Comp. Physiol. B* 172: 137–143.
- Ford, F. and Johnson, C. 2007. Eroding abodes and vanished bridges: historical biogeography of the substrate specialist pebble-mound mice (*Pseudomys*). – *J. Biogeogr.* 34: 514–523.
- Garza, J. C., Dallas, J., Duryadi, D., Gerasimov, S., Croset, H. and Boursot, P. 1997. Social structure of the mound-building mouse *Mus spicilegus* revealed by genetic analysis with microsatellites. – *Mol. Ecol.* 6: 1009–1017.
- Gutierrez, N. L., Hilborn, R. and Defeo, O. 2011. Leadership, social capital and incentives promote successful fisheries. – *Nature* 470: 385–388.
- Hamilton, W. D. 1964. The evolution of social behavior. – *J. Theor. Biol.* 7: 1–52.
- Hansell, M. H. 2005. *Animal architecture*. – Oxford Univ. Press.
- Hardin, G. 1968. The tragedy of the commons. – *Science* 162: 1243–1248.
- Harrison, N. M. and Whitehouse, M. J. 2011. Mixed-species flocks: an example of niche construction? – *Anim. Behav.* 81: 675–682.
- 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.
- Hirsch, B. T. 2011. Within-group spatial position in ring-tailed coatis: balancing predation, feeding competition, and social competition. – *Behav. Ecol. Sociobiol.* 65: 391–399.
- Hözl, M., Hoi, H., Darolova, A., Kristofik, J. and Penn, D. 2009. Why do the mounds of *Mus spicilegus* vary so much in size and composition? – *Mamm. Biol.* 74: 308–314.
- Humphries, S. and Ruxton, G. D. 1999. Bower-building: coevolution of display traits in response to the cost of female choice? – *Ecol. Lett.* 2: 404–413.
- Jackson, T. P. 2000. Adaptation to living in an open arid environment: lessons from the burrow structure of the two southern African whistling rats, *Parotomys brantsii* and *P. littledalei*. – *J. Arid Environ.* 46: 345–355.
- King, A. J., Narraway, C., Hodgson, L., Weatherill, A., Sommer, V. and Sumner, S. 2011. Performance of human groups in social foraging: the role of communication in consensus decision making. – *Biol. Lett.* 7: 237–240.
- Kleindorfer, S. 2007. Nesting success in Darwin's small tree finch, *Camarhynchus parvulus*: evidence of female preference for older males and more concealed nests. – *Anim. Behav.* 74: 795–804.
- Kosztolányi, A., Cuthill, I. C. and Székely, T. 2009. Negotiation between parents over care: reversible compensation during incubation. – *Behav. Ecol.* 20: 446–452.
- Maclean, G. L. 1973. The sociable weaver, part 2: nest architecture and social organisation. – *Ostrich* 44: 191–218.
- MacLean, R. C. and Gudelj, I. 2006. Resource competition and social conflict in experimental populations of yeast. – *Nature* 441: 498–501.
- Mainwaring, M. C. and Hartley, I. R. 2009. Experimental evidence for state-dependent nest weight in the blue tit, *Cyanistes caeruleus*. – *Behav. Process.* 81: 144–146.
- Manning, C. J., Wakeland, E. K. and Potts, W. K. 1992. Communal nesting patterns in mice implicate MHC genes in kin recognition. – *Nature* 360: 581–583.
- Martin, T. E. and Schwabl, H. 2008. Variation in maternal effects and embryonic development rates among passerine species. – *Phil. Trans. R. Soc. B* 363: 1663–1674.
- McGowan, A., Sharp, S. P. and Hatchwell, B. J. 2004. The structure and function of nests of long-tailed tits *Aegithalos caudatus*. – *Funct. Ecol.* 18: 578–583.
- McGowan, A., Sharp, S. P., Simeoni, M. and Hatchwell, B. J. 2006. Competing for position in the communal roosts of long-tailed tits. – *Anim. Behav.* 72: 1035–1043.

- Moreno, J., Lobato, E., Gonzalez-Braojos, S. and Ruiz-de Castaneda, R. 2010. Nest construction costs affect nestling growth: a field experiment in a cavity-nesting passerine. – *Acta Ornithol.* 45: 139–145.
- Navarro, J. L., Martella, M. B. and Bucher, E. H. 1995. Effects of laying date, clutch size, and communal nest size on the reproductive success of monk parakeets. – *Wilson Bull.* 107: 742–746.
- Nord, A. and Nilsson, J. A. 2011. Incubation temperature affects growth and energy metabolism in blue tit nestlings. – *Am. Nat.* 178: 639–651.
- Olsson, K. H., Kvarnemo, C. and Svensson, O. 2009. Relative costs of courtship behaviours in nest-building sand gobies. – *Anim. Behav.* 77: 541–546.
- Prokop, P. and Trnka, A. 2011. Why do grebes cover their nests? Laboratory and field tests of two alternative hypotheses. – *J. Ethol.* 29: 17–22.
- Rankin, D. J., Bargum, K. and Kokko, H. 2007. The tragedy of the commons in evolutionary biology. – *Trends Ecol. Evol.* 22: 643–651.
- Reid, J. M., Monaghan, P. and Ruxton, G. D. 2000. The consequences of clutch size for incubation conditions and hatching success in starlings. – *Funct. Ecol.* 14: 560–565.
- Reid, J. M., Cresswell, W., Holt, S., Mellanby, R. J., Whitfield, D. P. and Ruxton, G. D. 2002. Nest scrape design and clutch heat loss in pectoral sandpipers (*Calidris melanotos*). – *Funct. Ecol.* 16: 305–312.
- Sanz, J. J. and Garcia-Navas, V. 2011. Nest ornamentation in blue tits: is feather carrying ability a male status signal? – *Behav. Ecol.* 22: 240–247.
- Schaedelin, F. C. and Taborsky, M. 2010. Female choice of a non-bodily ornament: an experimental study of cichlid sand craters in *Cyathopharynx furcifer*. – *Behav. Ecol. Sociobiol.* 64: 1437–1447.
- Siedelmann, K. 1999. The function of the vestibulum in nests of a solitary stem-nesting bee, *Osmia rufa*. – *Apidologie* 30: 19–29.
- Soler, J. J., Møller, A. P. and Soler, M. 1998. Nest building, sexual selection and parental investment. – *Evol. Ecol.* 12: 427–441.
- Spottiswoode, C. N. 2005. Sociable weaver, *Philetairus socius*. – In: Hockey, P. A. R., Dean, W. R. J. and Ryan, P. G. (eds), Roberts – birds of Southern Africa. Trustees of the John Voelcker Bird Fund, Cape Town, pp. 1007–1010.
- Spottiswoode, C. N. 2007. Phenotypic sorting in morphology and reproductive investment among sociable weaver colonies. – *Oecologia* 154: 589–600.
- Szentirmai, I., Komdeur, J. and Székely, T. 2005. What makes a nest-building male successful? Male behavior and female care in penduline tits. – *Behav. Ecol.* 16: 994–1000.
- Ward, P. and Zahavi, A. 1973. The importance of certain assemblages of birds as “information centers” for finding food. – *Ibis* 115: 517–534.
- West, S. A., Griffin, A. S., Gardner, A. and Diggle, S. P. 2006. Social evolution theory for microorganisms. – *Nat. Rev. Microbiol.* 4: 597–607.
- White, F. N., Bartholomew, G. A. and Howell, T. R. 1975. The thermal significance of the nest of the sociable weaver *Philetairus socius*: winter observations. – *Ibis* 117: 171–179.
- Zahavi, A. 1995. Altruism as a handicap – the limitations of kin selection and reciprocity. – *J. Avian Biol.* 26: 1–3.