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**RESEARCH ARTICLE** 

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# Sex and age differences in the preference for materials for the communal nests of sociable weavers Philetairus socius

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## Abstract

Many animals build structures that are used for shelter, reproduction or to capture prey. The type of material used to build these structures is likely to influence their solidity, thermoregulation capacity and, in some species, may influence the attractiveness of the builders. In the case of animal nests, evidence for preference of nesting material has been documented in several species but, to date, few field experiments have been conducted, and it was seldom investigated whether individuals' attributes affected those preferences. We investigated these preferences in relation to individual attributes on sociable weavers (Philetairus socius) that build communally one of the largest known nest structures, using dry grass. We conducted an experiment where we presented two piles of straws, long and short, to wild individuals. We recorded 900h of video and used a deep learning method to automatically detect images where birds were present (266 colour-ringed individuals). Our results showed that males picked more straws than females and showed a preference for longer straws, while no preference was found for females. In addition, older males showed a preference for long straws compared to younger males. Finally, males displayed higher repeatability than females in their preference for longer straws. In conclusion, we show that choice of nesting material is not random, and that preferences are associated with individual attributes. Future studies should assess how building is associated with social status, mating and reproductive success of the individuals building, to investigate which of these factors could have shaped the evolution of these preferences.

#### **KEYWORDS**

animal architecture, behaviour, building, passerine, repeatability, selection

## 1 | INTRODUCTION

Many species of animals build structures that modify their physical environment in ways that serve various purposes for them and other

species. These structures, referred to as animal architecture, are widespread in nature, from invertebrates to humans (Laidre, 2021a). They can increase survival through protection against predators (Caro, 2005), provide thermal insulation (Hilton et al., 2004;

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Lombardo et al., 1995), help to capture prey, store food, roosting and/or be associated with courtship or reproduction (Laidre, 2021a). It is thus expected for the quality of these animal structures to be under strong selection, which has been supported by several studies (Mainwaring et al., 2014). For example, in hermit crabs (*Coenobita compressus*), shells from other individuals are used for shelter, being modified over successive generations of crabs. These modified shells were found to be associated with social dynamics and reproductive success (Laidre, 2019).

Among the examples of animal architecture, nests and burrows are widespread. They provide shelter for animals to raise their offspring, roost or hide from predators. These structures are found in most animal taxa, from invertebrates to mammals, fish and birds (Hansell, 2000; Heenan, 2013; Mainwaring et al., 2023). Evidence of preferences for nest material has been shown in different animal taxa, and it seems that both innate and acquired preferences exist (Breen et al., 2016). For instance, in blue tits (Cyanistes caeruleus), females with increased food availability put more moss, dead grass and other plant materials in their nest and less fine dry grass, hair, wool and feathers (Mainwaring & Hartley, 2009), while in termites Odontotermes nr. pauperans preference of soil types vary in relation to the part of the structure being built (Jouquet et al., 2002). However, it remains poorly known whether material preferences differ between individuals, and if individual attributes influence these preferences.

Sex differences in nesting material preference is rarely investigated (Sheard et al., 2023), one reason being that to date the sex of the builders is only known in 20% of the world's bird species (Healy et al., 2023). But, in species where both sexes construct the nest (Mainwaring et al., 2021), sexual differences may arise if males and females construct different part of the nests and this requires materials with different structural characteristics, such as increased or decreased flexibility, malleability, elasticity etc (Kern & Van Riper III, 1984; Biddle et al., 2017, 2018; Jouquet et al., 2002). For example, in captive village weavers (*Ploceus cucullatus*), males use palm fronds and giant Mexican reed grass to build the outer nest structures, while females use blue grass and small feathers to finish the inside of the nest (Collias & Collias, 1962). In addition, differences in nest material preference may exist if one sex also build to signal its quality to the other sex, and thus male and female building behaviour may not be exactly under the same selective pressures. For instance, in species where male nest building behaviour affects female preference, males may use conspicuous materials to attract females. This is the case in the cichlid fish *Neolamprologus multifasciatus*, where more shells used in nest building attract more females (Jordan et al., 2016).

Differences in preference for nest building material can also arise from differences in age and experience. For instance, an experimental study showed that failing or succeeding in previous breeding attempts affects the preference for nest building material on captive zebra finches (*Taeniopygia guttata*) (Muth & Healy, 2011, see also Muth & Healy, 2014 for similar result in this species).

Very few studies have used experiments to investigate choice for nest materials in a wild setting. In two experimental studies conducted on pied flycatchers (*Ficedula hypoleuca*), females showed a preference for deer hairs over wool and feathers (Briggs & Mainwaring, 2019) and birds were found to prefer white anthropogenic material over three other colours (Briggs et al., 2023).

In this study, we used a field experiment to study if birds display a preference in relation to their choice of nest material, and we investigate whether these preferences differ in relation to sex and age. We used as a model species the Sociable weaver (*Philaiterus socius*) that builds a remarkable communal nest structure, which is among the largest in the animal kingdom (Collias, 1964) (Figure 1c). Sociable weavers are ~28g passerines endemic to the Kalahari region of south-west Africa and live in large groups up to several hundreds of individuals of different ages (Maclean, 1973a). This species presents male philopatry,



FIGURE 1 Experimental design. (a) The treatment protocol, with trials 1 and 2, respectively, composed of 30 long and 30 short straws; and 30 long and 60 short straws; (b) A picture showing the pile of 30 long straws on the left and the pile of 30 short straws on the right; (c) The overall view of the communal nest and the straw piles' locations at four different positions. The position of the straw piles on the ground changed every day (for long-short, positions were 1–2; 2–1; 3–4 and 4–3, replicated two times per positions). leading to genetic structure among the resident males (Covas et al., 2006; van Dijk et al., 2015). The nest structure comprises a 'thatched' roof and numerous individual chambers (up to several hundreds in the largest nests), wherein the birds roost and breed (Maclean, 1973b). These communal nests are known to provide protection from the extreme temperatures known to occur in this region (very cold nights in winter and hot days in summer) (Lowney et al., 2020; van Dijk et al., 2013; White et al., 1975). They have been shown also to function as biodiversity hotspots, by providing foraging sites, shade or roosting sites to many other animals of the Kalahari Desert (Lowney & Thomson, 2021). The communal nest structures are built by inserting straws into the structure, and only the inside of the individual nest chambers is weaved (Collias & Collias, 1978; Maclean, 1973b).

In the field, sociable weavers build with varying straw sizes, from very short to very long straws, up to thrice their size. Nest materials are gathered around the colony, but very long straws can be brought from far away (authors' personal observations). In addition, nest materials can be stolen from other individuals or from the nest (either from the outer structure or from inside the nest chambers; authors' personal observations). Both sexes build but males generally build more than females, and build more on the outside of the structure (Collias & Collias, 1978; Leighton et al., 2015; van Dijk et al., 2014). An experiment conducted in captivity, suggested a preference to build with longer straws (Collias & Collias, 1978). However, the sample size was small (10 birds) and the observations were conducted for only 80min.

Here, we offered two sizes of straws underneath sociable weaver communal nests. We filmed the straws to investigate the birds' preference and recorded >3500 straw-picking events (over a total of 8 days at nine communal nests) for a total of 266 males and females. We used deep learning methods to automatically detect and pre-process these events. We tested (i) whether, as captive individuals, wild sociable weavers had a preference for longer straws, (ii) whether this behaviour varied with sex and (iii) age and (iv) if it was consistent over a short-term time scale. We expected sexual differences as males and females are known to build on different locations, as showed in finches and thrushes nests (Biddle et al., 2017, 2018), which may require different nesting materials. We further expected age differences as nest building skills, motivation to build and nest location (e.g. whether individuals acquire their own nest) should change with age.

## 2 | MATERIALS AND METHODS

## 2.1 | Study area

The study was conducted at Benfontein Nature Reserve, South Africa (-28°818 S, 24°816 E, 1190 m), which covers approximately  $15 \text{ km}^2$  of open savannah and at the time of the study contained about 30 active sociable weaver communal nests. In our study site, these nests are not equally spaced, varying from a few 100 m

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to ca. 4 km apart, and are located in a similar landscape. Most individuals in this population are ringed (93.5%, N = 514) and their age is known as a result of a long-term capture-recapture study initiated in 1993 (Covas et al., 2002) and detailed breeding monitoring (since 2010; e.g. Fortuna et al., 2021; Paquet et al., 2013). Birds are ringed with three colour rings and a numbered metal ring combination, which allows them to be visually identified in the field. Sex is obtained through genetic sexing (Covas et al., 2006; Doutrelant et al., 2004).

## 2.2 | Field experiment

To test for straw size preference, we simultaneously presented, under the communal nests, two piles of straw of different lengths (Figure 1a,b). The pile of short straws consisted of straws shorter than 12 cm in length (i.e. smaller than the birds' body length), whilst the long straw pile consisted of straws longer than 20 cm (i.e. longer than the birds body length). The experiment took place at nine communal nests between March and April 2021. This period corresponded to the end of the breeding season and coincided with a period where dry grass suitable for nest building was very scarce. This was mainly a result of very high rainfall during that summer (489 mm between August and February 2021, against 274mm on average for the same periods over the 27 previous years), resulting in the presence of very fresh green grass all around. The soil was cleared before placing the piles of straw to ensure that individuals mostly used straws from the experimental set-up and not straws that were already on the ground at this position. The straws were collected from a fallen communal nest nearby and placed under the communal nests being tested (Figure 1c). Both piles were spaced approximately 1 m apart.

We performed two trials (Figure 1a). Trial one: at five of the communal nests, we offered the same number of straws in both piles and thus placed one pile of 30 short straws and one pile of 30 long straws. However, these two piles differed in volume, and the pile of long straws might be more visible (Figure 1b). Trial two: at four other communal nests, we offered piles more similar in terms of volume and thus placed one pile of 60 short straws and one pile of 30 long straws. In parallel, to evaluate the potential effect of presenting different number/volume of straws, we examined in control trials the time it took to discover a pile of 60 short straws versus a pile 30 short straws. The results for this control trial (presented in Table S1) showed no difference in the time taken to find the two piles, and we concluded that straw pile volumes and number did not affect the weavers' behaviour. In consequence, we only control for the factor number of straws given (30 vs. 60) but not the factor 'trial' (one or two) in the statistical models that allowed us to detect whether the length of straws influence nest material preference in this species (see statistical section below).

Trials one and two were conducted over 8 days and the position of the straws' piles were repeated twice at four different positions under each communal nest used in the experiment WILEY-ethology

(Figure 1c). This means that on day one the two straw piles would be positioned in a given way, and the position was inverted on the consecutive day, resulting in a total of eight replicates ( $2 \times 4$  days) per communal nest. The control trials were conducted over 2 days at each of the communal nests and piles were presented at two positions under the nests.

We did not record what the birds did with the straws picked (i.e. whether they use them for building and where). However, observations conducted throughout the year showed that the vast majority of straws picked by the birds are used to build either inside the chambers or on the communal parts of the nest (on 12,724 building events observed for another study, 95.8% ended with a bird building with the straw it picked: authors' personal observations).

A camera (Sony Handycam HDR-CX240E–Camcorder– 1080p–2.51 MP–27× optical zoom) recorded each straw pile for approximately 5 h (as dictated by the battery lifespan) ((mean $\pm$ SD) 5h35 $\pm$ 0h51, N=123 videos). It allowed us to obtain the colour ring combinations of all the individuals visiting the piles of straw.

## 2.3 | Development of a deep learning pipeline to scan the videos and extract the sub-videos featuring birds

To help process the 850h of videos we collected, we developed a deep learning pipeline to scan the videos and extract the sub-videos that featured birds. We used a Yolov3 object detection system (Redmon & Farhadi, 2018) from the open-source neural network framework written in C and CUDA. Darknet (Redmon, 2013). This system was based on transfer learning from the COCO weights (Lin et al., 2014) that has been trained to detect 80 classes, including the class 'bird'. We run the detection on the videos for one picture per second of videos to only get individuals that were present more than a second. Once the detection frames were collected, we cut the full videos into multiple sub-videos according to the detection frames. We tested the method on ca. 100 individuals passing on the video footage and 100% of the birds recorded for more than a second on screen were retrieved. We used this threshold to avoid including individuals that were just passing by. There were also a few false positive sub-videos (when birds were wrongly detected by the deep learning network, as no birds are present on the sub-videos) (4%, N = 100 sub-videos).

## 2.4 | Individual identification

Within the sub-videos, individuals were identified by their colour ring combinations. For each individual identified, we used our long-term dataset to gather information on sex and age. We noted whether the identified birds were leaving the screen flying away with a straw in their beak. Sociable weavers always fly with only one-piece straw in the beak when transporting straws to build the nest.

## 2.5 | STRANGE statement

The STRANGEness of our test sample was evaluated as described by Webster and Rutz (2020). Our individuals are wild animals that were not raised by humans in specific conditions. Detailed breeding monitoring is conducted at our study site and some of the colonies have feeding stations nearby which are open to birds every third day to collect data on social associations, but we have no reason to think that these could affect the birds response to the treatments conducted in our experiment. These procedures have been approved by the Northern Cape Nature Conservation (permit FAUNA0059/2021) and the Ethics Committee of the University of Cape Town (permit 2020/2018/V22/RC/A1). Some birds could have not been present or not built over the days of experiments for random reasons, which could have influenced our results. However, by performing replicates of the experiment for 8 days at the communal nests, we reduced potential bias in sampling.

## 2.6 | Statistical analysis

All statistical analyses were conducted on R version 4.2.1 (Team, 2021) and mixed models were performed using the package glmmTMB (Brooks et al., 2017).

We conducted different analyses for the specific questions that are detailed below. For all the mixed models performed, we used as random factors: communal nest ID, the day of the replicate (one to eight) as well as the position on the ground (one to four). Additionally, for the models at the individual scale, we added the identity of the individuals as a random factor. As explanatory variables, we used the straws' length (short vs. long), sex and age. We also included as covariable the number of straws offered (30 vs. 60) and the length of the recording (varying due to battery capacities), ((mean $\pm$ SD) 5h35 $\pm$ 0h51).

Convergence issues in the mixed models were dealt with by changing the optimizer included in the packages used, and which allowed the models to converge. For each model, non-significant terms were kept, avoiding any *p*-hacking effects (Head et al., 2015). We used the DHARMA package to assess, both visually and with tests, residuals' normality and overdispersion (Hartig, 2017). All continuous explanatory variables in the models were scaled and centred before running the models, using the whole dataset.

## 2.6.1 | Do birds prefer longer straws?

We used the total number of straws of each length taken *per communal nest per day*, as the dependent variable. As fixed factors we used the straws' length (long versus short), the number of straws offered (30 vs. 60) and the length of the recording (to account for differences in video length). We performed a generalized linear mixed-effects model (GLMM) using a Negative-Binomial (link log) error structure. The analyses were performed on 123 videos (688h of recording) collected at nine communal nests. For 15 videos out the 123 recorded, the birds took more than the number of straws offered (due to wind strike bringing straws, or straws falling from the communal nest above the piles).

## 2.6.2 | Does sex influence straw size preference?

We used the total number of straws taken *per individual per communal nest per day* as the dependent variable. As fixed factors, we tested the length of straws taken, the sex of the individuals and the interaction between sex and straw's length. We performed a zeroinflated GLMM with a Negative-Binomial (link log) error structure. We analysed 1068 straw-picking events by 266 individuals, collected at nine communal nests. For each day of recording, we only included in the dataset the individuals who took at least one straw of a given length.

### 2.6.3 | Do older birds prefer longer straws?

We tested whether the bird's preference was influenced by their age relative to the other members of the communal nest, by comparing the number of straws of each length taken per male per communal nest per day. We included only males in this analysis because (i) our observations showed that females took six time less straws than males (see Results section), and (ii) we only had exact age for a smaller number of females (breeding females being mostly immigrants: van Dijk et al., 2015). For each day of recording, we only included in the dataset the individuals who took at least one straw of a given length. We performed the analyses on 547 straw-picking events with 88 individuals, at nine communal nests. We performed a zero-inflated GLMM with a Negative-Binomial (link log) error structure. Straw length and the bird's age were used as fixed factors. We tested the interaction between bird age and straw's length. Age (in days) was either exact age (for individuals ringed as nestlings) or minimum age if individuals were captured as juveniles (depending on the adult plumage development at the capture of the birds, their birth were estimated between 15 to 115 days before). 13 males out of 152 were excluded from the analysis because they were caught as adults, making it impossible to determine an accurate enough probable minimum age. In our dataset, age varied from 408 to 3706 days.

### 2.6.4 | Are preferences repeatable?

We analysed repeatability in preference for straw length through the rptR package (Stoffel et al., 2017), using a Poisson error structure. We computed four analyses to obtain repeatability for males versus females and long straws versus short straws. The day of the experiment, the position of the resource on the ground and the identity of the individuals were used as the random effects for the communal nest. We inferred confidence interval of this repeatability by performing 200 bootstrap repetitions. We also checked the nonrandomness of the repeatability by performing 200 permutation repetitions.

## 3 | RESULTS

## 3.1 | Do birds prefer longer straws?

We found that sociable weavers preferred longer straws (EST $\pm$ SE: -0.91 $\pm$ 0.16, *p* < .001; Figure 2). The birds took approximately 147% more long straws than short straws, with on average 17.01 long straws per day per communal nest (CI: 11.79-24.56) and an average of 6.88 short straws (CI: 4.95-9.56) (see Table S2). The number of straws offered during the experiment did not influence the number of straws taken by the birds (EST $\pm$ SE: -0.2 $\pm$ 0.24, *p*=.410, Table S2).

### 3.2 | Does sex influence straws size preference?

We found that males took more straws than females: 1168 straw picking events were recorded for 152 males versus 201 straw picking events for 114 females. In addition, we found a significant interaction between bird sex and straw size (Table 1) showing that males take on average 166% more long straws than females, taking

FIGURE 2 The figure shows that long straws are more frequently taken than short straws. Results were obtained from the GLMM that combines both trials. The red circles (long straws) and the blue triangles (short straws) correspond to the raw data used to run the model, black dots correspond to the estimates of the model and black vertical bars correspond to the confidence intervals at 95%. Value corresponds to *p*-value in a pairwise comparison test.



 TABLE 1
 Summary of the GLMM parameters to test the

 influence of sex on preference for nest building material length.

Fixed effect	Estimate	SE	z-Value	p-Value
Intercept	-0.57	0.14	-4.06	<.001
Straw length-Short	-0.24 0.19 -1.		-1.28	.200
Sex–Male	0.98 0.16 6.22		6.22	<.001
Straw length–Short: Sex–Male	-0.91	<.001		
Random effect	Variance			
Communal nest (N=9)	3e-09			
Day of the experiment (N=8)	2e-12			
Position of the straw pile ( $N = 4$ )	2e-03			
Individual (N=266)	4e-01			

Note: X:Y indicates interaction between variable X and Y. Bold values correspond to statistically significant terms. 'Length–Short' correspond to the variable straws' length and the value 'short'. 'Sex–Male' correspond to the variable sex and the value 'male'.

TABLE 2 Summary of the GLMM parameters to test the influence of age on males' preference for nest building material length.

Fixed effect	Estimate	SE	z-Value	p-Value
Intercept	0.48	0.14	3.56	<.001
Straw length—Short	-1.18	0.10	-11.31	<.001
Age	0.09	0.09	1.00	.320
Straw length—Short: Age	-0.28	0.10	-2.68	.007

*Note*: X:Y indicates interaction between variable X and Y. Bold values correspond to statistically significant terms. 'Length–Short' correspond to the variable straws' length and the value 'short'.

an average of 1.50 (CI: 1.26–1.79) per day. Females took an average of 0.56 (CI: 0.43–0.74) long straws per day (which is similar to the number of short straws that they take). However, males and females took approximately the same number of short straws per day (males: 0.47 (CI: 0.38–0.59); females: 0.44 (CI: 0.31–0.63)).

## 3.3 | Do older males prefer longer straws?

We found an interaction between bird age and straw length showing that the preference for longer straws is stronger for older individuals (Table 2). The number of straws taken by males per day is higher for long straws than for short straws and older males take more long straws and less short straws than younger individuals (Figure 3). On average, older males took more long straws (2.17 long straws (Cl: 1.17–4.02)) than younger males (1.47 long straws (Cl: 1.05–2.06)). Opposite results were observed for shorter straws, with older males taking fewer short straws (0.27 short straws (Cl:





**FIGURE 3** The figure shows that older males take fewer short straws than younger males. Red circles (long straws) and blue triangles (short straws) represent the raw data used to build the model. The red solid line and the blue dotted line correspond respectively to long straws and short straws' effect sizes of the mixed model.

0.12-0.58)) than younger individuals (0.61 short straws (CI: 0.42-0.90)) (Figure 3).

## 3.4 | Are preferences repeatable?

Both sexes showed a higher level of repeatability in their preference for long straws than for short straws (Table 3), with males showing a higher repeatability in the preference for longer straws than females. By contrast males had almost the same repeatability as females for short straws. Females' repeatability for short straws did not differ from what it would be under random sampling (Table 3, p=.180). However, the lack of difference from random sampling may also be due to the low number of females observed on more than 1 day.

## 4 | DISCUSSION

Our experiment revealed that in sociable weavers: (i) males took more straws than females, and had a preference for long over short straws, whilst females took equivalent number of short and long straws. In addition, (ii) this behaviour varied among individuals and males were more repeatable in their choice of straw length than females, particularly when taking longer straws. Finally, we found (iii) that older males took more of the long straws. Together these results indicate a preference for larger straws in males, and that preference for material increases with age in males.

## **TABLE 3** Individuals repeatability in relation to sex and straw size.

		Sinclegy			
	R	СІ	p-Value	Number of individuals	Number of events
Males-Length-Long	0.39	0.21-0.52	.010	138	439
Females—Length—Long	0.29	0-0.53	.030	99	173
Males-Length-Short	0.15	0-0.28	.040	121	349
Females-Length-Short	0.12	0-0.33	.180	61	107

Note: "R" is repeatability; "CI" is confidence interval; *p*-values are obtained from the permutation analysis and bold values correspond to statistically significant terms; "Number of ID" is the number of individuals on which the repeatability was measured; and "Number of events" is the number of lines (one individuals, one day) on which the repeatability was measured. "Length - Short" correspond to the variable straws' length and the value "short". "Length - Long" correspond to the variable straws' length and the value "long".

How attributes such as sex and age influence choice of materials or tools has been rarely studied in the wild (but see a study on tool using efficiency in termites-fishing in chimpanzees (*Pan troglodytes*) (Lonsdorf, 2005; Lonsdorf et al., 2004)). These preferences can arise from several non-exclusive factors that we discuss below.

## 4.1 | Sexual differences

The difference of preference between males and females for longer straws could arise from a sexual specialisation in the location or type of building undertaken, and the characteristics of the nest building materials can vary in relation to the part of the nest in which the materials are used (e.g. as seen in thrushes and finches (Biddle et al., 2017, 2018)). In sociable weavers, observations of four females in captivity suggested that, as in many other weaver species (Collias & Collias, 1964; Crook, 1960), females build mainly inside the individual chambers (Collias & Collias, 1978), which may require shorter straws. Males, however, mostly build on the outside (Collias & Collias, 1978; Leighton, 2014; van Dijk et al., 2014). Building the exterior structure might require longer straws if this helps increasing the solidity of the communal nest. These large structures require continuous maintenance and parts of the nest can fall when colonies are abandoned or when the number of birds inhabiting a colony declines, which leads to poorer maintenance of parts of the nest (authors personal observation). Future experiments could investigate how straws of different sizes could affect nests consecutively built by the same individuals.

Sex preference for some materials could also arise if building skills or ability to find nest materials are influenced by sexual selection. In other weaver species, males build several nests that are inspected and chosen by females. For instance, in village weaver (*P. cucullatus*), females choose their mate based on the freshness of the nests built by the male as well as nests built with stronger materials (Collias & Victoria, 1978). In sociable weavers, carrying very long straws is a conspicuous behaviour, frequently observable at the communal nests (authors' unpublished data). Females could prefer males that build with longer straws because they lead to the most durable communal nests, and/or because these longer straws are harder to carry, revealing the males' quality (see review by Mainwaring and Hartley (2013) arguing that nest building is a costly activity). Holding nest material was found to be used as a display in male estrildid finches, a group that is phylogenetically close to the weaver bird family (De Silva et al., 2017) and this behaviour was considered to be a display that indicates nesting ability (Soma, 2018).

The sex effect found here for preference could also arise from social selection that would be stronger in the philopatric sex (the males in this species (Covas et al., 2006; van Dijk et al., 2015)). Nest building in sociable weavers is a contribution to a 'public good' (the communal nest) (Ledyard, 1995) and it has been suggested that showing investment in a public good may allow reputation building and facilitate indirect reciprocity and trust (Covas & Doutrelant, 2019; Leighton & Meiden, 2016; Roberts, 2020; Taborsky et al., 2016). Further data linking nest building behaviour to social network position, for instance, would help to evaluate this hypothesis. This could also be tested in other species as communal nesting occurs in many taxa, such as rodents (Hayes, 2000), primates (Baden et al., 2013), lizards (Magnusson & Lima, 1984) or arachnids (Mori & Saito, 2006).

Another non-exclusive factor that may explain the sexual differences documented here is kin selection. The male-biased philopatry seen in sociable weavers leads to genetic structure among males, but not females (Covas et al., 2006; van Dijk et al., 2015). A previous study has suggested that sociable weaver males build more on the communal parts of the nest than females to gain indirect fitness benefits, as they were found to build more in parts of the communal nest occupied by themselves and their kin (van Dijk et al., 2014). If longer straws are better building materials, the males' preference for these materials could provide a better nest environment to their kin. Further studies could investigate whether the use of longer straws in communal parts is associated to the level of relatedness to the other males within the communal nest.

## 4.2 | Age difference

The different factors advanced above to explain the sexual differences can also explain the age effect found here. For instance,

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there could be a difference in building location (where the bird builds on the communal nest) between younger and older individuals, leading to a difference of straw sizes taken by the birds. In addition, or alternatively, if building with longer straws is better for the nest's structural stability, then older males may have learnt to use longer straws, and therefore, build less frequently with shorter straws. This has been shown in captive zebra finches where males that had previously attempted to reproduce, built more efficiently, with better materials (Muth & Healy, 2011, 2014), and with less nesting materials (Whittaker et al., 2023). Additionally, older male sociable weavers may also have more relatives in the communal nest than younger individuals due to a higher number of reproductive events, which could favour increased investment in nest building.

Finally, because older males are more dominant (Silva, 2017), if longer straws are superior materials, the age effect found here could arise from dominance itself, with dominant individuals monopolising the preferred resource (i.e. the longer straws). Sociable weavers are sometimes seen stealing straws from other individuals directly from their beak, and agonistic interactions to access building resources have been shown in other several species (e.g. satin bower birds (*Ptilonorhynchus violaceus*) (Borgia, 1986); baya weavers (*Ploceus philippinus*) (Crook, 1963); village weavers (*Ploceus cucullatus*) (Khan et al., 2019); the cichlid fish *Neolamprologus multifasciatus* (Jordan et al., 2016); and social hermit crabs (*Coenobita compressus*) (Laidre, 2021b)).

#### 4.3 | Repeatability

We found that regardless of age, males were more consistent in their preference for longer straws than females. Males showed a repeatability of 0.39 in their preference for longer straws over 8 days. However, long-term repeatability could differ from short-term repeatability (David et al., 2012). Therefore, more data would be needed to determine if this repeatability is stable over a long-term period. Previous research has also identified some consistency in nest building behaviour in other bird species (Schleicher et al., 1996) and in fish (Japoshvili et al., 2012; Rushbrook et al., 2008). Within individual repeatability in the propensity to perform a given behaviour can provide information on the propensity to build with the same materials or locations and the probability to perform the same behaviour in the future and thus on the reliability of the behaviour. This information could be important for instance for potential mates (Covas & Doutrelant, 2019; MacKinlay & Shaw, 2023; Schuett et al., 2010).

By contrast, females were not repeatable in their preference for shorter straws. This could mean that female building behaviour and location is more varied, requiring them to be more flexible in their choice of materials. Additional data on building behaviour is, however, needed to determine if this is a real pattern or a consequence of the smaller sample size that we obtained for females (N=61 for females versus N=121 for males, for short straws). Or the fact we

had not provided adequate nest material (e.g. females could prefer straws with a different diameter, or a different grass species; see

## 5 | CONCLUSION

also Bailey et al., 2016).

The field experiment conducted here adds to the small number of studies studying nesting material preferences in wild populations and shows that these vary in relation to individual attributes. Further data on breeding and social status, and mating and reproductive success of builders, as well as their level of relatedness to neighbouring communal nest members are required to further investigate which of these non-mutually exclusive selective pressures explain the evolution of nest building behaviour.

## AUTHOR CONTRIBUTIONS

Nicolas J. Silva: Conceptualization; methodology; data curation; writing – original draft; writing – review and editing; formal analysis. Fantine Benoit: Writing – original draft; formal analysis. Andrew Elliott: Data curation. Charlotte Rault: Data curation. Pierre Colençon: Data curation. Rita Covas: Funding acquisition; supervision; writing – review and editing; conceptualization; methodology; formal analysis; project administration. Claire Doutrelant: Funding acquisition; supervision; writing – review and editing; writing – original draft; conceptualization; methodology; formal analysis; project administration.

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#### DATA AVAILABILITY STATEMENT

Data available from the FigShare Digital Repository https://doi.org/ 10.6084/m9.figshare.23592363

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## SUPPORTING INFORMATION

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