Architectural traditions in the structures built by cooperative weaver birds

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Humans cooperate to build complex structures with culture-specific architectural styles. However they are not the only animals to build complex structures nor to have culture. We show that social groups of white-browed sparrow weavers (*Plocepasser mahali*), build structures (nests for breeding and multiple single-occupant roosts for sleeping) that differ architecturally among groups. Morphological differences are consistent across years and are clear even among groups with territories a few meters apart. These repeatable differences are not explained by among-group variation in local weather conditions, bird size, tree height, or patterns of genetic relatedness. Architectural styles are also robust to the immigration of birds from other groups.

INTRODUCTION

The limestone pyramid of the Kukulkan temple in Yucatan, Mexico, looks very different to its contemporary, St Andrews Castle, Scotland. The stylistic differences are not due to genetic differences between Mexicans and Scots or to environmental factors such as climate and material availability, as both were built with local stone around the 1200s. Rather, these differences in architecture are due to cultural differences. Indeed, such architectural traditions are considered a hallmark of human societies. However, we are not the only animals to either build structures or display culture (*1*, *2*). Once thought to be exclusive to humans and our closest relatives, it is now well documented that animal culture can explain many of the variations we observe in behavior [e.g. the social transmission across blue tits (*Cyanistes caeruleus*) in the UK of a novel foraging technique involving piercing the aluminum foil tops on milk bottles to access the cream (*3*)]. From fruit flies that copy the mate choices of others (4), whales that incorporate new vocal themes into their songs creating "cultural song ripples" across different populations (5), to birds that, like humans, have regional accents (6), social learning allows animals to maintain behavioral traditions independently from genes and the environment (*2*). Culture and traditions in birds have been observed across behavioral contexts such as vocal learning, foraging, and migration (*7*). Increasing evidence that animals' building behavior can be partly explained through social learning (*8–11*) begs the question of whether it can also become a cultural tradition (*12*).

Variation in birds' building and the nests they produce is often attributed to innate predispositions (*13–15*) or environmental differences (*16*, *17*), with only the latter supported by data. For example, birds building in colder climates may build larger and heavier nests than do birds that build in warmer places since nests containing more material can provide greater insulation (*16*, *18–21*). These correlational data have been reinforced by experimental manipulations of temperature, which lead laboratory zebra finches (*Taeniopygia guttata*), at least, to include more material when building their nests at lower temperatures than when building at higher temperatures (*22*). Having had experience of building and successful reproduction, however, zebra finches ignored the ambient temperature when they built their second nest. Indeed, increasing evidence shows that avian builders use both individual experience and social information (*8*, 10, *23–28*). For example, avian builders will copy the material choices of familiar conspecifics (*8*), change their material preferences having seen via a video screen a conspecific building (*25*), or even after viewing just a completed nest (*24*). Rather than environmental or innate predisposition alone, individual experience, social learning, and cultural processes might also help explain variation in building (*12*).

Cultural influences lead not only to variation among populations, but also to conformity within populations. For building (the behavior) and for nests (the behavioral product), however, there are very few data on the repeatability of either building behaviors or their product built by the same individuals or populations (*28–32*). The available data are somewhat mixed; for example, the morphology of nests built by three-spined sticklebacks (*Gasterosteus aculeatus*), sand gobies (*Pomatoschistus minutus*), and laboratory zebra finches is repeatable (*30, 33, 34*). However, the dimensions of nests built by weaverbirds (*Ploceus velatus* and *P. cucullatus*) and blue tits building in the wild have low or no repeatability (*27, 29;* but see evidence for distinctive weave signatures in weaverbird nests, *32*). Despite the ubiquity of bird nests, comparisons of the structures built by the same individuals remain rare. There are several reasons for this paucity: (i) building behavior is rarely quantified; (ii) many birds in the wild build a handful of nests in their

lifetime, typically one or two per season; and (iii) the interest in nests has been directed at the value of the structure (e.g. size, warmth, location) with regard to egg and chick survival, with the possibility that individuals may vary in their architectural style receiving little attention (*12, 22*).

Building by white-browed sparrow weavers (*Plocepasser mahali*) offers a unique opportunity to examine repeatability of structural morphology because these birds build many single-occupant sleeping roosts (hereafter referred to as roosts) throughout the year in addition to building one or two breeding nests (during the breeding season; hereafter referred to as nests). Additionally, these birds are cooperative breeders living in groups of two to 14 individuals (mostly kin), occupying year-round territories for up to a decade (*35, 36*). All structures are built around one or two trees within a group's territory. Roosts are made from grass and lined with feathers in an inverted "U" shape with an entrance and an exit tube (Fig. 1A-C) (*36*) and can shelter only a single sparrow weaver overnight. Nests are used only by the dominant female during the breeding season for laying and incubating her eggs. The nest has an entrance tube but the would-be exit tube of a roost is woven into a close-ended cup containing the egg chamber. At any one time it is clear which structure is a roost and which a nest, but birds renovate both into the other kind of structure: by removing material that formed the nest chamber the sparrow weaver converts a nest into a roost and by adding material to the exit tube, the birds turn roosts into nests.

Building and use of roosts occurs year-round, taking between five days and six weeks to complete a structure (*36,37*). Groups build around three times as many roosts as the number of group members. A previous report of building in two groups of sparrow weavers (*36*) suggested that building these structures may be cooperative, as more than one bird contributed to building (Fig. 1D). If these birds build together, we might expect structures within each group to be more similar to one another than to structures built by birds in other groups. As little is known from vertebrates as to how multiple individuals organize their behavior to build a structure from collected materials, white-browed sparrow weavers are useful for examining the dynamics of cooperative building.

In this study we tested whether (i) there is variation in morphology of structures built by white-browed sparrow weavers within and among different groups; (ii) local weather conditions, tree height, body size, or genetic relatedness could explain structural variation; (iii) multiple birds do build together; and (iv) incorporation of new individuals (offspring of the resident dominants, or immigrants) affects structural morphology. Existing data on animal building suggests that local weather conditions, the local environment, body size, and/or genetic relatedness could explain variation in structural morphology. If we could exclude all of these typical explanatory variables, we argue that cultural transmission is a plausible explanation for morphological variation we see in the structures built by the different groups of birds.

RESULTS AND DISCUSSION
We measured in situ structures (397 roosts and 47 nests) built by 43 different groups of sparrow weavers in the Kalahari Desert (*38*). We refer to both nests and roosts as "structures" and we combine data from both in the analyses unless specified otherwise (Supplementary Materials).

We measured the length of the entrance tube (straight line from the entrance opening to the back of the structure), length of the exit tube (straight line from the exit opening/end of the egg chamber to the structure top), total length (from the entrance to the exit hole or egg chamber), the width and diameter of the entrance and exit holes (or egg chamber), and the angle between the two tubes (Fig. 1, A to C). We found that structural morphology varied significantly among-groups across the population [one-way (ANOVA); $F_{42,436} = 4.55$, $p < 0.001$, Fig. 1, E to F, and table S1]. Structures differed in the lengths of entrance and exit tubes as well as the total

length of the structures (for each measurement we report mean, minimum-maximum range, and Coefficient of Variation; Length of entrance: 22.27 cm, 9.10-34.00 cm, 18.07; Length of exit:18.92 cm, 5.40- 29.60 cm, 16.90; Total length: 26.91 cm, 17.00-37.8 cm,12.58; Fig. 1E). Some groups built longer structures than others; for example, one group built structures with a mean total length of 23.77 ± 0.71 cm (mean $\pm$ S.E.), while the mean total length of another group's structures was 31.46 ± 0.71 cm (mean $\pm$ S.E.) (Fig. 2A). Variation in structural morphology among groups was mostly in entrance tube [33.47% contribution to the first axis of a principal component analysis: PCA)], exit tube (20.73%), and total length (20.36%). Variation of the entrance diameter and structure width among groups contributed the most to the second axis of the PCA (26.14% and 20.82% respectively; Fig. 2B, Fig.S1). The proportion of the total variation that was captured by the first component (PC1) was 31.5% (eigenvalue of 2.20); PC2 captured 21.8% of the variation. We therefore used PC1 as the response variable in all subsequent analyses. In the study of animal behavior, repeatability is used as a measure of behavioral consistency where R can take a value between 0 and 1 (with 0 as non-repeatable and 1 as highly repeatable within the grouping factor, in this case, each of the 43 groups). Importantly, structural morphology was significantly repeatable (consistent) within groups, with variation among groups greater than within groups (Adjusted Repeatability for Group accounting for year: $R = 0.26$, 95CI = 0.15-0.37, $p < 0.001$, mean group PC1 $\sigma^2 = 1.5$, all structures PC1 $\sigma^2 = 2.2$) (*39,40*).

There are several reasons why the structures built by different groups might vary morphologically. One is that builders respond to local weather cues. For example, birds may build shorter structures in warmer territories or longer structures in stronger winds. If so, because birds in neighboring territories are more likely to share local weather conditions, they should build more similar structures. Yet we found little variation in temperature and wind speed among the territories of the different groups. Temperature at different territories varied by only 0.06°C $\pm$ 0.2°C and wind speed by 0.59 ± 0.26 km hr^{-1} (both mean $\pm$ S.E.) compared to a central reference territory within the study site (Supplementary Materials). Temperature explained just 0.2% of the variation and wind speed 0.6% of the variation in structural morphology [Maximum-Likelihood Population-Effects model (MLPE): Temperature $r^2 = 0.002$, Fig. 3A; Wind speed $r^2 = 0.006$, Fig. 3B]. Similarly, differences in tree height explained less than 0.1% of the variation (MLPE: Tree height $r^2 < 0.001$; compared to a null model, Fig. 3C).These small effects are unsurprising since the distance between groups was small; the mean shortest distance among the territories of the groups in the study site was 97.7m, with the closest groups 11m apart and the furthest 1.52km (Fig. 4A, Fig. S2). Distance among the territories explained only 1.1% of the variation in structural morphology among different groups (MLPE Distance: $r^2 = 0.011$, Fig. 3D).

Alternatively, because larger species or larger birds typically build larger structures, e.g. village weavers (*P. cucullatus*) (*41*), body size may explain some of the variation in structure morphology across groups (here approximated by tarsus length). But while mean tarsus length from birds within each group differed between the groups (F$_{42,269}$ = 1.82 $p = 0.002$), tarsus length accounted for only 0.8% of the structural variation (MLPE Size: $r^2 = 0.008$, Fig. 3E). Compared to a null model, a model that included the difference in temperature, wind, distance among groups, difference in tree height, and bird size increased the fit of the model by ΔAICc = 6.54.

Finally, variation in structural morphology among different groups might be due to innate predispositions, such as a propensity to build short rather than long structures. As a proxy for testing whether a genetic component could explain variation in structure morphology, we assessed whether groups that were more closely related built structures that were more similar than did groups that were less closely related. We expected little variation in genetic distance

among groups because genetic isolation by distance has been shown in this population (*42*). We found that genetic relatedness explained 0.1% of the variation in structural morphology among different groups (MLPE Genetic relatedness: $r^2 < 0.001$; ΔAICc between the null and genetic models = 0.49; Fig. 3F).

Measurements of local weather conditions (temperature and wind speed), tree height, distance between groups, tarsus length, or relatedness, taken together explain very little variation in structural morphology among the groups (2.3%; Table S2). We hypothesize that the structures built by different groups differ morphologically because birds converge in their building behavior within each group. This possibility is supported by our behavioral data that show that sparrow weavers within a group build together (Fig.4 B to D). We recorded building in 19 groups, the colored leg rings of each group member identified using high-definition cameras. Multiple birds (up to eight) participated in building a single structure. Dominant birds built more than subordinates, and building actions were equally distributed among dominant and subordinate birds (fig. S3). Furthermore, birds that migrated into one group from other groups cooperated to build structures in the group they joined (fig. S4).

These behavioral data show that birds that live together also build together and that this creates a group's specific architectural style. Additionally, variation in structural morphology did not increase when new birds joined a group. The mean total number of different individuals that were recorded in a group across the study time was 12.57 individuals (± 0.27 SE) and varied in the number of individuals that joined as natal subordinates (n = 34 groups; max. per group = 5; fig. S4), as adults from other groups (max. per group = 5), or were new to the site (n = 12 groups; max. per group = 2). Neither group size, number of natal subordinates, nor number of new unrelated individuals affected structural variability (measured as the standard deviation of PC1; GLM: group size: $X^2_1 = 0.045$, p = 0.830; natal subordinates $X^2_1 = 0.67$, p = 0.420; unrelated individuals $X^2_1 = 0.33$, p = 0.560, table S3).

Birds that moved to new groups did not bring their own building style with them as the structures in the territories containing new birds did not vary more than the structures without new birds (n = 38 groups, Jaccard's group similarity index; Mantel test: $r^2 = -0.034$, n = 43, $p = 0.830$). Instead, migrants appear to conform to the architectural style of the group they join. Conformity, an increased tendency to adopt the most common trait among a sample, has been formally tested in foraging great tits (*Parus major*) as birds copied the technique for opening a feeder as they moved into a group with an established opening technique (*43*). In our data, the lack of increased variability in structural morphology when new birds moved from one group to another suggests that when building together, birds converge on an architectural style. This is further confirmed by the lack of impact of new birds joining a group on repeatability of structural morphology within groups.

Whenever a behavior is similar among individuals of a group but different among groups, the explanations for the observed shared traits include similarity in ecological conditions and genetic relatedness (*44*). However, none of the ecological factors we measured, bird size, or genetic relatedness, covaried with the morphology of the structures. We conclude that cultural transmission seems the most likely explanation of our results. Birds will copy the building behavior displayed by other group members. For example, in lab experiments, zebra finches copied the material color they observed other familiar builders use (*8, 10*). Furthermore, after having observed just a nest, zebra finches modified their subsequent building decisions and were more likely to use material of the color as that observed nest than to use material of a color they had previously preferred (*23, 24*). Field data are also consistent with social learning use in material-choice decisions. For example, the closer male spotted bowerbirds (*Chlamydera maculata*) build bowers to each other the more similar their decorations regardless of the local

availability of materials (*45*). This suggests that bowerbirds copy neighboring birds in their choice of decorative materials, while a heterospecific community of foraging tits also searched for nest-lining material together (*11*).

Social learning of nest-pertinent information was also observed when cross-fostered titmice copied the choices of their foster parents for both nest site and nestbox size rather than those of conspecifics (*46*). Social learning for nest decisions might also be interspecific, for example females of two migrant species, collared (*Ficedula albicollis*) and pied flycatchers (*F. hypoleuca*) preferred to use nestboxes bearing an arbitrary symbol that was also present on the nestboxes of resident tits [an avian version of "when in Rome, do as the Romans do" (*47*, *48*)].

Repeatability in structure morphology has been reported in other builders, both fishes and birds, building nests under experimental conditions and in the wild (*28,29,30,33,34*). In all these species nests were built by the same individuals or breeding pairs, while in the sparrow weavers studied here, we identified a group signature in the morphology of multiple structures built by multiple individuals. Cross-fostering and transmission chain experiments would be necessary to determine how different social interactions give rise to sustainable architectural styles in this species but we would expect that other species in which individuals cooperate to build (from bees and termites to beavers) also show within-group architectural signatures (*49,50*). Behavioral traditions in birds have been well documented for song, migration, foraging, and tool use (*7*, *51*). Here we add building behavior and show that architectural styles emerge from birds that build together.

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Supplementary Materials

Materials and Methods
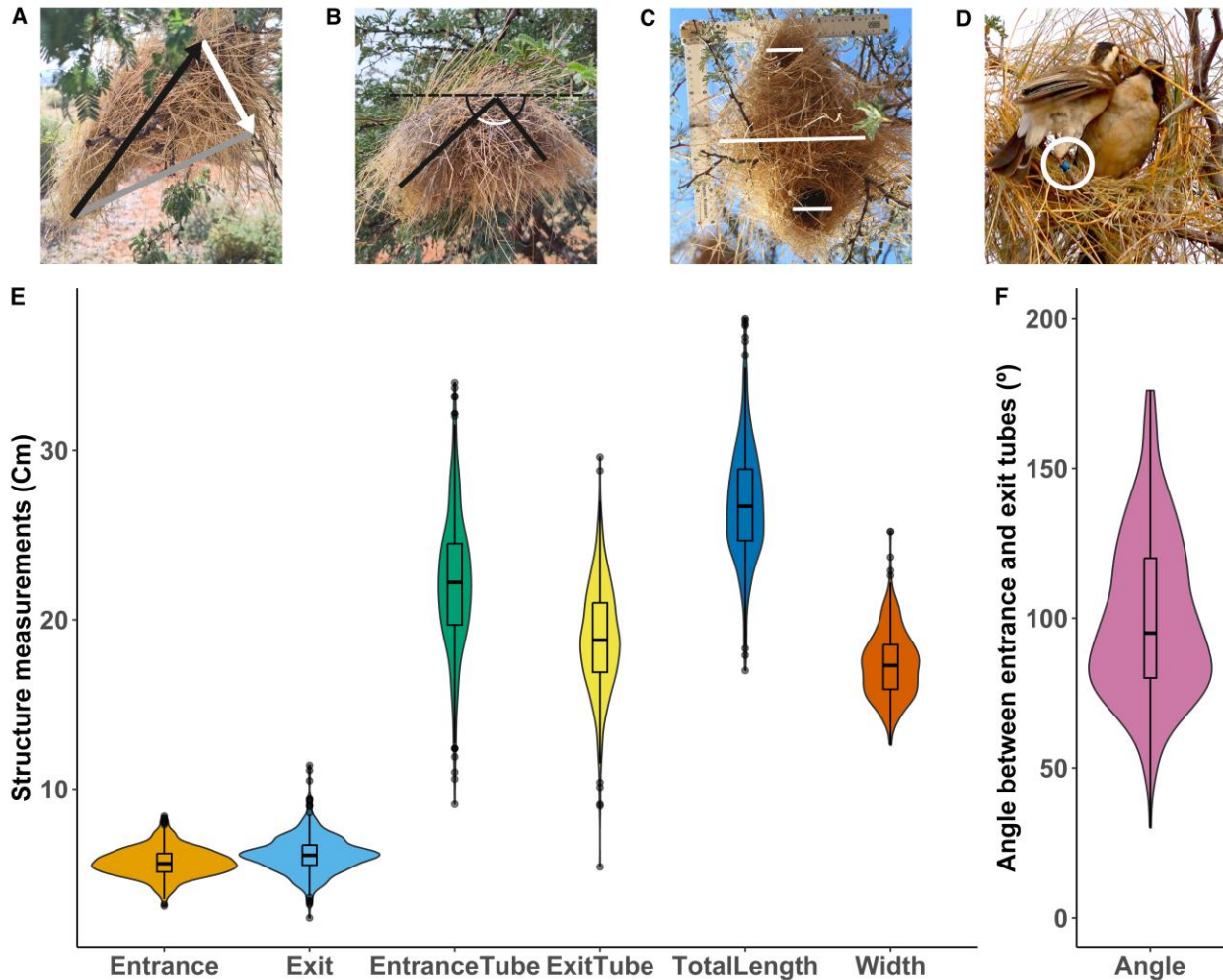
Figs. S1 to S5

Tables S1 to S3

FIGURES

5

Fig. 1. Measurements taken from structures and variation in the structures (both roosts and nests) built by white-browed sparrow weavers. (**A**) The black arrow shows the length of entrance tube, the white arrow shows the length of the exit tube, the grey lines show the total length. (**B**) The angle between the entrance and exit tube is shown in white. (**C**) Diameters of entrance and exit hole (upper and lower white horizontal lines). For a nest the lower white line represents the diameter of the exterior of the nest cup. The width of the structure is shown by the longer middle white horizontal line. (**D**) A still image from high-definition video showing two white-browed sparrow weavers passing each other a piece of grass while building. The white circle indicates the colored leg rings. (**E**) and (**F**) show the distribution in the seven measurements taken from the structures built by 43 different groups of white-browed sparrow weavers. Box plots show the median, first and third quartile for all the structures measured and the shaded areas represent kernel density distributions, while dots represent individual outliers.

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A

B
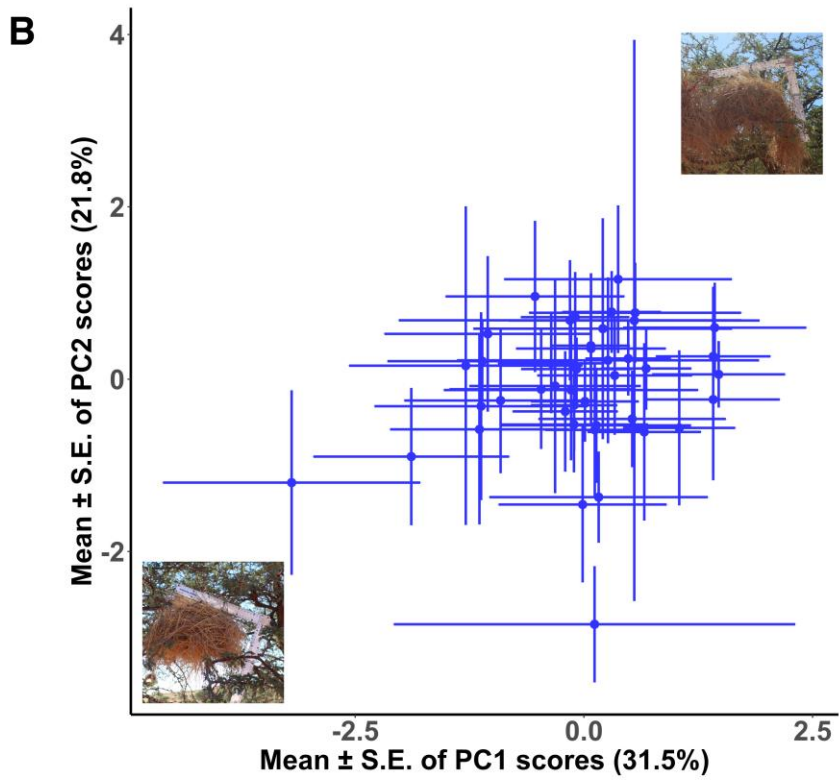
Fig. 2. Variation among the structures built by different groups. **(A)** Pictures of the structures built by three different groups of white-browed sparrow weavers. The two rulers show the difference in size between the structures built by the different groups. **(B)** Mean ± S.E. of PC1 and PC2 scores from the seven measures taken for the structures at each of 43 groups (one dot per group). The seven measures were: length of entrance and exit tube, the width, total length, diameters of entrance and exit hole, and the angle between the entrance and exit tube. Length of entrance and exit explain most of the variation in PC1 (53 %) while the diameter of the entrance hole and the width of the structure explains most of the variation in PC2 (50.7%). We have included two photographs of structures built by two different groups; there are two rulers next to each structure for scale.
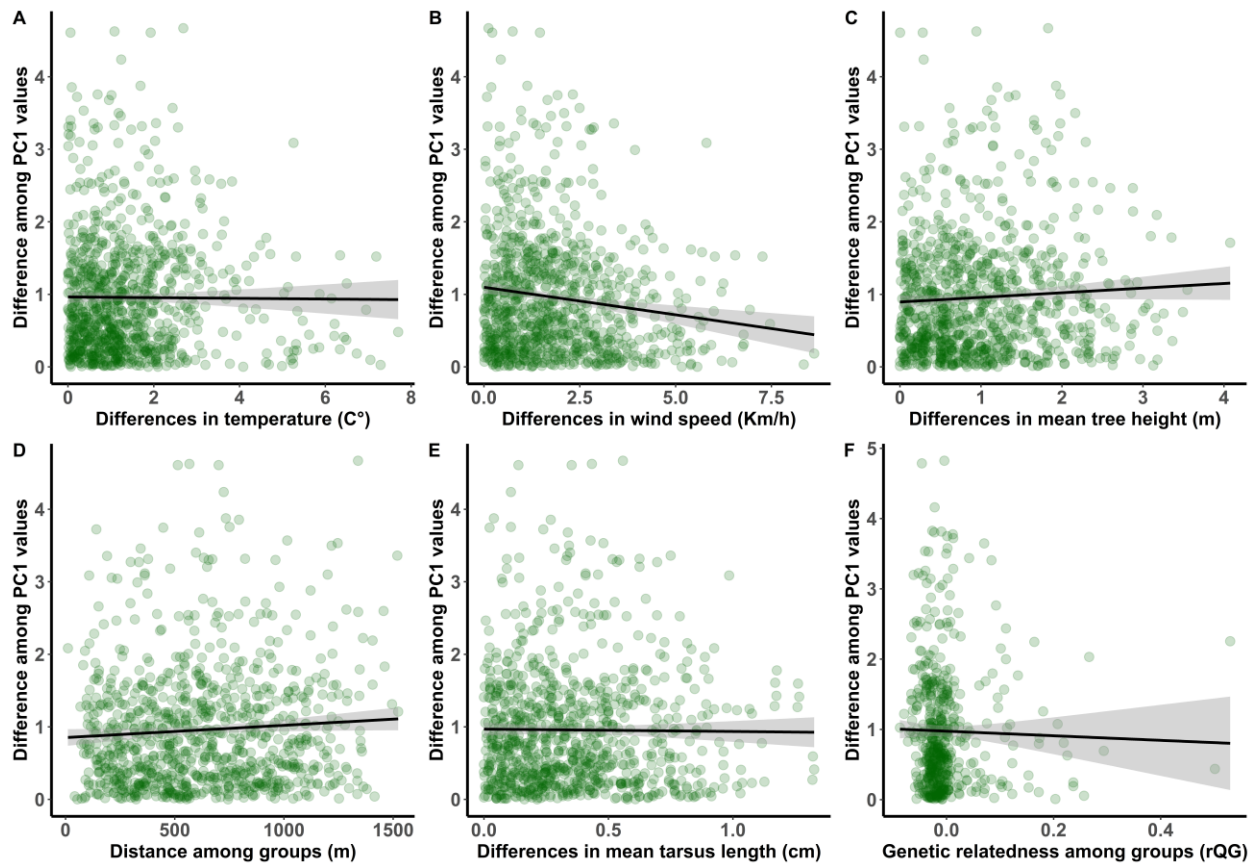
Fig. 3. Non-cultural factors do not explain architectural variations. Scatter plots illustrate the lack of significant correlation between the difference in PC1 values calculated from the seven measurements taken from the structures (i.e., length of entrance and exit tube, the width, total length, diameters of entrance and exit hole, and the angle between the entrance and exit tube). Each point represents the difference in PC1 values between the structures built by two different groups (a measure of variation in structure morphology among groups) and **(A)** the difference in temperatures at the territories of 43 groups, **(B)** the difference in wind speed, **(C)** the difference in the mean heights of the trees at each territory's group, **(D)** the distance in meters among groups, E) the difference in mean tarsus length of the groups, and **(F)** the distance in genetic relatedness among 33 groups. Regression lines represent a simple linear model between the difference in PC1 values and each of the six non-cultural factors.
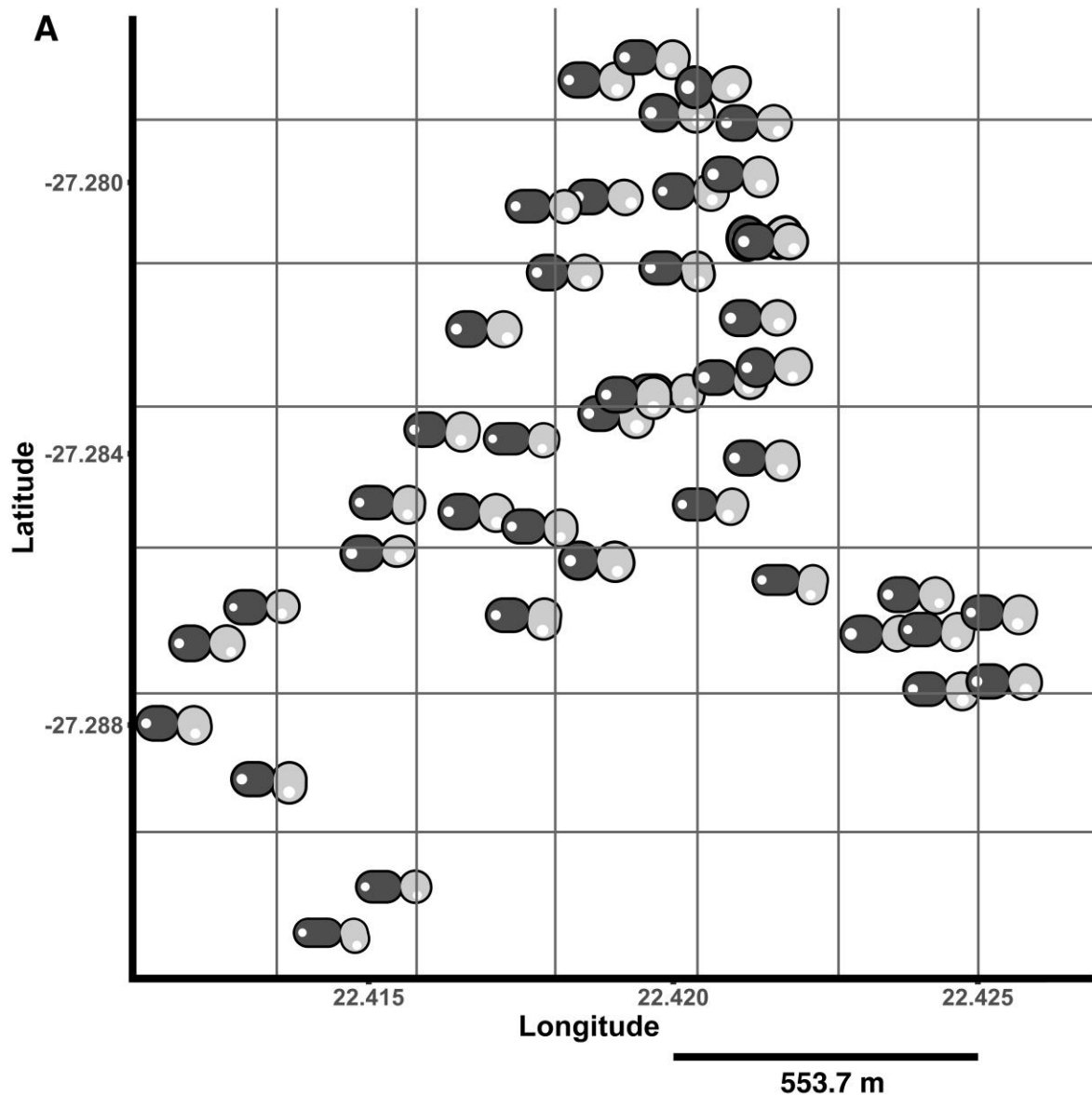
Fig. 4. Spatial distribution of the 43 groups studied and cooperative building in the white-browed sparrow weaver. (A) Each group is represented by a scaled schematic of the mean of the seven measurements (length of entrance and exit tube, the width, total length, diameters of

entrance and exit hole, and the angle between the entrance and exit tube) taken for all 43 groups across two years. The darker tube represents the entrance tube while the lighter one represents the exit tube. Groups that build only tens of meters apart build structures that are morphologically different with the entrance and exit tubes varying the most. **(B)** White-browed sparrow weavers building a structure (roost or nest) together. Birds take turns when incorporating material into a new structure with birds bringing material one after the other; **(C)** one bird passes the material to the bird at the building site; **(D)** two birds at the building site, one inside the unfinished structure, the other perching on the branch above.

Supplementary materials

Materials and Methods

Study population and site

The study population including the 43 social groups occupies ~2.5 km^2 in Tswalu Kalahari Reserve in the Northern Cape Province of South Africa (27°16′S, 22°25′E). The population has been monitored intensively since 2007 (*38, 53*). During this long-term study all birds in the population have been given color rings (SAFRING license 1444) and the group composition is known for each group. The data we describe were collected in December 2018-March 2019 and January to March 2020. During the period of this study 104 new birds were ringed in the population (13 of them as chicks). The monitoring of group-composition that occurred as part of the ongoing study of the social dynamics of this population allowed us to assess which birds were dominant. In each group the dominants are the reproductive pair (*38*). Subordinate individuals included all non-dominant individuals in a group such as birds that hatched in that group, birds from other groups within the populations (birds that had been ringed and their origin was known), and immigrants birds that came from outside the study population (birds without rings). As part of the routine demographic data taken for study population, all birds were weighed, and the length of the tarsus and wing were measured twice within the reproductive season. We use tarsus length as our measure of bird body size rather than body weight as tarsus length is much less variable across days and seasons. Blood samples were also taken to determine genetic relatedness. The study population has been successfully genotyped using 10 microsatellite markers as part of previous studies (see (*42, 53, 54*) for details of molecular protocols). Using the genotypes at these 10 loci for 1,383 individuals and COANCESTRY(*55*) (v 1.0.1.9), we calculated pairwise relatedness (*56*) available for focal birds (n = 227 individual birds from 33 groups for 2018 and 2019, combined).

Variation in structure morphology

We tagged and took measurements in situ for each structure that had been built within 3.5 m from the ground. We chose this height because we accessed the structures via a ladder placed in the sand below each structure and above this height, we considered the researcher to be at too great a risk of falling from the ladder. We were able to tag with colored beads 66% of all structures present at the site (1681 total structures, with an average of 38.2 ± 2.48 Mean, S.E., structures per group). Tagging the structures enabled us to keep track of the building status of each structure at the site across years. Forty-five percent of the structures that were tagged were also measured once they had been completed. The remaining 55% were not measured as they were either already broken, were not finished, or were too high to measure. For the structures that could be tagged and measured we took seven morphometric measurements (397 roosts and 47 nests; Fig. 1A-C). With a tree caliper (Häglof Mantax) we measured, total length (from the entrance to the exit hole), length of the entrance tube (straight line from the entrance opening to the back of the structure), length of the exit tube (straight line from the top of the structure to the opening of the exit tube) (Fig. 1A), the angle between entrance and exit tube (Fig. 1B), and the with, the diameter of the entrance and exit hole (Fig. 1C). We calculated the angle between the entrance and exit tube by measuring the angle of the entrance tube with a protractor perpendicular to the ground, the protractor was placed in parallel to the inclination of the entrance tube and a weighted string marked the angle of inclination (Fig. 1B). We repeated this procedure to measure the angle of the exit tube. We then summed both angles to determine the

angle between the entrance and exit tube. Each of the seven measurements was taken three consecutive times and the median of these measurement was used for all analyses. In the case of the nests, where there is no exit hole but instead an egg chamber, we measured the exterior diameter of egg chamber and the exterior length of the egg chamber.

5   To test whether there was variation in the morphology of the structures built within and among groups we used a principal component analysis to summarise the variation contained in all seven measurements taken from the structures. We used a correlation matrix and the data were rescaled to account for the fact that the variables were recorded in different scales (i.e., cm and degrees) and had different variances. We then used the resulting PC1 as the response variable for

10   subsequent analyses.

    We used a one-way ANOVA to determine whether there was a significant difference in the structures built by different groups using scores from PC1. To test whether the variation in structural morphology among groups was greater than that within groups we used a repeatability test (*39*, *40*). For this test, we ran a linear mixed model having PC1 as the response variable. This

15   model included Group identity as a random intercept and Year when the structure was first present at the site as a fixed effect to control for variation between years. We assessed the statistical significance of structure repeatability among groups using the rptR package in R (specifying 1500 permutations (*40*)). This repeatability can be interpreted as the proportion of the total variance in PC1 that is explained by consistent differences among groups (rptR package

20   (*40*)).

Local weather, distance, bird size, tree height, and genetic relatedness
We measured the temperature (in C°) and wind speed (Km/h) at each of the 43 group territories using portable anemometers with a temperature blogger built-in (SILVA ADC Summit). As we

25   had four anemometers to deploy at a time, we kept one location constant (at the center of the study site) and used the differences in temperature and wind speed among days between the group territories and the center measurement as the local weather variable. The anemometers were kept in each group's territory for two consecutive days. We hung the anemometers from a branch in the main tree for each group, at the same height from the ground (1.2 m).

30   We measured the latitude and longitude points for the tree that was used most often by each of the 43 groups using a GPS. This allowed us to calculate a distance matrix of the spatial distance in meters among the territories of all the groups within the study site.

    As the weight and the wing length measurements of individual birds are more variable than the length of the tarsus, we took the latter as the measurement of the size for each bird, as bigger

35   birds have longer tarsi. When the length of the tarsus had been recorded multiple times for an individual, we took the median of the length of the tarsus for that individual (and we only included the measurements from adult birds). If an individual was part of different groups at different times, we included that bird's measurements in both groups.

    Taller trees tend to have thicker branches, and thicker branches might allow birds to build

40   larger structures on those trees. To assess whether birds might build differently-sized structures based on tree morphology, we measured the height of the trees. Tree height was measured by using a clinometer using the formula, $a + b \tan \theta$, where a is the height at which the clinometer was held (1.52 m), b is the horizontal distance from the tree trunk and θ is the angle of inclination as measured by the clinometer.

45   Genetic sampling was performed by taking a small amount (< 25 uL) of blood from the wing vein and storing it in 96% ethanol at a minimum dilution of 1 part blood to 20 parts ethanol. We employed the Queller & Goodnight moment estimator (*56*) as our metric of individual relatedness based on 10 microsatellite genotypes, calculated using the program

COANCESTRY(55). Based on micro-satellite genotypes available for focal birds, we estimated relatedness values for 227 individual birds from 33 of the groups. We then calculated the average relatedness of all pairs of individuals between two focal groups. From the pairwise genetic relatedness between groups in the population we calculated a distance matrix of the relatedness between those 33 groups.

To evaluate the contribution that temperature, wind speed, distance among group territories, tarsus length, tree height, and genetic relatedness had on the differentiation of the structure morphology, we fitted two maximum-likelihood population-effects (MLPE) models as implemented within the mlpe_rga function using the R package ResistanceGA (version 4.2 (57)). One model included the temperature, wind speed, distance among territories, tree height, and size of birds as the explanatory variables and the other model, only used the genetic relatedness data as explanatory variable because such data were available for only 33 of the 43 groups. The MLPE test calculates the relationship among multiple distance matrices (one distance matrix per explanatory variable) explicitly accounting for non-independence of pairwise distances by including a random-effects term for the non-independent error structure of pairwise datasets (58). In both cases, as the response variable we used a distance matrix of PC1 calculated from the mean of the seven morphometrics of the structures built by each group, which defined how different the morphology of the structures was among the 43 groups (or 33 groups for the genetic relatedness model). Therefore, the response variable was a matrix with the difference in PC1 between each pair-wise group. We performed a model selection approach using Akaike's Information Criterion (AICc). The lack of independence is incorporated as a group-level factor to distinguish between data points shared by a group, and those that do not. All models were also run with PC2 as the response variable but only the distance between territories explained $> 1\%$ of the variation (maximum-likelihood population-effects model: $r^2 = 0.017$, compared to a null model (intercept model), including distance between territories improved the fit of the model $\Delta\text{AICc} = 13.55$).

We also tested whether there was a difference in the position of structures (both nests and roosts together) around the trees (from 0 to 359º) among groups. While we found a significant difference among groups (Mardia-Watson-Wheeler: $Wg = 83.79$ $p < 0.001$, Fig. S5), there was no correlation between the mean position in which different groups built their structures and the morphology (mean PC1 scores) of the structures (Mardia's Rank Test: $U_n = 1584.01$, $p = 0.79$, Fig. S5). Groups that contained more birds or older birds did not build structures with longer entrance or exit tubes. In addition, the structures were not wider (Pearson correlations between the mean number of birds in a group and: Length entrance tube, $r = -0.02$, $p = 0.85$; length exit tube, $r = 0.23$, $p = 0.12$; width, $r = 0.25$, $p = 0.09$; Pearson correlations between the mean age of birds in a groups and: Length entrance tube, $r = 0.15$, $p = 0.31$; length exit tube, $r = 0.11$, $p = 0.45$; width, $r = -0.04$, $p = 0.76$).

Building

We video recorded building by birds in 19 groups (and 21 structures) recording a total of 169 hours of building. To quantify building, videos were recorded opportunistically, whenever building was observed, often after or during rain. A camera tripod was left overnight to reduce the birds' response when the video camera was set up the following morning. The video camera was set up so that the entirety of a structure was captured and close enough so that individual birds could be identified from their unique color-ring combinations (Fig. 1D). Interobserver tests showed 95% reliability in identifying birds and their behaviors. As different groups varied in the time they took to build a structure, these recordings varied in duration. In addition, birds did not

build continuously throughout the season and sometimes completely stopped after a few days. We therefore stopped recording a structure if no bird had visited the structure for two consecutive days. Videos averaged 140 ± 17 minutes in length and groups were recorded on average 477 ± 104 (Mean $\pm$ S.E.) minutes, taking on average 3.13 ± 0.68 videos per group (Mean $\pm$ S.E.). To score building, we used the open-access software BORIS (Behavioural Observation Research Interactive Software ([59])). The sex, age, and dominance status (dominant or subordinate) for each bird were included during coding. We coded when an individual arrived at the structure, when it left the structure, and whether it brought any material (grass or feathers). To determine if building behaviors were performed differently by different birds within a group, we also coded whether a bird tucked, bent, pushed, pulled, cut, or dropped the material during its visit. Across all videos there were 15 visits made by an individual that could not be sexed or identified by its color rings and we excluded these visits from all subsequent analyses.

We used the number of visits as the response variable because a Spearman's rank correlation showed that the different building actions (tuck, bend, push, pull, cut, drop, and other) were correlated with the number of visits to the structure. To determine whether different categories of birds (dominant or subordinate) male or female built at different rates we used a generalized linear mixed model (GLMM). To control for the variation in the duration of recordings for the different groups we used hourly rate as the building variable. To calculate the hourly rate of building, we divided the total number of visits made by an individual by the length of the observation (i.e., video hours). We log-transformed the response variable Hourly building rate (to ensure normally distributed residuals), included bird identity as a random effect, and Sex (female, male and unknown), bird category (dominant, subordinate). Since we were interested in understanding if the birds at different groups contributed in different ways, we also included Group (19 groups) as a fixed effect. The significance of each model term was tested using the Wald chi-square statistic. To test whether there was a difference in how many individuals of each category (dominant females, dominant males, subordinate males, subordinate females) were recorded building across the 19 groups, we used a chi-square test. We also used a Spearman's rank correlation to investigate whether the number of individuals building in a group correlated with the total number of individuals in a group.

The more birds in a group, the more birds were recorded building a single structure together (Spearman's rho = 0.72, $P = 0.002$, n = 21 structures). In 17 out of 21 structures recorded, there were at least two birds building together, with up to seven birds building a single structure (Mean $\pm$ SE, 3.6 ± 0.8 individuals building per group). The mean proportion of birds within a group contributing to the building of a single structure was on average half of the group (Mean $\pm$ SE, 0.55 ± 0.05). Of all the birds observed building across the groups, 35 were female and 37 were male (72 individuals of 157 total birds in those groups). Across all groups, 19 of the birds building were dominants and 51 were subordinates. Even though subordinates outnumbered dominants, the dominant birds spent more time building than did subordinates (GLMM, main effect of bird category: $X_3^2 = 8.06$, $P = 0.04$). Overall, males and females contributed equally to building (GLMM, main effect of sex: $X_1^2 = 1.62$, $P = 0.44$). Two birds that were migrants from neighboring groups were also observed building together with the groups they have recently joined.

To determine whether there were differences in the frequency of different building actions (tuck, bend, push, pull, cut, drop, and other), we used generalized linear mixed model (GLMM; with building rate as the response variable with a Poisson distribution) with bird identity as a random intercept and including type of building action as a fixed effect. We categorized type of

building action as a seven-level factor. The significance of the fixed terms was tested using a chi-squared statistic.

When building, birds used different actions while manipulating grass brought for construction: tucking, bending, cutting, pulling, and pushing, as well as occasionally dropping the piece. The most common actions were tucking (n = 1869 individual observations) and bending material (n = 2077 individual observations) as these were used more often than the other actions (GLMM, type of building action: $X_8^2 = 6744.1$, $P < 0.001$). Only pulling or dropping the material was performed significantly less by the dominant bird (GLM, Interaction between bird status and building action: $X_{10}^2 = 33.3$, $P < 0.001$). All other building actions were performed equally by dominant and subordinate birds.

Group composition and movement of birds between groups
Group size was determined as the total number of individuals recorded for each group (by observations or capture in that group in a single year). To determine if group size, number of new natal subordinates, or number of new, unrelated individuals had an effect on the variation in the morphology of the structures built by different groups, we used a generalized linear model with the standard deviation of PC1 for each group as the dependent variable. The significance of the model terms was tested using the Wald chi-squared statistic. We compared group similarity by calculating a co-occurrence matrix of all individuals that moved between all of 43 groups. A Jacquard index of similarity matrix was calculated to compare pair-wise groups. This index considers the number of individuals that have moved from one group to another as well as the total number of birds in both groups. It therefore measures group similarity in terms of their composition ranging from 0 to 1, with 0 describing groups that share no individuals. A Mantel test was then used to test whether there was a correlation between the similarity of group compositions, as measured by the Jacquard index matrix, and the dissimilarity between the structures built by different groups calculated from the PC1 values. Referenced data and analysis scripts are archived in Dryad (*52*).
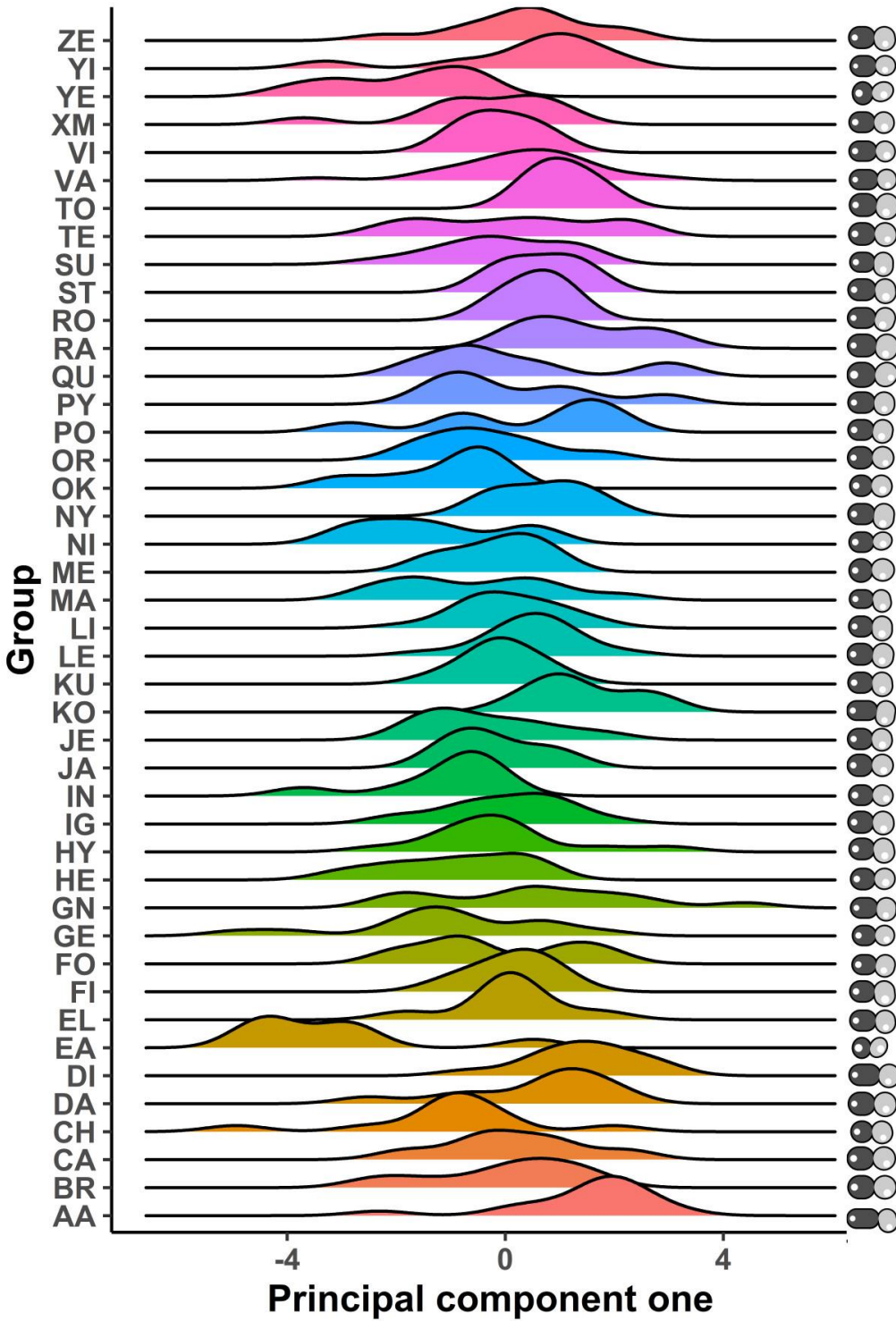
Fig. S1. **Histogram of the first principal component taken from seven measurements of the structures built by 43 groups of white-browed sparrow weavers**. Each group is represented by a different color and a scaled schematic of the mean of the seven measurements taken. The darker tube represents the entrance tube while the lighter one represents the exit tube.
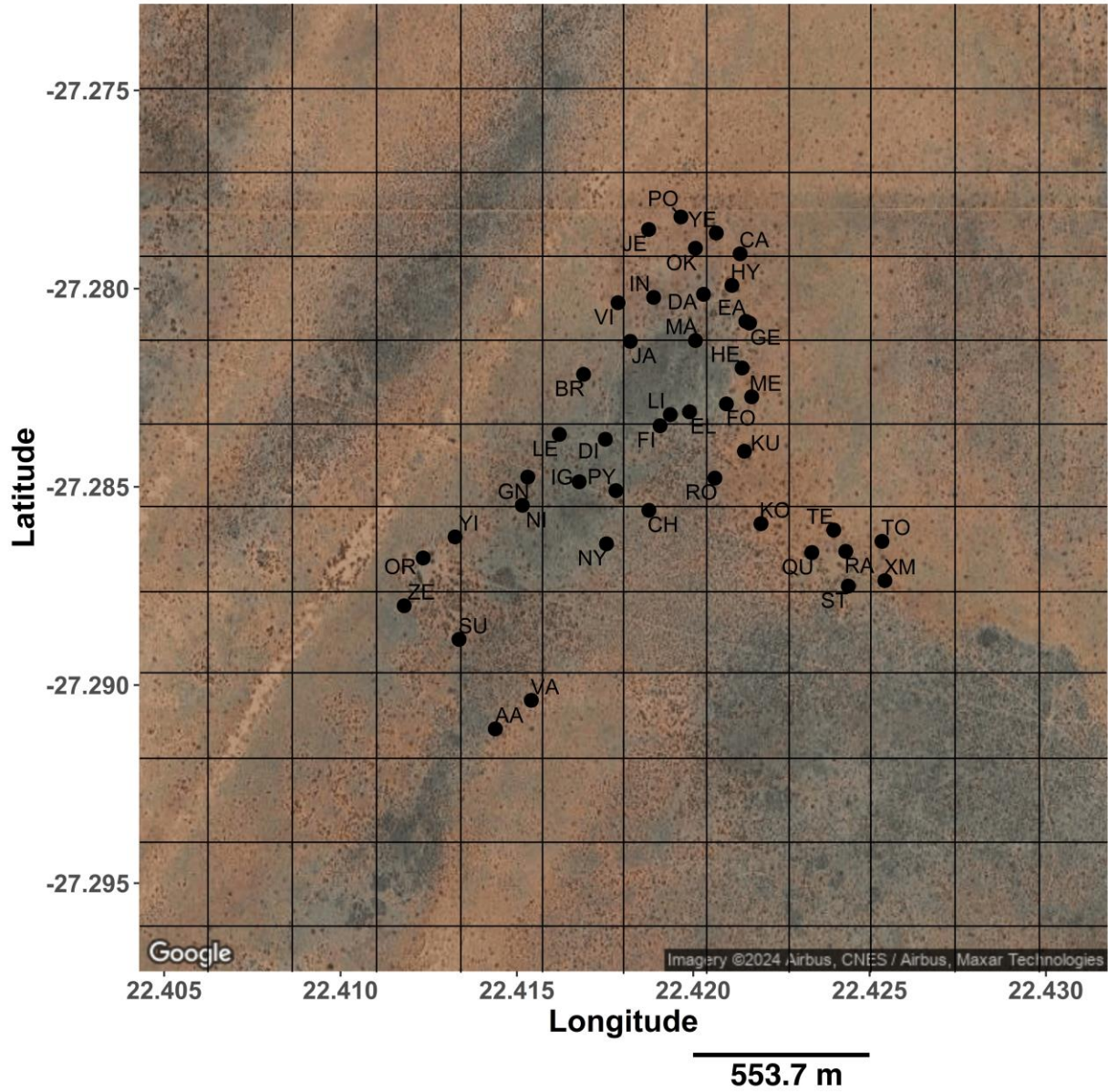
Fig. S2. Map of the study site. Aerial view of the site and the 43 groups showing the spatial relationship among the groups. The dots of different colors represent each of the groups.

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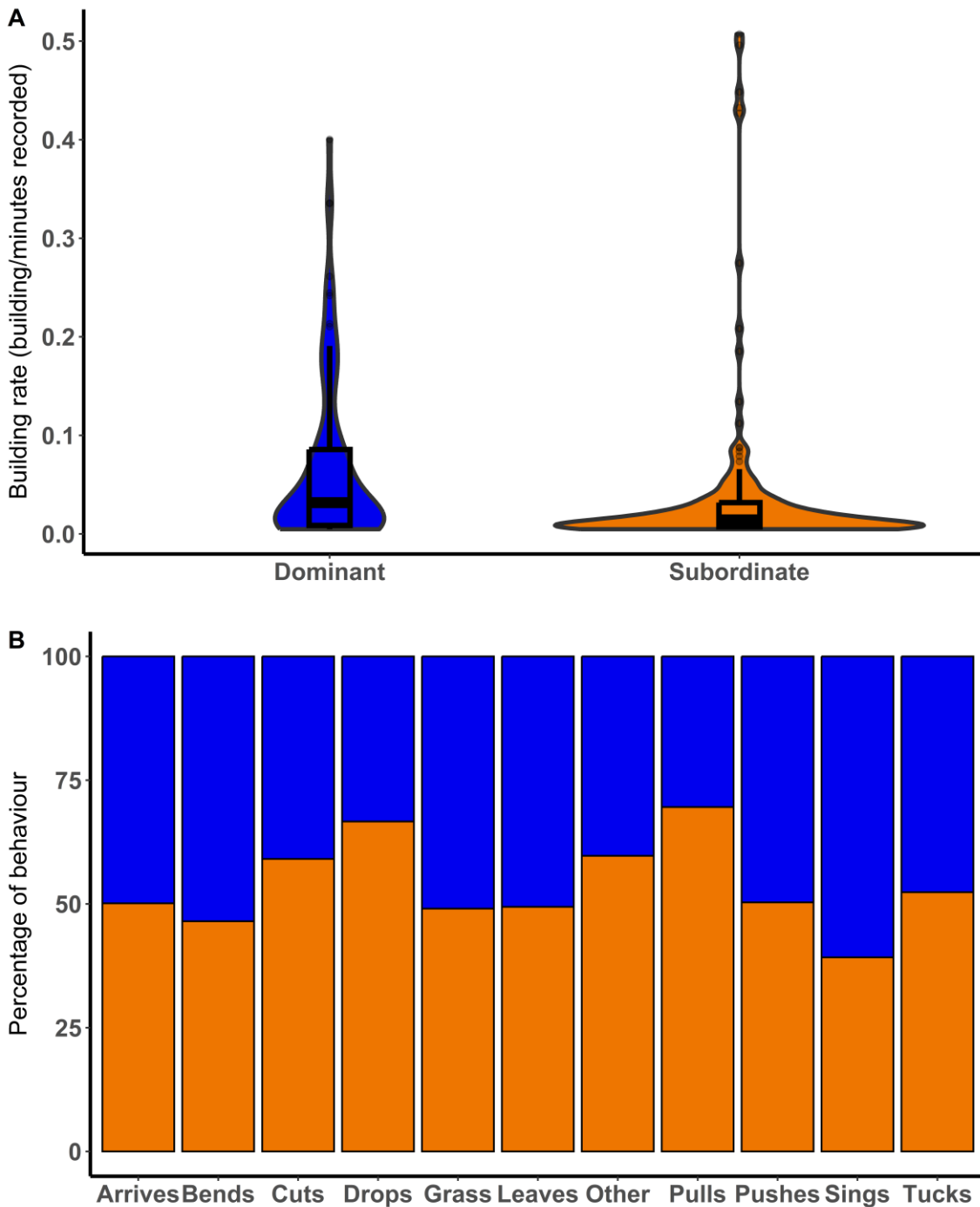
Fig. S3. All birds within a group build together. **(A)** Building rate of dominant (in blue) and subordinate (in orange) birds across all groups that were recorded (n=19, with dominants n=19 and subordinates n= 39). Box plots show the median, first and third quartile for all the structures measured and the shaded areas represent kernel density distributions, dots represent outliers. **(B)** The percentage that each of the behaviors was performed by either dominant (in blue) or the subordinate (in orange) birds.

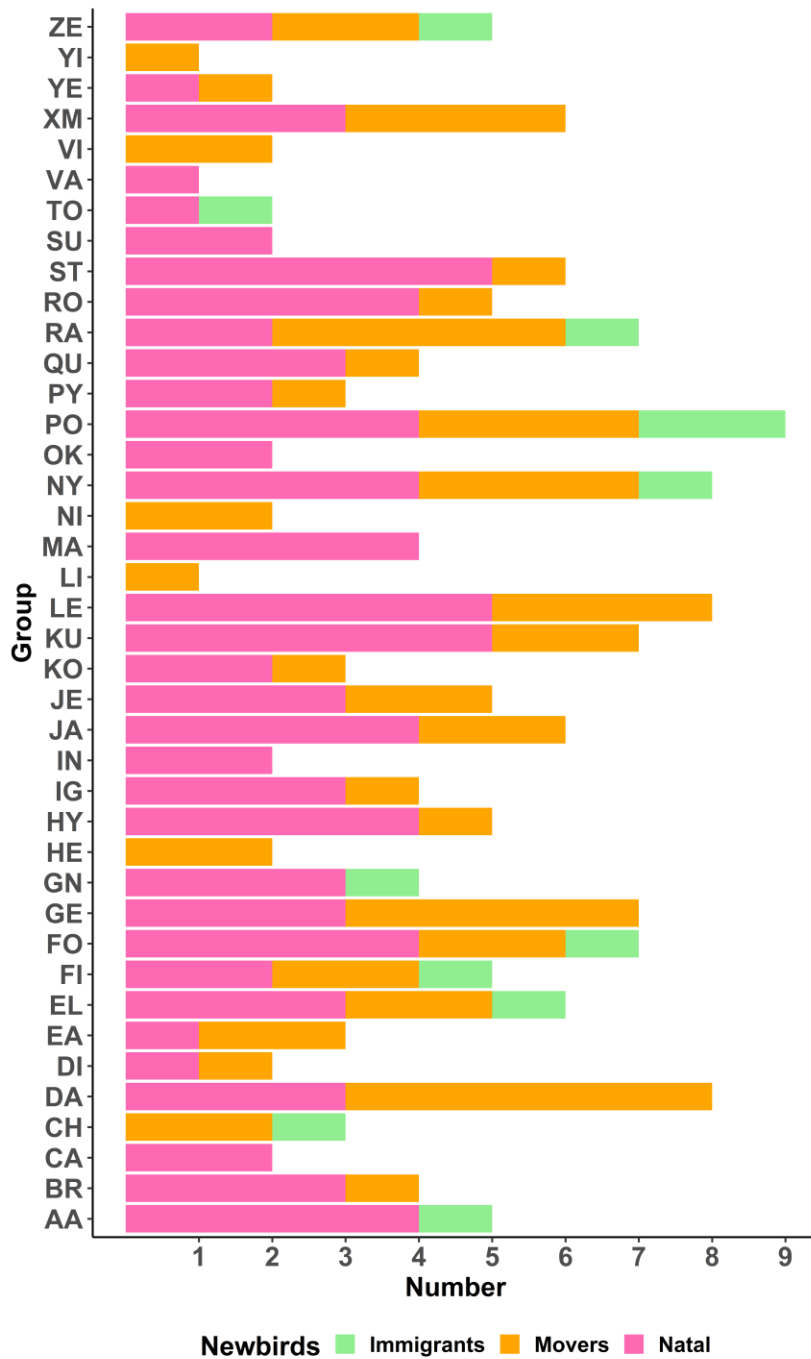**Fig. S4. Movement and group composition.** The total number of individuals that moved to each group for all groups that contained at least one new individual. The group origin of the individuals that moved is indicated by color: Blue represents natal subordinate, green represents birds that moved from other groups within the site, and red/orange represents birds that migrated into the site from elsewhere.

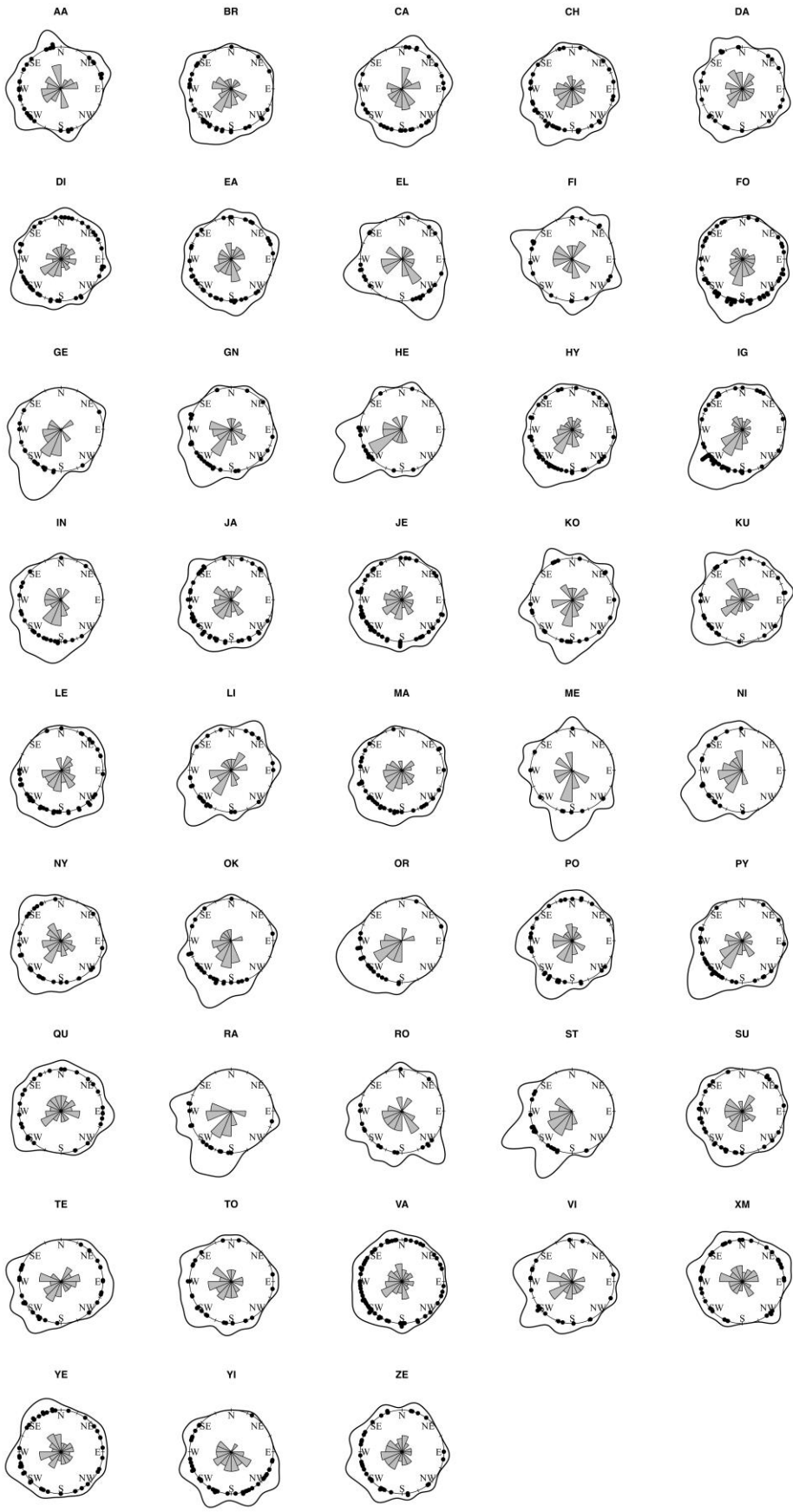**Fig. S5**. **The positions of structures differed between groups.** Raw circular data plots comparing the directions (degrees) where different groups of white-browed sparrow weavers built their structures around the trees in their territories. Inside each circle a rose diagram with the relative frequencies in 16 class intervals and outside a kernel density estimate of bandwidth 40.

Table S1. The morphology of the structures built by different groups of birds differed. Pairwise t-tests comparing the PC1 scores of all the groups with Bonferroni corrections. Only groups that were significantly different ($p < 0.05$) from each other are included.

Group	Groups with significantly different PC1 scores (pairwise t tests p <0.05)										
AA	CH	EA	GE	HE	IN	NI	OK	YE			
BR	EA										
CA	EA										
CH	EA	RA									
DA	EA										
DI	EA	GE	IN	NI	YE						
EA	AA	BR	CA	CH	DA	DI	EL	FI	FO	GN	HY	IG
	JA	JE	KO	KU	LE	LI	MA	NY	OR	PO	PY	QU
	RA	RO	ST	SU	TE	TO	VA	VI	XM	YI	ZE
EL	EA										
FI	EA										
FO	EA										
GE	AA	DI	KO	RA							
GN	EA	YE									
HE	EA										
HY	EA										
IG	EA										
IN	AA	DI	RA								
JA	EA	RA									
JE	EA										
KO	EA	GE	YE								
KU	EA										
LE	EA	YE									
LI	EA										
MA	EA										
ME	EA										
NI	AA	DI	RA								
NY	YE										
OK	AA										
OR	EA										
PO	EA										
PY	EA										
QU	EA										
RA	CH	EA	GE	IN	NI	YE					
RO	EA	YE									
ST	EA										
SU	EA										
TE	EA										
TO	EA										
VA	EA	YE									

VI	EA							
XM	EA							
YE	AA	DI	GN	KO	LE	NY	RA	VA
YI	EA							
ZE	EA							

Table S2. Non-cultural factors did not explain the differences in structure morphology among groups of birds. Summary of model selection using MLPE that evaluated the effects of different variables on the morphology of structures built by different groups. MLPE, the AIC, the ΔAIC, and the r^2 value, are given for the best models for each variable.

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Variables	AICc	ΔAIC	r^2
Distance	1390.7	0	0.011
All	1392.5	1.72	0.023
Wind	1396.7	6	0.006
Null	1399	8.26	NA
Temperature	1400.2	9.5	0.002
Tree height	1400.6	9.89	0.001
Size (tarsus)	1401	10.26	<0.000

Variables	AICc	ΔAIC	r^2
Genetic relatedness	827.2	0	<0.000
Null	827.7	0.49	NA

Table S3. White-browed sparrow weavers build more structures than the number of group members. The average number of total structures in each group, the average number of new structures for each group measured in 2019 and 2020, and the average number of birds in each group for the same years.

	2019	2020
Total structures	21.15 ±1.75 (Mean ± S.E.) Max 57, Min 3	14.82 ±1.07 (Mean ± S.E.) Max 32, Min 1
New structures	16.34 ±1.37 (Mean ± S.E.) Max 33, Min 1	4.51 ±0.53 (Mean ± S.E.) Max 14, Min 1
Number of birds	5.67 ± 0.47 (Mean ± S.E.) Max 14, Min 2	4.92 ± 0.42 (Mean ± S.E.) Max 13, Min 2