ANIMAL CULTURE

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.

The limestone pyramid of the Kukulkan temple in Yucatan, Mexico, looks very different from its contemporary, St. Andrews Castle, in 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 much of the variation we observe in behavior [e.g., social transmission across blue tits (*Cyanistes caeruleus*) 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 building by birds 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 those building in warmer places, as nests containing more material can provide greater insulation (*16*, *18*–*21*). These correlational data have been reinforced by experimental manipulation of temperature, which lead laboratory zebra finches (*Taeniopygia guttata*) to include more material when building their nests at lower temperatures than when building at higher temperatures (*22*). Having had experience in building and successful reproduction, however, the 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*, *9*, *10*, *23*–*26*, *27*). 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 (*9*), or even after viewing only a completed nest (*23*). 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 data that are available 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 weaver birds (*Ploceus velatus* and *P. cuculla* and blue tits building in the wild have low c repeatability (*27*, *29*), but there is evidence for distinctive weave signatures in weaver bird 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) interest in nests has been directed toward 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 an opportunity to examine repeatability of structural morphology, as 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 2 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. 1, A to 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 5 days and 6 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. Because little is known in 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.

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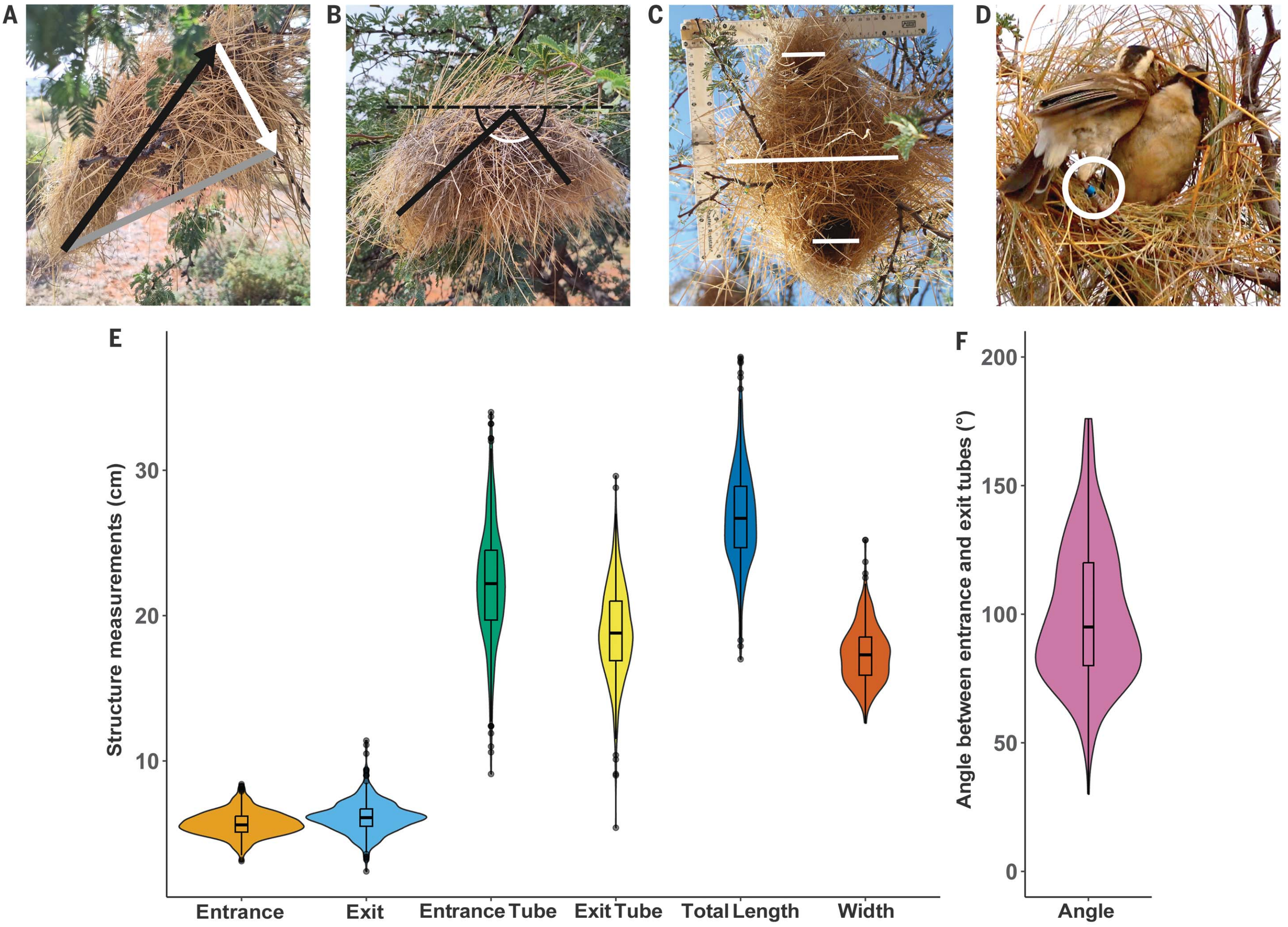

Fig. 1. Measurements taken from structures and variation in structures (both roosts and nests) built by white-browed sparrow weavers. (**A**) Side view of a roost. The black arrow shows the length of the entrance tube, the white arrow shows the length of the exit tube, and the gray lines show the total length. (**B**) Side view of a roost. The angle between the entrance and exit tube is shown in white. (**C**) View from below of a roost. 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; dots represent individual outliers.

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 suggest that local weather conditions, 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 the 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 (see 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 analysis of variance (ANOVA); $F_{42,436} = 4.55$, $P < 0.001$, Fig. 1, E to F, and table S1]. Structures differed in entrance and exit tube length as well as in 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 to 34.00 cm, 18.07; length of exit: 18.92 cm, 5.40 to 29.60 cm, 16.90; total length: 26.91 cm, 17.00 to 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 ± S.E.), while the mean total length of another group's structures was 31.46 ± 0.71 cm (mean ± S.E.) (Fig. 2A). Variation in structural morphology among groups was mostly in entrance tube length [33.47% contribution to the first axis

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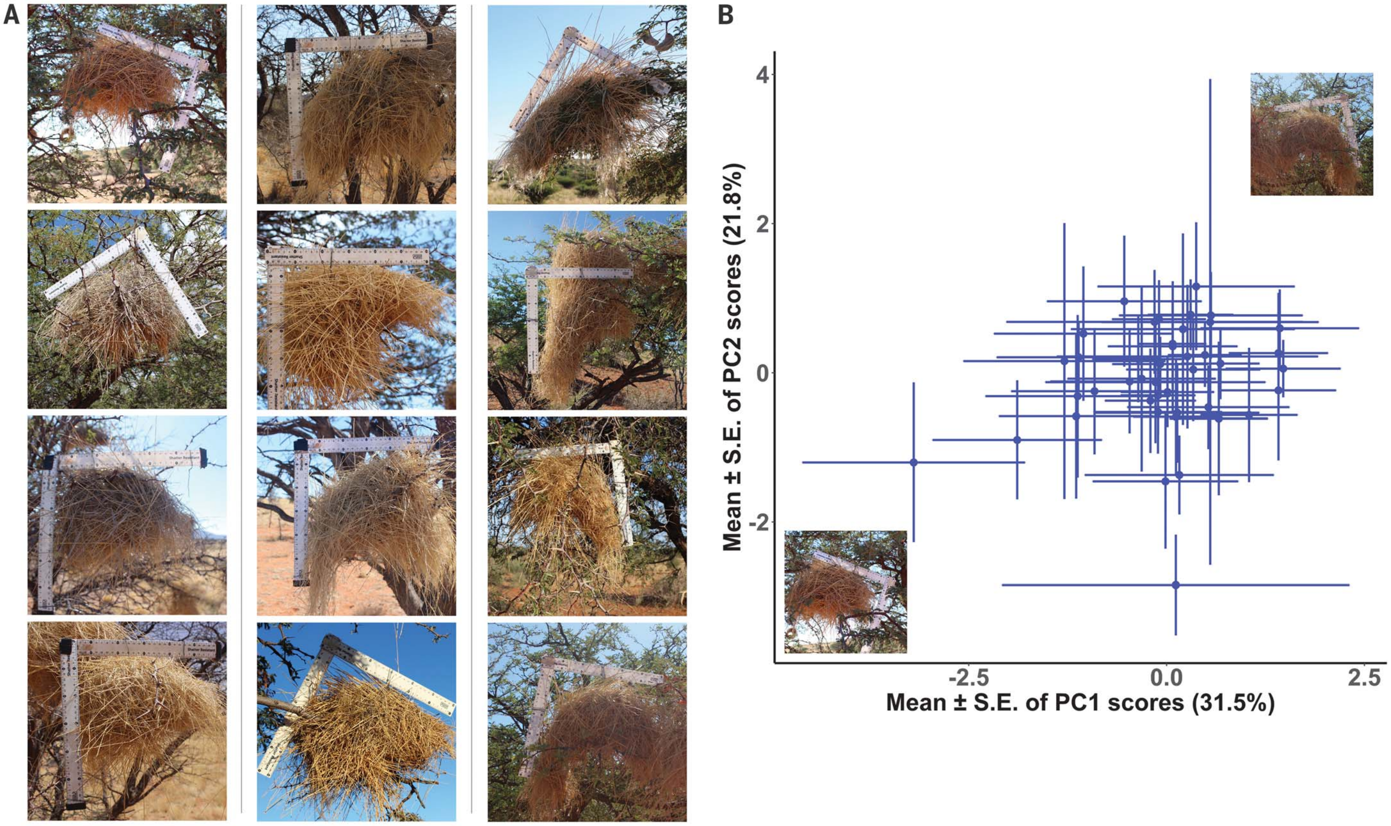

Fig. 2. Variation among the structures built by different groups. (**A**) Images of structures built by three different groups of white-browed sparrow weavers. The two rulers show the difference in size between the structures built by the different groups. (**B**) Mean ± S.E. of PC1 and PC2 scores from 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 and 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%), and the diameter of the entrance hole and the width of the structure explain 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.

of a principal component analysis (PCA)], exit tube length (20.73%), and total length (20.36%). Variation in 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 nonrepeatable and 1 as highly repeatable within the grouping factor, in this case, each of the 43 groups). Notably, structural morphology was significantly repeatable (consistent) within groups, with variation among groups greater than within groups [adjusted repeatability for group accounting for year: $R = 0.26$, 95% confidence interval (CI) = 0.15 to 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 ± 0.2°C and wind speed by 0.59 ± 0.26 km hr^{-1} (both mean ± S.E.) compared to a central reference territory within the study site (supplementary materials). Differences in temperature explained just 0.2% of the variation and differences in 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, as the distance between groups was small; the mean shortest distance among the territories of the groups in the study site was 97.7 m, with the closest groups 11 m apart and the furthest 1.52 km (Fig. 4A and 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 $\Delta\text{AICc} = 6.54$.

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

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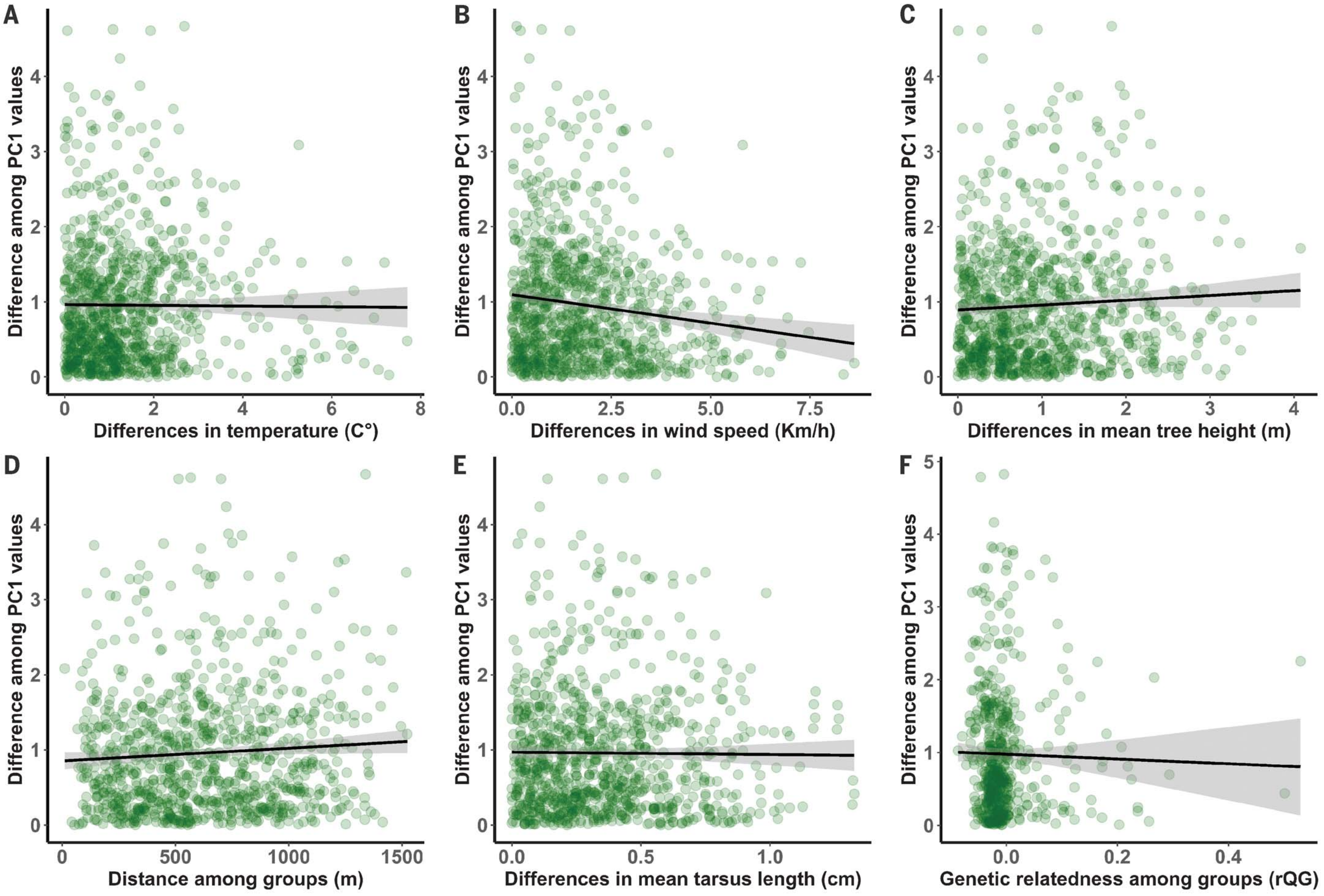

Fig. 3. Noncultural factors do not explain architectural variations. Scatter plots illustrate the lack of significant correlation between the difference in PC1 values calculated from the seven measurements taken from the structures (i.e., length of entrance and exit tube and width, total length, diameters 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**) difference in wind speed, (**C**) difference in the mean heights of the trees at each territory's group, (**D**) distance in meters among groups, (**E**) difference in mean tarsus length of the groups, and (**F**) 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 noncultural factors.

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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 variation in genetic distance between 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).

Taken together, measurements of local weather conditions (temperature and wind speed), tree height, distance between groups, tarsus length, or relatedness explain very little of the 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, using high-definition cameras to identify the colored leg rings of each group member identified. 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. Groups constituted a mean of 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). Group size, number of natal subordinates, and number of new unrelated individuals did not affect 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

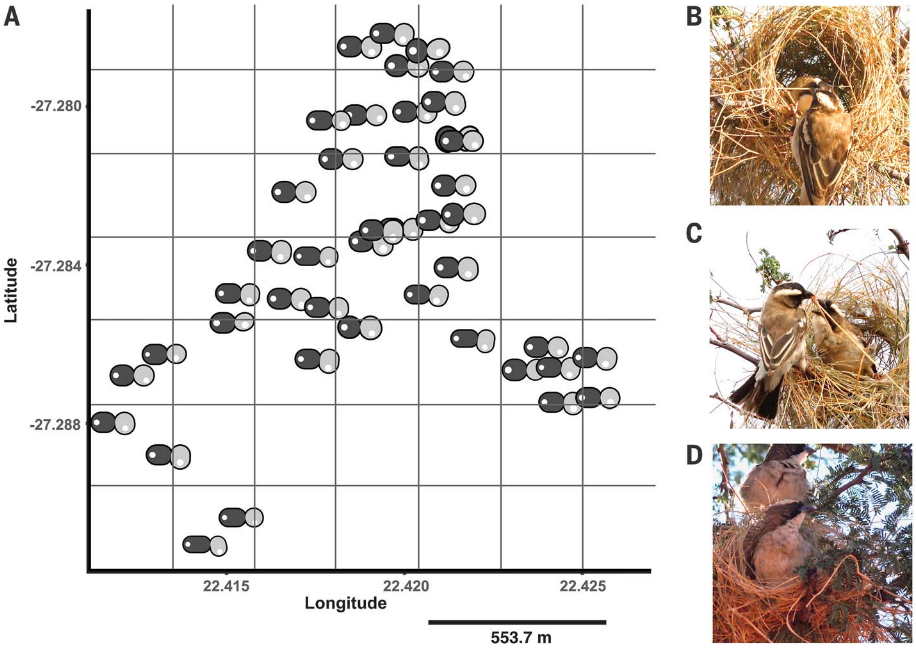

Fig. 4. Spatial distribution of the 43 groups studied and cooperative building in the white-browed sparrow weaver. (**A**) Each group is represented by a scaled schematic of the mean of the seven measurements (length of entrance and exit tube and width, total length, diameters of entrance and exit hole, 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.

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 for 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 same 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 in relation to material-choice decisions. For example, in male spotted bowerbirds (*Chlamydera maculata*), the closer bowers are built 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. Similarly, a hetero-specific community of foraging tits also searched and collected nesting material together, suggesting that in the context of building, birds can use social information gathered from other species (*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 (bees, termites, beavers, etc.) 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

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