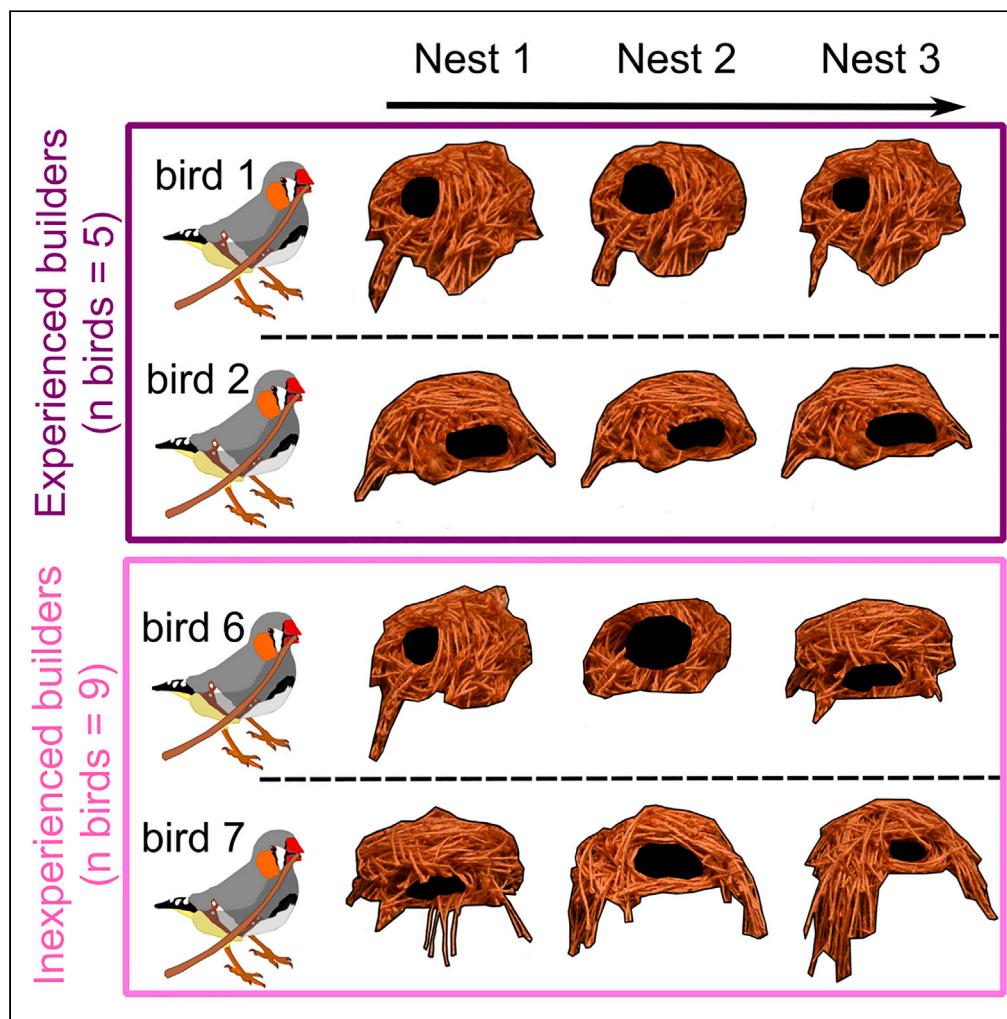


Article

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Highlights
Zebra finches build nests with repeatable styles of morphology

Experienced birds build nests with less varied morphology than naive birds

Experienced birds used less material to build nests than naive birds

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Article

Zebra finches have style: Nest morphology is repeatable and associated with experience

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SUMMARY

We investigated whether birds build nests in repeatable styles and, if so, whether styles were associated with past nest-building experience. Laboratory, captive bred zebra finches in an Experimental group were given nest-building experience, whereas, birds in a Control group were not. Each pair ($n = 20$) then built four nests that underwent image analyses for nest size, geometric shape and entrance orientation. Birds built nests in repeatable styles, with lower morphometric variation among nests built by the same pair and higher morphometric variation among nests built by different pairs. Morphology was not associated with construction time, body weight, nor age of birds. We found lower morphometric variation among nests built by the Experimental group, which also used less material to build nests compared to the Control group. Prior experience may therefore have been advantageous, as learning to reduce material usage while achieving a similar product (nest) may have lowered building costs.

INTRODUCTION

Animal architecture is taxonomically widespread and includes diverse structures that are built to serve a range of functions.¹ Chimpanzees (*Pan troglodytes*) construct nests to provide overnight shelter, orb web spiders (*Araneus diadematus*) spin webs to sense and trap their prey, and pufferfish (*Torquigener* sp.) create circular geometric patterns in sand to attract mates.^{2–4} Morphological variation exists among structures built by different individuals of the same species, despite their structures serving the same function.⁵ Animal architecture is therefore an extended phenotype, as intraspecific variation among structures is subject to natural and/or sexual selection.⁶ Potential sources for variation include intrinsic differences among the builders themselves.⁷ For example, larger gopher tortoises (*Gopherus polyphemus*) dig wider burrows than smaller conspecifics, female Bornean orangutans (*Pongo pygmaeus*) build closed nests whereas males build open nests, and unhealthy three-spined sticklebacks (*Gasterosteus aculeatus*) construct less compacted nests relative to their healthy counterparts.^{8–10} Measuring morphological variation among structures may provide insight on differences among the individuals which built them.

Bird nests are a ubiquitous form of animal architecture. Perez et al.¹¹ define three components of nest morphology: size, composition and shape. Here, we use these and incorporate two others to operationally define the five components (size, composition, class [termed "shape" by Perez et al.¹¹], shape, and orientation) of nest morphology used in the present experiment. First, nest size refers to linear dimensions of the structure, often measured as width, height and/or length, and are commonly associated with the body size of the builder(s).¹² Second, nest composition refers to the amount and type of material(s) that make up the structure, often measured as weight or volume.¹¹ Perez et al.¹¹ defined the categorical classification of a nest (e.g., cup, dome, cavity) as nest shape.¹¹ We redefine the categorical classification as nest class, our third morphological component. We re-use the term nest shape to define our fourth morphological component, which refers to geometric shape measured using landmark coordinates.¹³ Our fifth morphological component, nest orientation refers to the orientation of the nest relative to the position of a focal asymmetric feature, such as an entrance hole. By defining nest morphology as constituting the size, composition, class, shape and orientation of a nest we can assess how morphological styles of different nests vary along multiple dimensions. In the following paragraph we provide examples of variation in these five components of nest morphology.

Nest size and composition both show intraspecific variation. Yellow warblers (*Dendroica petechia*) breeding in northern Manitoba build larger nests (76.6 ± 3.8 mm exterior diameter) made from grasses, feathers, fireweed (*Epilobium* sp.) and willow (*Salix* sp.), whereas, yellow warblers breeding in southern Ontario build smaller nests (65.2 ± 4.4 mm exterior diameter) made from grasses and milkweed bark (*Asclepias* sp.).¹⁴ Nest class is phylogenetically conserved across taxa with closely related families building nests of similar shapes.^{15,16} The geometric shape of bird nests has received little attention and, to our knowledge, there are no published morphometric landmark analyses of bird nests. Notably, Jessel et al.¹⁷ digitized the structure of Dead-Sea sparrow (*Passer moabiticus*) nests using three-dimensional computed tomography

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(CT) and Bailey et al.¹⁸ pioneered computer-aided image texture classification analyses to quantify the texture of weaver bird (*Ploceus* spp.) nests. Lastly, the orientation of mud nests built by rufous hornero (*Furnarius rufus*) has been defined as left-oriented or right-oriented relative to the side of the nest on which the entrance hole is constructed.^{19,20}

Cognitive processes facilitate avian nest building.²¹ These processes include the development of motor skills (e.g., manipulating material), as seen in southern masked weaver birds (*Ploceus velatus*) which build lighter nests with increasing dexterity as they mature from juveniles to adults.²² Birds also use social information to learn about nest building. Wild blue tits (*Cyanistes caeruleus*), great tits (*Parus major*), and marsh tits (*Poecile palustris*) learn the location of nest material from conspecifics they associate with while foraging for food, and may choose the color of nest materials based on the color choices of neighboring conspecifics.²³ Memory also plays a role in nest building. Ravens (*Corvus corax*) recall the outcomes of past nests (e.g., success or failure of broods) and avoid nest sites that were disturbed and thus failed in previous breeding seasons.²⁴ Substantial work investigating cognitive processes in avian nest building has been conducted on captive bred zebra finches (*Taeniopygia guttata*) in the laboratory. These studies find that zebra finches develop motor skills to better manipulate nest materials as they gain nest-building experience, learn about the physical properties of different materials (e.g., color, length, flexibility), and choose materials that are best suited for building in specific contexts (e.g., selecting shorter string to fit through a narrow nest box hole).^{25,26} Zebra finches use social information from live demonstrators and social artifacts (e.g., abandoned nests) to inform decisions on nest material selection.^{27–29} The species also recalls the type and amount of material(s) used in previous nests, and adjusts subsequent material selection depending on past successes and failures.^{30–32} This accumulation of skills, learning and decisions is described as leaving a “behavioral fingerprint” on the structure of a nest.³³ We hypothesize there are repeatable styles in nest morphology that can reveal information about the skills, learning and decision-making of a bird and, as with fingerprints, can be analyzed to identify which individual built a specific nest.

In this experiment, we quantify the morphology of nests built by a captive population of zebra finches bred and housed in a laboratory. Zebra finches are an Australian species of estrildid finch that are widely used as a model for animal cognition, evolutionary biology, and neurobiology.^{34,35} Similarly to wild zebra finches, captive birds are opportunistic breeders that will readily build multiple nests in short succession.^{36,37} The species typically builds domed nests in both the wild and in the laboratory, which in the wild are constructed from grasses but in captivity are built using an array of provided materials including string, cotton, and coconut fiber.^{31,38,39} The male is the primary nest builder as he selects and deposits the majority of material into the nest.³⁸ Female zebra finches lay one egg per day and clutches are complete after the female has not laid any new eggs for a 24-h period.^{39,40}

We experimentally tested whether captive male zebra finches show repeatable styles in nest morphology. Style was defined as morphometric patterns seen across multiple nest components that were consistent to a specific individual across the nests they built, while also differing from the morphometric patterns of nests built by other individuals. Here, we examine repeatability in size, shape, and entrance orientation of successive nests built by the same pair, predicting that if styles are present in architecture we would find repeatability in one or more of these three components. We also experimentally test whether styles are associated with prior nest-building experience through manipulating the opportunity for birds to accumulate nest-building experience. We hypothesize that if learning processes influence nest style, then birds with prior nest-building experience would build nests with less varied style, as experience provides opportunities to develop skills and acquire information that facilitates subsequent nest building.

An Experimental group ($n = 10$ female-male pairs, the experienced group) first built five successive nests using 15 cm long pieces of white string, before then building four successive nests using coconut fiber. Whereas, the Control group ($n = 10$ female-male pairs, the inexperienced group) did not build any string nests before constructing four successive coconut fiber nests. Pairs in neither group handled nor built nests using coconut fiber prior to start of the study. Upon completion, coconut fiber nests were carefully taken from each cage and photographed under standardized conditions, in which the position and distance from camera, light levels, background, and position of a ruler for size calibration all remained the same. The next day, we added a clean nest cup and new building materials to the cage so that the pair could begin constructing their next nest. This process repeated until each pair built all required nests (experienced group = 5 string, 4 coconut fiber; inexperienced group = 4 coconut fiber). Pairs were excluded from the study if they did not successfully build four coconut fiber nests inside the nest cup. In total, five pairs from the experienced group and nine pairs from the inexperienced group successfully built the number of coconut fiber nests required for image analysis. The time taken (days) and amount (g) of coconut fiber used to build each nest was recorded, as was the body weight (g) and age (days) of all birds at the start of the study. Data on nest size, shape, and entrance orientation (see Table 1; Figures 1 and 2) was extracted from photographs of coconut fiber nests (n pairs = 14; n nests = 56) for statistical analyses. For further details on methodology and statistical analyses please see the [STAR Methods](#) section.

RESULTS

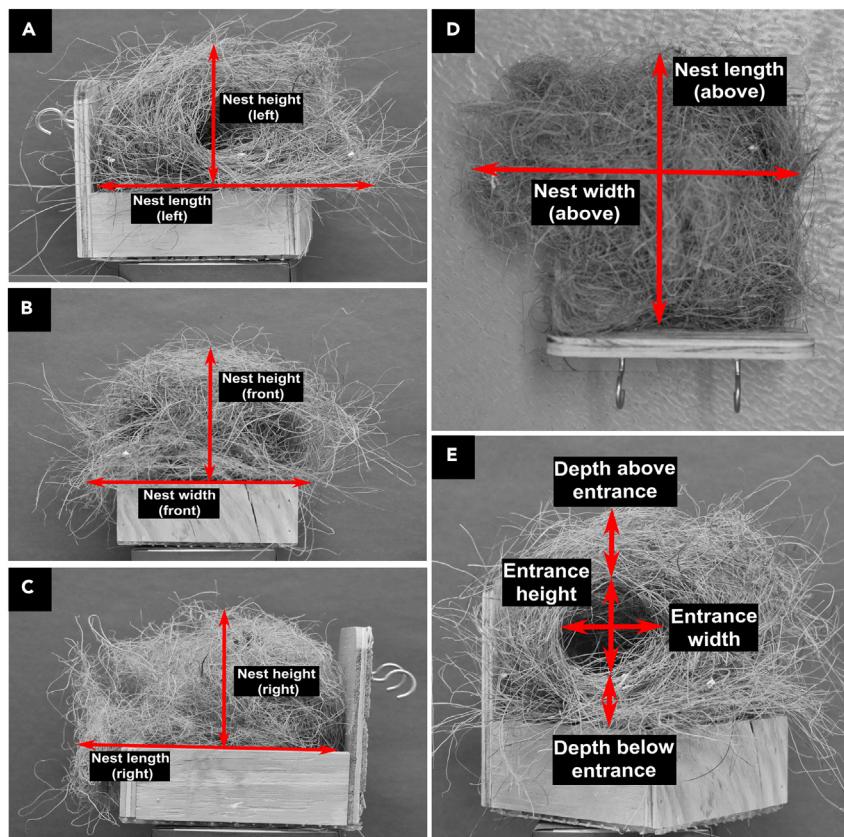
Repeatable styles in nest morphology

Coconut fiber nests were an average of $18.3 \pm SD 3.4$ cm long and $20.3 \pm SD 4.9$ cm wide as viewed from above, with an average height of $11.7 \pm SD 3.7$ cm as viewed from the front of the nest cup. We created a multivariate dissimilarity matrix which incorporated nest size (two Principal Component [PC hereafter] dimensions accounting for 83.6% of variance in eight measurements), nest shape (three PC dimensions accounting for 65.0% of variance in 22 Procrustes coordinates), entrance size (three PC dimensions accounting for 87.9% of variance in four measurements), entrance shape (four PC dimensions accounting for 79.2% of variance in 24 Procrustes coordinates), and entrance orientation (one quadrant location). A higher score in the matrix indicated a nest was less similar in terms of size, geometric shape, and entrance orientation relative to other nests.

Table 1. Definitions of 12 linear measurements of nest size taken across five images used in principle Component Analyses

Measurement	Definition	Nest Image(s)	PCA
Nest height	Distance between the highest point of the nest perpendicular to the cup	Left, Right, Front	Nest Size
Nest length	Distance between the backboard and furthest point of the nest, parallel to the cup	Left, Right, Above	Nest Size
Nest width	Distance between the furthest points the nest reaches parallel to the front corners of the cup	Front, Above	Nest Size
Entrance height	Distance between the highest and lowest points of the entrance, perpendicular to the cup	Entrance	Entrance Size
Entrance width	Distance between the leftmost and rightmost points of the entrance, parallel to the cup	Entrance	Entrance Size
Depth above entrance	Distance between the highest part of the entrance and highest visible part of the nest, perpendicular to cup	Entrance	Entrance Size
Depth below entrance	Distance between the lowest part of the entrance and lowest visible part of the nest, perpendicular to cup	Entrance	Entrance Size

Using the multivariate dissimilarity matrix as a response variable and pair ID as a grouping variable, we found significant differences in nest morphology among the fourteen pairs of captive zebra finches (PERMANOVA: $R^2 = 0.430$, $F = 2.435$, $p < 0.001$; 10,000 permutations). There was lower variation among nests built by the same pair than among nests built by different pairs (ANOSIM: $R = 0.342$, $p < 0.001$; 10,000 permutations; see Figure 3). We also ran univariate repeatability analyses that considered single PC dimensions or single measures as response

**Figure 1. Linear measurements (cm) collected from five images of the same coconut fiber nest**

(A-E) Measurements, shown as red arrows, were taken from the left side of the nest cup (A), front of the nest cup (B), right side of the nest cup (C), above the nest cup (D), and directly viewing the entrance (E). Images are shown here in greyscale to help illustrate linear measurements taken on color images.

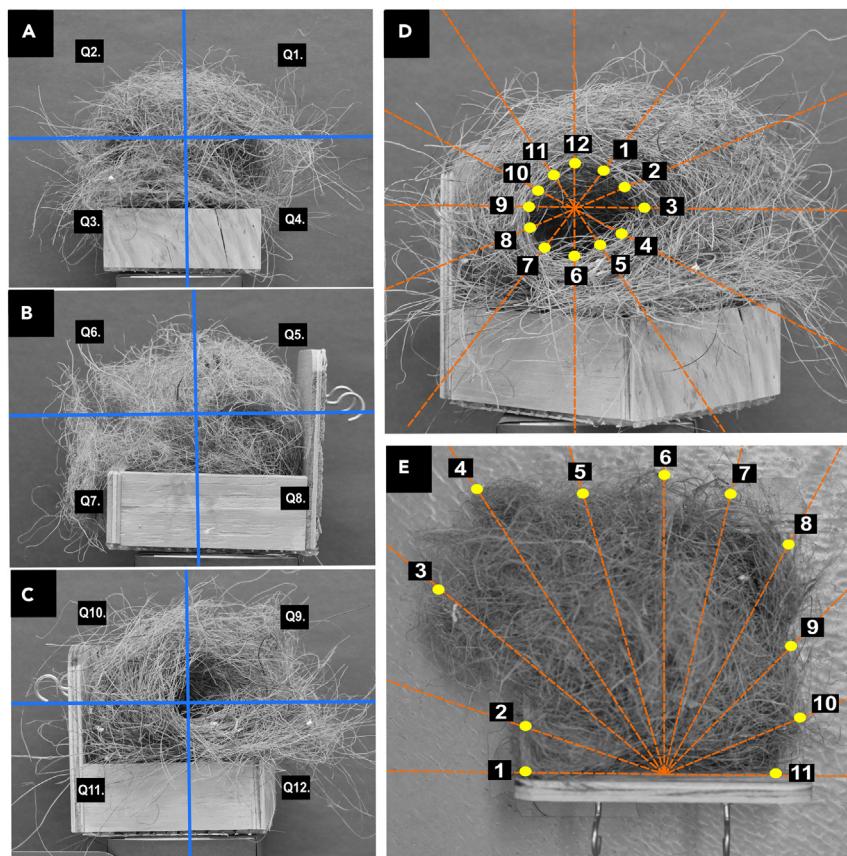


Figure 2. Quadrant and landmark positions superimposed over five images of the same coconut fiber nest

(A–C) Quadrant templates (Q1 – Q12), shown in blue, were positioned over images of the front of the nest cup (A), right side of the cup (B) and left side of the cup (C). The quadrant containing the largest area of the entrance was assigned as the entrance location.

(D and E) Landmarks, shown in yellow, were positioned on nest images using templates, shown in orange, to conduct geometric shape analyses on the entrance (D, landmarks = 12) and general shape of the nest viewed from above (E, landmarks = 11). Images are shown here in greyscale to help illustrate landmarks and templates placed on color images.

variables. We found strong repeatability for nest size (PC1 [69.5% of variance]: $R = 0.650 \pm SE 0.123$ [95%CI = 0.337–0.818], $p < 0.001$), entrance orientation ($R = 0.627 \pm SE 0.130$ [95%CI = 0.294–0.799], $p < 0.001$), and moderate repeatability for PC dimensions of nest shape (PC1 [37.5% of variance]: $R = 0.258 \pm SE 0.138$ [95%CI = 0.000–0.520], $p = 0.016$), entrance size (PC3 [22.6% of variance]: $R = 0.373 \pm SE 0.146$ [95%CI = 0.053–0.620], $p = 0.002$) and entrance shape (PC2 [20.2% of variance]: $R = 0.236 \pm SE 0.136$ [95%CI = 0.000–0.495], $p = 0.023$). Results from both the multivariate and univariate analyses showed that pairs consistently built bigger/smaller nests than others, had consistent differences in the geometric shape of nests and orientation of nest entrances. This supports the notion of repeatable styles in morphology among nests built by the pairs in our experiment (see Table 2).

As birds were weighed at the start of the experiment, we tested whether the body weight or age of birds was associated with differences in the morphology of the first nest they built. Using the multivariate dissimilarity matrix as a response variable, we found that neither the body weight (PERMANOVA: $R^2 = 0.041$, $F = 0.514$, $p = 0.891$; 10,000 permutations) nor age (PERMANOVA: $R^2 = 0.027$, $F = 1.492$, $p = 0.144$; 10,000 permutations) of males accounted for differences among nests. Likewise, neither female body weight (PERMANOVA: $R^2 = 0.059$, $F = 0.756$, $p = 0.671$; 10,000 permutations) nor age (PERMANOVA: $R^2 = 0.020$, $F = 1.089$, $p = 0.364$; 10,000 permutations) accounted for differences among nests.

Influence of experience on nest morphology

Using the multivariate dissimilarity matrix as a response variable with coconut fiber nest number (1–4) as a grouping variable and permutations restricted by pair ID, we found marginal, yet non-significant, differences among nests built by each pair over time (PERMANOVA: $R^2 = 0.024$, $F = 1.302$, $p = 0.065$; 10,000 permutations). Morphological variance among nests built by all pairs (both Experimental and Control groups) was lower among earlier nests (nest 1 distance to median centroid = 6.321, nest 2 distance to median centroid = 5.955) and higher among later nests (nest 3 distance to median centroid = 7.127, nest 4 distance to median centroid = 7.846). There were marginal, yet non-significant, morphological differences among coconut fiber nests built by all pairs across the four different time points (Permutation test: $F = 2.408$,

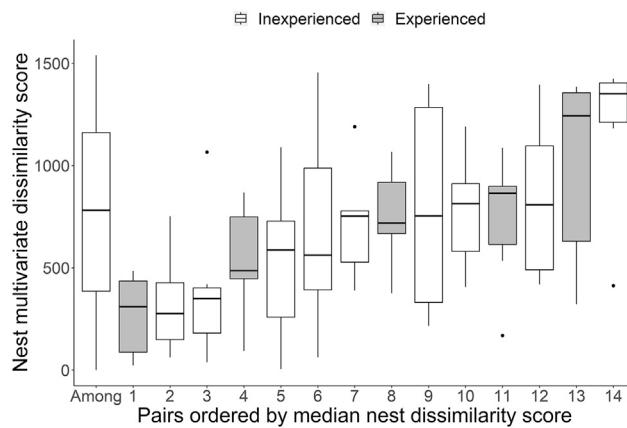


Figure 3. A multivariate dissimilarity matrix was created using measures of nest size, shape and orientation, dissimilarities were then analyzed among nests built by fourteen pairs of zebra finches

There were among-pair differences in morphology of coconut fiber nests (PERMANOVA: $R^2 = 0.430$, $F = 2.435$, $p < 0.001$). There were greater among-pair differences in nest morphology, shown in the first boxplot, than within-pair differences in nest morphology (ANOSIM: $R = 0.342$, $p < 0.001$). Pairs are ordered by median dissimilarity score, with prior experience building string nests being shown in gray and pairs without prior experience being shown in white. Bold horizontal bars represent medians, boxes show interquartile ranges, whiskers show values within 1.5 times the interquartile range, and outlying values are shown as circles.

$p = 0.078$; 10,000 permutations; see Figure S1). However, associated pairwise permutation tests found marginal differences when comparing the first nest to the last nest ($p = 0.055$) and significant differences when comparing the second nest to the last nest ($p = 0.029$; see Table 3). There were no further marginal nor significant pairwise comparisons among nests 1, 2 and 3, nor nest 3 and 4. Taken together, these results suggest that each pair was relatively consistent in the style of nest they built over time, though among-pair style was most different when comparing the last nest to the earlier nests.

There was significant heterogeneity in the multivariate dissimilarity matrix (Permutation test: $F = 4.991$, $p = 0.031$; 10,000 permutations) among coconut fiber nests built by the Experimental group (distance to median centroid = 6.127) and the Control group (distance to median centroid = 7.214). This shows there was less varied morphology among coconut fiber nests built by birds with prior experience building string nests compared to coconut fiber nests built by naive birds (Figure 4). It is important to highlight the small and uneven sample sizes used in this comparison, with five pairs in the experienced group and nine pairs in the inexperienced group.

Using the multivariate dissimilarity matrix as a response variable, we found differences among nests were accounted for by the amount of coconut fiber used to build the nest (PERMANOVA: $R^2 = 0.116$, $F = 7.066$, $p = 0.006$; 10,000 permutations). Pairs in the Experimental group used significantly less coconut fiber in their nests than pairs in the Control group (Linear Mixed Model: estimate for prior experience = $-0.386 \pm SE 0.136$, $t = -2.835$, $p = 0.013$; Figure 5). The amount of coconut fiber used in nests was not correlated with the time taken to

Table 2. Repeatability values (R) for 13 morphological variables over four nests built by the same pairs of zebra finches

Variable	R	$\pm SE$	95% CI	P	
Nest Size PC1	0.650	0.123	[0.337–0.818]	<0.001	***
Nest Size PC2	0.193	0.130	[0.000–0.460]	0.051	
Nest Shape PC1	0.258	0.138	[0.000–0.520]	0.016	*
Nest Shape PC2	0.000	0.069	[0.000–0.231]	1.000	
Nest Shape PC3	0.138	0.117	[0.000–0.397]	0.110	
Entrance Size PC1	0.020	0.077	[0.000–0.264]	0.393	
Entrance Size PC2	0.000	0.068	[0.000–0.234]	1.000	
Entrance Size PC3	0.373	0.146	[0.053–0.620]	0.002	**
Entrance Shape PC1	0.062	0.094	[0.000–0.314]	0.269	
Entrance Shape PC2	0.236	0.136	[0.000–0.495]	0.023	*
Entrance Shape PC3	0.082	0.100	[0.000–0.336]	0.220	
Entrance Shape PC4	0.000	0.070	[0.000–0.239]	1.000	
Entrance Orientation	0.627	0.130	[0.294–0.799]	<0.001	***

Included are the standard error (SE), 95% confidence intervals (CI), p value and significance threshold (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$).

Table 3. Pairwise comparison in morphological variance among four nests built by fourteen pairs of zebra finches

	Nest 1	Nest 2	Nest 3	Nest 4
Nest 1		0.640	0.264	0.055
Nest 2	0.639		0.149	0.029*
Nest 3	0.267	0.147		0.362
Nest 4	0.054	0.030*	0.358	

Included are observed t-test p values (lower diagonal), permutation test p values (upper diagonal) and significance threshold (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$).

complete the nest (Repeated Measures Correlation: $R^2_{(39)} = 0.054$, $p = 0.738$) nor did the time taken to complete the nest account for structural differences among nests (PERMANOVA: $R^2 = 0.034$, $F = 0.936$, $p = 0.301$; 10,000 permutations).

DISCUSSION

We find evidence for repeatable styles in bird nest morphology. These styles represent patterns in the size, geometric shape, and entrance orientation of nests that are consistent among nests built by the same individual and varied among nests built by different individuals. We did not find any association between nest morphology and the time taken to build a nest, nor the body weight or age of male and female zebra finches. Morphometric variance was lower among nests built earlier in the experiment and higher among nests built later in the experiment. There was lower morphometric variance among nests built by experienced birds compared to nests built by inexperienced birds. Experienced birds also used less material to construct nests than inexperienced birds.

Repeatable styles in nest morphology

Nest style represents repeatable variation in the extended phenotypes of the birds, potentially holding wider significance for processes of natural and/or sexual selection.⁶ Having found evidence for styles among nests, we are now faced with the question: what mechanism(s) led birds to build in repeatable style?

Our experiment controlled factors known to influence bird nest morphology, including climate and habitat variables. Common fitness indicators (body size and age) did not account for morphological differences between nests. These factors, discussed in the paragraphs later in discussion, are therefore highly unlikely to have been mechanisms that influenced nest style in the present study. Our study did not assess the role of heritability on nest morphology, so a genetic basis cannot be ruled out as a mechanism that influenced style. Future studies should quantify morphological components of nests built by genotyped birds from known early social environments to undertake pedigree analysis and ascertain values of genetic inheritance. Of the factors considered in our analyses, only prior nest-building experience accounted for differences in nest morphology. This supports our hypothesis that cognitive processes, specifically opportunities to learn from previous nest-building events, act as mechanisms influencing intraspecific variation in animal architecture.

Numerous studies demonstrate the effect of climatic variables on nest morphology, in particular temperature, humidity, and precipitation.¹¹ Nest size and composition often show adaptation to local climate conditions, with structures being built that optimize a stable microclimate for offspring development.⁴¹ Comparing nests collected across the range of widely distributed species shows that nests built in cooler environments are typically larger and more insulated than nests built in warmer environments.¹⁴ It is highly unlikely that climate affected nest style in the present study, as all the zebra finches were housed under laboratory conditions in the same room with a shared constant climate.

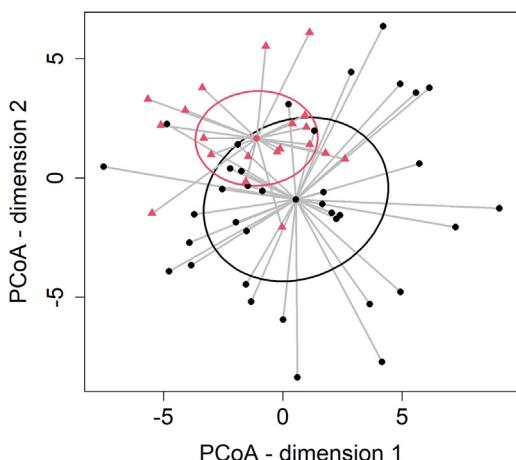


Figure 4. Morphological variance was lower among nests built by experienced birds relative to inexperienced birds

Principal coordinate analyses showed heterogeneous dispersion in the multivariate dissimilarity matrix (Permutation test: $F = 4.991$, $p = 0.031$; 10,000 permutations), with lower distances to the group centroid (median distance = 6.127) for nests built by birds with prior experience (shown as red triangles) and higher distances to the group centroid (median distance = 7.214) for nests built by inexperienced pairs (shown as black circles).

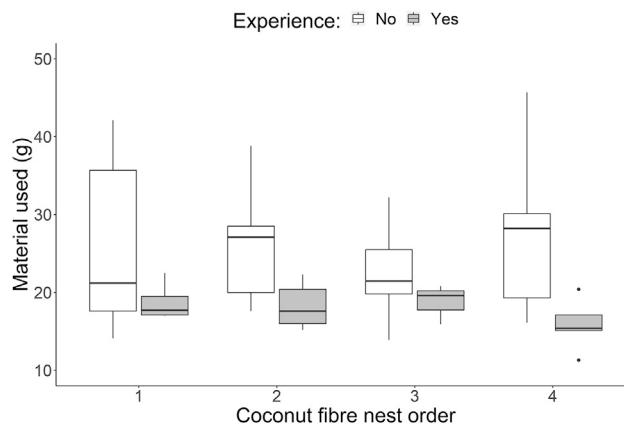


Figure 5. Experienced pairs used less coconut fiber to build nests than inexperienced pairs

The amount of coconut fiber (g) used to build the first, second, third and fourth nest by birds with past experience building string nests (shown in gray) and birds without prior nest building experience (shown in white). Bold horizontal bars represent medians, boxes show interquartile ranges, whiskers show values within 1.5 times the interquartile range, and outlying values are shown as circles.

Nest morphology is also influenced by the habitat in which a nest is constructed. For example, bearded reedlings (*Panurus biarmicus*) build thicker nests with a cone-shaped base in sites with dense vegetation and thinner nests in sites with less-dense vegetation.⁴² Habitat is unlikely to have affected nest style in the present experiment as pairs were housed in cages with a standardized layout and had *ad libitum* access to the same type of building material. We also controlled for possible variation among nest sites by omitting pairs from analyses that did not build at the same nest site (inside the nest cup).

Nests are required to support the combined weight of the incubating parent(s) and offspring, which accounts for the positive correlation between nest size and parent body weight observed across numerous species in the wild.^{41,43} We found no association between nest morphology and the body weights of captive female and male zebra finches. This might have been because the nest cups supported the weight of the birds from underneath the nest. It might be speculated that nest style was associated with other fitness traits. For example, intraspecific variation among three-spined stickleback nests is thought to reflect the ability of males to meet energetic costs incurred during the building process.¹⁰ Every pair of zebra finches in our study had *ad libitum* access to food, dietary supplements and water, and completed a 24-h rest period between building successive nests. Additionally, we found that the age (a common fitness indicator) of zebra finches did not account for morphological differences among nests.⁴²

A genetic basis for burrow morphology has been described in deer mice (*Peromyscus* spp.), with specific genomic regions shown to code for burrowing behaviors that determine burrow length and the presence/absence of escape routes.^{44,45} Comparable studies on a genetic basis for avian nest morphology are lacking, and there are contrasting reports on the heritability of nest morphology in wild birds. Blue tit (*Cyanistes caeruleus*) nests show low heritability in size (12%) and composition (13%), whereas, barn swallows (*Hirundo rustica*) show high heritability in components of nest size (33–66%).^{46,47} Our experiment was not designed to assess the heritability of bird nest morphology. Ten of the male zebra finches used in our study were unrelated, with two pairs of siblings among the remaining four birds.

Influence of experience on nest morphology

There were two ways in which captive zebra finches could gain nest-building experience during our experiment: (1) all birds could gain experience when building four successive nests using coconut fiber, (2) Experimental birds could gain prior experience when building five nests using white string, whereas, Control birds could not.

Although nest-building behavior was not directly observed in this study, it seems plausible that the birds became increasingly adept at manipulating material with each coconut fiber nest they built. This inference is supported by studies finding that captive male zebra finches became more consistent at handling and transporting material over time,²⁵ and also learned about the physical properties of materials such as flexibility and length.²⁶ Zebra finches recall morphological features of past nests, including the type and amount of material used in nest composition.^{30–32} In the current experiment, we find marginal, yet non-significant, changes in nest morphology over the four successive coconut fiber nests. We also find significant differences between earlier and later coconut fiber nests. Both of these pieces of evidence are congruent with the process of learning. Assuming that learning a style takes place over multiple nests, any differences would be incremental (therefore smaller) when comparing nests in construction order but cumulative (therefore larger) when comparing nests at the start and end of the sequence. A similar trend for nest morphology gradually changing over time has been described for southern masked weaver birds (*Ploceus velatus*). Walsh et al.^{22,48} found weaving dexterity increased as juveniles gained more nest-building experience, which coincided with nest size reducing as juveniles matured into adults.

There was lower morphological variation among nests built by the Experimental group than the Control group. This result is also congruent with the process of learning, as birds in the Experimental group had the opportunity to learn from the experience of building five string nests

whereas the birds in the Control group did not. This implies that the experience of building nests using one material (string) was generalized to building nests with another material (coconut fiber). The Experimental group used significantly less coconut fiber to build nests than the Control group. Taken together, these two results show that birds with prior nest-building experience built less varied nests that required fewer material resources, whereas, inexperienced birds built more varied nests that required more material resources. Construction is expensive in terms of energy, time and material resources, as the builder must source, transport and integrate materials into the structure.⁴⁹ Prior experience may therefore have been advantageous, as experienced birds learned to build nests with a similar style using fewer materials, potentially incurring lower building costs than the inexperienced birds which used more material to build nests with more varied styles. The amount of coconut fiber used in nests did not correlate with the time taken to complete the nest, nor did the time taken to complete the nest account for morphological differences among nests. This apparent independence between the amount of material used and time taken to complete nests may be an artifact of our experimental design. Wherein male finches, which deposit material into the nest,³⁸ had control over the amount of material used and we determined time to nest completion based on egg laying.^{39,40} Future studies could assess nest morphology at different time points to assess the rate of material use over the wider building process and also assess how each sex contributes to nest morphology.

Finding among-pair differences in style means that nest morphology was not fixed or shared among all pairs. In fact, we found among-pair differences increased from the first nest (distance to median centroid = 6.321) to the fourth nest (distance to median centroid = 7.846) meaning that, while pairs were relatively consistent in their own style, styles among-pairs diverged over time. One possible factor explaining style divergence might be that our experimental design prevented birds from successfully fledging chicks. Previous studies show captive zebra finches are more likely to repeat successful nest composition and change unsuccessful nest composition.^{30–32} Allowing pairs to have successfully fledged chicks may have increased style consistency among nests built by the same pair, resulting in higher estimates of repeatability. Whereas, a continual failure to hatch offspring may have contributed to shifts in style over repeated unsuccessful breeding attempts. The tendency to stick with successful morphometric components and shift from unsuccessful components could present a hypothetical mechanism for the development and reproduction of style in nest morphology. Further research should investigate whether different types of experience influence the divergence and convergence of styles among individuals over time. For example, providing opportunity for naive builders to gain experience and socially learn from the nests of conspecifics may lead to styles converging among pairs.^{27,28}

Here, we find support for consistent among-individual styles in the morphology of nests built by captive zebra finches. Of the variables considered in our analyses, only prior nest-building experience accounted for differences in nest style. Birds with experience built nests with less varied morphology and used less building material. Therefore, we provide empirical support for the role of cognition (learning and recall) as a mechanism influencing intraspecific variation in animal architecture. Additionally, we lay a framework for incorporating multiple components of nest morphology in multivariate analyses and also for conducting geometric landmark analysis on bird nests.

Limitations of the study

We examined nests built by captive zebra finches in a laboratory environment. This experimental system lacks many of the pressures faced by wild birds when building nests, however, achieves a much greater degree of control over potential confounding variables (e.g., temperature, predation risk). Quantifying the morphology of nests built by different species of wild and captive birds under different experimental scenarios would help determine whether styles persist across different contexts. One such context would be the site at which nests are built. We excluded pairs from analyses if they failed to build four coconut fiber nests inside the provided nest cup (e.g., nests built on the cage floor or inside food dishes), as this prevented nests from being photographed under standardized conditions. This exclusion criteria reduced our total sample size from 20 pairs to 14 pairs, and created unbalanced sample sizes between our Control ($n = 9$ pairs) and Experimental groups ($n = 5$ pairs). Developing methodologies for taking standardized photographs of nests *in situ* would provide a more flexible approach that would not have decreased our sample size. This would also allow nest site to be included as a variable in analyses, which could determine whether it is appropriate to pool data from nests built at different locations.

Few studies explicitly link cognition and animal architecture,^{50,51} fewer still assess how successive structures built by the same individual(s) change over time. Our study provides new insights on how learning processes may influence structure morphology, but literature to provide wider context is lacking. Our study focused on quantifying nest morphology and did not include direct observations of nest-building behavior. While this is a novel approach for testing animal cognition, further work is necessary to confirm the behavioral mechanisms that created styles in nest morphology. As discussed, one such mechanism may include the development of motor skills with accumulated building experience.⁴⁸ This could be assessed through video analysis to quantify the rate at which birds drop material when building early nests compared to later nests. While we provide initial insights on the role of cognition in animal architecture, some caution is needed when generalizing our findings on wider scales. For example, we considered nests to be completed once females had finished laying eggs and started incubation,³⁹ though it is possible nest morphology became fixed before/after this time point or alternatively remained fluid. Sampling nests at different time points during the building process would provide insight on how nest morphology does/does not change over time, better informing whether the current study can be generalized over the wider nest-building process.

STAR METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2023.108194>.

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AUTHOR CONTRIBUTIONS

LG conceived the idea for this study. LG and LNM developed experimental methodologies and data was collected by LNM, AN, DY, and SB. Formal analysis was undertaken by BW, CL and LG. Data were curated and visualized by BW. The first draft was written by BW, and all authors reviewed and edited subsequent drafts. LG and BW supervised research activity. LG acquired project funding, oversaw project administration, and provided all resources for this study.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

One or more of the authors of this paper self-identifies as an underrepresented ethnic minority in their field of research or within their geographical location. One or more of the authors of this paper self-identifies as a gender minority in their field of research. One or more of the authors of this paper self-identifies as a member of the LGBTQIA+ community. One or more of the authors of this paper received support from a program designed to increase minority representation in their field of research. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Nest morphometric data	This paper	NA
Experimental models: Organisms/strains		
Zebra finch	University of Alberta	NA
Software and algorithms		
R, version 4.1.2	R core team ⁵⁵	NA
TPSUtil, version 1.82	Rohlf J.F. ⁵²	NA
TPSDig, version 2.32	Rohlf J.F. ⁵³	NA

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Dr. Lauren Guillette (guillett@ualberta.ca).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Original morphometric data of bird nests ([Data S1](#)) and metadata ([Data S2](#)) are published as [supplemental information](#) and are publicly available as of the date of publication.
- All original code is available in this paper's [supplemental information](#) ([Methods S1](#)).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Zebra finches (*Taeniopygia guttata*)

Twenty adult female (mean weight = $15.7 \pm SD 1.2$ g, mean age = $745 \pm SD 66$ days) and twenty adult male (mean weight = $15.0 \pm SD 1.5$ g, mean age = $740 \pm SD 74$ days) zebra finches were bred and raised at the University of Alberta (Edmonton, Canada) from parent birds supplied by a commercial breeder (Eastern Bird Supplies, Canada). Individuals were identified using unique numbered plastic leg bands (Avian ID, UK).

Prior to the experiment birds were housed in same-sex colony cages ($184 \times 165 \times 66$ cm) with numerous perches and received *ad libitum* demineralized water, mixed seed (Hagen, Canada), grit (Grit 'n' Gravel, Canada), oyster shell (Pacific Pear Oyster Shell, Canada) and cuttlefish shell (Canadian Lab Diet, Canada). Diet was supplemented with greens (spinach, parsley) and vitamin water (Hagen, Canada) three times per week and spray millet (Hagen, Canada) once per week. The colony room was kept on a 14:10 light:dark cycle with overhead fluorescent lights (32 W, T8 full spectrum daylight), within a temperature range of 20 - 23°C and humidity range of 33 - 35%. During the experiment each pair was housed in a separate cage ($100 \times 50 \times 50$ cm, Kings Cages) with numerous perches and received the same *ad libitum* diet, supplements, lighting, temperature and humidity regimes as the colony cages. Opaque plastic curtains were placed between cages to visually isolate pairs, thereby removing the opportunity to observe and potentially learn nest building behaviour(s) from one another.²⁸ Wild zebra finches live in non-territorial groups and form socially-monogamous pairs and males are the primary nest builder.^{38,39}

All procedures in this study complied with the Canadian Council of Animal Care (CCAC) Guidelines and protocols were approved by the Animal Care and Use Committee at the University of Alberta (AUP 00002923). Subjects were involved with procedures prior to the experiment during which they had opportunity to handle string. All subjects were naïve to the focal nest-building material (coconut fibre) at the start of the present experiment. Subjects were not immune compromised and their health status was checked daily. Any birds that developed health concerns were withdrawn from the study and given appropriate veterinary care. Subjects were naïve to drugs and tests at the start of the experiment.

METHOD DETAILS

Nest building

Birds were randomly assigned into twenty unrelated different-sex pairs. Sex was determined by visually inspecting birds for sexually dimorphic plumage. Once paired, birds remained in the same pair for the duration of the experiment. We manipulated the nest-building experience of birds to assess whether the opportunity to learn from building nests using a different material (string) affected morphology of nests using a test material (coconut fibre). Ten pairs were randomly assigned to the Experimental group, which built five successive nests using pieces of 15 cm long white string prior to building four successive nests using coconut fibre. The remaining ten pairs were assigned to the Control group and did not build any string nests prior to building four successive coconut fibre nests.

After pairing, birds in the Experimental group were left to bond and acclimatize in cages inside the test room for seven days. A wooden nest cup (12.5 x 12 x 12 cm) was then hung centrally on the back wall of the cage and pieces of 15 cm long white string was placed in two bundles of 100 pieces each on the cage floor. The pairs were left to construct nests, with another bundle of 100 pieces of string added whenever approximately 50 pieces of string remained on the cage floor. Each nest was checked daily for eggs. Clutches are considered complete after no new eggs had been laid for a 24 hour period.⁴⁰ We considered nests completed once no new eggs had been laid for three consecutive days, at which point the pair had begun using the nest for incubation. This standardized nest removal at the same point in the reproductive cycle for all pairs. The nest cup was removed from the cage and, 24 hours later, a new nest cup and string was added to the cage. This process was repeated until each pair had built five nests using string (see Figure S5).

Building nests using coconut fibre followed the same procedure as string nests. Each pair was left to bond and acclimatize to the test room for one week, then a nest cup was placed in the cage. Coconut fibre (20 g) was placed in two bundles on the cage floor and each pair was left to construct a nest, with another 20 g of coconut fibre added whenever approximately 75% of the coconut fibre had been removed from the cage floor. Nests were considered complete after no new eggs had been laid for three days, standardizing nest removal at the same point in the reproductive cycle for both Experimental and Control pairs. The nest cup was then removed from the cage and the eggs carefully extracted so as not to compromise the structure of the nest. The day after removal, a new nest cup and coconut fibre was added to the cage. This process was repeated until each pair had built four consecutive nests using coconut fibre.

The time taken to build the nest (days) and amount of coconut fibre used in the nest (g) were recorded for each nest. Six of the twenty pairs were excluded from the study. This is because these pairs built at least one coconut fibre nest outside of the nest cup, typically on the floor or inside food dishes, which prevented these nests from being photographed under standard conditions. This occurred for one pair in the Control group and five pairs in the Experimental group. None of the pairs in the Experimental or Control group had opportunity to handle nest material before or aside from nest-building events, when a nest cup was placed inside the cage. None of the pairs in the Experimental or Control group experienced hatching, raising, or fledging chicks. Nests were removed at the same point in the reproductive cycle (three days after last egg had been laid) for each pair, regardless of whether the nest had been built using string or coconut fibre. In this sense, all birds experienced nest 'failure' in a standardized manner.

Image analysis

Coconut fibre nests were photographed in five standardized positions using a Nikon D5600 camera (Nikon DX 18-55mm lens) attached to a tripod. Photographs were taken under the same lighting conditions, with nests positioned at the same distance and orientation from the camera against a plain black background, with a ruler placed alongside the nest in each image for size reference. The standardized positions included directly facing the (1) front, (2) left and (3) right sides of the nest cup, (4) above looking down at the nest cup, and (5) facing the center of the nest entrance hole. Five TPS files were created from photographs using *TPSUtil*,⁵² software version 1.82. Each TPS file contained images taken from one of the five standardized positions, with images blinded and randomly sequenced to prevent order bias during data collection. TPS files were analyzed using *tpsDig*,⁵³ software version 2.32. The scale was set for each image using the ruler as a reference before taking linear measurements or placing landmarks.

A total of 12 linear measurements were recorded for each nest using photographs across the five different positions as shown in the main text. Several linear measurements were taken from different parts of a nest within a single photograph (e.g. height at the back and front at the left side of the nest cup), rather than taking one average measurement. This was done to more accurately quantify the asymmetric and non-uniform morphology of the nests. Each measurement was taken three times to ensure consistency and the median used as the final value. The left, front, and right images were also divided into quadrants and the position of the entrance hole recorded. Whenever the entrance hole spanned more than one quadrant it was assigned to whichever quadrant contained the greatest surface area. Using acetate templates, 11 landmarks were placed on images taken above nests to quantify nest shape, and 12 landmarks were placed on entrance images to quantify shape of the entrance hole. Generalized Procrustes Analyses (GPA) were performed on TPS files of above nest and nest entrance images using the *geomorph* package.⁵⁴ This controlled for possible variation in position, size and orientation of nest images and created a shared coordinate system between nest images. X and Y Procrustes coordinates were extracted for each landmark on each image for further analyses.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were performed in R,⁵⁵ software version 4.1.2. Unless specified, significance was defined at $P < 0.05$ and tests used a sample size of 56 nests (n pairs = 14, n nests per pair = 4).

Repeatable styles in nest morphology

We carried out four separate Principal Component Analyses (PCA) to condense the numerous morphometric variables into fewer dimensions, while retaining patterns of variation in (1) nest size, (2) nest shape, (3) entrance size, and (4) entrance shape. Nest size PCA included linear measurements ($n = 8$) taken from photos representing four of the five standardized positions. Nest Shape PCA included Procrustes coordinates ($n = 22$) obtained from landmarks placed on images taken above nests showing the overall shape of the nest (Figure 2). Entrance size PCA included linear measurements ($n = 4$) taken from photos of the entrance. Entrance shape PCA included Procrustes coordinates ($n = 24$) obtained from landmarks placed on images of the nest entrance. Missing values (2% of nest size, 10% of nest shape, 0% of entrance shape and 0% entrance size) were estimated through multiple imputation analysis using the *missMDA* package.⁵⁶ The optimal number of components used for imputations was calculated by the *kfold* method. Uncertainty surrounding the imputed data was assessed through multiple imputation analysis performed with 1000 bootstraps. Representation of individual nests, representation of each measurement/landmark, and projected stability along dimensional axes were evaluated through diagnostic plots. The *FactoMineR*⁵⁷ and *factoextra*⁵⁸ packages were used to visualize PCAs, determine the proportion of variance retained by each dimension, loadings of variables on each component, and extract PC scores of individual nests for further analysis (see Tables S1 and S2).

We tested whether zebra finches showed among-pair differences in nest style by creating a multivariate dissimilarity matrix. The matrix consisted of entrance position quadrant and scores from the first two dimensions of nest size PC (83.6% of variance), first three dimensions of nest shape PC (65.0% of variance), first three PC dimensions of entrance size (87.9% of variance), and the first four dimensions of entrance shape PC (79.2% of variance). The matrix scored pairwise distances between each of the morphometric variables measured in nests. A lower score in the multivariate dissimilarity matrix indicated a nest that had morphological features similar to other nests, whereas, a higher score in the matrix indicated a nest that had morphologically distinct features relative to other nests. We assessed multivariate homogeneity of group dispersion using the *betadisper* function in the *vegan* package,⁵⁹ with Pair ID used as the grouping factor. An ANOVA test was then performed on group dispersions. A non-significant result indicated homogenous multivariate compositions around the median centroids for each group, thus similar levels of variance in nest morphology built by each pair. Finding significant homogeneity satisfied assumptions to run PERMANOVA using the *adonis* function in the *vegan* package. This used the multivariate dissimilarity matrix as a response variable and a fixed term of pair ID, with 10,000 permutations. A significant result indicated differences in nest styles existed among pairs.

We assessed whether zebra finches showed within-pair consistency in nest style using two complimentary approaches. First, we conducted an ANOSIM test on the previously described multivariate dissimilarity matrix using 10,000 permutations in the *vegan* package. This test determined whether among-pair differences in nest style were greater than within-pair differences in nest style, with the group defined as pair ID. An R value closer to 1 would indicate greater dissimilarities among nests built by different pairs compared to nests built the same pair, an R value of 0 would indicate similarity among nests built by both different pairs and the same pair, and an R value closer to -1 would indicate greater dissimilarities among nests built by the same pair compared to nests built by different pairs. Second, we ran univariate repeatability analyses on nest style using the *rptR* package.⁶⁰ We fit 13 models, each of which used a variable from the multivariate dissimilarity matrix as a response variable and pair ID as a grouping factor. Each model was run using 10,000 bootstraps and 10,000 permutations. A significant R value less than 0.2 was considered to show weak repeatability, between 0.2 and 0.4 as moderate repeatability, and more than 0.4 as strong repeatability.⁶¹

Influence of experience on nest morphology

We tested whether differences in nest style was associated with two types of prior experience: (1) four successive building attempts with coconut fibre (nests 1 - 4), (2) prior experience building five nests using string (yes/no). We also assessed whether there were differences in style associated with traits of birds including: (3) male weight (above/below mean average weight), (4) female weight (above/below mean average weight), (5) male age (above/below mean average) and (6) female age (above/below mean average). We evaluated whether aspects of the construction process were associated with differences in nest morphology: (7) amount of material used (above/below mean average) and (8) time taken (above mean average, mean time taken, below mean average) to complete nest. For each of these eight factors we first tested multivariate homogeneity of group dispersion using the *betadisper* function in *vegan* package using 10,000 permutations, with the multivariate dissimilarity matrix as a response variable and the group defined as the factor of interest. Pairwise permutation tests were used when comparing variance among nests from successive building attempts in order to compare variance of nests built earlier and later in the process. An ANOVA test was performed on group dispersions, and a non-significant result indicated homogenous group dispersion and satisfied assumptions to run PERMANOVA (see Table S3). Of the eight factors tested, only prior experience building nests with string (i.e., test 2, the Experimental group vs. Control group) showed significant heterogeneous dispersion and was therefore excluded from PERMANOVA. Each of the PERMANOVA analyses used the multivariate dissimilarity matrix as a response variable and one of the seven factors of interest as a fixed term. Tests 1, 7, and 8 used the strata argument set to Pair ID to constrain permutations, thereby accounting for repeated sampling of the same pair of birds over time. Tests 3 – 6 only used subset data from the first nest built by each pair, as birds were weighed at the start of the experiment and therefore weights were most accurate when building the first nest. Tests 3 – 6, therefore, did not use the strata argument to account for repeated sampling. Each PERMANOVA used 10,000 permutations. A significant result would indicate differences among groups within the factor of interest (see Figures S1–S4).

We ran a linear mixed-model (LMM) using the *lme4* package⁶² to determine whether experience influenced the amount of material used to construct nests. The amount of coconut fibre (g) used in each nest was used as the response variable, with fixed terms included for experience building with string (yes/no), repeated building attempts (nests 1 - 4), and time taken to complete the nest (days), and a

random factor for pair ID ($n = 14$) to account for repeated measures (see Table S4). We used the *ggResidpanel* package⁶³ to assess model fit for assumptions of linearity, homogeneity of variance, and normality of residuals. The response variable was *log* transformed to satisfy assumptions of normality.

We undertook a repeated measures correlation test using the *rmcorr* package⁶⁴ to assess whether there was significant correlation among pairs for the amount (g) of coconut fibre used in nests and the time taken (days) to complete nests. The participant was specified as pair ID ($n = 14$) to account for the repeated measures design of our study.