

Zebra Finches build nests that do not resemble their natal nest

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ABSTRACT

Nests are built by nearly all bird species and can be extremely varied in their structural characteristics, both within and among species. As with a number of other avian behaviours, it seems plausible that early learning might be important in producing adult nest-building behaviour. To examine whether preferences that adults have for nest materials are related to their early-life experience, we experimentally manipulated the colour of the nest in which Zebra Finch pairs built and raised chicks. We then tested these chicks at maturity to determine whether they preferred the colour of the nest from which they had fledged or preferred the same colour as their father. We also examined the overall structure of nests that fathers and their sons built to determine whether the nest a male builds resembles that from which he hatched. When males and females naïve to building were paired as adults and tested for their nest material preferences, they did not prefer the colour of their natal nest. When these males were re-paired and their preference tested a second time, the majority then preferred the colour that their father had preferred (which was also the colour preferred by most of the males). The structural components of a male's nest did not resemble the nest built by his father, but neither did his father's nests resemble each other. We found no evidence that the experience of the nest from which a bird fledges influences his preferences for the colour of nest material or the structure of his first nest.

Keywords: early experience, imprinting, juvenile, learning, nest building, avian behaviour

1. INTRODUCTION

In 1867, Alfred R. Wallace wrote of nestlings, 'it would be very extraordinary if they could live for days and weeks in a nest and know nothing of its materials and the manner of its construction'. Although a number of adult behaviours observed in birds are influenced by early experience, such as song learning (Immelmann, 1969; Slater *et al.*, 1988; Slater, 1989), preferences for mates (Immelmann, 1972), food (Rabinowitch, 1968) and habitats (Klopfer, 1963; Teuschl *et al.*, 1998), as well as the type of nest box to nest in (e.g. Sargent, 1965; Herlugson 1981), it is not clear whether young birds learn anything about the construction of the nest itself while they are still in the nest.

One method of testing for the importance of early experience is to deprive young birds of nests and nest material by hand-rearing them and examining their subsequent nest-building skills, if any. American Robins (*Turdus migratorius*) and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) manipulated in this way were incapable of building nests (Scott, 1902; 1904), whereas domestic Canaries (*Serinus canaries*) appear able to build species-typical nests (Hinde and Matthews, 1958). Early nest material deprivation also affects young Village Weaverbirds (*Ploceus cucullatus*) with regard to their material handling skills, but not in their choices for appropriate nesting material (Collias and Collias, 1964). Young birds of this species also appear to spend time

watching the behaviour of adult males, and establishing 'play-colonies' in trees apart from adult colonies where they attempt to build nests (Collias and Collias, 1964; Collias and Collias, 1984). From these studies, however, it is unclear what specific role early experience plays in the development of nest-building behaviour.

Nest location, nest box type and nest material in Zebra Finches (*Taeniopygia guttata*), are all affected to some degree by experimental manipulation. Birds raised in green nests chose more green nesting material for building their nests than did birds raised in brown nests when given the choice between green, brown and red material (Sargent, 1965). There is more to adult colour preference, however, than just this early experience as, in the same experiment, birds raised in red nests did not prefer to build with red material as adults. Early experience also affected birds' preferences for their nesting location to some degree: although birds had strong unlearned preferences for nest cups located inside the cage, which experience did not override, when they could only choose between a cup outside *versus* a box inside the cage, birds then chose the location that matched that in which they were reared (Sargent, 1965). These data suggest a role for early experience in nest material choice by Zebra Finches, but only when specific colours of nest material are used, and it is not clear why that might be the case.

Both Sargent's data and those of Muth and Healy (2011) would suggest that Zebra Finches can have strong innate preferences for the colour of nest material. Here

we attempted to determine relative importance of innate preferences and of early experience on nest material choice for a male building his first nest. We did this by testing whether Zebra Finch adults preferred nest material of the colour of the nest they had experienced as a nestling or the colour that their father had preferred. Zebra finches are logistically useful for this type of experiment as they build nests readily in captivity and are reproductively mature at just three months of age (Zann, 1996), allowing for a cross-generation comparison. They will also build nests out of a range of nesting materials, both in the wild and in captivity (Zann, 1996).

We assessed male preferences for nest material colour (blue and yellow) before allowing them to build a nest with a female using either their preferred or non-preferred colour, and fledged chicks from these nests. This allowed us to examine whether their sons, when they were themselves adult nest builders, preferred the colour of the nest in which they developed or the colour of nest material their father had initially preferred. Furthermore, we measured the nests built by males in both generations to determine whether a son's nest resembled the structure built by his father.

2. METHODS

2.1. Subjects

Thirty-two pairs of birds, aged between three and four months, were paired in wooden cages measuring 44 × 30 × 39 cm (width × length × height). These birds had been bred in captivity at the University of St Andrews, UK, had fledged from nests built with undyed coconut fibre and hay and had not built a nest prior to this experiment. Of these 32 pairs, 19 built nests and fledged chicks in the current experiment, producing 59 offspring (21 females and 28 males).

The birds were kept on a 14:10 light:dark cycle, at a temperature of 19–32°C, with humidity levels of 50–70% and were given access to food (mixed seeds, cuttlebone, and oystershell grit) and water *ad libitum*. Pairs could not see neighbouring pairs but had a view of the occupants of other cages in the room.

2.2. Parent preference test

The pairs were provided with a wooden nest box sized 11 × 13 × 12 cm (w × l × h) hung in the centre of the back wall of the cage. A day later they were presented with two piles (each of 3 g) of nest material (coconut fibre), one dyed blue and the other yellow (Supercolor Ltd. food colouring). Zebra finches, like all birds, have tetrachromatic colour vision (Bowmaker *et al.*, 1997), and thus should be able to differentiate between these two colours. Each pile of material was placed either to

the far left or to the far right end of the cage on the cage floor. The end of the cage at which each colour of nest material was placed was alternated between cages. The birds were filmed using Sony Handycam camcorders until the male had taken at least 10 pieces of material to the nest box. After at least 10 pieces had been added, the nest box and all the nest material were removed from the cage. If the nest material was left untouched during this day of filming, it was removed and the piles of material were presented again the following day.

The video data were analysed using software for behavioural analysis (Noldus Observer, TrackSys Ltd., UK). We defined a male's 'colour preference' as the colour of at least eight of the first 10 pieces chosen. As well as recording when the male took nest material to the nest box, we also recorded the number of times he pecked at both colours of nest material on the cage floor and female responses to the nest material (pecks of material on the floor and taking material to the nest box).

2.3. Nest building

Once all of the males' nest material preferences had been determined, half of the pairs were provided with nest material of the male's preferred colour (blue: $n = 10$, yellow: $n = 6$), half were provided with nest material of the male's non-preferred colour (blue: $n = 4$, yellow: $n = 10$), and the pair in which the male had no preference were given yellow nesting material. In one pair the female died before their material preference had been determined, and this pair was removed from the experiment.

Material was provided twice daily until the female's first egg was laid. Nesting material was not provided after this time to prevent the male adding too much and burying the eggs (Zann 1996). If pairs failed to build or breed for any reason, they were removed from the experiment ($n = 12$ pairs: seven pairs building with the male's preferred colour, blue: $n = 4$, yellow: $n = 3$; and five pairs building with the male's non-preferred colour, blue: $n = 2$, yellow: $n = 3$).

2.4. Nest measurements

After the first egg had been laid, the nest was removed from the birds' cage for a maximum of 10 minutes and a number of measurements were made before it was replaced: the height of the front of the nest, height of the back of the nest (both taken from the bottom of the nest box to the top of the nest), width, length, and cup width and length. Single loose strands of coconut fibre sticking out of the nest were excluded from measurements. All measurements were made using digital callipers and measured to the nearest millimetre. The nests in their boxes were also weighed to the nearest 0.01 g. All measurements were repeated three times and we used the average measurement in the analyses. 19 nests were measured in total.

The nests were re-measured one week after the chicks fledged. The same measures were taken as previously and the nests were weighed after being removed from the wooden box, which was also weighed to determine the weight of the nest at laying.

After the chicks were independent and had been returned to stock cages, male and female parents were re-paired in the same pairs to build a second nest. This nest was removed when the first egg had been laid and measured using the same procedure as described for their first nest.

2.5. Offspring preferences and nest building

The male was left with the chicks for three weeks after fledging to prevent more eggs being laid by the female. The female was left for a total of four weeks after the chicks had fledged, as it takes up to a month until chicks feed independently (Zann, 1996). The fledglings were then moved to single-sex stock cages and at three months of age they were paired with a non-sibling individual from the same experimental treatment group. Their nest material colour preferences were tested using the same protocol as we used to examine material preferences in their parents.

Sixteen of the male offspring were initially paired with 16 of the female offspring and tested for their colour preferences (Block 1). However, in order to test the nest material preferences of all of the males using only female offspring produced in this experiment, the remaining males ($n = 18$) were paired with females that had been paired to males in Block 1. Eleven males (Block 2) were paired with females that had been paired once with a male from Block 1 and seven males (Block 3) were paired with females had been paired with a male in Blocks 1 and 2.

So as to assess preference without a confound due to the reuse of the female offspring, we determined the male's colour preferences a second time. For this preference test each of the male offspring was paired with a female taken from the parental generation. These pairs were provided with the colour of nest material that the male had preferred on this test (or given both colours if he had chosen them in equal amount during the preference test: $n = 3$), which was replenished regularly. As before, all nest material was removed once the first egg had been laid. At laying, the nests were measured using the same methodology as used for the males' parents' nests. At the end of the experiment all birds were returned to single-sex, group housing.

2.6. Data analysis and ethical note

All statistical analyses were carried out in IBM SPSS Statistics version 19. All of the work described here was approved by the University of St Andrews Animal Welfare and Ethics Committee.

3. RESULTS

3.1. Adult colour preferences

Of the 32 adult males tested, 21 preferred blue, 10 preferred yellow, and one (pair 3) chose both colours equally (Figure 1). For the 31 males with preferences, in most cases (25) the first 10 strands taken to the nest were of the same colour, in three cases 9/10 of the preferred colour were taken, and in three cases 8/10 of the preferred colour were taken. In one pair the female died, and so they were removed from the experiment (the male had preferred blue).

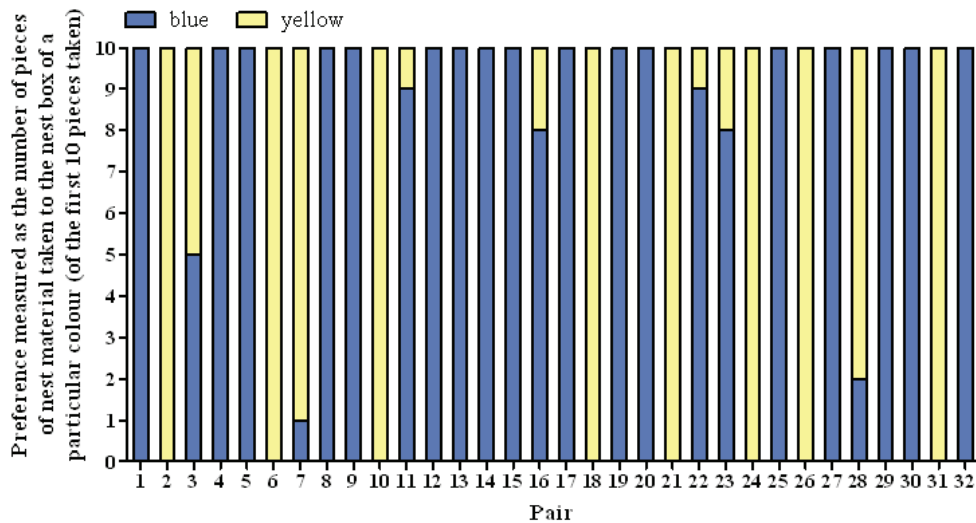


Figure 1 The preferences for blue or yellow nesting material of the parental males, measured as the colour he chose when adding his first 10 pieces of nest material to the nest box.

3.2. Adult nest building and breeding

Of the remaining 31 pairs, 19 pairs built nests, laid eggs and fledged chicks. The 12 other pairs were removed from the experiment for various reasons: two did not build, the females of two were pecked by their partners, one pair built but destroyed their nest, the eggs of one pair hatched but the parents threw the chicks out of the nest, four laid eggs that did not hatch, and two destroyed/ate their eggs. Of the 19 pairs that did build and breed successfully, nine built with their preferred colour (six blue and three yellow), nine built with their non-preferred colour (eight yellow and one blue), and the pair which had no preference built with yellow.

Fifty-nine offspring reached maturity: 21 females and 38 males. Of these individuals, 29 fledged from nests of their father's preferred colour (blue: seven females and 13 males, yellow: five females and four males), and 30 fledged from nests of their father's non-preferred colour (blue: two females and three males, yellow: seven females and 18 males).

3.3. First offspring colour preference test

In some pairs, females started building before or instead of males. Because of this unexpected behaviour, we addressed preferences both across all pairs (based on whichever individual built), and also by breaking the data down into three groups (where males were the sole builders, where females were the sole builders, and where both males and females built). Using the combined data from all builders ($n = 34$), the birds' colour preferences were not related to their father's preference: 20 birds preferred the same colour (all blue), 11 birds preferred the other colour (two blue and nine yellow), and three had no preference (Chi-square test: $\chi^2_1 = 2.613$, $P = 0.106$; Figure 2). The birds also did not prefer the colour of nest material of the nest from which they had fledged from: 11 birds preferred the colour of the nest they had fledged (eight blue and three yellow), 20 chose the other colour (15 blue and five yellow), and three had no preference (Chi-square test: $\chi^2_1 = 2.613$, $P = 0.106$; Figure 2).

For those cases in which the male was both the first of the pair to take the first piece of nest material and where he took 10 pieces to the nest box ($n = 23$), males did not prefer the same colour of material as had their father: 13 preferred the same colour as had their father (in all cases blue), nine did not (two preferred blue and seven yellow), and one had no preference (Chi-square test: $\chi^2_1 = 0.667$, $P = 0.414$). Males also were ambivalent to the colour of nest from which they had fledged: eight preferred the colour of their natal nest (five blue and three yellow), 14 preferred the other colour (10 blue and four yellow), and one male had no preference (Chi-square test: $\chi^2_1 = 1.636$, $P = 0.201$).

For eight of these 23 pairs the female pecked at the nest material on the ground before the male started building.

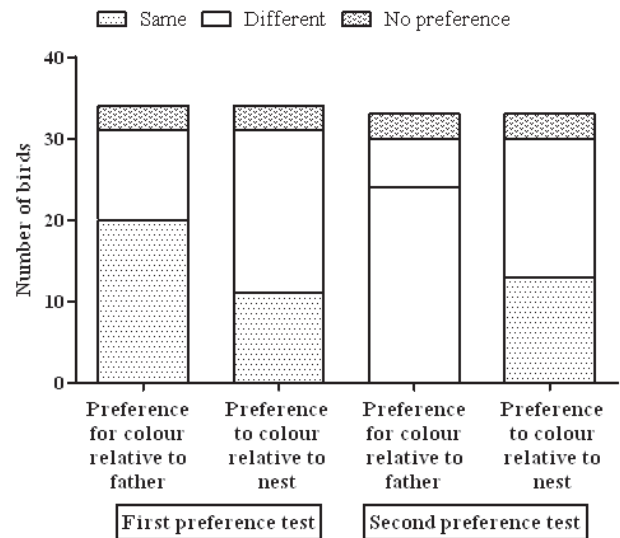


Figure 2 The colour preferences for nest material of all the builder offspring. The data are shown as relative to the colour preferences of their fathers and relative to the colour of the nest from which they fledged. Birds in the first preference test include both male and female offspring (only one builder per pair; $n = 34$). In the second preference test only males built the nest ($n = 33$).

In seven of these cases, she pecked at material of the same colour as was taken subsequently by the male (six times this was blue and once it was yellow). As the female behaviour may have influenced the male's material choice, we reanalysed the male preference data excluding these eight cases. The outcome did not change, however, eight males preferred the same colour as had their fathers (in all cases blue), while seven males did not (in six cases the offspring preferred yellow, and in one case blue; Chi-square test: $\chi^2_1 = 0.067$, $P = 0.796$). Similarly, males were ambivalent to the colour of nest from which they had fledged: five preferred the colour of their natal nest (two blue and three yellow), and 10 preferred the other colour (seven blue and three yellow; Chi-square test: $\chi^2_1 = 1.667$, $P = 0.197$).

In Blocks 2 and 3, there were five pairs where the female was the first of the pair to peck at the material, to take material to the nest box first and to take ten pieces to the nest box. For two of these pairs, the female was the same. She had no colour preference in Block 2 but preferred blue in Block 3. Three females preferred the same colour (blue) as their father had while one did not (yellow). One of these females preferred the same colour as the nest from which they had fledged (blue) while three females preferred the other colour (one yellow and two blue).

As these females had all been paired previously with males (in Blocks 1 and 2) we looked to see whether their preferences were related to the colour preferred by their previous partner. This did not seem to be the case, although the sample size was small: two females preferred the same colour as had their previous partner (blue), two

had different preferences (one preferred yellow when her previous partner chose blue and one preferred blue when her previous partner had no preference), while the fifth female, like her previous partner, had no colour preference.

There were also six cases in which both the male and the female added material to the nest box. Although in all of these cases the female started building before the male, the male always took 10 pieces to the nest box while the females took fewer than four pieces. In four pairs, the females added blue first, the males also added blue as their first piece, and then went on to take mostly blue pieces. In one pair, the female took a yellow piece, followed by a blue piece, the male then added a blue piece, and he went on to add mostly blue pieces. In the last pair, the female took a blue piece followed by two yellow pieces, the male then took a yellow piece, but he went on to take 9/10 blue pieces.

Taking all these cases together, in four cases the male preferred the same colour as his father (all blue), in one case he did not (he preferred yellow), and in one case he had no preference. In two cases he preferred the same colour as the nest he fledged from (blue), in three cases he did not (preferring blue), and in one case he had no preference.

3.4 Second offspring colour preference test

When males were re-paired and tested for their preferences a second time ($n = 33$), 24 males preferred the colour that their father had preferred (23 blue, one yellow), while six preferred the other colour (two blue, four yellow), and three had no preference (Chi-square test: $\chi^2_1 = 10.8$, $P = 0.001$; Figure 2). Males did not prefer the colour of the nest from which they had fledged: 13 chose the same colour (10 blue and three yellow), 17 chose the other colour (15 blue and two yellow), and three had no preference (Chi-square test: $\chi^2_1 = 0.533$, $P = 0.465$; Figure 2).

During this second preference test the females of eight pairs did some building. However, as in all of these cases the females took fewer than seven pieces, there were too few data to determine female colour preference. In five pairs, the female pecked the material before the male, and in four of these pairs the male then took that colour of material to the nest box while in the other pair, the female took a blue piece, then pecked at yellow, and the male then took 10 yellow pieces.

3.5 Sibling preferences

Siblings did not generally prefer the same colour as each other, either the first time they were tested or the second time ($n = 9$ parental pairs and 27 siblings, excluding cases where there was only one sibling). In the first preference test, there were two families where the siblings all

preferred the same colour, five families where the siblings chose different colours, and two families where at least one sibling had no preference. In the second preference test, siblings in four families preferred the same colour, siblings in two families differed in their preferences, and in three families at least one sibling had no preference (Table 1).

3.6 Nest measures

Most of the same measures taken from the same nest compared between laying and fledging were positively correlated (height at back, length, cup length, weight) or were trending towards significance (width, cup width;

Table 1 The preferences of offspring, divided into groups of siblings sharing the same parents (see text for full explanation) for yellow or blue nest material in their first and second preference tests

Sibling group	Sex	First preference	Second preference
1	Male	Blue	Blue
1	Male	Blue	Blue
1	Male	Blue	No preference
2	Male	Yellow	Blue
2	Male	Yellow	Yellow
2	Male	Blue	Blue
2	Male	Blue	Blue
2	Female	Blue	
3	Male	Blue	Blue
3	Male	Yellow	Blue
4	Male	Yellow	Blue
4	Male	Blue	No preference
4	Male	Blue	Blue
5	Male	Blue	Blue
5	Male	No preference	Blue
5	Male	Blue	Blue
6	Male	Yellow	Yellow
6	Male	Blue	Blue
6	Female	Yellow	
7	Male	Blue	No preference
7	Male	Blue	Blue
7	Male	Blue	Blue
8	Male	Blue	Blue
8	Female	No preference	Blue
9	Female	Blue	
9	Male	Yellow	Blue
9	Male	Blue	Blue

Table 2). The only measure that was not correlated between laying and fledging was the height of the front of the nest (Table 2). However, the nests generally became smaller between laying and fledging (in width, height at back, height at front and length; Table 2). The cup width did not change in size between laying and fledging, and the cup length was longer at fledging than when the eggs had just been laid (Table 2). The weight of the nest also became heavier at fledging (Table 2). None of these size measures nor weight was correlated with the number of eggs laid nor with the number of chicks fledged from that nest (all P values > 0.1).

The only measures that were correlated between the first and second nests built by parent pairs were the cup length, which was the same size (on average) in the first and second nest built, and weight, although the second nest was significantly lighter than the first (Table 3). All other measures were not significantly correlated and did not change in size between the two nests (Table 3).

The number of days before laying (as an approximate measure of the time a male took to build the nest) in the first or second nest was not correlated with any nest measurement from the first or second nest (respectively; first nest: all $n = 18$, all P values > 0.1 ; second nest: all n

Table 2 Comparison of measurements of the parents' first nest at laying and at fledging through Pearson correlations and paired t -tests using equivalent measures from both nests

	Pearson's r (df = 17) ^a		Mean \pm SD	t -value (df = 18) ^a
Width (mm)	0.445 (0.056)	Laying	211.8 \pm 47.3	4.429 (< 0.0001)
		Fledging	161.54 \pm 46.6	
Height at back (mm)	0.657 (0.002)	Laying	156.5 \pm 20.0	5.210 (< 0.0001)
		Fledging	130.0 \pm 29.3	
Height at front (mm)	0.181 (0.460)	Laying	96.8 \pm 18.0	4.459 (< 0.0001)
		Fledging	73.9 \pm 17.0	
Length (mm)	0.510 (0.026)	Laying	154.4 \pm 18.1	2.570 (0.019)
		Fledging	142.9 \pm 21.2	
Cup width (mm)	0.439 (0.060)	Laying	86.9 \pm 4.4	0.169 (0.867)
		Fledging	86.7 \pm 4.9	
Cup length (mm)	0.737 (< 0.0001)	Laying	69.8 \pm 13.2	-2.834 (0.011)
		Fledging	75.7 \pm 18.3	
Weight (g)	0.753 (< 0.0001)	Laying	48.24 \pm 20.90	-9.349 (< 0.0001)
		Fledging	87.29 \pm 34.82	

^a P -values are shown in parentheses.

Table 3 Comparison of measurements of the parents' firsts nests built to their second nests built through Pearson correlations and paired t -tests using equivalent measures from both nests

	Pearson's r (df = 16) ^a		mean \pm SD	t -value (df = 17) ^a
Width (mm)	0.206 (0.412)	1st nest	213.3 \pm 48.2	0.290 (0.776)
		2nd nest	209.1 \pm 48.7	
Height at back (mm)	0.273 (0.274)	1st nest	157.2 \pm 20.4	0.349 (0.731)
		2nd nest	155.3 \pm 18.0	
Height at front (mm)	0.264 (0.290)	1st nest	98.7 \pm 16.4	0.373 (0.714)
		2nd nest	96.7 \pm 20.1	
Length (mm)	-0.059 (0.816)	1st nest	156.7 \pm 15.7	-1.074 (0.298)
		2nd nest	165.5 \pm 30.2	
Cup width (mm)	-0.087 (0.731)	1st nest	87.1 \pm 4.4	1.298 (0.212)
		2nd nest	85.2 \pm 4.3	
Cup length (mm)	0.721 (0.001)	1st nest	69.9 \pm 13.6	-1.709 (0.106)
		2nd nest	73.7 \pm 9.5	
Weight (g)	0.519 (0.033)	1st nest	49.00 \pm 21.3	-3.249 (0.005)
		2nd nest	35.4 \pm 22.1	

^a P -values are shown in parentheses.

= 18, all P values > 0.06). There were two correlations: for the first nest built, the longer it took for eggs to be laid from the day building began, the heavier was the nest ($r = 0.504$, $n = 18$, $P = 0.033$), and the second nests were shorter in length the longer it took the birds to lay ($r = -0.492$, $n = 17$, $P = 0.045$). However, neither of these effects was significant after we corrected for multiple tests. Females took approximately the same length of time to lay in her second nest as she had in her first ($r = -0.248$, $n = 17$, $P = 0.337$).

The combined weight of the male and female (as both birds will sit in the nest simultaneously) did not correlate with any of the nest measures for either the first or second nest (first nest: all $n = 18$, all P values > 0.1, second nest: all $n = 18$, all P values > 0.2), except that the first nests were lighter the heavier the bird ($r = 0.554$, $n = 18$, $P = 0.017$).

We compared the measures from the nests of the offspring to those of their father's nests at laying, at fledging, and to his second nest at laying. Because we made three comparisons, we set the alpha value at 0.0167 (0.05/3). Of the 34 pairs of offspring, one pair did not build, two pairs added just a few strands to the nest box and one built in the corner of their cage on the floor. Of the remaining 30 pairs, none of the measures of their nests (width, height at back, height at front, length, cup width, cup length or weight) were significantly correlated with any of the respective measures from the parental male nests (Table 4).

4. DISCUSSION

When building their first nest, Zebra Finches that hatched in coloured nests did not prefer to build with material of the colour of nest from which they fledged. When these males were re-paired for building they preferred the same colour of nest material as had their father, which in most cases was the colour blue. Although the dimensions of

the nests these offspring built were not correlated with the dimensions of the nests their fathers built, the nests built by their fathers also did not resemble each other.

Although most of the birds in this experiment had strong preferences for one or other of the colours of nest material we provided, it is not clear what caused those preferences. It would appear that the colour of the nest in which the birds were raised did not lead to birds favouring that colour when they came to build their first nest. However, colour preferences can be affected by early experience as Zebra Finches raised in green nests chose more green material when building nests of their own than did birds raised in brown nests (Sargent, 1965). There are at least two possible explanations for this discrepancy. Firstly, it is possible that our Zebra Finches had colour preferences that were so strong (between 80 and 100%) that it was difficult to detect an effect of early experience. Sargent's birds did not appear to have such strong colour preferences. Secondly, it is possible that the difference is due to the way in which we assessed preference. We used the first ten pieces that the male took to the nest as our measure of preference, whereas Sargent assessed preference based on the proportion of each colour of material used in the nest by the end of nest building. It is possible that the strength of colour preferences wane across nest building. Testing this would require us to compare the two measures of preference directly.

Further work is required to determine why many of our Zebra Finches appeared to prefer blue to yellow nest material. Our data would suggest that there is either a familial basis to the colour preference or that Zebra Finches, in general, prefer blue to yellow when nest material is one of these two colours. Why this might be the case is also unclear. One possibility is that the blue material was more conspicuous against the cage floor than was the yellow material. This difference in conspicuousness could also explain why in Muth and Healy (2011), more Zebra Finches preferred green to brown material. However, given that birds in that experiment manipulated both colours of nest material on the floor equally, the

Table 4 Pearson correlation coefficients obtained by comparing measures taken from nests built by offspring to equivalent measures from their parents' nests; two parent nests were used for this comparison, the first nest was measured both at laying and at fledging, while the second nest was measured only at laying

Offspring nest measures	Parents' first nest at laying (df = 28) ^a	Parents' first nest at fledging (df = 28)	Parents' second nest (df = 25) ^a
Width (mm)	0.232 (0.216)	0.367 (0.046)	0.221 (0.267)
Height at back (mm)	0.041 (0.828)	-0.053 (0.781)	-0.069 (0.733)
Height at front (mm)	-0.136 (0.473)	-0.044 (0.819)	-0.053 (0.793)
Length (mm)	0.289 (0.122)	0.209 (0.268)	0.393 (0.043)
Cup width (mm)	0.299 (0.109)	0.336 (0.069)	0.127 (0.527)
Cup length (mm)	0.053 (0.783)	0.040 (0.833)	0.134 (0.506)
Weight (g)	0.109 (0.568)	0.172 (0.365)	0.313 (0.111)

^a P -values are shown in parentheses.

preference was not due to lack of experience with the 'inconspicuous' colour. Given that blue and green nesting material are both preferred, it is possible that there is a spectrum of colours they prefer, at least within the context of nest building. These are not colours that seem to be preferred in other contexts, such as mate choice (Burley *et al.* 1982, Burley and Coopersmith 1987, Burley 1988). It would be useful to determine whether these colour preferences are specific to the context of nest building, for example, through testing food colour preferences, or indeed, whether this particular colour preference is repeatable in other Zebra Finches. It would also be useful to examine colour preferences across a wider colour spectrum than we used.

Not only do young male Zebra Finches appear not to base their preference for the colour of nest material on the colour of nest material they have experienced, they also do not build nests that structurally resemble the nest from which they fledged. However, the two nests that their fathers built in succession also did not resemble each other, even though they were somewhat like the nests built by weavers in the wild, which got smaller across the season (Walsh *et al.*, 2010), in that the later nest did tend to be lighter. This might mean that Zebra Finches use less material with later nests. We would need to quantify the amount of material to determine whether this is the case. The lack of resemblance across nests might be because of the variability in measuring nests or it might be that males do not build the same nest at each attempt. Either of these possibilities would also be consistent with the lack of correlation between the structural measures of the nests of the offspring and that of their father's. There is certainly variability in nest measurements, even for the same nest between laying and fledging: all the measures became smaller, except cup width, which did not change and cup length and weight, which increased. The increase in cup length may reflect the distortion caused by the eggs hatching into chicks before they fledged, and the increase in weight is likely to be due to an accumulation of excrement across the nestling period. In an attempt to compare nests at the same stage, we used the laying of the first egg to indicate the completion of nest building. However, it may be that egg laying is not a good indicator of the stage of nest building. To address both of these issues, it would be useful to collect detailed observational data on nest building as has been done for Southern masked weaverbirds (Walsh *et al.*, 2011). Examining nest-building behaviour and the movements involved would also be useful. Attempting to replicate a structure from the finished product would seem a rather more difficult task than would the copying of nest building movements. There are some data from weaverbirds that suggest that young, inexperienced males may copy older males when learning to build (Collias and Collias, 1984). Again, there are, as yet, no substantial quantitative data to help us address this nest-building question.

Young Zebra Finches do not appear to acquire at least some of the components of nest building from early

experience of their natal nest. Whether they might watch adults manipulate material, choose nest sites or materials is not clear although the evidence is that the young of other species might do. It may be that, to acquire information as a juvenile, some sensory-motor feedback is required, as in both filial imprinting and song learning (e.g. Immelmann, 1972).

One surprising outcome of our experiments was the role played by females in manipulating the nest material and, in a few cases, taking on the job of building the nest. We are not sure why this occurred as it is typically the male who builds. Manipulations of oestrogen in female Zebra Finches will cause them to build nests (Rochester *et al.*, 2008), so it is possible that our experimental manipulation in which females experienced up to three males as frequently as over three successive days in a courting and nest building context, but without the opportunity to lay eggs increased oestrogen levels. A direct comparison between hormone and behavioural manipulations like those in our experiment would allow us to determine whether this was the case. An alternative explanation is that a proportion of female Zebra Finches build. Up until this experiment, this explanation seemed unlikely, since cases where females take material to build a nest have been reported rarely (Birkhead *et al.*, 1988; Zann, 1996). Again, more data are required to determine the circumstances under which female Zebra Finches take over building the nest.

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