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Zebra finches select nest material appropriate for a building task

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Across the animal kingdom, many animals build structures. One especially diverse example is that of nest building by birds. It remains unclear, however, what birds know or whether they learn about the structural aspects of the material with which they build a nest. Here we tested whether nest-building male zebra finches would choose the appropriate type of material when building in a novel situation. They did do this: males provided with a nestbox with either a small or a large entrance hole and with nest material of two types ('long' and 'short') chose the type of material that was appropriate for the box in which they built. Additionally, the birds' material use improved with experience: males building in nestboxes with small entrances became less choosy in their material choice as they became more skilled at inserting material of either length into their nestbox. The birds, therefore, first chose the appropriate materials for the nestbox in which they were building but then modified their handling skills so as to make use of all of the available material. How the cognitive abilities used in this nest-building context compare with those used in solving other physical problems such as tool use tasks is not yet clear.

Animal construction ranges from the microscopic casing built by the amoeba *Difflugia coronata* to the vast dams of beavers and tools constructed by chimpanzees, *Pan troglodytes*, and some birds (Hansell, 2005). One of the most widespread forms of construction behaviour, however, is nest building by birds. As far back as 1867, A. R. Wallace questioned whether nest building required more than an unlearned set of rules. Since then there has been relatively little work on what cognitive abilities, if any, might be involved in nest construction.

Nest construction involves the selection of appropriate material and the manipulation of that material by the bird or birds into a species-typical construction (Collias & Collias, 1984). For the selection of material, birds may have unlearned rules of what to choose, learn through trial-and-error learning, or use a combination of these. Nest-building male zebra finches, *Taeniopygia guttata*, appear to have unlearned preferences for particular colours of material (Muth & Healy, 2011, 2012; Muth, Steele, & Healy, 2013), which can be altered through experience: male nest builders switched their preference for one coloured material to another following a successful breeding attempt using the alternative material (Muth & Healy, 2011). Village weaverbirds, *Textor cucullatus*, may also have unlearned preferences for building materials, particularly that which is green, flexible and long (Collias & Collias, 1964). These preferences may represent the most appropriate type of material for building their nests (long, fresh, flexible strands of grass; Collias & Collias, 1984). However, although some birds appear to have preferences for material colour, which can change with experience, we do not know whether builders have preferences for the structural features of materials or whether these too may be altered through experience manipulating those materials.

Most studies addressing the role of experience in nest building have, to date, focused on the birds' building ability (motor skill) rather than on the selection of material, and these data do not support a general description for the role of experience relative to a set of unlearned rules. For example, hand-reared canaries, *Serinus canarius*, deprived of nesting material until maturity built nests that appeared 'as large and tidy' as those built by experienced birds (Hinde & Matthews, 1958, p. 45), while a pair of American robins, *Turdus migratorius*, and two pairs of rose-breasted grosbeaks, *Pheucticus ludovicianus*, that underwent a similar deprivation were incapable of building nests (Scott, 1902, 1904). Additionally, weaverbirds, which build relatively elaborate nests (Hansell, 2000), require a learning period when young to produce appropriate behaviour and structures as adults: males deprived of weaving experience as juveniles were less proficient at tearing off and weaving strips of material as adults than were nondeprived controls (Collias & Collias, 1964). First-time nest-building weaverbirds also built more loosely woven nests than adult males (Collias & Collias, 1964), which may also indicate a lack of dexterity in the

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manipulative skills involved in weaving. Furthermore, nests built by wild, free-living adult southern masked weaverbirds, *Ploceus velatus*, and village weaverbirds, *Ploceus cucullatus*, became smaller and lighter over time (Walsh, Hansell, Borello, & Healy, 2010). As this was concomitant with the birds dropping fewer blades of grass during building, the change in nest structure might have been due to refinement of the birds' manipulative skills (Walsh, Hansell, Borello, & Healy, 2011). Nest builders may also respond flexibly to their environment by incorporating man-made materials into their nest in a way that appears to benefit their chicks directly. A recent example of this comes from Mexico where house sparrows, *Passer domesticus*, and house finches, *Carpodacus mexicanus*, included smoked cigarette butts in their nests, possibly to act as a parasite repellent (Suárez-Rodríguez, López-Rull, & Garcia, 2012).

At least some aspects of nest construction behaviour in birds, then, can be refined through experience. However, there has been no test to determine whether birds choose material that is structurally appropriate to a building situation, or whether they can modify their choice, depending on the nature of that building situation. Here we tested whether nest-building male zebra finches are capable of choosing pieces of nest material that are structurally appropriate for building in a novel context. We used zebra finches as they readily build in captivity using a range of materials (Muth & Healy, 2011, 2012; Muth et al., 2013). We provided paired zebra finches housed in a laboratory with nestboxes that had either a large entrance or a small entrance through which the birds had to take the nest material to build their nest. All pairs were provided with two types of nest material, 'short' and 'long'. Both pieces could be readily taken through the entrance of the large-entrance nestboxes, as they could be held either in the middle or by the end of the piece. However, while the short pieces of material could be taken into the small-entrance nest irrespective of the way in which the birds held them, the long pieces would not fit through the entrance if a bird held them in the middle. A long piece would fit only if it was held at its end (see Supplementary Video S1).

If zebra finch males can choose nest material with the appropriate structural features, we expected the birds building in nestboxes with a small entrance hole to prefer to build with the short pieces of nesting material, while we expected the birds building in the boxes with the large entrance to be indifferent to the length of the material. Furthermore, as experience manipulating the material should both improve the birds' motor skills associated with material manipulation and provide an opportunity to learn the most effective way to hold the material, we also expected that, with increasing experience, birds would become more successful at getting nest material into the nestbox with the small entrance.

METHODS

Subjects

The subjects were 24 adult male and 24 adult female zebra finches, aged between 6 months and 2 years. All birds had been bred in captivity at the University of St Andrews, U.K. They were kept on a 14:10 h light:dark cycle, in rooms with full spectrum lighting, at a temperature of 19–22 °C with humidity levels of 50–70% and given ad libitum access to food (mixed seeds, cuttlebone and oyster shell grit) and water, as well as water dishes for bathing. Birds were paired in cages measuring 88 × 30 cm and 39 cm high. All work carried out was approved by the University of St Andrews Animal Welfare and Ethics Committee. Birds went on to be used in other behavioural experiments at the end of the study.

All of the males had built two nests previously, both in wooden, open-topped nestboxes (11 × 13 cm and 12 cm high), using coloured coconut fibre. None of the birds had previously encountered the type of nestbox or the material used in the current experiment.

Experimental Protocol

We carried out a 2 × 2 fully factorial experiment with two treatments: (1) 'experienced' versus 'inexperienced'; (2) 'large' entrance versus 'small' entrance. There were four treatment combinations, with six pairs of birds in each: 'experienced/large entrance'; 'inexperienced/large entrance'; 'experienced/small entrance'; 'inexperienced/small entrance' (for more details on the selection of these birds, see Nest-building Success in the Appendix).

The two large-entrance combinations were provided with nestboxes with an entrance 10 cm in diameter, and the small-entrance combinations were provided with nestboxes with an entrance 5 cm in diameter (Fig. 1a). Birds were also provided with both 'short' (20–22 cm long) and 'long' (25–27 cm long) nest material. Both types of material consisted of approximately 30 strands of coconut fibre bound together with wire to stiffen the middle section. The long material had a stiff middle wire section of 11.5–13.5 cm, and the short material had a stiff middle section of 4.5–5.5 cm in length (Fig. 1b). These nesting materials were designed so that when the bird held the material in the stiff middle section, the longer type would fit easily through the entrance hole of the large-entrance nestbox but not of the small-entrance one and the shorter material type would pass readily into both nestbox types when held in the middle. Because the material could also be held at the end, meaning it was held more perpendicular to the bird (rather than sticking out either sides of its beak), both types of material could fit into both nestbox entrance sizes when held in this way. Therefore, this means that there were two ways in which the birds could be selective about material for building in the small-entrance box: either by choosing short pieces (held either way), or by choosing long pieces and holding them by the end.

The two experienced groups (large- and small-entrance box) received 2 days of building experience with the experimental material and nestbox (specific to their treatment) prior to the first day of testing. During these 2 days, they were provided with 20 pieces of long and 20 pieces of short nest material and filmed for 3 h. The nest material was always placed on the floor of the cage below the nestbox, with the short pieces in one pile and the long pieces in another. For half the pairs, the short pieces were placed in a pile on the left-hand side of the cage floor and the long pieces on the right-hand side, and vice versa for the other half of the pairs. The side with the short pieces was also alternated on each day of testing within a pair. If, after 3 h, they had not touched the material (in $N = 6$ cases), they were filmed for a further 3 h to allow all birds to start building, which they did. After filming, they were provided with unlimited quantities of long and short pieces of nest material and allowed to build freely in the nestbox for 2 days.

Birds in the inexperienced groups were provided with a box but no nesting material for 2 days. After these 2 days, both experienced and inexperienced groups had their nestboxes (and nesting material in the case of the experienced group) removed from their cages. A day later, both groups were given empty nestboxes with an entrance of the same diameter as the one they had had previously. They were also provided with 20 pieces of nesting material (10 pieces of long and 10 of short) and filmed for 2.5 h, after which the nestbox and all the nesting material were removed. This procedure was repeated at approximately the same time (to within 1 h) on the next 2 days. These 3 test days are hereafter referred to as 'day 1', 'day 2' and 'day 3'.

Behavioural Coding

Using software for behavioural analysis (Noldus Observer, TrackSys Ltd, Nottingham, U.K.), we coded three nest-building

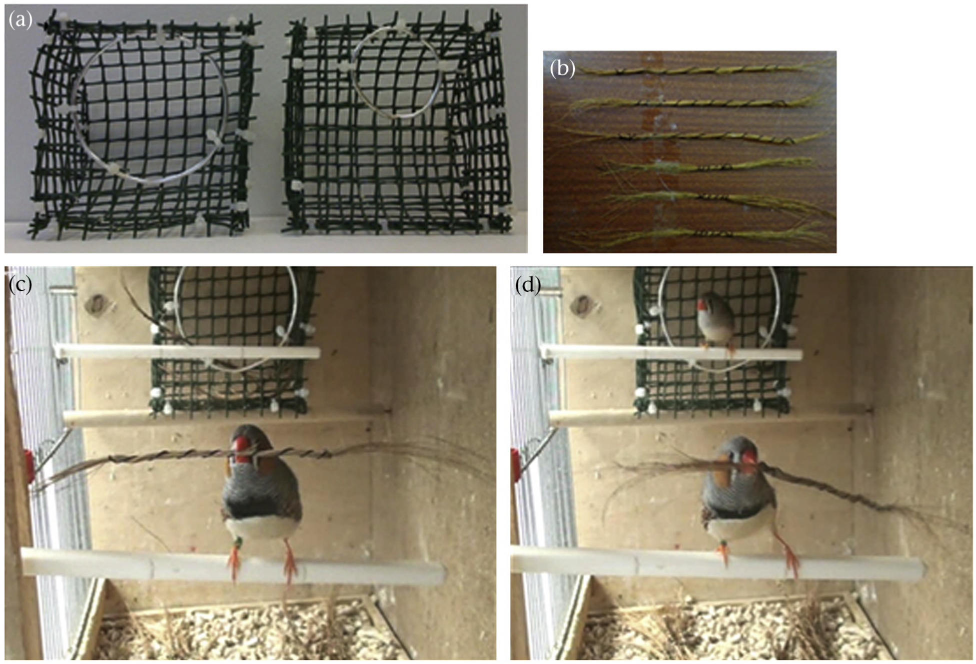

Figure 1. The two types of (a) nestbox (large entrance, left; small entrance, right) and of (b) nest material (long, above; short, below). (c) A male zebra finch building in the large-entrance nestbox, holding a long piece of material in the middle, which will be taken into the nestbox perpendicular to the bird. (d) The same male holding a long piece at the end, which will be taken into the nestbox end-first. Also see Supplementary Video S1.

behavioural outcomes from the videos: (1) which piece was taken to the nest (long/short); (2) whether the piece of nest material was successfully taken into the box (success/fail) and (3) how the piece of material was held (middle/end; Fig. 1b; see Supplementary Video S1). We also recorded the number of pieces that were 'knocked out' of the nest once placed inside. We considered that a piece had been knocked out when a piece of material fell out of the nest after making contact with a part of a bird's body. Additionally, we recorded the number of pieces that were 'pulled out' of the nest. We considered that a piece had been pulled out when that piece was removed from the nest by a bird holding the piece of material in its beak.

Data Analysis

All parametric analyses were carried out in R version 2.13.0 (R Development Core Team, 2010). GLMMs were carried out using the lmer() function in the lme4 package (Bates & Maechler, 2010) that gives z values and $\Pr(>|z|)$, an estimation of a P value, for each level of testing. AICc values for GLMMs were calculated from models using maximum likelihood estimation. LMMs were carried out using the lme() function in the nlme package, specifying type III sum of squares and sum contrasts in cases where there were interactions (Pinheiro, Bates, DebRoy, Sarkar, & the R Development Core Team, 2010). For all models, maximal models were run initially, and nonsignificant interactions were removed in a stepwise fashion. In cases where there were significant interactions, models were rerun dividing the data by one of the factors in the interaction, in order to determine the significance of the main effects without the interaction.

To determine whether males preferentially chose long or short pieces in the different treatments and whether this choice changed across days, we looked at the first 10 pieces that the male attempted to take into the nestbox. The proportion of long pieces (out of 10) was then compared using a GLMM with a binomial distribution. The model included three categorical explanatory variables: 'experience' (inexperienced or experienced), 'day number' (1–3) and 'nestbox size' (large or small), and the random factor 'male' ('Model 1'). A maximal model was used as the three-way interaction was significant. As there was a significant interaction between day number and size of nestbox entrance (GLMM: $z = 4.169$, $P < 0.0001$), two other models were run, using the data from the large- and small-entrance conditions separately.

To determine whether males became more successful at taking pieces into their nestbox across days and between experience treatment groups and whether this was different when building with short or long nest material, we looked at the proportion of the total number of successful attempts at taking pieces of material into the nest during the test period. These proportion data were normally distributed, so we used linear mixed models. A model ('Model 2') was fitted to the data for each of the two nest entrance groups (small and large) where the response was the proportion of successful attempts and the explanatory variables included were the fixed factors: 'experience' (experienced/ inexperienced), 'nest material length' (short/long) and 'day number' (1–3) and the random factor 'male'.

To determine whether birds changed their handling behaviour of material over successive days and whether this varied across different treatments, we carried out a GLMM with a binomial distribution for birds building in the small-entrance nestbox and another for birds building in the large-entrance nestbox, using the proportion of pieces held at the end as the response variable and with the same explanatory variables as in Model 2.

All nonparametric analyses were carried out in IBM SPSS Statistics version 19.

RESULTS

Nest Material Choice

When paired zebra finches were presented with either a small- or a large-entrance nestbox in which to build, males building in the small-entrance nestboxes generally chose more short pieces in their first 10 pieces than males building in the large-entrance nestboxes (entrance size: z: −2.730, $P = 0.006$; Fig. 2). This relationship changed over the 3 days of testing but how it changed differed for birds building in large- and small-entrance boxes (day number*entrance size: z value = 4.169, $P < 0.001$). To understand this interaction better, we ran two further models using the data from the large- and small-entrance conditions separately. Birds building in the small-entrance nestbox chose increasingly more long pieces of material across the 3 test days (day number: $z = 4.962$, $P < 0.001$; Fig. 2a). However, birds building in the large-entrance nestbox did not change the number of long pieces they took across test days (already choosing a high number on day 1; day number: $z = -1.877$, $P = 0.061$; Fig. 2b), although inexperienced birds tended to take more short pieces than the experienced birds on day 2 than on day 1 or day 3 (day number*experience: $z = 1.913$, $P = 0.056$; Fig. 2b).

Building Success

Males building in the small-entrance nestboxes generally became more successful over the 3 days of testing at getting pieces of material into their nestbox (day number: $F_{2,56} = 7.388$, $P = 0.001$; Fig. 3). Inexperienced males were more successful at getting short pieces into the nestbox than long pieces, while the experienced males were equally good at getting both lengths into the nestbox. Inexperienced birds were actually more successful at taking short pieces into the box than the experienced birds, although the groups did not differ in their ability to insert long pieces successfully (material length: $F_{1,56} = 13.112$, $P < 0.001$; experience: $F_{1,10} = 2.680$, $P = 0.133$; material length*experience: $F_{1,56} = 8.093$, $P = 0.006$; Fig. 3; see Appendix).

For birds building in the large-entrance nestbox, experienced males were more successful than inexperienced males at taking long pieces into the box but not more successful at taking in short pieces (experience: $F_{1,10} = 15.405$, $P = 0.003$; experience*material: $F_{1,56} = 7.256$, $P = 0.009$). Both experienced and inexperienced males were more successful at taking short pieces into the nestbox than at taking in long pieces (material length: $F_{1,56} = 59.263$, $P < 0.001$). They did not become more successful at taking pieces into the box over the 3 days (day number: $F_{2,56} = 2.292$, $P = 0.111$; Fig. 3).

Handling Material

Males were always more likely to hold material at the end than in the middle (average proportion held at end across days >0.7 in all cases). Despite this, males building in the small-entrance nestboxes held the material even more frequently at the end of the piece on later days (day number: $z = -6.341$, $P < 0.001$). Males in both experienced and inexperienced groups held the long pieces at the end more often than they held the short pieces at the end (material: $z = -4.378$, $P < 0.001$).

Males building in the large-entrance nestbox were more likely to hold short pieces at the end than they were to hold long pieces in this way (GLMM: $z = -8.031$, $P < 0.001$). Experienced birds were more likely to hold material at the end on later days (GLMM: $z = -2.367$, $P = 0.018$).

Exploratory 'Pecking' of Material before Building

To investigate the male's exploratory behaviour of the nest material before he took his first piece to the nestbox, we looked at his pecking of the material on the ground (prodding or picking it up with his beak) across all days and treatment groups. To address whether the male explored the material through pecking to a greater extent across days or with different levels of experience, we log transformed the data to normality and ran an LMM using the same explanatory variables as in Model 1.

All males explored the material more before taking their first piece to the nestbox (in terms of the total number of pecks) on day 1 than they did on day 3 (LMM: $F_{1,46} = 8.938$, $P < 0.001$; experience: $F_{1,21} = 1.496$, $P = 0.235$; nest-entrance size: $F_{1,21} = 0.544$, $P = 0.469$). The males pecked at the type of material they then took to the nestbox more than they did the other type (long taken: average ± SD proportion of pecks at long pieces = 0.93 ± 0.206, $N = 23$; short taken: average proportion of pecks at short pieces = 0.84 ± 0.241, $N = 44$). In five cases the male did not peck at the material before taking it to the nestbox.

Other Factors Investigated

In addition to the change in the way in which the birds held the material and their success at building, males also approached the material faster over the 3 test days (see Appendix). The amount of material they pulled out or knocked out of the nest did not change over the test days, but males building in the large-entrance nestboxes pulled out more material (see Appendix).

DISCUSSION

When zebra finch pairs were given artificial nestboxes that differed in the size of entrance and material of two lengths with which to build a nest in that box, males chose to build their nest using the type of nest material most appropriate for the size of the entrance of the nestbox in which they were building. On the first

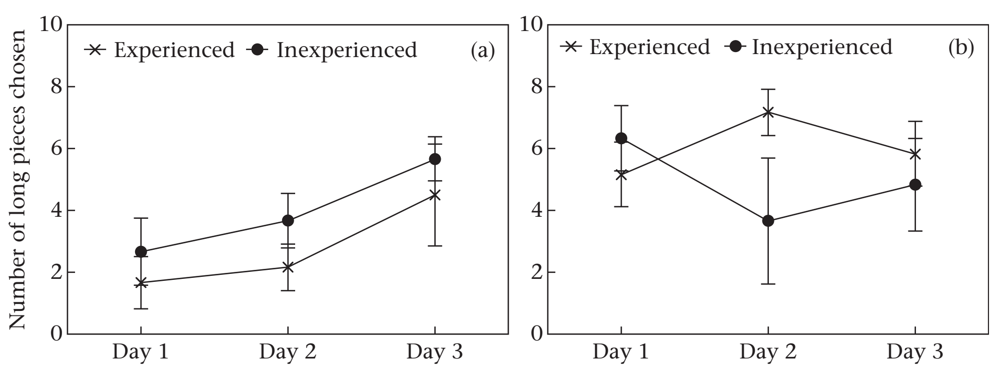

Figure 2. Mean ± SE number of long pieces of material chosen (out of the first 10 pieces taken to the nestbox) by inexperienced and experienced males building in (a) a small-entrance nestbox and (b) a large-entrance nestbox, across the 3 days of testing.

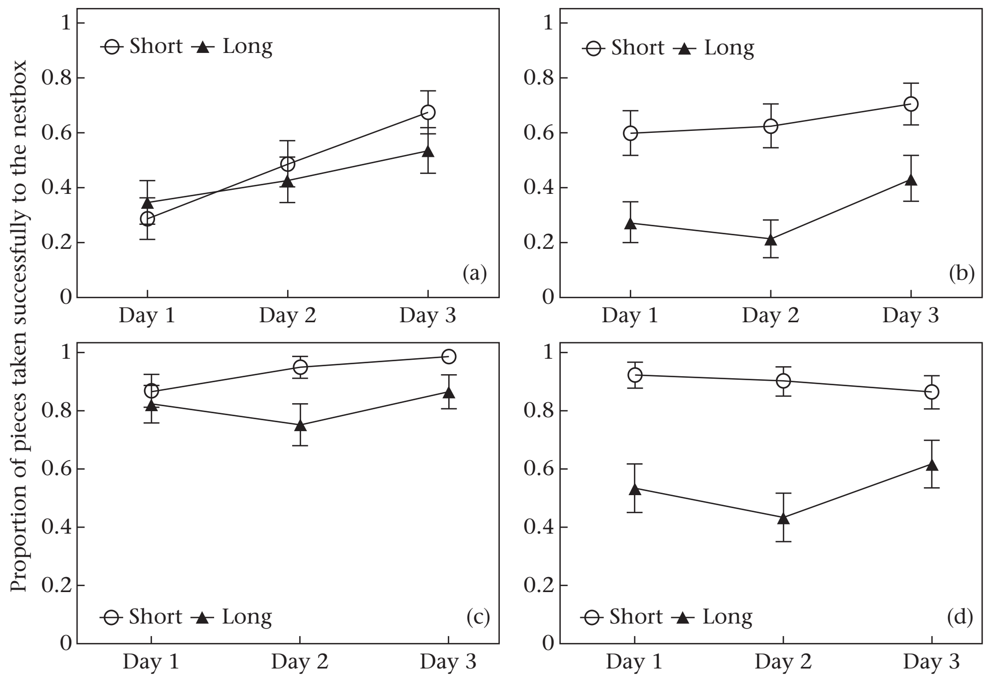

Figure 3. Mean ± SE proportion of nest material pieces that zebra finch males successfully took into the small-entrance nestbox (a: experienced group; b: inexperienced group) and the large-entrance nestbox (c: experienced group; d: inexperienced group) across the 3 days of testing.

day of building males building in boxes with a relatively small entrance chose short pieces more often than those birds building in a nestbox with a large entrance. Furthermore, handling of the material by the males building in the small-entrance nestboxes improved over the 3 test days as they increasingly became more successful at getting long pieces into their nestbox. As they became more experienced these males also became less choosy over material length. Additionally, males with 2 days of prior building experience were more successful than inexperienced males at getting long pieces into large-entrance nestboxes.

Zebra finch males, then, chose the appropriate material for solving this task. To achieve this, they may have assessed both the properties of the two types of material given to them as well as the situation in which they had to build through exploring the nestbox. Males manipulated both types of material on the floor of the cage prior to building and they did this on the first day of testing more than they did on the third day. This reduction might be due to the birds manipulating the material on the floor to assess the properties of the material prior to taking it to the nest, which, by the third day of building with that material, was unnecessary. Additionally, as all birds had access to the nestbox prior to testing, they may also have used this experience to assess the size of the entrance to the nestbox.

This judgement of which material was appropriate relative to the size of the entrance hole may have been based on the length, weight or flexibility of the building material, or a combination of these features. As the zebra finches did not choose the appropriate material on their very first choice, however, it would appear that they did not use this prior experience to inform their choice but rather indicates that there was some rapid trial-and-error learning. This is further supported by the increasing success of birds taking pieces of nest material into the small-entrance nestboxes. This success was due, at least in part, to males increasingly holding pieces by their end rather than in the middle and with this increase in dexterity, the birds were ambivalent to material length by day 3 of testing.

The increasing success of inserting material into the nest when building in the more constraining small-entrance box size is consistent with changes in dexterity seen in nest-building southern masked weaverbirds and village weaverbirds (Collias & Collias, 1964; Walsh et al., 2010, 2011). In our experiment, however, we saw changes in material choice in addition to these physical dexterity skills as the birds gained experience with the material and the nestboxes we provided. It appears, then, that as the zebra finches improved their ability to handle the material, so they were able to make greater use of all of the material we provided, rather than be restricted to a single type. This kind of flexibility in response to the availability of suitable materials would be useful to birds building in the wild where building materials may vary considerably in their structural characteristics. It seems likely that males that can rapidly improve their ability to identify suitable materials and to handle materials that differ in their physical properties would build their nest more effectively and efficiently than those less capable of such abilities.

One surprising result was that birds without previous experience building in the small-entrance box were more successful at taking short pieces into the nestbox on the first day of testing than birds with previous experience. It is not clear why this was the case as they did not differ from the experienced birds in how they held the nesting material, the number of pieces they added, or the number of pieces they knocked out or pulled out (see Supplementary material). It is possible that by excluding males from the inexperienced group that did not attempt to build on day 1 we inadvertently selected for more successful nest-building males, specifically in that group. This possibility is supported by the finding that birds in the experienced group were less successful at taking short pieces into the box on their first building occasion (on the pretesting days) than were birds in the inexperienced group on their first day of building. However, as the males in these two groups did not differ in their ability to take long material into the nestbox, this explanation is not entirely sufficient. Regardless of this unexpected finding, both our manipulation of experience (in terms of the 2 days of building prior to testing) and the birds' experience building in the experimental nestbox across the 3 days of testing affected the birds' building behaviour.

The choice and handling of materials for building nests bears at least a superficial resemblance to the choice of tools by primates and some birds, and the zebra finches in our experiment were able to choose material structurally appropriate to the task we presented them in a manner similar to tool selection (Chappell & Kacelnik, 2002, 2004; Fragaszy et al., 2010; Liu et al., 2011; Manrique, Gross, & Call, 2010; Manrique, Sabbatini, Call, & Visalberghi, 2011; Povinelli, Reaux, Theall, & Giambrone, 2000; Sabbatini et al., 2012; Visalberghi, Fragaszy, & Savage-Rumbaugh, 1995; Visalberghi et al., 2009). Furthermore, the trial-and-error learning they showed as they continued to build also resembled material choice by some primates (Povinelli et al., 2000). There is still little known about whether tool construction is a domain-specific ability, or might instead require more general cognitive abilities (Bird & Emery, 2009; Emery & Clayton, 2009; Tebbich, Seed, Emery, & Clayton, 2007; Teschke, Cartmill, Stankewitz, & Tebbich, 2011). The possibility that nest construction may require at least some of the same abilities as tool use requires further research.

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Supplementary Material

Supplementary material for this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2014.02.008.

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Appendix

Nest-building Success

Four pairs in the inexperienced/small-entrance treatment group and five pairs in the inexperienced/large-entrance group did not start building on day 1 of testing and were excluded from the experiment. Two pairs in the experienced/large-entrance group were also excluded because one pair did not build on day 3 and because the experimental set-up was not correct on day 3. As all of these pairs were replaced with pairs that did build, all of the results are from six pairs in each group that completed all days of building.

Additional Factors Investigated

Mechanism of material choice

To determine how males building in the small-entrance nestboxes might be selecting more short material on the first day of testing than those building in the large-entrance nestboxes, we addressed the possible influence of several other variables. First, we examined whether males made the 'correct' choice of the material appropriate for the nest entrance size from the very first piece of nest material. They did not: the first piece taken on day 1 of testing did not differ between groups, and nearly all birds took a short piece first: 1/6 birds in the large/experienced group took a long piece first; 2/6 large/inexperienced took long first; 1/6 small/experienced took long first; and 3/6 small/inexperienced took long first.

We then examined whether birds building in the small-entrance nestboxes on day 1 chose long pieces early on (ca. three of the first 10 pieces) and then switched to short pieces. To do this, we compared the lengths of the first five pieces chosen on day 1 with the lengths of the second five pieces chosen. The first and second five pieces chosen did not differ: males took the same number of long pieces on average in their first five choices as in their second five choices (Wilcoxon signed-ranks tests: experienced/small:

$W = -0.535$, $N = 6$, $P = 0.593$; inexperienced/small: $W = 0.000$, $N = 6$, $P = 1.000$).

To determine whether birds used a strategy to choose pieces (e.g. 'if you fail taking one type of material, then switch to the other type'), we compared the number of times that birds failed and then switched (to the other material) to the number of times they failed and stayed with the same type and the number of times they succeeded and then switched to the number of times they succeeded and stayed with the same type. We looked at the first 10 choices, addressing the treatment groups and nest material lengths separately. Birds in the experienced/large-entrance group were more likely to choose another long piece, whether or not they had failed or succeeded previously at taking a long piece into the nestbox, than they were to switch, but they showed no particular pattern of choice behaviour when the piece was short ('stay with the same length versus switch to the other': long/fail: $\chi^2_1 = 11.765$, $P = 0.001$; long/succeed: $\chi^2_1 = 7.053$, $P = 0.008$; short/fail: $\chi^2_1 = 0.091$, $P = 0.763$; short/succeed: $\chi^2_1 = 0.267$, $P = 0.606$). Birds in the experienced/small-entrance group, however, were more likely to choose another short piece regardless of their success with it previously, although these males showed no particular pattern of choice behaviour when the piece was long ('stay with the same type versus switch to the other': short/fail: $\chi^2_1 = 47.087$, $P < 0.001$; short/succeed: $\chi^2_1 = 10.246$, $P = 0.001$; long/fail: $\chi^2_1 = 0.667$, $P = 0.414$; long/succeed: $\chi^2_1 = 1.594$, $P = 0.695$).

The inexperienced/large-entrance group did not switch their choice of length based on success or failure (all χ^2 values >7.5, all P values <0.006). Males in the inexperienced/small-entrance group tended to choose short pieces irrespective of previous success with it. In contrast, when these males had previously failed at taking a long piece into the nestbox, they chose long pieces again, but when they had previously succeeded at taking a long piece into the box, there was no difference in their next choice (short/fail: $\chi^2_1 = 13.564$, $P < 0.001$; short/succeed: $\chi^2_1 = 7.667$, $P = 0.006$; long/fail: $\chi^2_1 = 5.000$, $P = 0.025$; long/succeed: $\chi^2_1 = 0.333$, $P = 0.564$).

Handling of short pieces

We explored further why the inexperienced birds building in the small-entrance nestbox might have been more successful at taking short pieces into the box on day 1 than the experienced birds. There was no difference between the groups in whether they finished building or not on day 1 (in both groups 3/6 pairs did not finish building). The groups also did not seem to differ in the time it took males to approach the nesting material on day 1 (although the sample size, $N = 6$ in each group, was too small to be compared statistically: mean ± SD: inexperienced: 33.4 ± 23.9; experienced: 16.4 ± 20.8). Although the means were far apart, there was a lot of variation in the data. We then looked at the first time that males in the experienced group had encountered the material (on day 1 of their 2 days of pretest experience) and their proportion of success with the short pieces then. The average success at taking short pieces into the nestbox did not differ between the first time the experienced group encountered the material (pretest) and when they built with it on test day 1 (excluding two cases where the pair took fewer than 10 pieces of short material in the time filmed: mean ± SD: pretest: 0.30 ± 0.22; day 1: 0.31 ± 0.09). Both of these means were smaller than the mean success of the inexperienced group on day 1 (0.63 ± 0.12). It thus seems that the difference between the experienced and inexperienced groups building with short material in the small-entrance boxes on day 1 was due to the inexperienced group being more successful from the outset than the experienced group, rather than the experienced birds becoming less successful between their first encounter with the material during the pretest and test day 1. The absolute number of times that short pieces were successfully taken to the nestbox did not vary between the two groups (mean ± SD: experienced group: 10.2 ± 1.8; inexperienced group: 11.2 ± 1.6; t test: $t_{10} = -1.006$, $P = 0.338$), and thus the experienced group had more unsuccessful attempts than the inexperienced group. The number of pieces pulled out and knocked out on day 1 by the males also did not vary between the two groups (Mann–Whitney U test: pulled out: $U = 25$, $N_1 = N_2 = 6$, $P = 0.212$; knocked out: $U = 11$, $N_1 = N_2 = 6$, $P = 0.181$). We also examined whether males tended to hold short pieces in the middle or at the end, and whether this could explain the difference in their overall success with pieces of that length. Although males in the experienced group held short pieces in the middle more often than at the end when they took them to the nestbox (mean ± SD: experienced: 10.33 ± 15.13, $N = 5$; inexperienced: 3.17 ± 4.58, $N = 4$; note that sample sizes were too small to be analysed statistically), when we looked at the pieces that both groups held at the end, the inexperienced group still had a higher proportion of success at taking them into the nestbox (t test: $t_{10} = -5.729$, $P < 0.0001$), and there was no significant difference in the absolute number successfully taken ($t_{10} = -0.896$, $P = 0.391$).

Time taken to approach the material and to add all pieces to the nestbox

To test whether males approached the nest material faster as days progressed, we measured the latency (in min) from when the material was first placed in the cage to when the male first pecked at it and log transformed them to normality. An LMM was then fitted with the same explanatory variables as in Model 1. All males approached the nest material more quickly over the 3 test days (LMM: $F_{2,44} = 12.429$, $P = 0.0001$), and experienced males were faster than inexperienced males on day 2, but not on day 1 or day 3 (experience: $F_{1,22} = 3.030$, $P = 0.096$; experience*day number: $F_{2,44} = 5.859$, $P = 0.006$).

As there were many cases where the pair did not finish building in the test time that we allocated to them, we compared the frequency of this across days, experience levels and size of nestboxes using chi-square tests and then corrected the alpha value for multiple tests. We did this to determine whether the speed of building differed between treatment groups. It did not, although, as expected, more males finished building on day 3 than on day 1 (day number: $\chi^2_2 = 8.857$, $P = 0.012$, $\alpha = 0.017$; experience: $\chi^2_1 = 0.429$, $P = 0.513$, $\alpha = 0.017$; nest entrance size: $\chi^2_1 = 0.429$, $P = 0.513$, $\alpha = 0.017$).

Knocking and pulling out material from nestbox

Males did not knock out more material over successive days (Friedman nonparametric test: $\chi^2_2 = 2.044$, $P = 0.360$, $\alpha = 0.017$; nest entrance size: Wilcoxon signed-ranks test: $W = -0.576$, $P = 0.564$, $\alpha = 0.017$; experience: Wilcoxon signed-ranks test: $W = -0.486$, $P = 0.627$, $\alpha = 0.017$).

Regardless of experience, males building in the large-entrance boxes consistently pulled out more material than the males building in the small-entrance boxes (nest entrance size: Wilcoxon signed-ranks test: $W = -2.948$, $P = 0.003$, $\alpha = 0.017$; day: Friedman nonparametric test: $\chi^2_2 = 3.805$, $P = 0.149$, $\alpha = 0.017$; experience: Wilcoxon signed-ranks test: $W = -0.884$, $P = 0.377$, $\alpha = 0.017$).

Female behaviour

We addressed female building behaviour using the same measures as described previously for the male: details of the nest material pieces taken to the box, pulled out and knocked out. As there were many cases in all treatment groups where the female did not knock out nesting material (experienced/large: 4, experienced/small: 9, inexperienced/large: 4, inexperienced/small: 6), these were removed from the data set before analysis. The data were then log transformed to normality before a general linear model (GLM) was carried out using the same explanatory variables as in Model 1. The female could not be included as a random factor as there were not enough data in this sample.

The females did not generally take any nest material to the nestbox, with the exception of two birds. In one case the female took a single piece, and in the other case a significant number were taken, but as it was after the male had taken his first 10 pieces and since the pair did not complete building, it is unlikely to have affected the results substantially. Although females did knock out material in some cases, they did not do this more often in any particular treatment group or more frequently across days (GLM: experience: $F_{1,44} = 2.044$, $P = 0.160$; nestbox entrance size: $F_{1,44} = 0.591$, $P = 0.446$; day number: $F_{2,44} = 1.136$, $P = 0.330$). The female rarely pulled nesting material out of the nestbox: this happened in a total of seven cases and in each case she pulled out only a single piece.