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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