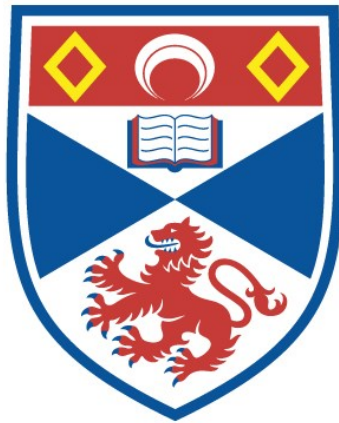


INVESTIGATING THE ROLE OF COGNITION IN NEST CONSTRUCTION IN BIRDS

Felicity Muth

**A Thesis Submitted for the Degree of PhD
at the
University of St Andrews**



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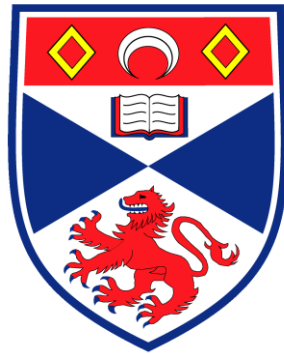
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Investigating the role of cognition in nest construction in birds

Felicity Muth



This thesis is submitted in partial fulfilment for the degree of PhD
at the
University of St Andrews

September 2012

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I, Felicity Muth hereby certify that this thesis, which is approximately 40, 000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

All data were collected by myself, with the exception of Chapter 3. This data was collected by the honours student Matthew Steele, under the supervision of Felicity Muth and Sue Healy.

Chapter 2 has appeared in print as "Muth, F. & Healy, S.D. (2011). The role of adult experience in nest building in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour* **82**: 185-189."

Chapter 4 is currently in print as "Muth, F. & Healy, S.D. (2012) Zebra finches build nests that do not resemble their natal nest. *Avian Biology Research* **5**: 218-226.

Chapter 6 will form part of the following manuscript: Walsh, P.T., Muth, F., Hansell, M., Borello, W.D. & Healy, S.D. Flexibility in behaviour and variation in structure: Confronting the myths of nest building.

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'I believe, in short, that birds do not build their nests by instinct... birds do change and improve when affected by the same causes that make men do so; and that mankind neither alter nor improve when they exist under conditions similar to those which are almost universal among birds... [but] the experiment has never been fairly tried'

– A.R. Wallace, 1867

Abstract

Nest building in birds has long been assumed to be a behaviour that is not learned, despite suggestive evidence to the contrary. In this thesis I investigated the role of learning in nest building in birds. I focused primarily on the choice of nest material made by zebra finches, in particular between two or more colours of nesting material. Using this aspect of behaviour, I found that adult nest building birds changed their preference for a particular colour of nesting material depending on their own nesting and breeding experience: males that built a nest using material of their less preferred colour later preferred that colour following a successful breeding attempt in that nest. In contrast to this role for learning in adults, in two other experiments I found no evidence that juvenile birds learned about the nest from which they had fledged or that birds learned about what material to nest with from conspecifics. Using wild Southern masked weavers, I also addressed variability in a particular aspect of nest building: the attachment of the very first blade of grass knotted onto a branch. I found that birds did not construct the same attachment each time they did it, even when building at the same location, but that males generally used more loops in their attachments as they built more nests, and when using longer pieces of grass. Finally, I tested zebra finches on a nest building ‘task’, using a paradigm often used to test cognitive abilities among tool-users. Birds were presented with two lengths of nest material, one of which was more appropriate for one of two sizes of nest box entrance. I found that nesting birds could choose the appropriate length of material and that the birds’ handling of material and their choice of material changed with experience. Taking these results together, it seems that there is a greater role for learning in nest construction than is generally acknowledged and that nest building might involve the same underlying cognitive processes as tool manufacture and use.

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Ethical note

All work carried out was approved by the University of St Andrews Animal Welfare and Ethics Committee.

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Chapter 1: Introduction

Animal constructions are found throughout the animal kingdom. From the microscopic casing of an amoeba, *Diffflugia coronata*, to the remarkably engineered dams of beavers, animal constructions exist across many scales and in many forms (Hansell 2000). Some of the most widespread constructions are birds' nests. Most of the roughly 10,000 species of birds build nests, which vary from the simple scrape in the ground of by terns, to the elaborate constructions of weaverbirds and tailorbirds. Bird nests have attracted a wide range of scientific interest in areas such as sexual selection (e.g. Hoi *et al.* 1994, Soler *et al.* 1998, Møller 2006, Quader 2006), the functional significance of nest structure and of the materials used (e.g. Schleicher *et al.* 1996, Palomino *et al.* 1998, Hilton *et al.* 2004, Heenan and Seymour 2011), and in the locations in which birds choose to nest (e.g. Herlugson 1981, Boulton *et al.* 2003, Hoover 2003, Loukola *et al.* 2012). However, we still know little about how birds know what nest to build and what role learning plays in nest construction.

Nest building by birds has traditionally been believed to be a behaviour that does not require any form of learning. In 1882, Darwin wrote '[Man] has to learn his work by practice; a beaver, on the other hand, can make its dam or canal, and a bird its nest, as well, or nearly as well, and a spider its wonderful web, quite as well, the first time it tries as when old and experienced' (Darwin 1882). A.R. Wallace, on the other hand, believed that birds might learn aspects of their nest building and went as far as saying that 'the mental faculties exhibited by birds in the construction of their nests are the same in kind as those manifested by mankind in the formation of their dwellings' (Wallace 1867). Wallace even suggested experiments to answer specific questions about what birds might learn and understand about nest building (Wallace 1867, 1870). However, since that time there have been few thorough investigations of how and what birds might learn about building nests.

One early approach to determine whether birds learn anything about building a nest from their early experience was to hand rear chicks and deprive them of nesting material until they were adults and then see what structure, if any, the birds built. Female canaries *Serinus canarius* that underwent this kind of deprivation could build nests as adults that were as 'large and as tidy' as the nests of females that were not deprived of this early nest experience (Hinde and Matthews 1958), whereas a pair of robins *Turdus migratorius* and two pairs of Rose-breasted Grosbeaks *Pheuticus ludovicianus* were incapable of building nests after being deprived in this way (Scott 1902, 1904). These experiments indicate that in some species early learning may be important in developing nest-building behaviour, but they do not reveal which specific aspects of building behaviour develop during through early experience in a nest. The cases where deprived birds do not build nests as adults might be due to a lack of motivation, an inability to choose appropriate materials or an inability to manipulate these materials appropriately. It is possible that even within a particular aspect of nest building such as material choice, some features are learned while others are not. For example, when village weavers *Ploceus cucullatus* were hand-reared and deprived of experience in manipulating building materials, this deprivation appeared to affect their ability to build as young adults (aged seven to 10 months), but not their choice of materials. When their material preferences were compared to those of control birds of the same age that had not been deprived of material, both groups had similar preferences for artificial nesting materials. Both groups of birds preferred the same colour of artificial building material (toothpicks): green over yellow, blue, red, black and white, although the birds that had had access to materials were more likely to choose yellow toothpicks than were the deprived birds. The two groups also did not differ in their preference for flexible over rigid material and for longer over shorter pieces when offered pieces varying in length between 2.5 and 20cm. Moreover, the preference for green material became stronger in the deprived group as they gained more

experience with the artificial building material. These preferences for artificial material reflect what this species chooses under natural conditions (long, flexible strands of fresh green grass). Therefore, it seems that in this species, birds have an unlearned set of criteria that they use for choosing nest material (green, flexible and long), which are consolidated through experience with the material. In contrast, the manipulation of the material itself seemed to require much more experience. When the two groups of birds were provided with natural nest materials (palm and reed grass) and a guava bush at one year of age, the deprived group did not build at all during the first week, whilst the control group wove nests into the bush and wire mesh of their cage. By the second and third week the deprived young wove a few stitches into the wire mesh, but still far fewer than woven by the non-deprived controls. After three months of being left with the building material, the deprived birds were able to carry and weave as much grass as did the control birds. However, over this three-month period, two deprived males only built two nests (one male never built), whereas the three control birds built 11 nests. While these experiments show that these birds need to experience building in order to manipulate nesting material appropriately, it is not clear what they learn in order to do this. Some of this learning is likely to involve refining their physical manipulation of nest material through motor learning but it may also involve learning about the physical properties or ‘folk physics’ of the objects being manipulated. These abilities, called ‘judgement’ by Collias and Collias (1964), includes learning that pushing one end of grass into the mesh before pulling the other end straight out again does not lead to a viable knot. Birds may also need to learn how materials connect together, or what building steps to follow, to build a complete nest: one deprived bird was seen to weave and then remove stitches repeatedly and after a week had produced nothing (Collias and Collias 1964).

How birds know how to proceed through particular stages of building to complete a nest has been investigated a little through addressing which cues they might use to signal the

end of one stage of building and to move on to a new behaviour. If nest building is entirely stereotyped, we would expect birds to follow a strict sequence of steps, triggered by internal or external cues. This proposition comes from the invertebrate literature where it appears to explain a substantial amount of building behaviour. For example, for the wasp, *Paralastor* (Smith 1978), which builds its funnel-shaped nest by executing a stereotyped sequence of behaviour, once the 'stem' of the nest (coming up from the ground out of a 'burrow') has been constructed to a specific height, the building of the neck is triggered. The wasp continues to this stage of building even if the nest is experimentally manipulated to make the building of this stage pointless: if the stem is buried in soil the wasp will continue to build the funnel into the soil, defeating the whole purpose of having the entrance on top of the stem (to prevent parasitic wasps entering; Smith 1978). However, building behaviour can appear stereotyped in that some motor patterns are repeatedly used, but the animal might still have flexibility in how it uses such motor patterns in response to external cues. Similarly, even if a particular building sequence is followed under 'normal' building conditions, the nest-building bird may still be able to change its behaviour if necessary (for example, if the nest is damaged). This seems to be the case in village weaverbirds, *Ploceus cucullatus*. These birds appear stereotyped in their building behaviour in that when building a nest they follow seven specific stages of building, each of which might be cued by stimuli from the previous stage. The sequence proceeds through the stages: initial attachment; ring stage; roof; egg chamber; antechamber; entrance and entrance tube (Collias and Collias 1984). When building the egg chamber, the male pushes long grass strips out from the ring to form the spheroid shape of the chamber, and weaves more grass into these strips. At this stage of building, the density of this mesh appears to act as the stimulus for the amount of grass still to be woven in, as was shown by the males' response to the removal of part of the roof and its replacement with artificial mesh. When the roof was replaced with a large mesh the male wove in more pieces, and

when it was a small mesh he wove in fewer. Once this mesh reached a certain density, the male started to add short pieces to thatch the roof; when part of the roof was cut away and replaced with extremely fine mesh, the male switched from adding long pieces to using short, thick pieces. However, experience also seems to play a role in the birds' responses to these cues, as more experienced birds thatched the ceilings of their nests more thickly than did younger birds (Collias and Collias 1984). Village weavers may also use stimuli from the entrance tunnel of their nests (loose hanging strands of grass) to determine the length of the entrance tube. Males generally continue weaving until these hanging grass pieces are woven to form the entrance tunnel with a neat, completed rim at the bottom. When more loose strands were experimentally added, the male continued to extend the tunnel to the bottom of the strand (making it up to six times longer than it would usually be), rather than just pulling out the loose hanging strands (Collias and Collias 1984). Although these examples indicate that males may build a nest by responding to stimuli from the nest to govern their behaviour, they also respond to experimental changes to the nest in a seemingly flexible manner, unlike unlike the *Paralastor* wasp. For example, when parts of the nest were cut away by an experimenter, the males did not simply continue to the next stage of building as did *Paralastor*, but instead repaired the nest. The only case where the male did not do this, but instead destroyed the nest, was when the experimenters destroyed the lower part of the ring. The authors concluded that this was because that part of the nest forms the essential scaffolding of the structure and the male needs to use it as a foot rest from which to work.

These results seem to indicate that the male does not simply follow a set of steps in building his nest, but may have some representation of what a complete nest should be, and can alter his behaviour in order to achieve this structure, except in cases where it is physically impossible. Nest building by another species of weaver, the Southern masked weaver *P. velatus* shows that although birds are repeatable in the nests they build (Walsh *et al.* 2010),

within the stages of building (especially the early stages), different individuals are extremely variable in their building behaviour, with regard to the way in which they handle building material (the side of their beak they held the grass, the side of the nest into which they inserted the grass and the part of the nest into which they wove the grass). Birds also varied in the speed at which they completed building stages of the nest (Walsh *et al.* 2011).

Therefore, it seems that behaviours need not be stereotyped to produce somewhat repeatable end-products (the nests of this species). These experiments with village and Southern masked weavers highlight the variability in this behaviour, the role for experience and the ability to respond flexibly to changes to the nest. However, while these birds may vary in the building of their nests, it remains unclear how it is that the end result is a nest that can be readily attributed to a Southern masked weaver.

Using a species that builds an apparently simpler nest than do weaverbirds, Hinde & Steel (1972) also attempted to look at whether rules governed the building behaviour by canaries, which build a cup-shaped nest. Hinde & Steel showed that the motivation to build is not maintained by feedback from nest building. In their experiment, birds were divided into three groups: one that could manipulate material (string) but could not carry it away (group G); a second, where the birds could manipulate and carry the string but had no nest pan (group GC), and a third group that could collect, carry and build with the string in the nest pan provided (group GCP). These three groups did not differ in the amount of ‘gathering’ (pecking and manipulation of material with the beak) or in the amount of carrying. Thus it seems that the birds will continue to attempt the earlier stages of building, even if there is not reinforcement from being able to carry out a later stage (e.g. group G continued to ‘gather’ material, even though they could not carry it and had nowhere to build with it). This implies that the birds can be motivated to build even when there is no immediate feedback from the nest. Canaries do use some key stimuli in cueing their nest building however, in a manner

similar to weaverbirds. At the first stage of building, the gathering of material, the canaries needed to manipulate the material in order to learn to return to it (Hinde and Steel 1972). This was established by presenting canaries with two sources of building material, one of which could be carried away for building, and one that was attached at one end and so could not be pulled away (although both could be manipulated). The canaries did not discriminate between the two sources, and continued to return to both the source where the material could be carried away, and the one where it was attached. However, when the birds had to jump to reach both sources of string, and could not manipulate the attached string, they did learn to visit the rewarding source rather than the source where the string was attached. This was the case even when they could pull the string down partially but could not carry it away. Both canaries and village weaverbirds, then, appear to use some cues from the nest in determining their building behaviour, and in the case of weaverbirds these responses may change with experience. However, whether species as different as weaverbirds and canaries use the same behavioural mechanisms in building their nests and vary in the extent to which learning is involved in the various aspects of building behaviour is not yet clear.

One of the few experimental investigations to examine the specific role of learning in building behaviour has been in the zebra finch, *Taeniopygia guttata* (Sargent 1965). While zebra finches used their early experience to inform their later nest building decisions, the experience of building a nest as an adult had larger effects on material choices: birds without building experience generally preferred brown material over green and red, but those that had recently built a green nest preferred green material to brown or red material. However, birds that had built a red nest did not then prefer red material to brown or green. Why males had these particular colour preferences, and whether they refer to functional properties of the material or are arbitrary, is not clear. Birds also developed preferences for a particular box type or location for building from their building experience: those that had nested in a

particular type of nest box (cup or box) or a particular location (inside or outside the cage) were more likely to choose that one rather than the alternative. In this study, early experience as a nestling appeared to have only a small effect on adult nest material preferences: birds raised in green nests chose significantly more green nesting material when building as adults than birds raised in brown, but still preferred brown overall. Whilst where they nested as chicks (location and box type) did not override unlearned preferences (for cups located inside their cages), 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 (choosing a box if it was inside). Thus the zebra finches in that study seemed to have both unlearned preferences (for brown material, nest cups, and nesting inside their cages), but these could be altered by early experience as a nestling in a nest, and to a larger degree, by adult nest building experience. These data, now some fifty years old, provide evidence that experience does indeed play a role in nest building, but it is not clear why they made so little impact on the current view of how it is that birds know what nest to build.

Given the little regard given to learning and memory in nest building, it might then seem surprising that another skill that also involves the manipulation of material external to oneself, namely tool use, has been extensively addressed in terms of what cognitive processes might be involved. The cognition that is usually studied in animal tool use is ‘physical’ cognition, a label used to describe the ‘understanding’ animals may have of the functional properties of the material they manipulate (‘causal understanding’ or ‘folk physics’; Povinelli *et al.* 2000, Bluff *et al.* 2007, Shettleworth 2010). This is often demonstrated by showing that an individual can choose an appropriate tool for a task (e.g. Chappell and Kacelnik 2002, Chappell and Kacelnik 2004, Cummins-Sebree and Frigaszy 2005, Hunt *et al.* 2006, Visalberghi *et al.* 2009, Fragaszy *et al.* 2010, Manrique *et al.* 2010, Manrique *et al.* 2011, Massaro *et al.* 2012) or that they can transfer knowledge about the use of one tool in one

context to its use in another or of another functionally similar tool (e.g. Fujita *et al.* 2003, Seed *et al.* 2011, Macellini *et al.* 2012, Sabbatini *et al.* 2012). Whether or not nest building behaviour requires similar types of physical cognition to tool construction has never been tested experimentally, despite the apparent similarity between these two behaviours (Hansell and Ruxton 2008). If nest-building birds solve physical cognition tasks using the same strategies as tool-using birds, this implies that the cognitive abilities needed for using tools may not be a specific adaptation, but rather an aspect of more general cognitive abilities.

In spite of the similarities between tool manufacture and nest building, most of the research effort has been focused on tool manufacture and use, and it remains unclear how similar the mechanisms are (psychological or otherwise) that enable animals to make tools or to build nests. However, as nest-building behaviour occurs in many more species than does tool use, addressing the role that cognition plays in this behaviour offers the opportunity for comparative studies and studying the evolution of cognition. As different species of birds build very different nests from one another in different environments, this variation may be reflected in the physical cognition involved in constructing these nests.

In this thesis, I set out to investigate the role of learning and memory in nest construction. I did this by carrying out a number of laboratory-based experiments using the zebra finch as a ‘model’ nest builder. I first addressed how adult learning, juvenile learning, and social learning affected nest material choice. I then investigated whether birds were able to choose material appropriate for a particular building context based on a physical property of that material. Finally, I used an experimental manipulation to examine variability in nest structure and the role of experience in nest building in wild, free-living, Southern masked weaverbirds *Ploceus velatus*.

I used zebra finches, *Taeniopygia guttata*, because although they are originally passerines native to Australia, they have been used extensively in experimental studies as a

model species to address questions in song learning, sexual imprinting and mate choice (Burley *et al.* 1982, Immelmann 1982, Burley and Coopersmith 1987, Catchpole and Slater 2008). They are useful for investigating nest building behaviour both for their short reproductive cycles (laying to fledging takes five weeks, and birds are reproductively mature at around three months of age; Zann 1996) and because they build nests readily in captivity, allowing experiments to commence quickly as well as the study of multiple nests per building pair. The nest is typically a spherical, domed structure with an entrance tunnel, constructed from dead grass stems (Zann 1996), although they can greatly vary in their structure both between and within colonies. Wild zebra finches typically nest in dense thorny shrubs or trees, but nests have also been found in clumps of dry seaweed, rabbit holes and cattle skulls (Zann 1996). This variation in their nest site choice in the wild is logistically useful as it might mean that their nesting location and nest box type is also flexible in the laboratory and therefore is amenable to manipulation. Zebra finches will also build with a variety of nesting materials, which is useful as it means that properties of material can be manipulated in learning experiments. Males typically bring the nest material to the nest site, and the female then manipulates the material in the nest cup, generally sculpting it into the species-typical dome-shape. Females will occasionally bring material to the nest as well or instead of the male (Zann 1996), but the reason she does this in only some cases is not clear. After all the material is added to the box or site, the male and female will generally both manipulate the material until the female lays her first egg. After the female has finished laying (an average of five eggs; Zann 1996), both sexes incubate and the male will occasionally add new pieces of nest material and manipulate the material in the nest. The female may also line the nest with feathers when the main structure of the nest is complete (Zann 1996). Because males are the primary nest builders, I focused on their building behaviour, specifically in the choices they made of nest materials.

I also looked at the building behaviour of wild Southern masked weaverbirds, *Ploceus velatus*. As this species constructs knots and weaves nests that appear complex and variable, it offers an excellent opportunity to study the factors determining the structure of their nests. Furthermore, males of this species build multiple nests over a single season, enabling the comparison of the structure of multiple nests built by the same individual (Collias and Collias 1984, Walsh *et al.* 2010). Southern masked weavers vary in their building behaviour, and while their nests are repeatable, their behaviour generally is not (Walsh *et al.* 2010, Walsh *et al.* 2011). However, there had been no detailed analyses of the product of their building behaviour (i.e. the knots they build).

Thesis aims

In the research I describe here, I aimed to address how learning might influence nest building, and gain a greater understanding of this little-investigated behaviour.

I first addressed what adult birds might learn from their individual breeding and building experiences (Chapter 2). To do this, I carried out an experiment where paired male zebra finches were tested for their colour preference between two colours of nest material. To test whether these birds could associate nest colour with breeding success, I then manipulated the success of that breeding attempt.

One of the questions that arose from that experiment was whether a male's colour preferences were specific to the context of nest building, or were instead general colour preferences, possibly transferred from a foraging context. To test this, in Chapter 3 I compared the preferences of paired male zebra finches for colour of nest material to their food colour preferences.

To determine whether nest material choice as an adult was affected by a bird's experience in a nest as a juvenile, I carried out an experiment where zebra finch offspring

fledged from nests of one of two possible colours of nest material (Chapter 4). I then tested the male offspring at maturity to determine which colour of nest material they preferred. I also compared the morphological structure of nests built by males to those of their father.

As social birds, such as zebra finches, often learn from one another (Lefebvre and Boogert 2010), in Chapter 5 I attempted to determine whether birds used the nest material choices of conspecifics when making their own decisions about which materials to use in nest building.

To determine how variable the very first part of the nest built by Southern masked weavers was, in Chapter 6 I describe the first attachments made of blades of grass to a branch when a male Southern masked weaverbird builds a nest. I removed the blades of grass knotted on to branches by male weavers as they added them, forcing birds to attach grass at the same site four times at each of four sites for several males. I looked at whether this attachment differed within and between males, across successive nests.

Finally, although zebra finch nests appear simpler than the intricately woven nests of weaverbirds, zebra finches still need to select appropriate nest material. In Chapter 7 I report an experiment where I addressed whether male zebra finches could select appropriate nesting material for a nest building ‘task’ using a procedure similar to those that have been used to determine whether tool-using animals are able to choose appropriate tools for a particular task. Paired birds were presented with two nest material types (‘long’ and ‘short’), and one of two possible boxes to build in (‘Large-entrance’ and ‘Small-entrance’). The short material was designed to be more appropriate for taking into the small-entrance nest box. If zebra finches are able to select material in a manner akin to tool-using animals, I predicted that they would choose the short material more frequently than the long material when building in the Small-entrance nest box. If experience played a role in males’ choices of material, then I predicted that this would be more so the case in experienced birds.

Chapter 2: The role of adult experience in nest building in the zebra finch, *Taeniopygia guttata*

Introduction

Nest building in birds often includes choosing nest materials, attaching the material to an appropriate site, and binding it all together into a species-specific structure (Collias and Collias 1984). Although this behaviour may result in a seemingly elaborate structure in many cases (Hansell 2000), it is far from clear whether learning plays a role. Indeed, it is generally considered that cognition is not involved in nest construction (Hansell and Ruxton 2008, Raby and Clayton 2009, Seed and Byrne 2010). Evidence for an unlearned predisposition for birds to build nests comes even from species that are considered to construct some of the most elaborate nests: as young chicks male village weaverbirds, *Textor cucullatus*, deprived of nest material, attempt to weave each other's feathers (Collias and Collias 1964). However, early experience also appears to be key in developing a number of nest-building skills in this species. For example, young males that were deprived of nest materials (palm strips or reed grass) for a month were not as proficient at ripping off strands for nest building as controls that had not been deprived of these materials. When males were further deprived for a year and then provided with nest materials, they wove less frequently and produced fewer nests than did control birds. The weaving skills of these deprived males did improve with experience but they never reached the standard of weaving shown by the control birds (Collias and Collias 1964). Like first-time builders, these males with early deprivation tended to build nests with loose loops and ends (Collias and Collias 1964) in comparison to the more tightly woven nests of adult males. This tighter weaving with more building experience is also reflected in the nests of wild, free-living Southern masked and village weavers (*Ploceus velatus* and *P. cucullatus*), which become smaller and lighter over time (Walsh *et al.* 2010).

A more tightly woven structure of nest may have better structural integrity, meaning nests are more tightly attached to branches and are more likely to hold the weight of a female and her developing offspring until they fledge. However, whether the tighter weaving (and smaller nests) males produce with more building experience do indeed serve these functions has never been tested experimentally.

In addition to changes in weaving ability with experience, male village weaverbirds become increasingly discriminating in their choice of nesting material as they mature, selecting grass and avoiding the toothpicks or raffia that they choose as juveniles (Collias and Collias 1964). Experience also appears to influence the choice of nest materials and building location in the zebra finch, *Taeniopygia guttata* (Sargent 1965). Captive zebra finches that were given green or brown nest material to build a nest always preferred that colour on a subsequent nesting attempt (although birds that built red nests did not later prefer red nest material). Similarly, birds offered the choice of a 'habitat' (inside or outside the cage) and 'substrate' (either a nest cup or box) preferred the habitat and substrate to which they had been allocated for nesting on their previous nesting attempt (Sargent 1965). Experience with the natal nest also appears to influence adult preferences, but to a lesser degree than does experience as an adult builder. For example, birds reared in green nests preferred green nest material more strongly than did birds reared in brown nests (Sargent 1965).

There is considerably more evidence for the effect of experience on the choice of habitat in bird nest building. Typically, birds that breed successfully in a particular habitat or type of nest box will return to breed in the same type in subsequent seasons, whilst those that are unsuccessful are less likely to do so (for example, Herlugson 1981, Gavin and Bollinger 1988, Haas 1998, Hoover 2003). However, it is not clear whether the success of a previous breeding attempt similarly influences decisions relating to nest building, such as the type of material used or how the nest is constructed.

Here we investigated whether the success of a breeding experience would affect the subsequent choice of nest materials in zebra finches. The zebra finch is a useful species for studying nest building behaviour as it has a short generation time and breeds readily in captivity. In the wild, zebra finches typically build domed nests from dead grass stems, although there is large variation both in the dimensions of their nests and in the materials used to build them (Immelmann 1962 in Zann 1996). There is also considerable variation in their choice of nest sites, including a range of shrub and tree species, in the foundations of raptor nests (Zann 1996). As they often suffer high levels of nest predation (Zann 1996, Griffith *et al.* 2008), an ability to learn to associate the success or failure of a breeding attempt with key aspects of the nest could reduce the risk of predation in later nesting attempts. In our experiment, we tested paired males for their initial preference for one of two colours of nest material shortly prior to nest building with either their preferred or non-preferred colour. We examined male behaviour because although both males and females manipulate nest material once it is in the nest, it is the male who takes material to the nest (Zann 1996). We manipulated the colour of nest material as colour is a relevant factor in nest construction for zebra finches (Sargent 1965) and we also manipulated breeding success by allowing half of the pairs to hatch eggs and rear chicks, and removing eggs from the other half of the pairs once they were incubating a completed clutch.

If zebra finches do learn to associate the colour of nest material with their breeding success in that nest, we would predict that males from pairs that bred successfully would prefer to use the same colour of nest material for a future breeding attempt, whilst males from unsuccessful pairs would have a reduced preference for that colour. If, on the other hand, experience alone with a particular colour of nest material causes males to prefer that colour for a second nest regardless of their breeding success, then initial preferences for nest material colour should change to whichever colour the male used for nesting.

Methods

Subjects

The subjects used in this experiment were 35 male and 35 female zebra finches. All birds used were aged between three and 15 months of age and had either been bred in captivity at the University of St Andrews or at the University of Glasgow, UK. None of the birds had had previous experience of building a nest, but had fledged from nests built with undyed coconut fibre and hay. 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*. Breeding pairs were provided with 1 tbsp. Haith's Egg Biscuit Food three times a week and daily once they had chicks. All breeding pairs were also given spinach once every one to two weeks. When not breeding, birds were housed in single sex cages in groups varying from 6 to 20 birds. When birds were paired for nesting, they were moved to wooden cages sized 44 × 30 × 39cm (width × length × height) and provided with a wooden nest box sized 11 × 13 × 12cm (width × length × height). As the walls of their cages were wooden, pairs were prevented from seeing building by neighbouring males. Pairs may have been able to see nest building occurring in the cages across the room. However, we arranged pairs such that they would have seen both brown and green material being built with if they could see into cages across the room.

Experimental protocol

None of the birds had had a previous opportunity to breed or interact with nest materials. Pairs were chosen such that they were no more closely related than first cousins and there were no two pairs where the four birds came from only two sets of parents (i.e. where two brothers were paired with two sisters). The experiment was carried out in three blocks (Block 1, $N = 11$ pairs; Block 2, $N = 20$ pairs; Block 3, $N = 4$ pairs). In all parts of the

experiment where preferences for nest material colour were tested, only the male's preference was addressed. All preference tests were recorded using Sony Handycam camcorders. The nest material used was coconut fibre and hay, as is standard procedure in our lab, and was dyed green and brown using food colouring (Supercook Ltd.).

Testing for initial colour preferences ('Test 1')

In order to determine whether males preferred a particular colour of nest material, pairs were presented with green and brown material after 24 hours of being caged together. Birds were provided with 3g (1.5g each of hay and of coconut fibre) of each colour of nest material. Each colour of nest material was placed either to the far left or to the far right end of the cage on the cage floor (alternated between cages) with the nest box hung in the centre of the back wall of the cage. The camcorder was focused on the nest box and cage floor, and pairs were filmed until the male had made at least 10 'choices' for material. Each 'choice' was defined as the male taking material (usually one or a few strands) from the pile on the floor to the nest box. The nest box was checked by eye without any disturbance to the birds once an hour for the first three hours and once every two to three hours after that. After at least 10 pieces had been added, the nest box and all the nest material were removed from the cage.

The video data were used to determine which colour of nest material the male preferred and were analysed using software for behavioural analysis (Noldus Observer, TrackSys Ltd., UK). We determined a males' preference based on the first 10 choices for material that he made. As well as recording when the male took nest material to the nest box, we also recorded the number of times he poked both colours of nest material as an indication of his tendency to explore both colours equally. We did not see females removing nest

material added by males, although in three pairs the females did all the nest building and the males did not take material to the nest. We excluded these pairs from the experiment.

Nest building with a preferred or non-preferred colour

Once all of the males' initial nest material preferences had been determined, half of the pairs were provided with the nest material of the male's preferred colour (green: $N = 14$, brown: $N = 2$) and half were provided with nest material of the male's non-preferred colour (brown: $N = 13$, green: $N = 3$) with which to build a nest (Figure 1).

Nest material was provided twice a day at 9:00 and 14:00 until the first egg was laid (at around six days: Zann 1996). If the female did not begin to lay within four weeks after nest material had been provided, the pair was removed from the experiment ($N = 8$). Pairs that laid eggs but then threw them out of the nest were also removed from the experiment ($N = 3$).



Figure 1: A zebra finch in a nest of green building material

Clutch manipulation

In order to manipulate apparent breeding success, half of the pairs experienced ‘successful’ breeding and were allowed to incubate their eggs, fledge chicks and care for them with their nest for a week ($N = 10$). They were then moved to a cage twice the size of their breeding cage without their nest. After two more weeks the female was moved to a single-sex stock cage whilst the male remained with the chicks for a further two weeks. One pair had their single chick die in the nest and was removed from the experiment. The remaining pairs experienced ‘unsuccessful’ breeding. Unsuccessful pairs were allowed to incubate eggs for six or seven days, at which point the eggs were removed and frozen ($N = 10$). These pairs were left with their nest for a following 24 hours before being returned to the single-sex stock cages. The manipulation of breeding success was counter-balanced across the two colours of nest material.

Testing for effects of experience on the preference for nest material colour (‘Test 2’)

Four weeks after the removal of their nest, pairs were re-united in individual cages with nest boxes as before. 24 hours later they were presented with 3g of brown and 3g of green nest material, filmed, and the male’s preference recorded using the same protocol as in the initial preference test. An experimenter blind to the treatment group of the bird scored the male’s preference.

Data analysis

To determine the role of both breeding experience and whether males had built with their preferred or non-preferred colour on the males’ new preference, we fitted a Generalized Linear Model with a binominal error structure and logit link function. The dependent variable was the number of choices made in Test 2 that were of the colour that was most preferred in

Test 1 (out of a total of 10) and the two independent variables were fixed factors each with two levels: the ‘nest material built with’ (preferred or non-preferred); the ‘breeding treatment’ (successful or unsuccessful), and the interaction between them.

We also addressed whether male preference in each treatment group changed from Test 1 to Test 2 by comparing the initial number of choices for the preferred colour to the new number of this colour chosen (in the second preference test) using Wilcoxon signed-rank tests.

We further addressed whether males explored both colours equally in Test 1 and Test 2 separately through comparing the number of times that males poked green and brown nest material during the time it took them to make 10 choices for nest material. This was addressed using Wilcoxon signed-rank tests for males that preferred green and males that preferred brown independently (for this test a ‘preference’ was 8 or more choices for a particular colour taken to the nest during the test). In order to determine whether the tendency to explore both colours equally in Test 2 differed for males in different treatment groups, the number of times males poked either the colour they had initially preferred, or the colour they had not initially preferred were also compared using Wilcoxon signed-rank tests.

We also addressed whether there was any difference in the time taken (in minutes) for males to make 10 choices for nest material between Test 1 and Test 2 (overall and within the different treatment groups) using 2-tailed paired *t*-tests on log-transformed data.

All statistical analyses were carried out in PASW v.18.0.0.

Results

Initial colour preferences

Of 35 pairs of birds tested in Test 1, the majority preferred green nest material (Chi-square test: $\chi^2_1 = 16.030$, $P < 0.001$). One male chose equal numbers of each colour and was removed from the experiment. Of the 19 pairs that were included in the second preference test, 15 preferred green and 4 preferred brown in the first test (Figure 2). In the majority of cases, the preferred colour was chosen in 10 out of 10 choices (Chi-Square test: $\chi^2_1 = 8.895$, $P < 0.01$; Figure 2), and in the 3 other cases 8 or 9 out of 10 choices were for this colour.

Whilst there was a trend to explore (through poking) green nesting material more often when the male was taking green to the nest, and likewise for brown, this was highly non-significant, and males explored both colours equally (Wilcoxon signed-rank test: males that preferred brown: $T = 0.365$, $N = 4$, $P = 0.715$; males that preferred green: $T = -1.108$, $N = 15$, $P = 0.268$).

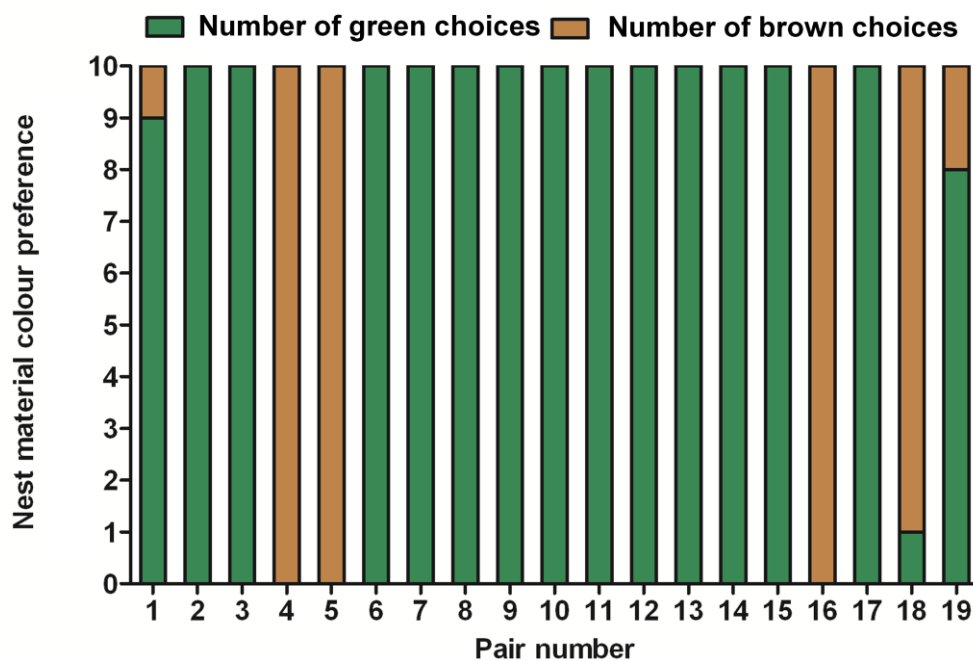


Figure 2: The number (out of a total of 10) of choices for two colours of nest material by males during the first test for their preferred colour of nest material. $N = 19$.

Colour preferences after a nesting and breeding experience

Males that were allowed to build their first nest with nesting material of the colour that they preferred in Test 1 were more likely to choose material of that colour in Test 2 than were males that had built with their non-preferred colour (GLM: LR: 7.559, $DF = 1$, $P = 0.006$; Figure 3). Overall, whether a male experienced successful or unsuccessful breeding did not affect his preference for a particular colour of nest material after nesting (GLM: LR: 0.408, $DF = 1$, $P = 0.523$; Figure 3). However, this was dependent on whether or not birds had built with their preferred or non-preferred colour (GLM: LR: 11.673, $DF = 1$, $P = 0.001$; Figure 3). Males that had built with their non-preferred colour of nesting material were more likely to develop a preference for it after nesting if they had experienced successful breeding, as they made fewer choices for the colour that they preferred initially, and therefore more of the other, initially-non-preferred colour they had just built with. However, this was not true for males in pairs, which had experienced unsuccessful breeding using their non-preferred nest material colour.

In all four treatment groups, the preference for the colour that was preferred prior to building the first nest tended to be reduced in Test 2. However, this difference was only significant for those males that had built with their non-preferred colour and then experienced successful breeding (Wilcoxon signed-rank tests: non-preferred/successful: $T = -2.032$, $N = 5$, $P = 0.042$; non-preferred/unsuccessful: $T = -1.841$, $N = 6$, $P = 0.066$; preferred/successful: $T = -1.342$, $N = 4$, $P = 0.180$; preferred/unsuccessful: $T = -1.069$, $N = 4$, $P = 0.285$; Figure 3).

Whilst in the initial preference test males explored both colours equally, in Test 2 males poked the material they chose to add to the nest significantly more than the other colour (Wilcoxon signed-rank tests: males that preferred brown: $T = 2.366$, $N = 7$, $P = 0.018$; males that preferred green: $T = -2.521$, $N = 8$, $P = 0.012$). In the four cases where the overall 'preference' was less clear (males made 6-7 choices for the preferred colour), they explored

both colours equally (Wilcoxon signed-rank test: $T = 0.000$, $N = 4$, $P = 1.000$). The treatment group a male was in did not affect his tendency to explore both colours in Test 2, as males poked the colour they had initially preferred as much as the other colour in all four treatment groups (Wilcoxon signed-rank tests: non-preferred/successful: $T = 0.674$, $N = 5$, $P = 0.500$; non-preferred/unsuccessful: $T = -0.210$, $N = 6$, $P = 0.833$; preferred/successful: $T = -1.461$, $N = 4$, $P = 0.144$; preferred/unsuccessful: $T = -0.365$, $N = 4$, $P = 0.715$).

Whilst there was a tendency for males to take longer to make 10 choices through taking material to the nest box in Test 2 than they had in Test 1, this difference was not significant (paired t -test: $t_{18} = -1.948$, $P = 0.067$). This held true when each treatment group was addressed separately (paired t -tests: non-preferred/successful: $t_4 = -1.505$, $P = 0.207$; non-preferred/unsuccessful: $t_5 = -1.132$, $P = 0.309$; preferred/successful: $t_3 = -0.670$, $P = 0.551$; preferred/unsuccessful: $t_3 = -0.347$, $P = 0.751$).

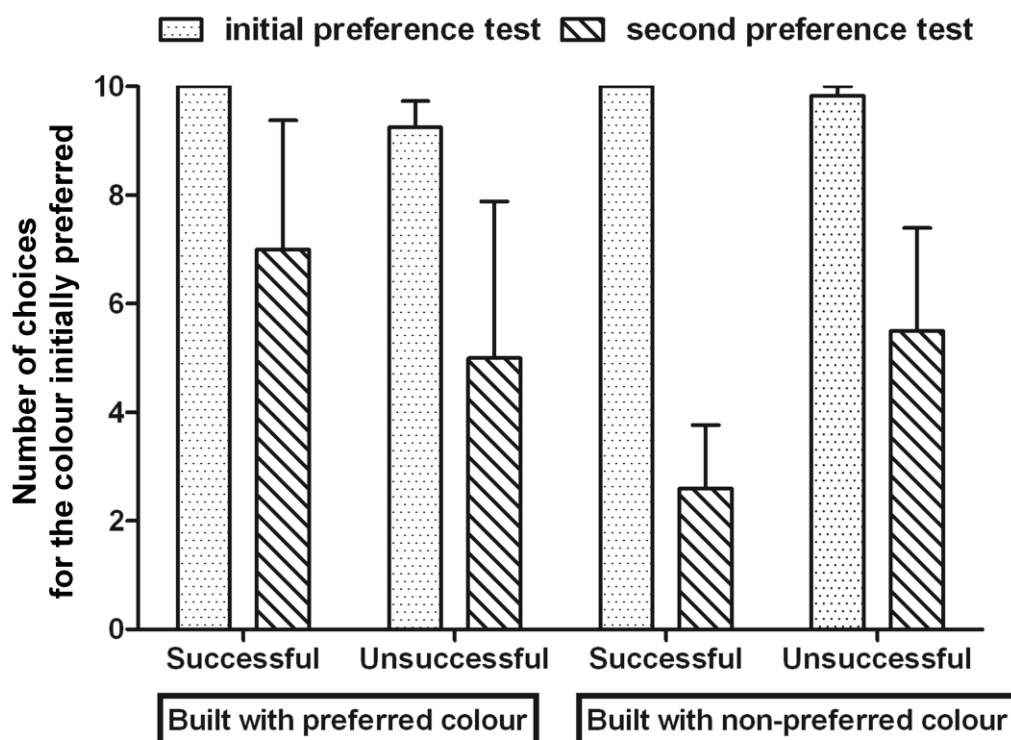


Figure 3: The average (+SEM) preference of males for the colour of nest material they preferred in the first preference test (measured as the number of choices/10 for this colour) before and after their breeding and nesting experience (in the four different treatments).

Discussion

When first-time nest-building male zebra finches were offered a choice between green and brown nesting material, most males (all but one) clearly preferred one or other colour of nesting material. When offered the same choice for their second nest, males that had built their first nest with their preferred colour continued to prefer that colour (albeit somewhat less so), regardless of whether they experienced successful or unsuccessful breeding. However, males that had built a nest with material of their non-preferred colour increased their preference for that colour, but only if they successfully raised and fledged chicks from their nest.

These data support our prediction that zebra finches can learn to associate the colour of nest material with their breeding success in that nest. They do not, however, support the prediction that experience alone with a particular colour of nest material leads males to prefer that colour when building a second nest, regardless of their breeding success. The effect of the experience is, then, context-dependent and choice of nest material appears to be flexible. Whilst males that built with their non-preferred colour and experienced successful breeding were significantly less inclined to choose their initially preferred colour in Test 2, all males' behaviour showed a trend in this direction. We do not have an explanation for this overall decline in preference for the initially preferred colour. That males that built a nest with their preferred colour still preferred that colour even after having had their nest fail may indicate that strong initial preferences are difficult to override if there is some nesting experience with the preferred colour of nest material. It is possible that a larger sample size would show that those initial preferences could be overridden by negative nesting experience.

Whether birds take into account breeding success when making decisions about which nest material to use has not been previously addressed (at least to our knowledge). However, birds do use breeding success when deciding where to build a nest. For example, 68.2% of

female wild mountain bluebirds (*Sialia currucoides*) that had reared offspring successfully in one year occupied the same territory and nest box the following year, whilst of those who moved territories, 71.4% chose the same type of nest box. Of the five unsuccessful breeders, two returned to the same territory and two out of three that moved used a different type of nest box (Herlugson 1981). It appears that these birds may learn features of their nest box and territory to use when selecting future nesting sites. Experimentally-simulated nest predation or nesting success (addition of offspring) had a similarly strong effect on the tendency of Prothonotary Warblers (*Protonotaria citrea*) to return to the same site in the following breeding season. The warblers' response was positively correlated with the level of experimental manipulation: birds fledged zero, one or two broods, which lead to them returning to study sites at low, moderate and high rates respectively (Hoover 2003). Additionally, the warblers responded to social cues: those that suffered experimental nest predation tended to remain in the same site if its neighbours did not lose their nest. It seems plausible that the flexibility in nest material choice we observed in the highly social zebra finch might also be affected by nest material preferences chosen or used by conspecifics building within sight.

The vast majority of males in our study strongly preferred one colour to the other in their first preference test, mostly for the green nest material. This preference is not due to males simply taking a particular colour of nest material to the nest once, and then returning to the same end of the cage to take it a further nine times, as males manipulated both colours of nest material equally. However, this was not the case on the second preference test: males were more likely to manipulate only the nest material of the colour with which they were building. It is possible that in the first preference test, males explored both colours before deciding which colour to build with but having built a nest, males already 'knew enough' to make a decision.

At least some passerines (e.g. European starlings *Sturnus vulgaris* and blue tits *Parus caeruleus*) include green plant material in their nests, reducing the deleterious impact that nest bacteria have on nestling growth (Brouwer and Komdeur 2004, Gwinner and Berger 2005, Mennerat *et al.* 2009a, Mennerat *et al.* 2009b). In these species, olfaction seems to be the main cue in choosing fresh green volatile herbs and they may learn from early experience (European starlings; Gwinner and Berger 2008) or from other individuals (Mennerat *et al.* 2009c), although this has not been shown experimentally. We do not know whether zebra finches would use volatiles in nest material when making nest material decisions but, as in our experiment all the material we provided was dry, we presume that olfaction was less salient than was colour for our nest-building males. The preference for green nest material of our birds contrasts with that of Sargent's (1965) zebra finches. His birds initially strongly preferred brown nesting material over green. There are multiple possible explanations for this discrepancy. Firstly, it could be due to differences in the nest material between experiments: Sargent used strands of coloured hessian whilst we used hay and coconut fibre dyed with food colouring, and the shades and reflectance of the colours used are likely to have differed between the two experiments. It is also possible that experience other than that with nest material differed between Sargent's zebra finches and ours, which may have affected males' preferences for nest material colour. For example, if a male's colour preferences are not specific to nesting material, but are more general colour preferences, then experience with foods of particular colours might affect his colour preferences in other contexts. Our birds are provided with green foods as treats, which may have led to the overall preference for green nesting material. This potential effect of colour preferences being generalised across contexts requires further investigation. A suggestion that zebra finches may not generalise in this way comes from the dislike of red nest material (when given the options of red, green and brown) (Sargent 1965), which is in striking contrast from the considerable evidence showing the

favour with which at least female zebra finches view red in the context of sexual selection: the redder the beak the more attractive the male is to females, and red-banded males are more attractive than are green-banded males (Burley *et al.* 1982, Burley and Coopersmith 1987, Blount *et al.* 2003). However, since males do not prefer the colour red in mate choice, a comparison between sexual and nesting contexts may be limited.

In conclusion, as in the choice of nest habitat and site, zebra finches also use the relative success of a breeding attempt to make decisions about the nest material they prefer to use to build subsequent nests. As with the changes with experience observed in nest structure in weaverbirds (Collias and Collias 1964, Walsh *et al.* 2010) it appears that there is a role for learning and memory in nest building in zebra finches. Whilst this is far from the apparent sophistication shown in decision making in tool use, where birds also have to decide amongst appropriate physical materials (for example, Chappell and Kacelnik 2002, Tebbich and Bshary 2004), it may be that nest building has a greater cognitive component than is typically assumed.

Chapter 3: Are the nest colour preferences of zebra finches context-specific?

Introduction

Birds construct nests to attract females (Jacobs *et al.* 1978) and to sleep in (Skutch 1961), but the most important function of the nest is to hold and protect eggs and offspring (Hansell 2000). A key aspect of nest construction is the selection of appropriate building materials. As different species of birds build structurally distinct nests in different environments that impose particular pressures, so the individuals of different species select and build with particular nesting materials. In some cases we know the reasons birds choose specific nest materials, for example to achieve a particular nest structure, or to serve another function such as mate attraction, camouflage or parasite deterrence (Wimberger 1984, Clark and Mason 1985, Clark and Mason 1988, Rodgers *et al.* 1988, Solis and De Lope 1995, Hansell 1996, 2000, Lafuma *et al.* 2001, Schuetz 2005). However, in other cases it is not clear why individuals of a species choose particular materials.

One particular feature birds appear to select in a potential nesting material is its colour. For example, domestic canaries *Serinus canaria domestica* prefer white to red string for building (Hinde and Steel 1972), some zebra finches *Taeniopygia guttata* prefer brown material to green and red (Sargent 1965), while others prefer green to brown (Muth and Healy 2011), or blue to yellow (Muth and Healy, *in press*) and village weaverbirds *Textor cucullatus* prefer green artificial building material (toothpicks) over other colours (yellow, blue, red, black and white). However, the reasons for such preferences are not always clear. In the case of village weaverbirds, it is possible that birds prefer green because the natural material chosen for building (fresh strips of grass) is also green (Collias and Collias 1962,

Collias and Collias 1964). Thus the colour may signal the mechanical properties of the material (i.e. fresh, flexible) that makes it most suitable for building this species' nests.

Birds might also use colour to select for potential nesting material for functional reasons other than mechanical qualities. For example, some species add green herbs to their nests that improve the condition of nestlings (e.g. European starlings *Sturnus vulgaris*; Gwinner *et al.* 2000, Gwinner and Berger 2005, blue tits *Parus caeruleus*; Mennerat *et al.* 2009b), in some cases through reducing the amount of bacteria (Mennerat *et al.* 2009a) or ectoparasites in a nest (e.g. European starlings; Clark and Mason 1985, Clark and Mason 1988, wood storks *Mycteria americana*; Rodgers *et al.* 1988, Corsican blue tits *Cyanistes caeruleus ogilastrae*; Lafuma *et al.* 2001). This plant material may also serve to attract females (e.g. European starlings; Gwinner 1997, Brouwer and Komdeur 2004). Nest material can also camouflage to the nest or eggs (e.g. Solis and De Lope 1995, Hansell 1996, Schuetz 2005), or even to threaten conspecifics through signalling the dominance of the builder (black kite *Milvus migrans*; Sergio *et al.* 2011).

Although these examples indicate that the colour of a material might act as a cue for selecting it for nest building, this colour preference might reflect a general colour preference resulting from another of the animal's experiences. For example, if a bird learns to associate a particular reward with a particular colour, that positive association might transfer to a preference for that colour in a nest-building context. The most likely context under which such associations might form is foraging.

To investigate whether a bird's preference for a particular colour of nesting material is specific to the building context, we compared the preferences of captive zebra finches for different colours of nest material to their preferences for different colours of food. We used zebra finches because this species can have strong preferences for particular colours of nest material (Sargent 1965, Muth and Healy 2011) and will also eat foods of different colours

(e.g. Katz and Lachlan 2003). We presented zebra finches with nest material of three different colours (blue, yellow and red) and, on another occasion, food of the same three colours in order to determine their colour preferences. If the birds differed in their colour preferences between the nest building and feeding contexts, this would support the suggestion that nest material colour preferences in zebra finches are specific to the nest-building context.

Methods

Subjects

We used 20 male and 20 female zebra finches in this experiment. All birds were aged between three and 15 months of age and had been bred in captivity at the University of St Andrews or at the University of Glasgow, UK. These subjects had built nests from green or brown material in an earlier nest-building experiment but they had not encountered the colours of nest material or food used in the present study. We kept birds on a 14:10 light:dark cycle at a temperature of 19-32°C, with humidity levels of 50-70% and gave them access to food (mixed seeds, cuttlebone, and oystershell grit) and water *ad libitum*, except for an hour before food colour preference tests.

24 hours after pairing males, we gave the pair a nest box. We housed pairs in cages measuring 44 × 30 × 39 cm (width × length × height). All walls of the cages were wooden, except for the front of the cage, which had vertical metal bars spaced 1cm apart. The cages were arranged such that birds could not see into neighbouring cages, although they did have a limited view of cages across the room.

Experimental protocol

To test colour preferences for food and nesting material in zebra finches, we dyed seed mix (Bucktons “foreign finch” seed, Cranswick Pet Products, UK) and nest material (coconut fibre) using blue, yellow, and red food colouring (Supercook Ltd.). To do this, we immersed the food or nest material in food colouring for around one minute, and then spread it on paper towel for at least 24 hours to dry prior to use. To confirm that dying both nesting material and food using the same food colouring lead to similar colours in both material and food, we took 10 measures of spectral reflectance for each colour of food and nest material using a Konica Minolta cm-2600d spectrophotometer. We then used averages of these measures to visualise the spectral reflectance of the food and nest material (Figure 1).

The 10 food trials and single nest trial were interspersed with each other, and the exact order in which they were carried out was randomised across birds. We conducted trials over a three-week period in November and December 2010, the birds were then returned to stock cages for six weeks, before we re-paired them in the same pairs and cages as before, and continued the trials for a further seven weeks.

We recorded all preference tests using Sony Handycam camcorders, and analysed videos using software for behavioural analysis (Noldus Observer, TrackSys Ltd., UK).

Nest material colour preferences

24 hours prior to the nest material colour preference test, we provided pairs with a wooden nest box measuring $11 \times 13 \times 12$ cm (width \times length \times height), which was hung in the centre of the back wall of the cage. At the start of the preference test, we gave birds 3g each of blue, red and yellow nest material. We placed each colour of nest material in a pile either to the far left, the far right, or centrally on the floor of the cage. The locations of the piles were alternated across pairs. We filmed the birds until the male had taken the majority

of the nesting material to the nest box, or until five hours had elapsed. We checked the nest box by eye every one to two hours without disturbing the birds. At the end of filming, we removed the nest box and all of the nest material from the cage. With zebra finches, only the male collects nest material during the initial stages of nest building (Zann 1996), so we tested only the nest material colour preferences of the male.

We used the video data to determine which colour of nest material the male preferred. We considered that a male had made a 'choice' each time he took nest material of a particular colour to the nest box and we determined his preference based on the first 10 choices of material that he made, with a minimum of eight of 10 choices for a single colour constituting a preference. One male attempted to build on his water dispenser rather than in the nest box and we included this data in the analyses.

Food colour preferences

We tested food colour preferences over 10 trials per pair. Each trial lasted five minutes, 30 seconds, as this time period was calculated as being long enough for both individuals to eat but short enough for multiple trials to be conducted. All pairs were given at least a day between consecutive food trials. Prior to each trial, we deprived pairs of food for an hour. During testing, we presented pairs with three transparent oval cylinder plastic food dishes (7.25 x 11 x 3.5 cm, width × length × height), placed along the front edge of the cage. Each dish contained 23g of either blue, red or yellow seed. The locations of the dishes were alternated across pairs and trials. After each trial we removed the three dishes and returned the birds' regular food. Each pair took part in only one food colour preference test per day and never underwent food and nest material colour preference tests in the same day.

We used the video data to determine whether the male and female had any food colour preferences. For each individual, we recorded the number of pecks at each colour of

food and the duration of time spent at each food dish. Pecks were counted only if they were directed to seeds inside a food dish (pecks at items outside the dishes or items birds brought into the dishes such as feathers, floor pellets etc. were not counted). We defined a visit to a food dish as starting when a bird sat in, or perched on the edge of, a dish and ending when the bird left. In the few instances where a bird pecked at food in a dish without sitting in it or perching on its edge, the start of its visit was taken from the time it first pecked at the food in the dish.

Statistical Analysis

As the number of pecks to a particular colour of food and the length of time birds spent visiting that colour of food dish in each trial were strongly positively correlated (Pearson's $r(199) = 0.950, p < 0.001$), we used the number of pecks to define food colour preferences. In order to test which colour was pecked most across the 10 trials, we used Friedman's tests for the data for each pair, as the data were not normally distributed. All statistical analyses were carried out in either PASW v. 18.0 or Minitab v. 15.

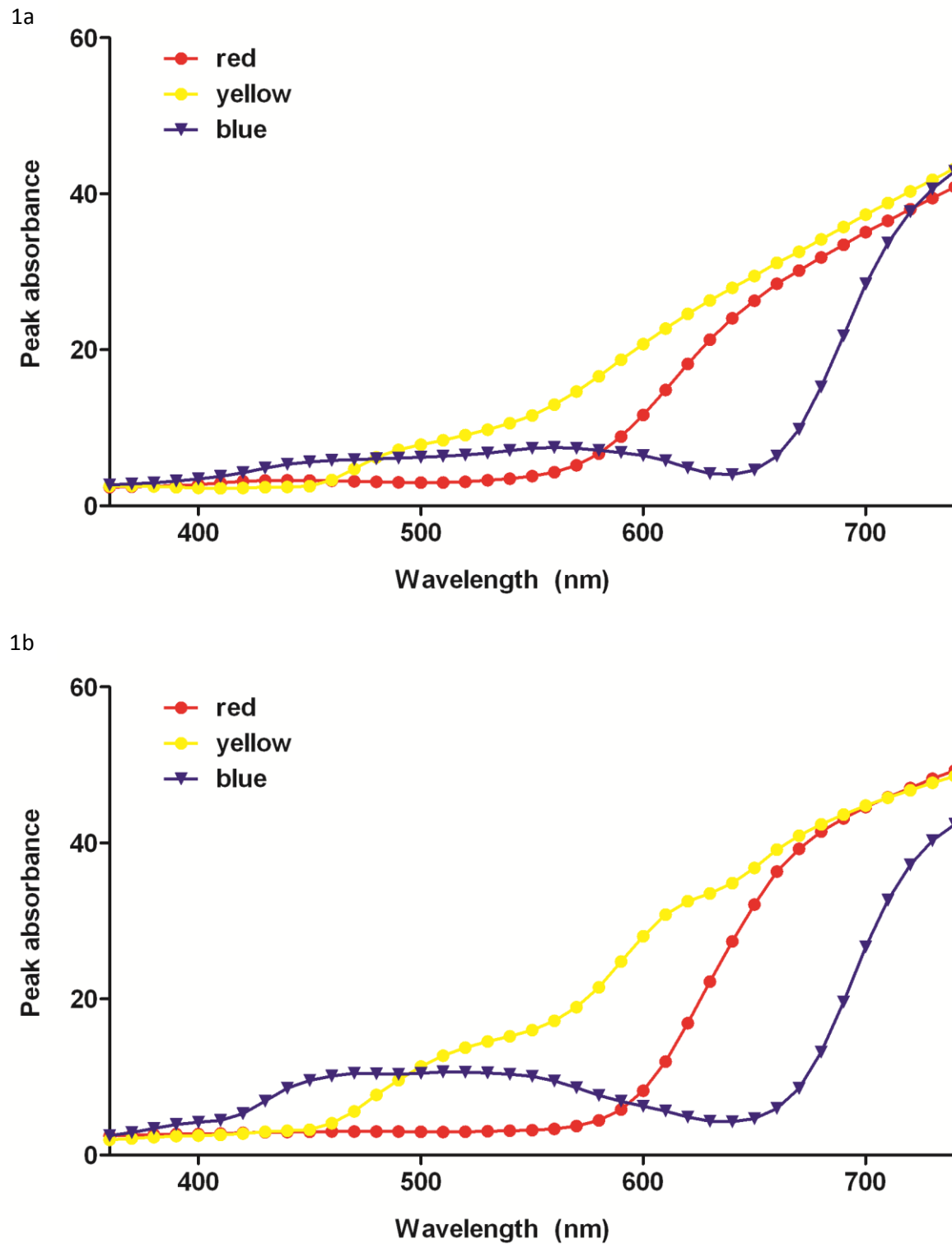


Figure 1: The peak absorbance across wavelengths of a) the three colours of nest material and b) the three colours of food.

Results

Nest material colour preferences

17 males preferred one colour of nesting material more than either of the other two (making eight or more choices for one colour): 15 males preferred blue, two preferred yellow and none preferred red. The other two males chose seven yellow, three blue and never chose red (Figure 2). The male from one pair did not build.

In three cases, females took nest material to the box in the time it took the males to make 10 choices. In one pair the female chose yellow and the male then chose seven yellow and three blue. In the second pair the female chose red and the male then took a majority of blue material. In the third pair the female took red, then yellow, then red, the male chose blue five times, the female chose blue, and the male then chose blue five more times.

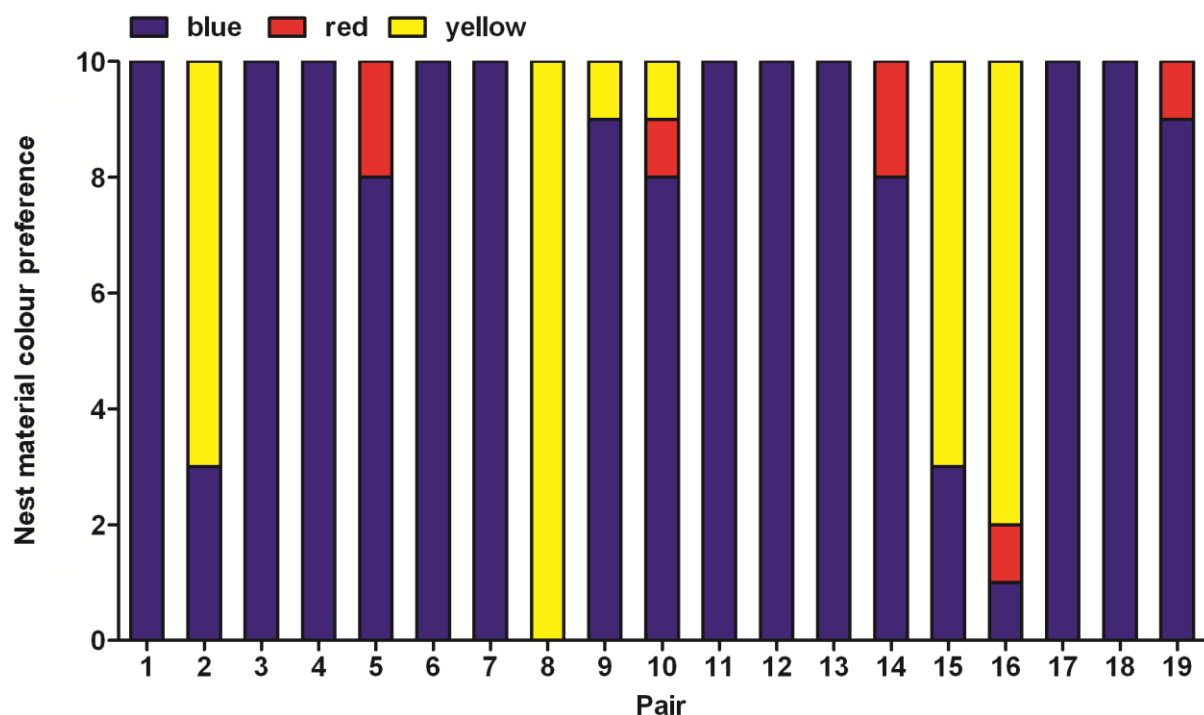


Figure 2: The nest material colour preferences of the 19 paired males, measured as the number of choices for each material colour (the colour of material taken in a single visit to the nest box) of the first 10 choices made.

Food colour preferences

In the food colour preference test, most of the males (16 of 20) had no colour preference (16 Friedman tests: $\chi^2_2 = 0.06 - 4.51$, $p > 0.05$; Figure 2). Of the four males that did have colour preferences, one preferred yellow and blue to red (Friedman test: $\chi^2_2 = 8.76$, $p < 0.05$), one preferred blue to yellow and red (Friedman test: $\chi^2_2 = 7.40$, $p < 0.05$), one preferred blue and red to yellow (Friedman test: $\chi^2_2 = 6.24$, $p < 0.05$), and one preferred red to yellow and blue (Friedman test: $\chi^2_2 = 6.24$, $p < 0.05$; Figure 3). The very first colour pecked did not differ across the three colours when looking across all males and trials (Chi-square test: $\chi^2_2 = 2.65$, $p = 0.266$).

Similarly, the majority of females (16 of 20) had no colour preference, pecking all colours equally (16 Friedman tests: $\chi^2_2 = 0.06 - 4.51$, $p > 0.05$). Of the four females that did prefer one colour over the others (these females were not paired to the males that displayed preferences), two preferred red to yellow and blue (Friedman tests: $\chi^2_2 = 6.22$, $p < 0.05$; $\chi^2_2 = 9.05$, $p < 0.05$), one preferred blue to yellow and red (Friedman tests: $\chi^2_2 = 6.22$, $p < 0.05$; $\chi^2_2 = 6.50$, $p < 0.05$), and one preferred yellow to blue and red (Friedman tests: $\chi^2_2 = 6.35$, $p < 0.05$). The very first colour pecked did not differ across the three colours when looking across all females and trials (Chi-square test: $\chi^2_2 = 0.88$, $p = 0.646$).

Across all the trials, females tended to peck the food before the males did (Chi-square test: $\chi^2_1 = 38.12$, $p < 0.001$). In 13 of 20 pairs, the females pecked at the food more frequently than did the males (paired t-tests across the 10 trials per pair: all $t_9 < -2.329$, all $p < 0.05$). In the remaining seven pairs, the female tended to peck more than did the male in two pairs ($t_9 = -1.881$, $p = 0.093$; $t_9 = -2.047$, $p = 0.071$) while there was no difference between the female and male in five pairs (all $t_9 > -1.6$, all $p > 0.1$). Males and females within a pair did not generally peck first at the same colour as each other (they pecked at the same colour in an average of 4 ± 1.8 trials of 10).

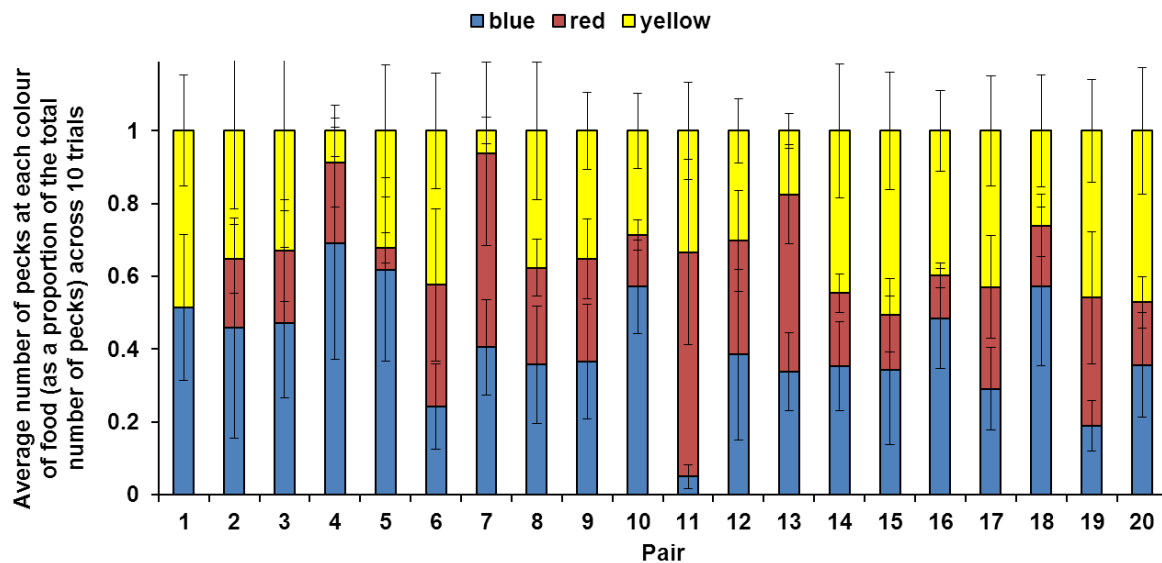


Figure 3: The food colour preferences of the 20 paired males, measured as the mean number of pecks at each colour of food across the 10 trials per male.

Food and nest colour preference compared

Nest material colour and food colour preferences were not the same, as the majority of males preferred a colour of nest material (most of the time blue), but did not prefer a colour of food. Of the four males that did prefer one colour of food, only one of these matched their preferred nest material colour (Table 1).

Table 1 The food and nest material colour preferences for the four males that preferred a particular colour of food.

Food colour preference	Nest material colour preference
blue/yellow	blue
red/blue	blue
blue	blue
red	blue

Discussion

The zebra finch males tested in this study preferred particular colours of nest material when constructing a nest: most preferred blue nest material and none preferred red material. In contrast, very few males had food colour preferences. Therefore, the colours nest-building birds preferred in this study may be specific to the building context.

The strong preference for blue nest material is consistent with birds' preferences in another study using a different group of zebra finches (Muth and Healy, Chapter 4), where 46/65 (of two generations) preferred blue nest material to yellow. These data are also consistent with Sargent's (1965) findings that zebra finch males did not choose red nest material when given a choice between brown and red material, even if they had fledged from a red nest or had previously built a nest with red material (Sargent 1965). In an earlier experiment, most of the birds used in the present study initially preferred green to brown nesting material but the birds that experienced a successful breeding attempt changed their colour preference in a subsequent colour preference test (Muth and Healy 2011, Chapter 2). It is possible that since the green material used in that study and the blue used in the present experiment are closer to each other in the colour spectrum, the blue material was preferred to brown and yellow and the green preferred to brown for the same reason. What that reason was, however, is not clear.

In contrast to their nest material colour preferences, the zebra finch males tested here did not prefer any of the three food colour options. This lack of preference is not likely to be due to an inability to discriminate between the different food colours, as the birds were capable of discriminating between nest material of the same colours. Zebra finches will also copy particular colours of food from watching conspecifics feeding and can discriminate between food colours and will use that information when choosing among foods (Katz and Lachlan 2003). Although zebra finches will prefer some foods over others, for example, they

eat a higher percentage of the largest, heaviest species of seeds available (such as Japanese millet *Echinochloa crus-galli*) over smaller seeds (e.g. Windmill Grass *Chloris truncata*) (Zann and Straw 1984, Zann 1996), there are no data prior to the current experiment on relative food colour preferences. Some food preferences may arise from the birds' early experience, as captive zebra finches prefer the food they experienced as a fledgling: birds raised on one of three types of seed (white millet, red millet or canary seed) generally prefer to eat that type of seed as adults, although it is not clear that the birds used the seed colour to discriminate among these options (Rabinowitch 1969). Given the possibility that early experience of food might lead to food colour preferences, of the colours we presented the birds, we might have expected them to prefer the yellow seed as it would seem most similar to the colour of the pale brown seeds that they ate as fledglings and up until this experiment. However, as our birds had experienced a range of colour in their foods (including green fresh vegetables such as spinach and cucumber and white and pink of the cuttlebone hanging in their cage), it is possible this experience with a diverse range of food colours reduced their neophobic responses to less familiar food colours.

Foraging is not the only context in which colour preferences might be developed. There is an extensive literature on the role that colour (both of morphological characteristics and leg rings) plays in mate choice in zebra finches: females prefer males with red leg rings and redder cheek patches and bills while males will prefer females with black or pink leg rings (Burley *et al.* 1982, Burley and Coopersmith 1987). However, given these colour preferences, mate choice preferences do not appear to be related to preferences for the colour of nest material.

In conclusion, nest-material colour preferences appear to be context-specific as they were not consistent with food colour preferences. It remains to be seen whether the birds use the colour of nest material as a cue to structural features of the material, or have another, non-

structural, function (e.g. camouflage). Future research might address the question of whether birds are able to learn to use the colour of material to determine the physical properties of possible materials. This could be tested by coupling different colours with different structural properties of material (e.g. size, flexibility), and seeing whether birds preferentially learn particular colour-structure combinations more readily than others.

Chapter 4: Does early experience affect adult nest building?

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 fledge 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.

Methods

Subjects

Thirty-two pairs of birds, aged between three and four months, were paired in wooden cages measuring $44 \times 30 \times 39$ cm (width \times length \times 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.

Experimental protocol

Parent preference test

The pairs were provided with a wooden nest box sized $11 \times 13 \times 12$ cm (w \times l \times 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 (Supercook 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, which have distinct peak absorbences across wavelengths (Chapter 3, Figure 1). 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 made at least 10 ‘choices’ for material. Each ‘choice’ was defined as the male taking material (usually one or a few strands) from the pile on the floor to the nest box. After at least 10 choices had been made, 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 choices made. 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).

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: $n = 3$).

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 (Figure 1) before it was replaced. 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.

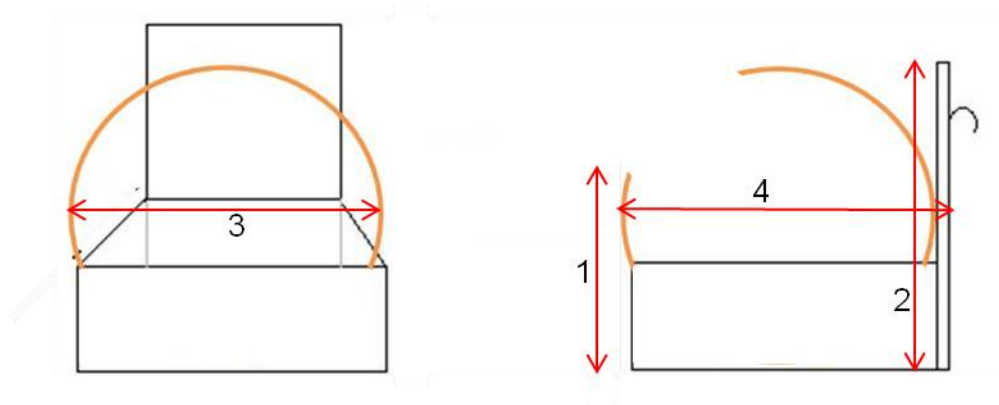


Figure 1: Diagram of nest box (in black) and nest (in brown) from the front (left) and side (right). The measurements taken are denoted by the numbers: 1: height at front; 2: height at back; 3: width; 4: length. Cup width and length were also measured.

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.

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.

16 of the naïve male offspring were initially paired with 16 of the naïve female offspring and tested for their colour preferences ('Group N', i.e. 'naïve'). However, in order to test the nest material preferences of all of the males using only female offspring from this experiment, the remaining males ($n = 18$) were paired with females that had been previously paired to males in Group N. 11 naïve males ('Group RP1', i.e. 're-paired once') were paired with females that had previously been paired once with a male from Group N. Seven males ('Group RP2', i.e. 're-paired twice') were paired with females that had previously been paired twice (once with a male in Group N and once with a male in Group RP1).

As we had an unexpected finding of females selecting the nest material in some cases, possibly caused by re-pairing them with multiple males, we re-paired all the males (from Groups N, RP1 and RP2) to test their nest material 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.

Data Analysis

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

Results

Adult colour preferences

Of the 32 adult males tested, 21 preferred blue, 10 preferred yellow, and one (pair 3) chose both colours equally (Figure 2). For the 31 males with preferences, in most cases (25) the first 10 choices made were for the same colour, in three cases 9/10 of the preferred colour were chosen, and in three cases 8/10 of the preferred colour were chosen. In one pair the female died, and so they were removed from the experiment (the male had preferred blue).

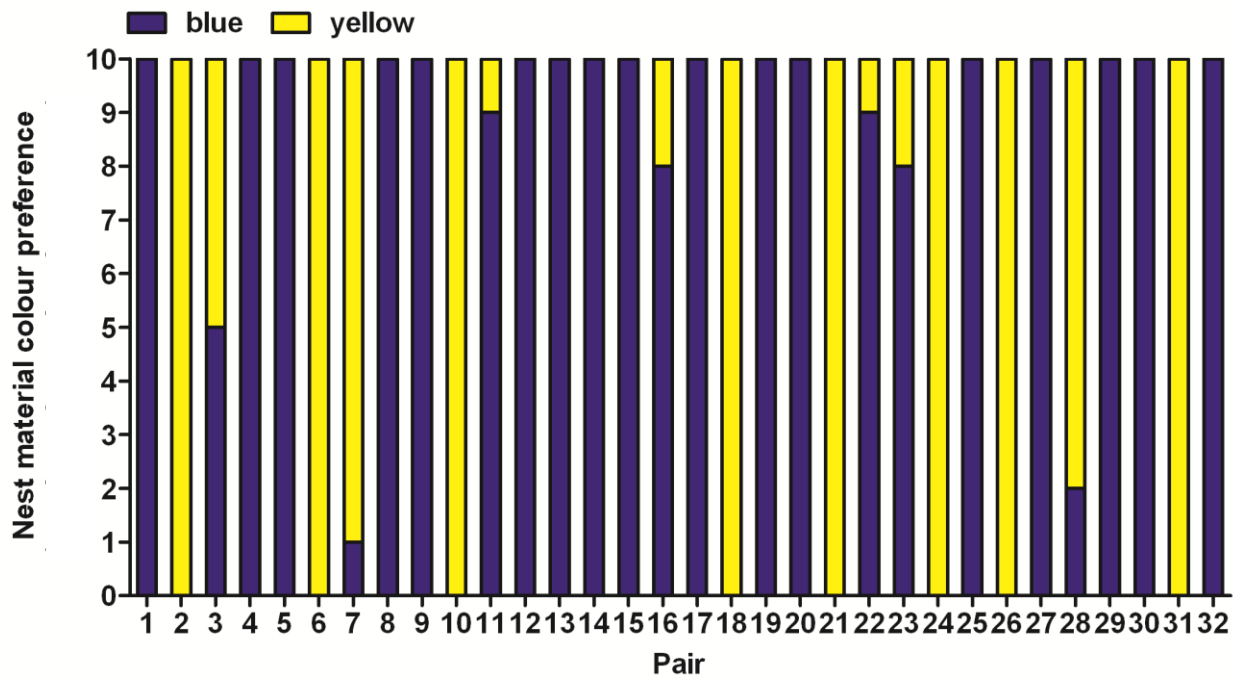


Figure 2: The preferences for blue or yellow nesting material of the parental males, measured as the colour a male chose the first 10 times he took material to the nest box.

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 (6 blue and 3 yellow), nine built with their non-preferred colour (8 yellow and 1 blue), and the pair which had no preference built with yellow.

59 offspring reached maturity: 21 females and 38 males. Of these individuals, 29 fledged from nests of their father's preferred colour (blue: 7 females and 13 males, yellow: 5 females and 4 males), and 30 fledged from nests of their father's non-preferred colour (blue: 2 females and 3 males, yellow: 7 females and 18 males).

Offspring colour preferences

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).

First preference test: male preferences

For those cases in which the male was both the first of the pair to make the first choice for nest material and where he made 10 choices ($n = 23$), 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 4 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. 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: $\chi^2_1 = 1.667$, $p = 0.197$).

First preference test: female preferences

In Groups RP1 and RP2, 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 make at least 10 choices. For two of these pairs, the female was the same. She had no colour preference in Group RP1 but preferred blue in RP2. 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 Groups RP2 and RP3) 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.

First preference test: pairs where both males and females built

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 made 10 choices for material while the females made fewer than four. In four pairs, the females added blue first, the males also added blue as their first choice, and then went on to take mostly blue material. In one pair, the female made a choice for yellow, followed by a

choice for blue, the male chose blue, and he went on to add mostly blue material. In the last pair, the female made a choice for blue followed by two choices for yellow, the male then made a choice for yellow, but he went on to make 9/10 choices for blue.

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.

First preference test: Male and female preferences combined

As we were interested in determining whether nest builders use information acquired during their time in the nest as nestlings, we re-did these analyses using the combined data from all builders, both males and females ($n = 34$). Using all of these data, the birds' colour preferences were not related to their father's preference: 20 preferred the same colour (all blue), 11 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 3). 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 3).

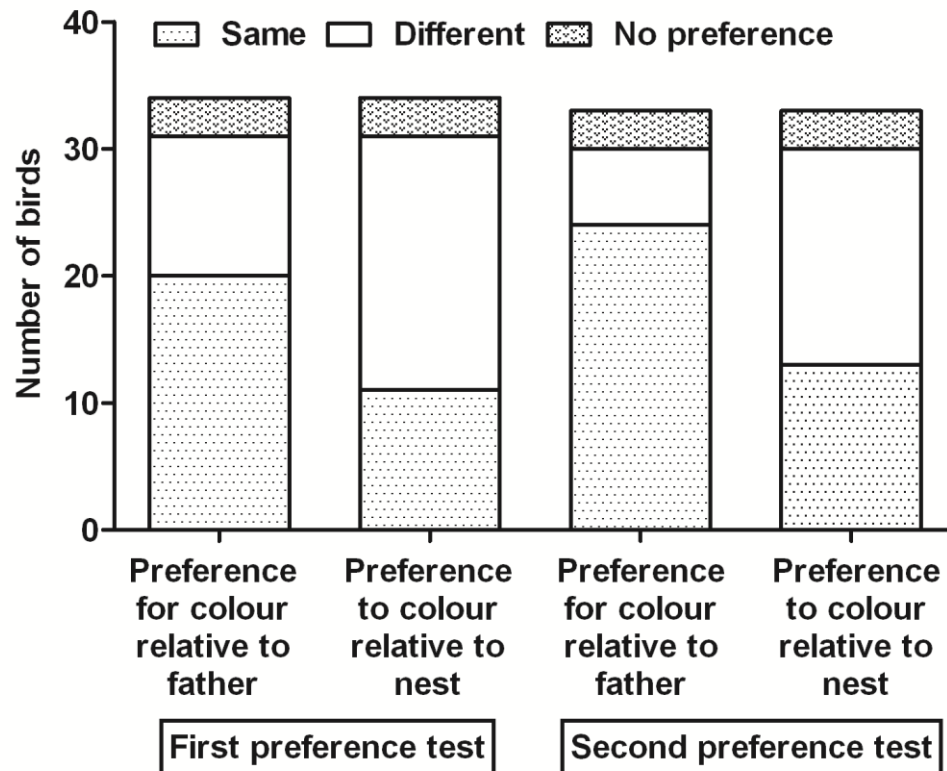


Figure 3: The colour preferences for nest material of all the builder offspring. The data are shown as relative to the colour preferences of their fathers and relative to the colour of the nest from which they fledged. Birds in the first preference test include both male and female offspring (only one builder per pair; $n = 34$). In the second preference test only males built the nest ($n = 33$).

Second 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 3). 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 3).

During this second preference test the females of eight pairs did some building. However, as in all of these cases the females made fewer than seven choices, 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 made a choice for blue, then pecked at yellow, and the male then made 10 choices for yellow.

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).

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

*Nest measures**Parents' nests at laying and fledging*

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 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 or weight was correlated with the number of eggs laid or with the number of chicks fledged from that nest (all p values > 0.1).

Table 2: Comparison of the parents' first nest at laying and at fledging through Pearson correlations and paired t-tests using equivalent measures from both nests. P-values are shown in parentheses.

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

Parents' first and second nests

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).

Table 3: Comparison of the parents' firsts nests built to their second nests built through Pearson correlations and paired t-tests using equivalent measures from both nests. P-values are shown in parentheses.

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

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 $n = 18$, 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 ($r = 0.554$, $n = 18$, $p = 0.017$).

The nests of the offspring

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).

Table 4: Pearson correlation coefficients (with p-values in parentheses) 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)	Parents' first nest at fledging (df = 28)	Parents' second nest (df = 25)
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)

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 80-100%) 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 10 colours a male took to his nest box 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 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 that 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. Despite all nests being built in nest boxes of equal dimensions, 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), but again, there are no substantial quantitative data to help us address this question.

In the current experiment, all zebra finches built in nest boxes of equal dimensions. Although these boxes did not seem to constrain the structure of nests (given the large variability we found in size both within and between pairs), it would be informative to know whether the same amount of variability exists when building under more natural conditions (e.g. in a tree or shrub).

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. One possibility is that, by re-pairing females multiple times in our experiment (as frequently as twice over three successive days), and allowing them to encounter males in a courting and nest building context, but not have the opportunity to lay eggs, we artificially increased their oestrogen levels. This may have affected their natural nest building behaviour, as manipulations of oestrogen in female zebra finches will cause them to build nests (Rochester *et al.* 2008). 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.

Chapter 5: Social learning in nest building?

Introduction

Social learning, where the behaviour of one animal is influenced by observation of, or interaction with, another individual (often, but not always, a conspecific) or its products (Heyes 1994), is used by birds in many contexts. These include methods of food extraction (e.g. pigeons *Columba livia*; Palameta and Lefebvre 1985), mate choice (e.g. black grouse *Tetrao tetrix*; Höglund *et al.* 1995, Japanese quail *Coturnix coturnix japonica*; White and Galef Jr 2004, zebra finches *Taeniopygia guttata*; Swaddle *et al.* 2005), mobbing of predators (Curio *et al.* 1978, Curio 1988), song learning (Catchpole and Slater 2008) and food preferences (burmese fowl *Gallus gallus*; McQuoid and Galef 1992, zebra finches; Coleman and Mellgren 1997, Benskin *et al.* 2002, Katz and Lachlan 2003, reviewed in Lefebvre and Boogert 2010, Shettleworth 2010). However, despite the widespread attention social learning has received, there has been little investigation into the role social learning might play in a key avian behaviour: nest building.

Birds appear to use information from conspecifics for deciding where to nest. For example, collared flycatchers *Ficedula albicollis* were more likely to settle in locations with seemingly higher breeding success (where nestlings had been experimentally added) than in locations where the breeding success was lower (where nestlings had been removed; Doligez *et al.* 2002). This attention to the breeding success of conspecifics has been seen in a range of species, including prothonotary warblers *Protonotaria citrea* (Hoover 2003), cliff swallows *Petrochelidon pyrrhonota* (Brown *et al.* 2000), great cormorants *Phalacrocorax carbo* (Frederiksen and Bregnballe 2001) and Black-legged Kittiwakes *Rissa tridactyla* (Danchin *et al.* 1998). However, while birds appear to pay attention to conspecifics in determining where

to nest, it is not clear whether birds also pay attention to conspecifics when learning how to construct the nest itself.

Given that zebra finches pay attention to the selection of nest sites by conspecifics, it seems plausible that nest builders might also pay attention to their neighbours' choice of nesting materials. Anecdotal descriptions suggest that young male weaverbirds seem to watch (and investigate) nest building by mature birds (Collias and Collias 1984).

Additionally, blue tits may attend to choices of nest material made by conspecifics, as birds tend to have more similar plant choices to their neighbours than non-neighbours, that could not be explained by patterns of plant availability (Mennerat *et al.* 2009c).

As a social species, zebra finches may have ample opportunity to observe other individuals both collect nest materials and build their nests. Although the distance between nests varies between colonies, in some wild colonies multiple zebra finch pairs may build in the same bush, separated by only about two metres, or share roosting nests at night (Zann 1996), which would provide an opportunity for observing and copying aspects of another's nest. Zebra finches will also attend to social information in other contexts. For example, female zebra finches copy male food choices, and both male and female zebra finches copy red-ringed (dominant) over green-ringed (subordinate) males and familiar over unfamiliar males in their food choices (Benskin *et al.* 2002, Katz and Lachlan 2003). Zebra finches also learn their songs from their fathers or other familiar males (Catchpole and Slater 2008), copy conspecifics' mate choices (Swaddle *et al.* 2005), and can even influence each other's exploratory behaviour (Schuett and Dall 2009).

Given that zebra finches use social information in many social contexts, and since multiple avian species are affected by social cues when deciding where to nest, here we addressed whether the actual construction of the nest itself was affected by social learning. Specifically, we investigated whether nest-building zebra finches copied the colour of nest

material used by neighbouring individuals when building a nest of their own. In our first experiment, ‘observer’ males chose between two available colours of material, before they observed ‘demonstrator’ males building with the colour of material they had preferred least. The observer pair were then presented with both colours of material for building to determine whether their colour preference had changed as a result of observing their building neighbour. In the second experiment we tested whether observer males would copy demonstrators building with a particular colour when the nest material was novel to the observers. We also addressed whether these same birds would copy food choices from each other by allowing observer males to choose between one of two food colours before observing a demonstrator pair eating food of the colour they did not choose. This allowed us to have a within-subject comparison of social learning in nesting and feeding contexts, so we could ascertain whether the tendency to learn from others depended on the individual. We expected that zebra finches that did copy food and nest material preferences from a demonstrator pair would preferentially choose the food or nest material of the colour eaten, or built with, by the demonstrators when feeding or nesting themselves. However, the amount of experience an individual has can also affect the tendency to copy other individuals (Boyd and Richerson 1985, Kendal *et al.* 2005). When an individual lacks their own experience with the stimuli in question, social information can help avoid situations such as encountering potentially poisonous foods (e.g. Mason and Reidinger 1982, Mason and Reidinger 1983, Johnston *et al.* 1998). Thus we would predict that if having prior experience affects the tendency to copy in nest building and feeding contexts in zebra finches, then individuals in the second experiment (those not given their own experience of the nest material or food colours) should copy demonstrators to a greater extent than did the individuals in the first experiment.

Experiment 1

Methods

Subjects

The subjects were 24 male and 24 female zebra finches. All birds had previously built one or two nests out of blue or yellow nesting material, but they had not encountered the colours of material used in the current experiment (green and brown). All birds were between five and 14 months of age (zebra finches are sexually mature by three months: Zann 1996) and had been bred in captivity at the University of St Andrews, UK. We kept the birds on a 14:10 light:dark cycle at a temperature of 19-22°C with humidity levels of 50-70% and gave them *ad libitum* access to water provided in a feeder fitted externally to the cage. We provided food (mixed seeds) *ad libitum* outside testing periods (detailed below). We used food colouring (Supercook Ltd., Leeds, UK) to dye all nest material and food. To do this, we immersed the food or nest material in food colouring for around one minute, and then spread it on paper towel for at least 24 hours to dry prior to use.

Experimental protocol

We paired birds at the end of February 2012, and started testing nest material and food preferences a week after this. We housed pairs in wooden cages sized 44 × 30 × 39 cm (width × length × height). The cages were designed such that two cages were next to each other, separated by a wooden divider, which could be removed and replaced with a divider made from chicken wire, allowing the pairs of birds to see each and interact with each other. In both sections there was a wooden nest box in the centre of the back wall of the cage and a food bowl on the floor of the cage. One of the pairs was the ‘demonstrator’ pair and the other was the ‘observer’ pair (12 ‘demonstrator’ pairs matched with 12 ‘observer’ pairs in total). Of

these 12 demonstrator-observer pairs, half were ‘experimental’ and half were ‘control’ pairs. Experimental pairs received demonstrations of nest building and feeding with particular colours, whereas the control pairs were exposed to another pair for the same amount of time, but did not see any building or feeding demonstrations. We tested six pairs for their food preferences first (three experimental and three control) and six pairs for their nest material preferences first.

First nest material preference test

To determine a male’s initial preferences for the two colours of nest material (green and brown), we presented all observer pairs with a pile of green and a pile of brown nesting material (3g of each) placed on the cage floor with one colour on the far left and the other on the far right (alternated across pairs). This took place with the opaque wooden dividers in place, so they could not see the demonstrator pair. We filmed the pairs until the male had made at least 10 ‘choices’ for material. Each ‘choice’ was defined as the male taking one or a few pieces of material to the nest box in a single visit, and we used the first 10 choices a male made to assess his ‘preference’ for a particular colour. We defined a preference for a particular nest material colour as when the male made at least 8 choices for one colour of material. These tests were conducted throughout daylight hours, as in our laboratory, at least, males will build at all times of the day.

First food preference test

At approximately 10:00 am (to within 20 minutes) on the day of testing, we removed all food from the observer pair. One hour later we presented this pair with seed in two transparent plastic food bowls. One bowl contained 10g of seed dyed with red food colouring and the other contained 10g of seed dyed with blue food colouring. The birds had never

encountered these colours of food before, and although they had encountered blue nest material before, a previous study showed no relationship between food and nest material colour preferences (Chapter 3). We placed the food bowls on the floor of the cage next to the front wall, either to the left or to the right of the cage door (Figure 1(A)). The side on which a bowl of food of a particular colour was placed was alternated between cages. We filmed the pairs for three hours and all pecks by both the male and female at the two colours of food were recorded during this time, as this has been found to correlate with time spent feeding and volume of seed eaten (Katz and Lachlan 2003).

Feeding and Nesting demonstrations

Once the initial food and nest material preferences of the 12 observer pairs had been determined, we carried out nest building and feeding demonstrations. Half the birds received a food demonstration before a nest demonstration, and half received a nest demonstration before a food demonstration (each separated by at least 24 hours). We started all demonstrations of feeding and nesting at approximately 11:00am (to within 20 minutes). One hour prior to this, we replaced the opaque wooden divider with one made of chicken wire, that allowed the birds to see the other pair, and in the case of the feeding demonstrations, we removed all food from the demonstrators at this time.

For the food demonstration, six pairs had visual contact with a demonstrator pair that fed from food of a particular colour, and six pairs (the control group) had visual contact with a pair without food. We exposed experimental and control pairs each to a pair of birds at the same time and for the same amount of time. The colour of food eaten by the demonstrators was always the observer pair's least preferred colour (red in all cases). At the start of the demonstration, we gave the demonstrator pair two food bowls, placed at equal distance to the observer pair (with 10g of each blue and red dyed seed as in the first preference test; Figure

1(B)). Rather than train the demonstrators to eat red food rather than blue food, we placed two bowls of food (one red and one blue) into the demonstrators' cage but only the red food was accessible. To render the blue food inaccessible, we placed a lid on the clear plastic bowl containing the blue food and inverted it, allowing the food to be seen, but not accessible. We removed the food from the observer pair at the start of the three-hour demonstration period, and replaced it immediately afterwards. We also removed the food from the control observer pairs (that had visual contact with another pair but no demonstration) for the three-hour demonstration period.

We used the same protocol for nest-building demonstrations, by providing six pairs with visual contact with pairs that had access to building material and providing six control pairs with visual contact with pairs without building material. Before the demonstration, we gave all pairs material of the male's least preferred colour (as determined by the preference test) to ensure they would build, and then removed it on the day prior to the demonstration. We used the same experimental and control pairs as were used in the food trials. We always used the observer pair's least preferred colour as the colour of material to be used by the demonstrators (brown in five cases and green in one case). For the nest-building demonstrations, we provided the demonstrator pair with 3g of nesting material of each of the two colours (as in the first preference test). We arranged the two colours of nest material so they could both be seen by the observer pair but only the colour to be used could be seen and accessed by the demonstrator pair. This was achieved by placing the inaccessible material in a cardboard box with the side facing the observer cage made of chicken wire, allowing only this pair to see the material. We placed the material that the demonstrator pair could access on top of the box, so that the observer pair could see both colours of material from a similar distance.

Second preference test

After the three-hour food and nest demonstrations, we replaced the opaque dividers and returned food to all the birds' cages. Immediately after this, the pair that had just been allowed to observe a demonstration of feeding or nest building, and the control pair that had observed another pair of birds at the same time and for the same amount of time but without a demonstration were both tested for their colour preference for food or nest material (of the demonstration they had just received). These preference tests were conducted in the same way as the first preference tests (Figure 1(C)).

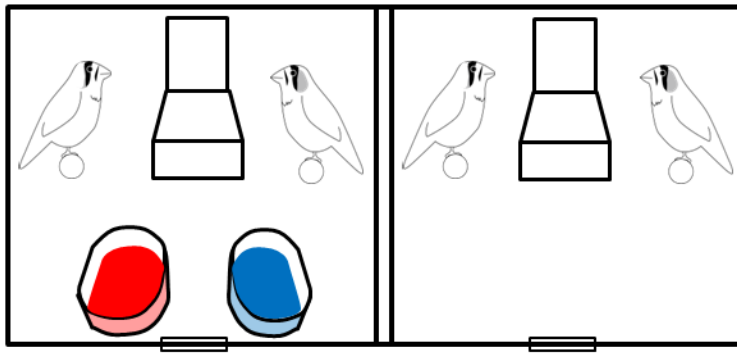
Behavioural analysis

We analysed the video-recorded behaviours using software for behavioural analysis (Noldus Observer, TrackSys Ltd., UK). For the food demonstrations we recorded the instances in which the demonstrator pair pecked at the demonstration colour and at the non-demonstration colour bowl (even though they could not access the food). We also recorded whether the observer pair might have seen the feeding behaviour of the demonstrator pair. We estimated this by recording the times at which the observer pair were in the half of their cage closest to the demonstrator pair and had their bodies facing towards their neighbours (although their heads could be either facing towards or sideways-on to the feeding birds). We then calculated the total number of pecks by the demonstrators that occurred during these time periods.

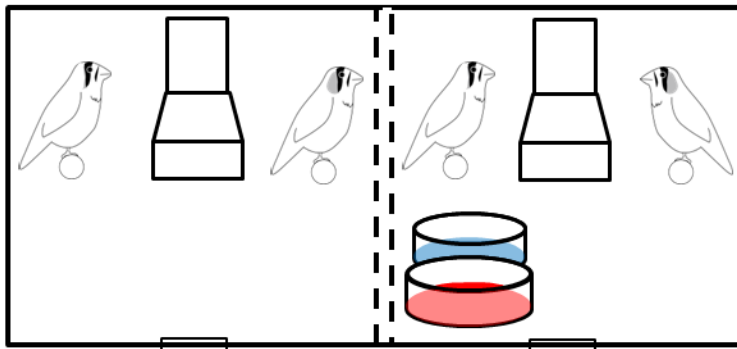
Statistical analysis

All of the statistical analyses were carried out either using R version 2.15.0 or IBM SPSS Statistics 19. We checked that the data in our models met parametric test assumptions prior to carrying out parametric analyses.

(A) First preference test (food)



(B) Demonstration (food)



(C) Second preference test (food)

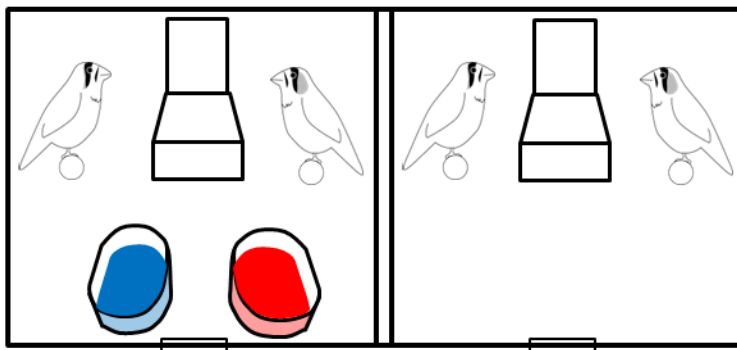


Figure 1: The experimental set-up for the food preference tests and demonstration. (A) The observer pair were tested for their preference for one of two colours of food. (B) The wooden divider was replaced with a chicken wire one, allowing the observer pair to see the demonstrator pair feed on one food colour for three hours. The red food was accessible to the demonstrator pair, and the blue food, whilst being seen by both pairs, was not accessible to the demonstrator pair. (C) The wooden divider was then replaced, and the observer pair were re-tested for their preference. The same set-up was used for the nest material testing and demonstration, except that the material was placed in a different location (see methods).

Results

Nest preference tests and demonstrations

In the initial preference test, five of the experimental observer males preferred green and one preferred brown. Of the six control observer males, four preferred green, one preferred brown, and one did not build.

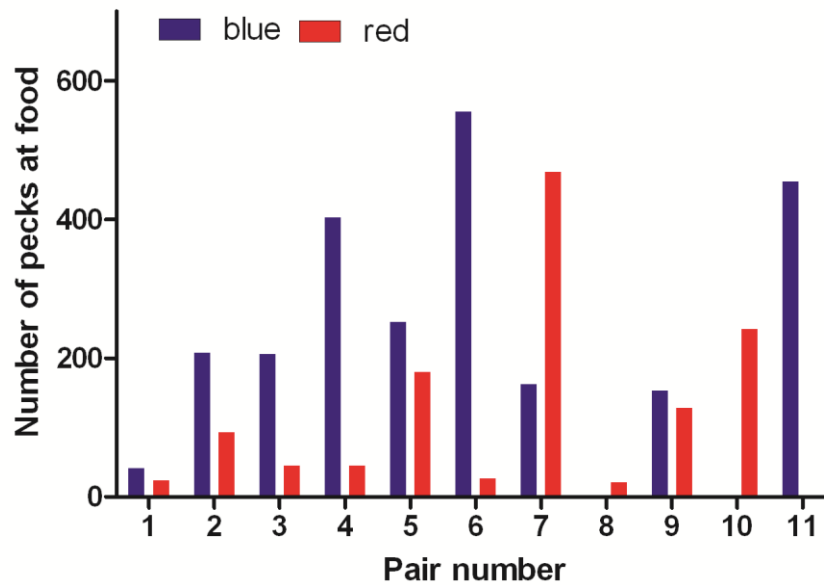
Prior to the start of the demonstrations, the six pairs of demonstrator birds all built readily when provided with material (five with brown and one with green). However, once the opaque dividers were replaced with transparent ones and the demonstration trial was started, none of the demonstrator birds built with or approached the material on the ground for the entirety of the three-hour demonstration period. Once the opaque dividers were replaced at the end of the demonstration, five of six male demonstrators then began building within three hours and the remaining male began building the following day.

Food preference tests and demonstrations

In the initial preference test, eight of the observer males pecked more times at the blue food than the red, two pecked more at the red than at the blue and one pecked equally at both (Figure 2a). Seven of the observer females pecked more frequently at the blue food than at the red, three pecked more at red than blue and one had no preference (Figure 2b). In one pair neither the male nor female ate during the testing period (this was the same pair that was the only pair not to build during their initial preference test). Males and females within pairs did not necessarily prefer the same colour: in six pairs, both individuals pecked more at blue than at red and in five pairs, their preferences differed. Females and males were equally likely to approach and peck at the food first: in six pairs, the female pecked first and in five, the male

pecked first. Males and females also did not differ in their total number of pecks at food (paired t -test: $t_{10} = -1.371$, $p = 0.200$).

2a



2b

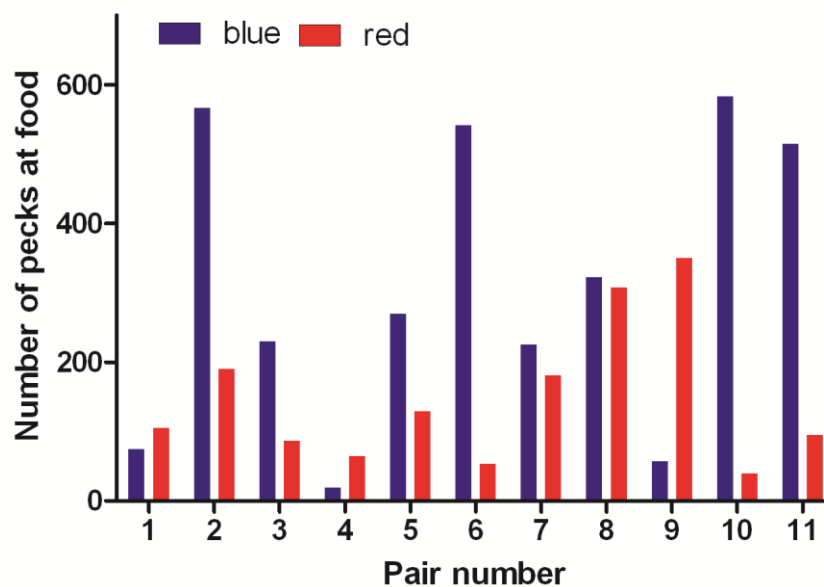


Figure 2: The preferences of (a) males and (b) females for the red or blue food, measured as the number of pecks at each type.

During the demonstrations, in four of the six demonstrator pairs both males and females pecked at the demonstration food, in one pair only the female pecked and in another pair only the male pecked (Figure 3a). The male observers only faced (and therefore had the possibility of seeing) females when they were pecking at the food in three cases, and males when they were pecking at the food in five cases, but in four of these cases it was for fewer than 10 pecks (Figure 3b). The female observers generally faced the demonstrators and so had the opportunity to see more pecks at the demonstration food than their male partners: five of six females potentially saw demonstrator females pecking and five of six females potentially saw demonstrator males pecking (Figure 3c).

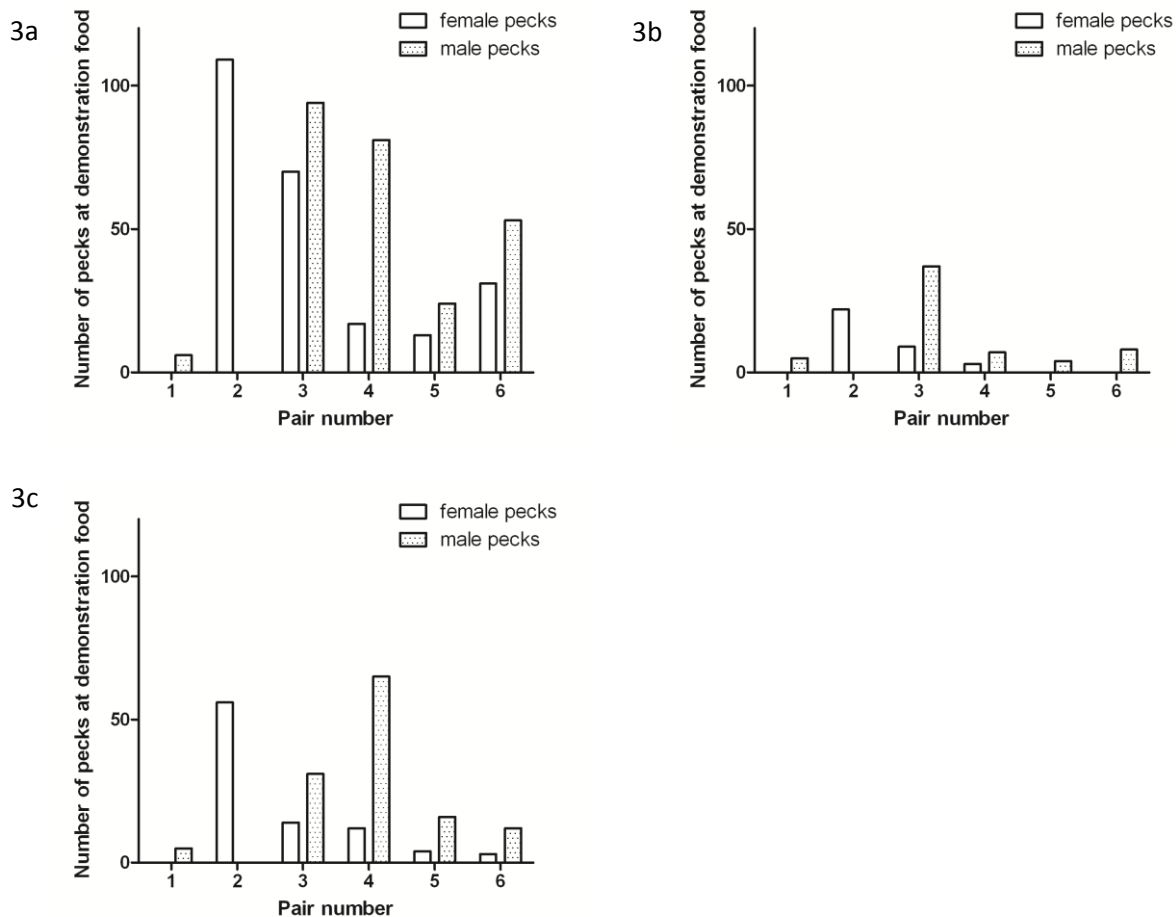


Figure 3: (a) The number of pecks by paired males and females at the demonstration food during the demonstration; (b) of these pecks, which were potentially seen by the observer males and (c) by the observer females.

To determine whether males and females chose more of the red demonstrated food after observing another pair feeding on it, we carried out a general linear mixed model, with the response variable being the difference in the proportion of the total number of pecks at red before and after the demonstration (measured in the two preference tests). We included the fixed factors: sex (male/ female) and treatment (experimental/ control), and pair number (1-11) as a random factor. Overall, pairs that had the opportunity to observe a pair feeding on food of one colour did not then change their preference for that colour (GLMM: treatment: $F_{1,9} = 0.00962$, $p = 0.924$; Figure 4). This was the same for both males and females (GLMM: sex: $F_{1,10} = 0.952$, $p = 0.352$; Figure 4). However, the experimental observers were often not facing the demonstrator birds when they were feeding. Therefore, we analysed only those data in which the observers were facing the demonstrators. Using the difference in the proportion of the total number of pecks at red before and after the demonstration as the response variable, we carried out general linear mixed models with the explanatory variables sex (male/ female), the random factor pair number, and number of pecks seen by males, females and males and females, in three different models respectively. Birds did not increase their preference for red to a greater degree when they had seen more pecks at red by the male demonstrator (GLMM: $F_{1,4} = 1.996$, $p = 0.231$), and this held true for both male and female observers (GLMM: $F_{1,4} = 0.0000328$, $p = 0.996$). Birds also did not increase their preference for red more when they had seen more pecks at red by the female demonstrator (GLMM: $F_{1,4} = 0.037$, $p = 0.856$), and this held true for both male and female observers (GLMM: $F_{1,4} = 0.216$, $p = 0.666$). Finally, birds did not increase their preference for red more when they had seen more pecks at red by both the male and female demonstrators (GLMM: $F_{1,4} = 0.892$, $p = 0.398$), and this held true for both male and female observers (GLMM: $F_{1,4} = 0.00109$, $p = 0.975$).

Furthermore, after having the opportunity to observe the demonstrator pair eating red food, this was not the first colour the observer pair pecked at in the majority of cases: observer males pecked at red food before blue in three of six cases and observer females pecked at red first in one of six cases. Control males and females that did not see a demonstration each visited red first in one of six cases.

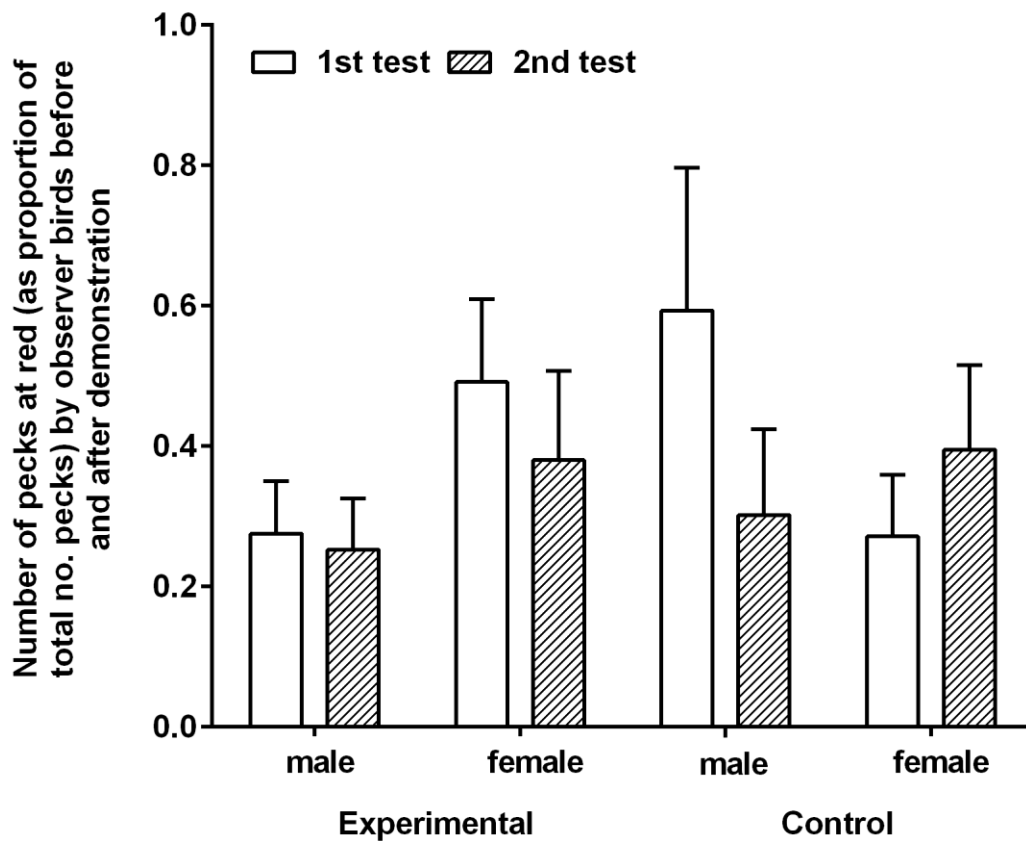


Figure 4: The proportion of the demonstrated colour (red) chosen by observer males and females before and after the demonstration for the experimental and control groups.

Of all experimental and control observer pairs, the females and males were equally likely to approach and peck at the food first (in seven cases the female pecked first, and in

four cases the male pecked first). Males and females within pairs did not tend to peck at the same colour as each other first (seven pairs did and four pairs did not).

During the demonstration, the demonstrator females generally pecked at the food before their male partner (in five of six cases), although male and female demonstrators did not differ in their absolute number of pecks to the food (paired t -test: $t_5 = -0.126$, $p = 0.905$). In the second preference test, the male and female observer birds (experimental and control) did not differ in their propensity to approach and peck at the food first (females pecked first in seven pairs, and males pecked first in four pairs). However, overall, females pecked more frequently at the food than did the males (paired t -test: $t_{10} = -2.879$, $p = 0.016$).

Discussion

Our attempt to examine the role of social learning in nest building was thwarted by an unexpected effect of social interaction: when in close visual proximity to neighbours, nest-building males stopped building. When the visual contact was cut, the builders soon recommenced building although one male did not begin again until the following day.

In contrast to nest building, paired zebra finches readily fed when in visual contact with another pair of birds. However, despite this, the zebra finches that had the opportunity to observe a feeding neighbouring pair feeding on food of a particular colour did not then prefer to peck at food of that colour (red). The observer pairs did not approach or peck at the red-coloured food first and they did not peck more in total at the red food than at the blue food. This result contrasts with evidence that female zebra finches will eat colour-dyed foods and feed from feeders of particular colours from which they have seen males feeding (Benskin *et al.* 2002, Katz and Lachlan 2003). It also contrasts with evidence that female and male zebra finches copy other males when the male is dominant or when he is familiar (Benskin *et al.*

2002) as even within pairs in our experiment males and female observers did not share preferences, and this male would have been the most familiar male to the female. One potentially significant difference between the study by Katz & Lachlan (2003) and our study was that we allowed our birds to experience the food themselves before observing others feeding. This may inhibit social learning, as the individual's own experience may be more important in determining its decisions than information obtained through social learning. This effect has been observed in other species: rooks (*Corvus frugilegus*) will copy a conspecific's food choice when the food is unfamiliar to them but not when the food is familiar (Dally *et al.* 2008). If our birds did not copy the demonstrator birds' choices because they had had their own experience of the food, birds without this individual experience might be more inclined to copy the demonstrator birds' choices. In order to test this, we conducted a second experiment where the observer pairs had not seen the two colours of food prior to having the opportunity to see the demonstrator pair eating food of one colour.

Experiment 2

This experiment was similar to Experiment 1, with two key differences. Firstly, we did not test observer pairs for their preferences for nest material or food colour prior to their observation of other birds nesting or feeding. Thus their experience of the food and material colour was restricted to seeing the other pair interact with it. Secondly, to maximise the chance that demonstrators would build during the demonstration, observers had visual access to the 'nest-building' demonstrators for up to five days rather than three hours.

Methods

Subjects

All the birds from Experiment 1 were separated after the second preference tests and kept in stock cages for a month. After this time we re-paired them in the same pairs (except the one male, whose mate had died, was given a new female, and the pair that had not built or fed in the first experiment were not used in the second experiment). The experimental set-up was the same as in Experiment 1. The pairs that had been observers and the pairs that had been demonstrators were again observers and demonstrators, respectively. We carried out the food demonstrations and preference tests first over a three-day period, and then commenced the nest demonstration and preference tests a week following this.

Experimental protocol

Food demonstrations and preference tests

Following the procedure as described for Experiment 1, we deprived the demonstrator birds of food and provided them with visual contact with the observer pair one hour prior to the demonstration. After this hour we gave the 11 demonstrator pairs one of two colours of food to eat in front of the observer pairs, which neither pair had experienced before (green, $n = 6$; brown, $n = 5$). After the three-hour demonstration, we presented the observer pair with both colours of food and tested them for their preference (Figure 1b and 1c).

Nest demonstrations and preference tests

The 11 demonstrator pairs were provided with one of two colours of nest material: purple and copper. We made purple by mixing red and blue food colouring, and copper by mixing red, yellow and green food colouring. After one hour of being in visual contact with

the observer pair, the demonstrators were provided with one of the two colours (purple: $n = 6$; copper: $n = 5$). The demonstrators were then checked once every two hours for up to five days for nest-building activity. When we saw that the nest material had been added to the box (in $n = 7$ cases), the opaque divider was replaced and the observer pair immediately tested for their nest material colour preference.

Results

Nest demonstrations and preference tests

In this experiment, seven of the 11 demonstrator males built nests. Of these males, one built in less than a day, two built in one day, three built in two days, and one male took three days to start building. However, once building had started in all cases it took less than two hours to add all of the material to the nest box. Of the seven observer pairs exposed to building by a demonstrator male, three preferred the demonstrator's building colour (in all cases purple) and four did not. Of the four males that did not prefer the colour used by the demonstrator male, three males had no preference and one preferred purple.

Food demonstrations and preference tests

Two demonstrator pairs did not eat any of the coloured food during the demonstration period, and so they and their accompanying observer pair were removed from the following analysis. Of the nine remaining demonstrating pairs, four ate brown food and five ate green food. However, this demonstration appears to have had little impact on the food colour preference of the observers, as the observers did not peck more at the colour they had the opportunity to observe being eaten than at food of the other colour (paired t -test: male: $t_8 = 0.385$, $p = 0.710$; female: $t_8 = 0.584$, $p = 0.576$; Figure 5).

We then addressed whether the observer pair's preference for the colour of food their demonstrator ate was related to the number of pecks the observers potentially observed. In this analysis we included the two cases where demonstrators did not feed at all. Birds did not choose a higher proportion of the demonstration colour when they had seen more pecks at that colour by the male demonstrator (GLMM: $F_{1,9} = 0.185$, $p = 0.677$), and this held true for both male and female observers (GLMM: $F_{1,9} = 0.310$, $p = 0.591$; Figures 6,7). Birds also did not choose a higher proportion of the demonstration colour when they had seen more pecks at that colour by the female demonstrator (GLMM: $F_{1,9} = 2.148$, $p = 0.177$), and this held true for both male and female observers (GLMM: $F_{1,9} = 0.520$, $p = 0.489$; Figures 6,7). Finally, birds did not choose a higher proportion of the demonstration colour when they had seen more pecks at that colour by both the male and female demonstrators (GLMM: $F_{1,9} = 0.989$, $p = 0.346$), and this held true for both male and female observers (GLMM: $F_{1,9} = 0.516$, $p = 0.491$; Figures 6,7).

In the demonstrations, neither demonstrator was more likely to peck at the food first (in five pairs the males pecked first, and in four pairs the females did). The male and female demonstrators also did not differ in their number of pecks at the demonstration food (paired t -test: $t_{10} = 0.655$, $p = 0.527$). However, in the preference tests, the observer females tended to approach and peck at the food first more often than did the males (in 9 of 11 cases). There was also a tendency for females to peck more frequently at the food than did the males, as did the observers in Experiment 1 (paired t -test: $t_{10} = -2.083$, $p = 0.064$). The colour that individuals within an observer pair pecked at first did not tend to be the same (in six cases they pecked the same colour and in five cases they did not).

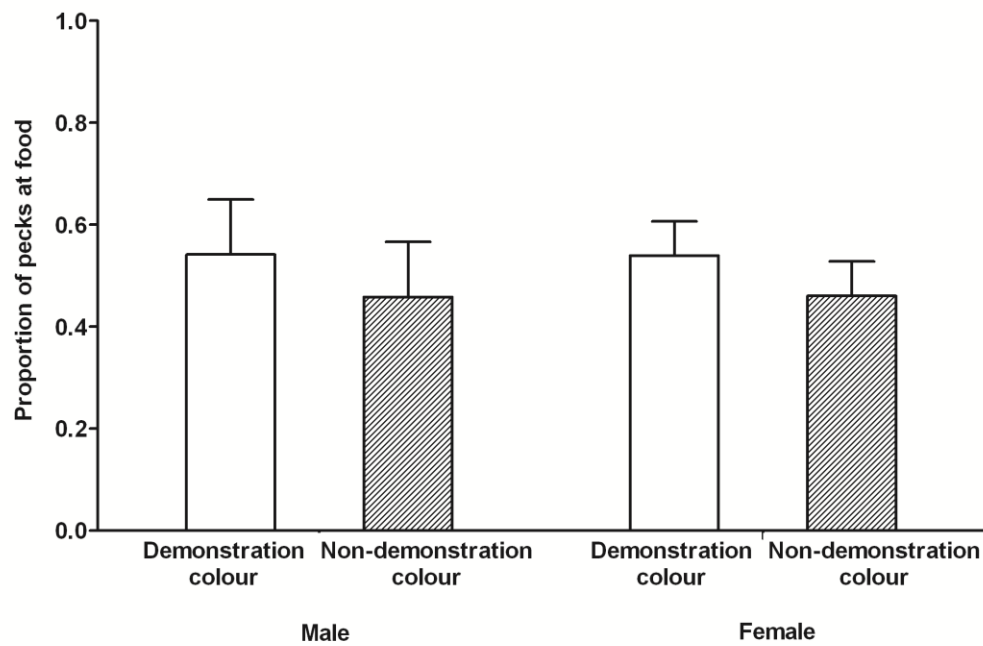


Figure 5: The proportion of the demonstrated and non-demonstrated colours chosen by observer males and females in their preference test.

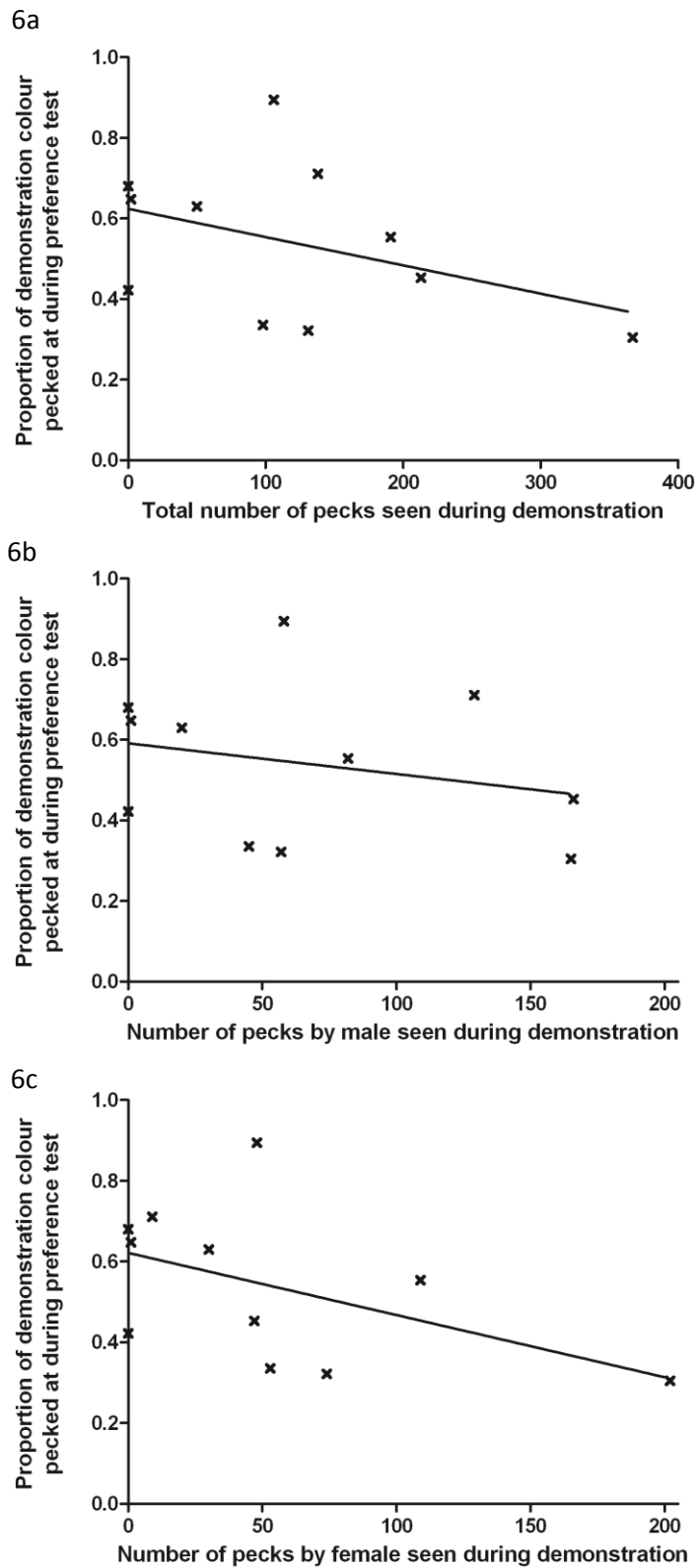


Figure 6: The relationship between the proportion of the demonstration colour pecked at during the preference test by the observer female and the total number of pecks potentially seen of that colour during the demonstration by (a) the demonstrator male and female combined, (b) the demonstrator male and (c) the demonstrator female.

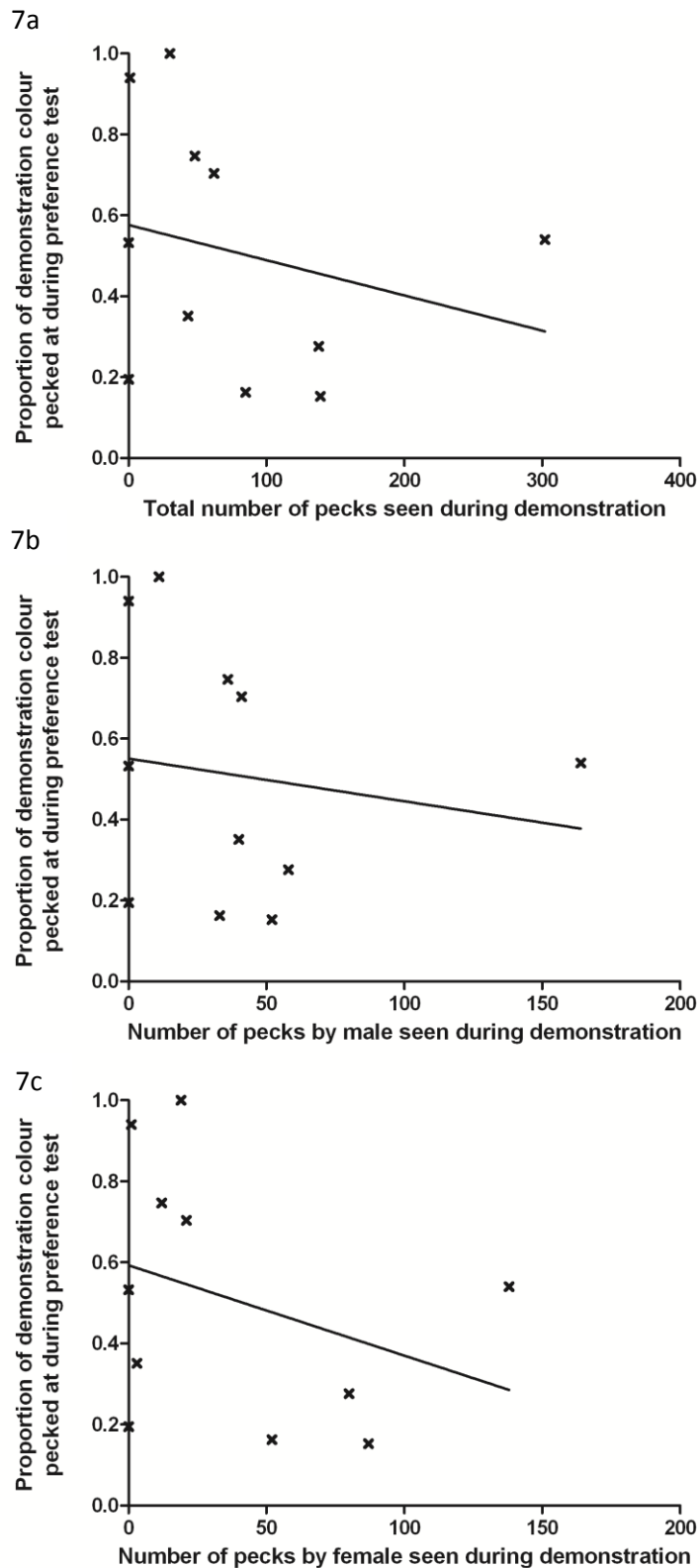


Figure 7: The relationship between the proportion of the demonstration colour pecked at during the preference test by the observer male and the total number of pecks potentially seen of that colour during the demonstration by (a) the demonstrator male and female combined, (b) the demonstrator male and (c) the demonstrator female.

Discussion

We found no evidence that birds copied either the colour of food eaten by demonstrators or the colour of nest material used for building by demonstrators, even though these colours were new to them. This result implies that the lack of copying of food colours of the birds in Experiment 1 was not due to their individual experience overriding any tendency to attend to the behaviour of conspecifics, as when the birds in the second experiment were denied their own experience and so only saw another pair's experience with the food, they still did not copy them. Instead, it seems that birds did either not attend to, or chose not to copy, the information they could have gained from the demonstrator birds.

General Discussion

We found no evidence that the zebra finches in this study used the information available to them via the behaviour of demonstrator birds in either a nest-building context or in a feeding context. In the first experiment, however, we found an unexpected effect of the presence of conspecifics, not on the observers but on the demonstrators, who stopped building once the opaque divider between the cages was replaced with a divider of wire mesh, through which the observers could now be seen. It appears that the demonstrator males were unwilling to build nests in front of the other pair, despite building readily both before and after being in visual contact with those birds. In order to see whether this was a temporary effect on the building behaviour, in the second experiment, the demonstrator birds were given more time to build. This did result in some of them building in anything from less than a day to up to three days. Subsequent to this building by the demonstrators, however, the observers did not then copy the demonstrator's nest material colour when building themselves. Although the impact of visual proximity appeared confined to the nesting

context, as the majority of demonstrator birds ate the coloured experimental food once the opaque divider was replaced with the wire mesh divider and both pairs could see each other, the observers also did not copy the food choices of their demonstrators.

Despite being a social species, zebra finch males in this study were unwilling to build with another pair in visual contact and in close proximity. There are a number of possible explanations for this: building may have been postponed because the demonstrators engaged in social behaviours with the neighbouring pair (for example, we often observed that demonstrator males sang to observer females). The chosen nesting site (the nest box provided) may also have become less favourable to the demonstrator pair now that another pair was in such close proximity. In the wild, zebra finches build breeding and roosting nests, the former of which are strongly defended from other pairs (Zann 1996). The distance between wild zebra finch nests varies between colonies, in some colonies multiple pairs build in a single tree, separated from each other by around two metres, whereas in other cases pairs prefer to nest in their own bush or tree. In the current study, the nest boxes of the two pairs were around half a metre from each other, and it is plausible that pairs would have been more willing to build if they had not been in such close proximity. It is also possible that, in the wild, zebra finch pairs may be more willing to build in close proximity to particular birds than in captivity. This may be the case if wild zebra finches choose which pairs to be in close proximity to (for example, more closely related individuals). However, under experimental conditions they are given no choice as to which pair they are closest to, and it is possible that this lack of choice disrupts their natural behaviour. In previous experiments, the nest-building birds we used were always in the same room, and were in visual contact from across the room, however this was at a much greater distance (around four metres) than the distance imposed on the neighbouring birds in the current experiment.

When the demonstrators were given more time to build in the second experiment, seven of the 11 pairs did start to build. Some birds took a day or less, whereas others took up to three days (we allowed them up to five). Birds may have built in Experiment 2 when they did not in the first experiment because of the additional time we gave them, increasing the probability that we would see building, or because this time allowed them to become habituated to the neighbouring pair, such that the demonstrator male learned that he could not gain access to the observer female and also that he did not need to defend his own female from the observer male. However, in the cases where the demonstrator pairs did build in front of their neighbouring observers, the observers did not copy the colour of the demonstrator's nest material when building themselves. Thus it seems that preference for a particular nest material colour (as observed in Chapters 2-4) is not due to adult males having observed other individuals build with material of that colour. This would seem to indicate that zebra finches may utilise social information when it comes to nest site choices but may not copy conspecifics when it comes to the structural aspects of building a nest, at least with regard to what nest material to use. However, it is possible that other factors, such as the identity of the observer, feed into this decision that we did not address in this study. For example, ravens (also a social species) spent more time observing demonstrators to whom they were closely affiliated than to individuals that they were not closely affiliated (Scheid *et al.* 2007). Zebra finches also preferentially copied particular individuals over others: females copied males over females and males and females copied dominant (red-banded) over subordinate (green-banded) and familiar over unfamiliar males (Benskin *et al.* 2002, Katz & Lachlan 2003). Therefore, it is possible that in our experiment if the demonstrator were dominant to the observer, the observer would be more inclined to copy them (Burley *et al.* 1982, Cuthill *et al.* 1997).

Another reason birds may not have copied conspecifics in our study could be because, given that the birds had already encountered nest material and built themselves, the information from the demonstrator birds was not as useful to them. An experimental situation that could make this information potentially more useful and therefore more likely to be copied could be created either by testing naïve birds that had never built before for their propensity to copy an experienced pair's building material colour, or by manipulating the information the building pair give to the observers. For example, if the observers were to see some pairs build with a particular colour and successfully fledge chicks, while others have poor breeding success, they may be more likely to choose the material associated with higher breeding success, as has been found for nest site choice (e.g. Danchin *et al.* 1998, Brown *et al.* 2000, Frederiksen and Bregnballe 2001, Doligez *et al.* 2002, Hoover 2003, Loukola *et al.* 2012). Thus it may be the case that this species would learn from the nesting behaviour of conspecifics, but just not under the conditions tested here.

In addition to the lack of social learning of nest colours, zebra finches also did not copy the food colour choices of conspecifics. This finding was particularly surprising in the second experiment, given that the birds had not experienced the food colours themselves prior to seeing another pair eat one of the coloured food types. In cases where individuals do not have adequate knowledge themselves (in this case, experience with food of these colours), theory predicts that they should copy (in this case, the food colour; Boyd and Richerson 1985). This has been found in other experimental studies, for example rooks that lack individual knowledge about a food (when it is unfamiliar to them) do copy a conspecific's food choice, but when they are familiar with the food, they do not (Dally *et al.* 2008). This is because when lacking one's own knowledge (such as when encountering novel foods), learning from others can help an individual avoid potentially poisonous food sources. Rats, for example, not only pay attention to other individual's food preferences (Galef and

Wigmore 1983), but can also transmit aversions to food down multiple generations (Galef & Allen 1995). Additionally, zebra finches in previous experiments both copied the colour of feeder used by conspecifics (Benskin *et al.* 2002), and the food colour (using dyed seed as we did in this experiment; Katz & Lachlan 2003). Although the birds in our study had not encountered the colours of food used before, it is possible that their previous experience with a number of different colours of food was sufficient as to override any aversion to novel foods. This lack of neophobia may have meant that birds were less likely to pay attention to the feeding decisions of conspecifics. It may be that if we imposed a cost to novel foods (e.g. by making some distasteful) then birds would use conspecifics' behaviour more to inform their own decisions, as has been recorded for other species.

Due to the apparent lack of copying of the demonstrators in either context, we cannot be sure whether birds simply did not attend to the information available to them from the demonstrators' behaviour or whether they paid attention but then chose not to use that information. We attempted to determine whether copying was correlated with the amount of behaviour the observer pair apparently saw, by addressing whether birds that had their heads directed towards the demonstrators and, therefore, could have seen what those birds were doing, then ate more of that food. This was not the case. This would seem, then, to imply that even in cases where birds were likely to have seen the demonstrators feeding, they still did not use this behaviour to inform their own feeding decisions. However, even in the cases where our birds could have seen a large proportion of the feeding behaviour of the demonstrator birds, they saw much less feeding behaviour (per unit of time) than in the study in which observational learning was found (Katz and Lachlan 2003). In that study, male and female demonstrators pecked between 51 and 355 times during the 30-minute observation period (two 15-minute periods separated by a 30-minute break), whereas in our study most birds pecked under 100 times in the three-hour demonstration and most of this was not when

the observer birds were facing towards the demonstrators. Indeed, the observer pairs faced the demonstrator pair for fewer than 20 pecks in most cases. However, although there were differences in the rates of feeding by the demonstrators between these studies and ours, those authors (Katz and Lachlan 2003) did not record how much of the feeding behaviour was actually seen by the observer birds. Without those data we cannot be sure that it is differences in the feeding behaviour of the demonstrators that explains the lack of copying in our observers.

One hypothesis for why some species learn from conspecifics more readily than others is that this is a reflection of their life history (reviewed in Shettleworth 2010). For example, Australian brush-turkey chicks, *Alectura lathami*, a species that receives no parental care and is independent from hatch, did not learn to copy a robot demonstrator in pecking food from a particular coloured bowl (Göth and Evans 2005). This contrasts with Burmese jungle fowl *Gallus gallus spadiceus* and domestic fowl *Gallus gallus domesticus*, that feed gregariously with their parents as chicks (and thus would have ample opportunity to learn from them), do copy food choices both from other individuals (Johnston *et al.* 1998) and from artificial demonstrators (Suboski and Bartashunas 1984), (McQuoid and Galef 1993). Our findings that zebra finches, also a social species, did not copy conspecifics' nest building or feeding behaviour do not support this hypothesis. However, material choice is only one aspect of nest building behaviour in birds, and we know virtually nothing about whether other aspects of building (such as the physical manipulation of materials) might be affected by social learning, and how this might vary between species differing in their gregariousness.

Chapter 6: Do weaverbirds vary in the knots they tie?

Introduction

How animals know how to construct objects such as tools, webs or nests is little understood. Addressing the cognition involved in these behaviours (how the animal perceives, processes, stores and acts on information from the environment (Shettleworth 2010)) would help us determine how animals construct such objects. However, a cognitive perspective has only been applied to one construction behaviour, the making and use of tools, even though birds' nests are comparatively ubiquitous and apparently biologically similar (Hansell and Ruxton 2008).

One way that constructed objects have been investigated in order to gain an understanding of the cognition involved in their construction has been to measure variability in the object constructed and to determine whether an animal constructs the same thing each time. However, how variable a constructed object is has been interpreted in different ways in different contexts, specifically whether or not the object in question is a tool. For example, crows following a few particular steps to construct highly standardised hooked tools (Hunt 1996) have been described as 'goal-directed' (Hunt and Gray 2004). However, nest-building birds often also follow a particular series of steps to achieve a standardised structure (e.g. village weaverbirds Collias and Collias 1984) and yet this behaviour has generally been considered not to require cognitive abilities (Hansell and Ruxton 2008), such as goal-directedness. Indeed, using the variability of constructed objects (the end-product of behaviour) to infer the variability of the behaviour that went into making them can be problematic, given that similar objects can be constructed using different behavioural patterns (Stuart and Currie 2002). Thus, using variability *per se* to infer cognitive processes is a

limited approach. Instead, in order to better understand the cognition involved in the construction of objects such as tools or nests, it does not seem sufficient just to examine whether there is variability within and between individuals of a species but also to ascertain what factors influence this variability. For example, it would be useful to know what cues the animal is responding to when making its constructed object, as well as knowing both internal factors (such as the animal's previous experience) and external factors (the environmental conditions under which it is building). This may allow us to be able to discern how animals construct the objects they do (be it tools or nests) and compare how this differs across species.

Weaverbirds offer a useful model in which to investigate variability in building behaviour, as the males build several seemingly complex nests across a single breeding season (Walsh *et al.* 2010). Individual male village weavers *Ploceus cucullatus* do not seem to build the same overall structure with each nest built, and Southern masked weavers *P. velatus* build nests that are only weakly repeatable in their structure (Walsh *et al.* 2010). However, the variation in the size of the nests built by these males is not random, as the nests become smaller across the breeding season (Walsh *et al.* 2010), which may reflect tighter weaving as the birds gain experience, as has been found in previous studies with village weavers (Collias and Collias 1984). Moreover, Southern masked weaver males are also variable in a number of aspects of their building behaviour, including their speed of building and how they handle building material (the side of their beak they hold the grass, the side of the nest into which they insert the grass and the part of the nest into which they weave grass; Walsh *et al.* 2011). Why these males vary in their building behaviour is not yet clear.

As a first step to examine how variability in the end product of weaving by Southern masked weavers might come about, we examined the behaviour of the birds at the very first stage of nest construction (the attachment of grass to a branch) to specifically address the

degree to which there was variation within and among males and what other factors might explain it. We focused on the initial attachment of grass made to a branch by male birds, as it was a clearly identifiable feature of the nest and was most readily manipulated. After photographing the initial grass attachments woven on to a branch by a male, we removed the grass while the male was away collecting his second blade of grass. We were interested in determining what form weaving this second blade of grass would take. By repeating this removal procedure several times (both within the same location and at different locations) for several males, we could assess how variable males were in their knotted attachments, and what other factors might help explain any variability there was. The factors we measured included the location on a branch in which a male built, how many nests he had already built that season, and how long the piece of grass was that he used.

Methods

Subjects and removals

We observed and manipulated nest building behaviour in seven individually identified male Southern masked weavers in South-eastern Botswana (Atholl Holme 11-KO, Gaborone) between October and December 2009. We observed a male until he had attached an initial blade of grass to a branch (Figure 1). When he flew off to collect a second blade, we then photographed the initial attachment from multiple angles and removed the blade of grass. We allowed the male to attach the second blade of grass, which we also photographed, again from multiple angles, before removing it once he had left to collect another blade. We followed this procedure until we had removed four consecutive ‘first’ blades of grass at each nest site (hereafter referred to as a ‘removal’) and at three to five nest sites per male (hereafter referred to as a ‘trial’) (mean: 4.14 ± 0.26). We measured the length of the blades

of grass after drying for a day to correct for potential differences in moisture content at the time of collection. We recorded the date each nest was built and the number it was in the sequence of nests built by the male in the season.



Figure 1: A Southern masked weaverbird making his first attachment of grass to a branch.

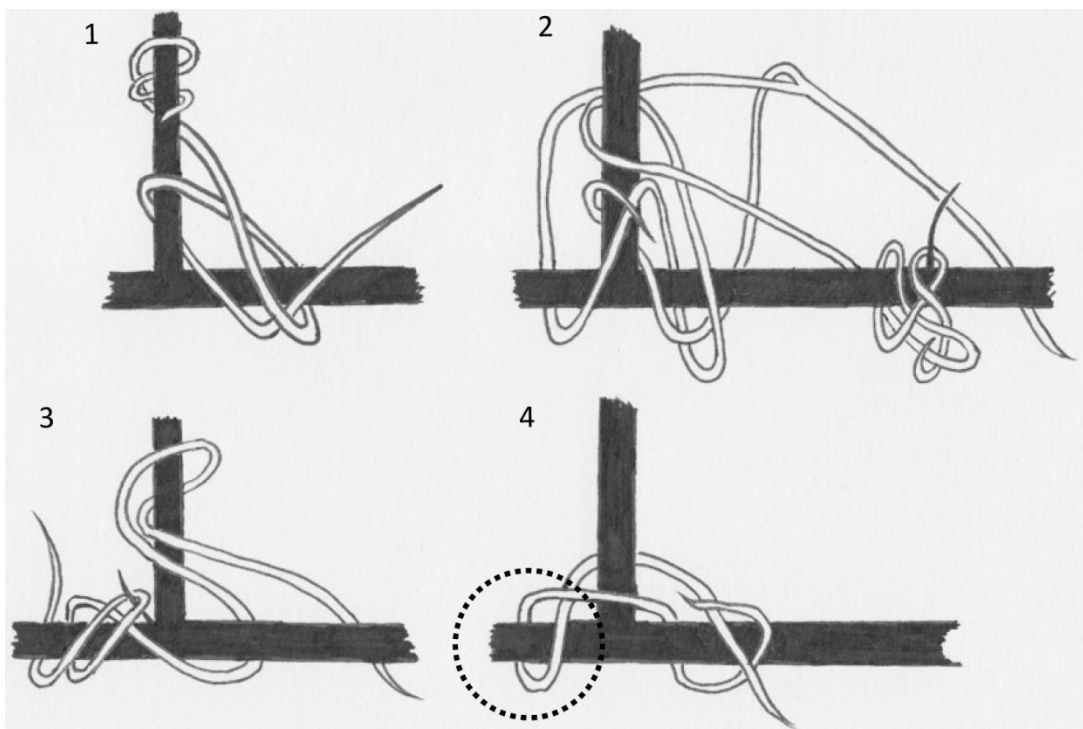


Figure 2: An example of the four subsequent initial attachments of grass made by a single male weaver bird at the same location. A 'loop' is circled in the diagram of the 4th attachment.

Quantification of attachments

We used the multiple photographs to make composite drawings of the grass attachments for measurement (e.g. Figure 2). These diagrams were drawn from the same angle for each of the four attachments in each location to aid comparison. The attachments were then quantified by counting the number of ‘loops’ in each attachment. A ‘loop’ was defined as the ‘simple loop’ stitch originally identified by (Collias and Collias 1962; Figure 2).

Statistical Analyses

We carried out all analyses in R version 2.15.0 (R Development Core Team 2010), using GLMMs with the `lmer()` function in the `lme4` package (Bates and Maechler 2010), which gives z-values and $\Pr(>|z|)$, an estimation of a *p*-value, for each level of testing.

To determine whether attachments changed across the four trials (at different sites), the four removals (within a site), the number of nests built by a male, or with the length of grass he was using, we looked at the number of loops in the attachments made by males. We fitted a generalized linear mixed model with a Poisson distribution with the response being number of loops in the attachment, and the explanatory variables included were the fixed factors: removal number (1, 2, 3 or 4) and trial number (1, 2, 3 or 4); the continuous variables nest number and grass length; and the random factor bird (1-7). We removed the interaction terms as none of them were significant and did not improve the fit of the model. We determined the significance of fixed effects through comparing models with and without the fixed effect in a likelihood-ratio test. ‘Trial number’ and ‘nest number’ were correlated because later trials were generally carried out on later nests built. However, we included both terms in the final model as removing ‘nest number’ from the model did not affect the significance of ‘trial number’.

Results

Males generally used more loops in their attachments as they built more nests (GLMM: z value = 2.030, p = 0.042; Figure 3) and when they used longer pieces of grass (GLMM: z value = 2.148, p = 0.032). Males did not, however, change the number of loops they used in each attachment with increasing number of removals at the same site, either within or across site (GLMM: trial (across-sites): χ^2_3 = 0.544, p = 0.909; removal (within-sites): χ^2_3 = 4.095, p = 0.251). Most of the male-to-male variation in the number of loops produced was due to one male (male 4: Figure 3) who put fewer loops into his attachments as he built more nests. However, when this male was removed from the analysis the results were unchanged but the nest number and grass length variables explain more of the variation in the data.

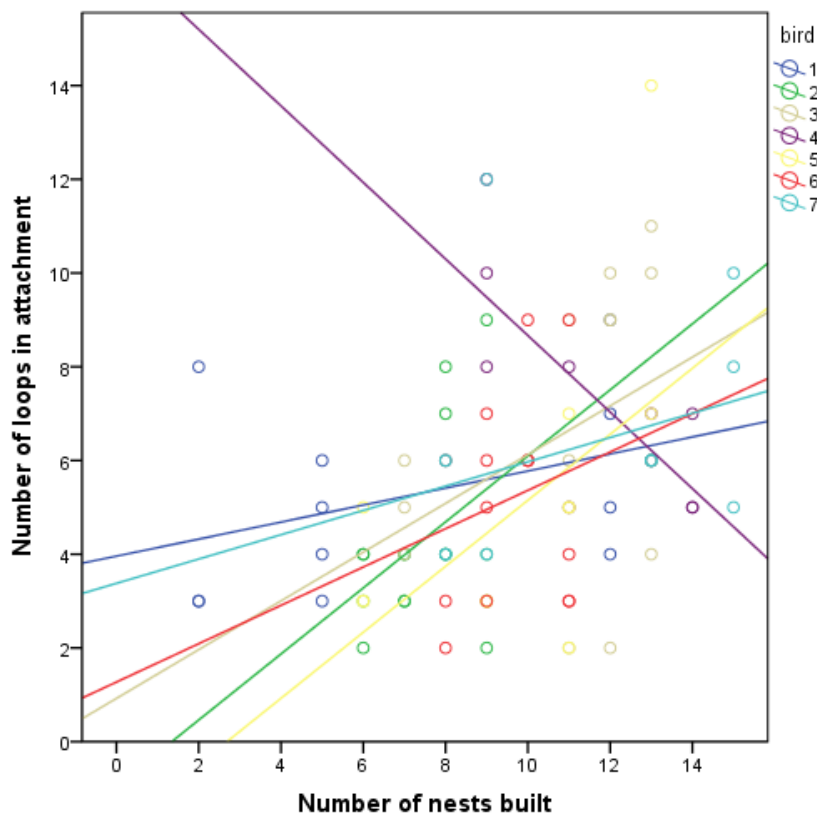


Figure 3: The relationship between the number of loops in a knot and the number of nests built by a male (n = 93 attachments across seven males).

Discussion

Male weaverbirds in our study varied in the attachments they constructed, even when building at the same site. However, as males built more nests, so they added more loops into their knotted attachments. They also produced more loops when using longer pieces of grass.

Males in the current study did not use the same number of loops in their attachments when building at a particular location. It appears, then, that when making their first grass attachment to a branch, males were not solely using either the immediate structure of the branch to determine their behaviour or doing the same thing each time as might be determined by an unlearned rule (e.g. ‘always do a clove-hitch when adding the first piece of grass to a straight branch’). Moreover, when building at a particular site, males did not increase or decrease the number of loops they used in their four consecutive attachments in a directional manner, as we might expect if the experimental manipulation we carried out influenced the males’ behaviour. For example, if after returning to a site where their first attachment had just been removed, males might have attempted to tie the second blade of grass more tightly (i.e. leading to more loops in it).

As males built more nests, and when they used longer strands of grass, so they incorporated more loops into their attachments. The latter of these findings makes intuitive sense: when males attach longer pieces of grass to a branch, so they are able to wrap it around a branch more times, thereby creating more loops in in the attachment. However, this does not explain why there were more loops in attachments as more nests were built, as males were not choosing longer pieces of grass as they built more nests. Instead, it seems that, for a given length of grass, males created a knotted attachment with more loops after having built more nests. Males of this species also build smaller nests with more nests built across a breeding season (Walsh *et al.* 2010). Both these results could be explained by birds weaving more tightly as they improve their motor skills involved in weaving through building

experience. This possibility is supported by observational data from another species, the village weaver, that builds more tightly woven nests the more they build (Collias and Collias 1984). Why one bird in our study (bird number 4) should be different, in that he made fewer loops in his attachments as he built more nests, is not clear. Other factors that we did not measure in the current study may also influence this aspect of the bird's nest building and the resultant structure of the attachment.

If more loops are being incorporated into attachments as more nests are built because birds refine their motor skills, it seems that it is not happening as quickly as within an experimental set of removals (taking a number of hours) or across the four repeated trials, but more slowly across the breeding season, as we only detected this effect when taking into account the absolute number of nests the individual has built. This includes nests where we did not carry out removals, meaning birds became more experienced builders between our experimental trials. There are other possible explanations for the pattern we found such as the birds responding to a seasonal change in the weather conditions. If, for example, the weather became increasingly windy, warmer or wetter, it is possible that this might have caused a directional change in the number of loops we found in the attachments.

The findings from this study suggest that learning plays a role in determining building behaviour by these birds, as has been found for other bird species (e.g. village weaverbirds, Collias and Collias 1964, zebra finches; Muth and Healy 2011). These findings refute the assumption that nest building does not require any learning (Hansell and Ruxton 2008). Given this evidence coupled with the outward similarities in material choice and the requirement for manipulative skills, it seems at least plausible that nest building may not be as dissimilar from tool manufacture and use. It has been argued that tool use requires 'advanced' cognition, not least because the tools produced are often very similar to each other. Indeed, similarity of tools made is sometimes suggested to be evidence of planning

(e.g. Hunt 1996, Hunt and Gray 2004). However, instead of using the variability in an object (i.e. a tool or a nest) to make inferences about how ‘intelligent’ or cognitively ‘complex’ an animal might be (which is not well-defined anyway; Shettleworth 2010), understanding why this variability might exist may be a more useful approach. Rather than placing animals in a hierarchy of how much they ‘understand’, we should attempt to elucidate the mechanisms underpinning nest construction and other construction behaviours. For example, we need to know how an animal perceives the object it manufactures, and what stimuli it uses to select and alter it. From here we can address how transferrable the animal’s skill is to other contexts other than construction of its particular object (i.e. nest or tool). Once we have a grasp of how animals perceive and process the objects they construct or manipulate we will be able to compare this across a wide range of species acting under different environmental pressures to determine how such cognitive abilities might reflect selection pressures.

One unexpected aspect of the knots the males wove was the difficulty we had in capturing quantitatively the amount of variation in the attachments both between birds and within them (e.g. Figure 2). Although we attempted to quantify knots through comparing them to human-made knots using knot-construction computer software, the complexity and variability in the weaver knots made this extremely difficult. It is perhaps ironic that in order to address the complexity of nest building in these birds we have had to simplify their behaviour for useful quantification.

Chapter 7: The right tool for the nest: Material choice in nest building

Introduction

Birds' nest-building behaviour is typically assumed to be inflexible and unaffected by learning (Hansell and Ruxton 2008, Seed and Byrne 2010). However, these assertions have been little tested despite their validity being questioned as early as 1867 by A.R. Wallace. This contrasts quite strikingly with the assumption that the manufacture and use of tools by birds requires 'complex' cognitive abilities (e.g. Hunt 1996, Chappell and Kacelnik 2002, Weir *et al.* 2002, Hunt and Gray 2003, Chappell and Kacelnik 2004, Hunt and Gray 2004, Weir and Kacelnik 2006, Taylor *et al.* 2007). Although neither 'complex' nor 'cognition' are usually clearly defined (Emery and Clayton 2004, Emery 2006, but see Hansell and Ruxton 2008), they usually include an understanding of 'folk physics' (Chappell and Kacelnik 2002, 2004) and goal-directedness (Hunt and Gray 2004). Tool use itself is generally defined as 'the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool' (Beck 1980). Whilst nests themselves are not considered to be tools, the construction of a nest may well entail the use of materials in ways that seem consistent with tool manufacture and use (Shumaker *et al.* 2011). This being the case, it seems plausible that, contrary to current opinion, the cognitive and or physical abilities that underpin tool use and manufacture may be similar to those underpinning nest building.

One of the key requirements for tool use is that the individual chooses the appropriate object for the task at hand. And, indeed, New Caledonian crows can select sticks of suitable width and length to retrieve food from a tube (Chappell and Kacelnik 2002, 2004). A range of

primate tool-users also solve this kind of task (Tomasello and Call 1997). For example, when chimpanzees *Pan troglodytes*, bonobos *Pan paniscus*, and orang-utans *Pongo pygmaeus* were given sticks tied together in a bundle and sticks tied in an H-shape and needed to untie the bundle or to remove a single stick from the H-shape to solve a task) they did so, whereas capuchin monkeys did not (Visalberghi *et al.* 1995). In other tests, wild bearded capuchin monkeys, *Cebus libidinosus*, chose stones of appropriate friability and weight for cracking open a nut (Visalberghi *et al.* 2009, Frigaszy *et al.* 2010) and selected suitable pits in which to crack these nuts (Liu *et al.* 2011). A number of great apes (chimpanzees, gorillas, bonobos and orang-utans) and capuchin monkeys can also choose tools based on rigidity (rigid or flexible) to meet particular task demands (Povinelli *et al.* 2000, Manrique *et al.* 2010, Manrique *et al.* 2011), while observational studies suggest that wild chimpanzees select hammers suitable for the resistance of the nut they have to crack (Boesch and Boesch 1989). Furthermore, chimpanzees manufacture and use tools appropriate for honey dipping and termite fishing (Sanz *et al.* 2009, Sanz and Morgan 2009, Sanz *et al.* 2010), while long-tailed macaques *Macaca fascicularis* use specifically shaped stones for scraping and hammering (Gumert *et al.* 2009). We contend that at least superficially similar to these descriptions is the choice of nest materials made by male village weavers *Ploceus cucullatus*. These birds construct intricate nests through weaving together long, green, flexible strips of grass. When tested between their preference for artificial materials, birds chose materials that seemed appropriate in that they matched the criteria for their natural materials (green over other colours, flexible over rigid materials, and longer over shorter strips; Collias and Collias 1959 in Collias and Collias 1964). However, these preferences might just reflect general preferences that weaverbirds have, as the birds did not have to build under any restrictions (thus making some materials more appropriate than others). Other potential evidence that birds might choose appropriate material for building is that birds appear flexible in their

choice of material in that they do not necessarily stick to choosing exactly the same type each time. Wire, plastic string and cigarette butts have all been used by birds in their nests (Igic *et al.* 2009, Antczak *et al.* 2010). However, we do not know whether this apparent flexibility is due to the artificial stimuli sharing a property that the birds use to select the natural material (e.g. the colour), or whether it is a reflection of the birds choosing an appropriate type of material based on the building situation. If the latter of these two hypotheses is true, this would provide support for ‘cognitive flexibility’: the ability to use knowledge from one context and apply it to a different one. While it seems then that there is the possibility that birds might be able to choose appropriate material of a range of possible types in a manner akin to tool using animals, this has never been experimentally tested.

In addition to the ability to select appropriate material, modifications of technique or improvements in performance with increasing experience of the task are also taken as a hallmark of tool-making abilities. For example, whilst it has been found that crows have strong predispositions towards tool use (Kenward *et al.* 2005), both wild and captive-reared New Caledonian crows also seem to learn some aspects of tool-using behaviours both individually and from their parents (Kenward *et al.* 2006, Bluff *et al.* 2007, Holzhaider *et al.* 2010). Similarly, some primates also improve their manipulative skill involved in tool-using behaviours, for example capuchin monkeys get better over time at pulling in hooked canes to retrieve food (Cummins-Sebree and Frigaszy 2005). Here again there seem to be similarities with nest-building: weaverbirds also refine their skills at physically manipulating objects, as young males deprived of weaving experience were less proficient tearing off strips of material and at weaving as adults than were non-deprived controls (Collias and Collias 1964). First-time nest-building weaverbirds also built more loosely woven nests than adult males (Collias and Collias 1964) and nests built by wild, free-living Southern masked weavers *P. velatus* and village weavers became smaller and lighter over time (Walsh *et al.* 2010). This

may be due to the birds weaving the grass more tightly, which they may be able to do as they refine their manipulative skill. However, although at least superficially nest building appears similar to tool use in the manipulative skills required, it is not clear whether nest builders could solve tasks akin to those solved by tool users.

We therefore examined whether nest-building zebra finches *Taeniopygia guttata* were able to choose the ‘right tool for the task’ and do so with increasing success in the context of nest building. We chose the zebra finch to address these questions as the male builds readily in captivity and will use a range of materials and nesting sites (Zann 1996). We provided paired zebra finches in the laboratory with nest boxes in which to build. The nest box had either a large entrance or a small entrance through which the birds had to take the nest material. All pairs were also provided with two types of nest material, ‘short’ and ‘long’. Both pieces could be readily taken through the entrance of the Large-entrance nest boxes, whether held by the end of the piece or in the middle. However, only the short nest material could be readily taken into the Small-entrance nest box held either way.

If zebra finch males can choose appropriate nesting material, we would expect the birds building in nest boxes with a small entrance hole to prefer to build with the short pieces of nesting material, which are easier to get into that nest box. We would expect the birds building in the boxes with the large entrance, on the other hand, to be indifferent to the length of the material. We would also expect birds to become more successful at getting nest material into the nest box with increasing experience.

Methods

Subjects

The subjects were 35 adult male and 35 adult female zebra finches (although only 24 males built on all test days and contributed data to the analyses). All males used were six to nine months old and all females were between six months and two years (zebra finches are sexually mature by three months: Zann 1996). All birds had been bred in captivity at the University of St Andrews, UK. They were kept on a 14:10 light:dark cycle at a temperature of 19-22°C with humidity levels of 50-70% and given *ad libitum* access to food (mixed seeds, cuttlebone, and oystershell grit) and water. The cages used throughout the experiment were sized 88 × 30 × 39cm (width × length × height).

All birds had fledged from nests built with coconut fibre and hay. All of the males had built two nests previously, both in wooden, open-topped nest boxes (11 × 13 × 12cm, width × length × height), using coloured coconut fibre. No birds had previously encountered the type of nest box or the material used in the current experiment.

Experimental protocol

Six pairs of birds were assigned to each of four treatment groups: ‘Experienced/Large entrance’; ‘Inexperienced/Large entrance’; ‘Experienced/Small entrance’; ‘Inexperienced/Small entrance’. The two Large-entrance treatment groups were provided with nest boxes with an entrance 10cm in diameter for the bird to enter through and the Small-entrance groups were provided with nest boxes with an entrance 5cm in diameter. Nest boxes were constructed using green garden wire mesh and modelling wire, held together with cable ties (Figure 2(a)). Birds were also provided with ‘short’ (20 – 22cm long) and ‘long’ (25 – 27cm long) nest material. Both types of material consisted of ~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 – 5.5cm in length (Figure 2(b)).

Prior to testing, the two Experienced groups received two days of building experience with the experimental material and nest box. These birds were each placed in the experimental cages for a day before being provided with a nest box with either a large or small entrance for a day. After this, the groups were provided with 20 pieces of ‘long’ and 20 pieces of ‘short’ nest material and filmed for three hours. The nest material was always placed on the floor of the cage below the nest box, with the short pieces in one pile and the long 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 of the cage on which the short pieces were placed was also alternated on each day of testing within a pair. If, after three hours, the male had not touched the material, they were filmed for further three hours 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 nest box provided for two days.

Birds in the Inexperienced groups were provided with a nest box without nesting material for two days. After these two days, both groups had their nest boxes (and nesting material in the case of the Experienced group) removed from their cages. A day later both groups were given empty nest boxes with an entrance of the same diameter as they had had previously. They were also provided with 20 pieces of nesting material (10 pieces of ‘long’ and 10 of ‘short’). The pairs were filmed for two and a half hours, after which the nest box and all the nesting material were removed. This procedure was repeated at approximately the same time (to within an hour) on the next two days. These three test days are hereafter referred to as ‘Day 1’, ‘Day 2’ and ‘Day 3’ (Figure 1). If birds did not touch the material at all on Day 1, Day 2 or Day 3 they were removed from the experiment.

Day number	
1	All zebra finches paired
2	All pairs given nest boxes (Large- or Small-entrance)
3	<div> <div>'Experienced' birds given 'long' & 'short' nest material</div> <div>'Inexperienced' birds left with box but no material</div> </div>
4	
5	All nest material and boxes removed
6	Testing Day 1
7	Testing Day 2
8	Testing Day 3

Figure 1: The experimental protocol. On testing days the birds were given 10 pieces of 'short' and 10 of 'long' material and a Small- or Large-entrance box of the type they experienced on days one to three.

For each testing day, the nest box was presented in a new location within the cage, rather than having the male return to the same site each time. We did this in an attempt to make each building event a 'new' nest to the male. There were four possible locations: high on the left wall, high on the right wall, low on the left wall and low on the right wall. Locations were pseudo-randomised across the four different occasions (pre-test exposure and the three test days), such that each location was first, second, etc. for at least one pair within

each treatment group and such that each pair experienced all four nesting locations. There were three perches: one in front of the nest box and two perches at 33cm and 55cm from this perch. The food bowl was in the centre of the cage floor and the camera was always fixed inside the cage at the opposite end to the nest box so that the nest box and the nest material below were in the field of view.

Behavioural coding

We used video software for behavioural analysis (Noldus Observer, TrackSys Ltd., UK) to code behaviours and record the time at which they occurred. We recorded each time a bird pecked at each type of nest material on the floor (touched or picked up with their beak), and each time they took a piece of nest material to the nest box. Taking a piece of material to the nest box was defined as a bird picking up a piece of nest material in its beak and carrying it to the perch placed directly in front of the nest box. Each time a piece of nest material was taken to the nest box, we recorded the type of material (long or short), where it was held (the ‘middle’ or the ‘end’; Figure 2(b), Figure 3) and whether it was taken successfully into the box (‘success’ or ‘fail’). If the bird held the piece in the ‘middle’ (the stiff wire section of the piece), this meant that the piece was held perpendicular to the bird, and therefore taken into the nest box such that the length of the piece was held across the entrance (Figure 3(a)). If the bird held the piece at the ‘end’ (any part of the material outside of the stiff wire section), this meant that the piece was held alongside the bird and, therefore, taken into the nest box end-first (Figure 3(b)). Long pieces held in the middle could be taken directly into the Large-entrance boxes but would not fit this way through the entrance of the Small boxes. Short pieces held in the middle could be taken into nest boxes with either entrance size. Both lengths held at the end could be taken into either size of nest box entrance. ‘Successful’ attempts were defined as any time that a bird both took a piece of nest material through the

entrance into the nest box successfully and then exited the box without that piece of nest material falling out.

We also recorded each time a male or female ‘knocked out’ nest material from the nest box (with their feet or body) or ‘pulled out’ material (with their beaks). The time it took birds to peck their first piece of nest material, and add all the nest material to the nest box (from when they first touched the material) was also recorded.



Figure 2(a) The two types of nest box (with a Large entrance and a Small entrance) and **(b)** the two types of nest material (long, above and short, below).



Figure 3 (a & b) A male zebra finch building in the Large-entrance nest box, holding **(a)** a long piece of material in the middle, which will be taken into the nest box perpendicular to the bird, and **(b)** the same male holding a long piece at the end, which will be taken into the nest box end-first.

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 and Maechler 2010) which 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 `nlme` package, specifying type three sum of squares and sum contrasts in cases where there were interactions (Pinheiro *et al.* 2010). For all models, maximal models were run initially, and then non-significant interactions were removed in a step-wise fashion. In cases where there were significant interactions, models were re-run splitting the data by one of the factors in the interaction, in order to determine the significance of the main effects without the interaction.

All non-parametric analyses were carried out in IBM SPSS Statistics version 19.

Results

Four pairs in the Inexperienced/Small treatment group and five pairs in the Inexperienced/Large group did not start building on Day 1 of testing so were excluded from the experiment. One pair in the Experienced/ Large group did not build on Day 3 and in one pair the experimental set-up was not correct on Day 3 so these two pairs were also removed from the experiment. As all of these pairs were replaced with pairs that did build, the following results are from six pairs in each group that completed all days of building.

In zebra finches it is males that collect the nest material and take it to the nest to build (Zann 1996), so we primarily focused on male behaviour.

Nest material choice

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 nest box. The proportion of long pieces (out of 10) was then compared using a generalized linear mixed model (GLMM) with a binomial distribution. The model included three categorical explanatory variables: 'Experience' (Inexperienced or Experienced), 'Day number' (1-3) and 'Nest box size' (Large or Small), and the random factor 'male' ('Model 1'). A maximal model was used as the three-way interaction was significant.

Males building in the Small-entrance nest boxes chose more short pieces in their first 10 pieces than did males building in the Large-entrance nest boxes (GLMM: z value = -4.747, $p < 0.001$; Figure 4). This relationship changed over the three days of testing but how it changed differed for birds building in Large- and Small-entrance boxes, as there was a significant interaction between day number and size of nest box entrance (GLMM: z value = 4.169, $p < 0.001$). In order to better understand this interaction, two further models were run using the data from the Large- and Small-box conditions separately. Birds building in the Small-entrance nest box chose increasingly more long pieces of material across the three test days (GLMM: z value = 4.962, $p < 0.001$). Birds building in the Large-entrance nest box did not change in the number of long pieces they took across testing days, although Inexperienced birds tended to take fewer long pieces on day 2 than on days 1 or 3 (GLMM: day number: z value = -1.877, $p = 0.061$; day number*experience: z value = 1.913, $p = 0.056$). Overall, previous experience with the nest-building task did not affect the number of long pieces taken to the nest box (GLMM: z -value = -0.435, $p = 0.663$).

To determine how males building in the Small-entrance nest boxes might be selecting more short material on the first day of testing than those building in the Large-entrance nest

boxes, we addressed a number of other variables. First we looked to see if males chose the 'correct' material 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 among the groups and nearly all birds took a short piece first: 5/6 birds in the Large/Experienced group; 4/6 Large/Inexperienced; 5/6 Small/Experienced; and 3/6 Small/Inexperienced.

We then looked to see whether birds building in the Small-entrance nest boxes began by choosing long pieces and then switched to short pieces. To do this, we looked at the lengths of the first five choices males building in the Small-entrance nest boxes made on the first day and compared this with the lengths of the second five pieces chosen. The first and second five did not differ: males took the same number of long pieces on average in their first five pieces as in their second five taken (Related-Samples Wilcoxon signed-rank tests: Experienced/Small: $n = 6$, $Z = -0.535$, $p = 0.593$; Inexperienced/Small: $n = 6$, $Z < 0.001$, $p > 0.999$).

In an attempt to determine whether there was any strategy in choosing pieces (e.g. if the bird failed at taking one type of material did he switch to the other type) we compared the number of times birds failed and then switched (to the other material) to the number of times they failed and stayed with the same type. We also compared the number of times birds succeeded and then switched to the number of times they succeeded and stayed. We looked at just the first 10 choices, addressing the treatment groups and nest material lengths separately. The Experienced/Large group were more likely to choose a another long piece whether or not they had failed or succeeded previously at taking a long piece into the next box, than they were to switch, but showed no particular pattern when the piece was short (Stay with the same length vs. 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: $\chi^2_1 = 0.267$, $p = 0.606$). The Experienced/Small group, however, were more likely to choose another short

piece regardless of their success with it previously but showed no particular pattern when the piece was long (Stay with the same type vs. 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 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 group tended to choose short pieces irrespective of previous success. With long pieces, counter-intuitively they chose long pieces after failing to insert a long piece into the box but were not more likely to choose long (or short) when they had succeeded inserting a long piece into the box (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: $\chi^2_1 = 0.333$, $p = 0.564$).

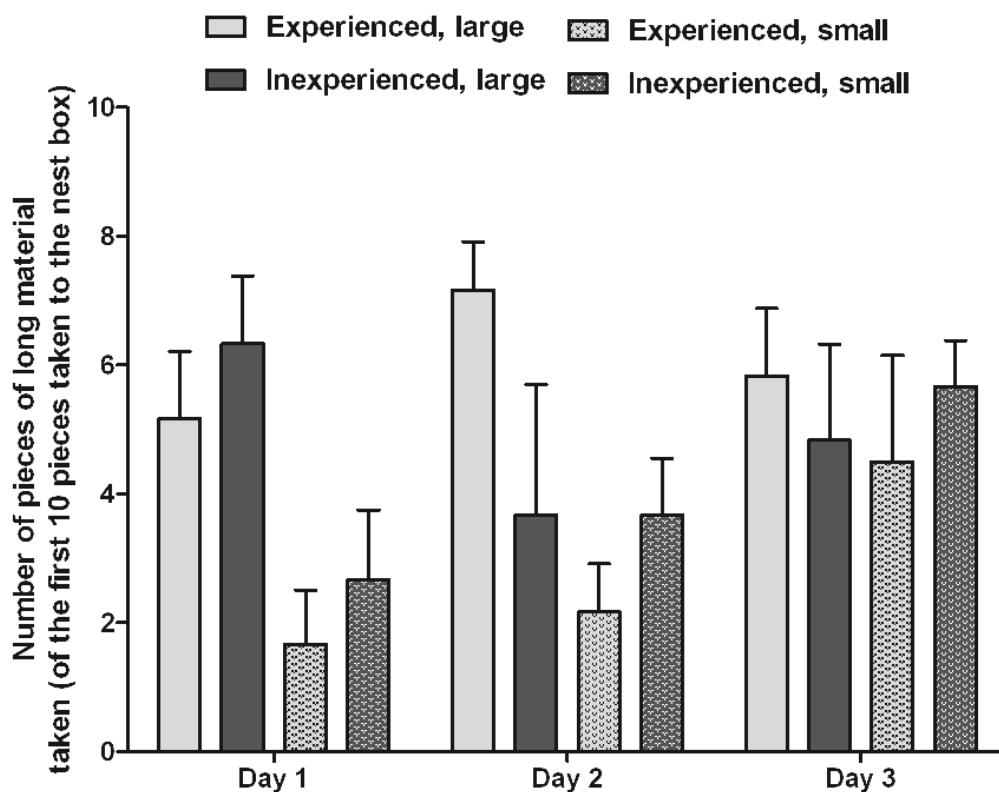


Figure 4: The mean (\pm S.E.) number of long pieces taken (out of the first 10 taken) across the four different treatment groups and across days.

Building success

To determine whether males became more successful at taking pieces into their nest box 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 during the testing period. A model 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 size' (short/long) and 'Day number' (1-3) and the random factor 'male' ('Model 2').

Males building in the Small-entrance nest boxes became more successful at getting pieces of material into their nest box over three days of testing (LMM: $F_{2,56} = 7.388$, $p = 0.001$; Figure 5). Inexperienced males were more successful at getting short than long pieces into the nest box while the Experienced males were equally good at getting both lengths into the nest box. Inexperienced birds were actually more successful at taking short pieces into the box than were the Experienced birds, although the groups did not differ in their ability to insert long pieces successfully (LMM: material length: $F_{1,56} = 13.112$, $p < 0.001$; experience: $F_{1,10} = 2.680$, $p = 0.133$; material length \times experience: $F_{1,56} = 8.093$, $p = 0.006$; Figure 5).

For birds building in the Large-entrance nest box, Experienced males were more successful than were the Inexperienced males at taking long pieces into the box, but not more successful at taking in the short pieces (LMM: Experience: $F_{1,10} = 15.405$, $p = 0.003$; Experience \times material: $F_{1,56} = 7.256$, $p = 0.009$; Figure 6). Both Experienced and Inexperienced males were more successful at taking short pieces into the nest box than at taking long pieces (LMM: $F_{1,56} = 59.263$, $p < 0.001$; Figure 6). They did not become more successful at taking pieces into the box over the three days (LMM: $F_{2,56} = 2.292$, $p = 0.111$; Figure 6).

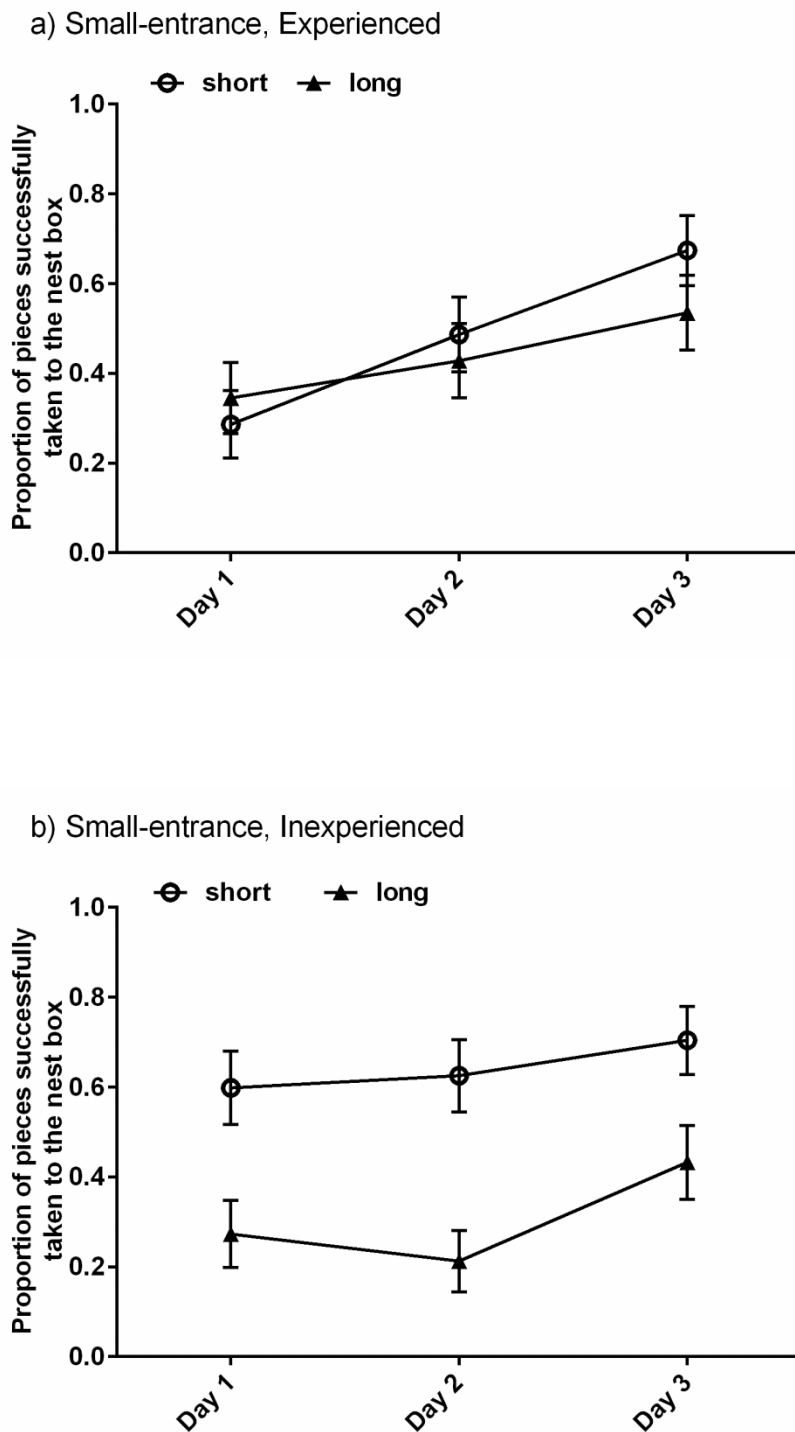


Figure 5: The mean (\pm S.E.) proportion of short and long nest material pieces successfully taken into the Small-entrance nest box by: a) Experienced and b) Inexperienced males across the three days of testing.

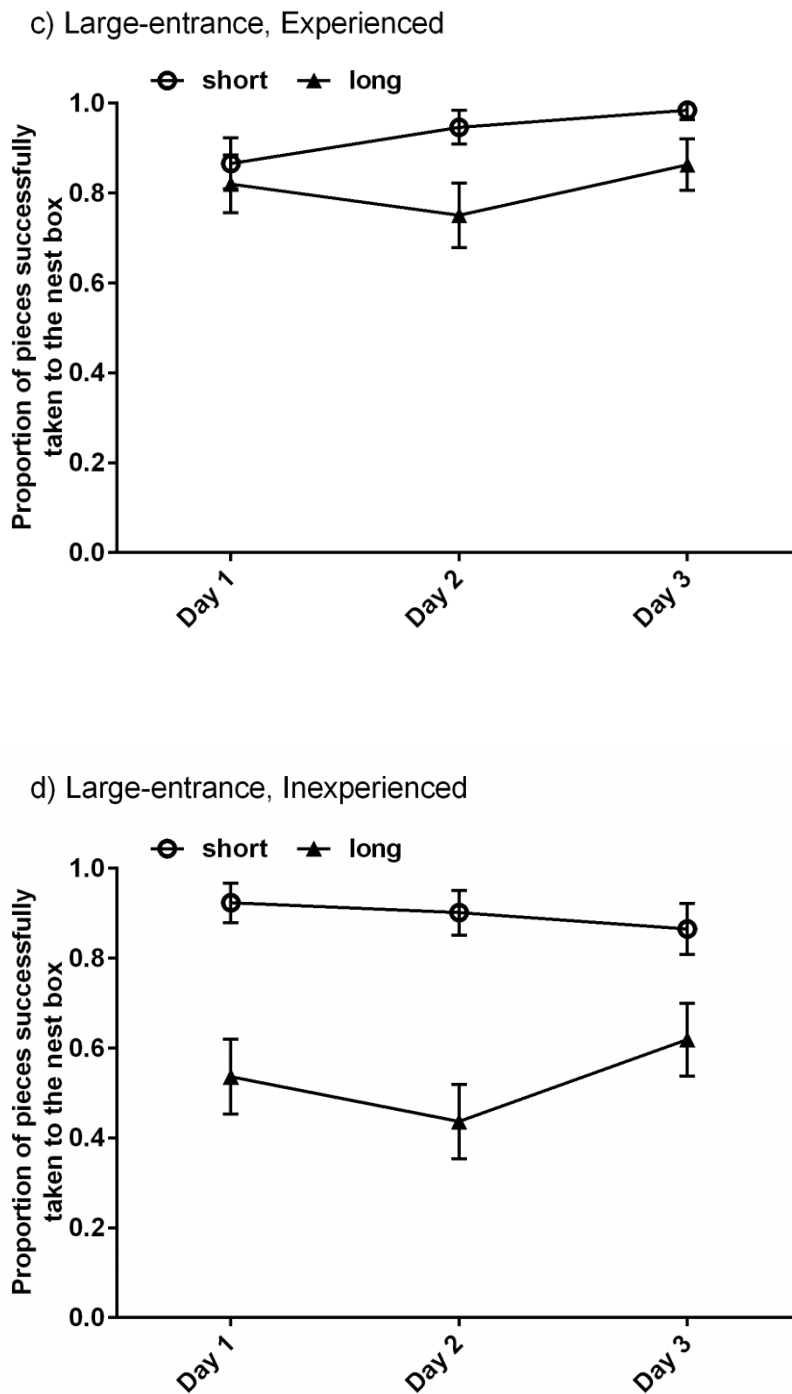


Figure 6: The mean (\pm S.E.) proportion of nest material pieces successfully taken into the Large-entrance nest box by males in each of the four treatment groups across the three days of testing.

We explored further why the Inexperienced birds building in the Small-entrance nest box might have been more successful at taking short pieces into the box on Day 1 than were 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 of $n = 6$ in each group was too small to be compared statistically: Inexperienced: $\bar{x} = 33.4$, $SD = 23.9$, Experienced: $\bar{x} = 16.4$, $SD = 20.8$). Although the means were far apart, there was a lot of variation in the data. We then looked at the first time males in the Experienced group had encountered the material (on the first day of their two days of experience) and their proportion success with the short pieces. The average success taking short pieces into the nest box did not differ between the first time the Experienced group encountered the material 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: 'Experience' $\bar{x} = 0.30$, $SD = 0.22$, Day 1 $\bar{x} = 0.31$, $SD = 0.09$). Both of these values are smaller than that of the Inexperienced group success on Day 1 ($\bar{x} = 0.63$, $SD = 0.12$). It therefore seems that the difference between the Experienced and Inexperienced groups building in with short material in the Small-entrance boxes on Day 1 (Figure 5) is due to the Inexperienced group being more successful from the outset than the Experienced group, rather than to the latter becoming less successful between its first encounter with the material during the two days of experience and Day 1. The absolute number of times short pieces were successfully taken to the nest box did not vary between the two groups (Experienced group: $\bar{x} = 10.2$, $SD = 1.8$, Inexperienced group: $\bar{x} = 11.2$, $SD = 1.6$, 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 or knocked out on Day 1 by the males also did not vary between the two groups (pulled out: Mann-Whitney U test: $U_{11} = 25$, $W = 46$, $p = 0.212$; knocked out:

Mann-Whitney U test: $U_{11} = 11$, $W = 32$, $p = 0.181$). The females did not pull out any short pieces on either of these days and only one short piece in each treatment group (across all pairs) was knocked out. We also addressed where the males were holding the short pieces, and whether this was explaining the difference in their overall success with it. Although males in the Experienced group may have taken more short pieces to the nest box held in the 'middle' than at the 'end' (Experienced: $\bar{x} = 10.33$, $SD = 15.13$ $n = 5$, Inexperienced: $\bar{x} = 3.17$, $SD = 4.58$, $n = 4$, sample sizes too small to be analysed statistically), when just looking at the pieces both groups held at the end, the Inexperienced group still had a higher proportion of success at taking them into the nest box (t-test: $t_{10} = -5.729$, $p < 0.001$) but not in the absolute number taken successfully (t-test: $t_{10} = -0.896$, $p = 0.391$).

Handling of material

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 nest box and another for birds building in the Large-entrance nest box, using the proportion of pieces held at the end as the response variable and with the same explanatory variables as in Model 2.

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 nest boxes held the material even more frequently at the end of the piece on later days (GLMM: z value = -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, but this was more the case in the Inexperienced groups (material: z value = -4.378 , $p < 0.001$; Experience \times material: z value = 5.412 , $p < 0.001$; Experience: z value = -0.299 , $p = 0.766$).

Males building in the Large-entrance nest box were more likely to hold short pieces than long pieces at the end (GLMM: z value = -8.031, $p < 0.001$). As the way in which the material was handled across days differed for the two levels of experience (experience \times day number = z value = -2.501, $p = 0.012$), the data were split by Experience and two models were carried out to determine significance of main effects. Experienced birds were more likely to hold material at the end on later days (GLMM: z value = -2.367, $p < 0.05$) whilst this was not the case in the Inexperienced group (GLMM: z value = 0.742, $p = 0.458$).

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 nest box, we looked at his pecking of the material on the ground (prodding or picking 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 a LMM using the same explanatory variables as in Model 1.

All males explored the material more before taking their first piece to the nest box (in terms of the total number of pecks) on Day1 than they did on Day 3 (LMM: $F_{1,46} = 8.938$, $p = 0.0005$; 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 nest box more than the other type (long taken: average proportion pecks at long = 0.93, SD = 0.206, $n = 23$; short taken: average proportion pecks at short = 0.84, SD = 0.241, $N = 44$). In 5 cases the male did not peck at the material before taking it to the nest box.

Time taken to approach the material and to add all pieces to the nest box

To test whether males approached the nest material faster as days progressed, we measured the latency (in minutes) from when the material was first placed in the cage to when the male first pecked at it and log-transformed them to normality. A LMM was then fitted with the same explanatory variables as Model 1. All males approached the nest material more quickly over the three test days (LMM: $F_{2,44} = 12.429$, $p < 0.001$) and Experienced males were faster than the Inexperienced males on Day two, but not on Days one or three (Experience: $F_{1,22} = 3.030$, $p = 0.0957$; Experience \times Day number: $F_{2,44} = 5.859$, $p = 0.006$).

As there were many cases where the male did not finish building in the testing time we allocated to him, we compared the frequency of non-completion across days, experience levels and size of nest boxes using chi-squared tests and then corrected the alpha value for multiple tests. 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 nest box

Males did not knock out more material over successive days ($\chi^2_2 = 2.044$, $p = 0.360$, $\alpha = 0.017$; Nest-entrance size: $n = 72$, $Z = -0.576$, $p = 0.564$, $\alpha = 0.017$; Experience: $n = 72$, $Z = -0.486$, $p = 0.627$, $\alpha = 0.017$).

Regardless of experience, males building in the Large-entrance boxes consistently pulled out more material than did the males building in the Small-entrance boxes (Nest-entrance size: $n = 72$, $Z = -2.948$, $p = 0.003$, $\alpha = 0.017$; Day: $\chi^2_2 = 3.805$, $p = 0.149$, $\alpha = 0.017$; Experience: $n = 72$, $Z = -0.884$, $p = 0.377$, $\alpha = 0.017$).

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 where the female did not knock out nesting material in all treatment groups (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 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 nest box, 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 her behaviour 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: $F_{1,44} = 2.044$, $p = 0.160$, nest box 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 nest box: this happened in a total of seven cases and in each case she pulled out only a single piece.

Discussion

When zebra finch pairs were given artificial nest boxes with two different entrance sizes and building material of two lengths, the males chose the type of nest material most appropriate for the size of the entrance to the nest box in which they were building. The first time they encountered this nest box, birds building in boxes with a small entrance were more

likely to choose short pieces than were those birds faced with building in a nest box with a large entrance. Furthermore, handling of the material improved over time as males building in the Small-entrance nest boxes increasingly held pieces at the end and became more successful at getting pieces into the nest box. These males became less choosy about material length. Additionally, males experienced at building in the Large-entrance nest boxes were more successful than were inexperienced males at getting long pieces into the nest box.

As males in the current study chose material of the appropriate length for the nest box entrance size in which they were building, even when they had never encountered the building context before, it would appear that zebra finch males are able to choose appropriate material in a manner equivalent to the appropriate choice of tools observed in New Caledonian crows (Chappell and Kacelnik 2002, 2004) and some primates (Visalberghi *et al.* 1995, Povinelli *et al.* 2000, Visalberghi *et al.* 2009, Frigaszy *et al.* 2010, Manrique *et al.* 2010, Liu *et al.* 2011, Manrique *et al.* 2011, Sabbatini *et al.* 2012).

How birds in the current experiment were able to select appropriate nest materials might be explained in a number of ways. For tool-using animals, choice of an appropriate tool is usually explained in one of three ways (Shettleworth 2010), by the animal having: (1) an unlearned rule of what choice is suitable for a particular situation; (2) previous trial-and-error learning leading to an associative rule; (3) causal ‘understanding’ of the functional properties of the tool, a ‘folk physics’ (e.g. Chappell and Kacelnik 2002, Chappell and Kacelnik 2004); or a combination of these explanations (Hunt *et al.* 2006). With regard to the performance of our nest-building birds, having an unlearned rule seems unlikely: although wild zebra finches may nest in thorny shrubs and trees, rabbit holes or even cattle skulls (Zann 1996) and build with both flexible and inflexible materials, which may mean that there was selection pressure on zebra finches to have an unlearned rule of what type of material will fit through a certain gap, our males did not choose the ‘appropriate’ piece from the very

first choice. As we only saw the effect of appropriate material choice when we looked at the first 10 pieces the birds took, it seems that they did not assess and solve the problem visually or through manipulating the material on the ground before starting to build. They also did not seem to respond to their immediate success at taking material into the nest box in the first 10 pieces. However, as the preference for short material by both groups building in Small-entrance nest boxes waned over the three days of testing there is some evidence for trial-and-error learning occurring over the testing days.

With regard to the third explanation, we cannot use these data to comment on whether males have any causal ‘understanding’ of the properties of the nest material and the box in which they built (as is often invoked as the explanation for tool selectivity (e.g. Chappell & Kacelnik 2002, 2004) as this experiment was not one designed to address that possibility. The data are, however, consistent with that explanation.

Like tool-users, some of the groups of zebra finches in our study improved their building behaviour with experience (Cummins-Sebree and Fragaszy 2005, Kenward *et al.* 2006, Bluff *et al.* 2007, Holzhaider *et al.* 2010). Although the birds building in the Small-entrance nest box that had two days of experience building prior to the start of the experiment did not differ in their material choice on Day 1 to the Inexperienced group, over the testing days males became better at manipulating material into the box, changed their handling of it, and with this improvement discriminated less in their choice of material. Similarly, the group with previous building experience were equally successful at taking both types of material into the nest box, whilst the group without the two days experience building in the experimental nest box were more successful taking the shorter, more easily manipulated, material into the Small-entrance nest box. Experience also seemed to impact on the behaviour of birds building in the Large-entrance nest boxes, even though overall it was easier for birds to build in these boxes than in the Small-entrance nest boxes, leaving less ‘room for

improvement'. Birds with two days of building experience prior to testing were more successful at taking the more difficult to manipulate, long pieces into the nest box than were birds without this building experience. One surprising result was that birds without previous experience building in the Small-entrance box were better at taking short pieces into the nest box 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, how many pieces they added, or how many pieces they knocked out or pulled out. It is possible that our exclusion of males from the Inexperienced group that did not attempt to build on Day 1 inadvertently selected for more successful nest-building males, specifically in that group. This possibility is supported by the finding that the Experienced group were less successful at taking short pieces into the box on their first building occasion (on the pre-testing days) than were 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 nest box, this explanation is not entirely sufficient, leaving the reason for the difference between the groups unclear. Regardless of this unexpected finding, both our manipulation of experience (in terms of the two days building prior to testing) and the birds' experience building in the experimental nest box across the three days of testing affected the birds' building behaviour.

We consider that these results make a useful contribution to the discussion concerning whether tool use is cognitively 'special' (Hansell and Ruxton 2008, Emery and Clayton 2009, Kacelnik 2009). It is not yet clear whether tool use requires general cognitive skills, not least because at least some animals not usually considered as tool users can use tools in captivity, seemingly as proficiently as well known tool users (Bird and Emery 2009b) as well as performing equally well as do tool users on physical cognition tasks (Tebbich *et al.* 2007, Teschke *et al.* 2011). It seems plausible, then, that the ability to manipulate and use tools may

utilize similar problem-solving capabilities (which may include both cognitive and motor skills) and be underpinned by a domain-general cognitive capacity rather than by an adaptive specialization (Bird and Emery 2009b, Emery and Clayton 2009). It may now be useful to consider much more carefully what exactly are the cognitive abilities required for tool manufacture and use.

Chapter 8: General discussion

In my thesis I investigated nest building behaviour in birds to gain a better understanding of the role of learning in this behaviour, primarily through laboratory-based experiments using the zebra finch. I addressed how nest material choice is affected by adult learning, juvenile learning, and social learning. I also carried out an experiment to see whether birds were able to choose appropriate material for a particular building context based on a physical property of that material. I further used wild, Southern masked weaverbirds to examine variability in building and the role of experience on nest building in the wild.

Main empirical findings

To investigate the role of learning in nest building, I primarily used the choice of nest material made by zebra finches, in particular between two or more colours of nesting material (Chapters 2-5). Using this aspect of behaviour, I found that, under some circumstances, adult zebra finches will modify their previous preference for the colour of nest material: males that built a nest using their less preferred colour later preferred that colour if they had a successful breeding attempt in that nest. However, despite using their own experience to inform their nest material choices, I found no evidence that adult birds attended to social information about nest material colours. Males were also not affected by their experience of the colour of the nest they occupied as a nestling, as they did not choose the colour of that nest when they subsequently built their first nest. Thus, the outcome of these experiments would suggest that the individual experience of building a nest plays a significant role in determining the nest material choices of zebra finches, but that birds attend less to the behaviour and nests of other birds, both as juveniles and as adults. However, we should be careful in the conclusions drawn from comparing individual to social learning in these adult birds, as the birds used in

the experiment on individual learning had not built nests before, while the birds in the social learning experiment had. This might have affected the birds' tendency to learn in the social learning experiment, and it is possible that if naïve birds had been used then they may have been more likely to learn. Furthermore, the building experience they had in the test of individual learning included breeding experience, whereas the opportunity to socially learn was based purely on seeing another pair nest. Our finding that adult learning played a larger role in nest material choice than juvenile learning from experience in the nest agrees with Sargent's (1965) data. In that experiment, the conditions under which a bird had previously built a nest (nest box type, location of nest and colour of nest material) were much more important in determining the behaviour relating to the decisions concerning the next nest than did the experience they had had in a nest as a juvenile. From our data it seems that, with regard to material choice at least, it is not just the experience building, but the nature of the experience (here, the breeding success when building with that material) that influence whether birds modify their choices of materials used for building future nests.

Across all of the experiments where I looked at choices between different colours of nest material (Chapters 2-5), males generally strongly preferred one colour over another (green over brown, blue over yellow and blue and yellow over red). As these preferences were not the same as males' preferences for food of the same colours (Chapter 3), the preferences for particular nest material colours might not be due to general colour preferences but instead be specific to the context of nest building. Why the males had these preferences is not clear. One possibility is that colour preference is genetically determined. This possibility is supported by our results from Chapter 3 where zebra finch males preferred the same colour as their fathers had (in most cases this was for the colour blue). However, this colour preference is flexible in that it can be affected by learning as an adult under particular conditions (Chapter 2). Thus it seems that there may be an interplay between unlearned

preferences, some of which are rather difficult to override through learning (a preferred colour was still preferred when the male experienced unsuccessful building in a nest of that colour; Chapter 2) and experience as an adult. Sargent (1965) also found that his birds did not prefer their least preferred colour (red) after building with it, but did for another also less-preferred colour (green; brown being the colour Sargent's zebra finches preferred). This flexibility in learning to use a different, previously less-preferred, colour may reflect the ecology of zebra finches, because in the wild they will build with a range of materials. Therefore, given this range of potential building material, it seems that males are not completely fixed in their initial colour preferences, and may only use them as a guide before learning from their own building experience

In addition to finding that young zebra finches did not copy the nest material colour of the nest from which they fledged, I also found that the nest structure was not copied from their father (Chapter 4). However, nests built by the same male were not similar to each other either. Village weaver males are also not repeatable in the nests they build, and Southern masked weavers are only repeatable to a small degree. In Chapter 6 I found that this lack of repeatability was also found in one particular aspect of this species' nest: the initial attachments. Individual birds did not use the same number of loops in their attachments, even when building at the same location on a branch. These findings, taken together, refute the assumption that nest-building is highly stereotyped, at least in the end-product of the behaviour. We now need to address why it is that such variability exists.

The number of nests a bird had built was important in explaining the variability I found in Southern masked weaver attachments (Chapter 6). As males used more loops when weaving their initial attachment as they gained building experience across a season, it is possible that they refined their motor skills involved in weaving as has been indicated to be the case in another species of weaver (Collias and Collias 1984). I also found that zebra

finches building with material and in a nest box they had not previously encountered, rapidly improved their handling skill of the material over a three-day test period (Chapter 7). These findings indicate that nest building in birds may involve some learning of the handling of the materials in question, and that this learning of the physical manipulation of material continues into adulthood and even after having built a few nests (as had the zebra finches in Chapter 7). Thus the finding in other species that birds are able to construct nests without the need for prior experience in a nest or building with nest materials (Hinde and Matthews 1958), is not evidence that learning plays no role in nest construction.

Nest building, tool use and construction behaviour

Construction behaviour is found across the animal kingdom, and as well as nest building includes web-building by spiders, dam-building by beavers, and many other behaviours (Hansell 2005). Past definitions of tool manufacture and use have been used to separate it from construction behaviour (Beck 1980), but there are at least some who consider that tool construction and nest building are both subsets of construction behaviour (Hansell and Ruxton 2008) and that nest construction involves the manipulation of materials in a manner synonymous to tool use (Shumaker *et al.* 2011). Indeed, even cases where the animal uses a tool without having constructed it itself could be considered to be similar to construction behaviour (Hansell and Ruxton 2008), as they both involve the manipulation of an unattached object external to the animal (Hansell 2005). Thus there is no *a priori* reason for assuming that tool manufacture and use and other animal constructions might have a different cognitive basis. However, despite this, tool manufacture and use have received a disproportionate amount of attention relative to other construction behaviours, because of the conjecture that they require more advanced cognitive abilities (Hansell and Ruxton 2008, Seed and Byrne 2010). There are two main reasons for this assumption. Firstly, some argue

that the rarity of tool use implies that only animals with specific cognitive abilities are capable of using tools (Hunt 2005). However, an opposing view to this is that tool use might have only evolved a few times because of the rarity of ecological situations where it is advantageous to use tools over anatomical adaptations (Hansell and Ruxton 2008). Secondly, because tool use is considered a hallmark of human cognition, some argue that ‘intelligence’ is a prerequisite for tool use, or at the very least tool-using animals can tell us something about the origins of human intelligence (Hunt 2000b). In contrast to this view, others have argued that animals that use tools are not cognitively ‘special’, and that there is no reason to assume that they should be more cognitively complex than animals that engage in other construction behaviour such as nest building (Hansell and Ruxton 2008).

Evidence that specific cognitive abilities are not required for tool manufacture and use but that they might depend on ‘domain-general’ cognitive abilities comes firstly from the evidence that non-tool users are capable of using tools in captivity (Tebbich *et al.* 2007, Bird and Emery 2009b, a, Emery and Clayton 2009, Auersperg *et al.* 2011) and can perform as well or even better than do tool-using species on tests of physical cognition (Seed *et al.* 2006, Teschke *et al.* 2011). Additionally, in Chapter 7 I demonstrated that zebra finches, which are not generally viewed as being particularly sophisticated in either their manipulation of material or in their physical cognition, performed in an equivalent manner to tool-using animals tested on a similar task (Chappell and Kacelnik 2002, 2004, Tebbich and Bshary 2004, Hunt *et al.* 2006). Just as tool-using animals have been shown to be able to select tools of ‘appropriate’ proportions (e.g. Chappell and Kacelnik 2002, Chappell and Kacelnik 2004, Visalberghi *et al.* 2009, Manrique *et al.* 2010, Manrique *et al.* 2011, Sabbatini *et al.* 2012), so zebra finches chose the most appropriate length of material suitable for building in a particular size of nest box (shorter material for the smaller entrance). These findings taken together suggest that since non-tool users have cognitive abilities that allow them to use tools

under certain circumstances, and nest builders behave in an equivalent manner, all these behaviours might arise from the same underlying processes. Tool use might then arise from particular ecological pressures providing the need or motivation for some animals to use tools, rather than from a capacity for specific abilities in physical cognition (Kacelnik 2009).

‘Advanced’ cognitive abilities for tool-using animals have been claimed in many cases but these are rarely set alongside other construction behaviours. For example, crows can use novel plants to function as tools (Hunt 2008) and chimpanzees can use one tool for multiple functions, as well using different techniques (Sanz and Morgan 2009), which have been reported as behavioural ‘flexibility’. However, birds can also use novel materials to build a nest (e.g. Igic *et al.* 2009, Antczak *et al.* 2010) and individuals may vary in how and what they build (Walsh *et al.* 2010, Walsh *et al.* 2011). Moreover, beavers respond flexibly and creatively to manipulations to their dams, weaverbirds mend experimentally damaged nests, and even spiders can flexibly alter their web-building to better catch flies (Wilsson 1976, Collias and Collias 1984, Heiling and Herberstein 1999). Tool-users within a particular geographical area sometimes vary in the tools they use in a manner that cannot be explained by ecological correlates (Hunt 2000a, Hunt and Gray 2003), which has been argued as evidence for social transmission and ‘culture’, but the same is true for some nest building birds (Mennerat *et al.* 2009c). Chimpanzees and New Caledonian crows can take years to learn how to make tools (Kenward *et al.* 2006, Lonsdorf 2006), but the same is true of chimpanzees and weaverbirds with regard to their nests (Bernstein 1962, Collias and Collias 1984, Fruth and Hohmann 1996, Videan 2006). However, these are simply examples and it is not until nest builders, tool manufacturers and other animal ‘architects’ are compared in thorough comparative analyses that speculations about the specificity of cognitive abilities relating to these behaviours can be confirmed.

Future work

There are a number of directions in which this research could be taken. Firstly, to answer the question of why it is that in zebra finches, adult learning seemed more important than juvenile or social learning in determining nest material choice, data should be obtained from other species. One hypothesis for why animals do or do not learn at particular stages of their life is that this reflects the animal in question's life history (reviewed in Shettleworth 2010). However, given that zebra finches both spend a number of weeks in their natal nest, and are a species that nests socially, it might be expected that these would be two opportunities for learning. In order to determine whether zebra finches are an anomaly in this regard, or if instead another factor explains why most learning of this aspect of building is through individual learning as an adult, nest building needs to be investigated in more bird species for comparison.

In parts of this thesis (Chapters 4, 6) and in previous studies (Walsh *et al.* 2010), we have attempted to elucidate building behaviour by looking at the end product. However, end-products that seem complex do not necessarily require complex behaviour (e.g. many invertebrate structures; Hansell 2005), and similar end-products can be constructed using different behaviours (Stuart & Currie 2002). Thus, in order to gain a greater understanding of the relationship between building behaviour and the end product (i.e. whether the behaviour of a species of bird reflects the nest it constructs), we need more detailed behavioural observations of the precise movements birds make in nest building and the steps they follow to complete a nest. We might expect that birds building more similar nests (e.g. all birds that build cup-shaped nests) would use more similar behaviours in creating those nests.

If different species of birds do differ in the movements they use to build their nests, a future experiment could address whether birds that build nests that require a greater repertoire of movements also have more 'advanced' physical cognition, or a superior causal

understanding of how objects relate to each other in contexts outside nest construction. This could be tested using standard tests of physical cognition (such as the trap tube task and variations of it; Visalberghi and Limongelli 1994, Povinelli *et al.* 2000, Tebbich and Bshary 2004, Seed *et al.* 2006, Bluff *et al.* 2007) on a range of bird species that differ in the size of their repertoire of movements and degree of physical manipulation needed for their nest building (e.g. varying from a species that uses just a few simple movements to a species that has a much larger repertoire). If a bird that builds a nest using a larger repertoire of physical movements also has a better causal understanding of how objects relate to each other in terms of ‘folk physics’, then we would expect these species to perform better on such tasks of physical cognition. Circumstantial evidence from tool-using birds would imply that this is not the case, as tool-using species (crows and woodpecker finches), which are typically thought to have the most ‘advanced’ physical cognition of avian species, do not build nests that appear the most complex. However, the reasoning behind this argument is questionable, given that animals that use tools do not necessarily have more ‘advanced’ physical cognition than animals that do not use tools (Tebich *et al.* 2007, Teschke *et al.* 2011), and since we are yet to compare nest building in tool-using and non-tool using species.

How birds causally ‘understand’ the nests they build (how they perceive and use cues from the nest) could also be investigated using experimental protocols that have been developed for testing whether tool-using animals ‘understand’ the tools they use (Seed *et al.* 2011). These tasks are designed to test whether an animal can transfer knowledge from one task to another (i.e. if they learn general rules about how objects relate to each other) or if instead they learn to associate more specific cues that do not transfer to another situation. For example, using a set-up similar to the one used in Chapter 7, birds could first be exposed to two or more different lengths of nest material appropriate for two or more different sizes of nest box entrance. After learning which materials are most appropriate for particular

entrances, non-functional properties of the materials could be changed (e.g. colour). The birds would then demonstrate whether they had learned the functional property (the size of the piece) or the non-functional (colour) cue associated with the piece by having to select between these novel materials. If birds use the functional features, they will continue to choose the most appropriate size of piece, regardless of the colour. The tendency of birds to learn a functional cue could further be investigated by manipulating the reliability of the non-functional colour cue. For example, capuchin monkeys learned to associate a non-functional feature (a handle) with a tool rather than the functional property of it (the length), however when non-functional feature was made variable such that it did not predict the function of the tool, then they learned the functional feature (Sabbatini *et al.* 2012). One caveat to such a protocol being applied to nest-building birds is that colour is also a cue by which birds select material. This means that if birds attend to colour more than to the structure of the material, this could be because colour is a more salient feature of the material to the birds than is the structure. To ensure this was not the case, birds would need to be tested prior to the experiment on a range of colours to pre-select colours that were not preferred over each other.

Finally, if we can discover which areas of the brain are involved in nest building, tool construction and tool use, this may help to reveal whether they share cognitive underpinnings. Although neuroimaging studies have highlighted some areas involved in human tool use (Lewis 2006) and crows have some enlarged brain structures compared to related non-tool using species (Mehlhorn *et al.* 2010) there have been no investigations into the areas involved in non-human tool use or manufacture. Similarly, to date there have been no studies investigating what areas of the brain might be involved in nest construction. Even if we find evidence (such as Chapter 7) that suggests that tool use and nest construction may be superficially similar under some experimental circumstances, data showing whether they

share neural substrates is needed to provide strong evidence for or against the specificity of the cognition involved in these behaviours.

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