



## The role of adult experience in nest building in the zebra finch, *Taeniopygia guttata*

Felicity Muth, Susan D. Healy\*

Schools of Biology and Psychology, University of St Andrews

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Whether learning plays a role in nest building in birds is largely unknown. Here we investigated whether the colour of nest materials used to build a first nest affected the subsequent nest material choices made by male zebra finches when building a second nest. Males were tested for their preference for green or brown nest material and then were provided with either their preferred or nonpreferred colour with which to build their first nest. The success of this nesting attempt was manipulated such that half of the breeding pairs had their eggs removed, while the other half were allowed to keep their eggs and fledge chicks. Males were then retested to determine which colour of nest material they now preferred. Males had strong initial preferences for one or other of the two colours of nest material. Males that built a nest with their preferred colour of nest material continued to prefer that colour after nesting, regardless of their breeding success in that nest. However, of the males that built a nest with material of their non-preferred colour, those that raised and fledged chicks from it subsequently preferred that colour of material for their second nest, while males that suffered a failed breeding attempt did not. Thus breeding experience can influence decisions relating to nest material choice in nest construction in the zebra finch. © 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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 & 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 & Ruxton 2008; Raby & Clayton 2009; Seed & 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 & 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 & Collias 1964). Like first-time builders,

these males with early deprivation tended to build nests with loose loops and ends (Collias & Collias 1964) in comparison to the more tightly woven nests of adult males. Similarly, nests built by wild, free-living southern masked weavers, *Ploceus velatus*, and village weavers, *Ploceus cucullatus*, become smaller and lighter over time (Walsh et al. 2010).

In addition to changes in weaving ability with experience, male village weaverbirds become increasingly discriminating in their choice of nest material as they mature, selecting grass and avoiding the toothpicks or raffia that they choose as juveniles (Collias & Collias 1964). Experience also appears to influence the choice of nest materials and building location in the zebra finch (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 nestbox will return to breed in the same type in subsequent seasons, while those

\* Correspondence: S. D. Healy, School of Psychology, University of St Andrews, St Mary's College, South Street, St Andrews, Fife KY16 9JP, U.K.  
 E-mail address: [sdh11@st-andrews.ac.uk](mailto:sdh11@st-andrews.ac.uk) (S. D. Healy).

that are unsuccessful are less likely to do so (for example, [Herlugson 1981](#); [Gavin & 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 logistically because 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 large variation has been documented both in the dimensions of their nests and in the materials used to build nests, within and among colonies ([Immelmann 1962](#) cited 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 well as in nestboxes ([Griffith et al. 2008](#)). 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 and its site could reduce the risk of predation in later nesting attempts. In our experiment, we tested males in breeding pairs for their initial preference for one of two colours of nest material shortly prior to nest building with either their preferred or nonpreferred colour. We examined only 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 has previously been shown to be 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, while 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 3 and 15 months of age and had been bred in captivity at either the University of St Andrews or the University of Glasgow, U.K. None of the birds had had previous experience of building a nest. Birds were kept on a 14:10 h 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 tablespoon of Haith's Egg Biscuit Food three times a week and daily once they had chicks. All breeding pairs were also given spinach once every 1–2 weeks. When not breeding, birds were housed in single-sex cages in groups varying from six to 20 birds. When birds were paired for nesting, they were moved to wooden cages (44 × 30 cm and 39 cm high) and provided with a wooden nestbox (11 × 13 cm and 12 cm high). 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. If so, they would have seen green and brown nest material being used.

### *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 no two pairs were of the same relatedness to each other. 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 Handy-cam camcorders. The nest material used was coconut fibre and hay, as is standard procedure in our laboratory, and was dyed green and brown using food colouring (Supercolor Ltd., Leeds, U.K.).

### *Test 1: Initial Colour Preferences*

To determine whether males preferred a particular colour of nest material, pairs were presented with green and brown material after 24 h of being caged together. Birds were provided with 3 g (1.5 g 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 with the nestbox hung in the centre of the back wall of the cage. The end of the cage at which each colour of nest material was placed was alternated between cages. The camcorder was focused on the nestbox and the area of the cage floor covered by the nest material, and pairs were filmed until the male had taken at least 10 pieces of material to the nestbox. The nestbox was checked by eye without any disturbance to the birds once an hour for the first 3 h and once every 2–3 h after that. After the male had added at least 10 pieces, the nestbox 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., Nottingham, U.K.). We considered that a male had made a 'choice' each time he took nest material of a particular colour to the nestbox and determined his preference based on the first 10 choices of material that he made. As well as recording when the male took nest material to the nestbox, 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 Preferred or Nonpreferred 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 nonpreferred colour (brown:  $N = 13$ ; green:  $N = 3$ ).

Nest material was provided twice a day at 0900 and 1400 hours until the first egg was laid (at around 6 days: [Zann 1996](#)). If the female did not begin to lay within 4 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 ( $N = 3$ ).

## Clutch Manipulation

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 2 more weeks the female was moved to a single-sex stock cage while the male remained with the chicks for a further 2 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 6–7 days, at which point the eggs were removed and frozen ( $N = 10$ ). These pairs were left with their nest for the following 24 h before being returned to the single-sex stock cages. The manipulation of breeding success was counterbalanced across the two colours of nest material.

## Test 2: Effects of Experience

Four weeks after the removal of their nest, pairs were reunited in individual cages with nestboxes as before. After 24 h, they were presented with 3 g of brown and 3 g of green nest material, filmed, and the male's preference was 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 effect of both breeding experience and whether males had built with their preferred or nonpreferred colour on the males' new preference, we fitted a generalized linear model (GLM) with a binomial error structure and logit link function. The dependent variable was the number of strands chosen 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 nonpreferred); 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 strands of the preferred colour chosen to the new number of this colour chosen (in the second preference test) using Wilcoxon signed-ranks tests.

We further addressed whether males explored both colours equally in Test 1 and Test 2 separately by comparing the number of times that males poked green and brown nest material during the time it took them to take 10 pieces of nest material to the nest. This was addressed using Wilcoxon signed-ranks tests for males that preferred green and males that preferred brown independently (for this test a 'preference' was eight or more strands of a particular colour taken to the nest during the test). To determine whether the tendency to explore both colours equally in Test 2 differed for males in different treatment groups, we compared the number of times males poked either the colour they had initially preferred or the colour they had not initially preferred, using Wilcoxon signed-ranks tests.

We also addressed whether there was any difference in the time (min) taken for males to take 10 pieces of nest material to the nestbox between Test 1 and Test 2 (overall and within the different treatment groups) using two-tailed paired  $t$  tests on log-transformed data.

All statistical analyses were carried out in PASW version 18.0.0 (SPSS Inc., Chicago, IL, U.S.S.).

## Ethical Note

All work carried out was approved by the University of St Andrews Animal Welfare and Ethics Committee. Eggs were removed from pairs at 6–7 days post incubation, as this is half way through the zebra finch gestation period (14 days), in accordance with Home Office regulations.

## RESULTS

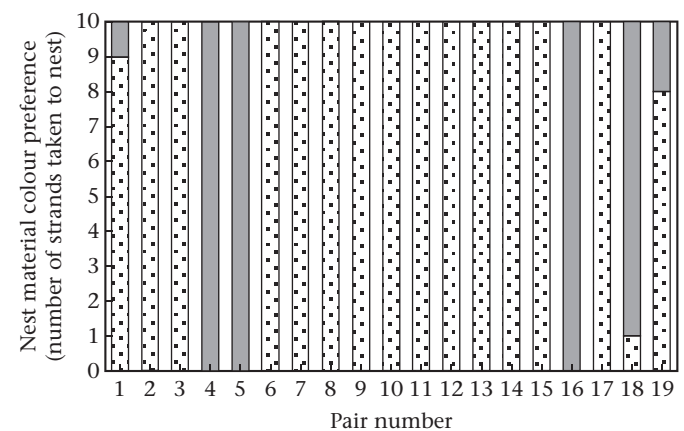
### Initial Colour Preferences

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 four preferred brown in the first test (Fig. 1). In the majority of cases 10 out of 10 strands of the preferred colour were chosen (chi-square test:  $\chi^2_1 = 8.895$ ,  $P < 0.01$ ; Fig. 1), and in the other three cases eight or nine out of 10 strands were chosen.

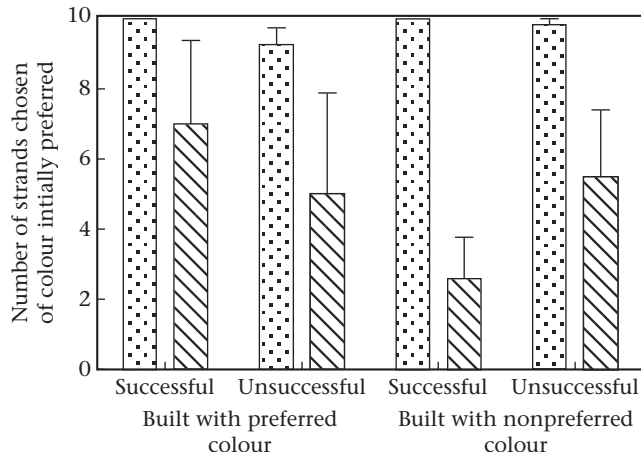
While there was a trend to explore (through poking) green nest material more often when the male was taking green to the nest, and likewise for brown, this was highly nonsignificant, and males explored both colours equally (Wilcoxon signed-ranks test: males that preferred brown:  $T = 0.365$ ,  $N =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

### Colour Preferences After Breeding Experience

Males that were allowed to build their first nest with nest 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 nonpreferred colour (GLM: likelihood ratio,  $LR = 7.559$ ,  $df = 1$ ,  $P = 0.006$ ; Fig. 2). Overall, whether a male experienced successful or unsuccessful breeding did not affect his preference for a particular colour of nest material after nesting (GLM:  $LR = 0.408$ ,  $df = 1$ ,  $P = 0.523$ ; Fig. 2). However, this was dependent on whether or not birds had built with their preferred or nonpreferred colour (GLM:  $LR = 11.673$ ,  $df = 1$ ,  $P = 0.001$ ; Fig. 2). Males that had built with their nonpreferred colour of nest material were more likely to develop a preference for it after nesting if they had experienced successful breeding, as they chose fewer strands of the colour they preferred initially, and therefore more of the other,



**Figure 1.** The number (out of a total of 10) of strands of nest material of the preferred colour taken to the nestbox by males during the first test for their preferred colour of nest material. Stippled bars: green strands; grey bars: brown strands.  $N = 19$ .



**Figure 2.** The average  $\pm$  SEM preference of males for the colour of nest material they preferred in the first preference test (measured as the number of strands of this colour taken to the nest) before (stippled bars) and after (striped bars) their breeding and nesting experience (in the four different treatments).

initially nonpreferred colour they had just built with. However, this was not true for males in pairs that had experienced unsuccessful breeding using their nonpreferred 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 nonpreferred colour and then experienced successful breeding (Wilcoxon signed-ranks tests: nonpreferred/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:  $T = -1.069$ ,  $N = 4$ ,  $P = 0.285$ ; Fig. 2).

Although 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-ranks 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 took six or seven strands of the preferred colour to the nest), they explored both colours equally (Wilcoxon signed-ranks test:  $T = 0.000$ ,  $N = 4$ ,  $P = 1.000$ ). Which treatment group an individual 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-ranks tests: nonpreferred/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:  $T = -0.365$ ,  $N = 4$ ,  $P = 0.715$ ).

While there was a tendency for males to take longer taking the 10 pieces of nest material to the nestbox 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: nonpreferred/successful:  $t_4 = -1.505$ ,  $P = 0.207$ ; nonpreferred/unsuccessful:  $t_5 = -1.132$ ,  $P = 0.309$ ; preferred/successful:  $t_3 = -0.670$ ,  $P = 0.551$ ; preferred/unsuccessful:  $t_3 = -0.347$ ,  $P = 0.751$ ).

## DISCUSSION

When first-time nest-building male zebra finches were offered a choice between green and brown nest material, most males (all but one) clearly preferred one or other colour. 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 nonpreferred colour increased their preference for that colour, but only if they successfully raised and fledged chicks from their nest.

These results support our prediction that zebra finches can learn to associate the colour of nest material with their breeding success in that nest. However, they do not 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. While males that built with their nonpreferred 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 curruoides*, that had reared offspring successfully in one year occupied the same territory and nestbox the following year, while of those that moved territories, 71.4% chose the same type of nestbox. Of the five unsuccessful breeders, two returned to the same territory and two out of three that moved used a different type of nestbox (Herlugson 1981). It appears that these birds may learn features of their nestbox 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 led 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 their 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, mostly green, to the other in their first preference test. 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 the further nine strands, 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, *Cyanistes caeruleus*) include green plant material in their nests, reducing the deleterious impact that nest bacteria have on nestling growth (Brouwer & Komdeur 2004; Gwinner &

Berger 2005; Mennerat et al. 2009a, b). 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 & 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 all the material we provided in our experiment 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 nest material over green. There are multiple possible explanations for this discrepancy. First, it could be because of differences in the nest material between experiments: Sargent used strands of coloured hessian while 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 nest 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 nest material. This potential effect of colour preferences being generalized across contexts requires further investigation. A suggestion that zebra finches may not generalize 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 to 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 green-banded males (Burley et al. 1982; Burley & Coopersmith 1987; Blount et al. 2003).

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 & Collias 1964; Walsh et al. 2010) it appears that there is a role for learning and memory in nest building in zebra finches. While this is far from the apparent sophistication shown in decision making in tool use, where birds also have to decide among appropriate physical materials (for example, Chappell & Kacelnik 2002; Tebbich & Bshary 2004), it may be that nest building has a greater cognitive component than is typically assumed.

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