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Colour preferences in nest-building zebra finches

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ABSTRACT

Some bird species are selective in the materials they choose for nest building, preferring, for example, materials of one colour to others. However, in many cases the cause of these preferences is not clear. One of those species is the zebra finch, which exhibits strong preferences for particular colours of nest material. In an attempt to determine why these birds strongly prefer one colour of material over another, we compared the preferences of paired male zebra finches for nest material colour with their preferences for food of the same colours. We found that birds did indeed prefer particular colours of nest material (in most cases blue) but that they did not generally prefer food of one colour over the other colours. It appears, then, that a preference for one colour or another of nest material is specific to the nest-building context.

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1. Introduction

Although birds construct nests to attract females (Jacobs et al., 1978) and to sleep in (Skutch, 1961), the nest's most important function is to hold and protect eggs and offspring (Hansell, 2000). A key aspect of nest construction is the selection of appropriate building materials. For example, materials may be chosen for their structural properties, such as using silk to bind other materials together or rigid sticks to form a stable platform (Hansell, 2000). Materials can also be chosen for a range of other functions such camouflaging the nest or eggs (Schuetz, 2005; Solis and De Lope, 1995; Hansell, 1996), attracting mates (Brouwer and Komdeur, 2004), reducing parasites and bacteria (Wimberger, 1984; Clark and Mason, 1988; Clark and Mason, 1985; Lafuma et al., 2001; Rodgers et al., 1988; Gwinner and Berger, 2005), increasing the condition of nestlings (Gwinner et al., 2000), or a combination of these. However, in some laboratory-reared birds, individuals have particular nest material preferences for reasons that are not always clear (Muth and Healy, 2011, 2012; Hinde and Steel, 1972; Collias and Collias, 1984).

One specific nest material 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, 2012) and captive-reared village weaverbirds *Textor cucullatus* preferred to build with green toothpicks rather than with toothpicks of other colours (yellow, blue, red, black and white). Perhaps, the most obvious explanation is that the birds use the colour of the material as an indicator of its function. 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 number of 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). Plant material can also be used to attract females (e.g. European starlings; Gwinner, 1997; Brouwer and Komdeur, 2004), threaten conspecifics (black kite *Milvus migrans*; Sergio et al., 2011) and act as camouflage (e.g. Solis and De Lope, 1995; Schuetz, 2005; Hansell, 1996). In these instances, it is plausible that the particular nest material is chosen based on a cue relating to the function that it serves (e.g. the particular colour or odour). Alternatively, a chosen cue such as colour may reflect the bird's visual capacities, whereby some colours are more conspicuous than others. Positive (or negative) experiences with food items or materials of particular colours might also lead to a general colour preference. If either of these were to explain preferences for particular colours of nesting material, then we would expect to see those preferences exhibited in contexts other than nest building.

To investigate this possibility, we compared the preferences of captive zebra finches for different colours of nest material to their

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preferences for food of the same colours, as zebra finches 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). To do this we presented the birds 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.

2. Methods

2.1. 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. All birds were reared in nests built from un-dyed material (hay and coconut fibre). The males and females had all been used in an earlier experiment (Muth and Healy, 2011) and in the current experiment were paired in the same pairs as for that earlier experiment. In the previous experiment, they encountered both green and brown nesting material and males chose between small amounts (3 g) of green or brown material, before building a nest of either entirely green or brown material (determined by the experimenter), where the females laid eggs. The males then chose between 3 g of green and 3 g of brown material a second time. Although none of the birds had encountered the colours of nest material or food that we used in the current study, we address possible effects of their earlier colour preferences and experience in the results section. 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 1 cm 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.

2.2. Experimental protocol

To manipulate the colour of the food and nesting material, 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 h 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 (Fig. 1).

We carried out the 10 food preference trials such that each food trial (e.g. trial 1, trial 2 etc.) for each pair was conducted within three days of each other, with at least one day between each trial per pair. We randomised the order of the nest material preference trials by randomising the order of the pairs, and then starting each trial after the previous pair had finished (filming one pair at a time). We conducted trials over a three-week period in November and December 2010 and the birds were then returned to stock cages

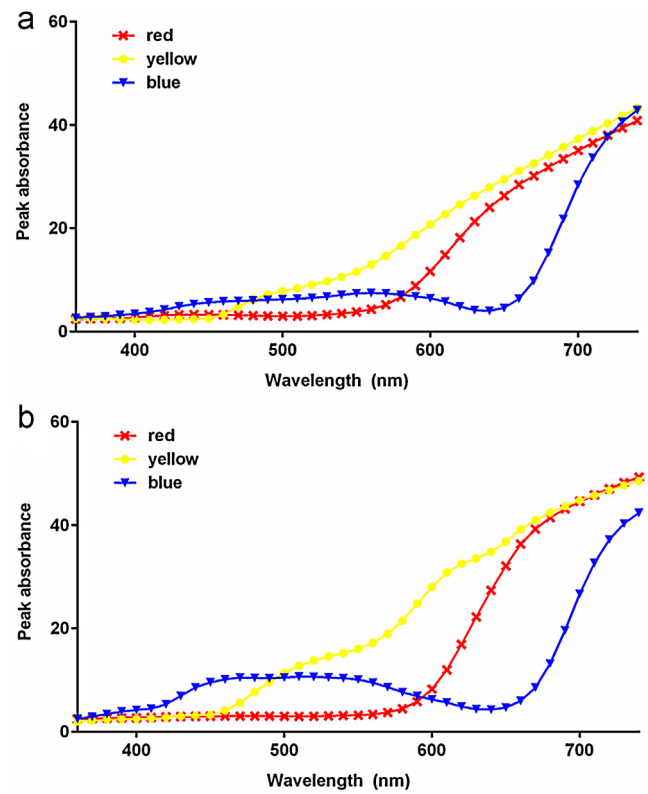

Fig. 1. The peak absorbance across wavelengths of (a) the three colours of nest material and (b) the three colours of food. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for six weeks. We then 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).

2.3. Nest material colour preferences

24 hours prior to the nest material colour preference test, we provided pairs with a wooden nest box measuring 11 × 13 × 12 cm (width × length × height), which was hung in the centre of the back wall of the cage. At the start of the preference test, we gave birds 3 g 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.

As in zebra finches only the male typically collects nest material during the initial stages of nest building (Zann, 1996), so we tested only the nest material colour preferences of the male but noted any instances of female building.

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 single or a few strands) 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 (see Muth and Healy, 2011). One male attempted to

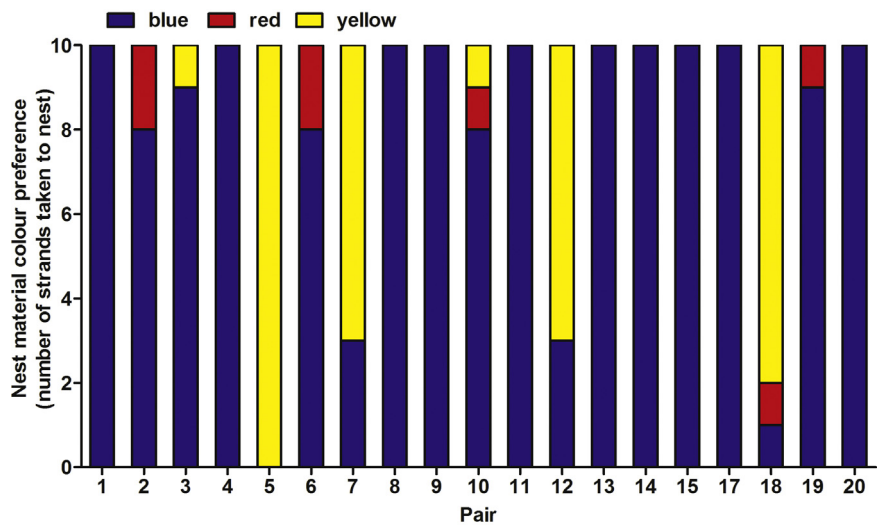

Fig. 2. The nest material colour preferences of the 19 paired males, measured as the number of pieces of each material taken to the nest box of the first 10 pieces taken. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

build on his water dispenser rather than in the nest box and we included these data in the analyses.

2.4. Food colour preferences

We tested food colour preferences over 10 trials per pair. Each trial lasted five minutes, 30 s, 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 × 11 × 3.5 cm, width × length × height), placed along the front edge of the cage. Each dish contained 23 g of blue, red or yellow seed. The locations of the dishes were pseudo-randomised 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.

2.5. Data analysis

Although we measured both the number of pecks to the food of each colour and the time spent visiting a food dish, these were strongly positively correlated (Pearson's $r(199) = 0.950$, $p < 0.001$). Therefore, we used the number of pecks as our measure of food preference in all further analyses. Parametric analyses were carried out in R version 2.15.1 and non-parametric analyses were carried out in PASW v. 18.0 and IBM SPSS 21.

3. Results

3.1. Nest material colour preferences

17 males preferred one colour of nesting material more than either of the other two (choosing eight or more strands of one colour): 15 males preferred blue, two preferred yellow and none preferred red. The other two males chose yellow material seven times, blue three times and did not build with red material (Fig. 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 yellow seven times followed by blue three times. In the second pair, the female took one red piece and the male then chose a majority of blue pieces. In the third pair, the female chose red, then yellow, then red material, the male then chose five blue pieces, the female then chose a blue piece, and the male then chose five more blue pieces.

3.2. 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 and contained a large number of zeros. 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: $\chi^2_2 = 6.24$, $p < 0.05$). As we conducted 16 tests, we might expect ~1 of these to find a male preference by chance. 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: $\chi^2_2 = 6.22$, $p < 0.05$;

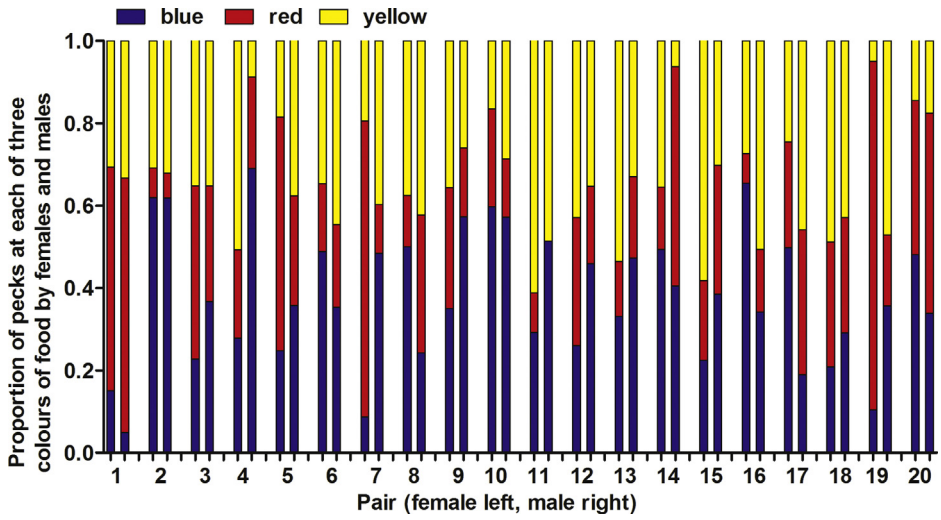

Fig. 3. The mean (+/− standard errors) proportion of blue, red and yellow food pecked at by paired males and females across the ten test trials. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$\chi^2_2 = 6.50$, $p < 0.05$), 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). Males and females within a pair also did not peck at the same colour as each other within each trial more often than chance (Fig. 3). To show this we carried out a generalised linear model using the glm() function, excluding the data from trials where the male or female did not peck at food at all ($n = 23$). With the proportion of pecks at a particular colour as the dependent variable, we included the categorical factors pair (1–20), trial (1–10), sex (male, female), colour (blue, red, yellow). Comparing models with and without the factor 'pair' using the anova() function and comparing AICs showed that including 'pair' did not improve the fit of the model (AIC with 'pair' included = 20180.85, without = 20142.94).

3.3. 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). As food colour preferences may have been weaker than nest colour preferences but still correlated with them, we also compared the proportion of blue, red and yellow food at which the birds pecked within the 15 individuals that preferred blue nest material. We carried out a general linear mixed model using the lme() function in the nlme package (Pinheiro et al., 2010) with the dependent variable being the mean proportion of pecks at a particular colour by a male (across the 10 trials), and included the fixed factor 'colour' (blue, red or yellow) and random factor 'pair' (1–15). The males that preferred blue nest material did not peck more at any particular colour ($F_{2,28} = 2.84$, $p = 0.075$; Fig. 4).

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

Pair number	Food colour preference	Nest material colour preference
11	Blue/yellow	Blue
14	Red/blue	Blue
10	Blue	Blue
1	Red	Blue

3.4. The role of previous experience

Although none of the birds used in the current experiment had experienced blue, yellow or red nest material prior to this experiment, they had experienced brown and green material (Muth and Healy, 2011). That previous building experience did not explain the overwhelming preference for blue material in the current experiment (of the 15 pairs of birds that preferred blue, nine had previously built with green and six with brown; χ^2 test: $\chi^2_1 = 0.6$, $p = 0.439$). In that earlier experiment, we tested their

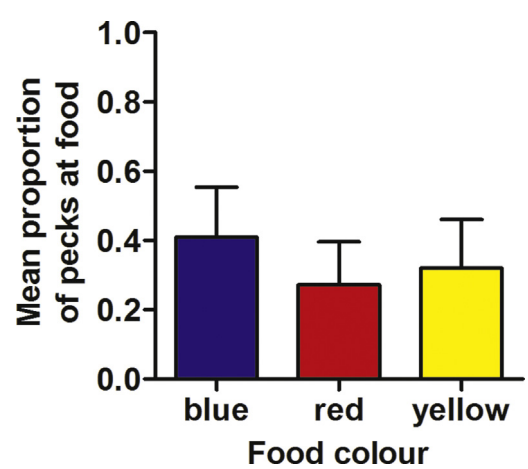

Fig. 4. The mean (+/− standard errors) proportion of pecks at blue, red and yellow food by the 15 birds that preferred blue nest material. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

colour preference twice but their second preference also did not explain the overall preference for blue material we observed in this experiment (of the 15 pairs of birds that preferred blue, eight had previously preferred green, six had preferred brown and one male did not demonstrate a preference; χ^2 test: $\chi^2_1 = 0.286$, $p = 0.593$; See supplementary material for summary table of previous nest material experience).

4. 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 (or females) preferred food of a particular colour. Therefore, it appears that the colours nest-building birds preferred in this study are specific to the building context.

The strong preference for blue (over red or yellow) nest material is consistent with birds' colour preferences in a previous study using a different group of zebra finches (Muth and Healy, 2012), where 46/65 males (of two generations) preferred blue nest material to yellow. The current 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). However, it is unclear why blue was the preferred colour in this or our earlier experiment. In another earlier experiment (Muth and Healy, 2011), most of the birds used in the present study initially preferred green over brown nesting material and as blue is relatively close to green on the visible spectrum, their preference for blue may be due to the birds generalising across the colours. However, some of those birds did switch their colour preference from green to brown material (a composite colour made up of green and red) after experiencing a successful breeding attempt, suggesting that that their colour preferences are not simply a product of their visual processing. Since there was little variation in the colour preferred in this experiment (as most birds preferred blue) we were unable to compare whether there was a relationship between the birds' previous preference (between green and brown) and their preference in the current experiment. An alternative sensory explanation might be that the blue material was more conspicuous than the yellow material relative to the background on which the materials were presented (a pale brown). However, if this was the case, it is unclear why the birds would prefer to build with a more conspicuous material.

In contrast to their marked preference for one of the colours of nest material, the birds did not prefer any of the three colours of food. We think it unlikely that the lack of preference is due to an inability to discriminate among the different food colours, as the birds were capable of discriminating among nest material of the same colours and other zebra finches in a previous captive study were able to use food colour (red and green) to discriminate among differently coloured foods (Katz and Lachlan, 2003). Moreover, we know of no previous studies in zebra finches finding a preference for food based on colour. Captive zebra finches may prefer the food they experienced as fledglings as in Rabinowitch's (1969) experiment where birds raised on one of three types of seed (white millet, red millet or canary seed) generally preferred to eat that type of seed as adults (Rabinowitch, 1969). However, even in this instance it is not clear that the birds used the seed colour to discriminate among these options. If early experience of food does lead to food colour preferences, in our experiment we would have expected the birds to prefer the yellow seed as it was most similar to the pale brown seeds that they ate as fledglings and up until this experiment. That they did not may be because they had also experienced a range of colour in their foods (including green fresh vegetables such as spinach and cucumber and the white and pink of the cuttlebone hanging in their cage), and this experience with a diverse range of food colours may have reduced any neophobic response they may have had to less familiar food colours, and thus reduced any strong colour preferences.

Foraging is not the only context in which colour preferences might be evident. 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 and Coopersmith, 1987; Burley et al., 1982; Hunt et al., 1997; Simons & Verhulst, 2011, Weisman et al., 1994). However, these mate choice colour preferences would not explain the preferences for the colour of nest material that we observed.

In conclusion, like colour preferences that occur in the context of mate choice, zebra finch 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 as an indicator of its function (e.g. for camouflage).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2013.07.002.

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