Food preference and copying behaviour in zebra finches, *Taeniopygia guttata*

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ABSTRACT
As a social species zebra finches might be expected to copy the food choices of more experienced conspecifics. This prediction has been tested previously by presenting observers with two demonstrator birds that differ in some way (e.g., sex, familiarity), each feeding on a different colour food source. However, if the observer subsequently exhibits a preference, it is unclear whether it has copied the choice of one demonstrator or avoided the choice of the other. Furthermore, this choice may actually be influenced by pre-existing preferences, a potential bias that is rarely tested. Here we examine whether apparent copying or avoidance can be explained by pre-existing preferences. In Experiment 1, observers had the opportunity to watch a conspecific forage from one of the two differently coloured food hoppers. In Experiment 2, the observers did not have this opportunity. In both experiments observers were subsequently tested for their food hopper preference and all but one preferred one colour over the other. In Experiment 1 some observers showed evidence for copying, while others seemed to avoid the colour preferred by the demonstrator. In Experiment 2 females generally preferred the white hopper. Pre-existing colour preferences could, therefore, explain the apparent copying/avoidance we observed.

Keywords: Avoidance; Colour preference; Copying; Food choice; Social learning; Zebra finch
1. INTRODUCTION

Zebra finches *Taeniopygia guttata* have served as a laboratory model for studying a range of psychological processes (Healy et al. 2010), most notably vocal learning (e.g., Immelman 1969; Slater et al. 1988; Mello and Clayton 1994) and mate choice (e.g., Adkins-Regan 2002; Riebel 2009). In addition to being vocal learners and perhaps because zebra finches are a highly social species (Zann 1996), it has been assumed that they should copy each other’s food choices (Giraldeau et al. 1990). Surprisingly, however, only a handful of studies have reported that zebra finches do, indeed, follow conspecifics’ food preferences and then only under some circumstances: zebra finch females copy food colour choice of demonstrators when they are male while males copy food colour choices of demonstrators of either sex (Benskin et al. 2002; Katz and Lachlan 2003). The decision as to which male to choose appears to depend on details such as colour of leg band and familiarity: males and females prefer the demonstrator’s food colour when the male demonstrator wears a red leg-band but not when he wears a green leg-band (Benskin et al. 2002) while males will also copy the food colour choice of familiar, but not unfamiliar, male demonstrators (Benskin et al. 2002).

Furthermore, zebra finches will also discriminate among demonstrators based on the size of the brood in which those demonstrators were reared: male observers copied males that were reared in large broods while female observers copied females from broods of a size similar to their own (Riebel et al. 2012). There appears to be little consistency in the variable by which demonstrators differ and on which choice is based, suggesting there are a number of specific, complex conditions under which social learning may occur in this social species (Laland 2004).

There is also an alternative explanation for these data. In all of these previous studies, observers were presented with two demonstrators, where one demonstrator fed from a food source of one colour and the other demonstrator fed from the alternate food source. By
showing conspecifics feeding from both colours to an observer, however, does not allow the experimenter to distinguish whether subsequent observer colour preferences are due to the observer copying the choice of one demonstrator or to avoiding the choice of the other demonstrator. Furthermore, it is not clear whether pre-existing biases would not explain the data just as well. As recent research shows that zebra finches have pre-existing colour preferences for both nesting material and food colour (Muth and Healy, 2011; 2012; Muth et al. 2013; Rosa et al. 2012) it remains unclear whether apparent copying behaviour found in previous studies might be explained by individuals’ pre-existing colour preferences because preferences for colour in absence of social demonstration were not assessed.

Therefore, here we examined firstly, whether zebra finches copy a demonstrated food option when that item is offered in the presence of a non-demonstrated item option. We presented male and female observer zebra finches with only one male or female demonstrator, which ate from only one of two differently coloured hoppers, to test whether hopper colour preferences shown by zebra finches are due to copying or to avoidance of the colour choice of conspecific demonstrators (Experiment 1). Secondly, we tested whether or not zebra finches have pre-existing colour preferences for food hoppers (Experiment 2).

2. METHODS

2.1 Subjects

The subjects were 85 adult zebra finches (42 male, 43 female) that were bred at the University of St Andrews (23 male, 20 female), the University of Glasgow (16 male, 17 female), or obtained from a local pet store (3 male, 6 female). All birds were housed in cages of same-sex individuals (8 - 26 individuals per cage, cage size either 140 × 71 × 122 or 100 × 50 × 50 cm) and kept on a 14:10 light:dark cycle with temperature at ~20˚C and humidity at ~ 50%. When not in the experiment birds were given free access to mixed seed, vitamin-
supplemented water, cuttle bone, oystershell, and vitamin block. At the end of the experiment, the birds were returned to single-sex group housing in the bird facility at the University of St Andrews.

All birds were tested between 04 March 2013 and 27 April 2013. All work described here is in accordance with ASAB ethical guidelines and was approved by the University of St Andrews Animal Welfare and Ethics Committee.

2.2 Apparatus

The experiments were carried out in two test rooms. Each test room contained a demonstrator cage, an observer cage, and stock cages of same-sex zebra finches (2 of each sex) located either 150 or 180 cm across the room from the experimental cages so that test birds were not visually or acoustically isolated from conspecifics.

The cages (100 × 50 × 50 cm) for the demonstrator and observer birds were identical except for the perch arrangement and the position of the coloured experimental food hoppers (see Fig. 1). Each cage contained two food and two water bowls, a cuttlefish bone and a vitamin block. A distance of 30 cm separated the demonstrator cage from the observer cage. A white opaque barrier between the cages prevented visual, but not vocal, interaction between the birds. The demonstrator cage contained three perches, two of which were located on the side of the cage that faced the observer cage. The observer cage contained six perches, two on each side of the cage and two on the back of the cage. During the observation and test phases (described below) coloured food hoppers (one black, one white, wrapped in coloured opaque electrical tape) were attached to each cage. Each cage contained two bird box cameras (SpyCameraCCTV, Bristol, UK) connected to a laptop computer.

Food was provided to the birds in the stock cages in the experimental room in transparent grey bowls, not food hoppers. These same grey transparent food bowls were used
in the observer and demonstrator cages before the experimental trial started. The birds that
served as observer in Experiment 1 and as controls in Experiment 2 were not housed in the
stock cages in the experimental room and did not view any experimental trials. In the stock
cages for observer and control birds’ food was delivered in metal, green, clear and white
bowls on the floor of the cage and transparent food hoppers attached to the side of the cage.

2.3 EXPERIMENT 1

2.3.1 Procedure

Each trial lasted approximately 24 hours. Between 14:30 and 15:30 hr on Day 1, one bird
was placed in the demonstrator cage and another bird was placed in the observer cage. At
this time, the opaque barrier was in place so the demonstrator and observer birds were not in
visual contact with one another, but both could see birds in the stock cages across the room.
On Day 2, food was removed from both cages for two hours, starting two hours after light
onset. Cage floor trays were replaced with clean ones so that birds could not eat spilled food
during this time.

There were two phases in each trial: the observation phase followed by the test phase.
The observation phase began after the two-hour food deprivation period. During the
observation phase, one black and one white food hopper were attached to the demonstrator
cage on the side of the cage facing the observer cage (Fig. 1). Only one food hopper
contained seeds. During the 30-minute observation phase the opaque barrier between the
demonstrator and observer cage was removed.

For the test phase, which occurred at the end of the 30 minute observation period, the
opaque barrier was returned and one black and one white food hopper, each containing seed,
were attached to the back of the observer cage (Fig. 1). The test phase lasted 60 minutes. At
the end of the test phase both birds were returned to their stock cages, food cups were
returned to the experimental cages, and a new bird was placed in each cage for testing the
following day. The colour and location of the black and white food hoppers were
counterbalanced across all conditions and the birds’ behaviour during the observation and test
phases was recorded via the cameras to be scored at a later date.

68 adult zebra finches, 34 males (18 from St Andrews, 13 from Glasgow, 3 from local
store) and 34 females (15 from St Andrews, 15 from Glasgow, 4 from local store) were used
in Experiment 1. A different demonstrator bird was used on all but two trials; two birds (one
male and one female, both from Glasgow) were used as a demonstrator in two trials each.

Birds were pseudo-randomly assigned to the following four experimental groups: (1) female
demonstrator with male observer (n = 9); (2) male demonstrator with female observer (n = 8);
(3) female demonstrator with female observer (n = 9); and (4) male demonstrator with male
observer (n = 9).

2.4 EXPERIMENT 2

2.4.1 Procedure

In Experiment 2, two cages were set up 30 cm apart, both laid out in the same way as for the
observer cage in Experiment 1 (see Fig. 1). We followed the same procedure as in
Experiment 1, except that during the observation phase both birds remained without food for
30 minutes, thus preventing them from acquiring social information about each other’s food
hopper preferences. We tested a total of 18 birds, 9 male (5 from St Andrews, 3 from
Glasgow, 1 from local store) and 9 female (5 from St. Andrews, 2 from Glasgow, 2 from
local store) in Experiment 2. None of the birds used in Experiment 2 were used in
Experiment 1 with the exception of one male from a local store that was used as a
demonstrator in Experiment 1 after being tested in Experiment 2.
2.5 Scoring and Statistical analysis

From the video recordings of each trial the number of pecks delivered to each food hopper by the demonstrator and the observer was measured and the latency in seconds, from the start of the trial until the first peck at a feeder. To quantify food hopper colour preference we calculated the following measures for Experiment 1: (1) for each demonstrator, the proportion of pecks delivered to the hopper containing seed, and (2) for each observer bird the proportion of pecks delivered to the food hopper colour used by the demonstrator.

We first ran tests to determine if demonstrators behaved differently towards the different coloured feeders and if male and female demonstrators behaved differently from one another because previous research has indicated that feeding activity of demonstrators affects observer behaviour (Katz and Lachlan, 2003). We conducted independent t-tests to test for differences in the proportion of pecks delivered by the demonstrators to the feeder that contained seed (1) when the demonstrated feeder was black or white, (2) when the demonstrator was a male or a female, and (3) when the demonstrator/observer pair was mixed-sex or same-sex.

We used the binomial test for dichotomous data to determine whether the proportion of responses differed significantly from no-preference (i.e., 0.5) for each observer. Each observer could then be classified as (1) having preferred the same colour food hopper as the demonstrator, (2) having preferred the hopper colour that was opposite to that of the demonstrator, or as (3) having no preference. Based on these three classifications we then used univariate ANOVAs to test for differences in demonstrator behaviour for each category of observers. This would allow us to examine whether observers were likely to behave according to differences in demonstrator behaviour. We carried out one-sample Wilcoxon signed-rank tests on the proportion of responses by the observer to the colour of feeder used by the demonstrator (in Experiment 1) or to the black feeder (in Experiment 2).
Experiment 1 we conducted a chi-square test to test for differences in observers’ behaviour (preferring the same or the opposite colour food hopper that was preferred by the demonstrator) according to the colour of the feeder (black or white). This allowed us to test if observer behaviour was due to the colour preference of the demonstrator. All the results that we report are means ± standard error. We scored preference for Experiment 2 as described for Experiment 1 but we scored all of the data according to proportion of pecks to the black feeder. We used the binomial test for dichotomous data to determine whether the proportion of responses differed significantly from no-preference (i.e., 0.5) for each observer. Each observer bird could then be classified as (1) having preferred the black hopper, (2) having preferred the white hopper, or as (3) having no preference. We carried out one-sample Wilcoxon signed-rank tests on the proportion of responses by the observer to the black hopper.

3. RESULTS

3.1 EXPERIMENT 1

Across all trials (N = 35, one trial per observer) one demonstrator and three observers did not feed, leaving the total number of trials for each experimental group as follows: (1) female demonstrator/male observer (n = 8), (2) male demonstrator/female observer (n = 7), female demonstrator/female observer (n = 8), and male demonstrator/male observer (n = 8). One female demonstrator had seed in the black hopper but pecked exclusively at the white hopper (total pecks = 92, proportion of pecks to white = 1.0), so we scored this trial as if the white hopper had been demonstrated.

3.1.1 Demonstrator performance
Although demonstrators preferentially pecked at the food hopper that contained seed (proportion of pecks 0.96 ± 0.010), they allocated a significantly greater proportion of pecks to the baited food hopper when the hopper colour was white (0.988 ± 0.009) than when it was black (0.931 ± 0.020, Independent-samples t-test: \( t_{29} = -2.545, P = 0.017 \)). Male and female demonstrators did not differ in the proportion of pecks they made to the baited food hopper (male: 0.969 ± 0.011; female: 0.951 ± 0.022, Independent-samples t-test: \( t_{29} = 0.738, P = 0.467 \)). Male and female demonstrators did not differ in the proportion of pecks delivered to the baited food hopper when demonstrating to a different-sex observer (i.e., female demonstrator/male observer or male demonstrator/female observer, 0.960 ± 0.065) or same-sex observer (i.e., male demonstrator/male observer or female demonstrator/female observer, 0.960 ± 0.072, Independent-samples t-test: \( t_{29} = 0.002, P = 0.999 \)).

### 3.1.2 Observer performance

#### 3.1.2.1 Individual data.

All birds preferred one coloured food hopper over the other. Across all trials (31 total, one per subject), using proportion of pecks (range: 81-620 pecks) as the behavioural measure, 24 birds’ preference scores differed significantly from 0.5. The binomial test could not be performed on the remaining seven birds because these individuals exclusively ate from only one food hopper colour (i.e., preference = 1.0) so these individuals clearly deviated from chance performance. Overall birds did not choose the same hopper colour as demonstrators: 51.61% (16/31) of the observer birds preferred the food hopper colour from which the demonstrator ate and 48.38% (15/31) preferred to eat from the food hopper colour that was not the colour of hopper from which the demonstrator ate (Wilcoxon signed-rank test, \( W = 256.5, N = 31, P = 0.867 \)).
3.1.2.2 Group data.

For males observing female demonstrators, seven of eight birds preferred the food hopper colour of the demonstrator (Fig. 2, panel a), and one preferred the food hopper colour that was not that demonstrated (Wilcoxon signed-rank test, $W = 28.5, N = 8, P = 0.141$). For females observing males, two of seven birds preferred the food colour hopper of the demonstrators (Fig. 2, panel b) and five preferred the food hopper colour that was not that demonstrated (Wilcoxon signed-rank test, $W = 9.5, N = 7, P = 0.443$). For the females observing females, four of eight birds preferred the food hopper colour of the demonstrator (Fig. 2, panel c) while the other four preferred the food hopper colour that was not that demonstrated (Wilcoxon signed-rank test, $W = 15.5, N = 8, P = 0.726$). For the males observing males, three of eight birds preferred the food hopper colour of the demonstrator (Fig. 2, panel d) while five preferred the food hopper colour that was not that demonstrated (Wilcoxon signed-rank test, $W = 15.0, N = 8, P = 0.674$). Across all birds, in the 16 trials where observer birds preferred the colour choice of demonstrator birds, 11 demonstrators ate from white and five ate from black food hoppers. A chi-square test indicated that overall, birds were more likely to prefer the colour used by the demonstrator if the demonstrator fed from the white, compared to the black feeder (Chi-square test: $\chi^2_{31} = 3.88, P = 0.049$, see Fig. 3).

The choices of the observers, whether they preferred the colour of the demonstrator (i.e., copy) or preferred the opposite colour (i.e., avoid), cannot be explained by differences in demonstrator behaviour: demonstrators’ proportion of pecks delivered to the demonstrated colour (copy $0.970 \pm 0.017$, avoid $0.951 \pm 0.018$, ANOVA: $F_{1,29} = 0.627, P = 0.435$); demonstrators’ latency to feed (copy $303.25 \pm 90$, avoid $438.8 \pm 93$, ANOVA: $F_{1,29} = 1.103, P = 0.302$); or demonstrators’ number of pecks to the demonstrated colour (copy $226 \pm 25$, avoid $178 \pm 26$, ANOVA: $F_{1,29} = 1.730, P = 0.199$).
3.2 EXPERIMENT 2

Across all trials (N = 18, one per bird), using proportion of pecks (range: 151-636) as the behavioural measure, six birds’ preference scores were significantly different from 0.5. One bird had no preference for feeder colour. The binomial test could not be performed on the remaining 11 birds because these individuals exclusively ate from only one food colour so these individuals clearly deviated from chance performance (see Fig. 4, panels a and b). Seven of eight females preferred the white feeder, and one female had no preference. Six of nine males preferred the white feeder, while three males preferred the black feeder. A Wilcoxon signed-rank test indicated that, as a group, females preferred the white feeder to the black one (Wilcoxon signed-ranks test: W = 1, N = 9, P = 0.01), while males, as a group, did not prefer one colour hopper over the other (Wilcoxon signed-ranks test: W = 14, N = 9, P = 0.299).

3.2.1 Further analysis of demonstrator behaviour from Experiment 1

In Experiment 1, above, demonstrators delivered a significantly greater proportion of pecks to the baited hopper when that hopper was white compared to black. Given that the females in Experiment 2 preferred the white food hopper in the absence of demonstration, while males did not, we conducted further analyses on the data from Experiment 1. Specifically, we now analysed female and male demonstrator behaviour separately with respect to behaviour towards the baited hopper when that hopper was white versus when the baited hopper was black. We re-ran this analysis separately for female and for male demonstrators and found that the result held for females but did not for males (Fig. 5). That is, female demonstrators allocated a significantly greater proportion of pecks to the baited food hopper when the hopper colour was white (0.998 ± 0.001) than when it was black (0.897
The male demonstrators did not peck the baited hopper more when it was white (0.976 ± 0.018) compared to black (0.961 ± 0.014, Independent-samples t-test: $t_{14} = -0.702, P = 0.494$).

4. DISCUSSION

In Experiment 1, zebra finch observers preferred one coloured food hopper over the other. This colour preference, however, cannot be explained by the colour preference of the demonstrator. In Experiment 2, all but one of the zebra finches without experience watching demonstrators preferred one colour hopper over the other. Furthermore, we found that female zebra finches preferred to feed from white food hoppers while male zebra finches did not.

In Experiment 1, we found apparent evidence for copying by some of the birds while the remaining birds’ strong preferences could be interpreted as avoidance. Superficially, these data might appear to contrast with the findings of Riebel et al. (2012) whose zebra finches tested (nine, both male and female) all copied the food colour choice demonstrated to them, regardless of the colour of hopper demonstrated (black or white). In that experiment, however, Riebel et al. used two demonstrator birds, housed individually, to demonstrate the same food hopper colour choice simultaneously to the observer. In line with the copy the majority strategy outlined in Laland (2004), two demonstrators both feeding on the same option as in Riebel et al. may have been a strong enough social stimuli to induce copying behaviour in the observer. Our sole demonstrator may not have provided sufficient social information to induce copying behaviour in the observer.

The outcome of Experiment 2 suggests that zebra finches have strong individual pre-existing colour preferences. Furthermore, evidence from both experiments show that females strongly preferred white food hoppers. The colour preference would be consistent with
Zann’s (1996) suggestion that the white colour of the rump of zebra finches, which are highly conspicuous against the background of grass when flocks are foraging in Australia, may serve as a releaser for birds flying overheard to join the foraging group. This visual signal may be particularly salient in a foraging context because zebra finch flocks, which are usually highly vocal, can be uncharacteristically silent. If this joining behaviour of wild zebra finches was conserved across lab bred populations, however, we would have expected our males, in addition to our females, to have preferred the white coloured food hoppers, which they did not. Strong colour preferences in zebra finches have been observed previously within and beyond food (green or purple millet: Rosa et al. 2012; blue nest material preferred to yellow: Muth and Healy 2012), although the reason for such colour preferences is not clear. Specific colour preferences do not, however, appear to be species-typical as Reibel et al. did not observe a female preference for white over black hoppers, hence our use of these colours in our experiments (Riebel et al. 2012).

Such strong unexplained pre-existing colour preferences suggest that the best approach might be to assess whether individuals have pre-existing preferences prior to exposure to a demonstration. Indeed, after observing pre-existing preferences led Rosa et al. (2012) to conclude that variation in social learning may not be due to circumstance but to the individual themselves. They found that zebra finches varied in the extent to which their initial preferences changed after viewing a demonstrator interacting with their initially un-preferred option and that the more an individual sampled its environment, presumably acquiring personal (asocial) information while doing so, the less likely that individual was to change its initial preference after viewing a conspecific demonstration. Furthermore, increasing levels of pre-natal stress in Japanese quail (Coturnix japonica) appear to result in individuals that are more likely to copy the food colour/location demonstrated to them than
are untreated individuals, whereas birds that had been subjected to post-natal stress are more likely to avoid the food colour/location demonstrated to them (Boogert et al. 2013).

Taken together, these studies suggest that we should not assume that, even if the species is considered to be social, all individuals do copy behaviour of conspecifics. Instead, ontogenetic factors (including those observed by Riebel et al. 2012) may contribute to individual differences in social information use. Such frequency-dependent use of social information is expected if social groups are composed of both individual who are likely to copy behaviour of others (*information scroungers*), and those individuals who avoid the behaviour of the demonstrators (*information producers*: Laland 2004). Coupled with our data, these recent findings suggest that acquisition and/or use of social information is dependent on both the observer and the demonstrator and not just qualities of the demonstrator as is often assumed.

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References


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Figure captions

Figure 1. Scale drawing of top-down view of the demonstrator and observer cages. The dashed line between the cages represents the opaque barrier that was in place at all times except during the observation phase. The food bowls on the front of the cage were removed two hours prior to the start of the observation phase. The location of the coloured food hoppers was counterbalanced between the two perch locations on each trial for both demonstrator and observer birds. During Experiment 1, there was always one demonstrator and one observer cage. During Experiment 2, both cages were set-up as observer cages.

Figure 2. Proportion of pecks to the demonstrated colour in Experiment 1. Panels a-d, the proportion of pecks by the observer bird to the food hopper colour of the demonstrator (y-axis) and the different experimental groups (x-axis). Filled circles represent when the demonstrator fed from the black food hopper and open circles represent when the demonstrator fed from the white feeder. The square represents the mean proportion of each group ± the 95% confidence interval. Triangles represent proportions that are not statistically different from 0.5 (no preference).

Figure 3. Proportion of pecks according to hopper colour in Experiment 1. Results for the 31 individuals run in Experiment 1. The y-axis indicates the proportion of pecks by the observer bird to the colour eaten by the demonstrator. A score of 0.5 indicates that the observer delivered an equal number of pecks to each coloured hopper. A score above 0.5 indicates that observer was copying the food colour of the demonstrator, while a score below 0.5 indicates that the observer was avoiding the food colour of the demonstrator. The filled bars represent trials where the demonstrator food hopper colour was black, and the open bars represent trials where the demonstrator colour was white.
Figure 4. Proportion of pecks to the demonstrated colour in Experiment 2. Panels a and b show the proportion of pecks (y-axis) to the black colour food hopper by female and male birds (x-axis). The square represents the mean proportion of each group ± the 95% confidence interval. Triangles represent proportions that are not statistically different from 0.5 (no preference).

Figure 5. Differences in demonstrator behaviour. The proportion of pecks (y-axis), directed towards the baited food hopper for female and male demonstrators when the baited hopper was white (white bars) and black (black bars; x-axis). The asterisk indicates a significant difference.
Figure 1.
Figure 2.
Figure 3.
Figure 4.

Proportion of pecks to black hopper

Female  Male
Figure 5.

Proportion of pecks to baited feeder

Female  Male

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