



Mechanisms of copying behaviour in zebra finches



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ABSTRACT

When an individual is faced with choosing between unfamiliar food options, it may benefit initially by choosing the option chosen by other animals so avoiding potentially poisonous food. It is not clear which cues the naïve forager learns from the demonstrator for choosing between food options. To determine firstly which birds (zebra finches, *Taeniopygia guttata*) would copy a demonstrator's choice, in Experiment 1 we presented each observer with a demonstrator feeding from one of two differently coloured feeders and then tested the observer's feeder colour preference. Of the same-sex/mixed-sex demonstrator-observer pairs tested only females copied male demonstrators. In Experiment 2, birds did not prefer either feeder colour in the absence of demonstrators confirming the social learning effect observed in Experiment 1. In Experiment 3, copying females fed significantly more at the feeder of the demonstrated colour, rather than at the location of the demonstrated feeder. These data point not just to the identity of the individual to be copied but also to the kind of information learned.

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1. Introduction

One of the potential advantages of group living is acquiring information from group mates. The information acquired may concern where and what objects with which to interact or how to behave in a way that results in a desirable outcome, for instance, obtaining food (Zentall, 2006). Social learning about foraging has been shown in a wide range of species (Danchin et al., 2004) and when an individual is faced with choosing between two unfamiliar food options, it may benefit initially by choosing the option chosen by other animals. Indeed, naïve rats prefer the flavour that matches that of food consumed by an experienced individual (Galef et al., 1998, 1984). In this way social learning enables the observer to consume a known, safe food while avoiding a potentially poisonous, unknown food. Moreover, one reason birds forage in flocks is because by doing so they find food more readily. For example, Burmese fowl (*Gallus gallus*) use both location and stimulus cues learned from an experienced demonstrator when foraging 48 h after observing the experienced bird (McQuoid and Galef, 1992).

Copying of food choices has also been demonstrated in zebra finches, *Taeniopygia guttata*, a species that forages in flocks on grass seed in Australia (Benskin et al., 2002; Katz and Lachlan, 2003;

Experiment 2, Riebel et al., 2012). There is evidence that the extent of food copying varies among individuals (Rosa et al., 2012) and depends on experimental conditions (Guillette et al., 2014). A possible interpretation for the variation in whether birds copy might be that birds do not encode and/or use all of the cues available to them at the time of observation/test. This could be because some cues, such as colour (of the feeder) or spatial location (of the feeder), are more salient, reliable or easier to learn. Some animals, then, may learn socially about the location of food (local enhancement; Galef and Giraldeau, 2001) but not the colour (stimulus enhancement; Spence, 1937) of food, which may explain why zebra finches used their own information to choose between unfamiliar coloured feeders rather than copy experienced conspecifics (Hoppitt and Laland, 2008). Furthermore, for some animals it may be that both of these cues are important: both budgerigars (*Melospittacus undulates*; Heyes and Saggerson, 2002) and starlings (*Sternus vulgaris*; Root-Bernstein, 2010), for example, copied a demonstrator's behaviour when the colour and location of food choices were held constant but failed to copy when colour and location were dissociated. In the zebra finch it is unclear which cues birds learn about while observing conspecifics: stimulus enhancement has been sufficient for social learning in some studies (Benskin et al., 2002; Katz and Lachlan, 2003) but not in others (Guillette et al., 2014). It is also not clear whether local enhancement plays any role in social learning in this species.

Our aim here was to determine what information copying zebra finches might acquire from their demonstrators. To do this, we used

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an experimental design in which the observer had the opportunity to watch a demonstrator forage at only one of two differently coloured feeders (Guillette et al., 2014). In Experiment 1 we tested both same-sex and mixed-sex pairs to determine if birds would copy the food choice of a demonstrator when the location, in addition to the colour of feeders was held constant across the demonstration and testing phases. If they do this, they should preferentially eat from the hopper of the same colour as that from which they observed the demonstrator to feed. In Experiment 2 we tested whether the apparent copying behaviour reflected initial colour preferences. If the birds have pre-existing preferences they should prefer one colour feeder over the other. We would not expect, however, that they would all show the same preference. Finally, in Experiment 3 we dissociated colour and location cues in the test phase to examine which cue was guiding copying behaviour.

2. Methods

2.1. Subjects

The subjects were 65 zebra finches (*Taeniopygia guttata*; 30 males, 35 females) bred at the University of St Andrews. All birds were housed in cages of same-sex individuals (8–10 individuals per cage, 100 cm × 50 cm × 50 cm) and kept on a 14:10 light:dark cycle with temperature at ~20°C and humidity at ~50%. Lights were fluorescent overhead bulbs. Birds were given free access to mixed seed, vitamin-supplemented water, cuttle bone, oyster-shell, and vitamin block. Each cage had several different perch sizes and types and the floor was covered with pressed wood pellets. At the end of the experiment all birds were returned to the group housing conditions described above. Birds were visually assessed for health at least two times a day by the researcher (LMG) and one additional time per day by the animal care staff. All birds were between 2 and 6 months of age at time of testing. All of the work described here was conducted with the approval of the University of St Andrews Animal Welfare and Ethics Committee.

2.2. Apparatus

The experiments were carried out in three test rooms. Each test room contained a demonstrator cage, an observer cage, and stock cages of same-sex zebra finches located 55 cm across the room from the experimental cages so that test birds were not visually isolated from conspecifics. All trials for Experiment 2 took place in one room. All trials for Experiment 3 took place in another room. Trials for Experiment 1 took place in the rooms where Experiments 2 and 3 took place, plus an additional room. The trials of the four experimental groups in Experiment 1 were randomized across all three rooms.

The cages (100 cm × 50 cm × 50 cm) for the demonstrator and for the observer bird were identical (see Fig. 1) and faced each other along the 100 cm side of the cage. A distance of 10 cm separated the demonstrator cage from the observer cage. A white opaque barrier between the cages prevented visual, but not vocal, interaction between the experimental birds. Each cage contained two water bowls, a cuttlefish bone and a vitamin block and six perches. The observer cage contained two grey food dishes on the side of the cage facing away from the demonstrator cage. During the observation and subsequently in the test phase (described below) coloured feeders (one pink, one purple, wrapped in coloured opaque paper) were attached to each cage. Each cage contained two bird box cameras (SpyCameraCCTV, Bristol, UK) connected to a laptop computer.

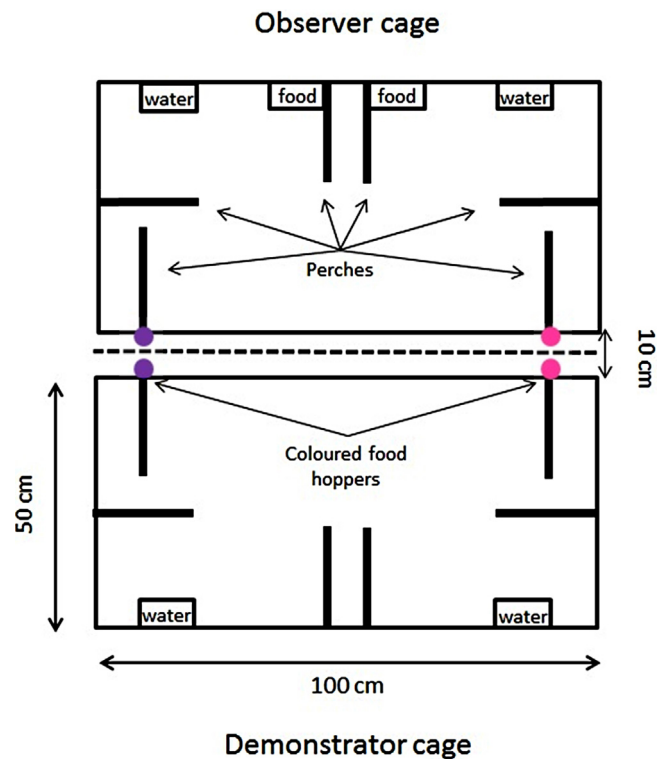


Fig. 1. Scale drawing top down view of the demonstrator and observer cages for Experiments 1 and 2. The dashed line between the cages represents the opaque barrier that was in place at all times except during the observation phase. We removed the food bowls on the front of the observer cage 2 h prior to the start of the observation phase. The location and colour of the feeders in the demonstrator and observer cage mirrored each other. In Experiment 3 the observer had 2 feeders (one of each colour) at each location.

2.3. Experiment 1

2.3.1. Subjects

The subjects for Experiment 1 were 46 adult zebra finches (24 male, 22 female) that were bred at the University of St Andrews. Birds were randomly assigned to the following four experimental groups: (1) female demonstrator with male observer ($n=8$); (2) male demonstrator with female observer ($n=7$); (3) female demonstrator with female observer ($n=7$); and (4) male demonstrator with male observer ($n=7$). Siblings were never paired. A different bird was used as a demonstrator in each trial. Once a bird had participated in a trial as an observer; it could then become a demonstrator bird in a subsequent trial.

2.3.2. Procedure

Each trial lasted approximately 24 h. Between 14:30 and 15:30 h on Day 1 one bird was placed in the demonstrator cage and another 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 male and female birds in the stock cages on either side of the experimental room. The only food available to the demonstrator bird was in one of two experimental feeders (pink or purple). Thus the demonstrator bird learned which feeder to 'demonstrate' during the observation phase (described below) the next day. On Day 2, food was removed from the both cages 2 h post light onset. The empty feeder (the non-demonstrated colour) remained in the demonstrator cage but was sham removed. The cage floors were replaced with clean floors so that the only food available to the birds was provided via the feeders. Across trials the location of the feeders remained fixed, but the colour at each location was randomized.

There were two phases in each trial, the observation phase followed by a test phase. The observation phase began after the two-hour food deprivation period. During the observation phase, the feeder that had been removed from the demonstrator cage during the food deprivation period was returned so that each demonstrator had two feeders, one pink and one purple, only one of which contained seeds. The empty feeder was also sham returned to the demonstrator cage so that both feeder locations were treated similarly. The 30-min observation phase started when the opaque barrier between the demonstrator and observer cage was removed.

During the test phase, which began immediately after the 30-min observation phase, the opaque barrier was returned and one pink and one purple feeder, each containing seed, was attached to the observer cage. The spatial location of the pink and purple feeders on the observers' cage mirrored that of the demonstrator cage. In this way, both colour and spatial cues point to the demonstrator's feeder choice. The test phase lasted 60 min. At the end of the test phase we returned both birds to their stock cages, food cups to the experimental cages, and placed a new bird in each cage for testing the following day. We recorded the birds' behaviour during the observation and test phases via the cameras for scoring at a later date.

2.4. Experiment 2

2.4.1. Subjects

The subjects in Experiment 2 were 12 adult (6 males, 6 females) zebra finches that had been bred at the University of St Andrews. None of these birds had acted as observers or demonstrators in Experiment 1.

2.4.2. Procedure

In Experiment 2, two cages were set up 10 cm apart and both were laid out as for the observer cage in Experiment 1 (see Fig. 1). We followed the procedure as described for Experiment 1, except that during the observation phase *both* birds remained without food for 30 min, preventing them from acquiring social information about each other's feeder preferences. During the test phase the opaque barrier was in place so the birds could not view each other.

2.5. Experiment 3

2.5.1. Subjects

The observers were 7 juvenile female zebra finches (at least 2 months old) bred at the University of St Andrews. The demonstrators were all adult males that had been subjects in Experiments 1 or 2.

2.5.2. Procedure

Experiment 3 was identical to Experiment 1 with the exception of the following two modifications: (1) during the test phase the observer was given two baited feeders at each location (one pink, one purple), and (2) a yellow piece of paper covered the mouth of all feeders. For birds to see and gain access to the food in the feeder, they first had to remove the cover. The mouth of the feeders was covered in this experiment so that the birds could not see that both feeders (the pink and the purple) contained seed once they had arrived at a particular location. Covering the mouth of the feeder let us assess the birds' choice of feeder location and colour prior to the birds learning that both feeder contained seed. Prior to the start of Experiment 3 we put transparent feeders in all of the stock cages of zebra finches. All of these feeders had a piece of paper covering the mouth of the feeder so birds could learn to remove the cover to gain access to seed.

2.6. Scoring

From the video recordings of each trial, the following measures were taken: (1) pecks: the number of pecks delivered to each feeder, and (2) latency: the time, in seconds, from the start of the trial until the first peck at a feeder. To quantify feeder colour preference we calculated the following measures: (1) the proportion of pecks to the feeder containing seed for the demonstrator bird and, (2) the proportion of pecks by the observer bird to the demonstrator's feeder colour. For Experiment 2 (no social demonstration) we calculated the proportion of peck to the purple feeder.

2.7. Statistical analysis

We used independent samples Mann–Whitney *U* tests to test for differences in the proportion of pecks by the demonstrators to the feeder that contained seed (1) when the demonstrated feeder was pink or purple, (2) when the demonstrator was a male or a female, and (3) when the demonstrator/observer pair was mixed-sex or same-sex. The binomial test was used to determine whether the proportion of proportion pecks for each observer bird differed significantly from no-preference (i.e., 0.5). Each observer bird could then be classified as having (1) copied the colour choice of the demonstrator bird, (2) avoided the colour choice of the demonstrator bird, or (3) having no preference. In Experiment 1 only one bird was classified as having no preference, therefore we used independent samples Mann–Whitney *U* tests to test for differences in demonstrator behaviour according to whether observers copied or avoided the feeder colour used by of the demonstrator. All the results that we report are mean \pm standard error. All analyses were conducted in IBM SPSS Statistics 20.

In Experiment 1, to test for systematic copying in the four experimental groups, we carried out one-sample Wilcoxon signed-rank tests on the proportion of pecks by the observer bird to the colour of feeder used by the demonstrator. We used a chi-square test to test for differences in observers' behaviour (copying or avoiding) according to the colour of the feeder (pink or purple) and an independent-samples Kruskal–Wallis one-way ANOVA to test for a difference in the proportion of pecks to the demonstrated colour among the experimental groups.

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 purple feeder. We used the binomial test for dichotomous data to determine whether the proportion of pecks differed significantly from no-preference (i.e., 0.5) for each observer. Each observer bird could then be classified as (1) having preferred the pink feeder, (2) having preferred the purple feeder, or as (3) having no preference. We carried out one-sample Wilcoxon signed-rank tests on the proportion of pecks by the observer to the purple feeder.

We scored the preference for Experiment 3 as described for Experiment 1, however, for the observers we calculated the proportion of pecks to each of the four feeders available during the test phase and used a one-sample Wilcoxon signed-rank test against a chance level of 0.25. We also calculated the proportion of pecks to the demonstrated colour, and the proportion of pecks to the demonstrated location, and used a Wilcoxon matched-pair signed-rank test to test for differences between the different cues available (i.e., colour and location of the demonstrator's food-only feeder).

3. Results

3.1. Experiment 1

Across all trials ($N=29$) one demonstrator and two observers did not feed. For the two observers that did not feed, they were

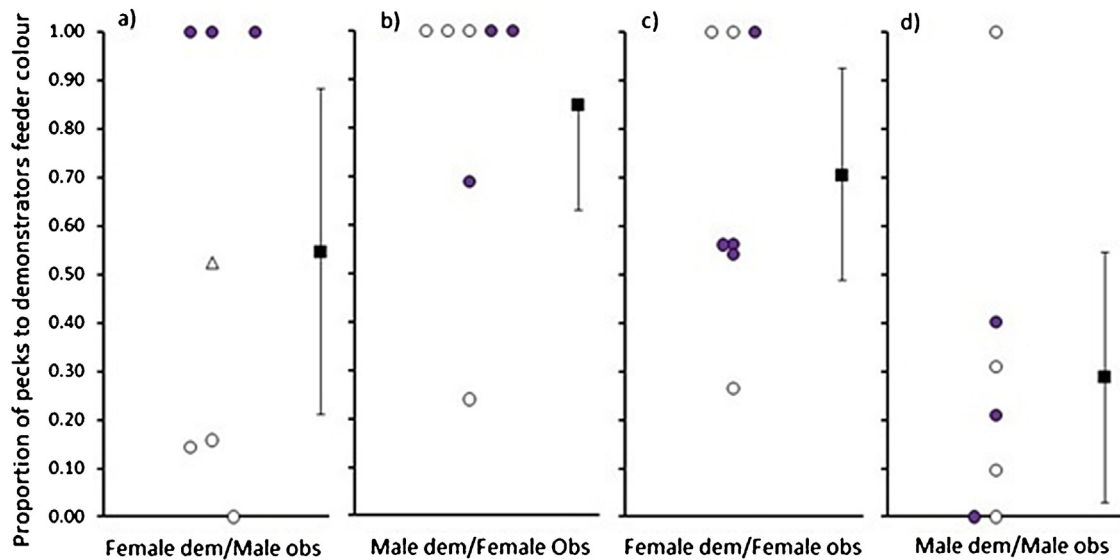


Fig. 2. The proportion of pecks to the demonstrated colour in Experiment 1. Panels a–d, the proportion of pecks by the observer bird to the feeder colour of the demonstrator (y-axis) and the different experimental groups (x-axis). Filled circles represent when the demonstrator fed from the purple feeder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

run in a second trial, either one or two days after the initial trial. Both observers fed in the second trial. The total number of complete trials for each experimental group was $n = 7$.

3.1.1. Demonstrator performance

Demonstrator birds preferentially pecked at the feeder that contained seed (0.998 ± 0.001) and did not peck more to one colour of baited feeder than to the other (pink feeder: pecks 1 ± 0.0 ; purple feeder: pecks 0.996 ± 0.008 ; Mann–Whitney $U_{28} = -1.931$, $P = 0.316$). Male and female demonstrators did not differ in the proportion of pecks to the baited feeder (male: pecks 0.999 ± 0.002 ; female: pecks 0.997 ± 0.002 ; Mann–Whitney $U_{28} = -0.642$, $P = 0.734$) or when the demonstrator/observer pair was mixed-sex (i.e., female demonstrator/male observer or male demonstrator/female observer, pecks 0.996 ± 0.008) or same-sex pairs (i.e., male demonstrator/male observer or female demonstrator/female observer, pecks 1 ± 0.0 ; Mann–Whitney $U_{28} = -1.797$, $P = 0.352$).

3.1.2. Observer performance

The number of pecks by all observers ranged from 51 to 858. All but one bird (group: female demonstrator/male observer, $z = 1.26$, $P = 0.20$) preferred one coloured feeder over the other. Twelve out of 27 birds' preference scores differed significantly from 0.5 (all z 's $> |3.04|$, P 's < 0.002). The binomial test could not be performed on the preferences of the remaining 15 birds because those individuals exclusively ate from one feeder colour only (i.e., preference = 1.0) so these individuals were treated as behaving differently from chance performance. Overall, the birds did not choose the same feeder colour as the demonstrators: although 57.1% (16/28) of the observers did prefer the feeder colour from which the demonstrators ate, 39.3% (11/28) preferred to eat from the feeder colour that was not the colour of feeder from which the demonstrator ate and 3.6% (1/28) had no colour preference (Wilcoxon signed-rank test, $W = 268.5$, $N = 28$, $P = 0.129$).

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 baited feeder (copy 0.997 ± 0.008 , avoid 1 ± 0 , Mann–Whitney

$U_{27} = -1.492$, $P = 0.422$); or demonstrators' latency to feed (seconds: copy 223 ± 324 , avoid 323 ± 250 , $t_{25} = 0.862$, $P = 0.397$).

3.1.2.1. Group data. In one of the four experimental groups we found systematic copying by observers of feeder colour/location used by the demonstrators. The proportion of pecks by female observers was significantly greater than chance for the colour/location used by male demonstrators (0.85 ± 0.29 , Wilcoxon signed-rank test, $W = 26$, $N = 7$, $P = 0.035$, see Fig. 2, panel b). For none of the other three experimental groups were the proportion of pecks by the observers significantly different than chance (male observer/female demonstrator 0.55 ± 0.45 , $W = 17.5$, $N = 7$, $P = 0.547$; female observer/female demonstrator 0.70 ± 0.29 , $W = 6$, $N = 7$, $P = 0.173$; male observer/male demonstrator 0.29 ± 0.35 , $W = 6$, $N = 7$, $P = 0.173$, see Fig. 2, panels a, c, and d).

Across all birds, in the 16 trials where observer birds preferred the colour choice of demonstrator birds, 10 demonstrators ate from purple and six ate from the pink feeder. A chi-square test indicated that, overall, birds were no more likely to prefer the colour used by the demonstrator if the demonstrator fed from the purple than they were to prefer the pink feeder (Chi-square test: $\chi^2_{28} = 2.673$, $P = 0.102$). The distribution of proportion of pecks to the demonstrated colour varied significantly across the four experimental groups, Kruskal–Wallis $H_3 = 7.9$, $P = 0.048$. Pairwise comparisons between the different experimental groups revealed that females observing male demonstrators pecked significantly more at the demonstrated feeder compared to males observing male demonstrators ($P_{\text{adj}} = 0.05$). There were no significant differences between any of the other experimental groups (P_{adj} 's > 0.253).

3.2. Experiment 2

The number of pecks for all birds ranged from 83 to 524. All but one male ($z = -0.22$, $P = 0.83$) preferred one coloured feeder over the other. Across the rest of the subjects ($n = 11$) six birds preference scores differed significantly from 0.5 (all z 's $> |3.67|$, P 's < 0.0002). The binomial test could not be performed on the remaining 5 birds because these individuals exclusively ate from only one feeder colour (i.e., preference = 1.0) so these individuals were treated as behaving differently from chance performance (see

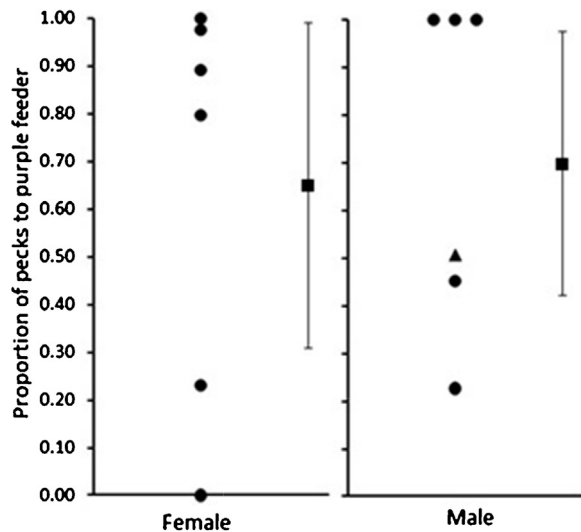


Fig. 3. The proportion of pecks (y-axis) to the purple colour feeder by female and male birds (x-axis) in Experiment 2. The square represents the mean proportion of each group \pm the 95% confidence interval. Triangles represent proportions that are not statistically different from 0.5 (no preference).

Fig. 3. A Wilcoxon signed-rank test indicated that, as a group, neither males nor females' proportion of pecks to the purple feeder differed from chance (females: 0.65 ± 0.42 , $W = 5.5$, $N = 6$, $P = 0.40$; males: 0.70 ± 0.34 , $W = 12$, $N = 6$, $P = 0.216$).

3.3. Experiment 3

3.3.1. Demonstrator performance

Demonstrator birds preferentially pecked at the feeder that contained seed (0.99 ± 0.018) and they did not prefer one colour of baited feeder to the other (pink feeder: pecks 0.985 ± 0.024 ; purple feeder: pecks 0.997 ± 0.006 ; Mann-Whitney $U_7 = 0.592$, $p = 0.629$).

3.3.2. Observer performance

The number of pecks for all observers ranged from 131 to 841. The proportion of observers' pecks to the feeder that was in same location but not of the colour of the feeder used by the demonstrator was significantly lower than chance (0.08 ± 0.14 ; Wilcoxon signed rank test: $W = 1$, $N = 7$, $P = 0.027$). The proportion of pecks by the observers to the three other feeders did not significantly differ from chance (same location and colour as the demonstrator: 0.28 ± 0.30 , $W = 9$, $N = 7$, $P = 0.752$; opposite location but same colour as the demonstrator: 0.45 ± 0.31 , $W = 24$, $N = 7$, $P = 0.091$; opposite location and colour as the demonstrator: 0.19 ± 0.15 , $W = 6$, $N = 7$, $P = 0.176$). The proportion of pecks by the observers to the demonstrated feeder colour, was not significantly different from chance (0.73 ± 0.22 , $W = 25$, $N = 7$, $P = 0.063$). Similarly, the proportion of pecks by the observers to the location of the demonstrated feeder, regardless of colour, did not differ from chance (0.36 ± 0.31 , $W = 7$, $N = 7$, $P = 0.236$). The proportion of pecks by the observers to the demonstrated colour was significantly greater than the proportion of pecks to the demonstrated location ($W = 2$, $N = 7$, $P = 0.043$; Fig. 4).

4. Discussion

In Experiment 1, all but one zebra finch observer preferred one feeder over the other. Observer preference was explained by demonstrator preference for females that had observed male demonstrators but not for those females that had observed female demonstrators or for males that had observed demonstrators of either sex. In Experiment 2, all but one zebra finch without the

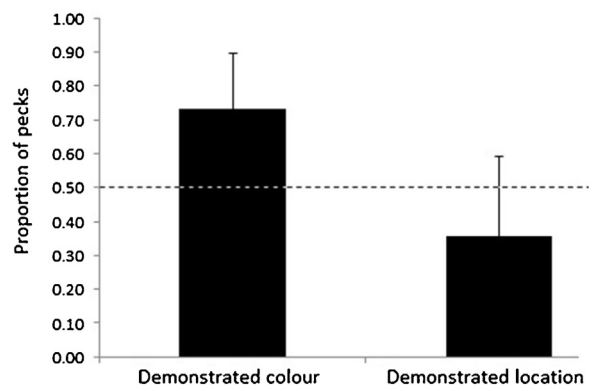


Fig. 4. The proportion of pecks (y-axis) by the observer to the correct feeder colour (collapsed across location) and the correct feeder location (collapsed across feeder colour; x-axis) in the test phase in Experiment 3. Chance performance is denoted by the horizontal dashed line.

experience of watching a demonstrator preferred one feeder over the other. However, one colour was not systematically preferred over the other. In Experiment 3, when colour and location cues were dissociated, zebra finches fed more at the feeder of the demonstrated colour than to the demonstrated feeder location.

These data are consistent with the finding that females copy the feeder colour fed on by males, whereas males, as a group, do not copy the feeder colour of either male or female demonstrators (Benskin et al., 2002; Katz and Lachlan, 2003). Unlike Riebel et al. (2012) and Rosa et al. (2012)'s findings, however, our females did not copy female demonstrators. It seems plausible that this difference may be due to context-dependence as one of several differences between our experiment and that of Rosa et al. (2012)'s, for example, was that Rosa et al. tested the extent that female zebra finches changed their preference (quantified previously) for an option after viewing a demonstrator interact with or consume the initially un-preferred male or food colour, respectively, while our observers had no prior experience with the experimental feeders before they had the opportunity to observe the demonstrators feeding. That the manipulation of the observers' prior experience with the to-be-tested stimuli can significantly affect whether individuals use subsequent socially provided information has been seen on multiple occasions. For example, guppies, *Poecilia reticulata*, without prior experience choose to eat at sites where they have seen conspecifics feed while guppies with prior experience (i.e., asocial information) did not (Kendal, 2004) and rats will use socially provided information when their personal information is ambiguous as to which of two food sources they have consumed resulted in illness (Galef et al., 2008).

We are not the first to find that females are more likely to copy than are males. For example, female blue tits *Parus caeruleus* and redfronted lemur *Eulemur rufifrons* females are more likely to learn to solve a foraging task by watching conspecifics than are males (Aplin et al., 2013; Schnoell and Fichtel, 2012). Perhaps surprisingly, however, most studies of social learning appear to use only same-sex observer-demonstrator pairs. As a result we may be missing something in our understanding of the ways in which information is transferred in gregarious animals.

If the function of food-choice copying is to assess whether novel food is safe for consumption (e.g., Galef et al., 1984) the sex of the demonstrator should not matter. Similarly, the benefits of joining a flock should not vary according to the sex of an individual. To explain the sex-dependent social learning seen in earlier work, Katz and Lachlan (2003) speculated that a male's food choice may provide a cue to his foraging ability, which may benefit his female mate when they are both feeding offspring; females should, perhaps therefore, pay attention to male foraging decisions. This

explanation seems unlikely, in our view, as zebra finches in the wild, at least, are monogamous and both parents play a significant role in parental care. It should, then, also pay a male to assess foraging ability of the female. A similar explanation based on attentional mechanisms was proposed by Benskin et al. (2002): as males are the more aggressive sex (Zann, 1996) they not only pay attention to females (potential partners) but also to males (potential rivals), while females need only to pay attention to potential mates and ignore behaviour of other females. This suggestion explained Benskin et al.'s results as in their two-demonstrator paradigm (one male, one female) and male observers copied either one or the other demonstrators' food choice, while female observers systematically copied the food choice of the male demonstrator. In our single-demonstrator design, however, which allowed observers a food choice that was not demonstrated, males did not copy any of their demonstrator's choices of feeder colour, counter to the prediction derived from Benskin et al.'s attentional hypothesis (2002). Indeed, especially given that males contribute almost equally to reproductive efforts in this species (Zann, 1996) attentional explanations do not satisfactorily explain our current results.

In Experiment 3 the birds used the colour of the feeder demonstrated to guide their food choice more than they used its location. This result at first appears somewhat at odds with earlier data where the choice of feeder colour was explained by prior preferences of the observers (Guillette et al., 2014). In that experiment, however, the feeder location was not coupled to its colour and in Experiment 1 here we intentionally confounded the two cues in the demonstration in order to enhance the likelihood of observing an effect of a demonstrator's choice of feeder on the observer.

We recognize that the procedure we employed in Experiments 1 and 3 did not allow us to control for the birds having pre-existing colour preferences. The drawback to testing for a pre-existing preference for food/feeder colour before the social learning phase is that the observer would have the opportunity to learn about the colours asocially and may, therefore, not need to learn from a conspecific which novel colour feeder to choose. For this reason, and to use methodology consistent with earlier studies in which social learning in a foraging context with zebra finches has been investigated (Benskin et al., 2002; Katz and Lachlan, 2003; Riebel et al., 2012), we did not examine whether observers had a pre-existing colour preference. Because we are aware that such preferences may exist (Guillette et al., 2014; Muth et al., 2013), in Experiment 2 we did examine colour preferences in other birds.

In sum, these experiments show that female zebra finches use social information provided by males about the properties, more so than the location, of objects to guide foraging behaviour. Social learning is expected to be context dependent (Laland, 2004), such that conspecific males and females would use social information to guide their behaviour only in some situations, but not others. One, as yet untested, context in which we might expect that male zebra finches would pay attention to choices made by conspecifics, specifically males, is nest building. In this species it is the male who is responsible for bringing nest material to the nest site. Whether or

not males do copy in a nest-building context, our data suggest that even when investigating learning in a social species, one cannot assume that the animals will learn from conspecifics.

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