

Sex and pairing status impact how zebra finches use social information in foraging



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ABSTRACT

Many factors, including the demonstrator's sex, status, and familiarity, shape the nature and magnitude of social learning. Given the important role of pair bonds in socially-monogamous animals, we predicted that these intimate relationships would promote the use of social information, and tested this hypothesis in zebra finches (*Taeniopygia guttata*). Observer birds witnessed either their mate or another familiar, opposite-sex bird eat from one, but not a second novel food source, before being allowed to feed from both food sources themselves. Birds used social information to make foraging decisions, but not all individuals used this information in the same way. While most individuals copied the foraging choice of the demonstrator as predicted, paired males did not, instead avoiding the feeder demonstrated by their mate. Our findings reveal that sex and pairing status interact to influence the use of social information and suggest that paired males might use social information to avoid competing with their mate.

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1. Introduction

Social learning allows animals to obtain information about novel resources quickly but the information obtained can be less reliable than that derived from personal experience (Danchin et al., 2004; Laland, 2004). Formal theory suggests that animals can maximize the reliability of acquired information, and hence their fitness, by selectively copying certain individuals (Boyd and Richerson, 1985; Laland, 2004). Thus, employing social learning entails the dilemma of choosing which particular individual(s) to copy (Galef, 2009; Hoppitt and Laland, 2013). Animals are known to base copying decisions on a number of factors, including the sex, dominance position, or familiarity of potential demonstrators (Laland 2004; Nicol and Pope, 1999; Swaney et al., 2001).

Given that familiarity encourages social learning (Guillette et al., 2016), it seems likely that pair bonds between mates would further promote mechanisms of information transfer and thereby impact 'who to copy' strategies (Coussi-Korbel and Fragaszy, 1995; Jolles et al., 2013), but this potential influence has rarely been examined. Two studies examined jackdaw (*Corvus monedula*) social foraging

and show that this species surprisingly did not learn faster or more from mates than other birds (Wechsler 1988; Schwab et al., 2008), potentially due to their fairly unusual degree of food sharing among affiliates (Schwab et al., 2008).

Here, we test whether pair bonding influences the likelihood of social learning in male and female zebra finches (*Taeniopygia guttata*). Pair-bonded zebra finches spend large amount of time foraging near their mates (Beauchamp, 2000), and individuals may use observations of their mates' feeding decisions when deciding where themselves to feed. These observations suggest that pair bonds could influence social learning in this species. In this study, naive birds (observers) watched trained conspecifics (demonstrators) eat from one of two available novel food sources. Observers were then given the opportunity to eat from both food sources to test whether they used social information to make foraging decisions. Each subject's demonstrator was either its pair-mate or a familiar, opposite-sex conspecific. We predicted that paired birds would be most likely to copy the demonstrator.

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2. Materials and methods

2.1. Experiment 1: social learning of a novel feeder

2.1.1. Subjects

Fifty-six adult zebra finches (28 male, 28 female) were housed at the University of St Andrews on a 14:10 light:dark cycle with 19–21 °C temperature, 42–50% humidity, and *ad libitum* food and water.

2.1.2. Treatment groups

Birds were randomly assigned to either the pair-bonded ($n = 28$) or non-bonded ($n = 28$) conditions. For the pair-bonded condition, one male and one female were placed together into a cage (130 × 35 × 28 cm) and monitored each day for signs of pairing (Silcox and Evans, 1982). If a successful pair had not formed after 10 days, we re-paired the birds with other individuals. All successful pairs built nests and began laying eggs.

The non-bonded condition housed two males together on one side and two females on the other side of the same sized cage. Birds were separated by a mesh partition but were in constant visual and auditory contact. Thus birds had a similar level of familiarity with a member of the opposite sex as the pair-bonded birds, but were physically prevented from forming pair-bonds or initiating breeding cycles. These males did not build nests when provided with material and these females did not lay any eggs.

2.1.3. Preference tests

Recent research suggests that individual preferences can obscure results of social learning experiments (Guillette et al., 2014; Rosa et al., 2012). To reduce these biases, we assessed baseline preferences in non-foraging contexts. Birds had previous experience with a variety of colours, so we selected novel horizontal vs. vertical 0.7 cm black/white striped patterns. Preference-testing cages had vertical striped 'wallpaper' on one side and horizontal striped on the other, with the specific cage sides balanced across trials. A white, opaque partition with a hole in the centre visually separated the two sides whilst allowing birds to move freely between them. The side where a bird was placed was counterbalanced between trials. Birds rapidly moved between sides, suggesting that this factor did not greatly impact individuals' preferences. Birds were tested singly for one hour at 9:30 a.m. and we scored the proportion of time spent on each side of the cage from video recordings.

Individuals showed a strong initial pattern preference during the preference-testing phase, spending $78 \pm 2.9\%$ (mean \pm SE) of their time on one side of the cage. Birds explored both sides of the cage (36.5 ± 4.3 movements between cage sides), so preferences were not likely due to initial placement or lack of exploration. There were no differences in initial preference strength between sexes, treatment groups, or stripe patterns (ANOVA $p > 0.8$).

2.1.4. Social learning tests

We used a 'single-demonstrator' paradigm (Guillette et al., 2014), as this allowed us to discriminate most effectively between copying and avoidance within pairs of demonstrators and observers. We trained demonstrators to forage from a feeder with their partner's (mate or familiar) non-preferred stripe pattern by placing them into a test cage that had feeders of both stripe patterns, but the preferred pattern of the observer blocked. Demonstrators were kept in this cage from 4 p.m.–9 a.m. (the same day as the preference test) to ensure ample time for training. Observers were housed together in same-sex pairs in the same room overnight. At 9 a.m. the next morning, a transparent mesh partition was added to divide the demonstrator's cage in two, and the demonstrator was food-deprived for one hour. After one hour, the observer was placed into the other side of the cage, without

access to food. The demonstrator was given the same two feeders (inappropriate choice again blocked, imperceptibly to the observer) and the observer witnessed the demonstrator feeding for one hour. Demonstrators performed at high levels, with $94 \pm 7\%$ of their foraging directed at the appropriate feeder. At 11 am, the demonstrator and mesh partition were removed and the two feeders were replaced with fresh, unblocked and unused, feeders marked with the same striped patterns. In the test phase, the observer was then free to forage on either feeder for one hour without further social stimuli.

2.1.5. Data analysis

We extracted the number of pecks to each feeder and the percentage of time spent at each feeder for both the demonstrator and observer from video recordings. To control for pre-existing individual biases, we subtracted the preliminary preference scores (% time) from the post-demonstration preference scores (% pecks). We focus our analyses on these differences because they most accurately reflect the change in preference following exposure to social information, but analysing just the post-demonstration data show the same patterns.

We accounted for other factors by running a linear mixed-model that included sex, treatment, and the sex*treatment interaction as fixed factors. In addition to these variables of interest, we also included feeder pattern (horizontal or vertical striped) and location (side of cage) as fixed factors, and demonstrator performance (% 'correct' demonstrations) as a covariate. In addition, we used one sample *t*-tests to compare each of the four group means to the expected value (0% change from initial preference). The results did not change if we examined the proportion of time instead of proportion of pecks (data not shown). Because the pattern for paired males was qualitatively different from other categories, we also used a one-sample *t*-test (expected proportion = 0.5) to test whether these males were avoiding the demonstrated location more than expected simply by chance. Four birds failed to feed during the trials, giving final sample sizes of: male pair-bonded ($n = 6$), female pair-bonded ($n = 6$), male non-bonded ($n = 7$), and female non-bonded ($n = 5$). Statistics were computed in SPSS v.21 (IBM Corp, Cary NC USA). We corroborated our hypothesis-testing approach using an information-theoretical approach by comparing potential models using Hurvich and Tsai's criterion to adopt Akaike's Information Criteria for small sample sizes (AICc).

2.2. Experiment 2: simultaneous foraging of mated pairs

2.2.1. Subjects

We studied 18 pairs of zebra finches, comprised of randomly chosen males and females not used in the previous study. Pairs were formed as above and we assessed pair-bond formation daily using the same methods. All pairs were housed in 50 × 50 × 50 cm cages, cared for in the same facilities and methods described above, and were tested during the egg-laying stage of the breeding cycle to best match the reproductive conditions of the previous experiment.

2.2.2. Experimental trials and analysis

We presented small pieces of cucumber (a favoured food of zebra finches, eaten by both males and females in the lab) to pairs of zebra finches to examine whether paired males would share or defer a limited food resource with their mates when housed together to allow simultaneously foraging. We presented a single small piece of cucumber (approx. 0.25 cm²) to each pair so that the food resource could not be shared. Cucumber was placed on the floor of the cage on a small white piece of paper to help facilitate collecting data from the video recordings. Each pair was videotaped for approximately 20 min and for each member of the pair, we extracted data on the latency to approach within one body length

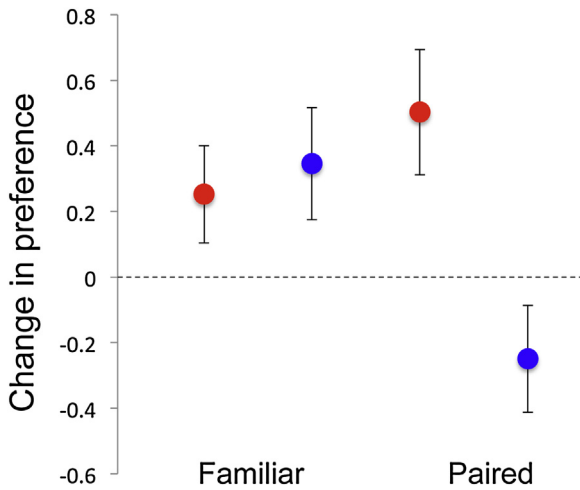


Fig. 1. Degree of social copying following foraging demonstrations. Mean \pm SE model estimates (GLMM, $df=24$; Table 1) for the change in preference are shown, with female observers indicated by red and male observers indicated by blue symbols. The dashed line designates no change in behaviour, with points above this line indicating social copying and those below it social avoidance of the demonstrated feeder. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Potential factors explaining the change in colour pattern preference following the foraging demonstration in the social learning experiment shown in the full model. Bold text indicates significant effects ($p < 0.05$).

| Model effect | df | F | p |
|---|----------|-------------|--------------|
| Intercept | 1 | 2.82 | 0.106 |
| Colour pattern (horizontal vs vertical stripes) | 1 | 0.20 | 0.659 |
| Feeder position (right vs left) | 1 | 0.93 | 0.344 |
| Demonstrator accuracy (%) | 1 | 2.19 | 0.152 |
| Observer sex (male vs female) | 1 | 2.39 | 0.135 |
| Treatment (paired vs familiar) | 1 | 0.93 | 0.344 |
| Sex * Treatment interaction | 1 | 9.37 | 0.005 |

of the cucumber as a measure of neophobia or the probability of encountering the new food source and the number of pecks on the cucumber. We used non-parametric Wilcoxon signed ranks test to compare the behaviour of each male-female pair because the data were not normally distributed.

3. Results

3.1. Experiment 1: social learning of a novel feeder

We found that birds varied in the degree to which they copied the demonstrator, with pairing status and sex of the observer interacting to affect copying ($p=0.002$; Fig. 1), but no other factors having significant influence (all $p > 0.19$; Table 1).

Pairing status did not clearly affect the degree of social copying in female birds (GLMM contrasts: $p=0.671$), with both paired and unpaired females shifting their preference towards the demonstrated feeder, although this shift was only statistically significant for paired females (t-tests, paired: $t_5=2.937$, $p=0.032$; familiar: $t_4=1.08$; $p=0.341$). However, pairing status had an effect on social copying in males (GLMM contrasts: $p=0.014$). Unpaired males switched their preference to copy the demonstrated feeder (t-test: $t_7=2.635$, $p=0.034$), whereas paired males did not copy the feeder demonstrated by their mate (t-test: $t_5=-0.231$, $p=0.827$), and instead appeared to avoid this feeder following the demonstration (Fig. 1; $t_5=-3.51$, $p=0.017$). We observed the same overall patterns if we ignored the initial preference data and simply examined the post-demonstration time period (GLMM: sex*treatment

interaction: $p=0.013$, all other factors: $p > 0.15$). Using an Information Theory approach yielded the same conclusion: the best model included sex, treatment, the interaction between these variables, and demonstrator accuracy ($k=10$, $AICc=31.13$). Removing demonstrator accuracy produced a model with a virtually identical $AICc$ ($k=9$; $\Delta AICc=0.1$). Adding other parameters (feeder position or color pattern) resulted in poorer-fitting models ($\Delta AICc > 4$).

3.2. Experiment 2: simultaneous foraging of mated pairs

We conducted a follow up experiment to test the hypothesis that paired males preferentially defer food resources to females, even when both pair members encounter the food resource at the same time (i.e. with no temporal delay between demonstration and choice test as in Exp 1). When foraging together in the same cage, a male or female member of a mated pair was equally likely to approach the supplemental food resource (cucumber; See Fig. 2a; Wilcoxon signed ranks, $N=18$, $Z=-0.63$, $p=0.53$). However, males allowed females to access the food first on 86% of trials, and females fed significantly more from the food resource than did males during the trial (Fig. 2b; Wilcoxon signed ranks, $N=18$, $Z=-2.93$, $p=0.003$), regardless of which sex initially approached the food.

4. Discussion

Our data show that forming pair bonds impacts how individuals use social information in foraging. Although we predicted that mated pairs would be more likely to copy from each other than would unmated pairs, we did not find this pattern. Instead, we found evidence for some degree of social copying in all treatment groups except mated males. Males who had formed pair bonds surprisingly avoided copying the feeder demonstrated by their mate. Lack of copying in this group does not necessarily indicate that males do not use social information from their mate in a foraging context, rather, they may use this information to avoid resources rather than directly copy her behaviour.

We suggest that males may have avoided feeding from the feeder that they had witnessed their mate use in an effort to reduce competition with her for valuable food resources. Paired birds were tested during egg laying, a stage that demands substantial energy investments from female birds (Monaghan et al., 1998). While male zebra finches help in many ways during nesting (Zann, 1996), including building the nest, incubating eggs, feeding the chicks, and even acting as sentinels (Mainwaring and Griffith, 2013), they cannot directly help with egg production. However, there are two potential ways in which males could help females obtain the necessary resources during this stage. First, a male could direct his female to new sources of food. Our data indicate that paired females do copy their mates' foraging demonstrations, changing their initial preferences in response to this social information. Second, a male could help ensure that his female obtains sufficient resources by avoiding competing with her over resources she has already located. Males in this study did just that—they both avoided the feeder they had observed their mate using and also deferred resources while simultaneously foraging with her. Anecdotal observations support this interpretation. When one male encountered the food, he appeared to look towards his mate and wait for her to approach. Another male immediately stopped feeding when his mate approached, allowing her access to feed on the cucumber. This is the first such demonstration that we are aware of showing this type of sex and pairing status specific avoidance of resources. We label the above explanation the 'chivalry hypothesis' and suggest that this type of 'chivalry—where males apparently sacrifice their immediate needs for the good of their

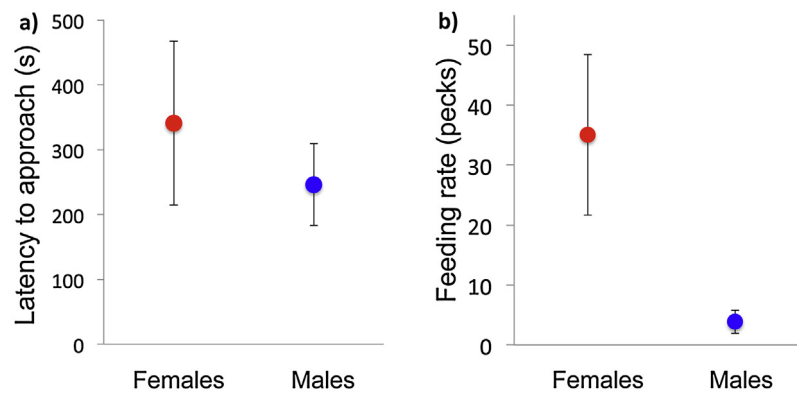


Fig. 2. Males deferred feeding opportunities to their mates when foraging together. a) One sex was not more neophobic or more likely to first encounter the food source (mean latencies \pm SE), but b) females fed significantly more from the resource than did males (mean # pecks to the cucumber \pm SE). Females are indicated with red and males with blue symbols. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mate or pair-bond—could be common among monogamous songbirds and perhaps even a trait selected for by females. This type of relationship was recently predicted theoretically (Desjardins and Dubois, 2015), further suggesting the potentially broad application of this idea for monogamous animals.

From a social learning perspective, these results suggest an unusual use of social information. Although most birds used the social information to change their preference and copy the demonstrator, paired males had the opposite reaction. While males still seem to use social information to make foraging decisions, this information appears to lead them to use the opposite choice of feeder, rather than display direct copying behaviour. The paired males' behaviour still meets definitions of social learning, but rather than the usual 'social transmission' (where social learning leads to matched behaviour), instead unmatched behaviour results (Hoppitt and Laland, 2013). A variety of different animals have been shown to learn to avoid predators (Griffin, 2004) or foods (Brown and Laland, 2002), in response to social information provided by conspecifics, a phenomenon known as 'social inhibition'. However, the present case differs from such examples in that the demonstrator's behaviour is not inhibitory, nor is it associated with inhibitory cues. Animals have been shown to learn from the mistakes of conspecifics (Darby and Riopelle, 1959; Templeton, 1998), leading to mismatched behaviour. In such instances animals are thought to avoid the demonstrated feeder in order to maximize their own feeding opportunities. However, this explanation seems unlikely in our experiment, given that the demonstrators consistently chose the 'correct' feeder and received a food reward each time, so there were no 'mistakes'.

The results from the second experiment test whether males also defer feeding opportunities to their mate under somewhat more ecologically relevant conditions. In the wild males and females often feed side by side and their foraging synchrony can even impact their nesting success (Mariette and Griffith, 2015). Thus the second test, which examined the behaviour of both individuals while foraging together in the same cage, was more natural than the first test. In this second experiment, regardless of which individual approached the cucumber first, most males preferentially allowed their mate to feed. This experiment was conducted under *ad libitum* access to see. More stressful conditions involving limited food availability have been shown to impact the importance of mated partnerships in birds for learning and scrounging (Firth et al., 2015; Jolles et al., 2013) and thus it is possible that 'chivalrous' behaviour might change depending on resource availability. Testing birds in larger flocks, as they are more commonly found in the wild, could also potentially change the findings of learning experiments (Templeton et al., 2014). While birds were not food

limited, the cucumber represented a highly valued food object that could be eaten or deferred to the mate, so the result that males deferred feeding opportunities to their mate corroborates the findings of the first experiment and provide further evidence for the hypothesis that males might 'chivalrously' defer food resources to their mate.

While alternative explanations to 'chivalry' may explain these surprising results, none appear very plausible. Animals in different states, or with different developmental histories or phenotypic characteristics can exhibit alternative copying strategies (Boogert et al., 2013; Riebel et al., 2012). Hormonal changes associated with mating have been found to change the use of social information in sticklebacks, shifting males towards asocial strategies (Webster and Laland, 2011), but the adaptive value of this change is tied largely to the mating system (exclusive male parental care versus biparental care in zebra finches). Another alternative explanation for the paired males' behaviour is the possibility that these birds inferred that the feeder had been depleted by the demonstrator. While there is support for the idea that animals should avoid copying potentially depleted resources (Boogert et al., 2013; Hopewell et al., 2010), this is a relatively unlikely explanation in the present study. First, there was no actual depletion during either the demonstration or test phase, with food constantly available in the feeder. Second, males also deferred resources to females when simultaneously tested together in the second experiment. Last, the depletion explanation does not explain why only paired males should infer that the feeder demonstrated by their partner was depleted.

That only one category of subjects—paired males—avoided the demonstrated feeder suggests that there is something special about their particular status or relationship with the demonstrator driving their unusual use of social information. The critical variable is likely to be this combination of pairing status and sex, where—especially, during egg-laying—paired males may benefit disproportionately by not competing with their mate. 'Chivalrously' deferring food resources to their mate could be a useful strategy for maximizing their own reproductive success.

Ethical note

All work carried out in this project was in line with the ASAB/ABS guidelines for use of animals in research and was approved by the St Andrews School of Biology Ethics Committee (11/05/2013).

Author contributions

CNT, SB-A, and KP designed experiment 1 and CNT, LMG designed experiment 2. Data were collected by KP (exp 1) and LMG

(exp 2) and analysed by KP and CNT. All authors contributed to interpreting the results and writing the manuscript.

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