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.

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 ± 2.9% (mean ± 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 ± 7% of their foraging directed at the appropriate feeder. At 11am, 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 cm^2) 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