

Review

'Sociability' affects the intensity of mate-choice copying in female guppies, *Poecilia reticulata*



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ABSTRACT

Selecting a quality mate can involve acquiring and accessing large amounts of information; information that can be obtained either independently or socially. One means of learning about mates socially is to attend to other members of one's sex and copy their mate choices. It is possible however that not all individuals of a species benefit equally from, or are equally effective at, copying. We examined whether female guppies copied the mate choices of other females. Then, in a separate context we measured each female's 'sociability': their proclivity to affiliate with other guppies. In the mate-choice copying procedure, 'focal' females chose to spend time near two putative mates. Next, focals observed another (model) female interact with the focal's non-preferred male. Finally, the focal again chose between the same two males. For sociability, we examined the time focal females spent near a trio of other guppies. Females did indeed mate copy: they spent more time with their non-preferred male when a model female had been seen interacting with that male. The effect however was highly variable. Sociability significantly predicted the intensity of mate-choice copying. Results suggest that individuals vary consistently in the types of information they use when making mating decisions.

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1. Introduction

The decision making processes involved in choosing a quality mate can be complex, requiring the integration of many types of information. Female mate choice has been studied across a wide variety of taxa and the number of male characteristics females use to select among putative mates is large; it includes males' secondary sexual characteristics (which often have to be integrated across modalities), their courtship behaviours, their courtship vigour, the resources they can provide, and the quality of their territory (Andersson, 1994; Bateson, 1983; Byers et al., 2010; Clutton-Brock and McAuliffe, 2009; Hebets and Papaj, 2005; Jennions and Petrie, 1997). In addition, females' search strategies, reproductive state, and developmental experiences all contribute to mate choice decisions (Badyaev and Qvarnstrom, 2002; Bateson, 1978; Lynch et al., 2005; Real, 1990; Riebel, 2000; ten Cate and Voss, 1999; Webster and Laland, 2011). Another valuable source of information about mates can come from the social environment. Attending to how a male behaves within a social context can reveal aspects of his dominance or social skills (Mennill et al., 2002; White

et al., 2010; Zuk and Johnsen, 2000). In addition, the behaviour of other females can provide public information about the quality of their mates (Nordell and Valone, 1998). Taken together, learning about the quality of a potential mate can be cognitively demanding and involve combining information acquired from private and public sources (Witte and Noltemeier, 2002).

One way females can use public information in mate selection is by copying the mate choice of other females (Losey et al., 1986). Copying females can learn about the quality of potential mates while avoiding the costs of engaging in independent search and assessment and end up mating with a male of no worse quality than the choosing female. This type of non-independent mate choice has the potential to skew reproductive success among males and impact the direction and intensity of sexual selection (Agrawal, 2001; Brooks, 1996; Kirkpatrick and Dugatkin, 1994; White, 2004; Witte et al., 2015). Mate-choice copying was initially proposed to explain the pronounced skew in male reproductive success of lekking birds (Gibson et al., 1991; Höglund et al., 1990), but has most often been examined under controlled laboratory investigations. Mate copying, or similar social processes have been demonstrated in fish, birds, insects, mammals and even humans (Alonzo, 2008; Bowers et al., 2011; Clutton-Brock and McComb, 1993; Drullion and Dubois, 2008; Dubois, 2007; Dugatkin, 1992; Fiske et al., 1996; Freed-Brown and White, 2009; Galef et al., 2008;

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Galef and White, 1998, 2000; Germaine et al., 2016; Goldschmidt et al., 1993; Grant and Green, 1996; Hebets, 2003; Heubel et al., 2008; Höglund et al., 1995; Jamieson, 1995; Mery et al., 2009; Munger et al., 2004; Schlupp et al., 1994; Swaddle et al., 2005; White, 2004; White and Galef, 1999a,b; Widemo, 2005).

One of the earliest and most extensive investigations of mate-choice copying was done by Dugatkin and Godin on guppies (Dugatkin, 1992, 1996a, 1996b, 1998; Dugatkin and Godin, 1992; Godin and Hair, 2009). Guppies lend themselves very well to examinations of mate choice. They mate and breed readily in captivity and the number of characteristics of mates to which females attend is extensive, including multimodal signals, size, colouration, and courtship intensity (Houde, 1997). In addition, they live in mixed-sex shoals, so the opportunity to use social information when making mate selections exists. To examine mate-choice copying, Dugatkin provided female guppies the opportunity to spend time swimming near two males, one of which had previously been observed to be interacting with another female. He found that the observation of the male with another female made that male more attractive to the subject female (Dugatkin, 1992). Since this first finding in guppies, Dugatkin and Godin have proceeded to show that the mate copying effect is strong enough to overwhelm an independent preference (Dugatkin and Godin, 1992), that the increased preference is for the male, not the location where the model female had been seen (Dugatkin, 1992), that the preference generalizes to the traits of the male (Godin et al., 2005), and that not all females engage in mate copying equally: younger females are more likely to copy older ones (Dugatkin and Godin, 1993) and large females are better models than small ones (Vukomanovic and Rodd, 2007).

Other labs, however, have failed to find mate-choice copying in guppies. Lafleur et al. (1997), using commercially bred guppies, and following Dugatkin's (Dugatkin, 1992) procedures closely, failed to find any social effect on female preferences. Brooks (1999), studying a feral population of guppies in Australia, also failed to find mate copying, instead finding that females avoided males seen mating with other females. Scarponi et al. (2015) also found females avoided males seen mating with other females (a similar effect as in male Japanese quail; White and Galef, 1999a).

There are several possible explanations for the discrepant findings across labs. First, perhaps subtle differences in the experimental methods or differences in the strain of guppies might introduce variability into the findings. Another possibility is that not all females engage in mate copying. There may be a subset of females who are more likely to attend to and use social information (as seen in foraging and habitat selection; Barnard and Sibly, 1981; David et al., 2011; Giraldeau et al., 1994; Hahn and Silverman, 2006). In many species, females show consistent and persistent individual differences in proclivity to seek out and be near others (Aplin et al., 2014; Dingemanse et al., 2010; Dosmann and Mateo, 2014; Keiser and Pruitt, 2014; Sih et al., 2004; Wolf et al., 2011). If females differ in this 'sociability' trait, it is possible that only some females would be influenced by social factors when making mate choice decisions (David and Cézilly, 2011; Trompf and Brown, 2014). Pronounced individual differences in attending to and using social information could influence assortative mating, and patterns of male reproductive success, and thus could influence the likelihood of researchers being able to detect mate-choice copying – especially based on the methodology most commonly used to study mate copying.

In most of the above-mentioned examinations of mate copying, the standards for detecting a social influence on mate choice were high: preference is measured as a binary variable, either the female prefers the male or she does not. This is done for good reason: if swimming near a male is a proxy for the likelihood of mating (Bischoff et al., 1985), then one male should succeed in securing the

female as a mate and the other should fail. Nevertheless, this procedure is not sensitive to small or moderate effects on the choosing female's behaviour. White and Galef (Galef and White, 1998; White, 2004; White and Galef, 1999a) created a procedure, derived from Dugatkin and Godin (1992), to investigate mate-choice copying in quail that was able to detect more subtle changes to females' mate choice decisions. Under this procedure, females were given a pre-test where they could evaluate the two males independent of any other female's presence. After this, a model female was added to the compartment of the male that the focal female had judged to be relatively less attractive (her 'non-preferred' male). After the observation phase, focal females again chose between the same two males and the change in the amount of time they spent near the initially non-preferred male from pre-test to post-test indicated the degree to which they were influenced by the presence of the model female. This was compared to the same female's consistency of preference when no model female was presented. In this procedure, the pre-test provides a measure of the focal female's independent assessment of the males and thus each female serves as her own control to compare how she weights public and private information when making a mate choice decision. In addition, the procedure provides a measure of the consistency of females' behaviour when not given access to social information. Here, even very small social influences on mate decisions can be detected. If females use information attained through copying for long-term changes to their mate selection decisions (Godin et al., 2005; Kneil et al., 2015; White and Galef, 2000), even a small effect on their probability of selecting a potential mate can be important.

In the current experiment we examined mate-choice copying in female guppies using White and Galef's (1999a) methodology described above in order to get a more sensitive measure of how females use public and private information when selecting a mate. Additionally, in a series of tests in a separate context, we examined each females' sociability: her tendency to approach and affiliate with conspecifics. We hypothesized that females' sociability would be predictive of the weight they would place on public information in the mate copying test.

2. Materials and methods

Twelve female guppies served as subjects in the experiments. In addition, we used twenty four male guppies in the mate choice experiments. We purchased fish from a commercial supplier (Big Al's Aquarium Supply, Kitchener, Ontario, Canada). All fish were non-gravid, sexually mature adults. Body size was very similar within sexes (all females were within 2 mm of each other, all males within 5 mm). We photographed fish to assist in identifying individuals and in measuring body size. We maintained all fish across six 10 L holding tanks in same-sex groups (randomly assigned, except for similar-looking females, which we separated to help track individual identity) in a computer-controlled housing rack (Pentair Aquatic Habitats, FL, USA). Water temperature in the housing tanks was maintained at 22–24 °C, salinity at 500–700 ppm, and the pH at 6.8–7.4.

Apparatus: We conducted all tests in a 40 × 20 × 25 cm glass aquarium. Two additional smaller 20 × 5 × 20 cm holding tanks, located at either end of the main aquarium were used to hold males for the mate-choice copying test. We used a standardized procedure to measure mate preferences (Bischoff et al., 1985; Dugatkin, 1992). We used a marker to divide the main aquarium into three sections for scoring purposes, two 10 cm preference zones at the two ends nearest the males and a 20 cm central neutral zone. A removable, clear 12 cm diameter Plexiglas cylinder was used to restrict fish movements in both the mate copying and sociability tests.

2.1. Procedure:

2.1.1. Mate-choice copying trials

The procedure was based on the methodology of mate copying experiments done on Japanese quail (White and Galef, 1999a) and guppies (Dugatkin and Godin, 1992). These trials consisted of a pre-test where a randomly selected focal female spent 10 min swimming in the mate choice aquarium. We measured the amount of time she spent in the two end areas of the aquarium near two randomly selected, size matched males. After the end of the pre-test, we placed the cylinder over the focal female which held her in the centre of the aquarium. At this point we placed a randomly selected, size matched female (the 'model' female) in the chamber of the male with whom the focal female had spent the minority of her time (her 'non-preferred' male). After another 10 min, the observation phase ended with the model female being removed. In the final post-test, we removed the cylinder and the focal female once again had 10 min to swim around the aquarium. Again we measured the amount of time she spent in the preference zones adjacent to the two males. We measured a mate-choice copying response for each female which we determined as the change from pre-test to post-test in the proportion of time she spent with her initially non-preferred male, excluding the time she spent in the neutral zone. We also conducted control trials that were identical to the experimental trials except that during the observation phase we did not place a model female into either male's container. Thus these control trials measured the consistency in focal females' preferences for spending time with the two males from pretest to post-test in the absence of any social information. Experimental and control trials were counterbalanced. All females served as focal females in both types of trials. All females served as both models and focals with the order of running randomized. The two males used in a trial were never re-paired for any other trial. No female was grouped with the same males or female across trials. One female died before completing both experimental and control trials. We removed her data.

2.1.2. Sociability tests

We placed three female guppies in the Plexiglas cylinder in the centre of the aquarium and then placed a focal female into one of the ends of the aquarium. After 2 min of acclimation, we recorded the amount of time the focal female spent within 4 cm of the cylinder. After 10 min we returned all fish to their holding tanks. We tested each female three times across two weeks in this manner. All females served as focals and as part of the group in the cylinder with order randomized. No fish was tested as a focal multiple times on the same day.

2.1.3. Other individual differences

It is possible that the sociability test was actually measuring aspects of the females' behavioural tendencies that were not specifically social. For example, our sociability task might actually have measured the females' tendency to explore their environment, their boldness, or merely their proclivity to be attracted to other moving objects. We therefore conducted two other tests on the females to control for these possibilities.

2.1.4. Exploration, boldness

Possibly, females who spent time near other guppies in the sociability test did so because they were more explorative or bold than the other females (or vice versa, spending time near other guppies for safety). To test these ideas, we conducted a test similar to the sociability test, but instead of using three female guppies in the cylinder, we placed a novel object into the centre of the tank. The novel object was a plastic coloured cylinder, 5 cm in diameter and 10 cm long. There were three different coloured cylinders:

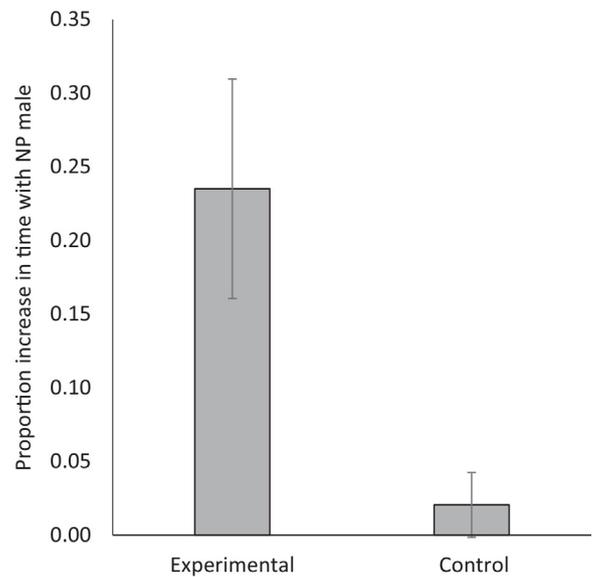


Fig. 1. Mean (± 1 SEM) change from pre-test to post-test in the proportion of time focal females spent with their non-preferred (NP) male in the experimental and control mate-choice copying trials in experiment 1.

green, pink and blue. Each fish was tested three times with different coloured cylinders used for the different trials. We measured the amount of time the fish spent within 4 cm of the cylinder. If this test correlated strongly with our sociability score it would call into question whether that test was validly measuring sociability.

2.1.5. Movement

It is also possible that females who affiliated with the other guppies were not attending to the other guppies specifically, but were just attracted to movement. We therefore conducted a heterospecific association test that followed the same procedure as the sociability test but, instead of having three female guppies present in the cylinder, we used three zebrafish (*Danio rerio*). All other procedures were identical. Two females died prior to completing these tasks, and one did not move around on any of the trials, thus we removed their data.

2.2. Data analysis

Analyses were conducted using SPSS. Repeatability analyses using the intraclass correlation coefficient (ICC) were conducted using the *psych* package in R (v.3.2.2).

3. Results

3.1. Mate-choice copying

Focal females spent a significantly higher proportion of time with their non-preferred male after observing him interact with a model female compared to when no model female was observed (paired *t*-test, $T(10) = 3.07$, $P = 0.012$; Cohen's $d = 1.24$; Fig. 1). The same pattern holds for comparisons using change from pretest to post-test in the number of seconds spent with the non-preferred male (mean increase in seconds spent with non-preferred male in experimental condition = 118.58 ± 42.73 , mean for control condition = 6.00 ± 12.8 s; paired *t*-test, $T(10) = 2.62$, $P = 0.026$; Cohen's $d = 1.18$). While the change in the amount of time focal females spent with their non-preferred male in the experimental trials was significant, it was also highly variable across females (in fact, the

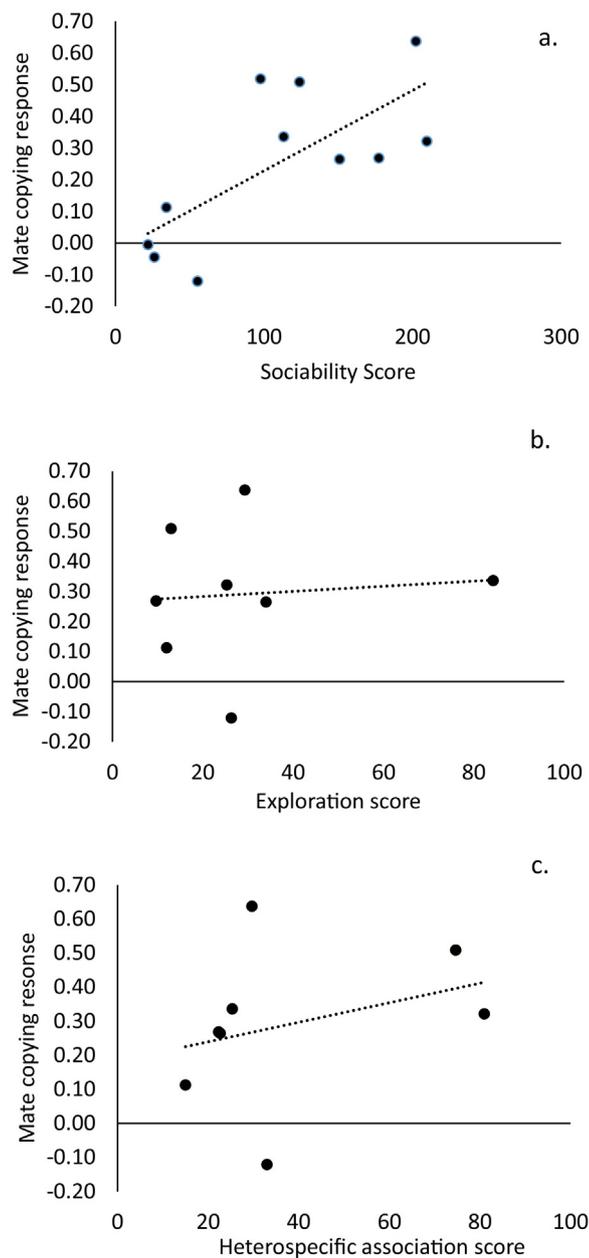


Fig. 2. Scatterplot depicting the relationship between each focal female's mate copying response (i.e., the change from pre-test to post-test in the proportion of time she spent with her non-preferred male in the experimental condition of the mate copying test) and her (a) sociability score (total seconds spent near guppy trio, averaged across the three trials), (b) exploration score (total seconds spent near novel object, averaged across the three trials), and (c) heterospecific association score (total seconds spent near zebrafish trio, averaged across the three trials). Best fit linear regression lines are overlaid on each scatterplot.

variance was 14.8 times greater than in the control condition). Eight out of 12 females increased the time they spent with their initially non-preferred male. In six of these cases focal females ended up spending more time with the non-preferred male than the preferred male in the post-test. Two females increased the time they spent with the non-preferred male, but only marginally, and three females spent less time with the non-preferred male in the post-test.

3.2. Sociability tests

We collected sociability measures from each of the 11 females. Across the three test trials females were consistent in their sociability scores ($ICC(3,1) = 0.34$, $F(10,20) = 4.49$, $P = 0.002$). Sociability was highly correlated with the change from pre-test to post-test in the proportion of time spent with the non-preferred male in the mate copying experimental trials (Fig. 2a; sociability scores were averaged across the three trials; Pearson $r = 0.72$, $P = 0.013$). The sociability scores for each of the three trials also correlated significantly with the mate copying scores, all $r_s > 0.60$, all $P_s < 0.05$).

There were no significant correlations among the measures of time spent with the fish (or cylinder) across the sociability, exploration, and heterospecific association tests (sociability and exploration, $r = -0.13$, $P = 0.76$; sociability and heterospecific association, $r = 0.29$, $P = 0.49$; exploration and heterospecific association, $r = -0.19$, $P = 0.65$), suggesting that the three tasks measured unrelated aspects of the females' behaviour. Females did not show consistency within measures across the three trials for exploration, but did so for heterospecific association (exploration $ICC(3,1) = -0.13$, $F(7,14) = 0.594$, $P = 0.751$; heterospecific association $ICC(3,1) = 0.42$, $F(7,14) = 3.41$, $P = 0.024$).

Neither the exploration or heterospecific association results correlated significantly with individual differences in the mate-choice copying response (exploration $r = 0.09$, $P = 0.83$; heterospecific association, $r = 0.31$, $P = 0.45$; Fig. 2b and c).

Since not all females were tested for the exploration test and heterospecific association test, the power to detect a relationship with mate copying was lower for these two tests than for the sociability measure. We therefore re-examined only the sociability data from the females from whom we had collected exploration and heterospecific association data. The correlation between sociability and the mate-choice copying response remained significant for these 8 females ($r = 0.76$, $P = 0.02$).

Overall, only the sociability of the females was predictive of their mate choice copying tendencies. Somewhat surprisingly, heterospecific sociability was not highly correlated with conspecific sociability, suggesting that female guppies react to other guppies differently than to zebra fishes. Also surprisingly, we, unlike other labs (see Réale et al., 2007), did not find across-trial consistency in exploration.

3.3. Experiment 2: controlling for shoaling tendencies

It was possible that the patterns of behaviour found in experiment 1 could be explained by females' tendency to shoal. Thus in both the mate copying trials and the sociability trials, focal females might have just been moving to an area where they saw other guppies, and not changing their mate choice decisions. We tested this possibility, following Dugatkin (1992), by conducting a mate-choice copying test with one procedural modification: we reversed the location of the two males after the observation phase. Thus for focal females to show mate copying they would have to swim to the area in which they had *not* seen a model female during the observation phase.

Subjects: We used 12 new females and 12 new males as subjects for this experiment. Fish were maintained in the same manner and tested in the same apparatus as fish in experiment 1.

Procedure: Fish were run through a mate-choice copying test similar to experiment 1. The one procedural difference came at the end of the observation phase. Prior to releasing the focal female for the post test, we reversed the positions of the two males. This allowed us to determine whether the change from pre to post test in the amount of time focal females spent near the two males was due to their preference to spend more time near the non-preferred male or near the location where she saw more fish.

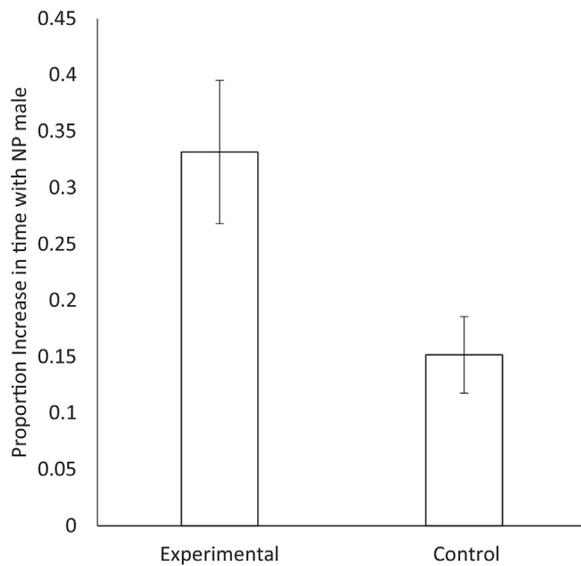


Fig. 3. Mean (± 1 SEM) change from pre-test to post-test in the proportion of time focal females spent with their non-preferred (NP) male in the experimental and control mate-choice copying trials in experiment 2 (males' locations reversed).

4. Results

When in the experimental condition, focal females spent more time near their initially non-preferred male after seeing him courting a model female. They did not increase their time spent in the location where the pair of fish had been seen during the observation phase (paired t -test, $T(11) = 3.147$, $P = 0.009$; Cohen's $d = 1.02$; Fig. 3).

5. Discussion

We demonstrated that female guppies are influenced by the presence of other females when making mate choice decisions, but the effect was highly individually variable. The best predictor of the strength of the response to the model female was the focal female's sociability.

Our results provided a potential solution for the question of why there are so many different mate-choice copying findings in the literature (Brooks, 1999; Dugatkin, 1992; Lafleur et al., 1997; Scarponi et al., 2015). Because the mate copying response was so highly variable among females, methodologies based on binary measures of preference may be less likely to demonstrate the social effect on preferences. We found some females who showed pronounced mate copying responses, some who showed very subtle ones, and some who did not mate copy at all (and may even have avoided the male associated with the model female). It is critical to be able to measure both the females' independent evaluation of the males and their reaction to the social information, all within one trial. This provides a way to place social and independent information in conflict and allows us to measure the magnitude of the mate-choice copying response within each female.

The finding that individual differences in sociability relate to mate choice decisions is intuitively clear and has some empirical support: females most likely to aggregate with other females in turn are most likely to use information acquired from others to influence their mate choice decisions (Trompf and Brown, 2014; Wolf and McNamara, 2013). It is unclear, however, what is driving this effect. Is it that sociable females are more likely to attend to other fish and thus have overall more social information to use, or do all females acquire the same overall amounts of all types of information but the sociable ones place more weight on the

social information over their own individually-acquired information when making mate choice decisions? Additionally, it is unclear what function the variability in social information use serves. It is possible selection has favoured sociability in another context and it emerges under mate selection tasks as a 'behavioural syndrome' (Sih et al., 2004). Alternatively, it is possible that more sociable females are more likely to use the social information in order to overcome less effective independent-assessment abilities, thus maintaining social information use vs independent information use in a frequency-dependent manner (a relationship recently found in nest selection patterns in cowbirds; White, et al. submitted). Perhaps, if there is a link between male characteristics and environmental conditions such that certain males vary in quality based on different environments, thus variability in information use might track different environmental circumstances (Boyd and Richerson, 1985). Mate copying has traditionally been considered a mechanism to simplify a cognitively complex decision; to remove some of the demands of independently assessing a potential mate. However it is possible that adding a social aspect to mate choice adds even more cognitive complexity to the decision, adding more information that must be acquired, evaluated, weighed and used. This could potentially lead to two distinct mate choice strategies, one based on independent assessment and one on copying, similar to the producer-scrounger relationships proposed to explain variation in foraging tactics (Barnard and Sibly, 1981; Giraldeau et al., 1994). In the wild, poeciliid fishes vary dramatically in their behaviour within and across populations (Dingemans et al., 2009; Riesch et al., 2009). It is possible that variation in their physical and social ecology could be driving variation in the use of social information in mate choice decisions.

Our laboratory-based investigation of mate choice in commercially bred subjects is limited in generalizability to wild population. 'Guppies' can be a vague category used by commercial suppliers to include several different kinds of breeding stock. These differences in breeding stock can be highly variable and might have contributed to the variability we found in our subjects. Our within-subject tests on this variability do contribute to a growing literature revealing that individual differences are important (Schuett et al., 2010; Sih et al., 2004; Smith and Blumstein, 2008; Wolf and Weissing, 2012) and need to be taken into account in theoretical models not only of sexual selection but of social evolution in general. If there are consistent differences among females in their tendency towards sociability, this might influence how they find food, move about in their environments, and select breeding grounds and mates. This could lead to the modification of selection pressures acting on population structure, secondary sexual characteristics, and social cognition.

Ethical statement

All work on animals conformed to the National Institutes of Health guide for the care and use of Laboratory animals and was done under Wilfrid Laurier Animal Care Protocols (Protocol number N14000).

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