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No evidence for mate copying in *Danio rerio*

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ABSTRACT

The zebrafish *Danio rerio* is an important model organism, but little is known about its mating preferences and how these are influenced by personality traits like boldness. In this study, we tested two strains of zebrafish and addressed whether females used social information to build a mating preference, a behavior called mate copying, and whether this social learning was affected by boldness. Thus, we provided positive social information for small males to test whether female zebrafish changed their mate preference after observing a pair of a small and a large male with a demonstrator female next to the small one. After that, we tested the observer female in a test maze to evaluate boldness. We found no significant evidence for mate copying as females did not change their preference for the small male after witnessing the large male alone and the small male interacting with another female and chose consistently larger males in a control without opportunity to copy. Whether the female was defined as shy or bold had no effect on mate copying. We conclude that mate copying is probably inexistent or only relatively weak in this species.

1. Introduction

The ability to find a mate and to reproduce is a universal challenge of animals and often results, within a population, in a strong competition for mating opportunities among individuals. Sexual selection, together with natural selection, contributes to the appearance of new traits and to species evolution. An approach to understand mate choice is to address this issue in model organisms that are easy to handle, and where pre-existing knowledge and a suite of genetic tools and experimental setups for behavioral studies are available. Among vertebrates, the zebrafish *Danio rerio* emerged as a powerful model to study genetics, developmental biology, neurophysiology and biomedicine (Dooley and Zon, 2000; Eisen, 1991; Nüsslein-Volhard, 2012; Streisinger et al., 1981). In particular, the zebrafish has been extensively used to study links between genetic and trait variations, and over the years, there has been increasing interest in the use of this model organism to understand the genetic basis of various behavioral patterns.

Only a few studies investigated the reproductive behavior of zebrafish with sometimes contradictory conclusions because the two

mechanisms of sexual selection, male-male competition and female preference, may operate in opposition (reviewed in Spence et al., 2008). A first study based on an analysis of offspring genotypes suggested that the opportunity for sexual selection is probably rather weak in this species (Spence et al., 2006a). In another study based on the analysis of courtship behavior, the same researchers concluded that sexual selection in zebrafish is unlikely (Spence et al., 2006b). Other studies, however, provide behavioral evidence for mate choice in this species (Hutter et al., 2010; Pyron, 2003). For instance, it was shown that zebrafish use visual information about body shape, stripe patterns and coloration for reproductive and shoaling behavior (Engeszer et al., 2004, 2007a; Hutter et al., 2011; Rosenthal and Ryan, 2005; Ruhl and McRobert, 2005; Snekser et al., 2006). Olfactory signals have also been shown to play a role in reproduction (Bloom and Perlmutter, 1977; Gerlach and Lysiak, 2006). Moreover, there is some evidence that female zebrafish prefer larger males (Pyron, 2003) and allocate more eggs to them (Skinner and Watt, 2007). Finally, the early social environment of zebrafish has been shown to influence shoaling, as individual fish prefer to shoal with fish with phenotypes similar to those it was raised with,

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regardless of their own phenotype (Engeszer et al., 2004; Moretz et al., 2007; Spence and Smith, 2007). Despite the importance of mate choice for sexual selection and evolution, very little is known about it in the zebrafish, and in particular, we have no information on whether and how zebrafish females inherit a mating preference.

Public information (i.e., “potential information that is accessible to all individuals”; Danchin and Wagner, 2010) is used by a wide range of taxa to evaluate prospective mates. One form of social learning in mate choice is mate copying (Danchin et al., 2004; Gibson and Höglund, 1992; Wade and Pruett-Jones, 1990). It occurs when an observer individual uses the mating preferences of conspecifics to build their own sexual preference. The observer copies the mate choice of conspecifics if it then tends to prefer as a mate the individual that it saw successfully attracting another partner (Dugatkin, 1992; Losey et al., 1986; Pruett-Jones, 1992; reviewed in Witte and Nöbel, 2011). Mate copying may also exist for rejection of a potential mate with the observer tending to dislike mates that it saw being rejected by others (Witte and Ueding, 2003). Copying the mate choice of others can be an efficient strategy to gather information about potential mate quality (Westneat et al., 2000). Mate copying has been experimentally demonstrated in several bird species (e.g., Galef and White, 1998; Gibson et al., 1991; Höglund et al., 1995; Kniel et al., 2015); mammals (e.g., Bowers et al., 2012; Galef et al., 2008); *Drosophila melanogaster* (e.g., Dagaëff et al., 2016; Danchin et al., 2018; Mery et al., 2009); as well as in several species of fish (reviews in Vakirtzis, 2011; Witte and Nöbel, 2011). A major result from these studies is that the influence of social information can be strong enough to reverse the initial predisposition for large males with, for instance, females copying the apparent mate choice for small males (Marler and Ryan, 1997), and females maintaining this socially learned mate preference for at least five weeks (Witte and Noltemeier, 2002). However, up to now, little is known about the parameters that could influence mate choice and mate copying (and nothing about its genetic basis).

We hypothesized that the ability of an individual to copy other individual's mate preference is influenced by variation in personality. Recently, we tested *Gambusia holbrooki* females in a standard mate-copying experiment while accounting for boldness (Nöbel et al., 2022). The shy/bold axis is one of the best-described continuums of behavioral variation (Dingemanse and Réale, 2005; Gosling, 2001; Groothuis and Carere, 2005; Réale et al., 2007; Sih et al., 2004). Boldness can be defined as the “propensity to move through and explore unfamiliar space” (Wilson et al., 1994; Fraser et al., 2001) while shy individuals rather respond to novel environment by retreating or freezing (Budaev, 1997; Wilson et al., 1993). Therefore, we expected bold and shy individuals to differ in their capacity to extract information from the environment and their behavior (Ariyomo and Watt, 2012; Biro and Stamps, 2008; Colléter and Brown, 2011; Dahlbom et al., 2011; Harcourt et al., 2009, 2010; Krause et al., 2010; Réale et al., 2009). In *G. holbrooki*, we found strong evidence for mate copying in shy individuals while no evidence in bold individuals (Nöbel et al., 2022). Here we used the same design to test for the existence of mate copying in zebrafish.

The zebrafish has emerged as a model to address the heritable components of behaviour (Ariyomo et al., 2013) and the genetic architecture underlying particular personality axis (Oswald et al., 2013). As a genetic model organism, the zebrafish could offer the possibility of studying mate copying and personality in a battery of different genetic background in order to correlate further personality patterns with mate copying. Such an approach, however, can only be developed if female zebrafish show robust mate copying. In the wild, zebrafish form small shoals of 2–30 individuals (Engeszer et al., 2007b; Pritchard et al., 2001; Spence et al., 2006a). Thus, they have the opportunity to observe and copy the mate choice of conspecifics. Like in most fish species, zebrafish females are visually attracted to large males (Pyron, 2003), which tend to be more territorial (Spence and Smith, 2005) and eggs sired by larger males have a higher hatching probability, hatch earlier and produce larger offspring (Uusi-Heikkilä et al., 2012). We tested females from two

zebrafish strains, AB and TL, in a standard mate-copying experiment and evaluate their boldness/shyness in a test maze. We found no significant evidence for mate copying and neither the strains nor the shy/bold score influenced females' preference for large males.

2. Methods

2.1. Fish lines and maintenance

The zebrafish is a diurnal shoaling species that lives in freshwater rivers in India, Bangladesh, Pakistan, Nepal and Bhutan (Barman, 1991; Engeszer et al., 2007b; McCann et al., 1971). Zebrafish have dark, bluish-black stripes alternating with light stripes. Zebrafish females and males display phenotypic differences, but the degree of sexual dimorphism is minimal. Males tend to be slender than females, which usually display an enlarged belly, and males tend to show more yellow coloration and darker stripes than females (Laale, 1977). However, these color and body shape traits can be affected by diet, age and strain and thus cannot be fully reliable for gender identification. Thus, to distinguish females from males unambiguously, we also used the presence of the urogenital papilla, a small protuberance in front of the genital pore that is well developed in females while poorly developed in mature males (Yossa et al., 2013).

We used two common zebrafish wild-type lab strains: the AB strain (with stripes pattern and short fins) and the TL strain (Tüpfel long fin; with leopard spotty pattern and elongated fins) to account for putative differences in social learning capacities in the two strains (Gorissen et al., 2015; van den Bos et al., 2017). Fish were purchased from the Centre de Biologie du Développement (Université Paul Sabatier in Toulouse, France) and were housed in mixed-sex shoals in tanks (60 cm × 40 cm × 30 cm) with a constant temperature of 26 °C and a 14:10 h light:dark cycle. They were fed twice a day ad libitum with flake food. Several days (3–6 days) before experiments fish were sexed and kept in same sex groups under the same conditions.

2.2. Ethical note

All animals were handled in accordance with the guidelines from the European directive on the protection of animals used for scientific purposes (2010/63/UE), French Decret 2013–118. Fish were raised in a facility certified by the French Ministry of Agriculture (approval ID B-31–555–10) and MR has received an authorization to experiment on vertebrate models (N° 311255556) from the ‘Direction Départementale de la Protection des Populations de la Haute-Garonne’. All efforts were made to minimize the number of animals used and their suffering, according to the guiding principles from the Decret 2013–118.

2.3. Mate-copying experiment

All experiments were performed with the classical mate-copying design used in most fish studies: a large test tank (50 cm × 30 cm × 30 cm) and four small stimulus tanks (15 cm × 10 cm × 25 cm) with two standing side by side at each smaller side of the large tank (Fig. 1). A mate-choice zone (15 cm × 15 cm) was marked in front of the small stimulus tanks on each side. The water in the tanks was 20 cm deep and had a constant temperature of 26 °C. The backsides of the tanks were covered with blue plastic foil to avoid any disturbances from outside. The design encompassed a series of steps that were similar to previous studies on mate copying in fish (e.g., Schlupp et al., 1994; Witte and Ryan, 1998).

First, opaque screens (white plastic boards) were inserted between the central compartment and the smaller tanks to prevent any visual contact between the tanks when the observer female was gently placed into the large test tank while a small and a large male were placed individually in one of the two small tanks, diagonally from each other to maximize distance. All three fish were allowed to acclimatize for

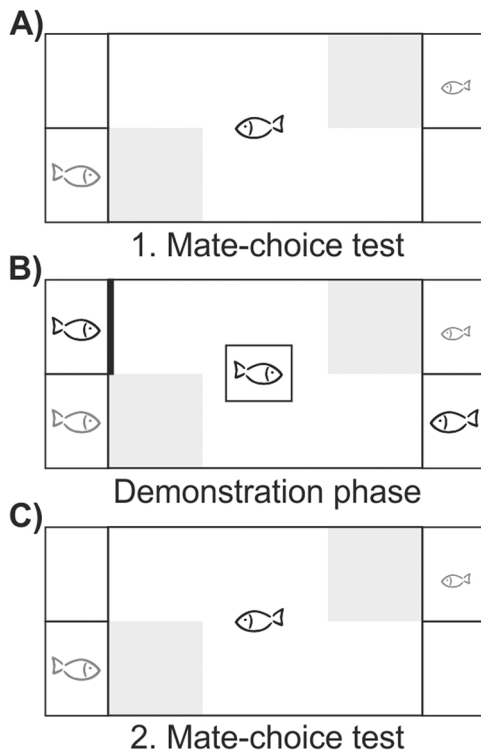


Fig. 1. Top view on the experimental set-up and design of the mate-copying experiment: (A) First mate-choice test: the grey fields are the two mate-choice zones. The observer female (black) is in the large test tank and two males (grey), a large (left) and a small (right), are placed diagonally in one of the small stimulus tanks at each end of the large test tank. (B) Demonstration phase for 10 min: A demonstrator female (black) is placed in a separate tank next to the small male (right here). A pseudo-demonstrator female (black, left) is placed in a separate tank next to the large male, but behind an opaque screen (black bar) and thus not visible to the observer female. (C) Second mate-choice test (similar to the first mate-choice test).

20 min. Then, the observer female was gently placed in a clear glass square (10 cm × 10 cm × 35 cm) in the middle of the central tank and the opaque screens were removed to allow visual contact. After an additional acclimation time of 10 min, the glass square was removed to free the observer female and the time the female spent within the mate-choice zone in front of each stimulus male was recorded for 10 min (first part of the mate-choice test, Fig. 1A). After 10 min, the opaque screens were inserted, and the observer female was placed back into the glass square in the center of the test tank. To control for potential observer female's side biases, stimulus males were switched between the two small stimulus tanks. Then the screens were removed, and the observer female had 5 min to acclimate to the new situation before she was released from the glass square, and again we recorded the time she spent in the mate-choice zones in front of the males for another 10 min. The time spent in front of a given stimulus male in both parts of the mate-choice test was added for each stimulus male separately. The observer female was considered to prefer a certain stimulus male if she spent more time in front of him during the total of 20-min of the mate-choice test.

After this first mate-choice test (comprising two 10-min trials), opaque screens were inserted, and the observer female was placed back into the glass square in the middle of the large tank. One demonstrator female was placed next to each male, but only the one close to the small male was visible to the observer female while the one next to the large male was hidden by an opaque screen (thick line in Fig. 1B). Fish were given a few minutes to calm down before the opaque screens (except the one in front of the pseudo-demonstrator female next to the large male) were removed. Then, the observer female was given the opportunity to

observe a demonstrator female near the small male and the large male apparently alone for 10 min (Fig. 1B). After this 10-min demonstration, screens were inserted again, and the demonstrator females removed. Finally, the opaque screens were removed, and the observer female was released from the glass square starting the second mate-choice test, which duplicated the first mate-choice test in all aspects (Fig. 1C).

After the experiments, male and female body lengths were measured from the tip of the snout to the caudal peduncle to the nearest mm. The demonstrator females used in the same test were matched for body length, while the mean difference of body length of stimulus males was 4.4 mm ± 0.2 mm, representing 17% ± 0.5% of the body length on average. For more details about the body lengths of fish used in the experiments please see Table 1 in the supplements. All fish were used only once.

2.4. Control for consistency in mate choice without opportunity to copy

Here, we tested if females were consistent in their mate choice when they were not given an opportunity observe another female's mate choice. We used the same set-up under the same conditions and with the same protocol as the experiments but both demonstrator females were hidden to the observer female during the demonstration phase by an opaque screen and thus not visible to the observer female.

The mean difference of male body length was 4.9 mm ± 0.2 mm, representing 18% ± 0.7% of the body length on average.

2.5. Calculation of the social-learning index (SLI)

We first calculated scores for each tested observer female separately for the first (MCT1) and the second mate-choice test (MCT2) using the following formula: $MCT = tS / (tS + tL)$, where tS is the time spent in front of the smaller male and tL the time spent in front of the larger male. Then a social learning score (SLS) was calculated for each observer female as the difference in scores of the first and second mate-choice test (MCT2 - MCT1). Positive values indicate an increase in time spent in front of small males (mate-copying), while negative values indicate a decrease in time spent in front of the small males (no mate-copying). The social learning index (SLI) is the mean of the SLS of all females within the same condition and was used for Fig. 4.

2.6. Personality test in a test maze

Directly following each mate copying or control experiment, we measured boldness as exploratory behavior in a test maze (Nöbel et al., 2022). The test maze consisted of a test tank (30 cm × 20 cm × 20 cm) separated in five chambers (chamber 3: 10 cm × 20 cm; the other four chambers: 10 cm × 10 cm) by four dark grey plastic boards (Fig. 2). Each plastic board had a hole in the middle (3 cm diameter) that allowed

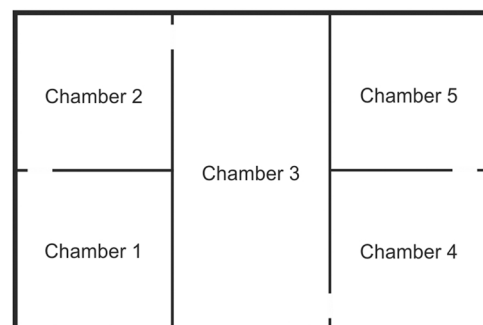


Fig. 2. Top view on the experimental set-up of the maze to test boldness. The tank was separated in five chambers by four dark grey plastic boards, each with an opening in the middle of each plastic board. A test female was gently placed into chamber 1 at the beginning of the test.

fish to swim from one chamber to the next. To avoid any disturbances from outside, the four sides around the test tank were covered with opaque foil. The water in the tanks was 10 cm deep and had a constant temperature of 26 °C.

A female was gently placed into chamber 1, and then, we recorded the time until the female reached chamber 5 or stopped after a maximum of 10 min and noticed the chamber the female reached in this time. A dichotomic definition separates individuals that reached the last chamber (Bold) from the ones that did not (Shy).

2.7. Statistical analysis

Data analyses were carried out with the R software (version 3.3.3; R Core Team, 2017). We tested a total of 120 observer females. Observer females that showed a strong side-bias independently from the fact that we swapped the males in the middle of the mate-choice test, i.e., whose total time spent on the mate-choice zone of one side represented more than 90% of the total time spent in the two mate-choice zones during the first mate-choice test, were removed from our study. This is a common criterion in mate-copying experiments (e.g., Witte and Noltemeier, 2002; Witte and Ueding, 2003). Fifteen females (14 AB, 1 TL) were excluded from the analysis because they showed a side bias in the first mate-choice test or did not move at all. Overall, we tested 105 females successfully: 65 in mate-copying experiments (30 AB, 35 TL) and 40 in control experiments (20 AB, 20 TL).

To analyze the data, we used a linear regression model (LM) without random effects. We started with an univariate analysis testing experimenter and body length of the observer female as confounding effects. Although the experimenter effect was significant (JT, MC, MG, SN: LM, $df = 1$, $F = 3.262$, $P = 0.025$) we did not include it in the final model as random effect because it increased the Akaike Information Criteria (AIC,

Akaike, 1969) of the models enormously. The body length of the observer female had no effect on SLS (LM: $df = 1$, $F = 1.485$, $P = 0.226$), and was thus, not included in the model. As we know from a study in mosquito fish (*G. holbrooki*) that size difference between males affect mate copying (Nöbel et al., 2022) we included this variable in our model, too. The starting model included the SLI as response variable and treatment (mate-copying (MC), control for consistency in mate choice (C)), personality (shy, bold), strain (AB, TL), male size-ratio (% normalized) plus its square and its interactions. Significance of fixed effects was tested using Wald chi-square tests implemented in the ANOVA function of the car package (Fox and Weisberg, 2011). We applied a stepwise backward selection method using P-values, by dropping out non-significant effects, starting with the highest order interaction. We used the AIC to determine the final model. We used t-tests as post-hoc tests to compare the SLI of the two treatments.

3. Results

The time spent in front of the males (Fig. 3) was used to calculate the social-learning scores (SLS) that were used for the analysis. To calculate the SLS, scores for each tested observer female were calculated separately for the first (MCT1) and the second mate-choice test (MCT2) using the following formula: $MCT = tS / (tS + tL)$, where tS is the time spent in front of the smaller male and tL the time spent in front of the larger male. The SLS for each observer female are the difference in scores of the first and second mate-choice test ($MCT2 - MCT1$). The starting model of variables explaining the SLS included 5 main effects, (i) treatment (MC, C), (ii) personality (shy, bold), (iii) strain (AB, TL) and (iv) male size-ratio plus its square, plus all possible interactions between treatment, personality, strain and size difference between males. The interaction between treatment, personality, strain and male size-ratio was non-

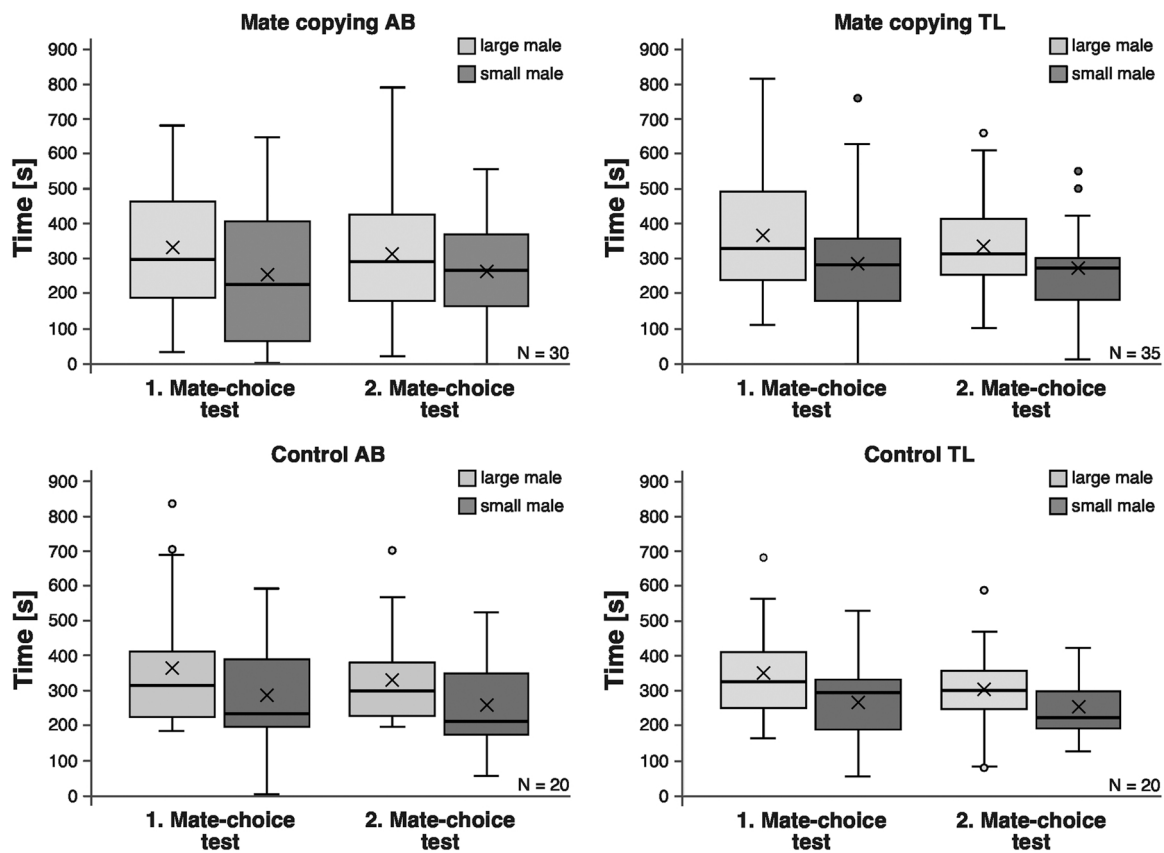


Fig. 3. Time spent in the mate-choice zones in front of large and small males of AB females and TL females in the mate-copying treatment and AB females and TL females in the control treatment. The upper and lower ends of the box are the lower and upper quartiles. The vertical line indicates the median and the cross marks the mean. Whiskers indicate min and max, while circles mark outliers.

significant (LM: $df = 1$, $F = 0.469$, $P = 0.530$). Neither the interactions were significant (LM: $P < 0.255$) nor the single fixed effects were significant (treatment LM: $df = 1$, $F = 0.001$, $P = 0.976$; strain LM: $df = 1$, $F = 0.021$, $P = 0.886$; personality LM: $df = 1$, $F = 0.691$, $P = 0.408$; male size-ratio LM: $df = 1$, $F = 0.422$, $P = 0.518$; male size-ratio²: LM: $df = 1$, $F = 1.859$, $P = 0.176$, see Table 1). Furthermore, the post-hoc comparison of the social-learning indices (SLIs, mean of the SLS) of the two treatments revealed that there was no difference between mate copying and control (t-test: $t = -0.297$, $df = 88.281$, $P = 0.768$, Fig. 4). Thus, we found no evidence for mate copying in our zebrafish.

4. Discussion

Despite of the improvements (see next paragraph) of the usual protocol for mate copying in fish (Schlupp et al., 1994; Witte and Ryan, 1998), we found no clear evidence for mate copying in female zebrafish of the two strains tested as observer females did not show any increase in the time spent close to the small males after observing them interacting with another female. Females preferred larger males, as already reported (Pyron, 2003), in both the first and second mate-choice test, respectively before and after the observer female received positive social information about the small male and negative about the large male. Also, in the control without opportunity to copy, observer females chose consistently the larger male. Thus, we found no evidence for mate copying of smaller males in either strain of zebrafish taken independently or after grouping them together.

4.1. Experimental design

We used the same set-up than Schlupp et al. (1994) and Witte and Ryan (1998) but made subtle changes to the protocol. These previous studies put the apparent demonstrator female near the male close to which the observer female spent the shortest amount of time during the first mate-choice test. As this protocol did not respect the general rule of attributing individuals randomly to the treatments, we decided a priori, as other authors (for instance Kniel et al., 2015), to show the demonstrator female next to the small male in all cases, as, in zebrafish, females have been shown to prefer larger males (Pyron, 2003). We believe that this change in the experimental set-up avoids the pervasive and subtle biases of the 'Regression to the Mean' (or RTM) fallacy that was first described by Galton (1886) and that kept on being rediscovered since (Stigler, 1999). Other protocols may generate artificially inflated mate-copying indices, just because the observer females having by chance spent a long time close to one male in the first mate-choice test are statistically more likely to spend less time close to that male only by chance, as average values are more common than extreme values. This change made our protocol immune to the RTM (Kelly and Price, 2005, see simulation studies in a different context in Danchin et al., 2014).

Our results clearly show that there is neither an increase nor decrease in time spent in front of small or large males between the two mate-choice tests. Thus, if females are influenced by public information about male mating success in that species, this influence must be rather low, suggesting that the zebrafish is probably not the best model species to study mate copying.

Table 1

Best fitting linear mixed regression model with the SLS as response variable. All interactions were removed. We tested 65 females in the mate copying treatment (30 AB, 35 TL) and 40 females in the control (20 AB, 20 TL).

	Sum Sq	df	F-value	P-value
Intercept	0.005	1	0.077	0.783
Treatment	0.001	1	0.001	0.976
Personality	0.045	1	0.691	0.408
Strain	0.001	1	0.021	0.886
Male size-ratio	0.028	1	0.422	0.518
Male size-ratio ²	0.121	1	1.859	0.176

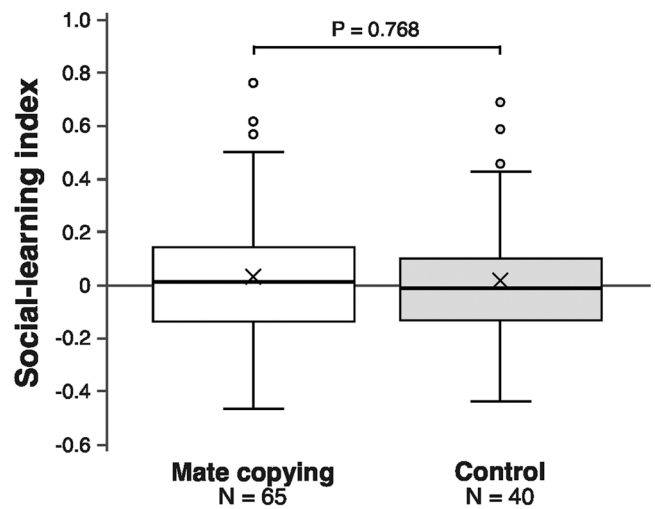


Fig. 4. Social-learning indices of the mate-copying experiment and the control pooled for both strains. We first calculated scores for each observer female separately for the first (MCT1) and the second mate-choice test (MCT2) using the following formula: $MCT = tS / (tS + tL)$, where tS is the time spent in front of the smaller male and tL the time spent in front of the larger male. Then a social learning score (SLS) was calculated for each observer female as the difference in scores of the first and second mate-choice test ($MCT2 - MCT1$). Positive values indicate an increase in time spent in front of small males (mate-copying), while negative values indicate a decrease in time spent in front of the small males (no mate-copying). The social learning index (SLI) is the mean of the SLS of all females within the same condition. The P-value above the horizontal bar is from a t-test comparing the two treatments. The upper and lower ends of the box are the lower and upper quartiles. The vertical line indicates the median and the cross marks the mean. Whiskers indicate min and max, while circles mark outliers.

We performed a control to assess the behavior of the observer female without any information about the two males during the demonstration (i.e., without any visible demonstrator female). Such a control would have been necessary to demonstrate that females do increase their preference for small males in the second mate-choice test because of the information provided during the demonstration and not for other reasons such as, for instance, the fact that they might have changed their mind and gone for the other male because at the first mate-choice test they did not manage to reach their preferred male. However, even if we found that female zebrafish do not show any mate-copying behavior we performed this control to show that females chose consistently the same male if they do not gain social information about males. In the control, females chose consistently the larger male.

4.2. Social learning index

As in previous studies in fish (e.g., Amlacher and Dugatkin, 2005; Dugatkin, 1992, 1998, 2007; Dugatkin and Godin, 1992, 1993; Nöbel and Witte, 2013; Schlupp et al., 1994; Schlupp and Ryan, 1997; Vukomanovic and Rodd, 2007; Witte and Noltemeier, 2002; Witte and Ryan, 1998, 2002) we used the amount of time a female spends close to a given male as a criterion of sexual preference. Every time that assumption was tested in previous studies authors found that the time spent close to a given male is a good predictor of the females' willingness to actually mate with that male (*Poecilia reticulata*: Bischoff et al., 1985; Kodric-Brown, 1993; *Syngnathus typhle*: Berglund, 1993; *Xiphophorus helleri*: Walling et al., 2010). The same assumption is made in the vast majority of species in all other taxa (Aspbury and Basolo, 2002; Clayton, 1990; Drickamer et al., 2000). We thus adopted the same convention, without testing the correlation between time spent close to a male and actual mating probability, as our study was essentially exploratory.

4.3. Influence of personality and male size-ratio on mate copying

We tested the influence of personality, especially boldness, on mate copying. We expected shy individuals to be better at gathering social information than bold individuals. However, in our experiments, boldness did not affect the mate-copying performance of our tested females. This is in accordance with a study in *Gambusia affinis* males where Gomes-Silva et al. (2017) did not find a correlation between personality measured as boldness, activity and shoaling tendency with mate copying. Contrastingly, when using the same approach in the Eastern mosquito fish (*Gambusia holbrooki*; Nöbel et al., 2022), we detected a significant effect of personality with only shy individuals performing mate copying. Similarly, White et al. (2017) found that sociability (defined as proclivity to be with other females) in guppy females (*Poecilia reticulata*) predicts mate-copying tendency. A study in zebrafishes (*Taeniopygia guttata*) showed that females that sample more actively their environment were less likely to copy in mating and foraging situations (Rosa et al., 2012).

We also included the size difference of stimulus males in the analysis because we previously showed that it influenced mate copying significantly in mosquito fish (Nöbel et al., 2022). However, in the current study male size-ratio was not affecting mate copying.

4.4. The reasons of the potential lack of mate copying in zebrafish

The lack of evidence for mate copying in that social species is rather surprising. One explanation is that our strains of zebrafish (AB, TL) need more time to learn socially. Alternatively it remains possible that another strain, or fish from the wild, would learn faster. In other species, the use of 10-minute demonstrations was sufficient to elicit detectable change in mate preference (Witte and Ryan, 1998); however, this demonstration period might have been too short in our case if zebrafish are 'slow' social learners. Another explanation might be that the proximity of the demonstrator female to the small male was not an appropriate stimulus to influence mate choice. Perhaps zebrafish females need real courtship and/or copulation as cues to copy the choice of other females. Although previous mate copying evidence in fish also did not involve actual copulation or courtship, experiments in the Japanese quail (*Coturnix coturnix japonica*) and the fruit fly (*D. melanogaster*) suggested that copulation is the main cue to elicit mate copying in these species (Dagaëff et al., 2016; Galef and White, 1998).

From a female perspective, mating with a male that already mated might be perceived as a risk of sperm depletion. In agreement with this hypothesis, *D. melanogaster* females avoid males immediately after seeing them copulating, but tend to prefer these males after 24 h, a delay sufficient for them to rebuild their sperm stocks (Loyau et al., 2012). Thus, there might be a possibility that some of our zebrafish females accounted for such risks of sperm depletion and avoided males they saw recently with another female. However, we did not find a significant increase in time spent with the larger male in the second mate-choice test which would hint at active avoidance of the smaller male they saw with a female. Perhaps females would need to observe spawning to cause an avoidance reaction.

Alternatively, male size might not play a major role in zebrafish, implying that we did not manipulate the right trait. This would also explain inconsistent results in previous studies in that species. Pyron (2003) provided evidence for female preference for large males, while Hutter et al. (2010) found no influence of male body size on female preferences. This suggests that, although existing, the preference for large males might not be a major determinant for female mating preference in that species.

Female preferences for males with larger body size are expected in species with mating systems in which males provide resources (e.g., guard territories or eggs; Andersson, 1994), which is not the case for male zebrafish. Male zebrafish are aggressive, and females may cue on aggressiveness or dominance more than on size (Qvarnström, Forsgren,

1998), a possibility that was prevented in our set-up, as males could not interact directly with each other. Nonetheless, our result suggests that in both strains females do have a preference for larger males.

Although in many other fish species, such as *Gambusia*, our design is efficient at demonstrating mate copying, it might be that our experimental design may have prevented the use of other major cues for mate choice in zebrafish. Although zebrafish have been shown to learn and discriminate visually in various contexts (Engeszer et al., 2004; Hutter et al., 2011; Rosenthal and Ryan, 2005), several studies also reported a major role of olfactory cues in reproduction (Bloom and Perlmutter, 1977; Gerlach and Lysiak, 2006). These cues were excluded in our set-up because males and females were in separate tanks during the experiments and water was not mixed. Thus, in order to investigate further the impact of mate copying in zebrafish, it might be necessary to characterize other determinants than body size potentially influencing mate preferences in zebrafish. Finally, it might also be that natural zebrafish populations possess the capacity for mate copying, and that laboratory strains have lost it.

We believe that it is important to accumulate results on various species to understand the ecological correlates of the presence versus absence of mate copying in multiple species. In the present study, we did not detect clear evidence for mate copying in the zebrafish despite the use of a robust set-up in fish and that we accounted for personality. At this stage, our conclusion is that the zebrafish is unlikely to be the best model species to study mate copying in vertebrates.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2023.104837.

References

- Akaike, H., 1969. Fitting autoregressive models for prediction. *Inst. Stat. Math.* 21, 243–247.
- Amlacher, J., Dugatkin, L.A., 2005. Preference for older over younger models during mate-choice copying in young guppies. *Ethol. Ecol. Evol.* 17, 161–169. <https://doi.org/10.1080/08927014.2005.9522605>.
- Andersson, M.B., 1994. *Sexual selection*. Princeton University Press, Princeton.
- Ariyomo, T.O., Watt, P.J., 2012. The effect of variation in boldness and aggressiveness on the reproductive success of zebrafish. *Anim. Behav.* 83, 41–46. <https://doi.org/10.1016/j.anbehav.2011.10.004>.
- Ariyomo, T.O., Carter, M., Watt, P.J., 2013. Heritability of boldness and aggressiveness in the zebrafish. *Behav. Gen.* 43, 161–167. <https://doi.org/10.1007/s10519-013-9585-y>.
- Aspbury, A.S., Basolo, A.L., 2002. Repeatable female preferences, mating order and mating success in the poeciliid fish, *Heterandria formosa*. *Behav. Ecol. Sociobiol.* 51, 238–244. <https://doi.org/10.1007/s00265-001-0443-1>.
- Barman, R.P., 1991. A taxonomic revision of the Indo-Burmese species of *Danio* Hamilton Buchanan (Pisces, Cyprinidae). *Rec. Zool. Surv. India*.
- Berglund, A., 1993. Risky sex: male pipefishes mate at random in the presence of a predator. *Anim. Behav.* 46, 169–175. <https://doi.org/10.1006/anbe.1993.1172>.
- Biro, P.A., Stamps, J.A., 2008. Are animal personality traits linked to life-history productivity. *Trends Ecol. Evol.* 23, 361–368. <https://doi.org/10.1016/j.tree.2008.04.003>.

- Bischoff, R.J., Gould, J.L., Rubenstein, D.I., 1985. Tail size and female choice in the guppy (*Poecilia reticulata*). *Behav. Ecol. Sociobiol.* 17, 253–255. <https://doi.org/10.1007/BF00300143>.
- Bloom, H.D., Perlmutter, A., 1977. A sexual aggregating pheromone system in the zebrafish, *BrachyDanio rerio* (Hamilton-Buchanan). *J. Exp. Zool.* 199, 215–226. <https://doi.org/10.1002/jez.1401990206>.
- Bowers, R.L., Place, S.S., Todd, P.M., Penke, L., Asendorpf, J.B., 2012. Generalization in mate-choice copying in humans. *Behav. Ecol.* 231, 112–124. <https://doi.org/10.1093/beheco/arr164>.
- Budaev, S.V., 1997. "Personality" in the guppy (*Poecilia reticulata*): a correlation study of exploratory behavior and social tendency. *J. Comp. Physiol.* 111, 399–411.
- Clayton, D.H., 1990. Mate choice in experimentally parasitized rock doves: lousy males lose. *Am. Zool.* 3, 251–262. <https://doi.org/10.1093/icb/30.2.251>.
- Colléter, M., Brown, C., 2011. Personality traits predict hierarchy rank in male rainbowfish social groups. *Anim. Behav.* 81, 1231–1237. <https://doi.org/10.1016/j.anbehav.2011.03.011>.
- Core Team, R., 2017. R: A language and environment for statistical computing. R. Found. Stat. Comput., Vienna, Austria.
- Dagaev, A.-C., Pocheville, A., Nöbel, S., Loyau, A.L., Isabel, G., Danchin, E., 2016. *Drosophila* mate copying correlates with atmospheric pressure in a speed learning situation. *Anim. Behav.* 121, 163–174. <https://doi.org/10.1016/j.anbehav.2016.08.022>.
- Dahlbom, S.J., Lagman, D., Lundstedt-Enkel, K., Sundström, L.F., Winberg, S., 2011. Boldness predicts social status in zebrafish (*Danio rerio*). *PLoS ONE* 6, e23565.
- Danchin, E., Wagner, R.H., 2010. Inclusive heritability: combining genetic and non-genetic information to study animal behavior and culture. *Oikos* 119, 210–218. <https://doi.org/10.1111/j.1600-0706.2009.17640.x>.
- Danchin, E., Giraldeau, L.-A., Valone, T.J., Wagner, R.H., 2004. Public information: from nosy neighbors to cultural evolution. *Science* 305, 487–491. <https://doi.org/10.1126/science.1098254>.
- Danchin, E., Wajnberg, E., Wagner, R.H., 2014. Avoiding pitfalls in estimating heritability with the common options approach. *Sci. Rep.* 4, 3974. <https://doi.org/10.1038/srep03974>.
- Danchin, E., Nöbel, S., Pocheville, A., Dagaev, A.C., Demay, L., Alphan, M., Isabel, G., 2018. Cultural flies: conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science* 362, 1025–1030. <https://doi.org/10.1126/science.aat1590>.
- van den Bos, R., Mes, W., Galligani, P., Heil, A., Zethof, J., Flik, G., et al., 2017. Further characterisation of differences between TL and AB zebrafish (*Danio rerio*): gene expression, physiology and behaviour at day 5 of the larval stage. *PLoS ONE* 12, e0175420. <https://doi.org/10.1371/journal.pone.0175420>.
- Dingemans, N.J., Réale, D., 2005. Natural selection and animal personality. *Behaviour* 142, 1165–1190. <https://doi.org/10.1163/156853905774539445>.
- Dooley, K., Zon, L.I., 2000. Zebrafish: a model system for the study of human disease. *Curr. Op. Genet. Dev.* 10, 252–256. [https://doi.org/10.1016/S0959-437X\(00\)00074-5](https://doi.org/10.1016/S0959-437X(00)00074-5).
- Drickamer, L.C., Gowaty, P.A., Holmes, C.M., 2000. Free female mate choice in house mice affects reproductive success and offspring viability and performance. *Anim. Behav.* 59, 371–378. <https://doi.org/10.1006/anbe.1999.1316>.
- Dugatkin, L.A., 1992. Sexual selection and imitation: females copy the mate choice of others. *Am. Nat.* 139, 1384–1389 (Available from). (<http://www.jstor.org/stable/2462347>).
- Dugatkin, L.A., 1998. Genes, copying, and female mate choice: shifting thresholds. *Behav. Ecol.* 9, 323–327. <https://doi.org/10.1093/beheco/9.4.323>.
- Dugatkin, L.A., 2007. Developmental environment, cultural transmission, and mate choice copying. *Naturwissenschaften* 94, 651–656. <https://doi.org/10.1007/s00114-007-0238-y>.
- Dugatkin, L.A., Godin, J.-G.J., 1992. Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proc. R. Soc. Lond. B.* 249, 179–184. <https://doi.org/10.1098/rspb.1992.0101>.
- Dugatkin, L.A., Godin, J.-G.J., 1993. Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. *Behav. Ecol.* 4, 289–292. <https://doi.org/10.1093/beheco/4.4.289>.
- Eisen, J.S., 1991. Determination of primary motoneuron identity in developing zebrafish embryos. *Science* 252, 569–572. <https://doi.org/10.1126/science.1708527>.
- Engeszer, R.E., Ryan, M.J., Parichy, D.M., 2004. Learned social preference in zebrafish. *Curr. Biol.* 14, 881–884. <https://doi.org/10.1016/j.cub.2004.04.042>.
- Engeszer, R.E., da Barbiano, Alberici, Ryan, L., Parichy, D.M., M.J., 2007a. Timing and plasticity of shoaling behaviour in the zebrafish, *Danio rerio*. *Anim. Behav.* 74, 1269–1275. <https://doi.org/10.1016/j.anbehav.2007.01.032>.
- Engeszer, R.E., Patterson, L.B., Rao, A.A., Parichy, D.M., 2007b. Zebrafish in the wild: a review of natural history and new notes from the field. *Zebrafish* 4, 21–40. <https://doi.org/10.1089/zeb.2006.9997>.
- Fox, J., Weisberg, S., 2011. An {R} Companion to Applied Regression, second ed. Sage Publishing, London, UK.
- Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N., Skalski, G.T., 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *Am. Nat.* 158, 124–135. <https://doi.org/10.1086/321307>.
- Galef jr., B.G., White, D.J., 1998. Mate-choice copying in Japanese quail, *Coturnix coturnix japonica*. *Anim. Behav.* 55, 545–552. <https://doi.org/10.1006/anbe.1997.0616>.
- Galef, B.G., Lim, T.C.W., Gilbert, G.S., 2008. Evidence of mate choice copying in Norway rats, *Rattus norvegicus*. *Anim. Behav.* 75, 1117–1123. <https://doi.org/10.1016/j.anbehav.2007.08.026>.
- Galton, F., 1886. Regression towards mediocrity in hereditary stature. *J. Anthropol. Instit.* 15, 246–263. <https://doi.org/10.2307/2841583>.
- Gerlach, G., Lysiak, N., 2006. Kin recognition and inbreeding avoidance in zebrafish, *Danio rerio*, is based on phenotype matching. *Anim. Behav.* 71, 1371–1377. <https://doi.org/10.1016/j.anbehav.2005.10.010>.
- Gibson, R.M., Höglund, J., 1992. Copying and sexual selection. *Trends Ecol. Evol.* 7, 229–232. [https://doi.org/10.1016/0169-5347\(92\)90050-L](https://doi.org/10.1016/0169-5347(92)90050-L).
- Gibson, R.M., Bradbury, J.W., Vehrencamp, S.L., 1991. Mate choice in lekking sage grouse revisited: the roles of vocal display, female site fidelity, and copying. *Behav. Ecol.* 2, 165–180. <https://doi.org/10.1093/beheco/2.2.165>.
- Gomes-Silva, G., Liu, K., Chen, B., Plath, M., Sommer-Trembo, C., 2017. Does individual variation in male mate choice copying reflect differences in social responsiveness? *Ann. Biol. Sci.* 5, 25–36.
- Gorissen, M., Manuel, R., Pelgrim, T.N.M., Mes, W., de Wolf, M.J.S., Zethof, J., Flik, G., van den Bos, R., 2015. Differences in inhibitory avoidance, cortisol and brain gene expression in TL and AB zebrafish. *Genes, Brain Behav.* 14, 428–438. <https://doi.org/10.1111/gbb.12220>.
- Gosling, S.D., 2001. From mice to men: what can we learn about personality from animal research? *Psychol. Bull.* 127, 45–86. <https://doi.org/10.1037/0033-2909.127.1.45>.
- Groothuis, T.G.G., Carere, C., 2005. Avian personalities: characterization and epigenesis. *Neurosci. Biobehav. Rev.* 29, 137–150. <https://doi.org/10.1016/j.neubiorev.2004.06.010>.
- Harcourt, J.L., Ang, T.Z., Sweetman, G., Johnstone, R.A., Manica, A., 2009. Leadership, personality and social feedback. *Commun. Integr. Biol.* 2, 335–336. <https://doi.org/10.4161/cib.2.4.8471>.
- Harcourt, J.L., Biau, S., Johnstone, R., Manica, A., 2010. Boldness and information use in three-spined sticklebacks. *Ethology* 116, 440–447. <https://doi.org/10.1111/j.1439-0310.2010.01757.x>.
- Höglund, J., Alatalo, R.V., Gibson, R.M., Lundberg, A., 1995. Mate-choice copying in black grouse. *Anim. Behav.* 49, 1627–1633.
- Hutter, S., Penn, D.J., Magee, S., Zala, S.M., 2010. Reproductive behaviour of wild zebrafish (*Danio rerio*) in large tanks. *Behaviour* 147, 641–660. <https://doi.org/10.1163/000579510x12632972473944>.
- Hutter, S., Zala, S.M., Penn, D.J., 2011. Sex recognition in zebrafish (*Danio rerio*). *J. Ethol.* 29, 55–61. <https://doi.org/10.1007/s10164-010-0221-5>.
- Kelly, C., Price, T.D., 2005. Correcting for regression to the mean in behavior and ecology. *Am. Nat.* 166, 700–707. <https://doi.org/10.1086/497402>.
- Kniel, N., Dürler, C., Hecht, I., Heinbach, V., Zimmermann, L., Witte, K., 2015. Novel mate preference through mate-choice copying in zebra finches: sexes differ. *Behav. Ecol.* 26, 647–655. <https://doi.org/10.1093/beheco/aru241>.
- Kodric-Brown, A., 1993. Female choice of multiple male criteria in guppies: interacting effects of dominance, coloration and courtship. *Behav. Ecol. Sociobiol.* 32, 415–420. <https://doi.org/10.1007/BF00168825>.
- Krause, J., James, R., Croft, D.P., 2010. Personality in the context of social networks. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 4099–4106. <https://doi.org/10.1098/rstb.2010.0216>.
- Laale, H.W., 1977. The biology and use of zebrafish, *BrachyDanio rerio* in fisheries research. *J. Fish. Biol.* 10, 121–173. <https://doi.org/10.1111/j.1095-8649.1977.tb04049.x>.
- Losey Jr, G.S., Stanton, F.G., Teley, T.M., Tyler III, W.A., Class, Z.G.S., 1986. Copying others, an evolutionarily stable strategy for mate choice: a model. *Am. Nat.* 128, 653–664 (Available from). (<http://www.jstor.org/stable/2461949>).
- Loyau, A., Blanchet, S., Van Laere, P., Clobert, J., Danchin, E., 2012. When not to copy: female fruit flies use sophisticated public information to avoid mated males. *Sci. Rep.* 2, 768. <https://doi.org/10.1038/srep00768>.
- Marler, C.A., Ryan, M.J., 1997. Origin and maintenance of a female mating preference. *Evolution* 51, 1244–1248. <https://doi.org/10.2307/2411053>.
- McCann, L.I., Koehn, D.J., Kline, N.J., 1971. The effects of body size and body markings on nonpolarized schooling behavior of zebra fish (*BrachyDanio rerio*). *J. Psychol.* 79, 71–75. <https://doi.org/10.1080/00223980.1971.9923769>.
- Mery, F., Varella, S.A.M., Danchin, E., Blanchet, S., Parejo, D., Coolen, I., Wagner, R.H., 2009. Public versus personal information for mate copying in an invertebrate. *Curr. Biol.* 19, 730–734. <https://doi.org/10.1016/j.cub.2009.02.064>.
- Moretz, J.A., Martins, E.L.P., Robison, B.D., 2007. Behavioral syndromes and the evolution of correlated behavior in zebrafish. *Behav. Ecol.* 18, 556–562. <https://doi.org/10.1093/beheco/arm011>.
- Nöbel, S., Witte, K., 2013. Public information influences sperm transfer to females in sailfin molly males. *PLoS ONE* 8, e53865. <https://doi.org/10.1371/journal.pone.0053865>.
- Nöbel, S., Wang, X., Talvard, L., Tariel, J., Lille, M., Cucherousset, J., Roussigne, M., Danchin, E., 2022. The importance of population heterogeneities in detecting social learning as the foundation of animal cultural transmission. *Proc. R. Soc. B.* 289, 20220431. <https://doi.org/10.1098/rspb.2022.0431>.
- Nüsslein-Volhard, C., 2012. The zebrafish issue of development. *Development* 139, 4099–4103. <https://doi.org/10.1242/dev.085217>.
- Oswald, M.E., Singer, M., Robison, B.D., 2013. The quantitative genetic architecture of the bold-shy continuum in zebrafish, *Danio rerio*. *PLoS ONE* 8, e68828. <https://doi.org/10.1371/journal.pone.0068828>.
- Pritchard, V.L., Lawrence, J., Butlin, R.K., Krause, J., 2001. Shoal choice in zebrafish, *Danio rerio*: the influence of shoal size and activity. *Anim. Behav.* 62, 1085–1088. <https://doi.org/10.1006/anbe.2001.1858>.
- Pruett-Jones, S., 1992. Independent versus nonindependent mate choice: do females copy each other? *Am. Nat.* 140, 1000–1009 (Available from). (<http://www.jstor.org/stable/2462930>).
- Pyron, M., 2003. Female preferences and male mate interactions in zebrafish (*Danio rerio*). *Can. J. Zool.* 81, 122–125. <https://doi.org/10.1139/z02-229>.
- Qvarnström, A., Forsgren, E., 1998. Should females prefer dominant males? *Trends Ecol. Evol.* 13, 498–501. [https://doi.org/10.1016/S0169-5347\(98\)01513-4](https://doi.org/10.1016/S0169-5347(98)01513-4).

- Réale, D., Reader, S.M., Sol, D., McDougall, P.T., Dingemanse, N.J., 2007. Integrating animal temperament within ecology and evolution. *Biol. Rev.* 82, 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>.
- Réale, D., Martin, J., Coltman, D.W., Poissant, J., Festa-Bianchet, M., 2009. Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J. Evol. Biol.* 22, 1599–1607. <https://doi.org/10.1111/j.1420-9101.2009.01781.x>.
- Rosa, P., Nguyen, V., Dubois, F., 2012. Individual differences in sampling behaviour predict social information use in zebra finches. *Behav. Ecol. Sociobiol.* 66, 1259–1265. <https://doi.org/10.1007/s00265-012-1379-3>.
- Rosenthal, G.G., Ryan, M.J., 2005. Assortative preferences for stripes in *Danios*. *Anim. Behav.* 70, 1063–1066. <https://doi.org/10.1016/j.anbehav.2005.02.005>.
- Ruhl, N., McRobert, S.P., 2005. The effect of sex and shoal size on shoaling behaviour in *Danio rerio*. *J. Fish. Biol.* 67, 1318–1326. <https://doi.org/10.1111/j.0022-1112.2005.00826.x>.
- Schlupp, I., Ryan, M.J., 1997. Male sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males. *Behav. Ecol.* 8, 104–107. <https://doi.org/10.1093/beheco/8.1.104>.
- Schlupp, I., Marler, C., Ryan, M.J., 1994. Benefit to male sailfin mollies of mating with heterospecific females. *Science* 263, 373–374. <https://doi.org/10.1126/science.8278809>.
- Sih, A., Bell, A., Johnson, J.C., 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* 19, 372–378. <https://doi.org/10.1016/j.tree.2004.04.009>.
- Skinner, A.M.J., Watt, P.J., 2007. Strategic egg allocation in the zebra fish, *Danio rerio*. *Behav. Ecol.* 18, 905–909. <https://doi.org/10.1093/beheco/arm059>.
- Snekser, J.L., McRobert, S.P., Murphy, C.E., Clotfelter, E.D., 2006. Aggregation behavior in wildtype and transgenic zebrafish. *Ethology* 112, 181–187. <https://doi.org/10.1111/j.1439-0310.2006.01139.x>.
- Spence, R., Smith, C., 2005. Male territoriality mediates density and sex ratio effects on oviposition in the zebrafish, *Danio rerio*. *Anim. Behav.* 69, 1317–1323. <https://doi.org/10.1016/j.anbehav.2004.10.010>.
- Spence, R., Smith, C., 2007. The role of early learning in determining shoaling preferences based on visual cues in the zebrafish, *Danio rerio*. *Ethology* 113, 62–67. <https://doi.org/10.1111/j.1439-0310.2006.01295.x>.
- Spence, R., Fatema, M.K., Reichard, M., Huq, K.A., Wahab, M.A., Ahmed, Z.F., Smith, C., 2006a. The distribution and habitat preferences of the zebrafish in Bangladesh. *J. Fish. Biol.* 69, 1435–1448. <https://doi.org/10.1111/j.1095-8649.2006.01206.x>.
- Spence, R., Jordan, W.C., Smith, C., 2006b. Genetic analysis of male reproductive success in relation to density in the zebrafish, *Danio rerio*. *Front. Zool.* 3, 5. <https://doi.org/10.1186/1742-9994-3-5>.
- Spence, R., Gerlach, G., Lawrence, C., Smith, C., 2008. The behaviour and ecology of the zebrafish, *Danio rerio*. *Biol. Rev.* 83, 13–34. <https://doi.org/10.1111/j.1469-185X.2007.00030.x>.
- Stigler, S.M., 1999. *Statistics on the Table: The History of Statistical Concepts and Methods*. Harvard University Press, Harvard.
- Streisinger, G., Walker, C., Dower, N., Knauber, D., Singer, F., 1981. Production of clones of homozygous diploid zebra fish (*Brachydanio rerio*). *Nature* 291, 293–296. <https://doi.org/10.1038/291293a0>.
- Uusi-Heikkilä, S., Kuparinen, A., Wolter, C., Meinelt, T., Arlinghaus, R., 2012. Paternal body size affects reproductive success in laboratory-held zebrafish (*Danio rerio*). *Environ. Biol. Fishes* 93, 461–474. <https://doi.org/10.1007/s10641-011-9937-5>.
- Vakirtzis, A., 2011. Mate choice copying and nonindependent mate choice: a critical review. *Ann. Zool. Fenn.* 48, 91–107. <https://doi.org/10.5735/086.048.0202>.
- Vukomanovic, J., Rodd, F.H., 2007. Size-dependent female mate copying in the guppy (*Poecilia reticulata*): Large females are role models but small ones are not. *Ethology* 113, 579–586. <https://doi.org/10.1111/j.1439-0310.2007.01343.x>.
- Wade, M.J., Pruett-Jones, S.G., 1990. Female copying increases the variance in male mating success. *Proc. Natl. Acad. Sci.* 87. <https://doi.org/10.1073/pnas.87.15.5749>.
- Walling, C.A., Royle, N.J., Lindström, J., Metcalfe, N.B., 2010. Do female association preferences predict the likelihood of reproduction? *Behav. Ecol. Sociobiol.* 64, 541–548. <https://doi.org/10.1007/s00265-009-0869-4>.
- Westneat, D.F., Walters, A., McCarthy, T.M., Hatch, M.I., Hein, W.K., 2000. Alternative mechanisms of nonindependent mate choice. *Anim. Behav.* 59, 467–476. <https://doi.org/10.1006/anbe.1999.1341>.
- White, D.J., Watts, E., Pitchforth, K., Agyapong, S., Miller, N., 2017. ‘Sociability’ affects the intensity of mate-choice copying in female guppies, *Poecilia reticulata*. *Behav. Proc.* 141, 251–257. <https://doi.org/10.1016/j.beproc.2017.02.017>.
- Wilson, D.S., Coleman, K., Clark, A.B., Biederman, L., 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *J. Comp. Psychol.* 107, 250. <https://doi.org/10.1037/0735-7036.107.3.250>.
- Wilson, D.S., Clark, A.B., Coleman, K., Dearstyne, T., 1994. Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* 9, 442–446. [https://doi.org/10.1016/0169-5347\(94\)90134-1](https://doi.org/10.1016/0169-5347(94)90134-1).
- Witte, K., Nöbel, S., 2011. Learning and mate choice. In: Brown, C., Laland, K., Krause, J. (Eds.), *Fish Cognition and Behaviour*. Wiley-Blackwell, Oxford, UK, pp. 81–107. <https://doi.org/10.1002/9781444342536.ch5>.
- Witte, K., Noltemeier, B., 2002. The role of information in mate-choice copying in female sailfin mollies (*Poecilia latipinna*). *Behav. Ecol. Sociobiol.* 52, 194–202. <https://doi.org/10.1007/s00265-002-0503-1>.
- Witte, K., Ryan, M.J., 1998. Male body length influences mate-choice copying in the sailfin molly *Poecilia latipinna*. *Behav. Ecol.* 9, 534–539. <https://doi.org/10.1093/beheco/9.5.534>.
- Witte, K., Ryan, M.J., 2002. Mate choice copying in the sailfin molly, *Poecilia latipinna*, in the wild. *Anim. Behav.* 63, 943–949. <https://doi.org/10.1006/anbe.2001.1982>.
- Witte, K., Ueding, K., 2003. Sailfin molly females (*Poecilia latipinna*) copy the rejection of a male. *Behav. Ecol.* 14, 389–395. <https://doi.org/10.1093/beheco/14.3.389>.
- Yossa, R., Sarker, P.K., Proulx, E., Saxena, V., Ekker, M., Vandenberg, G.W., 2013. A practical approach for sexing zebrafish, *Danio rerio*. *J. Appl. Aquacult.* 25, 148–153. <https://doi.org/10.1080/10454438.2013.792170>.