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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 one demonstrator female next to the small male. 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.

Keywords: public information; social learning; mate choice; mate copying; personality; zebrafish

## 1. Introduction

The ability to find a mate and to reproduce is a universal challenge of animal beings and this often results, within a population, in a strong competition for mating opportunities among individuals. Sexual selection, together with natural selection, is assumed to contribute to the appearance of new

animals' 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 in which one has access to a vast knowledge together with a panel of genetic tools and experimental set-ups for behavioral studies. 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 (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 that species (Spence et al. 2006a). In another study based, this time, on the analysis of courtship behavior, the same group 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, 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 this behavioral pattern 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 this context of 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 innate predisposition with, for instance, females copying the apparent mate choice for small males despite an innate preference for larger 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 comparing shy with bold individuals (Nöbel et al. under review). 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. under review).

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. This is why here we investigated whether zebrafish females copy the choice of their conspecifics for smaller males using the classical design in fish species and whether it is influenced by their personality. 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 a large male have a higher hatching probability, hatch earlier and the resulting offspring is larger (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 fresh water 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 x 40 cm x 30 cm) with a constant temperature of 26 °C and a 14:10 hours 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 x 30 cm x 30 cm) and four small stimulus tanks (15 cm x 10 cm x 25 cm) with two standing side by side at each smaller side of the large tank (Figure 1). A mate-choice zone (15 cm x 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 20 min. Then, the observer female was gently placed in a clear glass square (10 cm x 10 cm x 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, Figure 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 realize 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.

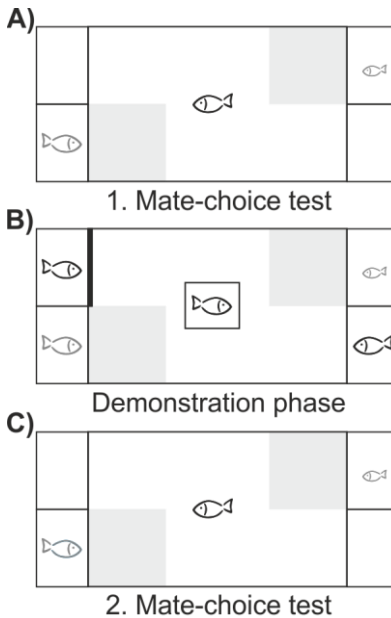
After this first mate-choice test (comprising two 10-min trials), opaque screens were inserted, and the observer female was placed back into the glass square in the middle of the large tank. One demonstrator female was placed next to each male, but only the one close to the small male was visible to the observer female while the one next to the large male was hidden by an opaque screen (thick line in Figure 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 (Figure 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 (Figure 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  $4.4 \text{ mm} \pm 0.2 \text{ mm}$ , representing  $17\% \pm 0.5\%$  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  $4.9 \text{ mm} \pm 0.2 \text{ mm}$ , representing  $18\% \pm 0.7\%$  of the body length on average.



**Figure 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).

### 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 figure 3.

### 2.5 Calculation of the observer female side-bias

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

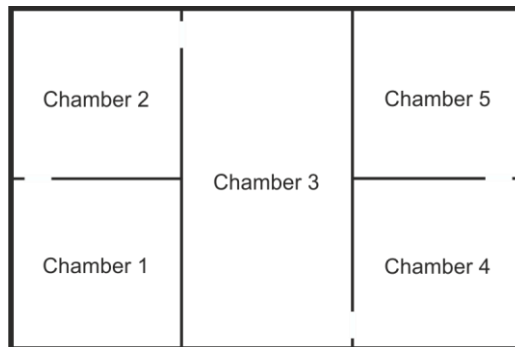
of one side represented more than 90% of the total time spent in the two mate-choice zones during the first mate-choice test, were removed from our study. This is a common criterion in mate-copying experiments (e.g., Witte and Noltemeier, 2002; Witte and Ueding, 2003).

Nonetheless, we calculated a side-bias (SB) for each observer female as  $SB = |(L1+L2)/(L1+L2+R1+R2)| - 0.5$ , where L1 and L2 are the time spent in the left mate-choice zone and R1 and R2 are the time spent in the right mate-choice zone respectively in the first (L1, R1) and second part (R2, L2) of the first mate-choice test. We removed 0.5 to the absolute value of the first term of this equation in order to be able to add the left and right deviations from the expected random distribution of 50% of their time in each mate-choice zone (Nöbel et al. under review).

### 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. under review). The test maze consisted of a test tank (30 cm x 20 cm x 20 cm) separated in 5 chambers (chamber 3: 10 cm x 20 cm; the other four chambers: 10 cm x 10 cm) by 4 dark grey plastic boards (Figure 2). Each plastic board had a hole in the middle (3 cm diameter) that allowed 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).



**Figure 2: Top view on the experimental set-up of the maze to test boldness.** The tank was separated in 5 chambers by 4 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.

### 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. Fifteen (14 AB, 1 TL) of them were excluded from the analysis because they showed a side bias in the first mate-choice test or did not move at all. Overall,

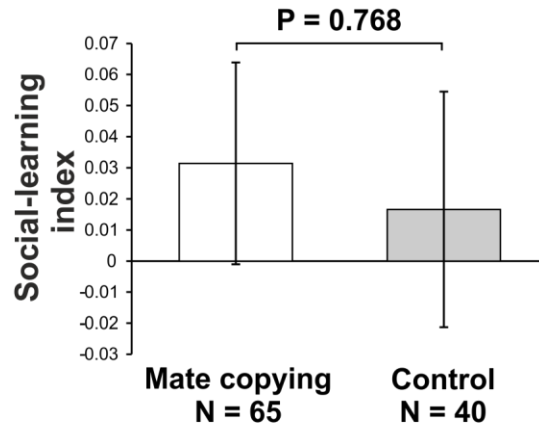


we tested 105 females successfully: 65 in mate-copying experiments (30 AB, 35 TL) and 40 in control experiments (20 AB, 20 TL).

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., under review) 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 the side-bias as fixed effects and its interactions. Significance of fixed effects was tested using Wald chi-square tests implemented in the ANOVA function of the car package (Fox & 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

For details about the mean time spent in front of the males please see table 2 in the supplements. The starting model of variables explaining the SLS included 5 main effects, (i) treatment (MC, C), (ii) personality (shy, bold), (iii) strain (AB, TL), (iv) male size-ratio plus its square, and (v) the side-bias, 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-significant (LM:  $df = 1$ ,  $F = 0.466$ ,  $P = 0.497$ ). Neither the interactions were significant (LM:  $P < 0.219$ ) nor the single fixed effects were significant (treatment LM:  $df = 1$ ,  $F = 0.003$ ,  $P = 0.960$ ; strain LM:  $df = 1$ ,  $F = 0.033$ ,  $P = 0.857$ ; personality LM:  $df = 1$ ,  $F = 0.607$ ,  $P = 0.438$ ; male size-ratio LM:  $df = 1$ ,  $F = 0.449$ ,  $P = 0.504$ ; male size-ratio<sup>2</sup>: LM:  $df = 1$ ,  $F = 1.917$ ,  $P = 0.169$ ; side-bias LM:  $df = 1$ ,  $F = 0.352$ ,  $P = 0.554$ ). Although the post-hoc comparison of the SLIs of the two treatments revealed that there was no difference between mate copying and control (t-test:  $t = -0.297$ ,  $df = 88.281$ ,  $P = 0.768$ ). Thus, we found no evidence for mate copying in our zebrafish.



**Figure 3. Social-learning index of the mate-copying experiment and the control.**

#### 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 did not find any evidence for copying the choice for smaller males in the female zebrafish.

##### 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 indexes, 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.

We performed a control in which we analyze 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), and again, every time that it was tested, studies reported that the time spent close to a male is a good predictor of mating probability (Berglund, 1993; Bischoff et al., 1985; Kodric-Brown, 1993; Walling et al., 2010). 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, male size-ratio and side-bias 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, personality 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. However, we observed the contrary in mosquito fish (*Gambusia holbrooki*; Nöbel et al., under review), and 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 zebrafinches (*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 or the side-bias of females in the analysis

because we have shown that they influenced significantly mate choice copying in mosquito fish (Nöbel et al., under review). However, none of these two variables was 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 and that another strain or fish from the wild 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 sufficient to elicit mate copying in these species (Dagaeff 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 hours, 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.

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 of male zebrafish. Male zebrafish are aggressive, and females may cue on aggressiveness or dominance more than on size (Qvanström and Forsgren, 1998), a possibility that was prevented in our set-up, as males could not interact directly with each other.

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 mate copying versus non-mate-copying 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. At this stage, our conclusion is that the zebrafish is unlikely to be the best model species to study mate copying in vertebrates.

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