

Klaudia Witte · Bianka Noltemeier

The role of information in mate-choice copying in female sailfin mollies (*Poecilia latipinna*)

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Abstract Female mate choice is a complex process involving both genetic and social factors. Extrinsic cues may play a role in determining how these factors interact. Mate-choice copying is a socially influenced mate-choice strategy in which females observe other females during mate choice and choose the same male as those females. Previous studies have shown that female sailfin mollies (*Poecilia latipinna*) prefer larger over smaller males, and this preference is assumed to be genetically based. In this study we tested, first, whether sailfin molly females changed their mate preference in favour of smaller males when they could obtain more information by observing two model females sequentially for 5 min each or one model female for 20 min next to the smaller male. Second, we tested if females that had changed their preferences in favour of smaller males maintained this learned preference afterwards. In copying experiments, females changed their preferences in favour of smaller males both when they could observe two model females each for 5 min near by a smaller male and when they could observe one model female for 20 min near the smaller male. In the latter case, females maintained this learned preference for smaller males up to 5 weeks after the copying experiment. This shows that mate-choice copying has a long-lasting effect on mate-choice decisions in sailfin molly females and that mate-choice copying can serve as a mechanism for cultural inheritance of mate preferences in females.

Keywords Sexual selection · Mate-choice copying · Information · Sailfin molly

Introduction

Most models of sexual selection assume that females exhibit a genetically based preference for males with specific traits (Kirkpatrick and Ryan 1991; Andersson 1994; Bakker 1999; Iwasa and Pominakowski 1999). Female mate choice, however, is a complex process involving not only genetic factors but also non-genetic factors (Freeberg et al. 1999; Ten Cate 2000; Westneat et al. 2000). There is increasing evidence that social factors have an important influence on mate-choice decisions. An important social influence is mate-choice copying (Galef and White 2000; Westneat et al. 2000). Mate-choice copying is defined as non-independent mate choice in which a female's probability of choosing a given male increases if other females have previously chosen that male (Pruett-Jones 1992). Females copy the mate choice of other females by observing a sexual interaction between a male and a female, and then mate with the same male as the observed female did before.

Several theoretical studies have investigated how copying could evolve and be maintained in a population (Losey et al. 1986; Wade and Pruett-Jones 1990; Gibson and Höglund 1992; Pruett-Jones 1992; Dugatkin 1996b; Nordell and Valone 1998; Stöhr 1998; Sirot 2001). Servedio and Kirkpatrick (1996) showed that an allele for copying can spread through a population via indirect selection even when there is a mild selection against it.

Empirical evidence for mate-choice copying exists in several fish species, including the guppy, *Poecilia reticulata* (Dugatkin 1992, 1996a, 1998; Dugatkin and Godin 1992, 1993), the Japanese medaka, *Oryzias latipes* (Grant and Green 1996, but see Howard et al. 1998), the livebearing fish *Limia perugiae* (Applebaum and Cruz 2000) and the sailfin molly *P. latipinna* (Schlupp et al. 1994; Schlupp and Ryan 1997; Witte and Ryan 1998), as well as in polygynous bird species such as the sage grouse *Centrocercus urophasianus* (Gibson et al. 1991), the black grouse *Tetrao tetrix* (Höglund et al. 1995), and the Japanese quail *Coturnix c. japonica* (Galef and White 1998; White and Galef 1999, 2000). Recently,

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K. Witte (✉) · B. Noltemeier
Lehrstuhl für Verhaltensforschung, Universität Bielefeld,
Postfach 100131, 33501 Bielefeld, Germany
e-mail: Klaudia.Witte@biologie.uni-bielefeld.de
Tel.: +49-521-1062835, Fax: +49-521-1062998

Witte and Ryan (2002) showed that sailfin molly males and females copy the mate choice of others in the wild. This study provides evidence that mate-choice copying in fish is a biologically relevant mate-choice strategy and not an artefact from the laboratory. Thus, mate-choice copying is an important factor in forming female mate preference.

Mate-choice copying can be a mechanism for cultural inheritance. Cultural inheritance is the acquisition of information by imitation of, or by being taught by, another individual (Boyd and Richerson 1985). Cultural transmission of mate preference is an important aspect in sexual selection because mate preferences can be transmitted between relatives and non-relatives within generations, while genetically based mate preferences can be transmitted only vertically from the mother to the daughter. Thus, cultural inheritance of mate preferences is a more dynamic process than genetic inheritance. Two prerequisites for cultural transmission of a mate preference by copying are that females copy the choice of a male type instead of a particular male, and secondly, that females should maintain their learned preference in order to be able to transmit it to other females (Brooks 1998).

In many fish species, females prefer larger over smaller males. In fishes with paternal care, females gain direct benefits by choosing larger males (Downhower and Brown 1980; Côté and Hunter 1989), as these males defend their brood more successfully (Bisazza and Marconato 1988; Hastings 1988). In fish species without parental care, females prefer larger over smaller males as well (Kodric-Brown 1990). This is the case in poeciliid fishes like the mosquitofish *Gambusia affinis* (McPeck 1992), the Gila topminnow *Poeciliopsis occidentalis* (Constantz 1975), the swordtails *Xiphophorus helleri* (Rosenthal and Evans 1998) and *X. nigrensis* (Ryan and Wagner 1987), the Amazon molly *Poecilia formosa* and the Atlantic molly *Poecilia mexicana* (Marler and Ryan 1997), as well as the sailfin molly *Poecilia latipinna* (Marler and Ryan 1997; Witte and Ryan 1998). Marler and Ryan (1997) provide strong indication that a preference for larger males is genetically based in sailfin molly females.

It is very likely that genetic and social factors interact to determine mate choice. The nature and extent of this interaction may depend on extrinsic cues. One possible extrinsic factor that might influence the decision of females to copy or not to copy is the amount of information a female gains by observing a sexual interaction between a male and a female. The more information the female gains, the more the female might be willing to copy the mate choice. A female can increase the input of information by observing a sexual interaction for a longer period of time, or by observing more than one female interacting with the same male. We manipulated the amount of information a sailfin molly female can obtain through observing a male and a female by altering the number of females interacting with a male, or by altering the time period for observing the male and the female. A second aim of our study was to investigate whether fe-

males maintained the learned mate preference over a period of time and how the amount of information might influence this maintenance. Thus, when females copied the choice of the model female and preferred the smaller male in the copying experiments, we tested whether those females maintained this learned preference for smaller males up to 5 weeks after the copying experiments.

Methods

Study species

The sailfin molly is a live-bearing poeciliid fish without parental care, living in mixed-sex shoals comprising 10–20 individuals. Thus, females have the opportunity to watch other females during mate choice and copy the choice of other females (Witte and Ryan 1998, 2002). All fish used in the experiments were at least 6 months old and descendants of wild fishes from the Comal River near New Braunfels, Texas, USA, caught in summer 1999. We maintained the fish separated by sex in tanks under 12:12 h light:dark regime with broad spectrum fluorescent light, at an average temperature of 25°C, and fed them ad libitum with daphnia and chironomid larvae once a day.

General procedure

We followed the protocol of Witte and Ryan (1998). All experiments were conducted in the same apparatus: a large tank (100×40×50 cm, L×H×W) for test females and four small tanks (20×40×25 cm) with two standing side by side at each end of the large tank. In each tank there was a layer of gravel and the water temperature was 25°C.

Before tests started, we gently placed a test female in the large tank. A smaller male and a larger male were placed into one of the two small tanks at each end of the large tank, so that they were placed diagonally from each other to minimise male-male competition. For the next 15 min all three fish could acclimatise to the new situation without seeing each other; the large tank was covered with white plastic boards. After the fish had acclimatised, we gently placed the test female in a clear Plexiglas cylinder (11 cm diameter) in the centre of the large tank and removed the plastic boards. During the 10 min starting period, females could observe the smaller and the larger males used in a test.

After this, we gently released the test female into the tank. We started the first preference test and measured the time the female spent within the preference zone in front of a male tank for the next 10 min. A preference zone was a 20-cm-wide zone in front of a small tank containing a male. Each preference zone was marked with two glass bars lying right-angled on the gravel and by a vertical black line on the front surface. Only the time the test female spent within the preference zone was scored as choosing a male. After 10 min, we switched the position of the males and repeated the preference trial. The test female was considered to prefer a particular male if she spent more than 50% of her time in the preference zone of that particular male during the 20 min of the first preference test. Although time spent is an indirect measure of female mate preference, Bischoff et al. (1985) and Kodric-Brown (1993) have shown in guppies that the time females spent together with a male correlates positively with the probability of copulation with that male. This was found in other species as well (Berglund 1993). In the sailfin molly, female association time with a male in a situation with no physical contact predicts the probability of copulation with that male (K. Witte, unpublished data).

A female was considered to show side biases when she spent more than 90% of her total time in front of both males in the same

preference zone although we had switched the position of the males. These test females were omitted from the analysis.

During the viewing period, test females were given the opportunity to observe another female, the so-called model female, next to the smaller male. We placed the test female back into the Plexiglas cylinder in the middle of the large tank and placed a model female in the small tank adjacent to the tank with the smaller male. The proximity of the model female to the smaller male should indicate her mate preference for the smaller male to the test female. Because males increased activity in the presence of females, however, it was necessary to place a pseudo-model female in the small tank adjacent to the larger male as well. But this pseudo-model female was covered behind a white plastic board and thus only visible to the larger male, but not to the test female. During the viewing period, the test female could observe a model female next to the smaller male and no female next to the larger male. The viewing period lasted 10 or 20 min (see below). After this we removed the model female, the pseudo-model female and the extra cover. For the second preference test, we released the test female from the cylinder and measured the time she spent with the larger and smaller males within the 2×10-min trials, as we did in the first preference test. Then we compared the time the test female spent with the smaller male in the second preference test (after the viewing period) with the time she spent with the smaller male in the first preference test. If females spent more time with the smaller male in the second preference test than in the first preference test, we concluded that females have copied the "choice" of the model female.

In the copying experiments, all females were used only once as test females, but they were used as model and pseudo-model females in other tests as well. Within an experiment, males were used only once, but they were used in other experiments as well. After each test, we measured the standard body length of males and females from the tip of the snout to the end of the caudal peduncle with a calliper. Measurements were taken after each trial to minimise effects on male behaviour. We performed three copying experiments with different viewing periods, two controls and two mate-choice tests for a maintenance of a learned mate preference.

Copying experiment with a 10-min viewing period and one model female

After the first preference test in which we determined the preference of the female for one of the two males, we presented one model female next to the smaller male during a 10-min viewing period. After the viewing period, we performed the second preference test as described above. The smaller males ($n=15$) used in this experiments had an average body length of 35.2 ± 4.4 mm (mean \pm SD), the larger males ($n=15$) 46.1 ± 5.8 mm. Thus, males used in a test differed on average by 10.8 ± 3 mm. We tested 15 females with an average standard body length of 43.6 ± 4.4 mm. Model females and pseudo-model females were on average 42.7 ± 7 mm and 41.6 ± 7.6 mm long, respectively.

Copying experiment with a 10-min viewing period and two model females

In the first preference test, females could choose between a smaller and a larger male. During the 10-min viewing period, we presented two model females one after another adjacent to the smaller male. Thus, we increased the amount of information available to the test female by presenting two different model females next to the smaller male. After the first 5 min of the viewing period, we covered both sides of the large tank, caught the model female and placed a new model female into the same small tank next to the tank containing the smaller male. We removed the cover and the test female could observe another model female next to the smaller male for 5 min. After the second 5 min, we covered the large tank again to remove the model and pseudo-model females.

We did not exchange the pseudo-model female next to the larger male; however, we dipped a net into this small tank and caught the pseudo-model female so that there was the same disturbance at both sides of the large tank.

After this 10-min viewing period, we removed the model and pseudo-model female as well as the cylinder, and performed the second preference test as described above. We tested 15 females (36.43 ± 5.4 mm) and used two sets of 15 model females (40.1 ± 4.5 mm and 43 ± 6.4 mm), and 15 pseudo-model females (34.4 ± 4.3 mm). The smaller males ($n=15$, 30.43 ± 4.6 mm) differed from the larger males ($n=15$, 42.7 ± 4.8 mm) on average by 12.2 ± 2 mm.

Copying experiment with a 20-min viewing period and one model female

In this experiment, we extended the viewing period to 20 min, in which the test female could observe one model female next to the smaller male. We tested 15 females (35.63 ± 3.6 mm) and used 15 model females (30.46 ± 4 mm) and 15 pseudo-model females (35.1 ± 5 mm). The smaller males ($n=15$, 31.9 ± 5 mm) were on average 12.26 ± 5 mm smaller than the larger males ($n=15$, 44.16 ± 5 mm).

Controls for consistency in female mate preference

In these two controls, we determined if females were consistent in their mate preference when they were not given an opportunity to copy. In these experiments, both the model female(s) and the pseudo-model female were covered behind a plastic board and not visible to test females but visible to the males during the viewing period between the first and second preference test.

In one control, the viewing period lasted 10 min. In this control, we tested 15 females (36.76 ± 3.7 mm) and used 15 model females (30.46 ± 4 mm) and 15 pseudo-model females (31.1 ± 5 mm). In this control, the smaller males ($n=15$, 31.0 ± 4.3 mm) differed from the larger males ($n=15$, 43.0 ± 5.8 mm) on average by 12.0 ± 3.7 mm.

In the other control, the viewing period lasted 20 min. Here we tested 15 females (35.6 ± 4.2 mm) and used 15 model females (37 ± 4 mm), as well as 15 pseudo-model females (37.5 ± 3.2 mm). The smaller males ($n=15$, 31.2 ± 4.74 mm) were on average 12.4 ± 3.6 mm smaller than the larger males ($n=15$, 43.6 ± 6 mm).

Controls for shoaling behaviour

In three controls we determined if females showed shoaling behaviour, that is, if females preferred to associate with a conspecific that they have seen together with a second conspecific during the viewing period in the experimental situation. We performed three different experiments in which we varied the duration of the viewing period and the number of model females, as we did in the copying experiments. Because shoaling is socially motivated, not sexually motivated, we used stimulus females instead of stimulus males. In one control, we presented one model female for 10 min next to the stimulus female with whom the test female ($n=10$, 34.1 ± 2.02 mm) had spent less time during the first preference test. The model and pseudo-model females we used were on average 36.1 ± 1.8 and 33.1 ± 2.5 mm long. In another control, we presented two model females, each for 5 min, next to the non-preferred female of the first preference test. In this control we tested ten females (34.35 ± 2.6 mm) and used two sets of ten model females (34.65 ± 2.2 and 34.7 ± 2.8 mm) and ten pseudo-model females (33.2 ± 4.9 mm). In the third control we presented one model female for 20 min next to the non-preferred stimulus female, i. e. the female with whom the test female ($n=10$, 34.0 ± 2.9 mm) had spent less time. Here, we used ten model females (34.5 ± 3.5 mm) and ten pseudo-model females (35.5 ± 2.6 mm).

Mate-choice tests for a maintenance of a learned preference

To test if females would maintain a learned mate preference for smaller males, we tested females in a binary choice situation in which they could choose between a larger and a smaller male. We used the same choice apparatus as in the copying experiments. A mate-choice test lasted 20 min, with switching the males after 10 min. Thus, we followed the protocol of the first preference test in a copying experiment. In one mate-choice test, we tested the same females we used in the copying experiment with an viewing period of 10 min and two model females on average 14.33 ± 4.88 days (7–21 days) after the copying experiment. In a second mate-choice test, we tested the females of the copying experiment with a 20-min viewing period on average 22 ± 8.6 days (between 12 and 36 days) after the copying experiment. In both experiments, we used different males than in the two copying experiments, so that females were unfamiliar with these individual males.

Analysis

We analysed the actual time a female spent in front of smaller and larger males and the relative time spent in front of males. We performed the Wilcoxon matched-pairs test with the actual time spent; values are means \pm SD. All *P*-values are two-tailed. Where necessary, we applied a Bonferroni correction for multiple comparisons.

Results

Copying experiment with a 10-min viewing period and one model female

In the first preference test of this copying experiment, all females ($n=15$) showed a clear preference for larger males (binomial test: $n=15$, $P<0.001$). Females spent on average significantly more time with larger males (487 ± 139 s, $=85.45 \pm 10.85\%$) than with smaller males (83 ± 60 s, $=14.55 \pm 10.85\%$) (Wilcoxon matched-pairs test: $n=15$, $Z=3.4$, $P=0.001$, Fig. 1a). None of the females changed their mate preferences in the second preference test, although they had seen a model female next to the smaller male during the 10-min viewing period (binomial test: $n=15$, $P<0.001$) and did not spend more time with the smaller male (Wilcoxon matched-pairs test: $n=15$, $Z=1.02$, $P=0.31$, Fig. 1a). Instead, females spent a similar amount of time in front of smaller and larger males in the second preference test as they did in the first preference test (Wilcoxon matched-pairs test: $n=15$, $Z=3.4$, $P=0.001$, Fig. 1a). The total time females spent with both males did not change between the first and second preference test (Wilcoxon matched-pairs test: $n=15$, $Z=0.68$, $P=0.49$). Thus, females did not copy the mate choice of the model female when they had observed the model female next to the smaller male for 10 min, and females still preferred the larger of two males.

Copying experiment with a 10-min viewing period and two model females

In the first preference test, all females showed a strong mate preference for the larger male (binomial test: $n=15$,

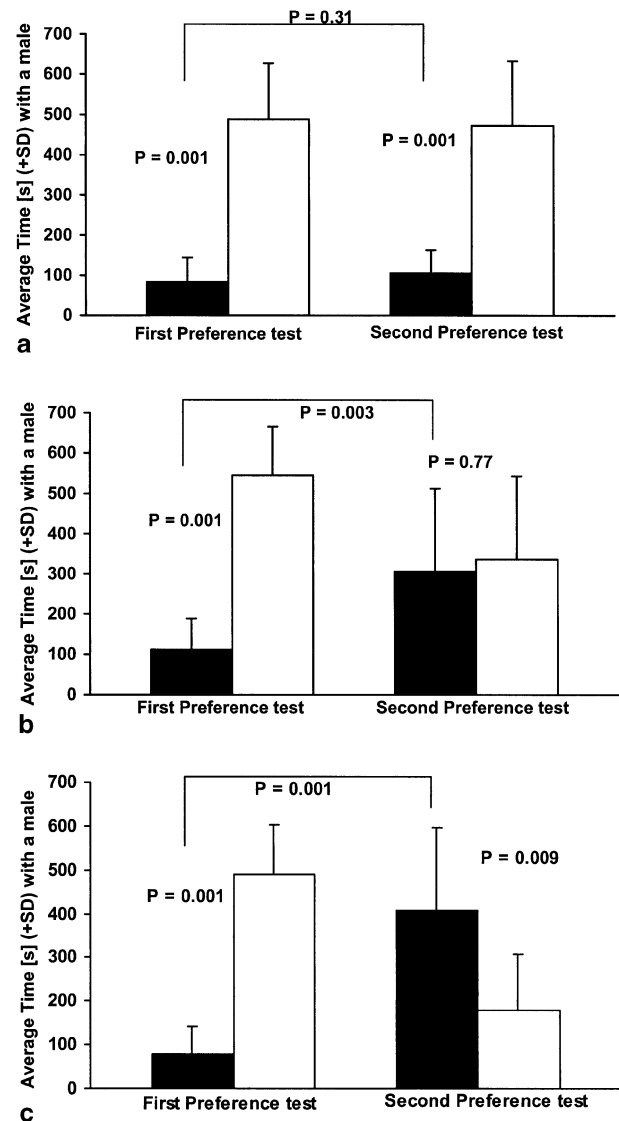


Fig. 1 **a** Average time a female spent with smaller males (black columns) and larger males (white columns) in the first and second preference test of the copying experiment when a model female was presented for 10 min next to the smaller male. **b** Average time a female spent with smaller males (black columns) and larger males (white columns) in the first and second preference test of the copying experiment when two model females were presented within 10 min next to the smaller male. **c** Average time a female spent with smaller males (black columns) and larger males (white columns) in the first and second preference test of the copying experiment when one model female was presented for 20 min next to the smaller male

$P<0.001$) and spent significantly more time with larger males (545 ± 120 s, $=83.03 \pm 10.11\%$) than with smaller males (111 ± 77 s, $=16.97 \pm 10.11\%$) (Wilcoxon matched-pairs test: $n=15$, $Z=3.4$, $P=0.001$, Fig. 1b). After the observation of two different model females next to the smaller male, however, seven females reversed their mate preference and preferred the smaller of the two males in the second preference test (McNemar: $n=15$, $P=0.016$). Females spent significantly more time with the smaller male in the second preference test

(305 ± 206 s, $=47.63 \pm 28.47\%$) than in the first preference test (Wilcoxon matched-pairs test: $n=15$, $Z=3.01$, $P=0.003$, Fig. 1b), and thus spent a similar amount of time with smaller and larger males in the second preference test (Wilcoxon matched-pairs test: $n=15$, $Z=0.28$, $P=0.77$, Fig. 1b). The motivation to choose between males, i. e. the total time females spent with both males, did not change between the first and second preference test (Wilcoxon matched-pairs test: $n=15$, $Z=0.45$, $P=0.65$). Thus, females copied the choice of the two model females under these conditions.

Copying experiment with a 20-min viewing period and one model female

As in the first two experiments, all females preferred larger males over smaller males in the first preference test (binomial test: $n=15$, $P<0.001$) and spent significantly more time with larger males (491 ± 111 s, $=86.21 \pm 9.87\%$) than with smaller males (78 ± 62 s, $=13.79 \pm 9.87\%$) (Wilcoxon matched-pairs test: $n=15$, $Z=3.4$, $P=0.001$, Fig. 1c). In the second preference test, however, 13 of 15 females reversed their preference and preferred smaller over larger males (McNemar test: $n=15$, $P<0.001$) and spent significantly more time in front of smaller males in the second preference test than in the first preference test (Wilcoxon matched-pairs test: $n=15$, $Z=3.35$, $P=0.001$, Fig. 1c). In the second preference test, females spent significantly more time with smaller males (407 ± 186 s, $=69.54 \pm 23.77\%$) than with larger males (178 ± 130 s, $=30.46 \pm 23.77\%$) (Wilcoxon matched-pairs test: $n=15$, $Z=2.61$, $P=0.009$, Fig. 1c). The total time spent with both males did not differ between the first and the second preference test (Wilcoxon matched-pairs test: $n=15$, $Z=0.74$, $P=0.46$). Thus, females copied the choice of the model female.

When comparing the results of these three copying experiments with different viewing periods and one or two model females, we found no copying effect when females could observe only one model female next to the smaller male for 10 min, and the strongest copying effect when females could observe one model female for a period of 20 min. Observing two model females each for 5 min had a weaker effect on copying behaviour with seven out of 15 females, which reversed their choice and preferred the smaller over the larger male. Almost twice as many females reversed their mate preference when observing one model female next to the smaller male for 20 min than did females viewing two females next to the smaller male, each one for 5 min.

To test whether the amount of information interacted with the copying effect, i. e. the increase in time spent with the smaller male from the first to the second preference test, we performed a repeated-measures ANOVA with the first and second preference test as dependent variables and the three copying experiments as independent variables. We applied a square-root transformation to the data, so that they were not significantly different

from a normal distribution (Shapiro Wilk-Test: first preference test: $n=45$, $P=0.76$; second preference test: $n=45$, $P=0.78$). The repeated-measures ANOVA shows that the three different viewing periods in the copying experiments interacted with the copying effect (repeated measure ANOVA: preference test*experiments: $F_{2,42}=11.04$, $P<0.001$).

Controls for consistency in female mate preference

To determine whether the increase in time spent with the smaller male is due to mate-choice copying or due to inconsistency in female mate choice, we repeated the copying experiments but with no opportunity for copying during the viewing period for the test females. Both, the model female and the pseudo-model female were hidden during the viewing period and visible only to the males but not to the test females. In this situation, females did not significantly increase their time spent with the smaller male, neither in the control with a viewing period of 10 min (Wilcoxon matched-pairs test: $n=15$, $Z=0.94$, $P=0.35$) nor in the control with a 20-min viewing period (Wilcoxon matched-pairs test: $n=15$, $Z=0.8$, $P=0.43$). In both controls, females preferred larger over smaller males in the first and in the second preference test. In the control with a 10-min viewing period, females spent on average 559 ± 101 s ($=85.32 \pm 6.81\%$) with larger males and only 96.3 ± 44.45 s ($=14.68 \pm 6.8\%$) with smaller males in the first preference test (Wilcoxon matched-pairs test: $n=15$, $Z=3.4$, $P=0.001$). This was similar in the second preference test. Females spent on average 584 ± 148 s ($=87.09 \pm 7.15\%$) with the larger of two males and only 86.6 ± 46.7 s ($=12.91 \pm 7.15\%$) with smaller males (Wilcoxon matched-pairs test: $n=15$, $Z=3.4$, $P=0.001$). In the control with a 20-min viewing period, females spent significantly more time in front of larger males (536 ± 103 s, $84.66 \pm 7.47\%$) than in front of smaller males (97.1 ± 55 s, $=15.34 \pm 7.47\%$) in the first preference test (Wilcoxon matched-pairs test: $n=15$, $Z=3.4$, $P=0.001$), and females showed a similar strong preference for larger males in the second preference test (smaller males: 92.86 ± 74.5 s, $=12.31 \pm 7.86\%$; larger males: 542.2 ± 134.5 s, $=57.74 \pm 39.76\%$) (Wilcoxon matched-pairs test: first preference test: $n=15$, $Z=3.4$, $P=0.001$; second preference test: $n=15$, $Z=3.35$, $P=0.001$). The motivation to choose between males did not change between the first and second preference test in both controls (Wilcoxon matched-pairs test: 10-min viewing period, $n=15$, $Z=0.11$, $P=0.91$; 20-min viewing period, $n=15$, $Z=0$, $P=1.0$). Thus, females chose consistently when they had no opportunity to copy regardless of whether the viewing period lasted 10 min or 20 min.

Controls for shoaling behaviour

In these controls, we determined whether the increase in time spent with smaller males was due to shoaling

behaviour. We performed three controls for shoaling behaviour. The model females were always next to the stimulus female with whom the test female spent less time during the first preference test. In one control, we presented one model female for 10 min. Females did not shoal and spent a similar amount of time in front of the less-preferred female in both preference tests (Wilcoxon matched-pairs test: $n=10$, $Z=0.97$, $P=0.33$). In another control, we presented two model females one after another for 5 min each. In this control, females did not change their preferences from the first to the second preference test either (Wilcoxon matched-pairs test: $n=10$, $Z=0.46$, $P=0.64$). In a third control, we presented one model female for 20 min next to the less-preferred stimulus female. Females did not shoal after viewing the model female (Wilcoxon matched-pairs test: $n=10$, $Z=0.36$, $P=0.72$). Thus, females did not shoal under three different experimental conditions. Shoaling behaviour, therefore, could not explain a significant change in female mate preferences. We therefore conclude that sailfin molly females copied the choice of model females in the copying experiments and changed their mate preferences in favour of smaller males.

Mate-choice tests for a maintenance of a learned preference

In two simple mate-choice tests, we tested whether those females that had preferred smaller males in the second preference test after viewing two model females or one model female for 20 min in the copying experiment, still preferred smaller over larger males on average 14.33 ± 4.88 days (7–21 days) or on average 22 ± 8.6 days (between 12 and 36 days) after the copying experiment. In the copying experiment with a 10-min viewing period and two model females, seven test females changed their mate preference and preferred a smaller over a larger male. One of these females did not enter the preference zones in the mate-choice test and was rejected from the analysis. The smaller males ($n=6$, 32.0 ± 5 mm) used in this test were on average 13.16 ± 3.1 mm smaller than larger males ($n=6$, 45.2 ± 5.9 mm). Three of the six remaining females still preferred the smaller over the larger male, but the other three spent more time with the larger male in the simple mate-choice test. On average, females ($n=6$) spent 320 ± 183 s ($=46.08 \pm 23.6\%$) with the smaller male and 374 ± 159 s ($=53.9 \pm 23.6\%$) with the larger male (Wilcoxon matched-pairs test: $n=6$, $Z=0.52$, $P=0.6$). In comparison to the second preference test of the copying experiment, the six females spent significantly less time with the smaller male in the mate-choice test for maintenance of a preference than in the second preference test of the copying experiment (Wilcoxon matched-pairs test: $n=6$, $Z=1.99$, $P=0.046$, Fig. 2a). Thus, these females did not maintain the learned preference 14.33 ± 4.88 days after the observation of two model females interacting se-

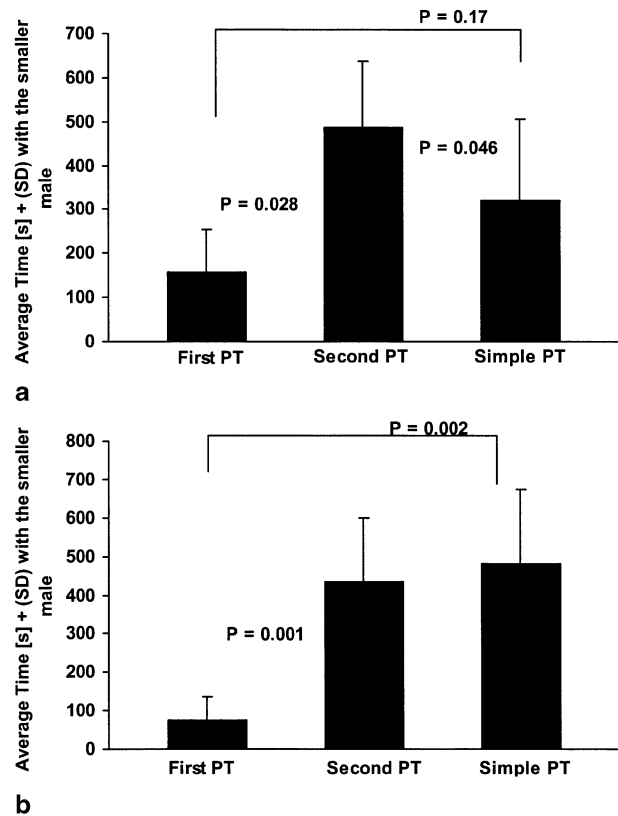


Fig. 2 **a** Average time spent by the test females in front of smaller males in the first and the second preference test in the copying experiment with two model females and in the mate-choice test (Simple PT). **b** Average time spent by the test females in front of smaller males in the first and second preference test in the copying experiment with one model female presented for 20 min and in the mate-choice test (Simple PT)

quentially with the smaller male. We found no significant correlation between the time period between the copying experiment and the simple mate-choice tests and the time spent with smaller males (Spearman rank correlation: $n=6$, $r=0.142$, $P=0.78$).

In the second mate-choice test for maintenance of a learned preference, we tested females that had changed their mate preferences after viewing a model female next to the smaller male for 20 min in the copying experiment. One female died during the waiting interval, so we tested 12 females. The smaller males ($n=12$, 32.3 ± 3 mm) differed from the larger males ($n=12$, 44.2 ± 5.3 mm) on average in 11.91 ± 4.6 mm. Females spent on average 327 ± 177 s ($=40.5 \pm 20.7\%$) with larger males and on average 480 ± 192 s ($=59.5 \pm 20.7\%$) with smaller males in the simple mate-choice test (Wilcoxon matched-pairs test: $n=12$, $Z=1.41$, $P=0.16$) and, therefore, spent significantly more time with the smaller male in the simple mate-choice test than in the first preference test of the copying experiment (Wilcoxon matched-pairs test: $n=12$, $Z=3.1$, $P=0.002$, Fig. 2b). Eight of 12 females still preferred the smaller over the larger male, and this mate-choice decision differed significantly from the mate-choice decision in the first preference test (McNemar:

$n=12$, $P=0.008$). We found no significant correlation between the time period between the copying experiment and the simple mate-choice tests and the time spent with smaller males (Spearman rank correlation: $n=12$, $r=0.235$, $P=0.46$).

Thus, females still showed a stronger preference for smaller males even up to 36 days after observing a model female next to the smaller male for 20 min than before this observation. These females therefore maintained the learned preference over this time period.

Discussion

In all experiments, sailfin molly females exhibited a strong mate preference for larger males when they had no opportunity to copy, or before they had the opportunity to copy. This strong preference for larger males has been shown in females from another sailfin molly population as well (San Marcos River, Martindale, Texas; Marler and Ryan 1997; Witte and Ryan 1998). Females still preferred larger over smaller males when they had observed one model female next to the smaller male for 10 min. This has been shown in previous experiments also (Witte and Ryan 1998). However, when females had the opportunity to observe two model females next to the smaller male for 5 min each, seven of 15 females switched their preferences in favour of smaller males. This effect was even stronger when females could observe one model female for 20 min interacting with the smaller male. In this situation 13 of 15 females reversed their preferences and spent most of the time with the smaller male in the second preference test of the copying experiment. Thus, when females obtain little or no information about the model female and the male, genetic factors appear to override social factors in the process of mate choice. When females obtain more information by observing two model females sequentially within 10 min or one model female for 20 min, social factors override genetic factors and females change their mate preferences in favour of smaller males, contradicting their genetically determined mate preference.

Our study parallels Dugatkin's (1998) previous work on guppies. Female guppies have a genetically based preference for the amount of orange body colour in males, and always prefer the more colourful male (Dugatkin 1996a). When females gained more information in a copying experiment by observing one model female for 10 min or two model females for 2×5 min next to the drabber male, females changed their preferences and preferred the less colourful male. Thus, the amount of information is an important factor for copying behaviour. What kind of information do females obtain during the viewing period? Females can gain information about both the male and the model female. The observation of a lone male did not seem to be relevant for copying (see controls for consistency). The observation of one or two model females with no sexual con-

text was not important for copying either (see controls for shoaling behaviour). By definition, the observation of an interaction between a male and a female is the cue for females to copy a choice of another female, whereas the number of model females and/or the duration of interaction between the male and the model female had a strong effect on copying behaviour. By observing an interaction between two individuals, the observer gains information about both participants that it would not get if it observes both individuals separately. This additional information gathering is a kind of eavesdropping, which can provide important information in communication networks between same-sex individuals and different-sex individuals (Doutrelant and McGregor 2000). Eavesdropping is defined as the behaviour of an observer extracting information from an interaction between two other individuals. If signals used in sexual interactions are assumed to be reliable, eavesdropping could be an effective way of evaluating the quality of potential mates. Mate-choice copying in which an individual gathers information from two interacting congeners is considered by us as a kind of eavesdropping. It is not clear what specific information females used to decide whether to copy or not. Our experiments show that two different females interacting with the same male provide the female with more information than observing one female for the same amount of time (10 min). Observing one model female for 20 min appears to provide the female with even more information, because 13 of 15 females reversed their previous mate preference.

How stable is a preference for a male type learned by mate-choice copying? The mate-choice tests showed that three of six females still preferred the smaller of two males even after 11, 14 and 16 days. Eight of 12 females that could observe one model female for 20 min next to the smaller male still preferred smaller over larger males after 12–28 days (on average, 18.75 days). It is surprising that one model female interacting with a male for 20 min had a stronger effect on copying behaviour than the observation of two different model females for a total of 10 min. Although females that had observed one model female for 20 min were re-tested after a longer period of time (12–36 days later) than the other females, they showed a stronger preference for smaller males than the females that had observed two model females. This is the first evidence that female fishes can maintain a mate preference learned by mate-choice copying that is opposite to a genetically based preference. This ability fulfils one of the prerequisites for cultural inheritance, the maintenance of a learned preference.

In the mate-choice tests, we presented novel males to females. Those females that still preferred the smaller males, therefore, did not copy the choice for an individual male. They copied the choice for a male type, i. e. a different male of similar body length as the male in the copying experiment. Thus, the second prerequisite for cultural inheritance by mate-choice copying was

fulfilled. White and Galef (2000) showed in Japanese quails that females not only copy the choice of a particular male but they copy also the choice for a male type, males with an artificial blue or red patch on breast feathers. Copying the choice of a male type is a requirement for a cultural transmission of mate preferences.

Our results show that a learned preference can be stable over the tested period of time. Hence, these females could serve as model females to other females, which might influence the mate preference of females and reproductive success of larger and smaller males within a population. The results of our study emphasise the significance of mate-choice copying for the evolution of female mate preferences. Mate-choice copying can lead to a cultural inheritance of mate preference (Brooks 1998) and is, therefore, significant for the dynamic of sexual selection.

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