Female sailfin mollies, *Poecilia latipinna*, remember males and copy the choice of others after 1 day

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Theoretical and experimental evidence indicates that females copy the mate choice of other females under certain conditions. In all mate choice copying experiments with fish to date, females were allowed to copy the choice of a model female immediately after the focal female had observed a model female interacting with a male. It is not known whether females continue to copy the choice of the model female after a longer interval. We investigated whether sailfin molly females also copy the choice of other females when they are prevented from copying immediately after observing a model female next to a previously nonpreferred male. We performed three copying experiments in which females could copy the choice of the model female immediately after, 1 h after or 1 day after observing the model female next to the previously nonpreferred male. In control experiments, we tested whether females chose consistently when they had no opportunity to copy, and whether females showed shoaling behaviour under these conditions. Females copied the choice of the model female immediately after, 1 h after and even 1 day after the observation of the model female interacting with the previously nonpreferred male. Females chose consistently between males when they had no opportunity to copy, and females did not shoal under these conditions. We conclude that females remember individual males with whom a model female had interacted, even after 1 day.

Most models of sexual selection assume that females have a genetically based preference for males with specific traits (Kirkpatrick & Ryan 1991; Andersson 1994; Bakker 1999; Iwasa & Pomiankowski 1999). Female mate choice, however, is a complex process involving not only genetic but also nongenetic factors (Freeberg et al. 1999; ten Cate 2000; Westneat et al. 2000). Increasing evidence suggests that social factors, such as mate choice copying, influence mate choice decisions (Galef & White 2000; Westneat et al. 2000). Mate choice copying is defined as nonindependent mate choice in which a female's probability of choosing a given male increases if another female has 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, then mating with the same male as the observed female did before.

Theoretical studies have investigated how copying could evolve and be maintained in a population (Losey et al. 1986; Wade & Pruett-Jones 1990; Gibson & Höglund 1992; Pruett-Jones 1992; Dugatkin 1996a; Stöhr 1998; Sirot 2001). Servedio & Kirkpatrick (1996) showed that an

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allele for copying can spread through a population by indirect selection even when there is mild selection against this allele for copying. Stöhr (1998) and Nordell & Valone (1998) showed in theoretical models that copying would be advantageous if some females had a poor ability to discriminate male quality. Evidence consistent with this notion comes from a mate choice copying experiment in guppies, *Poecilia reticulata*. Dugatkin & Godin (1993) showed experimentally that smaller females, which might be younger and less experienced in mate choice, copy the mate choice of larger females, which might be older and experienced in mate choice, but not vice versa. In other situations, copying might be advantageous because it reduces mate search time and thus reduces some costs associated with this behaviour (Gibson & Höglund 1992; Stöhr 1998).

Empirical evidence for mate choice copying exists in several fish species, including the guppy (Dugatkin 1992, 1996b, 1998a; Dugatkin & Godin 1992, 1993), the Japanese medaka, *Oryzias latipes* (Grant & Green 1996; but see Howard et al. 1998), the Perugia's lima, *Limia perugiae* (Applebaum & Cruz 2000) and the sailfin molly, (Schlupp et al. 1994; Schlupp & Ryan 1997; Witte & Ryan 1998, 2002; Witte & Noltemeier 2002; Witte & Ueding 2003), as well as in polygynous bird species including 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 & White 1998; White & Galef 1999, 2000). Copying, however, does not appear to occur in species with paternal care, such as the three-spined stickleback, *Gasterosteus aculeatus* (Patriquin-Meldrum & Godin 1998), and the sand goby, *Pomatoschistus minutus* (Forsgren et al. 1996), or in a biparental species such as the pied flycatcher, *Ficedula hypoleuca* (Slagsvold & Viljugrein 1999).

Some studies have investigated under what conditions females copy the mate choice of others. Dugatkin & Godin (1998) manipulated the level of hunger in guppy females, Briggs et al. (1996) studied mate choice copying in guppies under predation risk, and Dugatkin & Godin (1992) showed that small guppy females copy the choice of larger females but not vice versa. In experiments with the sailfin molly, females copied only when both males presented in a test were similar in body length (Witte & Ryan 1998). When males differed substantially in length, females always preferred the larger one, although the model female was presented next to the smaller male. However, if females obtained additional information by observing a model female for longer or two model females next to the smaller male, sailfin molly females copied the choice of another female for a smaller male and maintained this new preference (Witte & Noltemeier 2002). Under similar conditions, guppy females copied the choice for duller males, although females have a genetically based preference for orange males (Dugatkin 1998a). In the latter two studies a socially based mate preference overrode a genetically based mate preference. Witte & Ryan (2002) showed that sailfin molly males and females copy the mate choice of others in the wild, providing the first evidence that mate choice copying in fish is biologically relevant and not a laboratory artefact. Thus, mate choice copying is an important factor in forming female mate preference.

In all copying experiments with fish to date, females could copy the choice of the model female immediately after seeing her next to one of the two stimulus males. In nature, it is more likely that females may not be able to mate with a male they have seen interacting with another female immediately after this interaction. Instead, factors such as predation risk (Forsgren 1992; Candolin 1997), male harassment (Schlupp et al. 2001) or interacting shoal members are likely to prevent them from mating right away. If the female still prefers to mate with that particular male, she must be able to remember and recognize him later. In other mate choice strategies, females are also required to remember particular males. Different models of mate search strategies predict that females sample several potential mates before they choose one (Janetos 1980; Parker 1983; Real 1990). In the best-of-*n* tactic, females sample a pool of males, and they return to the highest quality one. In the fixed-threshold and one-step-decision models, females sequentially sample males and either reject or accept males as they are encountered, based on a fixed internal standard or the expected benefits of continued sampling. All of these

models predict that females can remember and compare previously encountered males. A few studies have considered how females sample and gather information about potential mates (Gibson & Langen 1996; Houde 1997). Female satin bowerbirds, *Ptilonorhynchos violaceus*, visit up to eight males before they choose one (Uy et al. 2001) and female great reed warblers, *Acrocephalus arundinaceus*, visit six males on average before they choose a mate (Bensch & Hasselquist 1992).

We tested whether sailfin molly females could remember a sexual interaction between a model female and a male after different intervals and then use this information for copying mate choice. Because sailfin molly females copy both the choices of other females (Witte & Ryan 1998) and the rejection of a male (Witte & Ueding 2003), and because mate choice copying is biologically relevant (Witte & Ryan 2002), they form an ideal system for investigating this question.

METHODS

Study Species

Sailfin mollies are a live-bearing poeciliid fish without parental care. They live in mixed-sex shoals of 10–20 individuals, so females have the opportunity to watch other females during mate choice and copy their choices. Our subjects were at least 6 months old and descendants of wild fish from the Comal River near New Braunfels, Texas, U.S.A., caught in February 1998. We maintained the fish, separated by sex, in several tanks (100 × 50 cm and 50 cm high) under a 12:12 h light:dark regime with broad spectrum fluorescent lighting, at an average water temperature of 25°C, and fed them ad libitum with flake food (Tetramin), tubifex worms, daphnia or *Artemia nauplii* once a day.

Experiments

General procedure

We performed three mate choice copying experiments with different intervals between the two preference tests. We also performed controls to test whether females chose consistently without an opportunity to copy, and whether females showed shoaling behaviour under the experimental conditions.

All experiments were conducted in the same apparatus: a large tank (100 × 50 cm and 40 cm high) for test females and four small tanks (20 × 25 cm and 40 cm high) with two standing side by side at each end of the large tank (Fig. 1). Each tank had a layer of gravel and the water temperature was 25°C.

Before tests started, we gently placed a test female in the large tank, then placed a male into one of the two small tanks at each end of the large tank, so that they were diagonally opposite each other, to minimize male–male competition. Within a test, the males were matched for body length and coloration. For the next 15 min, so that all three fish could acclimate to the new place without seeing each other, the large tank was covered
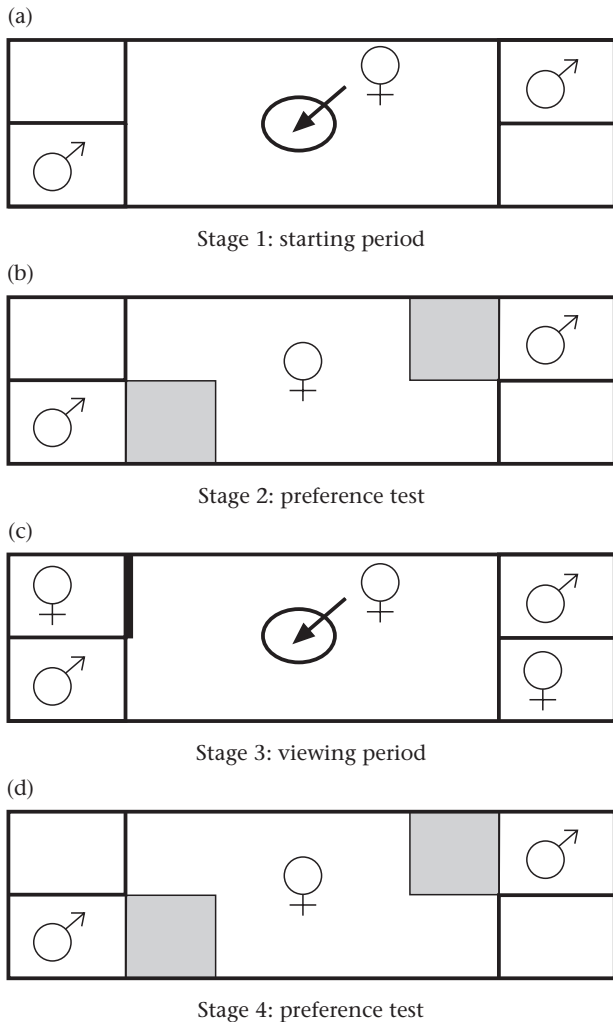
(a)

Stage 1: starting period

(b)

Stage 2: preference test

(c)

Stage 3: viewing period

(d)

Stage 4: preference test

Figure 1. Top view of the four stages of the copying experiment. Shaded areas indicate preference zones. In (c) thick black line indicates opaque board.

with white plastic boards. After the fish had acclimated, we gently placed the test female in a clear Plexiglas cylinder (11 cm diameter) in the centre of the large tank and removed the opaque boards. During the 10-min starting period (Fig. 1a) females could observe both males used in a test.

We then gently released the test female from the cylinder 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 area in front of a small tank containing a male (Fig. 1b). Each preference zone was marked with two glass bars at right angles on the gravel and by a vertical black line on the front and back surface of the test tank, 20 cm from each end of the tank. We scored the time the test female spent within the preference zone as choosing a male. After 10 min, we switched the positions of the males and repeated the preference trial. The test female was considered to prefer a particular male (preferred male), if she spent more than 50% of the total time spent in both preference zones

within that male's preference zone during the two 10-min periods of the first preference test. Although time spent with a male is an indirect measure of female mate preference, it correlates positively with the probability of copulation with that male (guppies: Bischoff et al. (1985); Kodric-Brown (1993); and gobies: Forsgren 1992; pipefish, *Syngnathus typhle*: Berglund 1993). In the sailfin molly, females are more likely to refuse a male when in physical contact with him, when they have spent less time with that male without physical contact before (K. Witte, A. Vaughan & M. J. Ryan, 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, even though we switched the positions of the males. These test females (12 over all experiments) were omitted from the analysis.

During the viewing period (Fig. 1c), test females were given the opportunity to observe another female (model female), next to the nonpreferred male (the male with whom the test female had spent less time in the first preference test). The model female was always presented next to the nonpreferred male. Thus, the side on which the model female was shown depended on the mate choice decision of the test female in the first preference test. We placed the test female back into the Plexiglas cylinder in the middle of the large tank and a model female in the small tank adjacent to the nonpreferred male. We assumed that the proximity of the model female to the nonpreferred male indicated her mate preference for that male to the test female. Because males increased their activity in the presence of females, however, it was necessary to place a second live female (pseudomodel female) in the small tank adjacent to the other male as well. This pseudomodel female was hidden behind a white plastic board and thus visible only to the preferred male, and not to the test female (Fig. 1c). During the 10-min viewing period, the test female could observe a model female next to the nonpreferred male and no female next to the preferred male. We then removed the model and pseudomodel females and measured their body lengths.

For the second preference test, we released the test female from the cylinder and measured the time she spent with the previously preferred and nonpreferred males within the two 10-min trials, as we did in the first preference test. Then we compared the time that the test female spent with the nonpreferred male in the second preference test (after the viewing period) with the time that she spent with him in the first preference test. If a female spent more time with the nonpreferred male in the second preference test than in the first, we concluded she had copied the 'choice' of the model female.

We performed three mate choice copying experiments in which we altered the interval between the viewing period and the second preference test.

Experiment 1: no time interval

In this experiment, we did the second preference test immediately after the viewing period and we followed the protocol as described above (N=15 females; Table 1). For each preference test there were two 10-min trials.

Table 1. Mean±SD standard body length (mm) of test females, model females, pseudomodel females and stimulus fish and sample sizes in parentheses

	Copying experiments			Control for consistency			Control for shoaling behaviour		
	No interval	1-h interval	24-h interval	No interval	1-h interval	24-h interval	No interval	1-h interval	24-h interval
Test females	43±2 (15)	38±5 (11)	39.9±3.9 (19)	41.1±2.8 (12)	41.8±5.3 (10)	40.8±3.7 (17)	33.6±2.4 (10)	34.4±2.2 (10)	36.3±3.6 (10)
Model females	43.3±1.9 (15)	40±1.8 (11)	38.4±3.8 (19)	40±4.3 (12)	42.7±5.3 (10)	38.2±2.7 (17)	42.2±7.4 (10)	37.4±4 (10)	30.9±4.8 (10)
Pseudomodel females	43±2.2 (15)	40.5±1.8 (11)	39.2±4.1 (19)	41.5±4.2 (12)	43±4.2 (10)	39.4±2.3 (17)	40.8±7.8 (10)	38±4 (10)	32.75±5.3 (10)
Males	43.3±5.5 (30)	40.4±6.3 (22)	41±4.5 (38)	46.5±2.2 (24)	43.7±5.7 (20)	49.5±9 (34)	—	—	—
Difference in male body length	2.7±2 (15)	2.5±1.8 (11)	1.6±1.6 (19)	1.5±1.1 (12)	3±2 (10)	1.7±1.7 (17)	—	—	—
Stimulus females	—	—	—	—	—	—	34.1±2.6 (20)	33.7±3.7 (20)	33.1±4.7 (20)

Experiment 2: 1-h interval

In experiment 2, we did the second preference test 1 h after the viewing period (N=11 females; Table 1). After the viewing period we removed the test female from the test tank and kept her visually isolated in a separate tank. We removed the model and pseudomodel females, measured their standard body lengths and kept them in another tank; we also removed the males and kept them in separate tanks for individual recognition. We removed all fish from the experimental tanks to use the apparatus for another test during the 1-h pause for the test female and stimulus males of the previous experiment. For this reason, both preference tests lasted for two 5-min trials each. Because males and test females were replaced into the test aquarium after 1 h they were allowed an extra 5 min to acclimate before the second preference test.

Experiment 3: 24-h interval

In this experiment, we did the second preference test 24 h after the first (N=19 females; Table 1). Between the first and second preference tests we kept test females in a separate tank, visually isolated from other males and females. We removed the males from the experimental apparatus and kept them in separate tanks for individual recognition, and we removed model and pseudomodel females and kept them in other tanks after measuring their body lengths. For the second preference test on the next day, males and test females were allowed 15 min to acclimate to the test tank. Preference tests lasted for two 10-min periods.

In all three experiments, each female was used only once as a test female, but test females were used as models and pseudomodels in other tests. Within an experiment, males were used only once, but they were used in other experiments as well. After each test, we measured, with callipers, the standard body length of males and females from the tip of the snout to the end of the caudal peduncle. After the experiments, males and females were maintained in the laboratory for other experiments.

Control for consistency in female mate choice

In this control we tested whether females chose consistently between the first and second preference tests when they had no opportunity to copy. This control was performed in the same manner as the three mate choice copying experiments. During the 10-min viewing period, however, both model and pseudomodel females were hidden behind an opaque board, so that they were not visible to test females but were visible to the males during the viewing period. We did three controls. In one control we started the second preference test immediately after the viewing period (control with no time interval; N=12 females; Table 1). Preference tests lasted for two 10-min periods. In a second control, we started the second preference test 1 h after the viewing period (N=10 females; Table 1). Preference tests lasted for two 5-min periods. In a third control, the second preference test was performed 24 h after the first (N=17 females; Table 1). Preference tests lasted for two 10-min periods.

In the controls with a time interval between the viewing period and the second preference test, we visually isolated test females from other females after the viewing period and presented the same stimulus males to test females in the second preference test. We compared the time the test female spent with the nonpreferred male in the first preference test with the time she spent in front of the same male in the second preference test.

Control for shoaling behaviour

In this control we tested whether females showed shoaling behaviour under the experimental conditions, that is, if females preferred to associate with a conspecific that they had seen with a second conspecific during the viewing period in the mate choice copying experiment. In this control, however, we used only females as stimulus fish to exclude any sexual motivation in females to swim within the preference zones. The control was performed in the same manner as in the mate choice copying experiment, but with stimulus females instead of stimulus males. In the first preference test we measured the time the test female spent with the two stimulus females. Then we presented a model female next to the stimulus female with whom the test female had spent less time during the 10-min viewing period. Next to the other stimulus female, we presented a pseudomodel female, but this was behind a screen and, therefore, not visible to the test female. We did three controls. In the control with no interval, preference tests lasted for two 10-min periods (N=10 females; Table 1). In the shoaling control with a 1-h interval, preference tests lasted for two 5-min periods (N=10 females; Table 1). In the third control with an interval of 24 h, preference tests lasted for two 10-min periods (N=10 females; Table 1). In the controls with an interval, we visually isolated test females from other females after the viewing period and presented the same stimulus females to test females in the second preference test. We compared the time the test female spent with the less preferred female in the first preference test with the time she spent in front of the same female in the second preference test.

We used a Wilcoxon signed-ranks test to compare the females' preference for males measured as the time (s) spent within a preference test and to analyse the relative time females spent (i.e. the percentage of time spent in both preference zones within two 10-min trials) in front of the nonpreferred males in the first and second preference tests. Actual time spent and relative times spent are given as medians and first to third interquartiles. All P values are two tailed.

RESULTS

Experiment 1: No Interval

With no interval between observing the model female and the opportunity to choose, females spent a median of 215 s (152–279 s) with the nonpreferred male and 522 s (343–603 s) with the preferred male in the first preference test (Wilcoxon signed-ranks test: actual time spent: $T=0$,
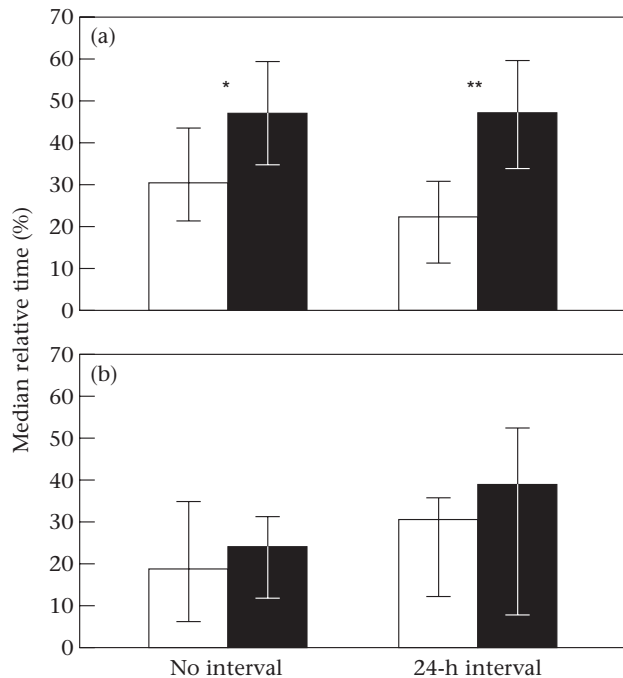
Figure 2. (a) Mate choice copying experiment and (b) test for consistency in female mate choice with no interval or after 1 day. Relative time (median) that a female spent in front of nonpreferred males in the first (□) and second (■) preference tests is shown. The second preference test was performed immediately after the viewing period or 24 h after the first preference test. First and third inter-quartiles are shown as the lower and upper tips, respectively, of each vertical line. *$P<0.05$; **$P<0.01$.

$N=15$, $P=0.001$). In the second preference test, after viewing a model female for 10 min next to the non-preferred male, females significantly increased the relative time spent in front of previously nonpreferred males (actual time spent: 245, 212–357 s; relative time spent: $T=17$, $N=15$, $P=0.015$; Fig. 2a), although moti-vation to choose between males (total time females spent in both preference zones within a test) decreased from the first preference test (713, 618–800 s) to the second (576, 514–793 s; $T=22$, $N=15$, $P=0.031$). Females spent signifi-cantly less time in front of previously preferred males in the second preference test (352, 113–429 s) than in the first (relative time spent: $T=17$, $N=15$, $P=0.015$). After viewing the model female, test females spent a similar time in front of preferred and nonpreferred males (actual time spent: $T=40$, $N=15$, $P=0.26$). Thus, females copied the choice of the model female immediately after observ-ing a sexual interaction between the model female and the nonpreferred male.

Experiment 2: 1-h Interval

With a 1-h time interval between observing the model female and the opportunity to choose, females spent a median of only 29 s (0–82 s) with the nonpreferred male and 320 s (242–379 s) with the preferred male in the first preference test (Wilcoxon signed-ranks test: actual time spent: $T=0$, $N=11$, $P=0.003$). One hour after viewing the

model female next to the nonpreferred male, females spent 117 s (95–100 s) in front of previously nonpreferred males in the second preference test (relative time spent: first test: 10, 0–25.3%; second test: 48.7, 35.2–62.3%; $T=2$, $N=11$, $P=0.006$). As a consequence, females signifi-cantly decreased the time spent in front of previously preferred males in the second preference test (130, 94–210 s; relative time spent: $T=2$, $N=11$, $P=0.006$). Females spent a similar time in front of preferred and nonpreferred males in the second preference test, 1 h after viewing the model females next to the non-preferred male (actual time spent: $T=26$, $N=11$, $P=0.53$). Motivation to choose between males did not change between the first (379, 290–410 s) and second preference tests (320, 199–370 s; $T=24$, $N=11$, $P=0.42$). Thus, females copied the mate choice of the model female 1 h after observing the sexual interaction between the model female and the male.

Experiment 3: 24-h Interval

Females spent a median of 406 s (361–595 s) with the preferred male and 137 s (39–201 s) with the non-preferred male in the first preference test (Wilcoxon signed-ranks test: actual time spent: $T=0$, $N=19$, $P<0.001$). In the second preference test, 24 h after observ-ing a model female next to the previously nonpreferred male, females significantly increased the relative time in front of the nonpreferred male in the second preference test (actual time spent: 282, 193–375 s; relative time spent: $T=18$, $N=19$, $P=0.002$; Fig. 2a). As a consequence, females spent less time with the previously preferred male in the second preference test (303, 217–550 s); relative time spent: $T=18$, $N=9$, $P=0.002$), and they spent a similar time with the preferred and nonpreferred males (actual time spent: $T=67$, $N=19$, $P=0.26$). Motivation to choose between males did not differ between the first (597, 431–773 s) and second preference tests (657, 522–762 s; actual time spent: $T=72$, $N=19$, $P=0.35$). Thus, females copied the choice of the model female a full day after they observed a sexual interaction between the model female and a male.

We compared the strength of copying, measured as the difference in time spent in front of the previously non-preferred male in the second versus the first preference test, in experiments 1 and 3. Strength of copying was not significantly different for females presented with a choice a day after viewing the model interaction and females allowed to choose immediately after viewing the model female (Mann–Whitney U test: $U=108$, $N_1=19$, $N_2=15$, $P=0.24$).

Control for Consistency

In the control with no time delay, females spent a median of 398 s (262–702 s) in front of preferred males and only 79.5 s (53–138.3 s) in front of nonpreferred males (Wilcoxon signed-ranks test: actual time spent: $T=0$, $N=12$, $P=0.002$). Females showed a similar prefer-ence and spent a similar relative time in front of

nonpreferred males in the first and second preference tests (98.5, 87.5–149.8 s; relative time spent: $T=31$, $N=12$, $P=0.53$; Fig. 2b), as well as with preferred males in the second preference test (375, 290.8–637.3 s; relative time spent: $T=31$, $N=12$, $P=0.53$). Motivation to choose between males did not differ between the first (501.5, 395–787 s) and second preference tests (520.5, 415.8–715.8 s; $T=32$, $N=12$, $P=0.58$).

In the control with a 1-h time interval, females spent a median of 166.5 s (120–263.3 s) with the preferred males and only 31.5 s (12.3–98.3 s) with nonpreferred males (actual time spent: $T=0$, $N=10$, $P=0.005$). They spent a similar time in front of preferred males in the first and second preference tests (110.5, 56.8–269 s) as well as in front of nonpreferred males in the first and second preference tests (77, 32–200 s; relative time spent: first test: 22.2, 7.7–31.5%; second test: 40.7, 23.2–54.2%; $T=11$, $N=10$, $P=0.093$). Motivation to choose between males did not change between the first (246.5, 143.5–314.8 s) and second preference tests (234.5, 124.3–408.5 s; $T=26.5$, $N=10$, $P=0.92$).

In the control condition with a 24-h time interval, females spent a similar time in front of nonpreferred males in the first (153, 50.5–213 s) and second preference tests (156, 42.5–280 s; relative time spent: $T=57$, $N=17$, $P=0.36$; Fig. 2b). Females also spent a similar time with the preferred male in the first (398, 334–495 s) and second preference tests (342, 223.5–438.5 s; relative time spent: $T=57$, $N=17$, $P=0.36$). Motivation to choose between males did not change between the first (554, 422.5–614 s) and second preference tests (549, 335.5–631.5 s; $T=73$, $N=17$, $P=0.87$).

Control for Shoaling Behaviour

Females did not shoal in any of the shoaling controls. In the control with no time interval, females spent a similar time with nonpreferred females in the first (189.5, 112.5–347.3 s) and second preference tests (280, 150–377.8 s; Wilcoxon signed-ranks test: relative time spent: first test: 32.7, 28.5–44%; second test: 45.3, 21.5–57.3%; $T=15$, $N=10$, $P=0.2$). In the control with a 1-h time interval, females spent a median of 102 s (53.8–161 s) with nonpreferred females in the first preference test and 129.8 s (57.4–183 s) with the same females in the second preference test (relative time spent: first test: 38.9, 24.4–46.8%; second test: 43.2, 23.7–60.6%; $T=22$, $N=10$, $P=0.57$). In the shoaling control with a 24-h interval, females spent a similar time with the female that was presented together with a model female during the viewing period in the first (181.5, 110.3–223.5 s) and second preference tests (207, 140.8–302 s: relative time spent: first test: 40.1, 36.3–48.9%; second test: 43.8, 35.5–47.4%; $T=26$, $N=10$, $P=0.87$).

DISCUSSION

Sailfin molly females copied the choice of the model female in three experimental conditions. In experiment 1, females that could choose a second time between the same two males immediately after observing the model female interacting with the previously nonpreferred male copied the mate choice of the model female. This situation is the standard one in mate choice copying experiments in fish. In almost all these fish studies females copied the choice of the model female when males presented in a test were similar in body length and coloration (e.g. Dugatkin 1992, 1996b; Dugatkin & Godin 1992, 1993; Witte & Ryan 1998). There are only three published exceptions to this rule. Brooks found no mate choice copying in feral guppy populations in South Africa (Brooks 1996) and Australia (Brooks 1999), and Lafleur et al. (1997) failed to replicate the result from Dugatkin's (1992) study (Dugatkin 1998b). The results of experiment 1 support findings in the sailfin molly (Witte & Ryan 1998): females copied the model's choice immediately after viewing a model female close to a particular male.

In experiment 2, we prevented the test female from copying immediately after viewing a sexually interacting model female and the previously nonpreferred male by isolating her for 1 h. These females also copied the choice of the model female. This indicates that the females had recognized the two males and recalled which male had interacted with the model female. Information on the model female's choice apparently overrode the current information available from the signalling males.

In experiment 3, females could choose between the two males a second time 1 day after observing the model female next to the nonpreferred male. Even then, females copied the choice of the model female; thus, females still recognized both males and which male had interacted with the model female. When females had no opportunity to copy, they chose consistently in the first and second preference tests on 2 successive days. Thus, inconsistency in female mate choice could not explain the copying effect in the mate choice copying experiment after 1 day. The strength of copying after 1 day was similar to the strength of copying of females that copied immediately after observing the sexual interaction. Recognizing potential mates and sexual interactions between conspecifics for at least a day represents an enormous memory capacity in female fish. In another mate choice study, Berglund & Rosenqvist (2001) showed that male pipefish had a similarly good memory for potential mates. Their experiment consisted of two trials on 2 successive days. On the first day, males could observe two fighting females. On the second, males could choose between the same females in a context where females were prevented from interacting with each other by an opaque divider, but showed courtship displays towards the male. Males preferred to associate with the dominant female. Thus, males remembered the fighting situation from the previous day and used this information on the next day, even though both females displayed towards the male. Subjects therefore used the earlier information about competition in preference to the more recent information about courtship display quality. This result parallels the result of our third experiment. Berglund & Rosenqvist's (2001) results and ours indicate that the memory capacity of fish in the context of mate choice might be better than has been thought.

In experiments 2 and 3, sailfin molly females were visually isolated for either 1 or 24 h between the two preference tests and could not interact with or smell other conspecifics. This is an artificial situation, but the isolation was necessary to exclude any other factors that might have influenced the outcome of the second preference test. In nature, females live with other conspecifics and heterospecifics and interact with them several times within an hour (K. Witte, personal observation). It is not clear if the females in our study would have still recognized a particular male after 1 h or even after a day, if they had been allowed to interact with other males in between. Nevertheless, our results show that sailfin molly females are able to remember individuals and use this information up to a day later.

What is the adaptive value of recognizing potential mates? A memory for potential mates is a prerequisite for several mate search tactics and mate choice strategies in females (Janetos 1980; Parker 1983; Real 1990). Numerous studies have shown that females can gain material, proximate and genetic benefits from choosing between males and have a higher fitness than nonchoosing females (reviewed in Andersson 1994). Thus, females must remember potential mates to find the optimal one.

Male courtship display to a female is a highly conspicuous behaviour not only for conspecifics, but also for predators (Houde 1997). Therefore, it might be risky for a copying female to mate with a male immediately after that male has courted another female and might have attracted the attention of a predator. Females might benefit from recognizing a particular male and mating with him at a safer time.

One cost of mate choice copying for females is that the male's sperm may be depleted. This is only the case, however, when copying females mate with the particular male immediately after observing other females mating with that male. Delaying a mating after observing a copying interaction may increase the likelihood that a male has stored sperm again. Thus, the risk of sperm depletion for copying females is not higher than for noncopying females.

We conclude that sailfin molly females can remember an observed sexual interaction between a male and a female for at least 24 h. This is an important point in understanding the mechanism of mate choice copying, and emphasizes the importance of mate choice copying in understanding female mate preferences.

Acknowledgments

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