

Sailfin molly females (*Poecilia latipinna*) copy the rejection of a male

Klaudia Witte and Kirsten Ueding

Lehrstuhl für Verhaltensforschung, Universität Bielefeld, Postfach 100131, 33501 Bielefeld, Germany

When females choose among males they often accept one male as a potential partner and reject others as nonacceptable mates. The rejection of “wrong” males and the acceptance of “right” males are equally important processes in mate choice. Sailfin molly females have been shown to copy the mate choice of other females when accepting a male. The present study used video playbacks to test whether or not sailfin molly females copy the rejection of a male. Test females spent significantly less time with previously attractive males after having observed their rejection by other females. Eight of 15 females even reversed their choice and preferred the male they had previously found unattractive. In control experiments, we showed that neither inconsistency in female mate choice nor escape behavior of a female in a nonsexual context could explain these results. This is the first study that shows that sailfin molly females copy the rejection of a male. *Key words*: male rejection, mate-choice copying, sailfin molly, sexual selection, video playback. [*Behav Ecol* 14:389–395 (2003)]

In most species, females are the choosier sex and discriminate between several males before they choose a mate (for overview, see Andersson, 1994). During the process of mate choice, females therefore either accept or reject males as potential mates. According to theories of sexual selection, the rejection of males as mates is as important as the acceptance of males because females might suffer low reproductive success when mating with the “wrong” male. In some species, females have developed tactics to reject a male after it has mounted, for example, in the seaweed flies *Coelopa nebularum* (Weall and Gilburn, 2000) and *Coleopa ursina* (Crean and Gilburn, 1998) and the termite *Zootermopsis nevadensis* (Shellman-Reeve, 1999).

Most models of sexual selection assume that females prefer mates on the basis of genetically determined, fixed mate preferences (Bakker, 1999; Bakker and Pomiankowski, 1995; Iwasa and Pomiankowski, 1999). There is increasing evidence, however, that social factors are important in influencing mate-choice decisions as well. Mate-choice copying is a socially influenced mate-choice strategy (Westneat et al., 2000) and can sometimes even override genetically determined mate preferences (Dugatkin, 1998). Experimental evidence for mate-choice copying has been shown in various polygynous fish species such as the guppy *Poecilia reticulata* (Dugatkin, 1992, 1996b, 1998; Dugatkin and Godin, 1992, 1993), the Japanese medaka *Oryzias latipes* (Grant and Green, 1996), and the sailfin molly *Poecilia latipinna* (Schlupp et al., 1994; Witte and Massmann, 2003; Witte and Noltemeier, 2002; Witte and Ryan, 1998, 2002) and 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). Theoretical studies have investigated how copying could have evolved and be maintained in a population (Dugatkin, 1996a; Gibson and Höglund, 1992; Kirkpatrick and Dugatkin, 1994; Losey et al., 1986; Nordell and Valone, 1998; Pruett-Jones, 1992; Servedio and Kirkpatrick, 1996; Stöhr, 1998). During mate-choice copying, females observe a sexual interaction between

a male and another female and choose the same male for copulation as the previous female. Thus, females base their mate choice decision on the mate choice of other females.

So far, studies regarding mate-choice copying in females have investigated whether a male becomes more attractive to a female after she had observed a sexual interaction between another female and that male (Dugatkin, 1992, 1996b, 1998; Dugatkin and Godin, 1992, 1993; Schlupp et al., 1994; Witte and Noltemeier, 2002; Witte and Ryan, 1998, 2002). These studies have shown evidence for copying mate acceptance. The process of mate choice decisions, however, involves not only the decision to accept males as potential partners but also the decision to reject specific males. By copying the rejection of a male, females might be able to learn which males are good potential partners and which ones are not (Pruett-Jones, 1992). If a female has observed another female rejecting a male and copies this mate choice decision, she might reject this male as well. Thus, a male may become less attractive to the observing female or even may be rejected. We tested this hypothesis in sailfin molly females. Previous studies have shown that sailfin molly females copy the acceptance of a male in the laboratory (Witte and Noltemeier, 2002; Witte and Ryan, 1998) and in the field (Witte and Ryan, 2002). Sailfin molly females show an obvious set of mate-rejection behaviors: They escape from males by fast swimming, move their body sideward to avoid a gonopodial thrust, or press their body to the bottom. Thus, this species provides an excellent system to study copying of male rejection. To simulate a situation in which a female rejects an attractive male by escape, we used video playbacks of males and females instead of live stimulus fishes. The rejection of a female was simulated by a female escaping from a male when he tried to court that female. First, we conducted a pretest to investigate whether sailfin molly females were able to distinguish between a conspecific male and a conspecific female presented on video monitors. Then we performed a copying experiment and two controls, which tested for inconsistency in female mate choice and for the influence of escape behavior in a nonsexual context.

Address correspondence to K. Witte. E-mail: klaudia.witte@biologie.uni-bielefeld.de.

Received 4 September 2001; revised 17 July 2002; accepted 28 August 2002.

© 2003 International Society for Behavioral Ecology

METHODS

Study species

Sailfin mollies are live-bearing poeciliid fish without parental care. They live in mixed-sex shoals comprising 10 to 20

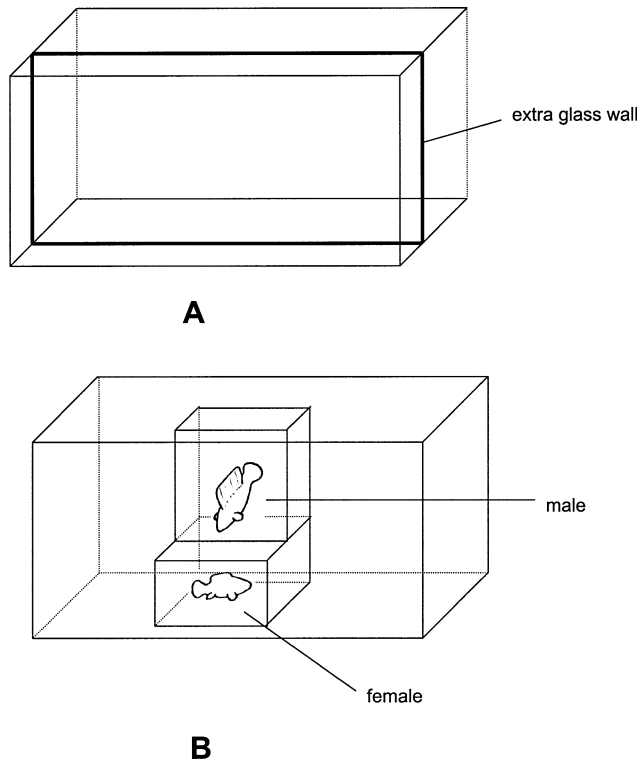


Figure 1
Side view of the recording tank. For recording single females (escaping and nonescaping females) and males together with the model female, we placed a transparent glass at 10 cm into the tank to facilitate focusing the stimulus fish (A). For recording single males we used a different setup (B).

individuals. Females have the opportunity to observe other females during mate choice and to copy the choice of other females (Witte and Ryan, 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 the summer of 1999. We maintained the fish separated by sex in tanks under 12-hour/12-hour light/dark regime with broad spectrum fluorescent light, at an average temperature of 23°C, and fed them ad libitum with daphnia and chironomid larvae once a day.

Video playbacks

All videos were recorded with a professional-quality Panasonic video camera (NV-MSE6) on high-quality S-VHS Fuji tapes (PAL video standard). The fish we used for the videos were recorded in a tank 60 cm long \times 30 cm wide \times 35 cm high (Figure 1A), with the longest side facing the camera and with an additional transparent glass at 10-cm depth to allow the stimulus fishes to swim only within 10-cm depth, which facilitated filming the fish stimuli (Figure 1A). The tank had a layer of gravel on the ground and a green paper sheet as a background. Dugatkin and Godin (1993) showed in guppies that small focal females copied the choice of large model females but not vice versa. To create good stimuli for the test females and to make sure that all model females on the screen appeared larger than test females, all fish were recorded 1.7 times larger than their natural body length. The apparent body lengths of the stimulus fish on the video monitors were still within the natural range of body lengths for sailfin mollies.

We created four sets of 12-min video tapes for (1) the pretest, (2) the copying experiment, (3) a control for consistency in female mate choice, and (4) a second control for escape behavior in a nonsexual context.

For the pretest and the escape behavior control, we recorded three single females (natural standard body length: 48, 50, and 54 mm) swimming slowly through the tank. For the escape behavior control, we recorded three other single females (natural standard body length: 48, 50, and 55 mm), which were chased by one of us and, therefore, swam rapidly through the recording tank (Figure 1A). The behavior of these females was defined as escape behavior, and this behavior was similar to the behavior of females escaping from males (see below).

For the copying experiment, we recorded each of four males. The males were similar in color and size (natural standard body length: 51, 52, 52, and 53 mm). We recorded each male together with a female (the model female) in the recording tank with the additional glass wall at 10-cm depth to facilitate focusing on both fish (Figure 1A). The model females had a natural standard body length of 43, 45, 45, and 48 mm. We recorded sequences in which model females escaped from the males (not provoked by one of us) when the males showed courtship displays to the females or tried to copulate with the females, and put these sequences together to form a 12-min video.

For the pretest and the copying experiment, we recorded the same four males again, but this time as single males that showed courtship displays to a female in an extra tank underneath. For these videos, we used a different setup (Figure 1B). We removed the additional glass wall from the recording tank and placed a small tank (15 \times 10 \times 15 cm) upside down on the bottom of the recording tank, with a female in it (Figure 1B). We placed a male in a similar small tank (15 \times 15 \times 10 cm) on top of the female tank. The males courted the female underneath through the glass bottom, facing the camera, so that their courtship displays appeared to be directed toward the test females viewing the videos in the pretests and copying experiments. We recorded only the male, not the female.

None of the females we used for the video tapes were used as test females. Test females and stimulus females were kept in separate tanks. Test females had no experience with stimulus males before testing.

General test procedure

All experiments were conducted in an aquarium (100 \times 50 \times 40 cm) with a layer of natural gravel on the ground and with a video monitor of 51 cm in diagonal (SABA, M5520C, 50 Hz, Type 630Z/TX91 GEU) at each side of the tank. Each monitor was connected to a JVC S-VHS video recorder (HR-S 7500 E/EH). The test tank was partitioned into three zones, that is, two preference zones at each end of the tank and a neutral zone in between (see Figure 2, grey areas indicate preference zones). Each preference zone was 20 cm deep and 50 cm wide. This preference zone was marked with a glass bar (49 cm), lying on the gravel parallel to the side of the test tank and 20 cm apart from the end of the tank, and by a vertical black line on the front surface 20 cm from the end of the tank.

Before a test started, test females had at least 20 min to adjust to the tank. During this period, the video monitors were covered by white plastic boards, and females moved freely in the tank. After the female had acclimatized to the test tank, we gently placed the female in a Plexiglas cylinder (11 cm diameter) in the center of the test tank, removed the white plastic boards, and started the videos on both sides

simultaneously. After 3 min, we released the test female from the cylinder and measured the time she spent within the preference zones in front of the videos for the next 5 min (9 min in the copying experiment). Then we covered the video monitors, placed the test female back into the cylinder, switched the videos, and removed the white plastic boards. Then we played the videos, released the female into the test tank after 3 min, and measured the time she spent within the preference zones within the next 5 or 9 min again. A female was considered to have chosen a stimulus fish when she spent more than 50% of the total time spent in both preference zones in front of that fish during the two 5- (or 9-) min test periods. 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 (Berghlund, 1993; Forsgren, 1992). In the sailfin molly, female rejection of a male in a situation in which physical contact was possible was correlated with time spent with that male in a situation in which physical contact was prevented (Witte K et al., in preparation).

Females that remained in the same preference zone at least 90% of the time, although we had switched the stimuli, were considered to have a side bias and were excluded from the analysis. Females that did not move around in the test tank after the acclimatization period were also excluded. After each test, we measured the standard length (from the tip of the snout to the end of the caudal peduncle) of each female. We did this after the experiment because this procedure was stressful for the fish.

Pretest

In the pretest, we investigated whether females were able to distinguish between a conspecific female and a conspecific male on the video monitor in a binary choice situation. We randomly selected a video showing a male on one side and a video showing a female on the other side. After the female had acclimatized to the test tank, we measured the time she spent within the preference zone in front of the male video and the time spent in front of the female video for the next two 5-min trials, as described above. A female was considered to have chosen the male when she spent more than 50% of the total time spent in both preference zones in front of the male during the two 5-min preference periods. We combined one of the three video tapes showing a female with one of the four male videos and used each combination three times. All pretests were conducted 1 day before the copying experiment. We tested 28 females. Twenty out of 28 females showed a preference for the male and were used in the subsequent copying experiment. The responding females ($n = 20$) had an average standard length of 46.7 ± 6 mm.

Copying experiment

Females ($n = 20$) were tested in the copying experiment 1 day after the pretest. In the copying experiment, we tested whether females copy the rejection of a male by another female. The copying experiment consisted of four phases: a starting period, the first preference test, a viewing period, and a second preference test (Figure 2). After the female had acclimatized to the test tank, the copying experiment began with a 3-min starting period in which the test female was kept within the Plexiglas cylinder (diameter, 11 cm) in the center of the tank, and could observe a video showing a male on one side and another male video on the other side. We used different videos in the copying experiment than in the

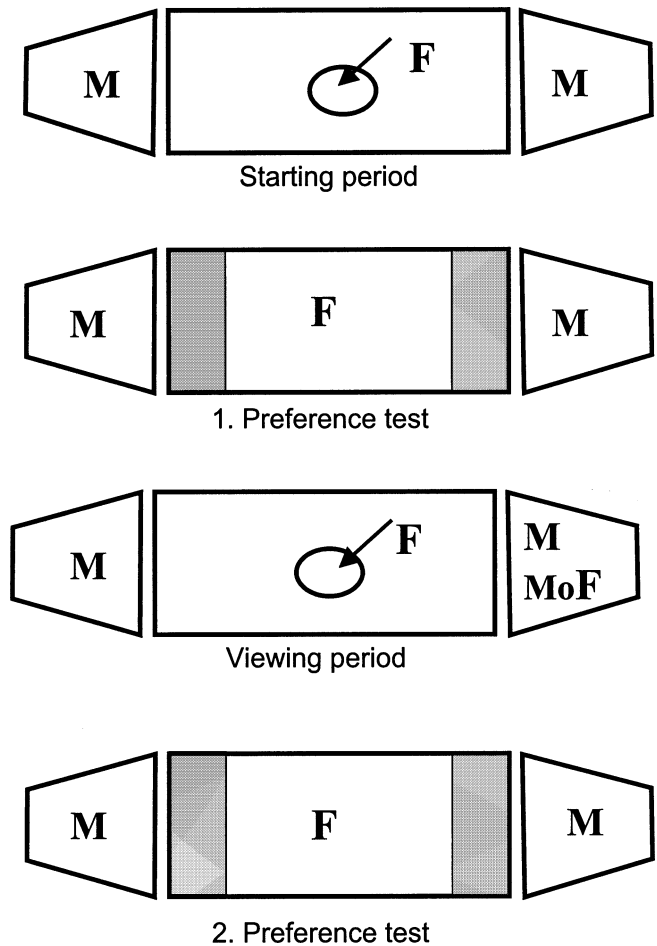


Figure 2

Top view of the four phases of a copying experiment. Starting period, 3 min: after the test female had acclimatized to the test tank, we gently placed the female in a Plexiglas cylinder (11 cm diam) in the center of the test tank, removed the white plastic boards, and started the videos on both sides simultaneously. First preference test: we released the test female from the cylinder and measured the time she spent within the preference zones indicated by grey areas in front of the videos for the next 9 min. Then we covered the video monitors, placed the test female back into the cylinder, switched the videos, removed the white plastic boards, played the videos, released the female into the test tank after 3 min, and measured the time she spent within the preference zones within the next 9 min again. A female was considered to have chosen a stimulus fish when she spent more than 50% of the total time spent in both preference zones in front of that fish during the two 9-min test periods. Viewing period: we removed the cover and presented a video sequence for 10 min showing the attractive male together with a female, the model female, that escaped from the male when he tried to copulate with her or showed courtship displays to her. The escape behavior of the model female should indicate her rejection of the male to the test female. On the other monitor, we presented the same video of the unattractive male as in the first preference test. Second preference test: we presented the same videos in the same manner as we did in the first preference test and measured the time the test females spent in front of both males.

pretest, so that test females had not previously seen these stimuli. After this starting period, we gently released the test female from the cylinder and began the first preference test. We measured the time she spent within the preference zones in front of each male within the two 9-min periods, as described above in General Test Procedure. The male with

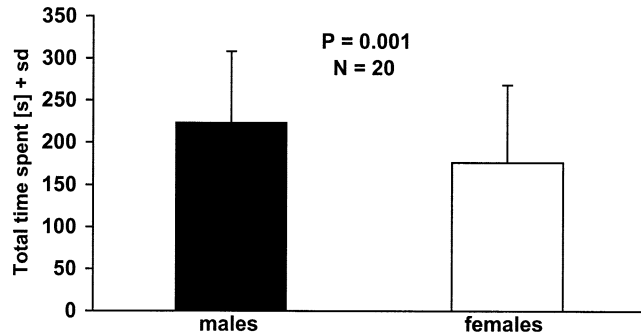


Figure 3
Average total time test females ($n = 20$) spent in front of a male video and a female video in the pretest. Females spent significantly more time in front of male videos.

whom the female spent more time within the two 9-min trials was considered to be the attractive male; and the other male, the unattractive one. Then we covered the video monitors and placed the test female back into the cylinder in the middle of the test tank. For the viewing period, we removed the cover and presented a video sequence for 10 min that showed the attractive male together with a female, the model female, that escaped from the male when he tried to copulate with her or showed courtship displays to her. The escape behavior of the model female should indicate her rejection of the male to the test female. On the other monitor, we presented the same video of the unattractive male as in the first preference test. After this viewing period, we covered the video monitors to exchange the video of the attractive male. Then we released the test female from the Plexiglas cylinder, removed the covers, and presented the same videos in the same manner for the second preference test as we did in the first preference test for two 9-min periods.

We compared the time the test female spent with the attractive male in the first preference test, before the viewing period, with the time she spent with that male in the second preference test after the viewing period. Test females were considered to copy the rejection of the model female when they spent significantly less time with the attractive males in the second preference tests than in the first preference tests.

Each of the four male videos was combined with the other three male videos, and all six combinations were randomly presented two or three times. Out of 18 females (average natural standard body length, 46.8 ± 6 mm) tested, 15 females met our criteria setup for accepting a trial and were used in the analyses.

Control for consistency in female mate choice

In this control experiment, we determined if females were consistent in their mate choice when they were not given an opportunity to copy. This control experiment was performed in the same way as the copying experiment, including a pretest 1 day before. During the 10-min viewing period, however, we presented the male videos of the first preference test. Thus, a model female was not presented, and test females had no opportunity to copy.

Each of the four male videos was used randomly and combined with the three other male videos. Each combination was used three times. Out of 21 females (average natural standard body length, 44.7 ± 5 mm) tested, 18 females met our criteria in the pretest. In this control, we used 15 out of 16 females (average natural standard body length, 43.3 ± 3 mm) that have chosen the male video in the pretest in the analysis.

A control for schooling behavior was not necessary because we wanted to test why a female spent less time on that side where two fishes, that is, the male and the model female, were presented. Previous copying experiments with live stimulus fishes showed that sailfin molly females do not shoal in such a choice situation (Schlupp et al., 1994; Witte and Ryan, 1998).

Control for escape behavior

Escape behavior of the model female might indicate to the test female that there is a predator nearby. Thus, escape behavior may lead the test female to avoid this side of the test tank where the model female was presented during the viewing period. This hypothesis is an important alternative explanation for a possible decrease in time spent with the attractive male. In this control experiment, we determined if females showed a response to an escaping female when no male was present. In a simple binary choice situation, we presented a video sequence of a female swimming slowly from side to side, the nonescaping female, and on the other video monitor, we presented a female swimming very fast with sudden movements. This female showed escape behavior, but in a nonsexual context. After the acclimatization period, the test female was gently placed in the Plexiglas cylinder in the middle of the test tank and could observe the slowly swimming (nonescaping) female on one side and the escaping female on the other side of the test tank for 3 min. Then, we released the female from the cylinder and measured the time she spent with both females for the next two 9-min test periods. We compared the time the test females spent in front of the escaping female with the time they spent in front of the nonescaping female. Each possible combination of the three videos with a slowly swimming female and the three videos with an escaping female was used in random order. We tested 12 females with an average standard length of 43.3 ± 5 mm.

RESULTS

Pretest: female video versus male video

Females ($n = 20$) swam several times within the preference zones and showed interest for the male and female videos. Eighteen females spent more time in front of the male video; two females spent more time in front of the female video. On average test females ($n = 20$) spent 223 ± 85 s ($56.6 \pm 17.5\%$, mean \pm SD) in front of the male videos and 176 ± 92 s ($43.4 \pm 17.5\%$) in front of the female videos (Wilcoxon matched-pairs test: $n = 20$, $z = -3.26$, $p = .001$; Figure 3). Thus, test females were able to distinguish between a conspecific female and a conspecific male on the video monitor and preferred to be close to a male, that is, were sexually motivated to choose a male.

Copying experiment

Although the two males presented in a test were similar in body length and color, females ($n = 15$) discriminated between them and showed a strong preference for one of the two males. On average, females spent 449 ± 120 s ($68.0 \pm 13.2\%$) of the time with the attractive male in the first preference test and only 205 ± 88 s ($32.0 \pm 13.2\%$) of the time with the unattractive male in the first preference test. After the viewing period, females spent significantly less time with the attractive male in the second preference test (303 ± 164 s, $44.0 \pm 18.5\%$) than in the first preference test (Wilcoxon matched-pairs test: $n = 15$, $z = -2.49$, $p = .012$;

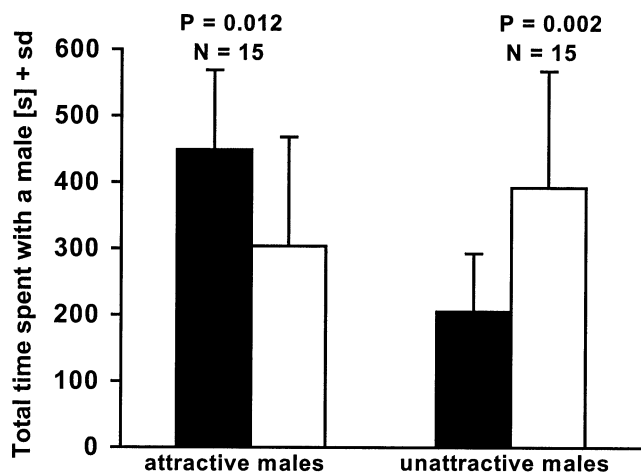


Figure 4

Average total time test females ($n = 15$) spent in front of the attractive and unattractive males in the first preference test (filled columns) and in the second preference test (open columns). Females spent significantly less time with the previously attractive males in the second preference test and significantly more time with the previously unattractive males.

Figure 4). On the other hand, females spent significantly more time with the previously unattractive male in the second preference test (392 ± 173 s, $56.0 \pm 18.5\%$) than in the first preference test (Wilcoxon matched-pairs test: $n = 15$, $z = 3.06$, $p = .002$; Figure 4). Eight of the 15 females reversed their preference and preferred the previously unattractive male in the second preference test over the previously attractive male, spending on average $65.9 \pm 14\%$ of their time with that male (McNemar-test: $n = 15$, $p = .008$). The eight females that reversed their mate choice in the second preference test were similar in body length (48.42 ± 7 mm) to the females that were consistent in their mate choice (46.37 ± 5.8 mm; Mann-Whitney U-test: $n = 8$, $m = 7$, $z = -0.64$, $p = .52$).

The total time a female spent with both males in a preference test did not change between the first and second preference test (Wilcoxon matched-pairs test: $n = 15$, $z = -0.35$, $p = .72$). Females spent on average 653 ± 103 s ($60.5 \pm 9.5\%$) of the 18 min in front of both males in the first preference test and on average 695 ± 159 s ($64.4 \pm 14.7\%$) in the second preference test. Thus, a possible decrease in motivation to swim to the stimuli cannot explain the decrease in attractiveness of the previously attractive males.

To test whether females avoided the side of the test tank where the escaping model female had been presented, we compared the time test females spent on the side where the escaping model female was shown before and after the viewing period. Females spent a similar amount of time on that side before the viewing period (121 ± 78 s, $43.9 \pm 18\%$) and after the viewing period (102 ± 66 s, $37.3 \pm 18\%$; Wilcoxon matched-pairs test: $n = 15$, $z = -0.86$, $p = .43$). Thus, females did not avoid to be on the side where the escaping model female was presented.

Consistency in female mate choice

In the pretest, females spent significantly more time in the preference zone in front of the male videos (186 ± 105 s, $62.5 \pm 14\%$) than in the preference zone in front of the female videos (111 ± 64 s, $37.5 \pm 14\%$), although two females spent more time near the female video (Wilcoxon matched-pairs test: $n = 18$, $z = -3.26$, $p = .001$).

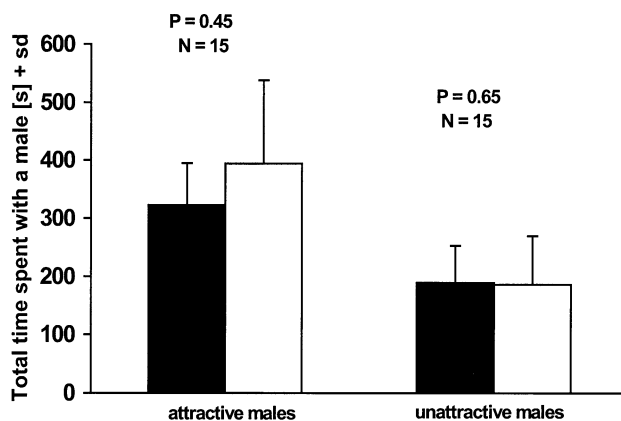


Figure 5

Control for inconsistency in female mate choice: Average total time test females ($n = 15$) spent in front of the attractive and unattractive males in the first preference test (filled columns) and in the second preference test (open columns). Females did not change their preferences with no opportunity to copy.

We performed the control for consistency with 15 out of 16 females that had preferred to be near the male video in the pretest. In this control, females ($n = 15$) showed a strong preference for one of the two males in the first preference test (Wilcoxon matched-pairs test: $n = 15$, $z = -2.55$, $p = .011$). They spent on average 323 ± 72 s ($64.2 \pm 12.5\%$) with the attractive male video and on average 189 ± 64 s ($35.8 \pm 12\%$) with the unattractive male video in the first preference test. Females showed a similar preference for attractive males in the first and second preference test (Wilcoxon matched-pairs test: $n = 15$, $z = -1.76$, $p = .45$; Figure 5) and for unattractive males in the first and second preference test (Wilcoxon matched-pairs test: $n = 15$, $z = -0.78$, $p = .65$; Figure 5). Thus, without the opportunity to copy, females chose consistently between males and spent a similar amount of time in front of the attractive male in both preference tests and in front of the unattractive male in both preference tests.

Control for escape behavior

Although females did not spend less time on the side where the escaping model female had been presented in the copying experiment, it was necessary to show that escape behavior without any sexual context could not explain the decrease in time spent with a particular male. In this control, females ($n = 12$) spent a similar amount of time with the nonescaping female (285 ± 215 s, $52.3 \pm 25.7\%$) and with the escaping female (247 ± 163 s, $47.7 \pm 25.7\%$; Wilcoxon matched-pairs test: $n = 12$, $z = 0$, $p = 1.0$). Thus, escape behavior in a nonsexual context cannot explain the decrease in time spent with the previously attractive male.

DISCUSSION

This is the first study showing that females copy another female's rejection of a male. This is a novel aspect in mate-choice copying. In our experiment, sailfin molly females spent significantly less time close to a video showing an attractive male after these females had observed another female that always escaped from that male when he tried to court her, that is, rejected that male. Interestingly, females not only spent less time with those males but also significantly reversed their preferences after observation of the escaping female and spent more time with the male they had previously found less attractive.

The reversal of preferences and decrease in time spent with an attractive male could not be explained by inconsistency in female mate choice or by escape behavior of a female in a nonsexual context.

Reversals of female mate preferences owing to mate-choice copying was shown in female guppies as well (Dugatkin and Godin, 1993), but in their study females copied the acceptance of a male, and a previously unattractive male became more attractive for females owing to copying.

Why did females copy the rejection of a male? As shown in a previous study (Witte and Ryan, 1998), mate-choice copying is a facultative mate-choice strategy. Sailfin molly females copy when both males presented in a test are similar in size and coloration. These females, however, do not copy when both males differ obviously in body length. In this case, females always prefer the larger males. In guppies, females copied the acceptance of a male when both males in a test did not differ by more than 24% in the amount of orange coloration of the body surface (Dugatkin, 1996b). When males differ by 40% in the amount of orange, females always prefer males having more orange, even if the model female is presented next to the drabber male (Dugatkin, 1996b). Thus, when it is difficult for females to distinguish between two males, females change their preferences and prefer the male they have seen together with a model female. Nordell and Valone (1998) showed theoretically that females do better to copy the mate choice of another female than to choose randomly between males, when it is difficult to distinguish between males. In our experiment, the males presented on the videos were similar in size and coloration. Although females showed a strong preference for one of the two males in the first preference test, they changed their preference after viewing a model female escaping from the attractive male. We assume that females would not copy the rejection of a male when both males differed in size in a test similar to the study regarding copying mate acceptance with males of different size (Witte and Ryan, 1998).

What is a possible advantage of copying the rejection of a male? Copying the rejection of a male might be one way for females to learn which type of male is "bad" as a potential mate. Dugatkin and Godin (1993) showed in guppies that small females, probably younger and relatively inexperienced in mate choice, copy the mate choice of large females, but not vice versa. In our experiment, test females were of similar body length, and all females had experience with males before starting the experiment. All model females, however, appeared larger than the test females because we played them back at an apparent size 1.7 times larger than their natural size. The rejection behavior of larger females might have led test females to change their mate preferences.

If females sample several males before choosing one of them, females might be able to save time for the process of mate choice by copying the rejection of a male. When females observe another female rejecting a male, females might ignore this male as well and concentrate on other males as potential partners. In addition, by saving time, females might be able to lower the risk of predation during mate choice.

Copying the acceptance of a male increases the variance in male mating success by enhancing the relative mating success of some males (Wade and Pruett-Jones, 1990). Copying male acceptance and male rejection would even stronger amplify this skewness in male mating success within a population. Rejected males are prevented from copulating with rejecting females, as well as with females that have observed this rejection.

Copying the rejection of a male is, therefore, an important factor for the process of mate choice that can influence the dynamic of sexual selection.

We thank Gil G. Rosenthal and two anonymous referees for their critical comments. K.W. is supported by the Deutsche Forschungsgemeinschaft (Wi 1531/2-3), and the project was supported by an innovation fund (FIF) of the University of Bielefeld.

REFERENCES

- Andersson M, 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.
- Bakker TMC, 1999. The study of intersexual selection using quantitative genetics. *Behaviour* 136:1237-1265.
- Bakker TMC, Pomiankowski A, 1995. The genetic basis of female mate preferences. *J Evol Biol* 8:129-171.
- Berglund A, 1993. Risky sex: male pipefishes mate at random in the presence of a predator. *Anim Behav* 46:169-175.
- Bischoff RJ, Gould JL, Rubenstein DI, 1985. Tail size and female choice in the guppy (*Poecilia reticulata*). *Behav Ecol Sociobiol* 46:169-175.
- Crean C, Gilburn AS, 1998. Sexual selection as a side-effect of sexual conflict in the seaweed fly, *Coelopa ursina* (Diptera: Coelopidae). *Anim Behav* 56:1405-1410.
- Dugatkin LA, 1992. Sexual selection and imitation: females copy the mate choice of others. *Am Nat* 139:1384-1389.
- Dugatkin LA, 1996a. Copying and mate choice. In: Social learning in animals: the roots of culture (Heyes CM, Galef BG Jr, eds). New York: Academic Press; 85-105.
- Dugatkin LA, 1996b. The interface between culturally-based preferences and genetic preferences: female mate choice in *Poecilia reticulata*. *Proc Natl Acad Sci USA* 93:2770-2773.
- Dugatkin LA, 1998. Genes, copying, and female mate choice: shifting thresholds. *Behav Ecol* 9:323-327.
- Dugatkin LA, Godin JGJ, 1992. Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proc R Soc Lond B* 249:179-184.
- Dugatkin LA, Godin JGJ, 1993. Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. *Behav Ecol* 4:289-292.
- Forsgren E, 1992. Predation risk affects mate choice in the gobiid fish. *Am Nat* 140:1041-1049.
- Galef BG Jr, White DJ, 1998. Mate-choice copying in the Japanese quail, *Coturnix coturnix japonica*. *Anim Behav* 55:545-552.
- Gibson RM, Bradbury JW, Vehrencamp SL, 1991. Mate choice in lekking sage grouse revisited: the roles of vocal display, female site fidelity, and copying. *Behav Ecol* 2:165-180.
- Gibson RM, Höglund J, 1992. Copying and sexual selection. *Trends Ecol Evol* 7:229-232.
- Grant JWA, Green LD, 1996. Mate copying versus preference for actively courting males by female Japanese medaka (*Oryzias latipes*). *Behav Ecol* 7:165-167.
- Höglund J, Alatalo RV, Gibson RM, Lundberg A, 1995. Mate-choice copying in the black grouse. *Anim Behav* 49:1627-1633.
- Iwasa Y, Pomiankowski A, 1999. Good parent and good genes models of handicap evolution. *J Theor Biol* 200:97-109.
- Kirkpatrick M, Dugatkin LA, 1994. Sexual selection and the evolutionary effects of copying mate choice. *Behav Ecol Sociobiol* 34:443-449.
- Kodric-Brown A, 1993. Female choice of multiple male criteria in guppies: interacting effects of dominance, coloration and courtship. *Behav Ecol Sociobiol* 32:415-420.
- Lossy GS Jr, Stanton FG, Telecky TM, Tyler WA III, 1986. Copying others, an evolutionary stable strategy for mate choice: a model. *Am Nat* 128:653-664.
- Nordell SE, Valone TJ, 1998. Mate choice copying as public information. *Ecol Lett* 1:74-76.
- Pruett-Jones S, 1992. Independent versus non-independent mate-choice: do females copy each other? *Am Nat* 140:1000-1009.
- Schlupp I, Marler C, Ryan MJ, 1994. Benefit to male sailfin mollies of mating with heterospecific females. *Science* 263:373-374.
- Servedio MR, Kirkpatrick M, 1996. The evolution of mate choice copying by indirect selection. *Am Nat* 148:848-867.
- Shellman-Reeve JS, 1999. Courting strategies and conflicts in a monogamous, biparental termite. *Proc R Soc Lond B* 266:137-144.
- Stöhr S, 1998. Evolution of mate-choice copying: a dynamic model. *Anim Behav* 55:893-903.
- Wade MJ, Pruett-Jones SG, 1990. Female copying increases the variance in male mating success. *Proc Natl Acad Sci USA* 87:5749-5753.

- Weall C, Gilburn AS, 2000. Factors influencing the choice of female mate rejection strategies in the seaweed fly *Coelopa nebulorum* (Diptera: Coelopidae). *J Insect Behav* 13:539–552.
- Westneat DF, Walters A, McCarthy TM, Hatch MI, Hein WK, 2000. Alternative mechanisms of nonindependent mate choice. *Anim Behav* 59:467–476.
- White DJ, Galef BG Jr, 1999. Mate-choice copying and conspecific cueing in Japanese quail, *Coturnix coturnix japonica*. *Anim Behav* 57:465–473.
- White DJ, Galef BG Jr, 2000. “Culture” in quail: social influences on mate choice of female *Coturnix japonica*. *Anim Behav* 59:975–979.
- Witte K, Massmann R, 2003. Females remember males and copy the choice of others after one day in sailfin mollies, *Poecilia latipinna*. *Anim Behav* (in press).
- Witte K, Noltmeier B, 2002. The role of information in mate-choice copying in female sailfin mollies (*Poecilia latipinna*). *Behav Ecol Sociobiol* 52:194–202.
- Witte K, Ryan MJ, 1998. Male body length influences mate-choice copying in the sailfin molly *Poecilia latipinna*. *Behav Ecol* 9:534–539.
- Witte K, Ryan MJ, 2002. Mate-choice copying in the sailfin molly (*Poecilia latipinna*) in the wild. *Anim Behav* 63:943–949.