ANIMAL BEHAVIOUR, 2002, **63**, 943–949
doi:10.1006/anbe.2001.1982, available online at http://www.idealibrary.com on IDEAL®

Mate choice copying in the sailfin molly, *Poecilia latipinna*, in the wild

KLAUDIA WITTE*† & MICHAEL J. RYAN*
*Section of Integrative Biology C0930, University of Texas at Austin
†Lehrstuhl für Verhaltensforschung, Universität Bielefeld

*(Received 8 February 2001; initial acceptance 21 March 2001;
final acceptance 28 November 2001; MS. number: 6835R)*

Mate choice copying has been documented extensively in the laboratory with almost no supporting data available from studies in the wild. We investigated male and female mate choice copying in a wild population of the sailfin molly, a species that shows copying in the laboratory. We set up two upside-down plastic tanks in a river, with two jars of water on each tank. In male mate choice trials we placed a female in one jar and a male in the other on one tank and a female in one jar on the other tank, leaving the last jar empty. In female mate choice trials we presented a male and a female on one tank and a male and an empty jar on the other. Males preferred to associate with a female adjacent to a male rather than a lone female and females preferred to associate with a male adjacent to a female rather than a lone male. In two controls for shoaling behaviour we presented two males on one side of the set-up and one male on the other or two females versus one female. These controls showed that shoaling behaviour could not explain the male and female preference. Thus both sexes of the sailfin molly show mate choice copying in the wild, much as they do in laboratory studies. At least in this species, mate choice copying is not a laboratory artefact.

Many models of sexual selection assume that females choose mates on the basis of genetically heritable mate preferences (reviewed in Kirkpatrick & Ryan 1991; Andersson 1994). There is increasing evidence, however, that social factors are also important in influencing mate choice decisions. Mate choice copying, which we refer to below as 'copying', is one such social influence on mate choice decisions (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 other females have previously chosen that male (Pruett-Jones 1992). In some cases mate choice copying can compromise genetically determined mate preferences (Dugatkin 1998a).

During copying, females observe a sexual interaction between a male and another female and choose the same male for mating as the previous female. Thus a female's mate choice depends on the mate choice of other females. Although studies on mate choice copying have focused on female mate choice, male sailfin mollies also copy the choice of other males (Schlupp & Ryan 1997). Copying differs from other types of nonindependent mate choice in that it is the observation of the sexual interaction between a male and a female, per se, that influences the mating decision of the observing individual, rather than some consequence of the sexual interaction. For example, female aggregations during mating might erroneously suggest copying (Shuster & Wade 1991; Clutton-Brock & McComb 1993; McComb & Clutton-Brock 1994). Also, a number of studies suggest that female fish prefer males with eggs in their nests from previous matings with other females and that such preferences are an indication of copying (Ridley & Rechten 1981; Constantz 1985; Bisazza & Marconato 1988; Unger & Sargent 1988; Goldsmith et al. 1993). But such behaviour probably results from selection to dilute the risk of predation for their own eggs (Rohwer 1978; Jamieson 1995). Eggs in a nest are a consequence of previous matings with other females and, therefore, cannot be a cue for copying by females (Kraak 1996).

Most of the evidence for mate choice copying is derived from studies of polygynous fish, such as the guppy, *Poecilia reticulata*, (Dugatkin 1992, 1996a, 1998a; Dugatkin & Godin 1992, 1993), the Japanese medaka, *Oryzias latipes*, (Grant & Green 1996; but see Howard et al. 1998) and the sailfin molly (Schlupp et al. 1994; Schlupp & Ryan 1997; Witte & Ryan 1998), as well as studies of polygynous bird species such as the sage grouse, *Centrocercus urophasianus* (Gibson et al. 1991), the black grouse,

Correspondence: K. Witte, Lehrstuhl für Verhaltensforschung, Universität Bielefeld, Postfach 100131, 33501 Bielefeld, Germany (email: Klaudia.Witte@Biologie.Uni-Bielefeld.de).

0003–3472/02/$35.00/0

Tetrao tetrix (Höglund et al. 1995) and the Japanese quail, *Coturnix c. japonica* (Galef & White 1998; White & Galef 1999, 2000).

To the extent that mate choice copying occurs in the wild, it could be an important factor in sexual selection through its influence on variance in reproductive success (Wade & Pruett-Jones 1990; Gibson et al. 1991; Kirkpatrick & Dugatkin 1991; Brooks 1998). Theoretical studies have investigated how copying could evolve and be maintained in a population (Losey et al. 1986; Gibson & Höglund 1992; Pruett-Jones 1992; Dugatkin 1996b; Stöhr 1998). Servedio & Kirkpatrick (1996) showed that an allele for copying can spread through a population via indirect selection even when there is mild selection against this allele for copying. These studies are not, however, based on any demonstrable selective advantage to copying.

For several good reasons mate choice copying is still a controversial concept. First, the function of copying is still under debate. Stöhr (1998) and Nordell & Valone (1998) showed in theoretical models that copying would be advantageous if some females were poor in their ability to discriminate male quality. Some evidence consistent with this notion comes from a mate-copying experiment in guppies. Dugatkin & Godin (1993) have shown 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 of the costs associated with this behaviour (Gibson & Höglund 1992; Stöhr 1998). In our view, however, there are no studies that offer strong evidence for a fitness advantage associated with mate choice copying in the laboratory or in the wild. Second, although guppies have emerged as the system most explored for copying, there is no evidence for copying in two feral guppy populations, and thus the generality of some previous studies has been questioned (Brooks 1996, 1999). Third, there has also been some argument as to the appropriateness of statistical analyses used in some studies (Lafleur et al. 1997; but see Dugatkin 1998b).

What we see as another, and perhaps more serious, issue in studies of mate choice copying is its generality. The majority of studies of copying have been conducted in the laboratory. There is only one study with black grouse in which mate choice copying was tested experimentally in the field (Höglund et al. 1995): more females were attracted to territories with a dummy female when males were able to copulate with the dummy.

The majority of studies of copying have been conducted with fish and all of these were done in the laboratory. To our knowledge, there is no evidence that mate choice copying in fish occurs in the wild. This is the issue we address here.

Previous studies in the laboratory have shown that female sailfin mollies copy the mate choice of other conspecific females (Witte & Ryan 1998) as well as the mate choice of heterospecific female *P. formosa* (Schlupp et al. 1994). Schlupp & Ryan (1997) have shown that male sailfin mollies copy mate choice as well. In this study we ask if patterns of mate choice copying seen in the laboratory also occur in the wild. In our study, stimulus and model animals were constrained in space, but all other aspects of the study replicate social and environmental conditions in nature. We conducted the study in the animal's home range where focal fish were free to move in and out of the experimental set-up. We feel such tests are now necessary to evaluate the proposition that mate choice copying is a real effect in nature, even if a poorly understood one.

METHODS

Study Species and Study Site

Sailfin mollies are live-bearing fish without parental care. They live in mixed-sex shoals comprising 10–20 individuals and males and females have the opportunity to observe other individuals during mate choice and copulation. We studied a population near the banks of the Comal River in the Landa Park in New Braunfels, Texas, U.S.A. between 20 July and 14 August 1999, that is, during the reproductive season (February to November, C. Hubbs, personal communication). The study site was part of the river, several hundred metres long, where we could observe several different shoals of sailfin mollies and single fish. The water was clear and only 60 cm deep at the bank. The population we studied was probably introduced from Louisiana in 1920 (Brown 1953).

The most common fish in this part of the river was a mosquitofish, *Gambusia geiseri*. The gynogenetic molly, *P. formosa*, is not present at this site. Observers could easily distinguish sailfin mollies from mosquitofish by body size and shape, coloration and behaviour. Female sailfin mollies were distinguished from males by their oval shape and lack of blue or black coloration at the tail fin. Females also have a bright line on the back and two bright spots on top of the mouth. Male mollies were distinguished from females by the blue colour on the tail fin. To ensure that we identified sex correctly, we ignored fish smaller than 30 mm, the majority of which would be juveniles.

Experiments

General procedure

We observed the fish's behaviour from the banks of the river, in areas lacking plants that would have obstructed the view. We designed the experiments to allow us to estimate mate preference by measuring the degree of association of free-ranging fish, the subject fish, with one of two stimulus fish of the opposite sex that either were or were not adjacent to a model fish. A preference for the stimulus fish adjacent to the live model fish was interpreted as evidence for mate copying.

The experimental set-up consisted of two plastic tanks (21 × 13 cm and 13.5 cm high) and four glass jars (9 cm in diameter, 17 cm high, 1 litre volume) and was located, on average, 70 cm from the bank. We placed the two plastic

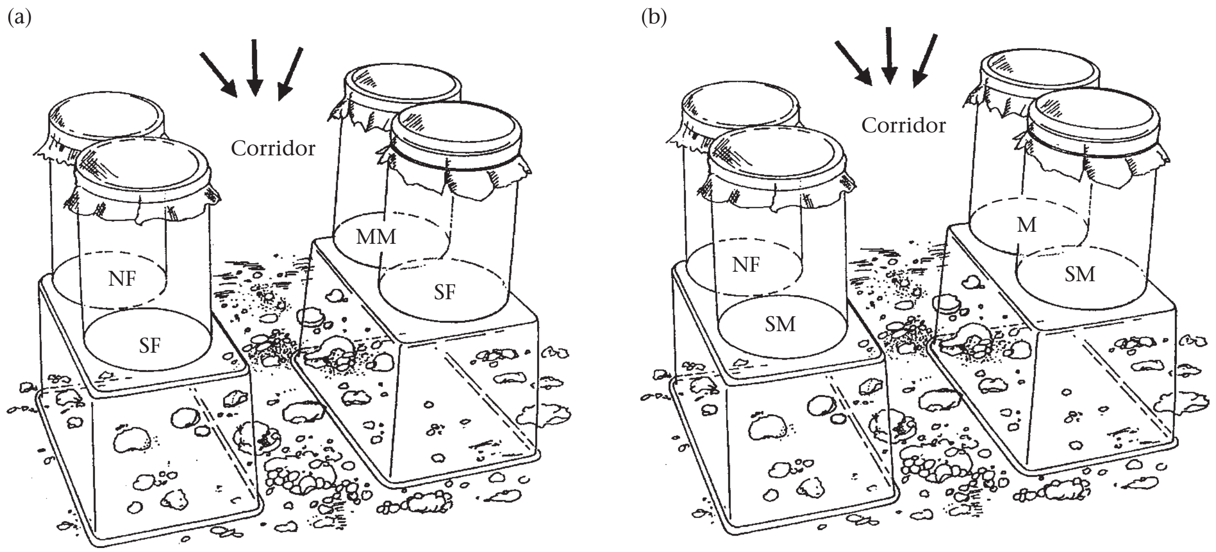

Figure 1. Top view of the set-up of (a) the male mate choice test and (b) the male control for shoaling in the water. Two jars stood on two upside-down plastic tanks. Each jar had a net on top and was filled with water from the river. In the male mate choice tests stimulus females (SF) were in two jars, the model male (MM) was in one jar next to a stimulus female and the fourth jar had no fish (NF). Only males were counted when they entered the set-up from the side with the empty jar and the model female (indicated by arrows), came through the 'corridor' and stopped within one body length of the jar with the stimulus females. In the set-up of the male control for shoaling there was a stimulus male (SM) and a jar with an extra male (M) on one tank and a stimulus male (SM) next to a jar with no fish (NF) on the other. Only males were counted when they entered the set-up from the side with the empty jar and the extra male (indicated by arrows), came through the corridor and stopped within one body length of the jar with the stimulus male. For the female mate choice test stimulus males replaced stimulus females and a model female the model male. In the female control for shoaling we presented two stimulus females and an extra female. Only females were counted, when they entered the set-up from the side with the empty jar and the model female (indicated by arrows), came through the 'corridor' and stopped within one body length of the jar with the stimulus males.

tanks upside down on the ground in the river (Fig. 1). The tanks stood parallel to each other with the longer sides 20 cm apart. There was no space between the jars, which were filled with water from the river. Each jar had a net on top so that olfactory cues could be transmitted, but fish could not escape the jars. The stimulus fish and the model fish were placed in one of two jars on the top of each plastic tank. The position and sex of stimulus and model fish are described in detail for each experiment below (Fig. 1). We performed male mate choice tests and a male control for shoaling behaviour, and female mate choice tests and a female control for shoaling behaviour.

The subject fish were able to approach the stimulus fish freely. The two jars with the stimulus fish were always facing the bank such that we had an unobstructed view of interactions between focal and stimulus fish. Each test started when the first focal fish entered the corridor from the side opposite the bank and lasted 20 min, during which we monitored additional subject fish in the corridor. After 10 min we halted the experiment, and within 30 s we carefully switched the jar with no fish with the jar containing the model fish to control for side preferences. We restarted the experiment when a focal fish entered the corridor. Thus, each stimulus fish within a test was next to the model fish. During the 20-min observation period we counted the number of fish that swam into the area between the two pairs of jars and interacted with the stimulus fish. We did not count fish that were within one body length of the stimulus fish but interacted with other free-swimming fish, and we did not count fish that interacted with the stimulus fish from outside the corridor or fish interacting with the model fish.

We caught stimulus fish and model fish from the experimental population a few days before the experiments. Between experiments, we released the model and stimulus fish from the jars and kept them in separate polystyrene boxes. Overnight we kept fish in tanks (100 × 40 cm and 50 cm high) segregated by sex at a temperature of 23°C and a 14:10 h light:dark regime with lights on at 0600 hours. We fed the fish once daily with flake food (Tetramin). We used stimulus fish as model fish and vice versa in other series of experiments.

All fish of the same sex in an experiment were matched for body length and coloration. Before tests we matched the fish of one sex by eye to minimize stress and disturbance for the fish. After each test we measured the body length of all stimulus and model fish as standard body length with callipers. We did this by gently pressing the fish's body against a plate with some water. The procedure lasted a few seconds. In all tests we used only nongravid females.

After each test we moved the experimental set-up ca. 20 m away to another location to minimize the risk of recording data from the same subject fish more than once between tests. We could not catch free-ranging fish that had been subjects, and any attempt to do so would have drastically affected water clarity. The order of the mate choice experiments and controls for shoaling was randomized. Because we did not mark fish individually it was possible, although we feel unlikely, that we had counted a fish twice within a 20-min experiment. Therefore, we did not compare the total number of fish associated with each stimulus fish. Instead, we used a binomial test to compare the number of tests in which the majority of subjects visited the stimulus fish adjacent to the model fish versus the stimulus fish adjacent to the jar with no fish. We used a two-tailed Wilcoxon signed-ranks test to compare the number of males visiting one or the other stimulus fish within the male mate choice experiments and within the male control for shoaling. We did the same for the female mate choice experiment and the female control for shoaling. We used a two-tailed Mann–Whitney *U* test to compare the total number of fish entering the set-up in the mate choice tests and the controls.

Male mate choice tests

In male mate choice tests we placed on one tank a jar with a stimulus female next to a jar with no fish. On the other tank we placed a jar with a stimulus female next to a jar with the model male (Fig. 1a). The proximity of the model male to the stimulus female should indicate his preference for that female to the free-living males. We did 20 tests. Each of the two stimulus females (N=40) had an average ± SD body length of 40.23 ± 5.33 mm. They differed in body length on average ± SD by 0.92 ± 2.8 mm. The model male was on average ± SD 37.62 ± 3.78 mm long.

Male control for shoaling

In this control, we tested whether males were more attracted by two conspecific fish than one conspecific fish of the same sex. We used only male stimulus fish for this control to exclude any sexual motivation to swim into the corridor of the set-up. In the male control we placed on one tank a jar with a stimulus male next to a jar with no fish. On the other tank we placed a jar with a stimulus male next to a jar with another male (Fig. 1b). We did 14 tests. In each test we used three males matched for colour and body length (average body length ± SD for one stimulus male: 33.32 ± 0.82 mm; for the other stimulus male: 33.4 ± 1.03 mm; for the third male: 33.32 ± 1.32 mm).

In the male mate choice tests and the male control for shoaling we counted the number of males that entered the corridor from the side where the empty jar and the model female or the third male were placed (see arrows in Fig. 1). To be scored, a subject had to swim through the area between the pairs of jars, stop at the jar with a stimulus fish, and in the male mate choice tests court the females in the jars. If a group of males entered the corridor (see Fig. 1) we took data only from the first male of this group and waited until this group left the corridor before collecting additional data.

Female mate choice tests

In female mate choice tests we placed on one tank a jar with a stimulus male next to a jar with no fish. On the other tank we placed a jar with a stimulus male next to a jar with the model female (Fig. 1). The proximity of the model female to the stimulus male should indicate her preference for that male to the free-living females. We did 20 tests. The stimulus males (*N*=40) were matched for colour and body length (average body length ± SD was 33.64 ± 3.2 mm, the average difference in body length between the two stimulus males in a test ± SD was 0.5 ± 2.95 mm), and the model female was on average ± SD 42.84 ± 4.55 mm long.

Female control for shoaling

In this control we tested whether females were more attracted by two conspecific fish of the same sex than one conspecific fish. We used only female stimulus fish for this control to exclude any sexual motivation of the focal females to swim into the corridor of the set-up. In the female control we placed on one tank a jar with a stimulus female next to a jar with no fish. On the other tank we placed a jar with a stimulus female next to a jar with another female (Fig. 1). We did 14 tests. In each control (*N*=14) we used three females which were matched for body length (average body length ± SD 41.84 ± 4.55 mm).

In female mate choice tests and the female control for shoaling we counted the number of females that entered the corridor from the side where the empty jar and the jar with a model male or the third female were placed (see arrows in Fig. 1). As above, to be scored, a subject fish had to come through the area between the pairs of jars and stop at the jars with the stimulus males or in the control, at the jars with the stimulus females. The focal females were required to swim to within one body length of the jar with a stimulus fish. If a group of females entered the corridor we took data only from the first female of this group and waited until the group was gone before commencing additional data collection. The majority of females touched the jar with the mouth. An association pattern is a good indicator of a sexual preference in sailfin molly females. We have shown in a laboratory study that females had the same preference for males constrained behind a glass barrier as they did in free-ranging laboratory experiments (K. Witte, A. Vaughan & M. J. Ryan, unpublished data). Kodric Brown (1993) and Bischoff et al. (1985) have shown that the time a female guppy spends with a male correlates positively with the probability of a copulation with that male.

RESULTS

Male Mate Choice Tests

In 19 out of 20 male mate choice tests more males ($\bar{X}$ ± SD=4.8 ± 3.7) associated with the female next to the model male. In only one case did more males visit the female next to the jar with no fish (binomial test: $P<0.001$; Fig. 2a). On average ± SD 12.7 ± 8.8 males visited the stimulus females in a test (range 2–32); 8.2 ± 6.1 males associated with the female next to the model male and 3.9 ± 3.4 with the female next to the empty jar (Wilcoxon signed-ranks test: $Z=-3.67$, $N=20$, $P<0.001$).

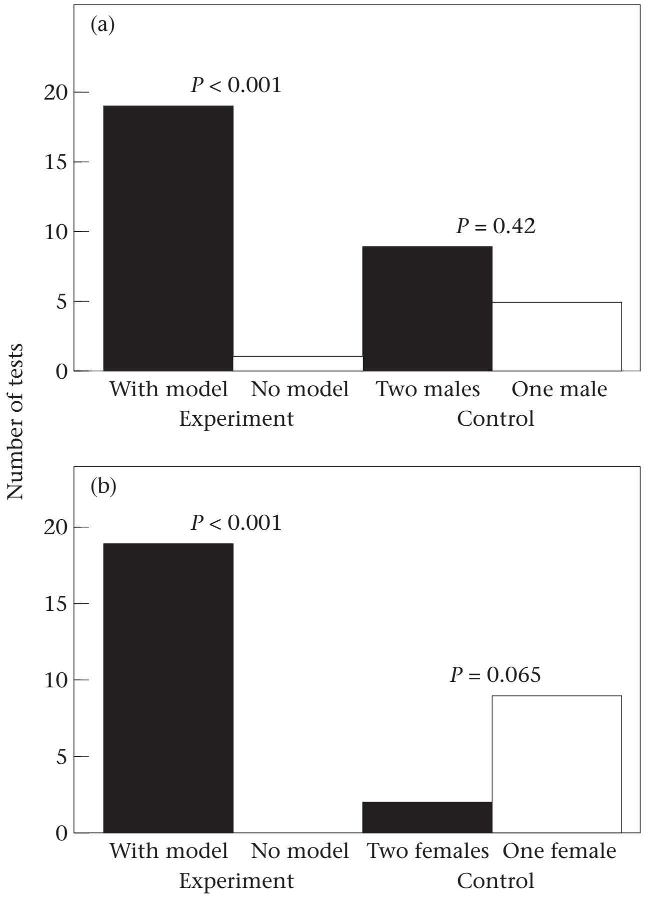

Figure 2. (a) Male mate choice tests: number of tests in which more males associated with the stimulus female next to the model male or with the stimulus female next to the jar with no fish. Male control for shoaling: number of tests in which more males associated with the stimulus male next to the other male or with the stimulus male next to the jar with no fish. (b) Female mate choice tests: number of tests in which more females associated with the stimulus male next to the model female or with the stimulus male next to the jar with no fish. Female control for shoaling: number of tests in which more females associated with the stimulus female next to the other female or with the stimulus female next to the jar with no fish.

Male Control for Shoaling

In the male control for shoaling (N=14), more males associated with the male next to another male in nine tests, and with the male next to the jar with no fish in five (binomial test: P=0.42; Fig. 2a). In this control, an average ± SD of 3.0 ± 1.8 males per test visited the stimulus males (range 1–7). On average ± SD 1.7 ± 1.3 males associated with the male next to the other male and 1.3 ± 1.0 with the male next to the empty jar (Wilcoxon signed-ranks test: T=37, N=14, P=0.30). Thus, males did not prefer to associate with two rather than one fish of the same sex. Shoaling behaviour, therefore, does not explain the preference of a male for the female next to a model male. Thus males copied the mate choice of the model male in the jar next to one with the female.

Significantly more males entered the set-up in the mate choice experiment than in the control (Mann–Whitney U test: U=42, N_1=20, N_2=14, P<0.001).

Female Mate Choice Tests

In 19 out of 20 female mate choice tests more females ($\bar{X}$ ± SD=11.0 ± 9.3) associated with the male next to the model female (binomial test: P<0.001; Fig. 2b). In one test an equal number of females visited the male next to the jar with no fish and the male next to the model female. The number of females that associated with one or the other male was on average ± SD 30.7 ± 23.9 (range 2–83). On average ± SD 20.9 ± 16.2 females associated with the male next to the model female and 9.9 ± 8.3 with the male next to the empty jar (Wilcoxon signed-ranks test: $Z=-3.83$, N=20, P<0.001).

Significantly more females than males entered the set-up in the female and male mate choice experiments (Mann–Whitney U test: U=113.5, N_1=N_2=20, P=0.02).

Female Control for Shoaling

In the female control for shoaling (N=14), on average ± SD 18.4 ± 24.5 females (range 1–96) visited the stimulus females in the jars. Females did not prefer to associate with two rather than one stimulus female. In nine tests more females visited the female adjacent to the jar with no fish, while in two tests more females associated with the female adjacent to a jar with another female; in three other cases an equal number of females visited both stimulus females (binomial test: P=0.065; Fig. 2b). On average ± SD 8.1 ± 11.5 females associated with the female next to the other female and 10.2 ± 13.5 with the female next to the empty jar (Wilcoxon signed-ranks test: T=20.5, N=14, P=0.14). This result is almost the opposite of what one would expect if shoaling behaviour were responsible for the female preference we found in the mate choice tests. We therefore conclude that females preferred to associate with a male that was next to a model female; thus, they copied the 'mate choice' of the model female.

In the female control for shoaling significantly fewer females visited the set-up than in the experiment for female mate choice (Mann–Whitney U-test: U=53.5, N_1=14, N_2=20, P=0.002).

DISCUSSION

To our knowledge, this is the first study to show mate choice copying in a fish in the wild, and the first situation in which mate choice copying has been shown for the same species in both the wild and the laboratory. Our results show that male and female sailfin mollies preferred to associate with a conspecific of the opposite sex adjacent to a model fish of the same sex as the focal fish. Thus, male and female sailfin mollies copied the mate choice of the model fish.

In our mate choice experiments significantly more females than males visited the set-up. This was probably because there are more females than males in the population, as is true in other populations of mollies (Snelson & Wetherington 1980).

As we discussed earlier, there has been speculation on the potential adaptive advantage to mate choice copying by females. The more popular suggestions are that copying reduces costs associated with searching for mates (Gibson & Höglund 1992; Stöhr 1998), or that younger animals acquire information from older animals (Dugatkin & Godin 1993; Nordell & Valone 1998; Stöhr 1998). Although the logic for an adaptive effect is strong, there are no data indicating that such scenarios are true.

The majority of studies on mate choice copying focus on female copying. The only exception is the study by Schlupp & Ryan (1997) that showed male sailfin mollies changed their preferences and preferred a gynogenetic, heterospecific female, *P. formosa*, when they have observed another male near that female. Males might copy because observing courtship of other males helps them to locate receptive females. Mate copying might lead to the mating frenzies in mollies in which three or four males simultaneously attempt to copulate with a female (Balsano et al. 1989; K. Witte, personal observation). In poeciliid fish there is last male sperm precedence (Rosenthal 1952; Farr & Travis 1986), so a copying male might be most likely to father the next brood.

One alternative explanation to our interpretation of mate choice copying is shoaling behaviour. Mollies and other fish species live in groups. Shoaling has many advantages for individuals, such as dilution of predation risk, predator confusion, information transfer among shoal members and the proximity of potential mates (reviewed in Godin 1997). In our two control experiments, males and females did not shoal, that is, did not prefer to associate with a fish next to another fish rather than a lone fish. In both controls, significantly fewer males and females entered the set-up than in the mate choice experiments with stimulus fish of the opposite sex. Thus, same-sex fish attracted significantly fewer focal fish than fish of the opposite sex. We conclude that in mate choice experiments the focal fish were mainly sexually attracted by the stimulus fish and thus social attraction such as shoaling cannot explain our results.

In a laboratory study, Schlupp & Ryan (1997) tested shoaling behaviour in sailfin molly females and found that a focal female preferred to associate with two rather than one conspecific female. This is in contrast to our results from the field. The studies, however, differed significantly. In the laboratory study the focal female was alone in her compartment and had no chemical contact with the stimulus females. Although females could acclimate to the test tank this was still a new environment for them. In our field study all focal and stimulus fish had visual and chemical contact. We tested all focal fish in the wild in the vicinity of other fish, such as mosquitofish and other sailfin mollies. These differences between the laboratory study and our field study might be responsible for the different results. In the standardized mate choice copying experiment in the laboratory (Schlupp et al. 1994; Witte & Ryan 1998) sailfin molly females do not shoal, that is, do not prefer the side where they have seen two females to the side with one female.

Another explanation for mate choice copying is that the subject fish prefer to associate with more active fish. In the mate choice experiments males and females associated with the stimulus fish that was adjacent to the model fish rather than the lone stimulus fish. The majority of both the male and the female stimulus fish adjacent to the model courted the model and moved up and down in the jar. The lone stimulus fish moved as well, but might have been less active than the other stimulus fish. In the controls for shoaling, we had a similar situation. The stimulus fish next to the third fish were more active than the lone stimulus fish. If focal fish prefer to associate with more active fish we would have expected a preference for the more active stimulus fish that were next to the other fish, that is, we would have found an effect in the controls for shoaling as well. However, we did not find any preferences for stimulus fish next to another fish. We therefore conclude that activity had, if at all, only a weak effect and cannot explain our clear results in the mate choice experiments.

A weakness of our experiment was that subject fish might have been sampled repeatedly. It seems unlikely, however, that those fish we tested would have moved to the next site, 20 m away, where we did the subsequent experiment. We did not remove the focal fish after testing because this would have disturbed the remaining wild fish, and free-ranging fish would thus subsequently avoid the set-up. Also, we moved the set-up to a different site after each 20-min test to help avoid repeated sampling of the same focal fish. Despite this potential weakness, we feel that our results support the hypothesis that male and female sailfin mollies copy the mate choice of other conspecifics in nature, and more generally support the notion that demonstrations of mate choice copying in the laboratory are not artefacts but that mate choice copying is biologically relevant to the mating systems of these animals.

Acknowledgments

We thank the Parks and Recreation Department of the Landa Park, New Braunfels, Texas, for permission to do the study in the Park. We also thank K. Weigel for the artwork in Fig. 1, and I Schlupp for comments on the manuscript. K.W. was supported by the DFG (Wi 1531/2) and M.J.R by NSF IBN 9630230.

References

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Balsano, J. S., Rasch, E. M. & Monaco, P. J. 1989. The evolutionary ecology of *Poecilia formosa* and its triploid associate. In: *Ecology and Evolution of Livebearing Fishes (Poeciliidae)* (Ed. by G. K. Meffe & F. F. Snelson), pp. 277–297. Englewood Cliffs, New Jersey: Prentice Hall.

Bisazza, A. & Marconato, A. 1988. Female mate choice, male-male competition and parental care in the river bullhead, *Cotus gobio*. *Animal Behaviour*, **36,** 1352–1360.

Bischoff, R. J., Gould, J. L. & Rubenstein, D. I. 1985. Tail size and female choice in the guppy (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology*, **46,** 169–175.

Brooks, R. 1996. Copying and the repeatability of mate choice. *Behavioral Ecology and Sociobiology*, **39,** 323–329.

Brooks, R. 1998. The importance of mate copying and cultural inheritance of mating preferences. *Trends in Ecology and Evolution*, **13**, 45–46.

Brooks, R. 1999. Mate choice copying in guppies: females avoid the place where they saw courtship. *Behaviour*, **136**, 411–421.

Brown, W. H. 1953. Introduced fish species of the Guadelupe River Basin. *Texas Journal of Science*, **2**, 245–251.

Clutton-Brock, T. & McComb, K. 1993. Experimental tests of copying and mate choice in fallow deer (*Dama dama*). *Behavioral Ecology*, **4**, 191–193.

Constantz, G. D. 1985. Alloparental care in the tessellated darter *Etheostoma olmstedi* (Pisces: Percidae). *Environmental Biology of Fishes*, **14**, 175–183.

Dugatkin, L. A. 1992. Sexual selection and imitation: females copy the mate choice of others. *American Naturalist*, **139**, 1384–1389.

Dugatkin, L. A. 1996a. Copying and mate choice. In: *Social Learning in Animals: the Roots of Culture* (Ed. by C. M. Heyes & B. G. Galef Jr), pp. 85–105. New York: Academic Press.

Dugatkin, L. A. 1996b. The interface between culturally-based preferences and genetic preferences: female mate choice in *Poecilia reticulata*. *Proceedings of the National Academy of Sciences U.S.A.*, **93**, 2770–2773.

Dugatkin, L. A. 1998a. Genes, copying, and female mate choice; shifting thresholds. *Behavioral Ecology*, **9**, 323–327.

Dugatkin, L. A. 1998b. A comment on Lafleur et al.'s re-evaluation of mate-choice copying in guppies. *Animal Behaviour*, **56**, 513–514.

Dugatkin, L. A. & Godin, J.-G. J. 1992. Reversal of female mate choice by copying in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London, Series B*, **249**, 179–184.

Dugatkin, L. A. & Godin, J.-G. J. 1993. Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. *Behavioral Ecology*, **4**, 289–292.

Farr, J. A. & Travis, J. T. 1986. Fertility advertisement by female sailfin mollies, *Poecilia latipinna* (Pisces: *Poeciliidae*). *Copeia*, **1986**, 467–472.

Galef, B. G. Jr & White, D. J. 1998. Mate-choice copying in the Japanese quail *Corturnix coturnix japonica*. *Animal Behaviour*, **55**, 545–552.

Gibson, R. M. & Höglund, J. 1992. Copying and sexual selection. *Trends in Ecology and Evolution*, **7**, 229–232.

Gibson, R. M., Bradbury, J. W. & Vehrencamp, S. L. 1991. Mate choice in lekking sage grouse revisted: the roles of vocal display, female site fidelity, and copying. *Behavioral Ecology*, **2**, 165–180.

Godin, J.-G. J. 1997. Evading predators. In: *Behavioural Ecology of Teleost Fishes* (Ed. by J.-G. J. Godin), pp. 214–220. Oxford: Oxford University Press.

Goldschmidt, T., Bakker, T. M. C. & Feuth-De Bruijn, E. 1993. Selective copying in mate choice of female sticklebacks. *Animal Behaviour*, **45**, 541–547.

Grant, J. W. A. & Green, L. D. 1996. Mate copying versus preference for actively courting males by female Japanese medaka (*Oryzias latipes*). *Behavioral Ecology*, **7**, 165–167.

Höglund, J., Alatalo, R. V., Gibson, R. M. & Lundberg, A. 1995. Mate-choice copying in the black grouse. *Animal Behaviour*, **49**, 1627–1633.

Howard, R. D., Martens, R. S., Innis, S. A., Drenvich, J. M. & Hale, J. 1998. Mate choice and mate competition influence male body size in Japanese medaka. *Animal Behaviour*, **55**, 1151–1163.

Jamieson, I. G. 1995. Do female fish prefer to spawn in nests with eggs for reasons of mate choice copying or egg survival? *American Naturalist*, **145**, 824–832.

Kirkpatrick, M. & Dugatkin, L. A. 1994. Sexual selection and the evolutionary effects of copying mate choice. *Behavioral Ecology and Sociobiology*, **34**, 443–449.

Kirkpatrick, M. & Ryan, M. J. 1991. The paradox of the lek and the evolution of mating preferences. *Nature*, **350**, 33–38.

Kodric-Brown, A. 1993. Female choice of multiple male criteria in guppies: interacting effects of dominance, coloration and courtship. *Behavioral Ecology and Sociobiology*, **32**, 415–420.

Kraak, S. B. M. 1996. 'Copying mate choice': which phenomena deserve this term? *Behavioural Processes*, **36**, 99–102.

Lafleur, D. L., Lozano, G. A. & Sclafani, M. 1997. Female mate choice copying in guppies, *Poecilia reticulata*: a re-evaluation. *Animal Behaviour*, **54**, 579–586.

Losey, G. S. Jr, Stanton, F. G., Telecky, T. M., Tyler, W. A. III & Zoology 691 Graduate Seminar Class 1986. Copying others, an evolutionary stable strategy for mate choice: a model. *American Naturalist*, **128**, 653–664.

McComb, K. & Clutton-Brock, T. H. 1994. Is mate choice copying or aggregation responsible for skewed distributions of females on leks? *Proceedings of the Royal Society of London, Series B*, **255**, 13–19.

Nordell, S. E. & Valone, T. J. 1998. Mate choice copying as public information. *Ecology Letters*, **1**, 74–76.

Pruett-Jones, S. G. 1992. Independent versus non-independent mate choice: do females copy each other? *American Naturalist*, **140**, 1000–1009.

Ridley, M. & Rechten, C. 1981. Female sticklebacks prefer to spawn with males whose nests contain eggs. *Behaviour*, **16**, 152–161.

Rohwer, S. 1978. Parental cannibalism of offspring and egg raiding as a courtship strategy. *American Naturalist*, **112**, 429–440.

Rosenthal, H. L. 1952. Observations on reproduction of the poeciliid *Lebistes reticulatus* (Peters). *Biological Bulletin*, **102**, 30–38.

Schlupp, I. & Ryan, M. J. 1996. Mixed-species shoals and the maintenance of a sexual-asexual mating system in mollies. *Animal Behaviour*, **52**, 885–890.

Schlupp, I. & Ryan, M. J. 1997. Male sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males. *Behavioral Ecology*, **8**, 104–107.

Schlupp, I., Marler, C. & Ryan, M. J. 1994. Benefit to male sailfin mollies of mating with heterospecific females. *Science*, **263**, 373–374.

Servedio, M. R. & Kirkpatrick, M. 1996. The evolution of mate choice copying by indirect selection. *American Naturalist*, **148**, 848–867.

Shuster, S. M. & Wade, M. 1991. Female copying and sexual selection in a marine isopod crustacean, *Paracerceis sculpta*. *Animal Behaviour*, **41**, 1071–1078.

Snelson, F. F. & Wetherington, J. D. 1980. Sex ratio in the sailfin molly, *Poecilia latipinna*. *Evolution*, **34**, 308–319.

Stöhr, S. 1998. Evolution of mate-choice copying: a dynamic model. *Animal Behaviour*, **55**, 893–903.

Unger, L. M. & Sargent, R. C. 1988. Alloparental care in the fathead minnows, *Pimephales promelas*: females prefer males with eggs. *Behavioral Ecology and Sociobiology*, **23**, 27–32.

Wade, M. J. & Pruett-Jones, S. G. 1990. Female copying increases the variance in male mating success. *Proceedings of the National Academy of Sciences U.S.A.*, **87**, 5749–5753.

Westneat, D. F., Walters, A., McCarthy, T. M., Hatch, M. I. & Hein, W. K. 2000. Alternative mechanisms of nonindependent mate choice. *Animal Behaviour*, **59**, 467–476.

White, D. J. & Galef, B. G. Jr. 1999. Mate copying and conspecific cueing in Japanese quail, *Courunix coturnix japonica*. *Animal Behaviour*, **57**, 465–473.

White, D. J. & Galef, B. G. Jr. 2000. 'Culture' in quail: social influences on mate choices of female *Coturnix coturnix japonica*. *Animal Behaviour*, **59**, 975–979.

Witte, K. & Ryan, M. J. 1998. Male body length influences mate-choice copying in the sailfin molly *Poecilia latipinna*. *Behavioral Ecolology*, **9**, 534–539.