

Mate-choice copying when both sexes face high costs of reproduction

Joachim G. Frommen · Anna K. Rahn · Stefanie H. Schroth ·
Nadine Waltschyk · Theo C. M. Bakker

Received: 12 June 2007 / Accepted: 3 January 2008 / Published online: 20 January 2008
© Springer Science+Business Media B.V. 2008

Abstract Mate choice is linked to costs such as time and energy effort or a higher risk of predation. Furthermore, reproduction with a partner of lower than average quality will reduce an individual's fitness. Copying the mate choice of others is assumed to reduce such costs. Most studies dealing with mate-choice copying focused on females, as they are usually expected to invest more into reproduction. However, in species where males provide brood care both sexes face high costs. Little is known about mate-choice copying in such mating systems. Male three-spined sticklebacks build nests and care for the offspring alone, facing a high-reproductive investment. Thus, one would expect that both males and females copy the mate choice of others. We gave male and female sticklebacks the opportunity to court either a partner that was visibly courted by another individual or a partner that was not visibly courted. Both spent significantly more time courting next to conspecifics after another individual has visibly courted them. Habituation effects, territorial defence or shoaling behaviour as alternative explanations were excluded by control experiments. The adaptive significance of mate-choice copying is not well understood. The results of this study indicate that in sticklebacks both sexes may reduce the costs of mate choice by copying the preferences of others.

Keywords Public information · Mutual mate choice · Sexual selection · Fish · Stickleback · *Gasterosteus aculeatus*

Introduction

Choosing a mating partner is known to be costly (Pomiankowski 1987; Gibson and Langen 1996). Such costs are for example time and energy spent searching for a mating partner (Milinski and Bakker 1992; Wong and Jennions 2003) or an increased risk of being

J. G. Frommen (✉) · A. K. Rahn · S. H. Schroth · N. Waltschyk · T. C. M. Bakker
Institute for Evolutionary Biology and Ecology, University of Bonn, 53121 Bonn, Germany
e-mail: jfrommen@evolution.uni-bonn.de

predated due to conspicuous courtship behaviour (Pomiankowski 1987; Magnhagen 1991). Furthermore, an individual choosing a mating partner of lower than average genetic quality will produce lower quality offspring, consequently facing costs due to a reduced fitness. Such expenses can be minimized using public information, that is cues produced by the performance of others (Danchin et al. 2004). While it is generally assumed that female preferences (Bakker 1993; Bakker and Pomiankowski 1995) as well as preferred traits show genetic variation (Kirkpatrick and Ryan 1991; Pomiankowski and Møller 1995; Bakker 1999; Iwasa and Pomiankowski 1999), influences of the social environment are also evident (e.g. Gibson and Höglund 1992; Jennions and Petrie 1997). Using mating interactions and decisions of others as cue influencing own mate-choice decisions (mate-choice copying) (Dugatkin 1992; Pruett-Jones 1992; Nordell and Valone 1998) is an example of using public information (Nordell and Valone 1998). Mate-choice copying is defined as the higher probability of an individual choosing a particular mate as a result of observing another individual choosing him or her (Gibson et al. 1991). Since the early 1990s mate-choice copying has become a field of increasing interest (Gibson and Höglund 1992; Galef and White 2000; Witte 2006). Although it has been demonstrated in several species of birds (e.g. Höglund et al. 1990, 1995; Galef and White 1998; Swaddle et al. 2005), mammals (McComb and Clutton-Brock 1994) and fish (Amundsen 2003; Witte 2006), the adaptive significance of mate-choice copying is still not completely understood (see Witte 2006 for a review of explanations). In fish, female mate-choice copying was demonstrated for example in sailfin mollies (*Poecilia latipinna*) (e.g. Witte and Massmann 2003) and Japanese medaka (*Oryzias latipes*) (Grant and Green 1996). In guppies (*Poecilia reticulata*), females prefer to copy the choice of larger conspecifics (Dugatkin and Godin 1993; Amlacher and Dugatkin 2005). As size in guppies correlates with age, the authors argue that the females copy the choice of older and consequently more experienced members of the same sex. Most studies on mate-choice copying focus on females as they are usually expected to invest more into reproduction and to be consequently the choosing sex (Trivers 1972). However, in species where males provide brood care both sexes face high costs and should therefore be choosy (Kokko and Johnstone 2002). Sailfin mollies are the only example for mate-choice copying in both males and females thus far (Schlupp and Ryan 1997; Witte and Ryan 1998, 2002; reviewed in Witte 2006). In this species, mate-choice copying can even lead to preferences for hetero-specific females (Schlupp and Ryan 1997). However, sailfin mollies are live-bearing fish where males do not provide any brood care. Thus, besides the danger of being predated during courtship, little is known about reproductive costs of males in this species. Broad-nosed pipefish (*Syngnathus typhle*) are another example for male mate-choice copying (Widemo 2006). In pipefish, males care for the eggs and are often the limiting factor in sexual selection (Berglund et al. 1989). Accordingly, males are often the choosier sex (Sandvik et al. 2000), while females are competing intensely for mating partners (Rosenqvist 1990). Widemo (2006) found that only male broad-nosed pipefish copy the mate choice of others and concluded that generally in fishes the sex facing higher costs should be more likely to show copying behaviour. However, data are lacking about mate-choice copying in species where both sexes face high reproductive costs.

During the mating season, reproductive three-spined stickleback (*Gasterosteus aculeatus*) males show a conspicuous nuptial coloration and defend a territory in which they build a nest. In nature, the distance between nests is often <1 m, so that males are able to observe each other (Kynard 1978; Goldschmidt et al. 1992; Mori 1995). When the nest is finished, males entice gravid females by performing a typical zig-zag courtship dance (Wootton 1976). After spawning, males do not court other females for up to 1 h

(Sevenster-Bol 1962). Males spend time and energy in building the nest, defending the territory, mainly against rival males (e.g. Bakker 1986; Sparkes et al. 2007), and caring for the brood (Wootton et al. 1995; Bakker et al. 2006). Consequently, males lose body mass during the breeding cycle (Sargent 1985; Smith and Wootton 1999), and often die afterwards (Allen and Wootton 1982).

Courtship is dangerous for males because their conspicuous coloration and behaviour attract predators (Candolin 1997). Candolin (1998) for example showed that in the presence of a predator fewer males bred, and males developed less nuptial coloration than in the absence of predators. Furthermore, courtship may attract rival males that compete for the courted female (Dziewieczynski and Rowland 2004), or steal fertilizations (Largiadèr et al. 2001). Males seldom collect more than 5–10 clutches (Wootton 1976; Smith and Whoriskey 1988; Bakker et al. 2006) per breeding cycle, mainly because space in nests is limited and high numbers of eggs lead to an increase of egg mortality (Kraak and Bakker 1998; Bakker et al. 2006). As males rarely complete more than 1–2 breeding cycles in their life (Wootton 1976; Bakker and Mundwiler 1994), most males have a relatively small total number of mating partners. Thus, choosing a female of lower than average genetic quality will lead to a severe loss of a male's fitness.

Females invest energy in producing eggs (Wootton 1973; Wootton and Evans 1976) and searching mates (Milinski and Bakker 1992), and suffer a higher risk of predation because of their reduced agility (Rodewald and Foster 1998). During courtship, females show a typical head-up position, presenting their silvery shining belly to the male (Wootton 1976), which may also increase the conspicuousness to predators (Kraak and Bakker 1998). Furthermore, females spawn all produced eggs as an entire clutch in a single nest (Wootton 1976). It takes several days to produce a new clutch, even under optimal food conditions (Fletcher and Wootton 1995), leading to a limited number of mating partners in females, too. Wootton et al. (1995) summarize averages of 3.4–4.5 spawnings per female during the breeding season. Thus, choosing a male of low quality will result in a severe loss of fitness for the female. Consequently, both males and females are choosy (Bakker and Rowland 1995; Kraak and Bakker 1998).

Mate-choice copying may reduce the costs of mate choice in several ways. For example both sexes may find mating partners faster due to copying the behaviour of others and thus reduce the risk of being predated (Magnhagen 1991; Candolin 1998), and minimize energy expenditure while searching for mates (Milinski and Bakker 1992). Furthermore, they may reduce the risk of erroneously choosing a mating partner of lower than average genetic quality. During courtship males and females often court each other without spawning (Wootton 1976; Kynard 1978; Kraak et al. 1999), while being observed by other females and males. Males are known to court females that are already courted by another male (Dziewieczynski and Rowland 2004). Thus, the possibility for the evolution of mate-choice copying is given for both sexes under natural conditions. However, until now studies have focused only on female sticklebacks with ambiguous results. Patriquin-Meldrum and Godin (1998) allowed females to choose between two males—either accompanied by another female or not—and found no convincing evidence of female mate-choice copying. In contrast, Goldschmidt et al. (1993) found that females preferred spawning in nests already containing eggs. However, this might not be sufficient evidence for copying behaviour (Kraak and Groothuis 1994), as males are known to cannibalize clutches containing few eggs (van den Assem 1967). Thus, spawning in nests that already contain eggs may be an assurance against egg cannibalism (Kraak 1996).

In this study we tested whether a less preferred male or female could be made more appealing by the presence of an individual of the opposite sex. This mate-choice copying

behaviour was examined using a set-up similar to that used by Patriquin-Meldrum and Godin (1998). As aggressive behaviour towards rival males (Bakker 1986; Rowland 1988) as well as habituation effects (Bakker and Rowland 1995) influence courtship of sticklebacks, control experiments were conducted concerning these points. The control experiments on habituation additionally served as a disruption control (see Applebaum and Cruz 2000 for details). Furthermore, because female sticklebacks form shoals during their whole life (Wootton 1976), and laboratory studies suggested that sticklebacks prefer the larger of two shoals (Krause et al. 1998), a control for shoaling behaviour was conducted.

Materials and methods

Experimental subjects

Experiments were carried out between April 19th and May 16th 2006. Sticklebacks were caught in the pond 'Stadtweiher' near Euskirchen, Germany (50°38' N/6°47' E) (Modarressie et al. 2006) on March 10th 2006 and brought to the lab. Here, females and males were kept together in large outdoor tanks (750 l) with air ventilation and a constant supply of tap-water at a flow rate of 3 l min⁻¹. One week before starting the experiments, groups of ~40 fish were transferred to smaller aquaria (160 l), which were equipped with sand, air ventilation and two internal filters (Hobby Aquaristic). Here, fish were kept under summer conditions (L : D 16:8, 17 ± 1°C) and fed with *Chironomus* larvae ad libitum. Males that developed breeding coloration were isolated into small aquaria (10 l), which contained 2 g of java moss *Vesicularia dubyana* and a Petri-dish filled with sand to build a nest in. Later, dishes containing nests could be transferred to the test aquarium without any problems of acceptance (Frommen and Bakker 2006; Rick et al. 2006). Male aquaria were separated by opaque plastic partitions. To stimulate nest building gravid females were presented to the males daily.

Experimental design

The test aquarium, measuring 100 cm × 40 cm × 40 cm (water depth 15 cm) was divided by sheets of transparent Plexiglas glued to the tank walls into five compartments (Patriquin-Meldrum and Godin 1998) (Fig. 1). Thus, visual contact was possible while olfactory communication between the compartments was excluded. This was done to reduce confounding olfactory effects to a minimum (e.g. Milinski and Bakker 1990; Rick et al. 2006). On the left and right end of the aquarium, we separated two stimulus sections that were again divided into two equal-sized compartments measuring 20 cm × 20 cm each. The central compartment measured 60 cm × 40 cm. Choice zones of 10 cm were marked on the bottom of the tank next to each stimulus compartment. In front of the Plexiglas dividers opaque plastic partitions were installed that could be lifted by nylon strings. These opaque partitions prevented visual contact among the fish. The set-up was illuminated using a fluorescent tube (30 W) placed 120 cm above the bottom of the aquarium. To exclude confounding influences of nuptial coloration on the females' mate choice, light tubes were wrapped with a red filter (Rosco, Supergel 73) during the female experiment. Excluding red light did not reduce male or female courtship intensity in previous studies (e.g. Milinski and Bakker 1990; Frommen and Bakker 2006). To prevent interactions with the environment, side and back walls of the aquarium were covered with

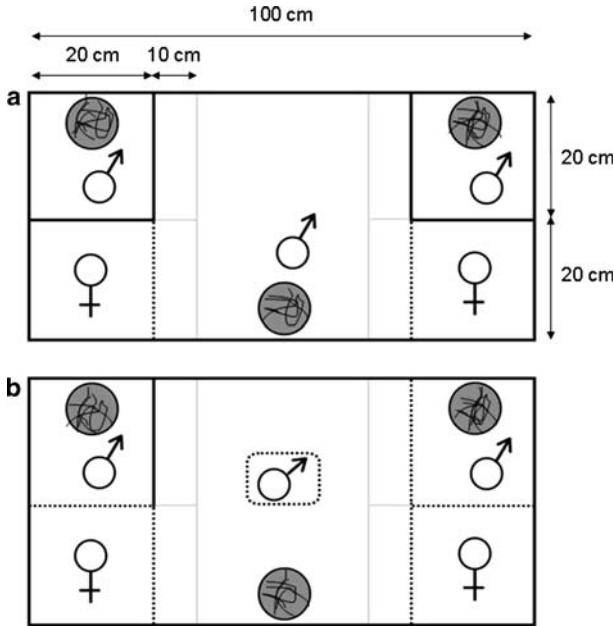


Fig. 1 Set-up for the male experiment. **(a)** The test aquarium (100 cm × 40 cm × 40 cm) was divided into five compartments, each separated from other compartments by both transparent (*dotted lines*) and opaque (*black lines*) dividers. Thin *grey lines* indicate association zones that were drawn on the bottom of the aquarium. The test fish was placed in the central compartment. Gravid females were placed in the front compartments, stimulus males in the rear. All male fish were placed in the respective compartments with their own nest (indicated by *dark circles*). **(b)** During the observation period, the focal fish was enclosed in a transparent Plexiglas cylinder. The female that was less preferred during the first measurement was allowed to visibly court with a rival male, while the male courting the more preferred female was not visible. Thereafter, male mating preferences were again measured as in **(a)**

opaque plastic sheets. Additionally, a black curtain surrounded the set-up. Fish movements were observed through a small spy-hole cut into the curtain.

Male experiments

In each trial a focal male and its nest was placed in the central compartment (Fig. 1) and one gravid female was placed in each front-side stimulus compartment. Females were size-matched to the nearest 2 mm. Stimulus males and their nests were placed in the rear-side stimulus compartments (Fig. 1).

An experiment started with an acclimatization period of 60 min (Frommen and Bakker 2006). After that, the opaque partitions between the test male and the two females were lifted (Fig. 1a). As soon as the test fish visited both choice zones once, the time the test male spent in each choice zone was measured for 15 min (Wagner 1998). Following this first measurement of males’ preferences, the opaque partitions were dropped again and the focal fish was caught and placed in a transparent plastic enclosure (10 cm × 7 cm, height 16.5 cm) in the middle of the central compartment. Thereafter, the opaque partitions between females and stimulus males were lifted. As soon as all females and stimulus males started courting, the opaque partitions between the central compartment and female

compartments were lifted again. If stimulus fish did not start courting within 30 min, the experiments were stopped and repeated the next day using new combinations of fish. When all fish courted, the opaque partition between the central compartment and the stimulus-male compartment on the side of the female less preferred (that is, that particular choice zone in which the male spent <50% of the total time that he spent in both choice zones) during the first measurement was lifted, too (Fig. 1b). Thus, the test male was allowed to see both females, but only one was visibly accompanied by a courting male (Witte and Ryan 1998). After 10 min, all partitions were dropped again and the test male was released from the enclosure. The opaque partitions between the test male and females were removed, and the second measurement started as described above. The person quantifying the choice behaviour of the test fish was naïve according to the side at which the female had been visibly courted by the stimulus male.

To exclude habituation effects, a control experiment was conducted as described above, but here the stimulus-male compartments did not include any fish. A second experiment was conducted to control for effects of territorial defence against the stimulus male. Here, subadult individuals not showing any reproductive behaviour substituted the gravid females.

Female experiments

Female mate-choice experiments were carried out analogous to the male experiments, but here gravid females were used as test and stimulus fish. The main compartment contained a gravid female, while the front-side stimulus compartments each contained a male with his nest and the rear-side stimulus compartments a gravid female each. As described above, experiments controlling for habituation effects were conducted excluding gravid stimulus females. Additionally, experiments controlling for a possible influence of female shoaling behaviour on the time spent on the side of the male that was visibly courted by another female were conducted analogous to the male territoriality-control experiment. Here, non-reproductive subadults substituted reproductive males. All test fish were used only once. However, some stimulus females and males were used in more than one trial, but never on the same day or in the same combination.

Data analysis

In three male and four female copying experiments the test fish did not visit both choice zones within 30 min or one of the stimulus fish failed to show courting behaviour during the first or second measurement. Furthermore, in 11 control trials the test fish spent no time at all in one choice zone. These experiments were excluded from analysis. To compare preferences within measurements, the time spent in the choice zones was used. In order to be able to compare preferences between the first and second measurement, in which the total time each individual spent in both choice zones was different, the relative time spent in the choice zone next to the less preferred individual was calculated ($\text{rel. time} = \text{time}_{\text{less preferred}} / (\text{time}_{\text{less preferred}} + \text{time}_{\text{preferred}})$). Parametric statistics were used for normally distributed data (according to Kolmogorov-Smirnov test with Lilliefors-correction). Data that deviated significantly from a normal distribution were transformed (log or square-root) to meet normal distribution. Given *p*-values are two-tailed throughout. All tests were performed using SPSS 12.0.

Results

Male mate-choice

Copying experiment

Time males spent in the choice zones differed significantly between the less and more preferred female before the presentation of a rival male (time in sec. \pm s. d., less preferred: $146.83 \text{ s} \pm 102.47$, more preferred: $325.33 \text{ s} \pm 153.53$, $t = -3.49$, $n = 12$, $p = 0.005$). This preference got lost after the male saw the less preferred female being courted by another male ($221.17 \text{ s} \pm 159.9$ and $208.5 \text{ s} \pm 165.18$, respectively; paired t -test: $t = 0.129$, $n = 12$, $p = 0.9$). Male test fish significantly increased the relative time staying in the choice zone next to the female that had been visibly courted by the stimulus male (mean relative time in % \pm s. d. before and after presentation of the rival male: $30.6\% \pm 14.8$ and $50.5\% \pm 22.6$, respectively; paired t -test: $t = -2.48$, $n = 12$, $p = 0.031$, Fig. 2). Total time spent in both choice zones combined in the first and second measurement (first: $472.17 \text{ s} \pm 91.71$, second: $429.68 \text{ s} \pm 214.64$) did not differ significantly (paired t -test: $t = 1.062$, $n = 12$, $p = 0.311$).

Control experiments

The habituation-control experiment, in which no rival courting male was shown, revealed no significant changes in the test fish's preferences for the less preferred female between the first and second measurement ($29.85\% \pm 13.01$ and $37.92\% \pm 25.16$, respectively; paired t -test: $t = -1.156$, $n = 13$, $p = 0.27$). Furthermore, no significant difference in association time before and after seeing the rival male in the aggression-control experiment, in which the females were replaced by subadult individuals, was found

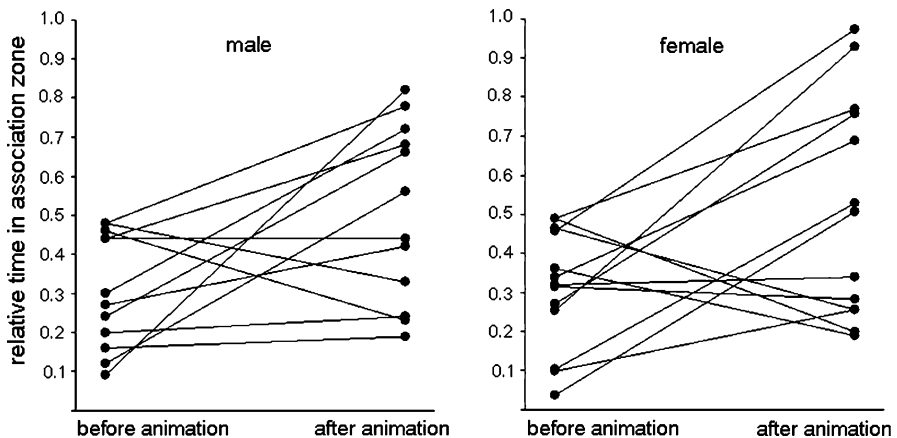


Fig. 2 Male and female preferences before and after animation. Relative time during the first and second mate-choice measurements each test fish (left: males, right: females) courted the fish that was visibly courted by a rival in the second measurement. During the second measurement both focal males and females spent significantly more time next to the fish that had been visibly courted by a rival than during the first measurement

(31.71% \pm 16.25 and 31.0% \pm 19.1, respectively; paired *t*-test: $t = 0.123$, $n = 14$, $p = 0.904$).

Female mate-choice

Copying experiment

During the first measurement, there was a significant preference of the test female for one of the two males (less preferred: 110.38 s \pm 96.34, preferred: 271.23 s \pm 202.83, paired *t*-test: $t = 3.333$, $n = 13$, $p = 0.006$). This difference disappeared after seeing a rival female courting the least-preferred male (184.85 s \pm 102.33 and 220.0 s \pm 182.71, respectively; paired *t*-test: $t = 0.639$, $n = 13$, $p = 0.535$). Females significantly increased the relative time staying in the choice zone next to the male that had been visibly courted by a rival female (30.69% \pm 15.26 and 51.38% \pm 28.30, respectively; paired *t*-test: $t = -2.37$, $n = 13$, $p = 0.035$, Fig. 2). Total time spent in both choice zones combined in the first and second measurement (first: 381.62 s \pm 253.30, second: 404.85 s \pm 220.0) did not differ significantly (paired *t*-test: $t = 1.25$, $n = 12$, $p = 0.235$).

Control experiments

The habituation-control experiment, in which no rival courting female was shown, revealed no significant difference in association time before and after animation (36.71% \pm 11.95 and 56.71% \pm 33.6, respectively; paired *t*-test: $t = -1.409$, $n = 7$, $p = 0.208$). The shoaling-control experiment, in which the courting males were replaced by subadult individuals, also showed no significant difference in association time with the less preferred subadult before and after it was shown with a receptive female (28.45% \pm 17.49 and 45.73% \pm 26.92, respectively; paired *t*-test: $t = -1.521$, $n = 11$, $p = 0.159$).

Discussion

The results of this study suggest that in three-spined sticklebacks both sexes copy the mate choice of others. In doing so they may reduce costs of reproduction, like time and energy invested in search for mating partners (Milinski and Bakker 1992) or the risk of being predated (Gibson and Langen 1996). Additionally, copying the mate choice of another fish could reduce the risk of choosing a mate of low quality (Dugatkin 2005). Alternative interpretations of our results such as aggression, habituation, shoaling, or disruption were excluded by control experiments.

Male mate-choice copying

The male copying experiment showed that the visible presence of a courting rival near a female significantly increased the male's interest in that female, indicating that males copy the mate choice of other males. An alternative explanation would be that males searched

for the rival which they had seen courting the female before, instead of copying its mate choice. To exclude this territoriality effect, in the aggression-control experiments non-reproductive subadults were used instead of gravid females. If the results of the copying experiment could be explained by the males' search for the rival, one would also expect a significant difference here. However, male sticklebacks did not significantly prefer the side where they had seen the rival over the side where no rival had been visible. A second alternative explanation would be that the male lost interest in the preferred female because she could not be reached (Bakker and Rowland 1995), and therefore changed his choice in the second part of the experiments. However, the habituation-control experiment, in which no rival male was presented, did not reveal any significant influence of time on males' mate choice.

Female mate-choice copying

The female copying experiment also showed a significant influence of the presence of a rival female on the test fish's mate choice. Again, gravid females courted the non-preferred male significantly longer after another gravid female had visibly courted him. Habituation or shoaling had no significant effects on this result, although sample sizes were rather small due to the exclusion of experiments in which the test fish did not spend time in both choice zones. However, females in the copying experiment showed courtship behaviour for most of the time, thus making it quite unlikely that the results can be explained by shoaling behaviour. Females in our experiments did not know whether the male's nests contained eggs or not. Reducing the risk of egg cannibalism can be excluded as an explanation of the results. In concordance with the results of Goldschmidt et al. (1993), it can thus be concluded that mate-choice copying influences preferences of female sticklebacks. At first sight this result seems to contradict earlier findings of Patriquin-Meldrum and Godin (1998) who found no significant ($p > 0.08$) evidence for female mate-choice copying in sticklebacks. However, the authors only compared the time females spent near a male that had been observed being courted by another female with the time the female spent near a male without a second female. This equals the second measurement of our experiment and is thus in concordance with our findings. Patriquin-Meldrum and Godin (1998) did not measure the changes in time females spent courting before and after they were allowed to view a male courted by a second female. Thus, they were not able to tell whether mate-choice copying changes the preference for a formerly unfavoured male.

In conclusion, this study shows to our knowledge for the first time that in a species with mutual mate choice and high reproductive costs, both sexes copy the mate choice of others. Reducing reproductive costs may be one reason why mate-choice copying evolved. Mate-choice copying might thus be more widespread among species in which both sexes are choosy than documented thus far.

Acknowledgements We would like to thank Ricarda Modarressie, Timo Thünken, Ingolf Rick and Julia Schwarzer for discussion. We thank Ricarda Modarressie for catching and Julia Strelau for caring for the sticklebacks and Peter Herold for help in building the set-up. Marion Mehlis assisted in conducting the experiments. Thomas Schaper and Jürgen Wittler gave the permission to catch sticklebacks at the field site. JGF is grateful to Klaus Peter Sauer for financial support. This study adhered to the Association for the Study of Animal Behaviour/Animal Behaviour Society Guidelines for the Use of Animals in Research. All experiments complied with the current laws of Germany.

References

- Allen JRM, Wootton RJ (1982) Age, growth and rate of food consumption in an upland population of the three-spined stickleback, *Gasterosteus aculeatus* L. *J Fish Biol* 20:95–105
- Amlacher J, Dugatkin LA (2005) Preference for older over younger models during mate choice copying in young guppies. *Ethol Ecol Evol* 17:161–169
- Amundsen T (2003) Fishes as models in studies of sexual selection and parental care. *J Fish Biol* 63(Suppl. A):17–52
- Applebaum SL, Cruz A (2000) The role of mate-choice copying and disruption effects in mate preference determination of *Limia perugiae* (Cyprinodontiformes, Poeciliidae). *Ethology* 106:933–944
- Bakker TCM (1986) Aggressiveness in sticklebacks (*Gasterosteus aculeatus* L.)—a behaviour-genetic study. *Behaviour* 98:1–144
- Bakker TCM (1993) Positive genetic correlation between female preference and preferred male ornament in sticklebacks. *Nature* 363:255–257
- Bakker TCM (1999) The study of intersexual selection using quantitative genetics. *Behaviour* 136:1237–1266
- Bakker TCM, Mundwiler B (1994) Female mate choice and male red coloration in a natural three-spined stickleback (*Gasterosteus aculeatus*) population. *Behav Ecol* 5:74–80
- Bakker TCM, Pomiankowski A (1995) The genetic basis of female mate preferences. *J Evol Biol* 8:129–171
- Bakker TCM, Rowland WJ (1995) Male mating preference in sticklebacks: effects of repeated testing and own attractiveness. *Behaviour* 132:935–949
- Bakker TCM, Mazzi D, Kraak SBM (2006) Broods of attractive three-spined stickleback males require greater paternal care. *J Fish Biol* 69:1164–1177
- Berglund A, Rosenqvist G, Svensson I (1989) Reproductive success of females limited by males in two pipefish species. *Am Nat* 113:506–516
- Candolin U (1997) Predation risk affects courtship and attractiveness of competing threespine stickleback males. *Behav Ecol Sociobiol* 41:81–87
- Candolin U (1998) Reproduction under predation risk and the trade-off between current and future reproduction in the threespine stickleback. *Proc R Soc Lond B* 265:1171–1175
- Danchin E, Giraldeau LA, Valone TJ, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. *Science* 305:487–491
- Dugatkin LA (1992) Sexual selection and imitation—females copy the mate choice of others. *Am Nat* 139:1384–1389
- Dugatkin LA (2005) Mistakes and the evolution of copying. *Ethol Ecol Evol* 17:327–333
- Dugatkin LA, Godin JGJ (1993) Female mate copying in the guppy (*Poecilia reticulata*)—age dependent effects. *Behav Ecol* 4:289–292
- Dzieweczynski TL, Rowland WJ (2004) Behind closed doors: use of visual cover by courting male three-spined stickleback, *Gasterosteus aculeatus*. *Anim Behav* 68:465–471
- Fletcher DA, Wootton RJ (1995) A hierarchical response to differences in ration size in the reproductive performance of female three-spined sticklebacks. *J Fish Biol* 46:657–668
- Frommen JG, Bakker TCM (2006) Inbreeding avoidance through non-random mating in sticklebacks. *Biol Lett* 2:232–235
- Galef BG, White DJ (1998) Mate-choice copying in Japanese quail, *Coturnix coturnix japonica*. *Anim Behav* 55:545–552
- Galef BG, White DJ (2000) Evidence of social effects on mate choice in vertebrates. *Behav Process* 51:167–175
- Gibson RM, Höglund J (1992) Copying and sexual selection. *Trends Ecol Evol* 7:229–232
- Gibson RM, Langen TA (1996) How do animals choose their mates? *Trends Ecol Evol* 11:468–470
- 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
- Goldschmidt T, Foster SA, Sevenster P (1992) Inter-nest distance and sneaking in the three-spined stickleback. *Anim Behav* 44:793–795
- Goldschmidt T, Bakker TCM, Feuth-de Bruijn E (1993) Selective copying in mate choice of female sticklebacks. *Anim Behav* 45:541–547
- 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, Lundberg A (1990) Copying the mate choice of others—observations on female black grouse. *Behaviour* 114:221–231
- Höglund J, Alatalo RV, Gibson RM, Lundberg A (1995) Mate choice copying in 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
- Jennions MD, Petrie M (1997) Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev Camb Philos Soc* 72:283–327
- Kirkpatrick M, Ryan MJ (1991) The evolution of mating preferences and the paradox of the lek. *Nature* 350:33–38
- Kokko H, Johnstone RA (2002) Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philos Trans R Soc Lond B* 357:319–330
- Kraak SBM (1996) ‘Copying mate choice’: which phenomena deserve this term? *Behav Process* 36:99–102
- Kraak SBM, Groothuis TGG (1994) Female preference for nests with eggs is based on the presence of the eggs themselves. *Behaviour* 131:189–206
- Kraak SBM, Bakker TCM (1998) Mutual mate choice in sticklebacks: attractive males choose big females, which lay big eggs. *Anim Behav* 56:859–866
- Kraak SBM, Bakker TCM, Mundwiler B (1999) Sexual selection in sticklebacks in the field: correlates of reproductive, mating, and paternal success. *Behav Ecol* 10:696–706
- Krause J, Godin JGJ, Rubenstein D (1998) Group choice as a function of group size differences and assessment time in fish: the influence of species vulnerability to predation. *Ethology* 104:68–74
- Kynard BE (1978) Breeding behavior of a lacustrine population of threespine sticklebacks (*Gasterosteus aculeatus* L.). *Behaviour* 67:178–207
- Largiadèr CR, Fries V, Bakker TCM (2001) Genetic analysis of sneaking and egg-thievery in a natural population of the three-spined stickleback (*Gasterosteus aculeatus* L.). *Heredity* 86:459–468
- Magnhagen C (1991) Predation risk as a cost of reproduction. *Trends Ecol Evol* 6:183–185
- McComb K, Clutton-Brock T (1994) Is mate choice copying or aggregation responsible for skewed distributions of females on leks? *Proc R Soc Lond B* 255:13–19
- Milinski M, Bakker TCM (1990) Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature* 344:330–333
- Milinski M, Bakker TCM (1992) Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. *Proc R Soc Lond B* 250:229–233
- Modarressie R, Rick IP, Bakker TCM (2006) UV matters in shoaling decisions. *Proc R Soc Lond B* 273:849–854
- Mori S (1995) Factors associated with and fitness effects of nest-raiding in the three-spined stickleback, *Gasterosteus aculeatus*, in a natural situation. *Behaviour* 132:1011–1023
- Nordell SE, Valone TJ (1998) Mate choice copying as public information. *Ecol Lett* 1:74–76
- Patriquin-Meldrum KJ, Godin JGJ (1998) Do female three-spined sticklebacks copy the mate choice of others? *Am Nat* 151:570–577
- Pomiankowski A (1987) The costs of choice in sexual selection. *J Theor Biol* 128:195–218
- Pomiankowski A, Møller AP (1995) A resolution of the lek paradox. *Proc R Soc Lond B* 260:21–29
- Pruett-Jones S (1992) Independent versus nonindependent mate choice—do females copy each other? *Am Nat* 140:1000–1009
- Rick IP, Modarressie R, Bakker TCM (2006) UV wavelengths affect female mate choice in three-spined sticklebacks. *Anim Behav* 71:307–313
- Rodewald AD, Foster SA (1998) Effects of gravidity on habitat use and antipredator behaviour in three-spined sticklebacks. *J Fish Biol* 52:973–984
- Rosenqvist G (1990) Male mate choice and female-female competition for mates in the pipefish *Nerophis ophidion*. *Anim Behav* 39:1110–1115
- Rowland WJ (1988) Aggression versus courtship in threespine sticklebacks and the role of habituation to neighbors. *Anim Behav* 36:348–357
- Sandvik M, Rosenqvist G, Berglund A (2000) Male and female mate choice affects offspring quality in a sex-role-reversed pipefish. *Proc R Soc Lond B* 267:2151–2155
- Sargent RC (1985) Territoriality and reproductive tradeoffs in the three-spine stickleback, *Gasterosteus aculeatus*. *Behaviour* 93:217–226
- Schlupp I, Ryan MJ (1997) Male sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males. *Behav Ecol* 8:104–107
- Sevenster-Bol ACA (1962) On the causation of drive reduction after a consummatory act (in *Gasterosteus aculeatus* L.). *Arch Néerl Zool* 15:175–236
- Smith C, Wootton RJ (1999) Parental energy expenditure of the male three-spined stickleback. *J Fish Biol* 54:1132–1136
- Smith RS, Whoriskey FG (1988) Multiple clutches: female threespine sticklebacks lose the ability to recognize their own eggs. *Anim Behav* 36:1838–1839

- Sparkes TC, Rush V, Foster SA (2007) Reproductive costs, condition and carotenoid-based colour in natural populations of threespine stickleback (*Gasterosteus aculeatus*). Ecol Freshw Fish publ online: doi: [10.1111/j.1600-0633.2007.00279.x](https://doi.org/10.1111/j.1600-0633.2007.00279.x)
- Swaddle JP, Cathey MG, Correll M, Hodkinson BP (2005) Socially transmitted mate preferences in a monogamous bird: a non-genetic mechanism of sexual selection. Proc R Soc Lond B 272:1053–1058
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man: 1871–1971. Aldine, Chicago, pp 136–179
- van den Assem J (1967) Territory in the three-spined stickleback, *Gasterosteus aculeatus* L. An experimental study in intra-specific competition. Behav Suppl 16:1–164
- Wagner WE (1998) Measuring female mating preferences. Anim Behav 55:1029–1042
- Widemo MS (2006) Male but not female pipefish copy mate choice. Behav Ecol 17:255–259
- Witte K (2006) Learning and mate choice. In: Brown C, Laland K, Krause J (eds) Fish cognition and behavior. Blackwell Publishing, Oxford, pp 70–95
- 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
- Witte K, Massmann R (2003) Female sailfin mollies, *Poecilia latipinna*, remember males and copy the choice of others after one day. Anim Behav 65:1151–1159
- Wong BBM, Jennions MD (2003) Costs influence male mate choice in a freshwater fish. Proc R Soc Lond B 270:S36–S38
- Wootton RJ (1973) Fecundity of three-spined stickleback, *Gasterosteus aculeatus* (L.). J Fish Biol 5: 683–688
- Wootton RJ (1976) The biology of the sticklebacks. Academic, London
- Wootton RJ, Evans GW (1976) Cost of egg-production in three-spined stickleback (*Gasterosteus aculeatus* L.). J Fish Biol 8:385–395
- Wootton RJ, Fletcher DA, Smith C, Whoriskey FG (1995) A review of reproductive rates in sticklebacks in relation to parental expenditure and operational sex ratios. Behaviour 132:915–933