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ORIGINAL ARTICLE

Mate-choice copying in sailfin molly females: public information use from long-distance interactions

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Abstract

Animals may use public information gained by observing sexual interactions between conspecifics and use this information for their own mate choice. This strategy, called mate-choice copying, is considered to play an important role for the evolution of mate preferences. Mate-choice copying is defined as non-independent mate choice, in which a female's probability of choosing a given male increases if other females have chosen that male previously. Using the livebearing sailfin molly (*Poecilia latipinna*), we asked if increasing the distance between a model female and a male would affect copying behaviour of focal females. We tested focal females in two different treatments: (1) model female and male in close proximity and able to interact at close range and (2) model female and male positioned apart from each other and restricted from close-range interactions. We could show that focal females copied the choice of a model at short distance to the prior non-preferred male as predicted from previous experiments. Surprisingly, focal females also copied the choice of a model when positioned 40 cm apart from the male. When no model female and, hence, no public information were provided (choice consistency control), focal females were consistent in their mate choice, indicating that changes in mate preference observed in the two treatments were due to the simulated mate choice of the model female. Our results demonstrate that females gain and use public information and copy the mate choice of other females even when heterosexual conspecifics interact from a distance.

Significance statement

Animals can copy the mate choice of conspecifics by observing their sexual interactions and, hence, choose the same mate as the other individual did before. So far, mate-choice copying was investigated when the so-called model female and the male were in close proximity. Here, we investigated whether female sailfin mollies (*Poecilia latipinna*) copy the choice of a model female for a male when the model female can only interact with a male at distance. We show for the first time that even interactions of heterosexual conspecifics at distance provide public information for an observing focal female to copy the choice of the model. Our results imply an even wider information transfer in sailfin molly social networks than previously thought.

Keywords Mate-choice copying · Public information · Distance · Sailfin molly · Poeciliidae

Introduction

Animals can use public information to receive information about the environment like resources, predators, parasites, and conspecifics as competitors or mates. Public information can be acquired by observing the performance or decisions of others and used to assess the quality of resources (Nordell and Valone 1998; Danchin et al. 2004; Valone 2007). In a feeding context, a forager can for example assess the behaviour of its group mates to get information about food availability without personally sampling the whole food patch (Clark and Mangel 1986; Valone 1989; Giraldeau et al. 1994; Valone and Templeton 2002). Public information gained by observing

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interactions between other individuals or the environment is also frequently described as inadvertent socially acquired information, since the observed interactions are not deliberately directed to the observer (Dall et al. 2005). Here, the observer eavesdrops on its surrounding individuals. Therefore, the opportunity to acquire and use public information is especially high in group-living animals (Valone and Templeton 2002; Danchin et al. 2004; Dall et al. 2005; Valone 2007; Ioannou et al. 2011).

One form for the use of public information is mate-choice copying (hereafter abbreviated as MCC; Westneat et al. 2000; Witte and Nöbel 2011; Witte et al. 2015). Here, individuals observe heterosexual conspecifics during sexual interaction and choose the same individual as a mate as the so-called model (of same sex as the observer) did before (Dugatkin 1992) or an individual of the same phenotype as the chosen one (Kniel et al. 2015a). MCC is an alternative non-independent mate-choice strategy that shows that not only genetically-based mate preferences for a certain trait determine mate choice, but that mate choice can also be influenced by non-genetic factors like social learning (Nordell and Valone 1998; Danchin et al. 2011). MCC is considered to have wide implications on the evolution of phenotypic traits (Agrawal 2001; Danchin et al. 2004; Verzijden et al. 2012; Witte et al. 2015), as it could not only be shown to favour the potential spread of preferences for novel phenotypes (Kniel et al. 2015a, b) but also the avoidance of certain phenotypic traits by copying the rejection of a mate (Witte and Ueding 2003). Moreover, it has been shown that MCC can even override genetic preferences under certain conditions (Dugatkin 1996, 1998; Witte and Noltemeier 2002; Godin et al. 2005).

So far, MCC has been demonstrated in mammals: humans (Waynforth 2007; Place et al. 2010), Norway rats *Rattus norvegicus* (Galef Jr et al. 2008); birds: Japanese quail *Coturnix coturnix japonica* (Galef Jr and White 1998; White and Galef 2000); zebra finches *Taeniopygia guttata castanotis* (Kniel et al. 2015a, b, 2017); and invertebrates, fruit fly *Drosophila melanogaster* (Mery et al. 2009; Dagaeff et al. 2016). An extensive amount of work was also done in fish where MCC seems to be a widespread alternative mate-choice strategy.

Since Dugatkin (1992) first experimentally demonstrated that female guppies (*Poecilia reticulata*) copy the mate choice of conspecific females, MCC has been detected in several other species of fish: in three-spined sticklebacks *Gasterosteus aculeatus* (Frommen et al. 2009), in ocellated wrasses *Symphodus ocellatus* (Alonzo 2008), in the white belly damselfish *Amblyglyphidodon leucogaster* (Goulet and Goulet 2006), in the pipefish *Syngnathus typhle* (Widemo 2006), in Atlantic mollies *Poecilia mexicana* (Heubel et al. 2008; Bierbach et al. 2011), in sailfin mollies *Poecilia latipinna* (Witte and Ryan 1998; Witte and Noltemeier 2002; Witte and Massmann 2003; Witte and Ueding 2003), in Amazon mollies *Poecilia formosa* (Heubel et al. 2008) and in the humpbacked limia *Limia nigrofasciata* (Munger et al. 2004). MCC can be considered as a biologically meaningful strategy, since it was found to occur in the wild as well (Witte and Ryan 2002; Goulet and Goulet 2006; Alonzo 2008; Godin and Hair 2009). Further, it was demonstrated that not only females use MCC but that, despite the risk of sperm competition, also males copy the mate choice of conspecific males (Schlupp and Ryan 1997; Witte and Ryan 2002; Bierbach et al. 2011; reviewed by Plath and Bierbach 2011).

Until now, not much is known about what exact aspects of quantity and quality of public information affects MCC (Witte et al. 2015). Initial findings have shown that the quality of the model, whose choice is observed and potentially copied, seems to play an important role (age: Dugatkin and Godin 1993; Amlacher and Dugatkin 2005; species: Hill and Ryan 2006; size: Vukomanovic and Rodd 2007; phenotype: Kniel et al. 2017), as well as the quantity of public information available for the observer (number of models and duration of observation: Witte and Noltemeier 2002). It is defined that a sexual interaction between the model and the male/female has to be observed to count as MCC and not the resulting consequences, as for example, the number of eggs in a nest (Pruett-Jones 1992). But numerous previous studies in fish following an experimental approach similar to Schlupp et al. (1994) also proved that it is sufficient when sexual interactions are restricted (e.g. by a transparent partition), meaning that no actual copulation needs to be observed to trigger copying behaviour in the observer. So far, in all experiments regarding MCC, the model individual was always presented directly next to a heterosexual conspecific — a potential mate (but see also Bierbach et al. 2013 for homosexual copying behaviour and Schlupp et al. 1994 for copying of a heterospecific model). In nature, however, individuals may also interact with each other at distance. Long-distance communication might be more prominent in cases of acoustic signals (reviewed by Naguib and Haven-Wiley 2001; see Ladich 2004 for fishes) or chemical cues, e.g. pheromones for mate attraction (see Shorey 2013). Nevertheless, visual signals can also be used to communicate from a distance, as seen by the long-distance jumping display in the lekking Jackson's widowbird (*Euplectes jacksoni*) used to attract females (Andersson 1989).

Here, the question arises whether females would still copy the mate choice when two conspecifics sexually interact at distance. In our current study, we used female sailfin mollies (*P. latipinna*) to test whether females use public information in mate choice even though conspecifics are interacting at distance. In the wild, sailfin mollies form loose shoals of around 20 individuals that change quickly through time and space (Travis 1994). Therefore, longer distances between individuals can be expected. Natural sailfin molly courtship displays of males, however, involve individuals in direct or very close contact of about 1 cm (Parzefall 1969; Baird 1974). Male courtship displays typically include the following behavioural patterns: (I) approaching and (II) following of a female, (III) lateral displays (dorsal and caudal fin raised) and so-called sigmoid displays (IV) in front of or next to the female, (V) gonopore nipping, (VI) gonopodial thrusting and (VII) copulation (Parzefall 1969; Baird 1974). In commonly used experimental designs to study MCC in fish, model and stimulus males are restricted in direct contact but are still able to communicate visually through glass at a distance of around 1 cm at the nearest. Standard designs were previously used to demonstrate copying behaviour in sailfin mollies (Schlupp et al. 1994; Schlupp and Ryan 1997; Witte and Ryan 1998, 2002; Witte and Noltemeier 2002; Witte and Massmann 2003), and therein, model female and stimulus male were frequently observed to interact visually at the closest possible distance.

Marler and Ryan (1997) showed a genetically predefined preference for larger over smaller males in sailfin molly females. Later, MacLaren (2006) showed that female sailfin mollies were able to perceive and distinguish between a large and a small dummy male positioned at a distance up to 68 cm by showing a preference for the larger male. Therefore, sailfin molly females are generally able to assess visual information necessary for mate choice at a distance up to 68 cm.

But the questions remain whether (I) sailfin molly conspecifics do interact sexually over larger distances, and if so, (II) is this distant interaction sufficient for an observing female to extract public information for her own mate choice decision? Therefore, we investigated whether sailfin molly females would copy a choice of a model female when this model female is either close to a stimulus male (1 cm) or 40 cm away from that male. We predicted that females will copy the choice when the model female is next to the stimulus male as found in previous experiments. However, we further predicted that females will not copy the choice of a model female positioned farther away from the stimulus male (40 cm), since close sexual interactions (courtship) between the model female and the male are not possible.

Material and methods

Study organism

Sailfin mollies are small neotropical fish inhabiting fresh and brackish water (Meffe and Snelson 1989). They are livebearers of the family Poeciliidae without parental care. Both males and females copy the mate choice of others (Schlupp et al. 1994; Schlupp and Ryan 1997; Witte and Ryan 1998, 2002). Male and female sailfin mollies used in experiments were mature descendants of wild mollies caught from a shallow freshwater drainage ditch at Mustang Island near Corpus Christi (TX, USA) in 2014. In the lab, fish were kept in mixed-sex shoals in large housing tanks (80 cm × 35 cm × 40 cm; approx. 30 individuals each) under a light-dark cycle of 14:10 h and a constant temperature of 26 ± 1 °C. They were fed daily with flake food (JBL GmbH & Co. KG, Germany), frozen *Artemia* sp., and chironomid larvae alternately. Prior to experiments, focal females were kept separated from males in small groups for several weeks to increase their choosing motivation. All experiments were performed in 2016. After experiments, all fish were returned to their home tanks.

General experimental procedure

For testing the effect of distance on public information use in MCC, we used a square paddling pool for children to provide a large area (Intex Kinderpool Frame Pool Mini, blue, 122 cm × 122 cm × 30 cm). We filled the pool with tap water as used for fish housing. Water was aerated and filtered between experiments and partly changed once a week. Water temperature was 26 ± 1 °C, and the water level was 19.5 ± 1 cm in height, resulting in a total volume of approximately 280 L. Illumination during experiments was provided by two fluorescent tubes positioned approximately 138 cm above the middle of the pool (Philips TL-D 90 De Luxe, 58 W).

The following treatments and the control were modified after the classic copying experiment described by Schlupp et al. (1994), Schlupp and Ryan (1997), Witte and Ryan (1998) and Witte and Noltemeier (2002). Prior to the start of a trial, four clear Plexiglas cylinders (11 cm diameter) were positioned in the test pool (Fig. 1). Cylinders were used to keep each fish at a specific place inside the pool and to ensure a constant distance between them during experiments. All cylinders were large enough for fish to move around and behave normally. To mark a circular mate choice zone (34 cm diameter) around each cylinder containing a stimulus male, we used flexible tubes (8 mm in diameter) filled with sand that lay on the ground of the pool. Both choice zones comprised around 12% of the total pool area.

First, two stimulus males were positioned in two cylinders on opposite sides of the pool for acclimatisation (Fig. 1). Two opaque frames made of white plastic were put around them to prevent the test female from seeing them, which was released into the pool beforehand. Each trial started with an acclimatisation period of 25 min, in which the focal female was allowed to swim freely and explore the pool (Fig. 1, stage 1). The focal female was then placed in a clear Plexiglas cylinder (11 cm diameter) in the middle of the pool and the frames were lifted to give view to the stimulus males. The focal female was allowed to watch both stimulus males for 10 min (Fig. 1, stage 2). After we lifted and removed her cylinder, the first preference test (P1) started and the focal female could swim freely for 10 min to spend time with both males. We measured the time the focal female spent within the mate choice zone around the cylinder containing a stimulus male with

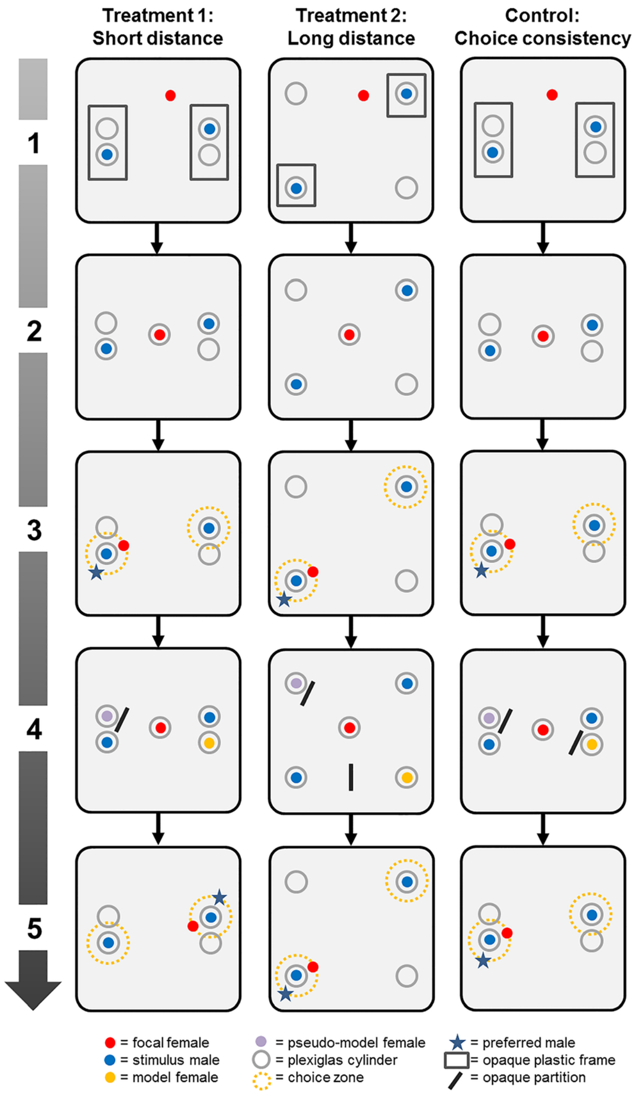


Fig. 1 General overview of the experimental procedure for treatment 1, treatment 2 and the control. The figure describes the presence and position of fish in the experimental pool per treatment, depending on the experimental phase: (1) acclimatisation period, (2) focal female watches stimulus males, (3) first preference test (P1), (4) observation period, and (5) second preference test (P2). The position of the preferred male is shown exemplarily for each treatment

stopwatches (Fig. 1, stage 3). After 10 min, the focal female was gently put back into the cylinder in the middle of the pool and a white and opaque plastic frame was put around her cylinder to block her view. The position of the stimulus males was switched to control for a possible side bias in the focal female. Males could be easily switched as their cylinders were closed at the bottom and they could be lifted out of the water to change position. This was done to decrease handling time for the experimenter and to reduce stress from handling the fish with a net. We lifted the plastic frame around the focal female and the focal female was given 5 min to get accustomed to the new situation before she was released again. She was given 10 min time to spend with the males. After P1, the focal female was placed back inside the Plexiglas cylinder in the middle of the pool and the plastic frame was put around her cylinder to block her view to the other cylinders. Time spent for both halves of P1 was summed up, and it was calculated which stimulus male was preferred by the female during P1. The preferred male was defined as the male the focal female spent more than 50% of the time she spent in both mate choice zones within the two mate-choice trials of 10 min. After this first preference test, we put the focal female back into her clear cylinder in the middle of the pool and put an opaque white frame around her cylinder. To provide public information to the focal female during the observation period, a model female was introduced to the cylinder next to the male that was not preferred. To handle both males equally and to prevent the case that one male was more active than the other, a so-called pseudo-model female was placed next to the preferred male in a clear Plexiglas cylinder (Fig. 2). The pseudo-model female was obscured by a white plastic barrier in front of the cylinder and, hence, not visible to the focal female. The pseudo-model female, however, was still visible to the stimulus male next to her. The frame surrounding the focal female was lifted and an observation period of 10 min started in which the focal female could watch the simulated mate choice of the model female for the non-preferred male (Fig. 1, stage 4). After the observation period, the view of the focal female was again obscured; the model females were removed from their cylinders, and the second preference test (P2) started. Here, the procedure was identical to P1 in which the focal female could again spend 10 min with both males (Fig. 1, stage 5). Then, the position of the stimulus males was switched and the female was given 5 min to observe the new situation before she was again given 10 min time to spend with both males. Time spent was again summed up for both halves of P2, and it was calculated which stimulus male was preferred by the female during P2.

Observation and data recording were done by a single experimenter (MK) during all experiments; therefore, no blinded methods were used. The experimenter was sitting 100 cm away from the pool to reduce disturbance of the fish. Observation of obscured areas in the pool (e.g. by the pool wall) was provided by a mirror positioned in 80 cm height at the upper rear of the pool (see supplementary Fig. S1). Per stimulus male, we measured the absolute association time (in seconds) a focal female spent within a choice zone with a stopwatch. Association time is a well-established measure to determine mate choice in sailfin mollies when no direct contact is provided (Witte and Noltemeier 2002; Witte and Klink 2005; Nöbel and Witte 2013; Gierszewski et al. 2017). Association time is an indirect measure of female mate preference and several studies showed that the time females spent with a male was positively correlated with the probability of copulation with that same male in different species of fish (Bischoff et al. 1985; Forsgren 1992; Berglund 1993;

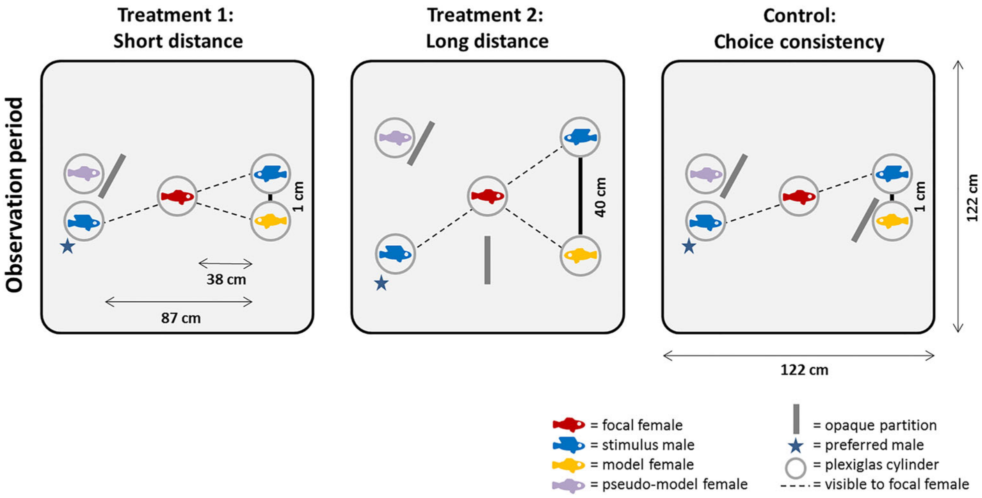


Fig. 2 Position of fish during the observation period in treatment 1, treatment 2 and the control. The figure describes the position of each fish in the experimental pool during the observation period for each treatment and the control

Kodric-Brown 1993). After Pruett-Jones (1992), focal females were considered to copy the choice of the model female if they showed a significant increase in time spent with a prior non-preferred male after the observation period, since an increase in association time directly results in a higher probability of mating with that same male.

If a focal female spent more than 90% of the total time in only one choice zone, even if males were switched, her choice was judged to be side biased and the experiment was terminated. All females with a side bias were retested once after 2 days with different stimulus males and further excluded from the analysis if their side bias persisted. Focal females that spent less than 10% of the total time of a mate-choice trial (20 min total) in both choice zones combined were excluded due to lack of interest in the stimulus males. Focal females that were too stressed during mate-choice trials and only stayed in one corner of the pool were excluded from analysis due to stress. To evaluate the effect of distance between the model female and the non-preferred stimulus male on MCC, we performed two different treatments and a control as described below.

Treatment 1: short distance — model female next to non-preferred male

During the observation period in treatment 1, cylinders containing the prior non-preferred male and the model female were set at a distance of 1 cm (short distance), measured between the outer rims of the cylinders (see Fig. 2 and supplementary Fig. S2). The same was true for the distance between the prior preferred male and the pseudo-model female. This distance is common in most MCC experiments and also describes a typical distance between male and female during courtship with direct contact (Parzefall 1969; Baird 1974; SG, personal observation). The cylinder of the focal female was 38 cm apart from stimulus males and model females. We tested whether females copy the mate choice of other females under these experimental conditions. We assumed that focal females would copy the mate choice of the model female, as shown in previous studies.

Treatment 2: long distance — model female apart from non-preferred male

During the observation period in treatment 2, cylinders containing the prior non-preferred male and the model female were set at a distance of 40 cm (long distance), measured between the outer rims of the cylinders (see Fig. 2 and supplementary Fig. S3). The same was true for the prior preferred male and the pseudo-model. The focal female was 43 cm apart from stimulus males and model females. The pseudo-model female was covered with a white opaque barrier and hence not visible to the focal female inside her clear cylinder. We made sure that, although the pseudo-model female was 40 cm apart from the previously preferred male and covered to the focal female, the male could see the pseudo-model female (see Fig. 2). Additionally, we added a second barrier to block the line of sight between the prior preferred male and the model female on the opposite side of the pool (Fig. 2).

So far, this distance was never tested in copying experiments in the lab before; however, this distance between conspecifics can be commonly observed in natural sailfin molly shoals (KW, personal observation). Here, we tested whether females copy the mate choice of other females although model females were 40 cm apart from stimulus males. We assumed that focal females would not copy the mate choice of the model female due to the lack of close contact with the stimulus male.

Control for choice consistency

We performed a control for choice consistency in which the general procedure of the copying experiment was identical to that of treatment 1 with the exception that both the model female and the pseudo-model female were not visible to the focal female during the observation period and, hence, no public information was provided for MCC (see Fig. 2 and supplementary Fig. S4). This procedure is a common control to test mate-choice consistency in studies on MCC (Witte and Ryan 1998; Witte and Noltemeier 2002; Witte and Massmann 2003; Witte and Ueding 2003; Heubel et al. 2008), and it is important to show that a change in preference can be linked to the absence/presence of a model female and, hence, the absence/presence of public information provided during observation. Here, we assumed that focal females would choose consistently and not alter their preference for the prior preferred male in P2.

In all experiments, we used females (focal, model and pseudo-model females) that were around the same size (see supplementary Table S1). Stimulus males used in the same trial were of similar size as well (see supplementary Table S1). Stimulus males were unknown to the respective focal females and chosen to be similar in fin sizes and colour. Stimulus males were always presented simultaneously in a binary choice situation and the position of the Plexiglas cylinders containing the stimulus males was alternated between trials. Due to the limited amount of fish available for experiments, we re-used stimulus males but always together with a different male a second time. In each experiment and trial, females were used first and only once as the focal female but were later re-used as model or pseudo-model female. Standard length of each fish participating in a trial was measured after testing. All fish were later returned to their home tanks.

Statistical analysis

R 3.2.2 (R Development Core Team 2015) and SPSS v. 24 (IBM Statistics) were used for data analyses. Descriptive statistics for sizes and association time are given as mean ± SD or median with first and third quartile. Per experiment, we compared sizes of focal females, models and pseudo-models using a Kruskal-Wallis rank sum test and sizes of the two stimulus males using a Wilcoxon rank sum test for unpaired samples.

For each treatment and the control, we analysed whether the overall choosing motivation (total time spent in both mate-choice zones within a preference test) differed between mate-choice tests using a paired Wilcoxon signed-rank test. When choosing motivation differed in any experiment, all further analysis was done using relative values (preference scores) rather than absolute association times to ensure comparability within and between treatments. Association time, i.e. time spent within mate-choice zones, was used as a measure of mate choice for a given stimulus male. For each preference test (P1 and P2), a preference score for the preferred and non-preferred male was calculated as the absolute time spent with a male divided by the total time spent with both males. To analyse whether mate choice for either stimulus male differed from chance, we tested the preference score for either stimulus male against a 50% expectation using a one-sample *t* test. Preference scores for the prior non-preferred stimulus male were further used to test whether these scores changed between the first and second preference tests when public information was provided, compared to the control treatment in which public information was absent. Since it was not possible to gain normally distributed data by using common transformation methods, we used paired Wilcoxon signed-rank tests. A Holm-Bonferroni correction was applied when multiple testing occurred and adjusted *p* values were calculated using the *p.adjust* function in R.

To compare both distance treatments, we analysed whether choosing motivation in P2 (after observation) was different across treatments, as a result of the varying distances in which the model female was presented using a Mann-Whitney *U* test. Furthermore, we tested whether a change of preference for the prior non-preferred stimulus male (copying score = score for prior non-preferred male in P2 − score for non-preferred male in P1) was different between treatments using a Mann-Whitney *U* test. Since we were also interested in whether a change of preference (copying score) for the prior non-preferred male was correlated with focal female's standard length (SL), we performed a Spearman rank correlation.

Additionally, Fisher's exact test was calculated to test whether the number of focal females that changed their mate preference in P2 and, hence, copied the choice of a model female differed between the control and both distance treatments. *p* values were considered significant if $p < 0.05$. All *p* values are two-tailed. Data are available in the supplementary material (Table S1).

Results

Detailed information on standard length of all fish used, absolute time spent of focal females with stimulus males and relative time spent (preference scores) for all experiments can be found in the supplemental material (Table S1). Although we only used preference scores for analysing a potential change of focal female's preference for the prior non-preferred male, a graphical overview of the absolute time spent with each stimulus male for all treatments and the control is found in supplementary Fig. S5.

Treatment 1: short distance — model female next to non-preferred male

In treatment 1, we tested 16 females. Three females showed a side bias and were all successfully re-tested. One female had to be excluded due to stress. We could analyse data from 15 focal females. Focal females ($n = 15$) spent 840 ± 293 s in both choice zones in P1 and 851 ± 306 s in P2. Overall choosing motivation did not differ between P1 and P2 (Wilcoxon signed-rank test: $V = 51$, $p = 0.639$).

During P1, focal females ($n = 15$) spent on average 644 ± 316 s with the preferred male and 203 ± 176 s with the non-preferred male, resulting in a preference score of 0.68 (0.55, 0.98) and 0.32 (0.02, 0.45), respectively. Focal females showed a significant preference for one stimulus male (one-sample t test: $T = 4.937$, df = 14, $p < 0.001$). In P2, focal females spent on average 510 ± 303 s with the prior preferred male and 343 ± 213 s with the prior non-preferred male [scores: 0.49 (0.41, 0.68) and 0.51 (0.32, 0.59)]. Preference scores for the prior non-preferred male significantly increased from P1 to P2 (Wilcoxon signed-rank test: $V = 0$, $p = 0.003$; Fig. 3). Preference for the prior preferred male did not differ from chance in P2 (one-sample *t* test: $T = 1.122$, df = 14, $p = 0.281$). We found no correlation between the copying scores for the prior non-preferred male and focal female's SL (Spearman rank correlation: $n = 15$, $r_S = -0.095$, $p = 0.736$). Nine out of 15 focal females (60%) reversed their initial mate choice for a male and copied the choice of the model female in the short-distance treatment.

Treatment 2: long distance — model female apart from non-preferred male

In treatment 2, we tested 20 females. Four females showed a side bias, three females were successfully re-tested and one had to be excluded from analysis. Four females were excluded due to lack of interest. Overall, focal females ($n = 15$) spent 722 ± 293 s in both choice zones in P1 and 736 ± 302 s in P2. Choosing motivation did not differ between preference tests (Wilcoxon signed-rank test: $V = 52$, $p = 0.67$).

In P1, focal females ($n = 15$) spent on average 527 ± 308 s with the preferred male and 193 ± 131 s with the non-preferred male [scores: 0.6 (0.57, 0.83) and 0.4 (0.16, 0.43)]. Focal females showed a significant preference for one stimulus male in the first preference test (one-sample t test: $T = 4.197$, df = 14, $p = 0.001$). In P2, focal females spent on average 390 ± 302 s with the prior preferred male and 346 ± 200 s with the prior non-preferred male [scores: 0.47 (0.34, 0.64) and 0.53 (0.36, 0.66)]. Preference scores of time spent with the prior non-preferred male significantly increased from P1 to P2 (Wilcoxon signed-rank test: V = 16, $p = 0.025$; Fig. 3). The prior preferred male of the first preference test was not preferred anymore in the second test (one-sample *t* test: $T = -0.042$, df = 14, $p = 0.967$). Copying scores for the prior non-preferred male were not correlated with focal female's SL (Spearman rank correlation: $n = 15$, $r_S = 0.054$, $p = 0.847$). Nine out of 15 focal females (60%) reversed their initial mate choice for a male and, hence, copied the choice of the model female in the long-distance treatment.

Control for choice consistency

In the control, we tested 17 females. Two females were excluded from analysis, one due to lack of interest and one due to stress. Two females that showed a side bias were later successfully re-tested. Focal females ($n = 15$) spent 987 ± 167 s in both choice zones in P1 and 890 ± 241 s in P2. Choosing motivation significantly differed between preference test (Wilcoxon signed-rank test: $V = 102$, $p = 0.015$), with females spending less time in both choice zones in P2.

During P1 of the control, focal females ($n = 15$) spent on average 694 ± 240 s with the preferred male and 294 ± 151 s with the non-preferred male [scores: 0.68 (0.56, 0.76) and 0.32 (0.24, 0.44)]. Focal females showed a significant preference for one stimulus male in P1 (one-sample t test: $T = 4.197$, df = 14, $p = 0.001$). In P2, females spent on average 571 ± 232 s with the prior preferred male and 319 ± 165 s with the prior non-preferred male [scores: 0.62 (0.53, 0.71) and 0.38 (0.29, 0.47)]. There was no change in preference scores of time spent with the prior non-preferred male in P2 (Wilcoxon signed-rank test: $V = 40$, $p = 0.554$; Fig. 3). Preference for the prior preferred male in P1 was still significant in P2 (one-sample *t* test: $T = 3.661$, df = 14, $p = 0.003$). One out of 15 focal females (6.6%) reversed her initial mate choice for a male in P2. Overall, focal females were consistent in their mate choice for a male when no opportunity for copying and, hence, no public information was provided during the observation period.

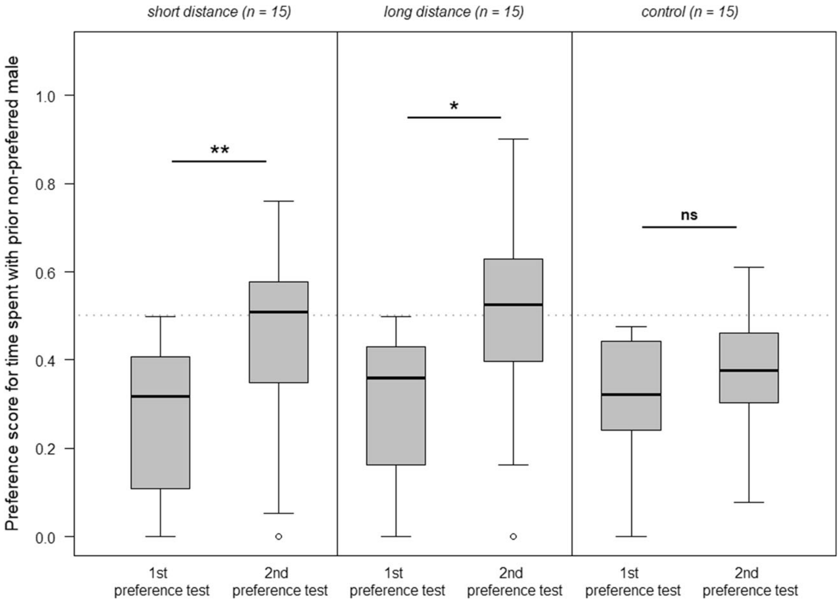
Comparison of distance treatments and control

There was no difference in the change of preference (copying score) for the prior non-preferred male from P1 to P2 across distance treatments (Mann-Whitney *U* test: $Z = -0.104$, $p = 0.917$). Further, choosing motivation in P2 (after observation of a model female) did not differ across treatments (Mann-Whitney *U* test: $Z = 0.995$, $p = 0.317$). The number of focal females that copied the choice of a model female and also reversed their initial preference in favour for the prior non-preferred male in P2 was significantly higher in both treatments than compared to the control for choice consistency (short-distance vs. control: Fisher's exact test: $p = 0.005$; long distance vs. control: Fisher's exact test: $p = 0.005$; Fig. 4).

Discussion

In the present study, we investigated whether the distance between a model female and a male would affect the use of public information and alter the mate choice of an observing female in favour of that male. As predicted, focal females significantly increased time spent with the prior non-preferred male after the observation period and copied the

Fig. 3 Preference scores for treatment 1, treatment 2 and the control. Boxplots of median, quartiles and whiskers (1.5 × interquartile range) are shown for preference scores for the time spent with the (prior) non-preferred stimulus male in preference test 1 (P1) and preference test 2 (P2). The grey dotted line represents a preference score of 0.5. Circles indicate outliers. $N = 15$; $*p \leq 0.05$, $**p \leq 0.01$, ns not significant



mate choice of the model female when the model female was in close distance (1 cm) to the stimulus male. Regarding the distance between the model female and the stimulus male, the short distance treatment resembled the classic procedure in experiments on MCC and illustrates a natural distance between male and female during courtship (Parzefall 1969; Baird 1974). Nevertheless, our experimental design differed from the classical MCC experiment in a way that focal females had much more space to swim around during preference tests and hence was more similar to the situation in the field in this aspect. Yet, focal females copied the mate choice of the model. This result supports the previous finding of MCC in sailfin molly females. Focal females originally came from a population from Mustang Island near Corpus Christi. This is the third population of sailfin mollies from Texas exhibiting MCC (Comal River: Witte and Ryan 2002; Witte and Noltemeier 2002; Witte and Massmann 2003; Witte and Ueding 2003; San Marcos River: Schlupp and Ryan 1997; Witte and Ryan 1998).

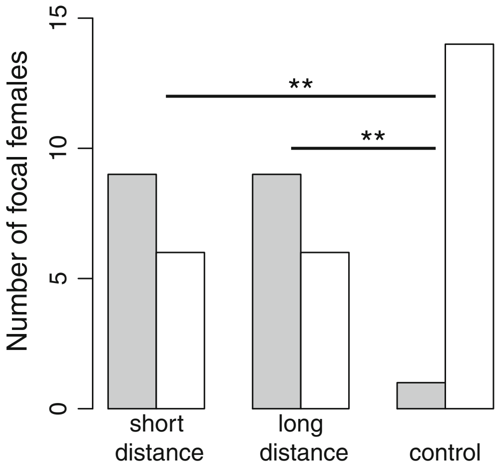


Fig. 4 Number of focal females that reversed their initial mate choice after observation. Bar plots show the absolute number of females (total of $n = 15$ for each treatment and the control) that either did copy and reversed their mate choice (grey bars) or did not copy (white bars) the choice of a model female in both distance treatments and the control. $**p < 0.01$

In contrast to previous studies on MCC in fish, where model female and stimulus male could either directly interact (Bierbach et al. 2011; observations from the wild: Witte and Ryan 2002; Goulet and Goulet 2006; Alonzo 2008, Godin and Hair 2009) or at least had close range contact through a clear wall or partition (Schlupp et al. 1994; Witte and Ryan 1998; Witte and Noltemeier 2002; Witte and Massmann 2003; Widemo 2006; Frommen et al. 2009; Moran et al. 2013; Auld and Godin 2015), we here increased the distance between the model female and the prior non-preferred stimulus male during observation and, as a result, prevented close range sexual interactions. Surprisingly and contrary to our prediction, focal females significantly increased time spent with the prior non-preferred male when the model female was positioned 40 cm away from the stimulus male (long-distance treatment) as well. Despite prevention of close-range contact between the model female and the stimulus male during the observation period, public information was still available to affect the mate choice of observing focal females who copied the choice of the model.

Since focal females were consistent in their mate choice when no model female was visible, and hence, no public information was provided during the observation period (control for choice consistency), we conclude that the change in preference in favour of the prior non-preferred male in both distance treatments was due to MCC. Additionally, in all previous standard experiments testing MCC in the sailfin molly, we never found any effect of local enhancement or shoaling that might have explained a change in preference in focal females (Witte and Ryan 1998; Witte and Noltemeier 2002; Witte and Ryan 2002; Witte and Massmann 2003; see also Schlupp et al. 1994; Heubel et al. 2008).

The presence of a model female simulating a choice for the prior non-preferred male in both distance treatments altered the mate choice of focal females irrespective of the distance provided. Experiments on MCC already showed that it is not necessary that an actual copulation is observed to elicit copying behaviour in the observer (classic experimental procedure without direct contact), but our results further show that even interactions in distance provide enough information to affect the mate choice of an observer. Sailfin molly females were shown to perceive and respond to dummy males in a distance up to 68 cm (MacLaren 2006); therefore, it can be assumed that the focal female, the model female as well as the non-preferred male were able to see each other and respond to each other as potential mates. For this reason, it was important to block the view of the prior preferred male to the model female on the other side of the pool. In zebra finches, Kniel et al. (2015b) found that females copy the choice for a male phenotype when the model female and the stimulus male could acoustically and visually interact through a transparent barrier. Zebra finch females, however, did not copy the mate choice of a model female when an opaque barrier was inserted between the model female and the stimulus male, preventing visual interactions. This shows that visual cues or signals between the model female and stimulus male provide important public information used in mate choice by the observing female. Although behaviour of stimulus and model fish was not quantified in this study, all fish were observed to be visually interacting during all experiments (MK, personal observation). The fact that focal females showed copying behaviour indicates that distant visual interactions between stimulus male and model female were still perceived as sexually motivated. We assume that sexual interest between the stimulus male and the model female was expressed by an increase in swimming activity. During experiments, fish were observed actively swimming up and down the walls of the clear Plexiglas cylinders (MK, personal observation). It was also observed that stimulus males and model females were facing each other while visually communicating (MK, personal observation) which suggests that focal females might have assessed to whom the sexual interest was directed. A list of possible behavioural patterns of interacting sailfin mollies, which might have been visible and, therefore, influencing to an observing female, can be found in the supplementary material (see sheet "Behavioural patterns" in Table S1).

In both treatments, the focal female was farther away from the stimulus male and the model female than they were to each other. In treatment 1, the cylinder of the focal female was 38 cm away from stimulus males and model females whereas model female and stimulus male were only 1 cm apart. In treatment 2, the cylinder of the focal female was 43 cm away from the stimulus males and model females, whereas model female and stimulus male were 40 cm away. If focal females were able to assess these distances, then the model female was always perceived as being nearer and, hence, more closely interacting with the stimulus male than the focal female herself. However, it is, so far, not known whether the behaviour of the stimulus male or that of the model female is more important for an observing sailfin molly female's decision to copy the choice of the model or not.

We did not find a difference in strength of preference (copying scores) between the two distance treatments, meaning that an increase in distance from 1 to 40 cm between the prior non-preferred male and the model female did not weaken the strength of copying behaviour in our study. As our analysis shows, focal female's motivation to choose between stimulus males was also not affected. A weakening effect of distance between sender and receiver on information transfer could, for instance, be found in a foraging context in starlings, *Sturnus vulgaris* (Fernández-Juricic and Kacelnik 2004). Fernández-Juricic and Kacelnik (2004) used two distance treatments from 0 to 3 m within the natural range of starling flocks and showed that individual foraging and scanning behaviour was less affected when birds were farther away. To our knowledge, comparable results for public information use in mate choice over distance are not apparent.

In our experimental setup, visual conditions were very good and might have facilitated public information use. The experimental pool was well illuminated and the shallow water was clear, providing excellent visibility that was also stable over time. Long and Rosenqvist (1998) showed that guppy males vary their courting distance depending on the light environment with a two to three times larger distance (6–9 cm) at higher light levels. Therefore, courting distance may vary without losing information for the receiver and, presumably, for an observer in the case of MCC. It is, however, likely that under natural conditions, the perception of distant interactions and, hence, public information use over distance are limited by individual visual capacities and environmental factors like water turbidity, which has, e.g. shown to affect mate choice in sailfin mollies (Heubel and Schlupp 2006) and in three-spined sticklebacks (Engström-Öst and Candolin 2007). Therefore, it can be assumed that, depending on the respective habitat and particularly depending on differences in visual conditions, it is likely that different populations of sailfin mollies differ in public information use. There may exist a high variability of public information use within populations of sailfin mollies, due to, e.g. seasonal and geographical differences in turbidity and, hence, visibility as well (see Heubel 2004). Turbidity can lead to different mate choice decisions in different populations of the same species. Basolo (2002) found a preference for males with an artificial sword in sailfin molly females of a population in Louisiana living in murky water. Witte and Klink (2005) tested a latent preference for males with an artificial sword in sailfin mollies of a population from the Comal River in New Braunfels, Texas, living in clear water. In contrast to Basolo (2002), Witte and Klink (2005) found no latent preference for artificially sworded males in sailfin molly females. This difference in female mate choice between these two populations may be due to adaptations to the environment with bad or good visual conditions.

Conclusion

In our study, we could show that close range contact between a model female and a male is no prerequisite for MCC in sailfin mollies. Public information gained from interactions between two heterosexual conspecifics at distance still provides public information to affect the mate choice of an observing female. Our results indicate a much wider transfer and use of public information in sailfin molly groups than previously thought as 40 cm exceeds the, for fish typically described, social interaction distance for group members of four body lengths (Croft et al. 2008). Further, our results raise the question of what specific behavioural features communicate sexual interest in sailfin mollies at distance, apart from commonly described courtship displays in this species. Future studies should evaluate this aspect in more detail. Since MCC is regarded as an important evolutionary driver for both the transmission of phenotypic traits as well as the preference for those (Danchin et al. 2004), our findings underline even more far-reaching consequences of MCC for the evolution of sexually selected traits in sailfin mollies. This is especially important when regarding the presumably high variability of public information use due to varying environmental constraints. The use of public information from distance does not lower the risk of the detection of an observer by the interacting individuals, which can lead to the audience effect. Thus, apart from MCC, a wider information transfer might also lead to implications for other behavioural phenomena like, e.g. audience effects (reviewed in Plath and Bierbach 2011), and should be evaluated in more detail in the future.

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Compliance with ethical standards

Ethical approval The performed experiments and handling of the fish were in line with the German Animal Welfare legislation (Deutsches Tierschutzgesetz) and approved by the internal animal welfare officer Dr. Urs Gießelmann, University of Siegen, and the regional authorities (Kreisveterinäramt Siegen-Wittgenstein; Dr. Wilhelm Pelger; Permit number: 53.6 55-05).

Conflict of interest The authors declare that they have no conflict of interest.

Data accessibility statement All data generated or analysed during this study are included in the supplementary material (Table S1).

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