

The role of model female quality in the mate choice copying behaviour of sailfin mollies

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Female mate choice copying is a socially mediated mate choice behaviour, in which a male's attractiveness to females increases if he was previously chosen by another female as a mate. Although copying has been demonstrated in numerous species, little is known about the specific benefits it confers to copying females. Here we demonstrate that the mate choice behaviour of female sailfin mollies (*Poecilia latipinna*) is influenced by the phenotypic quality of model females with whom males are observed consorting. Test females choosing between two males of similar body length were found to significantly increase time spent with previously non-preferred males after having observed them with a relatively high-quality female. Conversely, females were found to significantly decrease time spent with previously preferred males after having observed them with a relatively low-quality female. Female mate choice copying might be maintained by selection based on the heuristic value it provides females choosing between males whose quality differences are not easily distinguishable.

Keywords: sexual selection; mate choice; non-independent mate choice; mate choice copying

1. INTRODUCTION

Female mate choice copying is a type of non-independent mate choice, in which females observe a sexual interaction between a male and another female (referred to as the model female) and preferentially choose that male for a mate (Pruett-Jones 1992). Most evidence for copying comes from polygynous fishes such as the guppy, *Poecilia reticulata* (Dugatkin 1992, 1996), medaka, *Oryzias latipes* (Grant & Green 1996) and sailfin molly, *Poecilia latipinna* (Schlupp *et al.* 1994; Witte & Ryan 1998, 2002). Copying is typically understood to benefit females by decreasing time and energy required to find suitable mates and lessening predation and injury risks while doing so (Slagsvold *et al.* 1988; Gibson & Höglund 1992; Stöhr 1998). A key assumption of this advantage is that the model provides the copying female with information about the male's quality. Here, we test the prediction that the model female's quality influences copying by serving as a surrogate of male quality when quality differences

between males are difficult to distinguish. In this study, female quality is determined by quality assessments performed by males themselves.

The sailfin molly (*P. latipinna*) is a live-bearing poeciliid fish without parental care that lives in mix-sexed shoals of 10–20 individuals (Witte & Noltemeier 2002). Sailfins have a promiscuous, non-resource based mating system that includes female choice and male–male competition (Ptacek & Travis 1997; Gabor 1999). There is a positive relationship between female size and fecundity (Travis *et al.* 1990) and male *P. latipinna* preferentially choose larger females as mates (Ptacek & Travis 1997; Gabor 1999) and produce more sperm in response to these females (Aspbury & Gabor 2004a). Females preferentially choose larger males as mates, but will copy the mate choice of other females when males are similar in body size. Copying does not override female preference for larger males, however (Witte & Ryan 1998). Females also copy the mate choice of Amazon mollies (*Poecilia formosa*), a heterospecific gynogen that requires sperm from sailfin males to induce embryogenesis (Schlupp *et al.* 1994). Both male and female sailfin mollies discriminate between conspecific and heterospecific females and males preferentially choose conspecifics as mates (Schlupp *et al.* 1994; Ptacek & Travis 1997; Gabor 1999) and produce more sperm in response to those females (Aspbury & Gabor 2004b).

In the case of copying, we propose that females do not just evaluate the presence of a model female with a potential mate (Witte & Ryan 1998), but rather use the model's quality as a mate assessment heuristic. Given that males compete for the most desirable mates and females exercise mate choice, the quality of a male's mate probably provides an honest signal of his own quality. We hypothesize that when differences between males are difficult to discern, females use the model's quality to guide mate choice in favour of the male with the higher-quality model. Others have argued that copying represents the mechanism by which animals learn mate choice (i.e. younger females copy preferences of larger adults to learn correct mating behaviours; Dugatkin & Godin 1993). To avoid confounding experience with quality as judged by size, conspecific and heterospecific females will serve as high- and low-quality models in this experiment. We predict that the quality of female with whom a male consorts will influence female assessments of quality differences between similarly sized males. More specifically, we predict that if one male consorts with a conspecific female and another with a heterospecific female, females will assess the former as being of higher quality since males view conspecifics as more desirable mates.

2. MATERIAL AND METHODS

(a) Origin of fishes

All female and all but four male fishes were collected in 1993 from central Texas, USA (Martindale, San Marcos River) and maintained in outdoor breeding tanks under natural conditions at Brackenridge Field Laboratory, University of Texas. The remaining four males were from another central Texas population (Spring Lake, San Marcos). In the laboratory all fishes resided in species- and sex-specific tanks to ensure that fishes were sexually receptive and not gravid. Fishes were fed commercially available food

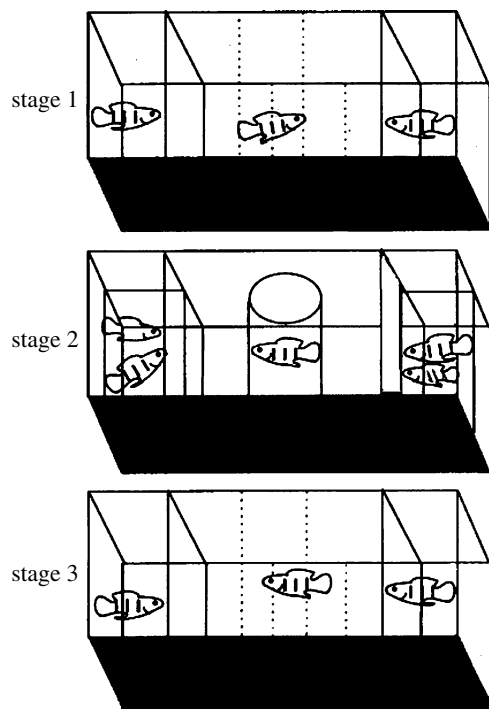


Figure 1. Side view of experimental tank.

(TetraMin) and maintained a 12:12 h light:dark cycle that supplemented natural light. Tanks were maintained a temperature of about 25 °C. After experiments, all fishes were returned to their stock tanks.

(b) General procedure

Our method was similar to that used by Schlupp *et al.* (1994). We divided a large (122 × 32 × 52 cm) aquarium into five equally sized sections. The sections on each side were partitioned from the rest of the tank with clear Plexiglas (figure 1) and constituted the two male compartments. The central sections were open, demarcated only by markings on the sides of the tank. One male molly (*P. latipinna*) was placed in each male compartment; males were approximately matched in standard length (mean difference, 2.20 mm). A female sailfin molly was placed in a clear container in the tank's central section and observed males for 20 min. To test for initial preference, the clear container was removed from the tank and the amount of time the female spent adjacent to each male compartment during the 10 min following the female's initial departure from the central section was quantified. The female was considered to prefer a male if she spent more time in that male's 24.4 cm preference zone during the 10 min preference test. Although time spent is an indirect measure of mate preference, others have demonstrated that it correlates positively with the probability of copulation in guppies (Bischoff *et al.* 1985; Kodric-Brown 1993). The female was then placed back in the centrally placed clear container. Each male compartment was divided in half, parallel to the long end of the tank and a female Amazon molly (*P. formosa*) was placed in the empty half of the preferred male's section of the tank. A female sailfin molly was placed in the empty half of the non-preferred male's section of the tank (figure 1). The test female observed both males and both females behaving for 20 min. The researcher made note which (if either) male was displaying more vigorously (e.g. male swimming toward the female and following her movements along the glass, making zigzag motions in front of her) every 2 min throughout the 20 min viewing session. After the 20 min observation, the testing aquarium returned to its original condition and a second 10 min preference test was performed to test whether the quality of model affected the female's subsequent mate preference.

After each test, standard body length of all fishes was measured from the tip of the snout to the end of the caudal peduncle with callipers. The average (\pm s.d.) difference in standard length between males within a pair was 2.20 ± 1.17 mm. The average body length of all males used in this experiment ($n=48$) was 34.10 ± 3.35 mm. The test female and model sailfin in any one test were also matched in size (test females, $35.09 \text{ mm} \pm 3.91$; model females, $35.74 \text{ mm} \pm 3.04$). Amazon models were larger than sailfins in each trial, as they are in nature (Heubel 2004; average model Amazon,

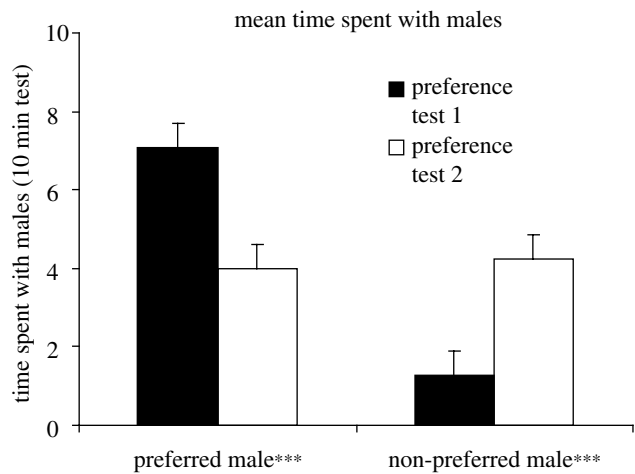


Figure 2. Mean time (± 1 s.e.) spent with males in first and second preference test. *** $p < 0.001$.

$41.63 \text{ mm} \pm 3.11$). Sailfin females ($n=26$) were used once as a test female and once as a model female. New Amazon model females were used for each trial ($n=26$) and new males were used for each trial except for two trials, in which males from previous trials were re-used ($n=48$).

3. RESULTS

During the initial 10 min preference test, females did not allocate their time evenly between the two males despite the males' similarity in body size. Females ($n=26$) spent significantly more time with the preferred male (7.07 min; 2.21 s.d.) than the non-preferred male (1.26 min; 1.21 s.d.; independent samples *t*-test: $t=11.76$, d.f.=38.75, $p < 0.001$). After this test, females then observed the preferred male consorting with a model Amazon female and the non-preferred male consorting with a model sailfin female for 20 min. A trained research assistant tabulated differences in courtship behaviour between the two males every 2 min throughout this 20 min viewing period. The numbers of times that one male was courting more vigorously than the other were summed at the end of each experiment. Within each viewing period, male courtship behaviour differed in intensity an average of 4.18 ± 2.71 times. Ninety-six per cent of these differences represented instances of the preferred male increasing display behaviour in response to the very aggressive courtship displays exhibited by model Amazons. A second 10 min preference test was then performed. After observing the non-preferred male with the model sailfin, females spent significantly more time with this male ($M=4.22$ min, 3.23 s.d.) than in the initial preference test (paired samples *t*-test: $t=-4.77$, d.f.=25, $p < 0.001$), with 13 of the females reversing their initial mate preference completely. Conversely, females spent significantly less time with the preferred male ($M=4.00$ min, 3.29 s.d.) than they did in the initial preference test (paired samples *t*-test: $t=-4.96$, d.f.=25, $p < 0.001$; see figure 2). However, no significant differences were found between time spent with the preferred and non-preferred male in the second preference test (independent samples *t*-test: $t=-0.24$, d.f.=50, $p=0.81$).

4. DISCUSSION

Prior research has demonstrated that female sailfin mollies prefer large males as mates and will mate copy when males are similarly sized, but not when male size differs substantially (Witte & Ryan 1998). From the findings presented above, it appears that test females do not just evaluate a model female's presence with a potential male mate. Rather, test females appear to use the model's desirability to males as a surrogate of male quality when choosing mates. Given that males compete for sexual access to females, the presence of a highly desirable female with a male signals that male's own quality. Our results are consistent with the hypothesis that a model female's quality has heuristic value to females in mate choice.

An alternative hypothesis is that females invoke a mate choice strategy that alternately favours each of the two males independent of copying (i.e. females prefer male A at time 1 and male B at time 2). Although not tested, there is little support for this strategy in this species. Numerous experiments have found female mollies are consistent with their mate choice in the absence of an opportunity to copy (e.g. Schlupp *et al.* 1994; Witte & Ryan 1998; Witte & Noltemeier 2002), with some data demonstrating a trend for females' initial preferences to be strengthened rather than ameliorated by a second viewing (e.g. Schlupp *et al.* 1994). It is additionally possible that the reported results can be attributed to the focal females' original preferences diminishing due to the preferred males' vigorous courtship behaviour toward the heterospecific females (i.e. to avoid the cost of mate competition). The observed preference switch by females may represent active avoidance of the preferred males, rather than an active preference for the previously non-preferred male. It is also possible that females, after having lost their original preference, do not show any preference and choose randomly between the two males. It is difficult to distinguish between the loss of any preference and the loss of preference for the high-quality males due to low-quality model females in the current paper. Future research must address these issues to rule out these alternatives.

Additional research is needed to explore whether females of other copying species are influenced by the quality of females to whom males are mated, especially in those where male quality differences are not readily observable. Further research is also needed to explore potential interactions between male and model quality to understand the heuristic value of model female quality in mate choice copying. The findings presented in this study provide preliminary support for the hypothesis that female mate choice copying might be maintained by selection due to the heuristic value it provides copying females when choosing between potential mates of similar quality.

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- Aspbury, A. S. & Gabor, C. R. 2004a Differential sperm priming by male sailfin mollies (*Poecilia latipinna*): effects of female and male size. *Ethology* **110**, 193–202. (doi:10.1111/j.1439-0310.2003.00963.x)
- Aspbury, A. S. & Gabor, C. R. 2004b Discriminating males alter sperm production between species. *Proc. Natl Acad. Sci. USA* **101**, 15 970–15 973. (doi:10.1073/pnas.0405653101)
- Bischoff, R. J., Gould, J. L. & Rubenstein, D. I. 1985 Tail size and female choice in the guppy (*Poecilia reticulata*). *Behav. Ecol. Sociobiol.* **46**, 169–175.
- Dugatkin, L. A. 1992 Sexual selection and imitation: females copy the mate choice of others. *Am. Nat.* **139**, 1384–1389. (doi:10.1086/285392)
- Dugatkin, L. A. 1996 Interface between culturally based preferences and genetic preferences: female mate choice in *Poecilia reticulata*. *Proc. Natl Acad. Sci. USA* **93**, 2770–2773. (doi:10.1073/pnas.93.7.2770)
- Dugatkin, L. A. & Godin, J. G. J. 1993 Female mate copying in the guppy (*Poecilia reticulata*): age dependent effects. *Behav. Ecol.* **4**, 289–292.
- Gabor, C. R. 1999 Association patterns of sailfin mollies (*Poecilia latipinna*): alternative hypotheses. *Behav. Ecol. Sociobiol.* **46**, 333–340. (doi:10.1007/s002650050627)
- Gibson, R. M. & Höglund, J. 1992 Copying and sexual selection. *Trends Ecol. Evol.* **7**, 229–232. (doi:10.1016/0169-5347(92)90050-L)
- Grant, J. W. A. & Green, L. D. 1996 Mate copying versus preference for actively courting males by female Japanese medaka (*Oryzias latipes*). *Behav. Ecol.* **7**, 165–167.
- Heubel, K. U. 2004 Population ecology and sexual preferences in the mating complex of the unisex Amazon molly *Poecilia formosa*. Dissertation, University of Hamburg, Hamburg, Germany.
- Kodric-Brown, A. 1993 Female choice of multiple male criteria in guppies: interacting effects of dominance, coloration, and courtship. *Behav. Ecol. Sociobiol.* **32**, 415–420.
- Pruett-Jones, S. 1992 Independent versus non-independent mate choice: do females copy each other? *Am. Nat.* **136**, 1000–1009. (doi:10.1086/285452)
- Ptacek, M. B. & Travis, J. 1997 Mate choice in the sailfin molly, *Poecilia latipinna*. *Evolution* **51**, 1217–1231.
- Schlupp, I., Marler, C. & Ryan, M. J. 1994 Benefit to male sailfin mollies of mating with heterospecific females. *Science* **263**, 373–374.
- Slagsvold, T., Lifjeld, J. T., Stenmark, G. & Breiehagen, T. 1988 On the cost of searching for a mate in female pied flycatchers *Ficedula hypoleuca*. *Anim. Behav.* **136**, 1000–1009.
- Stöhr, S. 1998 Evolution of mate-choice copying: a dynamic model. *Anim. Behav.* **55**, 893–903. (doi:10.1006/anbe.1997.0674)
- Travis, J., Trexler, J. C. & Mulrey, M. 1990 Multiple paternity and its correlates in female *Poecilia latipinna* (Poeciliidae). *Copeia* **1990**, 722–729.
- Witte, K. & Noltemeier, B. 2002 The role of information in mate-choice copying in female sailfin mollies (*Poecilia latipinna*). *Behav. Ecol. Sociobiol.* **52**, 194–202. (doi:10.1007/s00265-002-0503-1)
- Witte, K. & Ryan, M. J. 1998 Male body length influences mate-choice copying in the sailfin molly *Poecilia latipinna*. *Behav. Ecol.* **9**, 534–539.
- Witte, K. & Ryan, M. J. 2002 Mate choice copying in the wild. *Anim. Behav.* **63**, 943–949. (doi:10.1006/anbe.2001.1982)