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Male fish use prior knowledge about rivals to adjust their mate choice

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Mate choice as one element of sexual selection can be sensitive to public information from neighbouring individuals. Here, we demonstrate that males of the livebearing fish *Poecilia mexicana* gather complex social information when given a chance to familiarize themselves with rivals prior to mate choice. Focal males ceased to show mating preferences when being observed by a rival (which prevents rivals from copying mating decisions), but this effect was only seen when focal males have perceived rivals as sexually active. In addition, focal males that were observed by a familiar, sexually active rival showed a stronger behavioural response when rivals were larger and thus, more attractive to females. Our study illustrates an unparalleled adjustment in the expression of mating preferences based on social cues, and suggests that male fish are able to remember and strategically exploit information about rivals when performing mate choice.

Keywords: audience effect; familiarity; mate choice; *Poecilia mexicana*; communication networks; sexual selection

1. INTRODUCTION

Cognitive abilities in non-primate animals have received growing scientific interest [1,2]. For example, many fishes can recognize individuals [3–6] as well as certain behavioural characteristics [7–9]; males can estimate the fighting abilities of rivals by evaluating their body size [7], or by watching other males fight [10,11]. Nonetheless, it remains to be studied whether males of non-primate species may assess and remember rivals' sexual competitiveness and attractiveness to females and adjust their own behaviour accordingly.

To study this question, we used the livebearing fish *Poecilia mexicana* [12], as previous studies revealed that males respond to the presence of an unfamiliar rival male (i.e. an audience) when choosing a mate [12,13]. It seems that males respond to the risk of being copied [14–16] and thus, cease expressing

mating preferences [12,13]. We asked whether males would gather information about rivals when allowed to familiarize themselves with other males. Based on the assumption that audience effects are a counter-strategy employed by males to reduce the risk of sperm competition arising from male mate choice copying [12,14], audience effects should occur only when the audience male is either (a) unfamiliar (i.e. its sexual competitiveness is unknown) or (b) familiar, but had been perceived as sexually active and attractive to females. To test prediction (a), we compared the response of focal males to familiar or unfamiliar rivals (experiment 1), while prediction (b) was tested by confronting males with familiar rivals that had been perceived as either sexually active or inactive (experiment 2).

2. MATERIAL AND METHODS

Poecilia mexicana used in this study were descendants of fish collected near Tampico (Tamaulipas) in northeastern Mexico [17]. In experiment 1, familiarity was induced by keeping two males together in 25 l aquaria prior to the mate choice tests for a period of one week. For experiment 2, one male was kept together with a female for one week, so this male could interact sexually with the female, while the other male resided in an adjacent compartment, where it was able to observe the pair interact (electronic supplementary material).

Using a dichotomous choice test [18], all focal males were first tested for their preference for a particular female (large or small) by measuring association times. In experiment 1, focal males were then randomly assigned to one of three treatments: they were tested with an audience male present (familiar or unfamiliar) or without an audience (control). The audience was confined in a Plexiglas cylinder, while in the control treatment, an empty cylinder was used instead.

In experiment 2, males were tested on 2 consecutive days as focal and audience male and vice versa. We thus obtained paired data, where the audience within each male dyad had either been perceived by the focal male as sexually active or inactive.

We compared the decrease in strength of individual male preferences by calculating a score expressing changes in focal males' preferences for the initially preferred female ([13]; see also electronic supplementary material). Scores from experiment 1 were compared among treatments using one-way analysis of variance (ANOVA). For a post hoc comparison across treatments, Fisher's protected least significant difference (PLSD) tests were employed. We also analysed the absolute time males spent in the neutral zone during both parts of the tests (electronic supplementary material). Paired *t*-tests were used to compare scores obtained from experiment 2. We employed Spearman rank-order tests to detect potential effects of male body size differences. Additional information on total time spent interacting with both stimulus females can be found in the electronic supplementary material.

3. RESULTS

When comparing the decrease in strength of individual male preferences before and after presentation of an audience, we detected a statistically significant difference among treatments in experiment 1 (ANOVA: $F_{2,85} = 11.11$, $p < 0.0001$). Post hoc pair-wise comparisons revealed that males responded with a marked decrease in the expression of preferences only during the unfamiliar treatment (figure 1a). Male body size difference (audience–focal) had no significant effect (Spearman rank-correlation, unfamiliar audience: $r_s = -0.05$, $p = 0.79$, $n = 36$; familiar audience: $r_s = -0.20$, $p = 0.37$, $n = 23$).

In experiment 2, no audience effect was detected when the familiar audience was perceived as sexually inactive, while a familiar sexually active audience clearly induced a response (paired *t*-test, $t_{20} = -2.10$; $p = 0.049$; figure 1b)—similar to the

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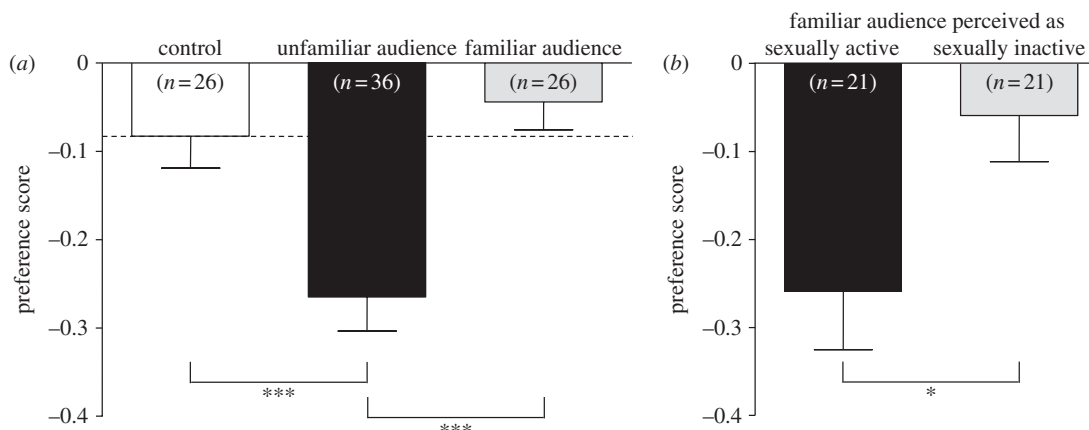


Figure 1. Changes in *P. mexicana* male mating preferences induced by the presence of an audience male. (a) Experiment 1: during the second part of the choice tests either no audience (left), an unfamiliar (middle) or a familiar audience male (right) was presented. Results from Fisher's PLSD tests. (b) Experiment 2: males of a dyad (one familiar sexually active and one familiar sexually inactive male, see main text) were tested for their preferences while successively serving both as focal and audience males. Results from paired *t*-test. Depicted are preference scores (fraction of time near preferred female during second part–first part, see main text), whereby negative values indicate that male preferences decreased in strength. * $p < 0.05$, *** $p < 0.001$. Data are means \pm s.e.m.

effect of unfamiliar audience males in experiment 1. Furthermore, when confronted with a sexually active familiar audience, focal males adjusted their mate choice decisions according to rivals' relative body size (Spearman correlation: $r_s = -0.57$, $p = 0.006$; figure 2), with larger audience males leading to stronger changes in mating preferences. No such correlation was found when the audience male was perceived as sexually inactive ($r_s = -0.18$, $p = 0.44$).

4. DISCUSSION

Males responded by exhibiting weaker mating preferences when faced with an unfamiliar rival, i.e. with a male whose motivational state/competitiveness they could not evaluate before the tests. No such effect was found with familiar audience males, but familiarity *per se* cannot account for this effect, as focal males in experiment 2 did respond to familiar audience males they had perceived as sexually active during the familiarization period. By contrast, familiar sexually inactive audience males—probably representing a low sperm competition risk—did not evoke a response. It appears that familiarizing with rivals allows the gathering of information about their motivational state that will be remembered by males when exercising mate choice. We argue that, during the familiarization period in experiment 1, focal males never saw the audience male interact sexually with a female, so they may have evaluated the rival as sexually inactive and thus, less competitive. Males clearly responded to the presence of an audience male as indicated by an increase in time males spent in the neutral zone (electronic supplementary material). Nevertheless, mate choice decisions were affected differentially (see above), and thus, general distractions by the audience rival cannot sufficiently explain the effects observed here.

In addition, audience males' body size affected focal males' mate choice, but only when the familiar rival was perceived as sexually active. Although familiarity

among males is known to reduce the intensity of fights in some poeciliids [7], an effect of aggression can be ruled out, as body size effects did not play a role when focal males were confronted with an unknown rival. Furthermore, established dominance hierarchies and, therefore, avoidance of encounters with dominant males by smaller, subordinate males [19] are unlikely, as males also had an opportunity to establish a dominance relationship in the 'familiar treatment' of experiment 1, where also no effect of body size differences was seen. Our data, therefore, suggest that focal males responded to the audience males' sexual attractiveness. *Poecilia mexicana* females prefer to mate with larger males [20], and focal males may also directly assess females' differential responses to males during the familiarization phase.

In conclusion, we suggest that cognitive abilities at least in teleost fishes are by no means restricted to the mere recognition of familiar individuals [5,21,22], but rivals' sexual activity and attractiveness to females are also being assessed, remembered and integrated in mating decisions.

Mate choice is of central interest in research on sexual selection [23], and our results underscore the importance of considering the social context in which individuals perform mate choice, as the (observable) strength of mating preferences can depend on (i) the presence of competitors and (ii) various forms of socially acquired information. Our study prompts the question of what other non-primate species are capable of a comparable 'higher order' assessment of their social environment, which will be an exciting topic for future research.

The experiments reported here comply with the current laws of Germany (approved by Regierungspräsidium Darmstadt V-54-19c-20/15-F104/Anz.18).

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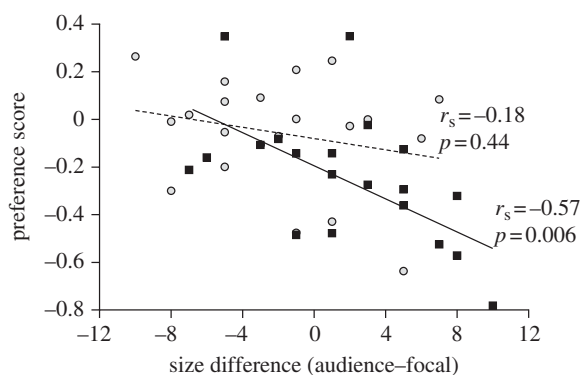


Figure 2. Correlation between body size differences and changes in *P. mexicana* male mating preferences relative to the perceived sexual activity of the familiar audience male. Depicted are preference scores (see main text), whereby negative values indicate that male preferences decreased in strength. Body size differences in the tested male dyads ($n = 21$) were determined as (SL audience male–SL focal male). The r_s - and p -values are from Spearman rank-order tests. The strength of males' preferences decreased with increasing rival males' body size when the familiar audience was perceived as sexually active, but not in the case of familiar sexually inactive audience males. Filled squares, sexually active audience; filled circles, sexually inactive audience.

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