



ISSN: 2348-1927

RESEARCH ARTICLE

Annals of Biological Sciences
2017, 5 (1): 25-36

Does Individual Variation in Male Mate Choice Copying Reflect Differences in Social Responsiveness?

Guilherme Gomes-Silva^{1,2}, Kai Liu¹, Bojian Chen¹, Martin Plath¹ and Carolin Sommer-Trembo^{1,3*}

¹College of Animal Science and Technology, Northwest A&F University, Yangling, P.R. China

²Master Study Program Saude Ambiental, Universidade Federal de Uberlândia, Minas Gerais, Brazil

³Department of Ecology and Evolution, J.W. Goethe University Frankfurt, Max-von-Laue-Straße, Frankfurt am Main, Germany

ABSTRACT

During mate choice copying (MCC), individuals evaluate the attractiveness of potential mating partners while observing if they are preferred or rejected by other individuals. Numerous studies have examined female MCC, while its role during male mate choice received far less attention. Using western mosquitofish (*Gambusia affinis*) as our study organism, we asked if individual focal males would spend more time associating with the previously rejected female of a pair of stimulus females (a large- and a small-bodied female) after they had observed another (model) male consort the rejected female. We used the resulting 'copying scores' to test if individual variation in MCC can be explained as part of a larger behavioral syndrome (i.e., social responsiveness). In one experiment, we assessed focal males' copying tendencies and then tested them in another context of socially-dependent mate choice (audience effects). Males with high copying tendencies were also more likely to respond to rival presence by showing audience effects (concealment of mating preferences). In another experiment, we assessed copying tendencies and behavioral correlates of boldness, activity and sociability (shoaling tendencies) of the focal males. All three traits were correlated, but did not predict male copying tendencies. Altogether, our results suggest that male MCC may indeed be part of a social responsiveness syndrome (explaining correlated responses in two contexts of socially-dependent mate choice), but this syndrome seems to be independent of standard behavioral parameters widely used to quantify animal personality traits.

Keywords: Animal personality, Audience effect, Non-independent mate choice, Social learning, Social responsiveness

INTRODUCTION

Male mate choice copying

Animals use social information in a variety of contexts [1-5]. This includes learning about predation risk and foraging, as exemplified by studies on social learning in a live bearing fish, the guppy [6,7]. Animals also integrate social information when searching for mates, whereby individuals observe how potential mating partners interact with other individuals in their social environment [8,9]. This strategy helps to evaluate the quality of potential mating partners and also reduces the costs associated with mate searching [9,10] (but see 11,12 for potential costs of socially-dependent mate choice). Usually, studies on socially-dependent mate choice reported considerable variation among individuals in social information use in natural populations [13-17], raising the question as to whether this variation is consistent across different contexts of socially-dependent mate choice. In other words, the question arises if some individuals consistently respond more to social information during mate choice than others.

Our present study focused on a widespread form of socially-dependent mate choice: mate choice copying (MCC). During MCC, choosing individuals accept or reject potential mating partners after they had observed how their potential mates were preferred or rejected by other members of their own sex, respectively [13,18-20], and it is widely accepted that MCC is operationally a form of non-independent mate choice resulting from social learning [21]. MCC can be found in both invertebrates [22] and vertebrates [23,24]. Empirical evidence for MCC was first reported for guppy females [25] and subsequent studies have largely continued to focus on female MCC [13-16,26,27]. More recent studies, however, have started to acknowledge that also males copy the mate choice of other males [9]. Examples of male MCC come from an array of species, including a sex-role reversed pipefish, sticklebacks, darters and especially live bearing fishes [14,28-35].

In this study, we used relative changes in the strength of mating preferences as a means to assess the effect of MCC on individual males' mate choice decisions. We asked if individual focal males would spend more time associating with the previously rejected female of a pair of stimulus females after focal males had been able to observe another (model) male consort the rejected female. Previous studies confirmed that information obtained during MCC can indeed weaken or override intrinsic preferences for certain phenotypes during female [26,36-38] and male mate choice [14,31-34].

Our study for the first time reports male MCC in Western mosquitofish (*Gambusia affinis*; Poeciliidae). We gave individual focal males an opportunity to choose between two different-sized females in a binary, dichotomous association preference test and predicted males to exhibit an intrinsic preference for large female body size as reported for the closely related *G. holbrooki* [39,40]. We then asked if focal males would alter their initial preferences after they had an opportunity to observe an interaction between another (model) male and the initially non-preferred female. Our major aim was to identify behavioral correlates of the observed variation in MCC.

Copying tendencies-part of a social responsiveness syndrome?

The first part of our study tested the hypothesis that the observed variation in males' tendency to copy is non-random and can be explained by consistent differences among individuals in their general propensity to respond to social information (i.e., social responsiveness; [41]). In our first experiment, we considered another context of male mate choice during which individual differences in social responsiveness should also affect the degree to which males alter their choices in response to social information [42]. We investigated so-called 'audience effects' [43,44] during which males alter their mate choice behavior strategically in response to rival presence [45-47]. Poeciliid males, when faced with a rival male during their mate choice (which may observe and later copy their mating decisions) lower their sexual effort and conceal their mate preference, or they even trick their observers by interacting with the previously non-preferred female [32,48-54].

We observed a correlation between males' copying tendencies and strength of audience effects—alluding to the existence of a 'social responsiveness syndrome'. The second part of our study, therefore, asked if variation in male MCC can also be linked to classical personality traits [55]. This question was motivated by studies suggesting that personality traits can define individuals' propensity to use social information [41,56,57] and may thus lead to consistent differences in social responsiveness [58]. For example, when private and social information about the optimal food searching strategy were conflicting, bolder guppies were relying more on private than social information compared to shyer ones [59]. Likewise, in a study on barnacle geese (*Branta leucopsis*), bold individuals used social information to a lesser extent than shy ones [60]. Hence, there is increasing evidence that shy individuals rely more on social information than bold ones, a possible explanation being that sampling of private information bears risks [10,61-63], which shy individuals are less likely to accept. However, studies exploring how individual differences in social information use (especially in a mate choice context) relate to individual differences in personality traits are scarce [64] and no study to date has made an attempt to link variation in males' tendency to show MCC to variation in personality traits but see [65] for an investigation of the link between personality and female MCC in zebra finches. In our study, we explored the relationship between male MCC and three behavioral parameters that are widely used to characterize animal personality in fish, namely boldness [66-70], activity [42,68,70,71] and sociability [68,69,72-74].

In summary, our present study reports on two experiments that were designed to detect potential behavioral correlates of individual differences in MCC in *G. affinis* males (testing both aspects in one comprehensive experiment was unpractical, as it would have required keeping focal males isolated from females for an extended period of time). We predicted a positive correlation between individual males' tendency to show MCC and their tendency to respond to rival presence (audience effects). We further predicted a positive correlation between MCC and sociability (assuming

that general sociability correlates with social responsiveness), but a negative correlation with boldness, as bolder individuals tend to be less sociable [72,74] and to respond less to social information [59,60].

METHODS

Test organisms and general housing conditions

Test fish were wild-caught *G. affinis* from the species invasive range in China [see Electronic Supplementary Material 1 (ESM 1) for details]. We maintained fish in groups comprising both sexes, at densities of around 40 fish per tank, in several aerated and filtered 200 L aquaria at 25°C under a 12:12 h light/dark regime. Aquaria were well equipped with plants, twigs and stones. Fish were fed twice a day ad libitum with commercially available flake food, frozen blood worms (chironomid larvae), as well as *Artemia salina nauplii* and shrimps.

Behavioral tests were conducted between 22nd December 2015 and 10th March 2016. Test fish were acclimated to laboratory conditions for about eight months at this point. We isolated small groups of 3 individually recognizable focal males from the same stock tank for 1–2 days before the tests in 50 L tanks, to which they were returned between subsequent tests until a test sequence was completed. Poeciliid males are continuously sexually active but increase sexual activity after a short period of isolation from females [75]. We tested each focal male only once for MCC and once for their tendency to show audience effects; however, due to the limited number of males available from our stocks, some focal males were also used once as model or audience males 2–4 days after they were used as a focal male. When former focal males were re-used as a model or audience male, they were not paired with the same male during a subsequent trial.

BEHAVIORAL EXPERIMENTS

To demonstrate that males do not alter their mate choice during two identical, successive mate choice tests without an opportunity for MCC, we first tested $n=15$ males in a control experiment [42]. In experiment 1, we tested whether males' propensity to copy correlates with the strength of their tendency to respond to rival presence during mate choice by showing audience effects. To this end, $n=29$ focal males were tested in two mate choice situations (one to quantify MCC and one to quantify audience effects), whereby the order of the two assessments was balanced (i.e., half of the focal males were first tested for MCC, and half first for audience effects). In experiment 2, we tested whether standard behavioral parameters used to characterize animal personality affect male copying tendencies. Therefore, we assessed personality traits of another $n=30$ focal males before they were tested for MCC.

To minimize observer bias, blinded methods were used when recording behavioral data in a way that the experimenter(s) did not know the outcome of a previous behavioral assessment (e.g. personality traits) for a given focal male when conducting a trial. Specifically, a team of experimenters collected the data, and the different behavioral assessments for the same focal male were conducted by different persons, who were naïve with respect to the previous assessments.

In the following, experimental procedures are explained in a comprehensive (condensed) form. An extended description of our experimental setup and details on the experimental procedures can be found in the Electronic Supplementary Material (ESM 2-4).

Assessment of males' tendency to copy

We assessed males' tendencies to copy as the degree to which they alter their mating decisions after a copying situation [26]. The test for MCC was divided into three consecutive phases: (1) 1st dichotomous mate preference test, (2) observation phase, and (3) 2nd preference test. During the 1st test, the focal male (mean \pm SE standard length, SL: 21.89 ± 0.34 mm) was allowed to visually associate with either of two unfamiliar stimulus females of different body size (large female: 39.66 ± 0.29 mm; small female: 31.02 ± 0.24 ; paired t-test: $t_{73}=28.81$, $P<0.0001$) for 10 min, whereby stimulus females were interchanged between sides after 5 min to detect potential side biases. We measure times spent by the focal male in proximity of each stimulus female (i.e., in both of the preference zones; see ESM Figure S1a). During the observation phase, the focal male could observe a visual interaction between the non-preferred female and an unfamiliar model male (22.41 ± 0.57 mm; experiments 1, 2). The 2nd preference test was identical to the 1st preference test and enabled us to determine if focal males' preferences changed from the 1st to 2nd test part.

To evaluate the strength of MCC, we calculated a copying score [38]. No change in male preferences would lead to a copying score of zero, negative values would indicate that the focal males spent less time near the initially non-preferred female in the 2nd part of a trial and positive values would indicate that males spent relatively more time near the initially non-preferred female (i.e., copied the model male's mate choice).

To demonstrate that focal males' preferences remained unchanged when there was no opportunity to copy, we ran a control experiment in which we did not include model males during the observation phase (such that the focal male could not observe behavioral interactions between other males and either of the stimulus females; see ESM Figure S1a).

Assessment of audience effects

We tested the same focal males for MCC and for their tendency to respond to rival presence during mate choice by exhibiting audience effects (weakening of male preferences and less time spent engaging in mate choice altogether) [48]. Test for audience effects consisted of two phases: (1) 1st preference test and (2) 2nd preference test, during which an audience male could observe the focal male's mate choice (ESM Figure S1b). The 1st preference test was identical to the 1st part in tests for MCC (see above). Again, we noted the time the focal male spent associating with each of the two (unfamiliar) stimulus females that differed in SL (mean \pm SE, large female: 38.38 ± 0.48 mm; small female: 30.90 ± 0.43 ; paired t-test: $t_{28}=11.68$, $P<0.0001$). The 2nd preference test was different in that another male (audience male) was placed in a transparent Plexiglas cylinder in the central back of the test tank.

We compared association times near either females during the two preference tests and calculated an 'audience score' [48,50] as the difference between the relative association time near the initially preferred female with an audience (2nd preference test) and the relative association time near the same female without an audience (1st preference test). No change in male association times lead to a score of zero, negative values indicate that the focal males spent less time near the initially preferred female in the 2nd part of a trial and positive values indicate that males spent relatively more time near the initially preferred female. This score, therefore, represents an equivalent to the copying score described before while being negative instead of positive when focal males changed their preferences. However, to keep our data comparable to previous studies [48,50], we kept those two different designations and formulas.

Personality assessment

In experiment 2, focal males (mean \pm SE standard length, SL: 22.73 ± 0.58 mm) were characterized along three personality axes before they were tested for MCC: boldness as latency to emerge from shelter and enter an unknown area [76-79], activity in an open field tank [42,80,81] and sociability (i.e., shoaling tendencies) as time spent in the vicinity of a group of conspecifics [72,82,83]. All tests were performed consecutively in the same arena to minimize handling stress. We conducted personality assessments twice, allowing us to calculate behavioral repeatability (see ESM 4 for details).

STATISTICAL ANALYSES

All statistical analyses were conducted in SPSS 19. All relative data were arcsine (square-root)-transformed prior to statistical analysis. Assumptions of normal error distribution and homogeneity of variances and covariances were met for all analyses performed.

Direction of males' initial preferences and individual preference scores

Males of the related *G. holbrooki* tend to prefer large-bodied over small-sized females as mating partners [39,40]. We confirmed a significant preference for large (302.67 ± 15.18 s) over small stimulus females in *G. affinis* (215.93 ± 13.86 s; paired t-test: $t_{73}=3.05$, $P=0.003$). However, not all males preferred the larger female (i.e., 40.5% preferred the small female), and so we calculated copying and audience scores independent of which of the stimulus females (large or small) was preferred in the first preference test.

Comparing copying and control treatments

Multi-step experiments in which the outcome of one step might influence following steps are especially prone to a statistical phenomenon called 'regression to the mean' (RTM), which was first described by Galton [84] and repeatedly discussed in the context of biological disciplines [85,86]. Unusually large or small measurements tend to

be followed by measurements that are closer to the mean [85], which in our study might have caused changes from the 1st to 2nd test parts that are not necessarily due to treatment-effects (i.e., due to MCC). To exclude this possibility, we included a control group without copying situation. Our first analysis specifically tested whether males responded to the copying treatment by increasing the time spent with the initially non-preferred female and whether they would show more consistent behavior (i.e., whether they did not change their mate choice decisions) in the control treatment. Copying scores were treated as the dependent variable in a General Linear Model (GLM), in which ‘copying treatment’ [‘copying’ (experiments 1 and 2) vs. ‘control’] was coded as a factor and ‘focal male body size’ as a covariate. A significant main effect of the factor ‘copying treatment’ would indicate that RTM can be ruled out as the sole explanation for changes in males’ mate choice behavior from the 1st to 2nd test parts. Note that we could not include ‘model male body size’ in this analysis, as no model males were involved in the control treatment.

Moreover, to prevent over-interpretation of our results in light of potential effects caused by RTM, we included the ‘relative time spent with the non-preferred female during the 1st test part’ (i.e., before males could copy) as a covariate in all analyses. This decision was made because our experimental design used relative changes in mate choice as a means to determine males’ tendency for mate choice copying and focal males with strong initial mating preferences (i.e., males that had strongly rejected the initially non-preferred female) were more likely to show an increase in relative time spent near the initially non-preferred female (leading to higher copying scores that would actually reflect an effect of RTM).

We initially included all possible two-way interactions but removed non-significant interactions from the final model when $P > 0.1$ (all excluded interactions: $F < 2.17$, $P > 0.12$), leaving only the interaction effect of ‘copying treatment \times focal male body size’ in the final model. To quantify the relative importance of model terms, we calculated effect sizes using Wilks’ partial eta squared (η_p^2).

Correlation between copying tendencies and audience effects

Our second analysis asked if there is a correlation between MCC (expressed as the copying score) and males’ tendency to respond to rival presence by showing audience effects. We analyzed the subset of data from experiment 1 and again used the copying score as the dependent variable in a GLM, in which the ‘strength of audience effects’, ‘focal male body size’, ‘model male body size’ and ‘relative time spent with the non-preferred female during the 1st test part’ were included as covariates. Again, we initially included all two-way interactions but excluded them from the final model as all interactions were non-significant ($F < 2.77$, $P > 0.11$).

Repeatability of personality traits and correlation with copying tendencies

Repeatedly measured traits can be evaluated regarding their consistency by calculating repeatability (R)-values, defined as: $R = \text{variance among individuals} / (\text{variance among individuals} + \text{variance within individuals})$. R was calculated from variance estimates obtained from linear mixed models (LMMs) for each personality trait assessed in experiment 3. Significant deviations of R from zero were tested with likelihood ratio tests (LR-tests).

To test for correlations between all three measures of personality, we used mean values from both assessments and calculated Pearson correlations. We corrected α -levels for multiple testing as $\alpha' = 0.05/2 = 0.025$. As we found evidence for a correlation structure between all three variables, we condensed the data into a single variable for further statistical analysis. A correlation-matrix based principal component analysis retrieved one single PC with an Eigen value > 1 (1.83; eigenvalue of PC 2 = 0.69) that explained 61.0% of the total variance. Axis loadings were -0.78 for emergence times (boldness) +0.72 for activity and +0.84 for sociability.

We used another GLM to estimate the effects of our measures of animal personality on males’ tendency to copy. Again, copying scores were coded as the dependent variable, while ‘focal male body size’, ‘model male body size’ and ‘relative time spent with the non-preferred female during the 1st test part’ were included as covariates. To test for personality effects, the personality-related PC was included as another covariate. We initially included all two-way interactions but excluded them from the final model as all interactions were non-significant ($F < 1.51$, $P > 0.23$).

RESULTS

Comparing control and copying treatments

In our first analysis, we tested if males change their association preferences when given an opportunity to copy (experiment 1: $n = 29$; experiment 2: $n = 30$), but retain their initial preferences when given no opportunity for copying

(control experiment: $n=15$). In the General Linear Model (GLM) using the copying score as the dependent variable, ‘copying treatment’, ‘focal male body size’, the ‘relative time spent near the non-preferred female during the first test part’, and the interaction term ‘copying treatment \times focal male SL’ had significant effects (Table 1a). The significant treatment-effect reflects that males showed positive copying scores after they had an opportunity to copy (experiment 1: 0.211 ± 0.064 ; experiment 2: 0.130 ± 0.041), while copying scores were close to zero in the control group (0.040 ± 0.073). Even though copying scores were (qualitatively) slightly different in the two copying experiments, post hoc Fisher’s LSD tests detected no significant difference between experiments 1 and 2 ($P=0.59$), while there was a statistically significant difference between the control and experiment 1 ($P=0.035$) and between the control and experiment 2 ($P=0.011$). More information on behavioral consistency can be found in the Electronic Supplementary Material (ESM 5).

Table 1: Results from General Linear Models (GLM) using ‘copying scores’ (see main text) as the dependent variable. (a) Comparison of copying and control treatments ($r^2=0.41$), (b) test for a correlation between males’ tendency to show mate choice copying and audience effects within the subset of trials from experiment 1 ($r^2=0.74$), and (c) correlation between copying tendencies and three behavioral correlates of animal personality (boldness, activity and sociability, combined in one PC, see main text; $r^2=0.36$). Non-significant interaction terms and main effects were excluded from the final models if $P>0.1$. Significant effects are highlighted in bold typeface.

Factor	df	F	P	Wilks’ partial η^2
(a) Copying vs. control treatments				
Copying treatment	2	3.43	0.038	0.093
Focal male body size (SL)	1	4.45	0.039	0.062
Relative time spent with non-preferred female (1st test part)	1	35.32	<0.0001	0.345
Copying treatment \times focal male SL	2	3.4	0.039	0.092
Error	67			
(b) Experiment 1				
Strength of audience effect	1	12.62	0.002	0.336
Focal male body size (SL)	1	15.84	0.001	0.388
Relative time spent with non-preferred female (1st test part)	1	56.24	<0.0001	0.692
Error	25			
(c) Experiment 2				
Focal male body size (SL)	1	3.77	0.062	0.123
Model male body size (SL)	1	12.07	0.002	0.309
Error	27			

The direction of both other significant main effects in the GLM will be outlined below. The significant interaction term (‘copying treatment \times focal male body size’) reflects absence of a true copying situation (in which ‘focal male body size’ does play a role, see below) during the control runs.

Correlation between copying tendencies and audience effects

We tested for a correlation between the strength of male mate choice copying and audience effects (experiment 1). We excluded ‘model male body size’ from the final GLM, as it had no significant effect ($F_{1,24}=0.11$, $P=0.75$). The final GLM using copying scores as the dependent variable detected significant effects of the covariates ‘strength of audience effects’, ‘focal male body size’ and the ‘relative time spent near the non-preferred female during the first test part’ (Table 1b).

We used residuals from reduced models to analyze those effects further and found a negative relationship between copying scores and the strength of audience effects (Pearson correlation: $r_p=-0.56$, $P=0.002$, $n=29$; Figure 1). This indicates that males that were more likely to copy (i.e., showed high and positive copying scores) also were more

likely to respond to rival presence by showing audience effects (i.e., they showed strong and negative audience scores).

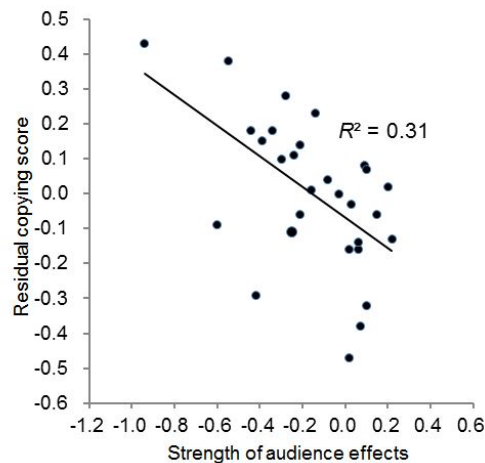


Figure 1: Scatterplot illustrating the relationship between males' tendency to copy the mate choice of a model male (resulting in positive 'copying scores') and their tendency to alter their mate choice in response to rival presence during the mate choice tests (resulting in negative 'audience scores'). Depicted are unstandardized residuals of copying scores from a GLM similar to the final analytical model (see main text); the solid line represents a linear regression ($R^2=0.31$).

Considering the 'relative time spent near the non-preferred female during the first test part', our post hoc correlation analysis confirmed the predicted negative relationship ($r_p=-0.78$, $P<0.001$, $n=29$), suggesting that males that initially strongly rejected one of the two stimulus females were more likely to show copying compared to males with less clear-cut initial preferences (thus, inclusion of this covariate corrected for effects of 'regression to the mean'; Galton [84]). Moreover, copying tendencies decreased with increasing focal male body size ($r_p=-0.58$, $P=0.001$, $n=29$), suggesting that large males copied less than smaller ones.

Repeatability of and correlation between personality traits

In experiment 2, we found moderate to high estimates of repeatability (R) for boldness (i.e., emergence time; $R=0.39$, LR-test: $P=0.016$) and activity (numbers of squares crossed; $R=0.61$, $P<0.001$), while the R -value for sociability (time spent shoaling) was lower and only bordered statistical significance ($R=0.27$, $P=0.088$).

When considering mean values from both personality assessments, all three measures of personality showed pronounced variation within the cohort of focal males (emergence time: 57.9 ± 8.3 s, range: 10.0–213.5 s; activity: 158.2 ± 9.5 squares, range: 64.5–272.0 squares; shoaling time: 182.5 ± 11.3 s, range: 0.0–260.5 s). A correlational structure between personality traits became evident (Figure 2a), whereby emergence times tended to correlate negatively with activity levels (Pearson correlation, $r_p=-0.32$, $P=0.090$, $n=30$, $\alpha^2=0.025$) and showed a significant negative correlation with our measure of sociability ($r_p=-0.50$, $P=0.005$, $n=30$, $\alpha^2=0.025$). Note that bold individuals typically show short emergence times, while shy individuals should exhibit longer emergence times. Hence, our results suggest that bolder individuals were more active but—counter to prediction—spent more time shoaling than shy individuals. Finally, activity levels were positively correlated with sociability ($r_p=+0.42$, $P=0.020$, $n=30$, $\alpha^2=0.025$).

Correlation between copying tendencies and personality traits

The covariate 'relative time spent near the non-preferred female during the first test part' was excluded from the final GLM as it had no statistically significant effect ($F_{1,26}=1.01$, $P=0.33$); the same was true for the personality-related PC ($F_{1,25}=0.48$, $P=0.50$; Figure 2b). We ran independent GLMs using only one of the three personality traits as a covariate in each model, but also found no significant effects ($F<1.04$, $P>0.32$). In the final model, only 'model male body size' was significant. Our post hoc correlation analysis using residuals from a reduced model uncovered a positive correlation between model male body size and focal males' tendency to copy (Pearson correlation: $r_p=+0.42$, $P=0.020$). 'Focal male body size' bordered statistical significance (i.e., $P<0.1$; Table 1c), which was reflected by a negative (but also non-significant) correlation coefficient in our post hoc analysis ($r_p=-0.27$, $P=0.15$).

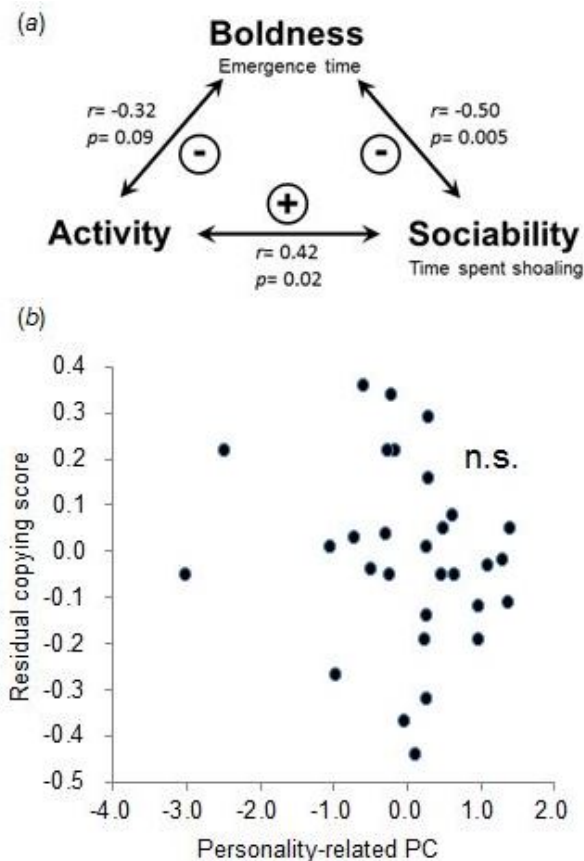


Figure 2: (a) Pearson correlations between three behavioral parameters used to characterize focal males' personality traits (boldness, activity and sociability). Note that 'boldness' was assessed as time focal males needed to emerge from shelter. Hence, negative correlations between our measure of 'boldness' and both other personality traits suggest that bolder males were more active and spent more time shoaling than shy males. (b) Personality traits (condensed into one principal component, PC) did not predict male copying tendencies. Depicted are unstandardized residuals of 'copying scores' from a GLM similar to the final analytical model.

DISCUSSION

Copying the mate choice of others is thought to benefit individuals by decreasing time and energy required to find suitable mates and lessening predation and injury risks associated with individual information sampling (sensu [10,61-63]). An open question in this context is whether and how the observed variation among individuals in their tendency to copy the mate choice of others can be explained. In the following, we discuss this question by scrutinizing the evidence for both predictions outlined in the introduction regarding (1) the correlation between copying tendencies and strength of audience effects, and (2) the (non-existent) correlation between personality traits (including sociability) and copying tendencies. Additional discussion of the observed effects of focal male body size and model male body size on focal males' copying tendencies can be found in the Electronic Supplementary Material (ESM 6).

We used two different-sized stimulus females in our mate choice copying tests. Previous studies on female mate choice copying found that copying does not completely reverse the female preference for large-bodied males [87] however; choosing individuals can rate the relative attractiveness of previously rejected mating partners differently, spending more time in association with them (see Introduction). In our study, we found a significant male preference for large female body size in *G. affinis*. Studies using the related mosquitofishes *Gambusia sexradiata* and *Heterophallus milleri* found focal males to show no preference for large-bodied mating partners [88], while the sister species *G. holbrooki* exhibited a preference for large female body size in some [39,40,47,89], but not all studies [90]. Our analyses of copying tendencies were independent of the average (population-wide) direction of male preferences and were based on the relative attractiveness of both stimulus females during the 1st preference test independent of

their body size (i.e., we calculated individual ‘copying scores’ from the relative times spent near the initially non-preferred female independent of whether or not it was the smaller of both stimulus females).

Copying tendencies-part of a social responsiveness syndrome?

The major question of our present study was whether (and to what extent) individual variation in males’ tendency to copy could be explained as part of a behavioral syndrome [91-93], i.e., whether we would uncover a correlation with another measure of social responsiveness [56-58], assessed in another experimental situation that tested for socially-dependent mate choice (audience effects). We then asked whether the observed ‘social responsiveness syndrome’ can be related to classical personality traits like boldness, which have been hypothesized previously to play a role in the evolution of consistent differences in social responsiveness [41].

Social responsiveness describes the extent to which individuals respond to social information [58]. Theoretical considerations suggest that different forms of selection give rise to consistent individual differences in (social) responsiveness [57,94] (1) benefits of responding to social information (rather than collecting private information) are likely negatively frequency-dependent, which could explain why responsive and less responsive individuals coexist within a population. (2) The costs of being responsive are likely reduced by positive-feedback mechanisms. Hence, being responsive becomes less costly for individuals that have been responsive before, which could explain why individuals differ consistently in their behavioral strategies. In our present study, we found males’ copying tendencies to be correlated with their tendencies to respond to rival presence by showing audience effects (concealment of preferences and reduced sexual activity overall) [43,44]. Our present study, therefore, provides empirical evidence for the existence of a social responsiveness syndrome during mate choice, i.e., consistent individual differences across different situations of socially-dependent mate choice. This is in congruence with a study on female zebra finches [65], which showed that the propensity of social information use was consistent across two different contexts (MCC and foraging).

We also predicted a correlation between sociability/shoaling and males’ tendency to use social information, assuming that those individuals that are more likely to seek the proximity of conspecifics are also more likely to observe conspecifics’ behavior and to use social information. However, we detected no effect of any of our three measures of personality (sociability/shoaling, boldness and activity) on males’ propensity to copy. While we are lacking a compelling answer for the lack of the predicted correlation, we tentatively argue that our assessment of ‘shoaling tendencies’ may not have adequately captured sociability: shoaling mainly serves as a strategy to protect fish from predators [96-98] and so bolder individuals are predicted to spend less time shoaling than shyer ones [72,74]. In our present study, we used stimulus shoals consisting of three males to avoid effects of sexual attraction, and it seems likely that the focal male’s decision to approach the stimulus shoal was coupled with the decision to accept increased competition levels—which bolder individuals may be more likely to do. This would explain the unexpected finding of bolder males spending more time in the vicinity of the stimulus shoal than shy males.

Social responsiveness as a proximate explanation for individual variation in audience effects

We found males’ tendencies to show mate choice copying and audience effects to be correlated (i.e., to be part of a social responsiveness syndrome). In the following, we will discuss how this result seemingly contradicts earlier hypotheses for the evolution of audience effects especially [35,48]. We will then provide a unifying framework to reconcile existing hypotheses.

Poeciliid females store sperm from multiple inseminations for fertilization [99,100]. Therefore, male mate-choice copying is associated with considerable costs for both the copying and the copied male as it leads to increased sperm competition (sensu [101]). Evolution of male mate choice copying despite associated costs has been explained by the fact that only a small portion of females within a shoal is receptive at the same time [102], which increases costs of private assessment of potential mating partners [33]. However, while the copying male faces both costs and benefits, the copied male only faces an increased sperm competition without gaining any benefits [103].

Previous studies found poeciliid males to respond to the presence of a potential copier male with (1) reduced sexual effort, (2) concealment of their mating preference for a given female by associating less with that female, and (3) spending more time with the previously non-preferred female when observed by a rival. Those effects have been interpreted as a strategy to reduce sperm competition arising from male mate choice copying [43,44]. In support of this interpretation Bierbach et al. [88] found audience effects to be widespread when comparing ten species of poeciliids, but the degree of effect (3) was correlated with species-level sexual activity—a likely correlate of average sperm competition intensity across species.

Our finding of a social responsiveness syndrome involving both copying tendencies and strength of audience effects, at first sight, seems to contradict earlier (adaptive) interpretations for the existence of audience-induced changes in male mate choice behavior [35,43,103]. However, we argue that those hypotheses can be viewed as ultimate explanations, i.e., hypotheses regarding the adaptive significance of audience effects, while our present study provides a potential proximate explanation for audience effects (i.e., a causal linkage to social responsiveness). Consistent variation in social responsiveness among individuals may actually represent the substrate on which selection acts to create differences among populations and species in average levels of male MCC and the degree to which males respond to rival presence by showing audience effects. Establishing this correlation empirically by comparing different poeciliid species or independently evolving populations of the same species represents a logic next step to test our hypothesis.

ACKNOWLEDGEMENT

We like to thank Jiancao Gao, Xu Ouyang, Lihong Wang, Linjun Zhou, Meifeng Xie, Binghua Liu, Diana Umutoni and Xiaoqin Wang for help with animal care.

ETHICAL STATEMENT

All experiments reported here comply with current laws and regulations of the PRC and were approved by the Animal Welfare commissioner at the Department of Animal Science of the College of Animal Science and Technology. Our research was supported by Talent Support Funding (Z111021403 and Z111021501) and Scientific Start-up Funding for Doctors (2452015350) of Northwest A&F University. The authors declare no conflict of interest. All authors agreed on the publication of the data presented here and contributed during manuscript writing.

REFERENCES

- [1] Brown, C., and Laland, K.N., *Fish Fisheries*, 2003. 4: pp. 280-288.
- [2] Danchin, E., et al., *Science*, 2004. 305: pp. 487-491.
- [3] Laland, K.N., *Learn Behav*, 2004. 32: pp. 4-14.
- [4] Valone, T.J., *Behav Ecol Sociobiol*, 2007. 62: pp. 1-14.
- [5] Bshary, R., Gingins, S., and Vail, A.L., *Trends Cogn Sci*, 2014. 18: pp. 465-471.
- [6] Laland, K.N., and Williams, K., *Anim Behav*, 1997. 53: pp. 1161-1169.
- [7] Swaney, W., et al., *Anim Behav*, 2001. 62: pp. 591-598.
- [8] Westneat, D.F., et al., *Anim Behav*, 2000. 59: pp. 467-476.
- [9] Witte, K., Kniel, N., and Kureck, I.M., *Curr Zool*, 2015. 61: pp. 1073-1081.
- [10] Gibson, R.M., and Höglund, J., *Trends Ecol Evol*, 1992. 7: pp. 229-232.
- [11] Rendell, L., et al., *Science*, 2010. 328: pp. 208-213.
- [12] Dubois, F., Drullion, D., and Witte, K., *Behav Ecol*, 2012. 23: pp. 225-231.
- [13] Höglund, J. et al., *Anim Behav*, 1995. 49: pp. 1627-1633.
- [14] Witte, K., and Ryan, M.J., *Anim Behav*, 2002. 63: pp. 943-949.
- [15] Goulet, D., and Goulet, T.L., *Behav Ecol*, 2006. 17: pp. 998-1003.
- [16] Alonzo, S.H., *Anim Behav*, 2008. 75: pp. 1715-1723.
- [17] Godin, J.-G.J., and Hair, K.P.E., *Behaviour*, 2009. 146: pp. 1443-1461.
- [18] Galef, B.G., and White, D.J., *Anim Behav*, 1998. 55: pp. 545-552.
- [19] White, D.J., and Galef, B.G., *Anim Behav*, 1999. 57: pp. 465-473.
- [20] Witte, K., and Ueding, K., *Behav Ecol*, 2003. 14: 389-395.
- [21] Witte, K., and Godin, J.-G.J., *Behav Ecol*, 2009. 21: pp. 193-194.

- [22] Mery, F., et al., *Curr Biol*, 2009. 19: pp. 730-734.
- [23] Pruett-Jones, S., *Am Nat*, 1992. 140: pp. 1000-1009.
- [24] Dugatkin, L.A., 1996. *Academic*, San Diego: pp. 85-105.
- [25] Dugatkin, L.A., *Am Nat*, 1992. 139: pp. 1384-1389.
- [26] Dugatkin, L.A., and Godin, J.-G.J., *Proc R Soc Lond B*, 1992. 249: pp. 179-184.
- [27] Schlupp, I., Marler, C., and Ryan, M., *Science*, 1994. 263: pp. 373-374.
- [28] Widemo, M.S., *Behav Ecol*, 2006. 17: pp. 255-259.
- [29] Frommen, J.G., et al., *Evol Ecol*, 2009. 23: pp. 435-446.
- [30] Moran, R.L., von Ende, C.N., and King, B.H., *Behaviour*, 2013. 150: pp. 1255-1274.
- [31] Zimmer, C., et al., 2014. *Nova Science Publishers, Hauppauge*, NY: pp. 69-92.
- [32] Auld, H.L., and Godin, J.-G.J., *Behav Ecol Sociobiol*, 2015. 69: pp. 1795-1807.
- [33] Schlupp, I., and Ryan, M.J., *Behav Ecol*, 1997. 8: pp. 104-107.
- [34] Bierbach, D., et al., *Behav Ecol Sociobiol*, 2011. 65: pp. 1699-1707.
- [35] Plath, M., and Bierbach, D., *Comm Integr Biol*, 2011. 4: pp. 276-280.
- [36] Godin, J.-G.J., Herdman, E.J.E., and Dugatkin, L.A., *Anim Behav*, 2005. 69: pp. 999-1005.
- [37] Witte, K., and Noltenmeier, B., *Behav Ecol*, 2002. 52: pp. 194-202.
- [38] Heubel, K.U., et al., *Behaviour*, 2008. 145: pp. 1041-1064.
- [39] Bisazza, A., Marconato, A., and Marin, G., *Ethology*, 1989. 83: pp. 335-343.
- [40] Head, M.L., et al., *Anim Behav*, 2015. 103: pp. 99-105.
- [41] Wolf, M., van Doorn, G.S., and Weissing, F.J., *Proc R Soc Lond B*, 2011. 278: pp. 440-448.
- [42] Bierbach, D., et al., *Behav Ecol*, 2015. 26: pp. 1314-1325.
- [43] Plath, M., and Schlupp, I., *Comm Integr Biol*, 2008. 1: pp. 199-203.
- [44] Plath, M., Kromuszczynski, K., and Tiedemann, R., *Behav Ecol Sociobiol*, 2009. 63: pp. 381-390.
- [45] Dosen, L.D., and Montgomerie, R., *Behav Ecol Sociobiol*, 2004, 55: pp. 266-271.
- [46] Wong, B.B.M., and McCarthy, M., *Behav Ecol*, 2009. 20: pp. 278-282.
- [47] Mautz, B.S., and Jennions, M.D., *Behav Ecol*, 2011. 22: pp. 769-775.
- [48] Plath, M., et al., *Anim Behav*, 2008. 75: pp. 21-29.
- [49] Plath, M., et al., *Curr Biol*, 2008. 18: 1138-1141.
- [50] Ziege, M., et al., *Front Zool*, 2009. E6:17.
- [51] Makowicz, A.M., Plath, M., and Schlupp, I., *Behav Proc*, 2010. 85: pp. 36-41.
- [52] Nöbel, S., and Witte, K., *PlosOne*, 2013. 8:e53865.
- [53] Makowicz, A.M., Plath, M., and Schlupp, I., *Behaviour*, 2010. 147: pp. 1657-1674.
- [54] Auld, H.L., Jeswiet, S.B., and Godin, J.-G.J., *Behav Ecol Sociobiol*, 2015. 69: pp. 1191-1199.
- [55] Réale, D., et al., *Biol Rev*, 2007. 82: pp. 291-318.
- [56] Johnstone, R.A. and Manica, A., *Proc Natl Acad Sci USA*, 2011. 108: pp. 8373-8378.
- [57] Wolf, M., and McNamara, J.M., *Trends Ecol Evol*, 2013. 28: pp. 253-254.
- [58] Taborisky, B., and Oliveira, R.F., *Trends Ecol Evol*, 2013. 28: pp. 254-255.
- [59] Trompf, L., and Brown, C., *Anim Behav*, 2014. 88: pp. 99-106.

- [60] Kurvers, R.H.J.M., et al. *Ecol Lett*, 2010. 13: pp. 829-837.
- [61] Slagsvold, T., et al., *Anim Behav*, 1988. 136: pp. 1000-1009.
- [62] Stöhr, S., *Anim Behav*, 1998. 55: pp. 893-903.
- [63] Dall, S.R.X., et al., *Trends Ecol Evol*, 2005. 20: pp. 187-193.
- [64] Schuett, W., Tregenza, T., and Dall, S.R.X., *Biol Rev*, 2010. 85: pp. 217-246.
- [65] Rosa, P., Nguyen, V., and Dubois, F., *Behav Ecol Sociobiol*, 2012. 66: pp. 1259-1265.
- [66] Brown, C., and Braithwaite, V.A., *Anim Behav*, 2004. 68: pp. 1325-1329.
- [67] Riesch, R., et al., *Behav Ecol Sociobiol*, 2009. 63: pp. 1515-1526.
- [68] Côte, J., et al., *Proc R Soc Lond B*, 2010. 277: pp. 1571-1579.
- [69] Côte, J., et al., *Proc R Soc Lond B*, 2011. 278: 1670-1678.
- [70] Wilson, A.D.M., Godin, J.-G.J., and Ward, A.J.W., *Ethology*, 2010. 116: pp. 96-104.
- [71] Burns, J.G., *J Comp Psychol*, 2008. 122: pp. 344-356.
- [72] Ward, A.J.W., et al., *Behav Ecol Sociobiol*, 2004. 55: pp. 561-568.
- [73] Côte, J., Fogarty, S., and Sih, A., *Anim Behav*, 2012. 83: 1469-1476.
- [74] Jolles, J.W., et al., *Anim Behav*, 2015. 99: pp. 147-153.
- [75] Franck, D., *Z Tierpsychol*, 1975. 38: pp. 472-481.
- [76] Brydges, N.M., *J Anim Ecol*, 2008. 77: pp. 229-235.
- [77] Wilson, A.D.M., and Godin, J.-G.J., *Behav Ecol*, 2009. 20: 231-237.
- [78] Biro, P.A., Beckmann, C., and Stamps, J.A., *Proc R Soc Lond B*, 2010. 277: pp. 71-77.
- [79] Harris, S., et al., *Oikos*, 2010. 119: 1711-1718.
- [80] Moretz, J.A., Martins, E.P., and Robison, B.D., *Behav Ecol*, 2007. 18: pp. 556-562.
- [81] Archard, G.A., and Braithwaite, V.A., *J Fish Biol*, 2011. 78: pp. 593-601.
- [82] Plath, M., and Strecker, U., *Behav Ecol Sociobiol*, 2008. 62: pp. 1727-1737.
- [83] Dziewczynski, T.L., and Crovo, J.A., *J Fish Biol*, 2011. 79: pp. 776-788.
- [84] Galton, F., *J Anthropol Inst GB Ireland*, 1886. 15: pp. 246-263.
- [85] Barnett, A.G., van der Pols, J.C., and Dobson, A.J., *Intern J Epidem*, 2005. 34: pp. 215-220.
- [86] Kelly, C., and Price, T.D., *Am Nat*, 2005. 166: pp. 700-707.
- [87] Witte, K., and Ryan, M.J., *Behav Ecol*, 1998. 9: pp. 534-539.
- [88] Bierbach, D., et al., *Research*, 2013. 2:75.
- [89] Callander, S., Backwell, P.R.Y., and Jennions, M.D., *Behav Ecol*, 2012. 23: pp. 355-360.
- [90] McPeck, M.A., *Behav Ecol*, 1992. 3: pp. 1-12.
- [91] Sih, A., Bell, A., and Johnson, J.C., *Trends Ecol Evol*, 2004. 19: pp. 372-378.
- [92] Sih, A., et al., *Quart Rev Biol*, 2005. 79: pp. 241-277.
- [93] Bell, A.M., *Proc R Soc Lond B*, 2007. 274: pp. 755-761.
- [94] Wolf, M., van Doorn, S., and Weissing, F.J., *Proc Natl Acad Sci*, 2008. 105: pp. 15825-15830.
- [95] Brock, V.E., and Riffenburgh, R.H., *J Cons Perm Int Explor Mer*, 1960. 25: pp. 307-317.
- [96] Seghers, B.H., *Evolution*, 1974. 28: pp. 486-489.
- [97] Magurran, A.E., *Annal Zool Fenn*, 1990. 27: pp. 51-66.

- [98] Magurran, A.E., and Seghers, B.H., *Behaviour*, 1991. 118: pp. 214-234.
- [99] Evans, J.P., and Magurran, A.E., *Proc Natl Acad Sci USA*, 2000. 97: pp. 10074-10076.
- [100] Greven, H., Ecology and evolution of poeciliid fishes (book), 2010. *The University of Chicago press, Chicago and London*: pp. 3-17.
- [101] Parker, G.A., *Biol Rev*, 1970. 45: pp. 525-567.
- [102] Houde, A.E., Sex, colour, and mate choice in guppies (book), 1997. *Princeton University Press*.
- [103] Dubois, F., *Behav Ecol Sociobiol*, 2015. 69: pp. 183-191.