1 Different preference functions act in unison: mate 2 choice and risk-taking behaviour in the Atlantic 3 molly (*Poecilia mexicana*)
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Abstract

14 Consistent individual differences in behaviour (animal personality) are widespread throughout
15 the Animal Kingdom. This includes variation in risk-taking versus risk-averse behavioural
16 tendencies. Variation in several personality dimensions is associated with distinct fitness
17 consequences and thus, may become a target of natural and/or sexual selection. However, the
18 link between animal personality and mate choice—as a major component of sexual
19 selection—remains understudied. We asked (1) whether females and males of the livebearing
20 fish *Poecilia mexicana* prefer risk-taking mating partners (directional mating preference), (2)
21 or if their preferences are dependent on the choosing individual's own personality type
22 (assortative mating). We characterized each test subject for its risk-taking behaviour, assessed
23 as the time to emerge from shelter and enter an unknown area. In dichotomous association
24 preference tests, we offered two potential mating partners that differed in risk-taking
25 behaviour but were matched for other phenotypic traits (body size, shape, and colouration).
26 Females, but not males, exhibited a strong directional preference for risk-taking over risk-
27 averse mating partners. At the same time, the strength of females' preferences correlated
28 positively with their own risk-taking scores. Our study is the first to demonstrate that a strong
29 overall preference for risk-taking mating partners does not preclude effects of choosing
30 individuals' own personality type on (subtle) individual variation in mating preferences. More
31 generally, two different preferences functions appear to interact to determine the outcome of
32 individual mate choice decisions.
33

34 ***Keywords***: Animal personality, sexual selection, female choice, male mate choice, boldness

35

Introduction

37 Behavioural differences among individuals that are consistent over time and across contexts

38 (animal personality or temperament) can be found throughout the Animal Kingdom (Gosling,

39 2001; Kralj-Fišer & Schuett, 2014; Weiss, 2018). Additive genetic effects contribute to

40 variation in animal personality traits (Dochtermann, Schwab & Sih, 2015), and heritability

41 estimates are often comparable to those reported for life-history and physiological traits

42 (Dochtermann, Schwab, Anderson Berdal, Dalos & Royauté, 2019). This renders animal

43 personality a potential target of both natural and sexual selection (Dingemanse & Réale, 2005;

44 Schuett, Tregenza & Dall, 2010). Accordingly, several empirical studies demonstrated fitness

45 consequences for different personality dimensions, such as boldness (risk-taking behaviour),

46 exploration and sociability (Ballew, Mittelbach & Scribner, 2017; Cote, Dreiss & Clobert,

47 2008; Dingemanse, Both, Drent & Tinbergen, 2004).

48   A meta-analysis across taxonomic groups suggested that individual variation along the

49 continuum between risk-taking and risk-averse behaviour—the most studied animal

50 personality dimension—tends to be associated with an increased reproductive success of risk-

51 taking individuals, particularly males (Smith & Blumstein, 2008). It remains controversial,

52 however, what mechanisms might explain fitness variation among behavioural types and

53 whether sexual selection (e.g. female choice in favour of risk-taking mating partners) plays a

54 role in this context (Schuett, Tregenza & Dall, 2010; Smith & Blumstein, 2008). Female

55 guppies (*Poecilia reticulata*), for example, preferred risk-taking over risk-averse males when

56 risk-taking tendencies were experimentally manipulated by presenting single males close to

57 (or away from) predators (Godin & Dugatkin, 1996). The question remains as to whether

58 females would be able to assess actual male personality types independent of males'

59 behavioural responses to predators. Females could base their mate choice on correlated

60   phenotypic traits, as risk-taking behavioural tendencies (and other personality traits) can be

61   associated with variation in traits like body colouration, or size (Brown, Jones & Braithwaite,

62   2007; Schweitzer, Montreuil & Dechaume-Moncharmont, 2015). However, even if those

63   phenotypic traits are carefully matched between experimentally presented potential mating

64   partners—as we did in our present study (see below)—systematic co-variation between risk-

65   taking behavioural tendencies and other behaviours could be used for mate assessment. This

66   includes differences in swimming patterns (Kern, Robinson, Gass, Godwin & Langerhans,

67   2016; Wilson & Godin, 2009), body posture, or readiness to resume normal swimming

68   behaviour after disturbance (Brown, Jones & Braithwaite, 2005; Sommer-Trembo & Plath,

69   2018; this study).

70   While some studies suggest the existence of a directional preference for risk-taking

71   mating partners, others reported contrasting patterns in that risk-taking females preferred risk-

72   taking males and *vice versa*, leading to assortative mating (Jiang, Bolnick & Kirkpatrick,

73   2013). Assortative mating can affect individuals' reproductive success (Both, Dingemanse,

74   Drent & Tinbergen, 2005; Kralj-Fišer, Sanguino Mostajo, Preik, Pekár & Schneider, 2013;

75   Scherer, Kuhnhardt & Schuett, 2017). For instance, guppy females that were paired with

76   males showing similar risk-taking tendencies had a higher parturition success than females

77   that were paired disassortatively (Ariyomo & Watt, 2013).

78   Here, we present a test for directional mate choice and/or assortative mating based on

79   individuals' risk-taking behaviour in the livebearing fish *Poecilia mexicana*. For the first time,

80   we assessed both male and female mating preferences. While the importance of male mate

81   choice is increasingly acknowledged (Edward & Chapman, 2011), studies on male mate

82   choice for female personality types are virtually absent. We used emergence tests (Brown,

83   Jones & Braithwaite, 2005; Sommer-Trembo & Plath, 2018) to assess individuals' risk-taking

84   behaviour. *Poecilia mexicana* (including the population studied here) has repeatedly been

85   characterized for risk-taking behaviour, and previous studies reported high behavioural

3

86   repeatability, with R-values ranging between 0.53 and 0.64 (*freezing time after a simulated*

87   *predator attack*, R = 0.64, Sommer-Trembo et al., 2016a; repeatability across *time to emerge*

88   *from shelter* and *freezing time after a simulated predator attack*, R = 0.53, Sommer-Trembo

89   & Plath, 2018). Slightly lower, yet significant R-values were reported for the related guppy

90   (*time to emerge from shelter*, R = 0.51, Brown & Irving, 2013; *time to emerge from shelter*, R

91   = 0.51 for females and R = 0.36 for males, Irving & Brown, 2013; *time to emerge from*

92   *shelter*, R = 0.33, White, Kells & Wilson, 2016) and other poeciliid fishes (e.g., *Gambusia*

93   *affinis*, *time to emerge from shelter*, R = 0.29 in Cote, Fogarty, Weinersmith, Brodin & Sih,

94   2010 and R = 0.39 in Gomes-Silva, Liu, Chen, Plath & Sommer-Trembo, 2017; *Poecilia*

95   *vivipara*, *time to emerge from shelter*, R = 0.70, Sommer-Trembo et al. 2016b). For our

96   present study, we initially screened a large number of potential stimulus and focal individuals

97   so as to be able to select stimulus pairs with contrasting behavioural type (see methods). This

98   time-consuming approach led us to decide to not assess behavioural repeatability, but we

99   argue that behavioural repeatability of risk-taking tendencies is well established in our study

100 species.

101   We performed dichotomous mate choice tests in which focal individuals could choose

102 between two stimulus individuals of the opposite sex that differed in risk-taking tendencies

103 but were matched for other phenotypic traits known to be involved in mate assessment (body

104 size, shape and colouration; Rios-Cardenas & Morris, 2011). This left only behavioural

105 characteristics correlated with risk-taking tendencies as a potential source for mate

106 assessment. We asked whether focal individuals prefer risk-taking over risk-averse mating

107 partners (directional preference) and/or whether a pattern indicative of assortative mating

108 would be uncovered. Either result would indicate that focal individuals were able to assess the

109 behavioural type of potential mating partners within the short time period of our mate choice

110 tests (focal and stimulus individuals were unfamiliar prior to the tests) and without an

111 opportunity to observe interactions with predators.

112   While predictions may seem to be mutually exclusive when considering the potential

113   occurrence of directional mating preferences or assortative mating, we argue that this is

114   actually not the case: focal individuals [at least females (Godin & Dugatkin, 1996)] could

115   show an overall (directional) preference for risk-taking mating partners. Still, 'hidden' within

116   the individual variation in mating preferences, focal individuals' own risk-taking tendencies

117   might predict the strength at which individuals express this mating preference. Our present

118   study confirms that both preference functions indeed act in unison and jointly explain female

119   (but not male) mate choice for risk-taking mating partners.

120

Materials and methods

Test subjects and general testing procedure

123   Test subjects were laboratory-reared descendants of wild-caught Atlantic mollies (*Poecilia*

124   *mexicana*), which we collected in the southern Mexican Río Oxolotán in 2013. We

125   maintained the fish in several aerated and filtered 200-L stock tanks at 28°C under a 12/12 h

126   light/dark cycle. Our stock tanks comprised juveniles and adults of both sexes at densities of

127   50–70 adult individuals per tank. We fed the fish twice a day *ad libitum*-amounts of

128   commercially available flake food (Tetra Min®), frozen spinach, *Artemia* naupliae and frozen

129   bloodworms (*Chironomus* larvae). Aquaria were equipped with live and artificial plants and

130   stones. To maintain water quality, we replaced half of the water by aged tap water every 2

131   weeks. Focal and stimulus fish for the mate choice tests were taken from different stock tanks

132   and were thus unfamiliar prior to the tests.

133   We conducted our behavioural experiments in 2016. Before the behavioural

134   assessments, test subjects were held for three days in same-sex groups at densities of 20

135   individuals per tank. We initially tested a large number of fish ($n = 300$) for risk-taking

136   tendencies, after which they were given three days for recovery before focal individuals and

137   stimulus pairs were selected. We tested a sub-set of $n = 54$ focal individuals (27 females and

138   27 males) for their mating preferences by using dichotomous mate choice tests (see below for

139   details on which individuals were selected for the mate choice tests).

140

Assessment of risk-taking tendencies

142   We used time to emerge from shelter and enter an unknow area as a proxy of individuals'

143   risk-taking tendency (Brown, Jones & Braithwaite, 2005; Sommer-Trembo & Plath, 2018).

144   To this end, the test subject was gently transferred into the shelter compartment of the test

145   tank, which was equipped with stones and artificial plants (see Sommer-Trembo & Plath,

146   2018 for details). After a 3-min acclimatization period (after which all tested individuals

147   showed normal swimming behaviour), we lifted an opaque Plexiglas divider and measured

148   the time until the fish entered the open field area with a uniformly grey bottom and no

149   opportunities for hiding. Based on a pilot study, fish were given a maximum of 60 s to emerge

150   from shelter. We calculated individual risk-taking scores as: [maximum emergence time (60

151   s) – individual emergence time], which resulted in high sores for risk-taking and low scores

152   for risk-averse individuals. 85% of test subject emerged from shelter within 60 s, whereas the

153   other 15% reached the ceiling value of 60 s.

154

Assignment of focal and stimulus individuals

156   Initially, we assessed risk-taking tendencies of $n = 150$ females and $n = 150$ males. We

157   randomly selected 60 of those individuals ($n = 30$ per sex), based on the flip of a coin, which

158   did not undergo any further behavioural test before they served as focal individuals (see

159   below). Of the remaining 240 individuals, we disregarded individuals with intermediate

160   boldness-scores (emergence times between 21 and 39 s) and retained those individuals as

161   potential stimulus fish that could be characterized unambiguously as either risk-taking

162   (emergence times ≤ 20 s) or risk-averse (≥ 40 s).

6

163   We measured the standard length (SL) of all individuals meeting these criteria to the

164   nearest millimetre by laying the fish flat on moist laminated millimetre paper and matched

165   stimulus pairs according to their SL (difference ≤ 3 mm). Body size is known to be an

166   important criterion of mate choice in poeciliids (Bisazza, Marconato & Marin, 1989;

167   Herdman, Kelley & Godin, 2004; Plath, Seggel, Burmeister, Heubel & Schlupp, 2006).

168   Additionally, we visually matched the respective stimulus pairs with respect to body shape

169   and colouration (Fig. 1). However, we refrained from analyses such as spectroradiometric

170   assessments of body coloration (e.g., Dugatkin & Godin, 1996; Jordan et al., 2004) so as to

171   avoid stressful anaesthesia or other forms of handling before the mate choice tests. Following

172   this procedure, we successfully assigned 54 stimulus pairs ($n = 27$ per sex).

173   Of the 60 fish that were initially selected to serve as potential focal individuals, we

174   randomly selected $n = 27$ individuals per sex as focal individuals for our mate choice tests and

175   tested each focal individual with a different stimulus pair. To keep stress levels before the

176   mate choice test as low as possible, SL of the focal fish was measured only after the mate

177   choice tests. Upon completion of the behavioural tests, all fish were retransferred into their

178   original stock tanks.
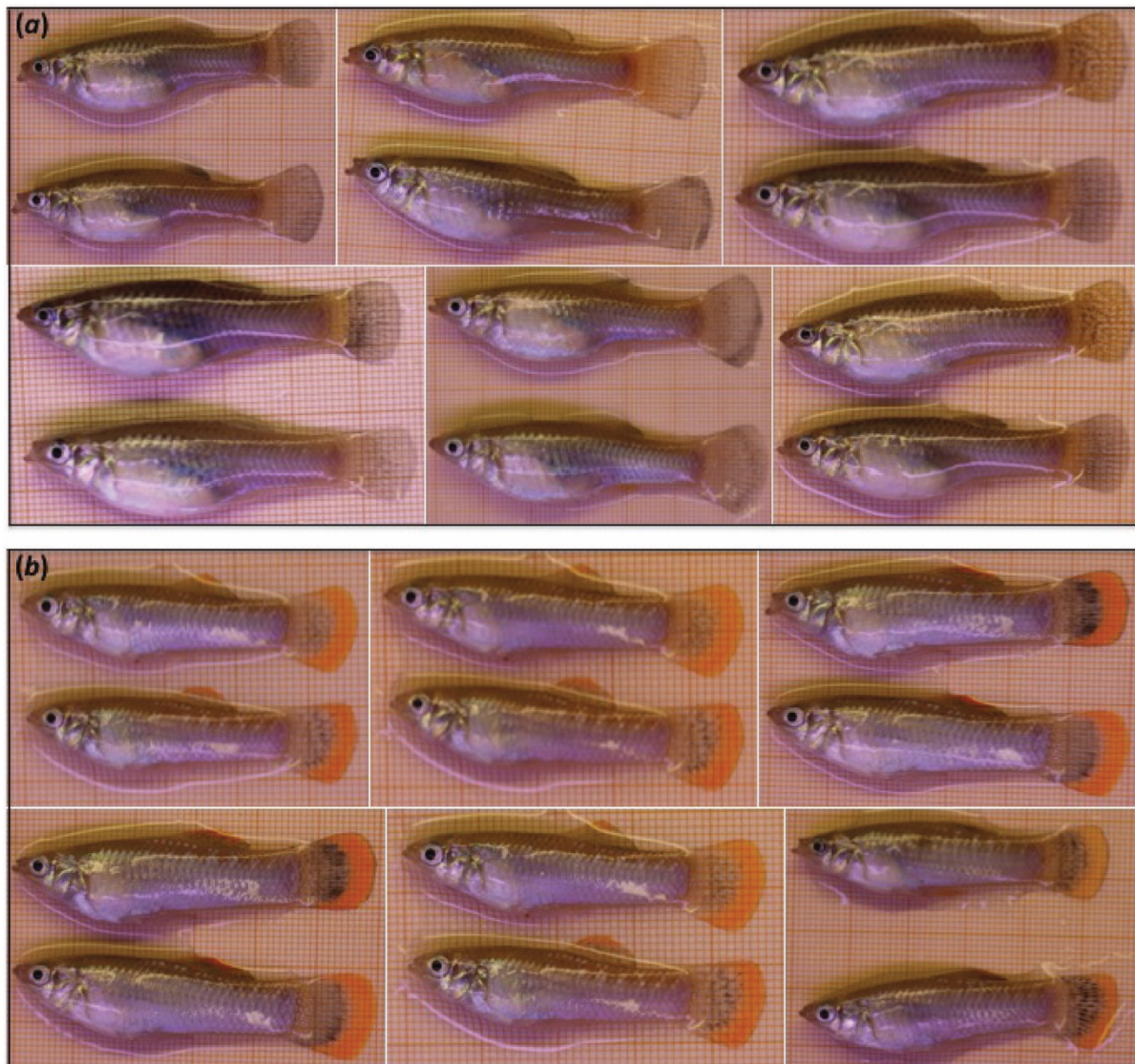
Figure 1

Examples of stimulus pairs (*a* females; *b* males), matched for standard length, body shape and colouration.

Mate choice tests

During the association preference tests, a focal individual could choose between a risk-taking and a risk-averse mating partner. The test tank ($60 \times 25 \times 35$ cm) was divided into a central neutral zone (30 cm) and two lateral preference zones (15 cm each) adjacent to the stimulus compartments, which were separated from the main tank by transparent Plexiglas sheets (see Sommer-Trembo et al., 2016 for details). The focal fish was allowed to move freely between zones during a 5-min observation period, during which we scored times spent in either of the preference zones. We then switched side assignments of both stimulus individuals to avoid

8

191 potential side biases and repeated measurement of association times. We summed times spent

192 in association with either stimulus individual during the entire 10-min testing period.

193 We calculated strength of preference (SOP)-scores for risk-taking mating partners as:

194 (time spent with risk-taking stimulus – time spent with risk-averse stimulus) / total association

195 time. Thus, an SOP-score of +1 reflects maximal preference for the risk-taking stimulus and -

196 1 maximal preference for the risk-averse stimulus fish.

197

Statistical analyses

199 All statistical tests were conducted using SPSS version 24.0. Where parametric tests were

200 used, dependent variables met the assumptions of normal error distribution and

201 homoscedasticity. Analyses were conducted separately for males and females.

202 To test for a directional preference for risk-taking mating partners, we used paired *t*-

203 tests and compared association times near both types of stimulus individuals. We compared

204 risk-taking scores and SOP-values between sexes using non-parametric Mann-Whitney *U*-

205 tests. To test for potential effects of choosing individuals' own personality (assortative mate

206 choice), we ran univariate General Linear Models (GLM) using SOP-scores as the dependent

207 variable and focal individuals' risk-taking behaviour as a covariate. Due to limited sample

208 sizes, we could not include all potentially biologically meaningful additional explanatory

209 variables (size difference of risk-taking stimulus – risk-averse stimulus; focal individuals'

210 SL). However, when those covariates were included alongside focal individuals' risk-taking

211 behaviour in alternative GLMs, neither their main effects ($F_{1,24} < 0.54$, $P > 0.47$) nor

212 interactions with risk-taking scores ($F_{1,23} < 0.70$, $P > 0.41$) were significant. Hence, in our

213 main GLMs, the mean SL of the stimulus individuals and focal individuals' risk-taking scores

214 served as covariates. We excluded the non-significant interaction terms (females: $F_{1,23} = 0.58$,

215 $P = 0.46$; males: $F_{1,23} = 2.19$, $P = 0.15$).

216

Results

Males tended to be more risk-taking than females (Mean ± S.E. risk-taking-scores, females: 31.2 ± 4.6 s; males: 42.5 ± 3.4 s), but the difference was not statistically significant (Mann-Whitney U-test: $z = 1.60$, $p = 0.11$). Focal females showed a directional preference for risk-taking males and spent 263.4 ± 20.9 s in association with the risk-taking and 151.7 ± 16.9 s near the risk-averse stimulus male (paired t-test: $t_{26} = 3.31$, $p = 0.003$; Fig. 2a). By contrast, focal males did not show a directional preference related to females' propensity to take risks (time spent with risk-taking female: 266.8 ± 23.0 s; with risk-averse female: 220.9 ± 22.8 s; paired t-test: $t_{26} = 1.04$, $p = 0.31$; Fig. 2b). However, strength of preference (SOP)-scores did not differ significantly between sexes (Mann-Whitney U-test: $z = 1.54$, $p = 0.12$).
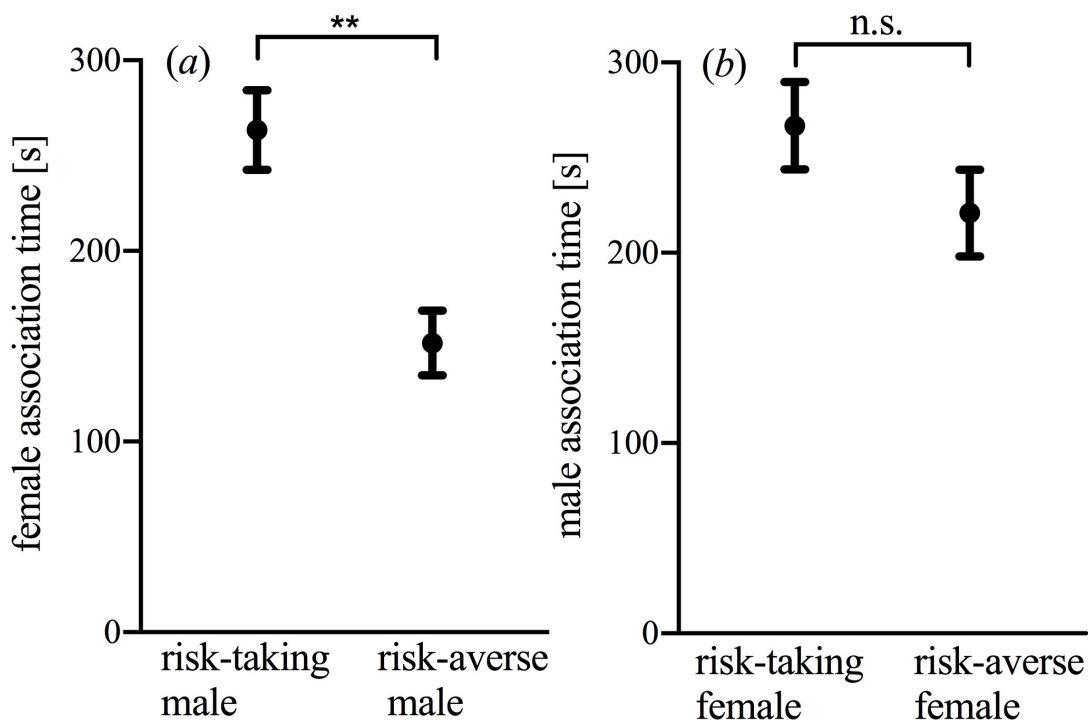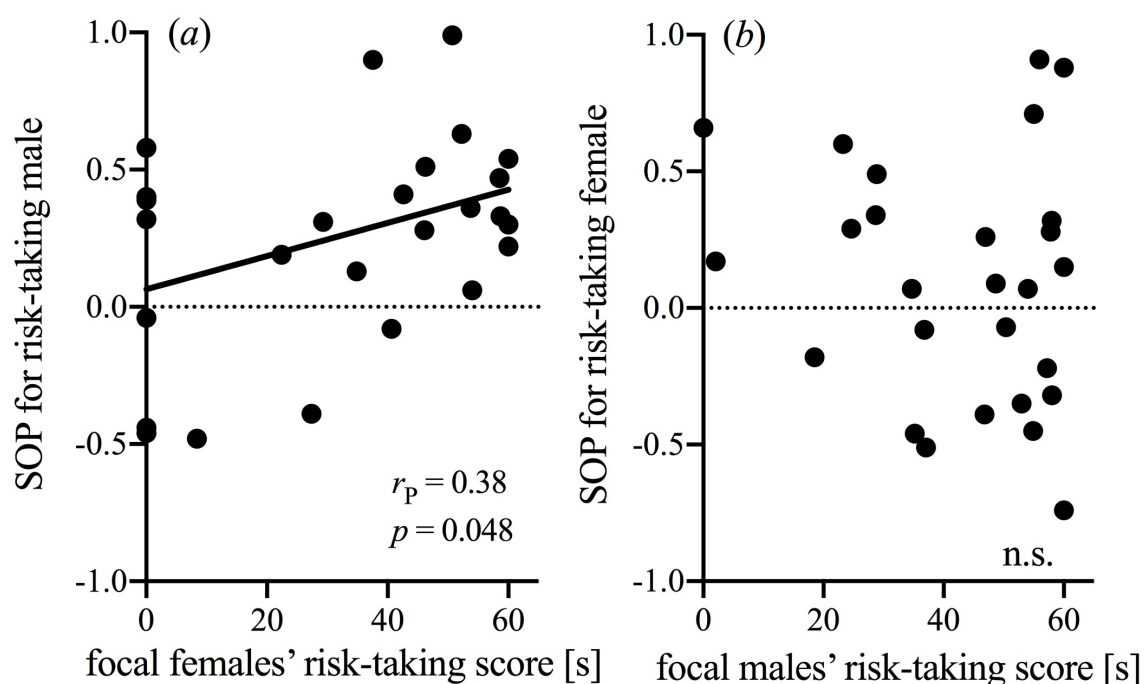

Figure 2
Results of dichotomous preference tests to assess directional mating preferences for risk-taking mating partners. Shown are the mean (± S.E.) times focal individuals (a females, b males) spent associating with risk-taking and risk-averse stimulus individuals of the opposite sex.

234   Focal females' risk-taking tendency had a significant effect on their SOP (GLM, $F_{1,24}$

235    $= 4.94$, $p = 0.036$; mean SL of stimulus males: $F_{1,24} = 2.28$, $p = 0.14$). A *post-hoc* Pearson

236   correlation confirmed a significant, positive correlation between both variables (Fig. 3*a*).

237   Neither focal males' risk-taking tendency ($F_{1,24} = 0.56$, $p = 0.46$; Fig. 3*b*) nor the stimulus

238   females' mean body size (SL; $F_{1,24} = 0.21$, $p = 0.65$) had statistically significant effects on

239   males' SOP.

240

Figure 3
Scattergrams showing the correlation between focal individuals' own risk-taking scores and their strength of preference (SOP) for risk-taking mating partners (testing for assortative mate choice). Females (*a*) but not males (*b*) showed a pattern where the choosing individual's risk-taking tendency predicted variation in SOP-values, and risk-taking females showed stronger preferences for risk-taking stimulus males (*post-hoc* Pearson correlation).

Discussion

250   Animal personality represents a major component of intraspecific phenotypic variation (Wolf

251   & Weissing, 2012), but whether and how sexual selection (e.g., through mate choice) affects

252   personality distributions remains understudied (Schuett, Tregenza & Dall, 2010). Using the

253   livebearing fish *Poecilia mexicana*, we investigated whether a directional mating preference

254   for risk-taking mating partners provides those individuals with a reproductive advantage

255   (Godin & Dugatkin, 1996; Kortet, Niemelä, Vainikka & Laakso, 2019) and/or if the strength

256   of preference for risk-taking individuals would be dependent on the choosing individuals'

257   own tendency to take risks (assortative mate choice; Scherer, Kuhnhardt & Schuett, 2017).

258   We found a pattern in which both preference functions appear to interact: female (but not

259   male) *P. mexicana* generally preferred risk-taking over risk-averse mating partners, but the

260   strength of preference (SOP) for risk-taking males was dependent on the choosing females'

261   own personality type (i.e. risk-taking females exhibited stronger preferences for risk-taking

262   males than risk-averse females).

263   A multitude of studies on mate choice considered mean preferences across individuals

264   and inferred the existence of directional preferences for certain phenotypic traits (e.g., Kodric-

265   Brown, 1985; Maan & Cummings, 2009; Marler & Ryan, 1997). In those cases, it often

266   remains difficult to explain how additive genetic variance of the traits under sexual selection

267   is maintained in natural populations (Brooks & Endler, 2001; Hoekstra et al., 2001; Morris,

268   Nicoletto & Hesselman, 2003; Gasparini, Serena & Pilastro, 2013). Our results suggest that

269   effects of the choosing individuals' personality type could contribute to the maintenance of

270   this variation, as they produce individual variation in mating preferences. Future studies in

271   this and other species will need to consider the fact that the effects we describe here can easily

272   be overlooked when research merely focusses on (more obvious) directional preferences,

273   neglecting the potential drivers/correlates of individual variation in those preferences.

274   In our current study, personality differentially affected female and male mate choice.

275   We argue that the adaptive significance of choosing risk-taking mating partners differs

276   between sexes: in group-living animals, risk-taking is often associated with aggression and

277   dominance (Colléter & Brown, 2011; Dahlbom, Lagman, Lundstedt-Enkel, Sundström &

278   Winberg, 2011). Social dominance, in turn, can be a correlate of mating success in fish and

279   other animals, especially in males (Ellis 1995; Jacob, Evanno, Renai, Sermier & Wedekind,

280   2009; Paull et al., 2010). In *P. mexicana*, dominant males monopolize and defend groups of

281   females (Bierbach et al., 2014), and females receive less sexual harassment from those males

282   (Plath, Parzefall & Schlupp, 2003). Choosing risk-taking mating partners, therefore, likely

283   provides both direct and indirect (genetic) benefits to females. Moreover, females likely base

284   their mate choice on certain phenotypic traits of males that are correlated with/indicative of

285   risk-taking (including behaviour, see below), and the strength of this correlation could simply

286   be weaker or absent in females.

287   Why did risk-taking females show a stronger preference for risk-taking males than

288   risk-averse ones? One possible explanation would be that a trade-off between benefits of

289   mating with risk-taking males and reproductive benefits of assortative mating (Ariyomo &

290   Watt, 2013; Both, Dingemanse, Drent & Tinbergen, 2005; Kralj-Fišer, Sanguino Mostajo,

291   Preik, Pekár & Schneider, 2013; Scherer, Kuhnhardt & Schuett, 2017) explains females' mate

292   choice. Moreover, risk-taking males tend to be more aggressive (Sih, Bell & Johnson, 2004)

293   and risk-taking females could be more willing to accept the risk of interacting with aggressive

294   males than risk-averse females.

295   Our results prompt the question of how exactly females discriminated between risk-

296   taking and risk-averse males. We carefully matched stimulus males for morphological traits

297   known to be involved in mate assessment. Nevertheless, females could differentiate between

298   bold and shy males within the short time (10 min) of our behavioural tests. We may have

299   overlooked subtle variation of certain (non-behavioural) traits that might correlate with

300   differences in risk-taking tendencies, such as the intensity of male sexual ornamentation, but

301   we consider this explanation unlikely. We argue in favour of another explanation: while

302   females could not assess males' responses to predators (Godin & Dugatkin 1996; Scherer,

303   Kuhnhardt & Schuett 2017), variation in risk-taking likely correlates with other behavioural

304   traits that females could evaluate during mate choice, especially males' swimming patterns

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305   (Kern, Robinson, Gass, Godwin & Langerhans, 2016; Wilson & Godin, 2009), body posture,

306   or time to emerge after disturbance (Brown, Jones & Braithwaite, 2005; Sommer-Trembo &

307   Plath, 2018; this study), as slight disturbances occurred during the mate choice tests through

308   handling, e.g. when switching stimulus males between the lateral compartments. Tracking

309   programmes based on deep learning are currently being developed, which will enable us to

310   analyse movement patterns of fish in unparalleled detail (e.g. Graving et al., 2019). It would

311   be desirable to conduct a follow-up study using this state-of-the-art technology to investigate

312   what components of movement patterns characterize different personality types and how

313   these affect mate choice decisions.

314   Overall then, while mate choice based on directional preferences (Godin & Dugatkin

315   1996; Kortet, Niemelä, Vainikka & Laakso 2012; Reaney & Backwell) and assortative mate

316   choice (Ariyomo & Watt, 2013; Both, Dingemanse, Drent & Tinbergen, 2005; Kralj-Fišer,

317   Sanguino Mostajo, Preik, Pekár & Schneider, 2013; Scherer, Kuhnhardt & Schuett, 2017)

318   seem to be mutually exclusive mechanisms, our results suggest that the existence of a

319   directional preference does not preclude effects of choosing individuals' personality on

320   individual variation in mating preferences.

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