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Male phenotypic diversity experienced during ontogeny mediates female mate choice in Trinidadian guppies

Abbreviated title: Male diversity and female mate choice in guppies

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Abstract

Early social experience can be important in shaping female mate choice. Previous work has shown that females adjust their decisions based on the distribution of male sexual trait values encountered during development. However, other phenotypic features could be important in the formation of mate preferences if, for example, they provide additional information about the males available. Here, we examined how the level of overall phenotypic variance (independent of trait values) experienced during ontogeny, mediated female choice in guppies, *Poecilia reticulata*. Developing females were reared with males either all different in colouration or all similar in colouration or with adult females representing high variance, low variance and no experience of male variance respectively. We found that females were more sexually responsive when reared with females only than in either of the male treatments. When reared with males, responsiveness was greater in the low-variance compared to the high variance treatment. Moreover, females had stronger sexual preferences following rearing in the high variance compared to the low variance condition. In turn, males switched mating tactics, increasing the rate of coerced copulation attempts when facing choosier females, possibly to balance the loss in mating opportunities. Taken together, these results demonstrate the adaptive plasticity of female mating decisions and the dynamic selection pressures they might impose on the evolution of male sexual traits, potentially contributing to the maintenance of the extreme polymorphism found in male colour patterns.

Keywords: Mate choice, early social environment, ontogeny, adaptive plasticity, colour pattern polymorphism, *Poecilia reticulata*
Introduction

Research on female mating preferences has historically focused on the role of average preferences on the evolution of elaborated male traits and species recognition (Andersson and Simmons, 2006; Andersson, 1994). However, a growing body of evidence suggests there is substantial phenotypic variation among and within females in mate choice behaviour and this can have significant ecological and evolutionary implications (Ah-King and Gowaty, 2016; Brooks, 2002; Brooks and Endler, 2001; Jennions and Petrie, 1997; Widemo and Saether, 1999). This variability has been linked to genetic differences (Bakker and Pomiankowski, 1995; Brooks, 2002; Jennions and Petrie, 1997; Widemo and Saether, 1999), environmental factors (e.g. perceived predation risk (Johnson and Basolo, 2003; Kim et al., 2009), signalling environment (Endler, 1991; Gordon and Uetz, 2011)), intrinsic factors (e.g. female age and condition (Coleman et al., 2004; Cotton et al., 2006), cost of sampling males (Milinski and Bakker, 1992)), social experience (Jirotkul, 1999; Mery et al., 2009; Rutledge et al., 2010; Witte and Nöbel, 2011) and distinct developmental trajectories (Bailey and Zuk, 2008; Macario et al., 2017). The conditions experienced early in life strongly influence the development of an individual’s morphology, behaviour and cognition (Buchanan et al., 2013; Stamps, 2016; West-Eberhard, 2003), however, some gaps remain in the understanding of the effects of the social context experienced during ontogeny on mate choice.

Developmental plasticity enables juveniles to evaluate environmental conditions and adapt their behaviour accordingly to maximize fitness once adult, especially in variable environments (Kasumovic and Brooks, 2011; West-Eberhard, 2003). In species with parental care, young individuals may use visual (Kendrick et al., 1998), acoustic (Riebel, 2003, 2009) and olfactory (Penn and Potts, 1998) cues displayed by their parents to adjust mate preferences, allowing for the
recognition of conspecifics as prospective partners. However, mate preferences can also be formed during ontogeny in group living species with no parental care referred to as “oblique imprinting” (Hebets and Sullivan-Beckers, 2010). This type of mate choice imprinting in which juveniles learn characteristics of nonparental adults encountered during development has received considerably less attention than “parental imprinting” and its potential evolutionary consequences have not been fully explored.

Previous studies on oblique imprinting have investigated how the manipulation of secondary sexual traits known to be good predictors of mating success affected the outcome of mate choice. For example, Macario et al. (2017) found that, in the Trinidadian guppy (Poecilia reticulata), both the values of male coloration experienced as juveniles and the duration of exposure influenced females’ preferences and choosiness. Walling et al. (2008) varied the size of the sword – an important criterion of mate choice in the genus Xiphophorus - to which growing females were exposed and demonstrated that the preference for long swords could be reversed if female experience was restricted to short-sworded males. A similar effect has been observed in the wolf spider Schizocosa ocreata where females shifted their preferences towards males displaying the sexual trait they experienced as juveniles. Hence female S. ocreata previously exposed to only large-tufted males or only small-tufted males chose, as adults, large-tufted and small-tufted males respectively (Stoffer and Uetz, 2016). In the related species S. uetzii, females preferred to associate with the phenotype of males – either brown or black painted legs - encountered while maturing (Hebets, 2003). Moreover, it has been shown that female S. ocreata exposed to males with a mixture of tuft sizes (Stoffer and Uetz, 2016) and female guppies exposed to males with low- and high-orange colouration (Rosenqvist and Houde, 1997) both increased the strength of their mating
preferences. Thus, previous work has considered how ontogenetic exposure to sexual traits that vary quantitatively (e.g. short or long sword, small or large tufts) or qualitatively (e.g. brown or black legs) influenced mate choice. It has also highlighted the importance of perceiving variation in a sexual trait for the development of mate preferences. However, there are still some aspects of the social environment that, to our knowledge, have not been investigated and could potentially drive variation in individual preferences. Sexual displays are often complex, consisting of many different signal components and in species where males display such complex traits, female mate choice is based on these multiples cues (Candolin, 2003). For instance, in guppies, a species in which males display multicomponent colour signals, females favour groups of colours rather than individual colours independently and the preferences for different colour combinations vary depending on the environment (Cole and Endler, 2015). Unlike previous studies which focused on the influence of variation in a single sexually selected trait, we aimed here to analyse how being exposed during development to different levels of variation in overall phenotypes affects the process of mating decision.

We examined how the frequency distribution of whole male phenotypes (independently of the value or salience of any specific secondary sexual trait), experienced during development shaped female mate choice in adult life. Using the Trinidadian guppy, we tested the hypothesis that females adjust their responsiveness to males’ sexual solicitation and preference functions (how potential mates are ranked based on inherent characteristics) following exposure to males with similar colour patterns (low between-male variance) or males with entirely different colour patterns (high between-male variance). The extreme polymorphism found in their coloration (Houde, 1997) and a strong environmental component accounting for phenotypic variation in
female mate choice (Brooks, 2002; Brooks and Endler, 2001) provide an excellent model system to address the developmental trajectory of female preferences and its potential evolutionary implications, such as the maintenance of variation in male ornamentation and population divergence. We predicted that females would be choosier, that is less responsive, after exposure to high variance in male phenotype because they would learn as juveniles that their social environment provided relative diversity in males, improving the benefits of sampling multiple males prior to making mating decisions. Similarly, we predicted that females would increase the strength of their preference functions as it paid off to invest in prospecting for the best possible mate. Furthermore, to more fully understand the implications of female choice behaviour, we investigated the possibility that males shift their reproductive tactics – courtship display versus sneak matings (e.g. forced copulation attempts) – in response to changes in female sexual behaviours. Guppy males exhibit a high level of plasticity in their mating behaviour driven by multiple factors such as the operational sex ratio (Jirotkul, 1999), male trait distribution (Jirotkul, 2000), female reproductive status (Guevara-Fiore et al., 2010) and social experience (Guevara-Fiore, 2012; Price and Rodd, 2006). We predicted that males would shift from courting females to sneaky attempts as females become choosier and variance in male reproductive success increases.

**Methods**

**Study organisms**

Guppies are small livebearing freshwater fish native to the coastal streams of the north-eastern part of South America. We used descendants of individuals collected in the lower part of the Aripo River on the island of Trinidad (N 10°39’03’’; W 61°13’40’’). Neonates were selected from housing tanks at day 5 post-birth and placed into treatment groups. All fish housed in the laboratory
were maintained on a 12h light:dark cycle at 24-25°C and were fed twice daily: in the mornings with commercial flake and in the afternoons with brine shrimp (*Artemia nauplii*). Plastic plants were placed into the tanks to physically enrich the environment and provide shelter for the fish.

**Rearing setup**

Neonates were evenly distributed into one of three types of rearing groups composed of adult fish representing two levels of phenotypic variance and a control group (high and low between-male variance and a female-only condition, respectively, N=6 stimuli fish/group, Fig. 1) and reared for 84 days (all females were sexually mature at this point: A.M., personal observation). The “high variance” treatment was composed of males that differed distinctly in their colour patterns. The “low variance” treatment was achieved by assembling similar males for which nearly all the coloured patches coincided in both colour classes and topographic position although could slightly vary in their shape. The “no male” treatment was composed of mature non-virgin females with no secondary body colouration. Due to the Y-linked inheritance of a large part of the colour pattern alleles (Haskins and Haskins, 1951; Houde, 1992; Winge, 1927; Yamamoto, 1975), the “low variance” condition was represented by collections of half or full brothers unlike “high variance” males that were unrelated or very distantly related. The experiment consisted of four replicates of each treatment. The rearing tanks were divided into two compartments of unequal size (30x30x18cm + 15x30x18cm). The developing fry were housed in the large compartment and through a perforated, transparent Perspex sheet were exposed to groups of 6 stimulus fish representing the three different conditions. The partition allowed olfactory and visual cues to pass from one compartment to the other. Males were removed from rearing groups before reaching sexual maturity (i.e. before the gonopodial hood extended beyond the tip of the fin (Reznick,
The number of focal females varied across treatments and across replicates depending on brood size and brood sex ratio (see Table 1 in electronic supplementary method).

**Behavioural trials**

Following the 84-day rearing period, we assessed mate choice in a 42 litre open arena (60x35x20cm). In each trial an equal number of stimulus males and experimentally reared females were placed in the arena (see electronic supplementary methods for details on number of males and females used in each trial) as an even sex ratio reduces male-male competition which in turn facilitates the full expression of female preferences. Stimulus males for these trials were randomly drawn from different stock tanks and chosen by eye to differ in colour patterns and size. Females were from the same rearing treatment and had not been exposed during development to the colour patterns of the stimuli males used in the behavioural trials. In total 4 replicate groups for each treatment were observed. As females show little discrimination prior to their first mating, focal females were mated with an unfamiliar male (i.e. neither represented in the rearing treatments nor in the behavioural trials) the day before testing to ensure the full expression of their preferences (Daniel and Rodd, 2016; Endler and Houde, 1995; Houde, 1997). On the day of the trial, females were released in the test tank two hours before observation to acclimatize them to the novel environment.

We recorded sexual behaviour following standard methods (Endler and Houde, 1995; Houde, 1997; Houde and Endler, 1990). During a trial we carried out five minutes of focal sampling on each male during each of 6 sessions across a single day: 3 sessions in the morning and 3 in the afternoon. The order in which males were sampled in a session was randomized. Two male behaviours were recorded: the number of courtship displays and the number of sneak mating
attempts. The courtship display, or “sigmoid” display (Houde, 1997), takes the form of a male quivering stiffly in front of a female while he bends his body into an S-shape potentially ending with a consented insemination. Alternatively, a male can adopt a sneaker strategy, attempting copulation without female cooperation by thrusting his gonopodium at the female’s gonopore (Houde, 1997). Males that performed less than five displays (seven males in total) throughout the 6 observation sessions were excluded from the analysis. Male displays were registered only if they were directed toward a particular female, if other males did not interrupt them and if they started after the male became the focal male. Moreover, during focal observations we recorded the sexual responses of females to the courtship display of the male being observed. The relative attractiveness of a given male was evaluated as the proportion of his displays that elicited at least a “glide” response from the females in the group (coined the “fraction response” D; see electronic supplementary methods for details on a female sexual response and on the measurement of D). Individual females within an experimental group were not distinguishable so D represents an aggregate measure of overall female responsiveness for that particular male. The fraction response is a reliable predictor of male mating success in guppies (Houde, 1987, 1988). The degree of preference for a sexual trait was calculated as the regression of D on that trait for all males used in a given experimental group (see below and electronic supplementary methods). At the end of the day, females were placed back in their housing tanks and males were kept in the observational arena.

**Male trait analysis**

Male colour patterns were photographed with a digital camera (Nikon coolpix 8800) in a custom-made box filled with a small volume of water where fish were free to swim. All the pictures were
taken under the same light conditions when the fish was parallel to the glass face of the box and
the images analyzed with UTHSCSA ImageTool (http://compdent.uthscsa.edu/dig/itdesc.html).
Colour patches were grouped into the following colour classes: black, orange (including red),
yellow, iridescent (including silver/white, blue, violet, and bronze-green) and total colour area.
Colour classes were measured as relative total area (relative to the body + caudal fin). Total body
length (from the tip of the snout to the tip of the longer lobe of the caudal fin) was recorded using
a digital caliper. A measure of diversity of the colour pattern was also calculated for each male.
This male trait, which is rarely examined in the study of female preference, was computed with
Simpson’s Reciprocal Diversity Index. The values span from 1 to X with X being the number of
categories being used (with 5 colour classes, the highest possible value, X=5, when each of the 5
colours have equal areas). The lower the value the less diversity and vice versa (see electronic
supplementary method for more detailed explanations).

Female preference analysis

We divided female sexual behaviour into two measurable components (Brooks and Endler, 2001;
Jennions and Petrie, 1997; Widemo and Saether, 1999). Choosiness is the effort an individual is
prepared to invest in mate assessment and is represented in this study by females’ responsiveness
D. The preference function is the ranking order of the male sexual signal, measured as the
relationship between female responses D and the male trait they are evaluating (see method in
electronic supplementary).

Statistical analyses were performed in R version 3.3.2 (The R Foundation for Statistical
Computing, Vienna, Austria). To determine the effects of the rearing treatments on female
responsiveness (D), we used a generalized linear mixed model (GLMMs, ‘glmer’ function of the
‘lme4’ R package) fit by maximum likelihood (Laplace approximation) with a binomial error
distribution and logit link. A model selection procedure, using the ‘LMERConvenienceFunctions’
R package that performed backward selection of fixed effects and forward fitting of the random
effect kept in the final model Treatment, Orange, Yellow and Total Colour as fixed effects. To
establish whether the total number of male courtship displays varied across treatments we used a
generalized linear mixed model (GLMMs, ‘glmmadmb’ function of the ‘glmmADMB’ R package)
with a negative binomial error distribution and logarithmic link to account for overdispersion. The
fluence of the rearing conditions on total number of gonopodium thrusts was examined
performing a generalized linear mixed model (‘glmmadmb’ function of the ‘glmmADMB’ R
package) with a Poisson error distribution and logarithmic link. To determine the most adequate
model, we used Likelihood Ratio Tests via the ‘drop1’ R function. Based on Akaike Information
Criterion (AIC) criterion, we kept in our final model the fixed effects Treatment, Black and Total
Colour. Experimental group was included as a random term in all models to account for the non-
dependence of the behaviours of males and females within the same trial. To adjust for multiple
testing and decide which differences were significant across treatment groups, we corrected \( p \)-
values following a Holm procedure.

For each sexual trait, the overall degree of female preference was analysed among
treatments. To do so, preference slopes of these traits were compared using a Kruskal-Wallis
procedure performed with the “qn.test” function developed in the “kSamples” R package. Post-
hoc analyses were carried out applying the Nemenyi test found in the “DescTools” R package.
Finally, we tested for a correlation between female preference slopes and the level of variance
experienced as juveniles using a spearman rank correlation.
Results

Responsiveness

The females from the no-male group (reared with females) were significantly more responsive than those from both the low- and high-variance groups and females from the low-variance condition were more responsive than females from the high-variance group ($\chi^2 = 25.8$, df=2, p<0.0001, Fig. 2). Female responsiveness was thus greatest when the level of phenotypic variance experienced during development was lowest in the case of females that had experienced males, or non-existent in the case of females’ naïve to male variance. There was no significant difference in the intensity (i.e. display rate) of male courtship towards females reared in the different treatments ($\chi^2 = 0.73$, df=2, p=0.69) so it is unlikely that variation in female responsiveness among treatments was due to differences in male display behaviour.

Linear preference functions

Female preferences were estimated as the linear regression slope coefficients of female response (D) on the male trait being evaluated. We estimated the female preference function for each male trait (orange, yellow, black, iridescent, total colour area, total body length and diversity of colour pattern) separately within each trial. Our four replicates yielded four slope coefficients per treatment per male trait. Females that had experienced different phenotypes during development showed stronger preferences for yellow (p=0.02), black (p=0.08) and total colour area (p=0.01) than females exposed to similar males (Table 1). Moreover, females with no male experience preferred smaller males relative to females reared with similar males (p=0.03). In contrast, there were no significant differences with respect to preference for body size between females from the high variance treatment and the two other experimental groups (Table 1, Fig.3). We also found a
positive correlation between the strength of Yellow (p=0.04), Total Colour (p=0.08) and Total Body Length (p=0.06) preferences and the level of phenotypic variability experienced as juveniles (Table 1). Finally, we analysed whether the observed differences between treatments resulted from variation in the overall phenotypic variance \textit{per se} or because of variation in a particular sexual trait experienced during rearing. To do so, we compared the average values of sexual traits experienced in the low and high variance treatments and for which females displayed a preference during the behavioural trials. Independent t-tests did not reveal any differences between the two experimental conditions ruling out the possibility that the observed effects resulted from exposure to variation in the value of a particular sexual trait (yellow: \textit{t}_{46}=1.35, \textit{p}=0.18; black: \textit{t}_{46}=0.95, \textit{p}=0.35; total colour: \textit{t}_{46}=0.29, \textit{p}=0.78; total body length: \textit{t}_{46}=1.85, \textit{p}=0.07).

\textit{Male alternative reproductive tactic}

When males were in contact with females from the “high variance” group, they attempted more sneak copulations than when in contact with females reared in the two other conditions ($\chi^2=16.8$, \textit{df}=2, \textit{p}=0.0002; high-variance vs. no-male group: \textit{p}=0.07, and high- vs. low-variance group<0.001, Fig. 4). Moreover, males attempted fewer gonopodium thrusts towards females reared in the “low variance” than in the “no male” condition (p<0.001). There is a possibility that less attractive males (males not bearing preferred traits) would switch from courtship displays to gonopodium thrusts in order to offset an initial reduced mating success. Although we found a significant effect of Black and Total Colour covariates, these did not drive the differences observed among treatments as signified by the lack of interaction.
Our findings demonstrate for the first time that variation in female mate preferences can arise through early social experience with different degrees of phenotypic variability found in males and independently of variation in any particular sexual trait. Females differed in both aspects of mate preference under scrutiny (responsiveness and preference functions) after prior exposure to two different levels of male phenotypic variance and to a control group of females (i.e. naïve to male phenotypic variation). We present evidence that female guppies were less responsive when reared with males than when reared in the absence of males. Following exposure to different levels of variance in male phenotypes, females were more responsive if males were less variable in their phenotypes. Moreover, the strength of preference for male traits such as yellow body colouration or total colour area increased for females having experienced a higher level of phenotypic variance. In response, males shifted their reproductive tactics, augmenting the rate of forced copulation in the presence of those females.

**Phenotypic variance and responsiveness**

Females were more responsive to males’ solicitations as the overall level of phenotypic variance experienced during development decreased. Females from the no-male group (no experience of male variance) were more responsive than females from both the “low-” and “high-variance” male treatments possibly emphasizing that males are a limited resource in the local environment. This may work to augment the willingness of females to respond positively (e.g. be more responsive) and thus engage more in sexual behaviours. These findings support a previous study (Bailey and Zuk, 2008), which showed that female field crickets *Teleogryllus oceanicus* reared in silent conditions (comparable to our “no male” treatment) are more responsive to playbacks than females.
reared with male song (comparable to our “low” and “high” variance treatments). Secondly, we found that after being exposed to similar males (“low variance”), females responded more to male displays than females exposed to different males (“high variance”). Zajitschek & Brooks (2008) and Hampton et al. (2009) investigated how sexually mature females accommodated their preferences to different levels of colour pattern rarity (common or redundant vs. unique vs. novel colour pattern) encountered within their social environment and showed that females found unique and novel phenotypes equally more attractive relative to common phenotypes. In our experiment, although adult females were tested only with novel phenotypes, the effects of early social experience were not overridden by the immediate experience of surrounding males.

**Phenotypic variance and preference functions**

There were no differences between treatments in the direction of preferences for the different traits under investigation (no difference in the sign of the median preference slopes). Females were applying the same ranking criteria independent of their early experience and male attractiveness did not vary as a function of the amount of phenotypic variance that females observed during development. In contrast, there were clear-cut differences in the strength of preferences (magnitude of the slopes) between treatments. Overall, females tended to increase their degree of preferences for sexual cues as the level of phenotypic variance experienced as juveniles increased. Females from the “high variance” condition had stronger preferences for greater amount of yellow, black and total colour relative to females from the “low variance” condition. In other words, the level of phenotypic variance displayed by males during female maturation influenced female choosiness (measured here as the magnitude of preference slopes). Even if rather uncommon, females may base their choice on male size in some guppy populations (Endler and Houde, 1995;
Magellan et al., 2005; Reynolds and Gross, 1992), favoring larger males (but see Endler & Houde (1995) for Paria river). Here, we report results showing that females were indifferent to male size when reared in contact with males but preferred smaller males when reared without male contact. It is not clear why this preference arose and further examination in the acquisition of preference for male size in guppies is needed.

*Implications for sexual selection*

Our results suggest that phenotypic variation found in the social environment during development is unlikely to alter the direction of sexual selection, as females from the three different treatments tended to use the same sexual cues. It may, however, change the strength of sexual selection since choosiness increased when developing females had experienced more variation in male phenotypes.

Developmental plasticity in the degree of choosiness can generate dynamic fluctuations in the selection exerted on male traits following this scenario: in a population where phenotype diversity is relatively high, females increase their choosiness, leading to more variance in mating success between males. After a while the diversity in sexual phenotypes is eroded by the strong directional selection imposed by females that are now experiencing less diversity during ontogeny. Less variance in male phenotypes drives females to be less choosy, decreasing the threshold at which they accept males, which in turn relaxes sexual selection on male traits, allowing for more or different sexual phenotypes to spread in the population. The importance of this feedback loop between plasticity in female preferences, environmental variation and selection can explain the maintenance of the polymorphism found in male colour patterns alongside other mechanisms such as frequency-dependent selection or antagonistic pleiotropy for fitness-related traits. From a
female perspective, plasticity in choosiness as a function of male phenotypic variance could represent an adaptive strategy diminishing the cost associated with the process of mate choice. Indeed, widening the range of accepted stimuli (e.g. decreasing choosiness) when the variability in male phenotypes is low allows females to spend time and energy on other activities than searching and assessing potential partners. The effect of plasticity in female preferences was balanced, to some extent, by plasticity in the reproductive tactics adopted by males. In response to females being choosier, males attempted more unsolicited copulations in the form of gonopodium thrusts, which are less costly than courtship rituals. High relative rates of sneak copulation diminish the importance of mate choice as a determinant of male mating success (Kelly et al., 1999; Magurran, 2001), potentially decreasing the strength of sexual selection which in turn can undermine population divergence (Evans et al., 2003; Matthews and Magurran, 2000). Our finding supports previous work showing that the relative importance of sneak attempt versus courtship display within population depends on environmental factors (Endler, 1987; Farr, 1976; Gamble et al., 2003; Godin, 1995; Jirotkul, 1999), morphological characteristics (Karino and Kobayashi, 2005) and prior sexual experience with females (Balaban-Feld and Valone, 2018).

More surprisingly, our results suggest that males surrounded by females from the “low variance” treatments attempted significantly less gonopodium thrusts than males with females from the two other treatments. These differences cannot be explained by differences in male size (Becher and Magurran, 2004; Houde, 1997) or male attractiveness, as there were no correlations between different colour classes used as sexual cues and the rate of thrusts. Females from the “low variance” treatment were exposed during rearing to similar males closely related to each other. We cannot rule out that being exposed to half- or full-siblings affected female behaviours (for other
reasons than their similar phenotypes and not observable in our measures) that would in turn affect the rate at which males performed their gonopodium thrusts.

To conclude, we have demonstrated that the frequency distribution of males’ phenotype experienced before reaching maturity (independent of the values of sexual signals) affected female mate choice in guppies; females were choosier when reared with more diverse male phenotypes. Our work adds to the growing literature on phenotypic plasticity in mate choice highlighting the importance of focusing on the physiological, social and ecological conditions of the choosing subject rather than only on the traits of potential mates to understand reproductive decision-making (Ah-King and Gowaty, 2016). This plasticity can have substantial ecological and evolutionary implications such as variation in the relative strength of sexual selection. Most traditional sexual selection models assume that mate choice is directional, fixed within a species and static within individuals over time, missing important properties of the mate choice process. A recent review (Ah-King and Gowaty, 2016) pointed towards the need for elaborating state-dependent models such as the one developed by Gowaty and Hubbell (2009) to study the flexible nature of mate choice. This model, in which our results fit, has the advantage of capturing the variation induced by chooser intrinsic features and ecological and social situations while categorizing the large number of variables associated with within-individual plasticity into few unifying parameters.

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References


Figure legends:

**Figure 1**: Example of one replicate made of a control group and two different levels of male phenotypic variance to which fry were exposed to. The scale among the different pictures in the figure varies.

**Figure 2**: Females responsiveness in the 3 different treatments. Bars represent estimated marginal means +/- 1SE. ***p<0.0001, **p<0.01, *≤0.05.

**Figure 3**: Degree of female preference for different male sexual traits after exposure to no male (■), low variance (▲) and high variance (●) treatments. Each data point represents the degree of preference in one observation session.

**Figure 4**: Gonopodium thrusts attempted by males to females reared in the 3 different treatments. Bars represent estimated marginal means +/- 1SE. ***p<0.001, *<0.1.
Table 1: Median of the preference slope for the three treatments. Each row represents a trait that could affect the linear preference function of females. K-W is the Kruskall-Wallis statistic testing for differences in degree of preference between treatments; multiple comparisons between treatments; $r_s$ is the spearman rank correlation coefficient between preference slope and the treatments ordered from “no male” to “high variance”; n is the total number of observation session.

<table>
<thead>
<tr>
<th>Preference Differences</th>
<th>Multiple comparisons</th>
<th>Preference and Treatment</th>
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<tbody>
<tr>
<td></td>
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<td>No male - Low variance</td>
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<tr>
<td></td>
<td></td>
<td>K-W (df)</td>
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<td>Simpson's Reciprocal Index</td>
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<td>0.06</td>
</tr>
</tbody>
</table>

* *The significance level is based on the exact distribution of the test statistic providing an exact $p$-value
* Significant after Bonferroni correction for number of tests in column
- No pairwise comparisons when no overall significant differences across treatments
† $p<0.1$
‡ $p<0.05$