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Selection for relative brain size affects context-dependent male preference for, but not discrimination of, female body size in guppies

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ABSTRACT

Understanding what drives animal decisions is fundamental in evolutionary biology, and mate choice decisions are arguably some of the most important in any individual's life. As cognitive ability can impact decision making, elucidating the link between mate choice and cognitive ability is necessary to fully understand mate choice. To experimentally study this link, we used guppies (*Poecilia reticulata*) artificially selected for divergence in relative brain size and with previously demonstrated differences in cognitive ability. A previous test in our female guppy selection lines demonstrated the impact of brain size and cognitive ability on information processing during female mate choice decisions. Here, we evaluated the effect of brain size and cognitive ability on male mate choice decisions. Specifically, we investigated the preference of large-brained, small-brained and non-selected guppy males for female body size, a key indicator of female fecundity in this species. For this, male preference was quantified in dichotomous choice tests when presented with dyads of females with small, medium and large body size differences. All types of males showed a preference for larger females but no effect of brain size was found in the ability to discriminate between differently sized females. However, we found that non-selected and large-brained males, but not small-brained males, showed a context-dependent preference for larger females depending on the difference in female size. Our results have two important implications. First, they provide further evidence that male mate choice also occurs in a species in which secondary sexual ornamentation is present only in males. Second, they show that brain size and cognitive ability have important effects on individual variation in mating preference and sexually selected traits.

KEY WORDS: Mate choice, *Poecilia reticulata*, Decision making, Context-dependent choice

INTRODUCTION

Animal decisions are central to the study of animal behavior. However, little is known about the underlying mechanisms of animal decision making. Recently, the theoretical framework of human decision making has been suggested as a model for animal behavior research, defining the decision-making process as how individuals use information to judge a situation and behave in a particular way (Mendelson et al., 2016). This framework identifies preference, ranking certain options over others, and choice, selecting an option given a set of alternative options, as the two major components of animal decisions (Mendelson et al., 2016).

Despite the important conceptual difference between the two components of decision making (preference and choice), dissimilarities between the two are seldom recognized in classic sexual selection theory (Kirkpatrick et al., 2006). Commonly, selective pressures are believed to drive positive reinforcement between the preference for a particular trait and the choice of mates bearing those traits (Andersson, 1994). However, current sexual selection theory acknowledges that mate choice can be context dependent and therefore does not necessarily correlate with absolute preference functions (Jennions and Petrie, 1997; Widemo and Sæther, 1999). Indeed, empirical studies across different taxa have demonstrated that, for instance, social context can shift mate preference and mate choice (Royle et al., 2008; Reaney, 2009; Lea and Ryan, 2015; Locatello et al., 2015; Griggio et al., 2016). Intrinsic condition and acquired experience have additionally been suggested to be important factors shifting innate preference functions and generating variability in mate choice (Ryan et al., 2007; Verzijden et al., 2012; Gilman and Kozak, 2015). Cognitive ability is central to decision making (Shettleworth, 2010), and likewise an important modulator of mating decisions (Akre and Johnsen, 2014; Cummings and Ramsey, 2015; Corral-López et al., 2017a). Yet, the impact of cognitive ability on mating decisions has mostly been assessed through studies of sensory perception and their effects on information-acquiring processes (Kirkpatrick et al., 2006; Ryan et al., 2007, 2009).

The influence of cognitive ability is seldom considered in sexual selection theory, as it is often assumed that selective pressures lead to mating with individuals who maximize fitness (Bateson and Healy, 2005; Castellano et al., 2012). However, cognitive ability probably plays a fundamental role in many aspects of sexual selection, as the ability to acquire information, and make judgments based on such information, can influence the outcome of an individual's behavior prior to, during and after mating. Yet, our understanding of the proximate factors that affect animal decision making during mate choice is still incomplete. Based on the economic concept of rationality, where decision making is based on maximizing benefits (Hurley and Nudds, 2006), it has been suggested that animals are adapted to perform optimal mate choices. Such rationality in mate choice implies that individuals use absolute preference decision rules to maximize fitness in their choice based on current information. Recent studies have shown optimal choice in diverse taxa such as cichlid fish (Dechaume-Moncharmont et al., 2013), fruit flies (Arbuthnott et al., 2017) and bats (Hemingway et al., 2017). However, these patterns remain inconsistent in the literature as irrational mate choice has also been

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reported (Royle et al., 2008; Reaney, 2009; Lea and Ryan, 2015; Locatello et al., 2015; Griggio et al., 2016). An alternative explanation for this inconsistency is that rationality is context dependent. Individual optima may vary and can lead to individual variation in mate choice (Fawcett et al., 2014). Indeed, studies applying theoretical modeling demonstrate an evolutionary advantage of not using absolute preference rules when incorporating environmental heterogeneity into animal decisions (Trimmer, 2013; McNamara et al., 2014). In line with this, constraints in cognitive resources can likewise affect mate choice decisions (Sasaki and Pratt, 2011). The development and maintenance of neural tissue is energetically demanding (Aiello and Wheeler, 1995; Isler and van Schaik, 2009; Kotrschal et al., 2013; Tsuboi et al., 2015). Hence, simplification of information processing resulting in lower neural investment can be beneficial from an evolutionary point of view. For instance, instead of the use of absolute functions, proportional processing of stimuli mainly influence decision making in animals (Bateson and Healy, 2005; Akre and Johnsen, 2014), a neuronal process previously demonstrated to require less neuronal coding (Dehaene, 2003; Nieder and Miller, 2003).

The brain, as the central organ in the neural network, is essential in animal decision making. Indeed, brain size has been shown to impact cognitive ability (Kotrschal et al., 2013, 2015; Benson-Amram et al., 2016), which in turn might influence animal decisions related to mate choice and mate preference (Ryan et al., 2007). This view has recently been empirically demonstrated in female guppies artificially selected for relative brain size. Cognitive differences between large-brained and small-brained females (Kotrschal et al., 2013; Buechel et al., 2018) impact the judgment of attractiveness of male guppies (Corral-López et al., 2017a). Yet, better mate quality assessment should present an advantage not just for female choice, as variation in female quality could potentially also drive the evolution of male preference and their choice of specific traits (Edward and Chapman, 2011). Female body size is commonly positively correlated with female fecundity (Houde, 1997; Edward and Chapman, 2011). Hence, under classic sexual selection theory it would be expected that males develop a preference for larger females when such a preference yields fitness benefits. Previous studies documented a clear relationship between female fecundity and female size in the guppy (e.g. Reznick, 1983). In situations with no male–male competition, male guppies prefer to mate with larger females (Dosen and Montgomerie, 2004; Jeswiet et al., 2012; Auld and Godin, 2015; Auld et al., 2016). However, such male preference is often only observed when the difference in body length between females exceeds a certain threshold, commonly around 10% difference in body size (Dosen and Montgomerie, 2004; Jeswiet and Godin, 2011). It is thus evident that better judgment of mate quality can play a major role in maximizing reproductive fitness not only in terms of female choice but also for male mate choice in this species. Hence, male guppies artificially selected for divergence in relative brain size present a suitable model system to study the impact of brain size and cognitive ability in adaptive mating decisions.

In this study, we exposed large-brained, small-brained and non-selected males to three different female pairs with small, medium and large differences in body size. Previous studies in these fish showed that large-brained males outperformed small-brained males in a cognitive test (Kotrschal et al., 2015), but large-brained and small-brained males did not show differences in body condition or visual ability (Kotrschal et al., 2013; Corral-López et al., 2017b). Likewise, cognitive differences between large-brained and

small-brained males are unlikely to be attributable to hitchhiking of deleterious alleles in the selection process, as several assays have shown that the lines do not differ in a range of physiological and behavioral traits (Kotrschal et al., 2013, 2014; Corral-López et al., 2015); the small-brained lines have even presented some immunological and life-history advantages (Kotrschal et al., 2013, 2016). Here, we assessed male innate preference for larger females, as experimental males did not have previous mating experience in our set-up. Our experimental approach tests the role of brain size and cognitive ability in sexual preference of male guppies for female body size. We performed dichotomous choice tests with no male–male competition based only on visual cues and in male guppies of similar age and experience. Given the previous validation of the correlation between preference and choice in a similar set-up for this species (Houde, 1997; Jeswiet and Godin, 2011), our study allowed us to focus on evaluating the ability of males to judge female quality to make adaptive mating decisions, i.e. preferring a larger female. In particular, if relative brain size affects the ability of male guppies to judge differences in female body size, we predict a stronger preference for larger females in large-brained males regardless of the size difference between the females presented in dichotomous choice tests. In addition, if judgment of differences in female body size becomes more difficult when the difference is smaller than 10%, we predict that only large-brained males will prefer larger females when presented with small size differences between female pairs in our test.

MATERIALS AND METHODS
Study system
The experiment complied with Swedish law and was performed in accordance with ethical applications approved by the Stockholm Ethical Board (Dnr: N173/13 and 223/15). We studied the preference for female body size in male guppies, *Poecilia reticulata* W. Peters 1859, from laboratory-reared descendants of Trinidadian guppies from high predation areas of the Quare River. We used non-selected wild-type female and male guppies from this laboratory population, together with males artificially selected for small and large relative brain size. Briefly, the artificial selection experiment was based on indirect selection for parental brain mass corrected for body size, which was used to generate replicated lines with large and small relative brain size (three replicates for large-brained individuals and three replicates for small-brained individuals, six populations in total). See Kotrschal et al. (2013) for full details on the selection experiment. These selection lines have up to 13.6% difference in the fourth generation (Kotrschal et al., 2015). After the fourth generation, 30 non-related males and females from each population were paired to generate a fifth generation of brain size-selected offspring. All offspring were removed from their parental tanks after birth. Males were isolated from females and grouped in 12 l tanks before they were sexually mature. We allowed visual contact between tanks to avoid social stress from isolation. However, males did not have visual contact with any female prior to the experiment. All males were approximately 6 months old when tested and had been kept in similar conditions in the laboratory. The laboratory was maintained at 26°C on a 12 h:12 h light:dark schedule, which resulted in 25°C water temperature. Fish were fed an alternating daily diet of flake food and live *Artemia*.

Selection of female pairs
To form female pairs with differences in body size, we measured standard body length in 60 lab-reared descendant wild-type female guppies that ranged between 7 and 9 months of age. All females had

no prior experience with males, as they had been isolated from males prior to sexual maturity. Based on these measurements, we used 18 females to create three female pairs for each of the three experimental treatments: (i) large difference in body size (7 mm; 25% difference), (ii) medium difference in body size (3.4 mm; 12.5% difference) and (iii) small difference in body size (1.6 mm; 6.25% difference). To avoid potential differences in motivation to mate in the males across the three treatments and because absolute female size in the test can drive the preference for larger females (Dosen and Montgomerie, 2004), the combined body length of the two females was kept equal to 50 mm in every pair (large difference: 28.5 versus 21.5 mm; medium difference: 26.7 versus 23.3 mm; small difference: 25.8 versus 24.2 mm).

Preference test

Using a dichotomous choice test, we assessed the preference of male guppies for larger females when exposed to the three different treatment conditions. Our set-up consisted of eight plain glass tanks of 42×20×20 cm in which males were allowed to observe both females in adjoining plain glass tanks of 11×10×20 cm over a period of 10 min. Following the method used in Corral-López et al. (2017a), the male experimental tank was divided into three zones to determine female position: (i) left choice zone, the area adjacent to the left female tank up to a maximum distance of 10 cm from it; (ii) right choice zone, the area adjacent to the right female tank up to a maximum distance of 10 cm from it; and (iii) no-choice zone, the area between the left and right choice zones and all areas further than 10 cm from the female tanks (Fig. S1). Females did not see each other during trials to avoid female–female competition effects. For 12 consecutive days, we measured for every male the time spent associating with the larger and the smaller female when exposed to a large, medium and small difference in female body size. We measured eight males each day for a total of 24 trials daily. Males and female pairs were placed in their respective experimental tanks 24 h prior to the test to allow for acclimation. The right and left position of the larger female in each trial and the daily order of presentation of the female size difference treatment were randomized. Three large-brained, three small-brained and two non-selected males were tested every day. The impossibility of testing nine individuals daily in our experimental set-up resulted in a lower sample size of non-selected males tested. In total, we used 22 non-selected males, and 36 large-brained and 36 small-brained males from the fifth generation of the brain size selection lines (12 individuals from each of the three up- and down-selected lines). We selected this methodology to maximize the number of large-brained and small-brained males tested, and to ensure a balanced design between non-selected and brain size treatments in the female pairs that they interacted with, and in the order of presentation of the female size difference treatments. Every trial was broadcast live using a Logitech HD webcam C615 located above the tanks and viewed from a distance on a laptop to avoid disturbance. Following Corral-López et al. (2017a), the position of the male was scored by a single observer using the live observation mode in BORIS v 2.72 (Friard and Gamba, 2016). Quantification of behaviors was performed blind to the treatment as only running numbers identified the males. A preference ratio was obtained as the difference in time spent with each female, standardized by the total amount of time in any of the choice areas. Trials in which males did not move in the experimental tank (n=42) or in which males did not visit both female choice areas (n=19) were excluded from analysis (Houde, 1997). Final analyses included a total of 221 trials corresponding to 19 non-selected, 26 small-brained and 29 large-brained males.

Every day, after trials were completed, we measured the body size (standard length) of the tested male guppies to the nearest 0.1 mm using a vernier caliper. We found no differences in body size between large-brained and small-brained males, but non-selected males were slightly larger than selected males (mean±s.e.m. body size; small brained: 17.95±0.10 mm; large brained: 17.78±0.10 mm; non-selected: 18.26±0.12 mm; small brained versus large brained t=1.17, P=0.244; small brained versus non-selected t=−2.96, P=0.065; large brained versus non-selected t=−1.85, P=0.003). In order to control for the potential effect of body size differences between treatments in the time spent associating with larger females, we statistically controlled for male body size in our statistical analyses (see below).

Statistical analyses

We assessed potential behavioral differences between large-brained, small-brained and non-selected males in our study using a linear mixed model (LMM) approach. To study male mating preference for larger females, we used a LMM that included preference ratio as the dependent variable. Brain size and the difference in size between females were used as fixed effects. The full model included two covariates, male body size and the number of tests previously performed by the same male. Likewise, all interactions between fixed effects and the female pair size difference covariate were included in the full model. In addition, the full model included female pair identity and male identity as random factors, as well as a random intercept for each replicate selection line and a random slope for brain size within each replicate. We performed a backward elimination of non-significant fixed factors of LMM by means of Satterthwaite's approximation for degrees of freedom (Kuznetsova et al., 2015; Appendix 1). Model diagnostics showed that residual distributions were roughly normal with no signs of heteroscedasticity. All analyses were performed in R version 3.3 (http://www.R-project.org/). To evaluate whether large-brained, small-brained and non-selected males independently preferred larger females regardless of female body size differences, we obtained *post hoc* contrasts of the best fitted preference model using the lsmeans package (Lenth, 2016). To reduce Type I error, *post hoc* analyses included multiple testing correction applying the false discovery rate procedure (Benjamini and Hochberg, 1995).

To assess whether large-brained, small-brained and non-selected males differed in their ability to judge female body size differences, we used three independent LMMs for data on small, medium and large body size differences following the above-mentioned procedure. Full models included brain size as a fixed effect and male body size and the number of tests previously performed by the same male as covariates. We included female pair identity as a random factor, as well as a random intercept for each replicate selection line and a random slope for brain size within each replicate. This statistical procedure was also followed to analyze five other behavioral patterns of the males during the test: side bias, time of no choice, total movement, number of visits and visit ratio (see Appendix 2).

RESULTS

Preference for larger females

The quantification of male preference in a standard dichotomous choice set-up regardless of the percentage size difference between females revealed that small-brained, large-brained and non-selected guppy males showed a significant preference for larger females (mean±s.e.m.: small brained: 0.20±0.07, t=2.82, P=0.02; large brained: 0.15±0.07, t=2.22, P=0.04; non-selected: 0.25±0.08,

t=3.14, P=0.01; Fig. 1). No significant differences in the preference for larger females were observed between small-brained, large-brained and non-selected males (LMM preference: brain size: $F_{2,68.53}$=0.60, P=0.552). Males reduced their preference for larger females in their second test. However, the number of tests performed did not affect preference across the different male types (mean±s.e.m.: first test: 0.27±0.08, t=2.82; second test: 0.06±0.07; third test: 0.25±0.08; LMM preference: test number×brain size: $F_{4,137.7}$=1.38, P=0.248).

We did not find any effect of brain size in the preference of males for larger females when the body size difference between females presented in the test was small (Fig. 1B; LMM preference: brain size: $F_{2,72}$=1.89, P=0.317). We also did not find any difference in male preference for larger females between large-brained, small-brained and non-selected males for any of the female body size difference treatments (Fig. 1B; LMM preference: medium size difference: brain size: $F_{2,72}$=0.97, P=0.495; large size difference: brain size: $F_{2,72}$=0.65, P=0.522). Likewise, we found no effect of the percentage size difference between the females presented in the dichotomous choice test on the preference for larger females (LMM preference: female pair size difference: $F_{2,5.91}$=1.25, P=0.352). However, analysis of the preference for larger females showed a significant interaction between the percentage size difference between the females and male brain size (LMM preference: female pair size difference×brain size: $F_{4,138.70}$=2.53, P=0.043). We observed large individual variation in context-dependent preference for all male groups (see Fig. S2). However, visual inspection of the results suggests that the significant interaction effect was due to two factors. First, average preference of non-selected males for larger females increased when the size

difference between females presented was intermediate (12.5%). Second, average preference of large-brained males for larger females increased as the size difference between females increased, whereas the preference of small-brained males for larger females remained on average similar across female size difference treatments (Fig. 1B).

Behavioral patterns during preference test

Analysis of how individuals behaved during the preference tests showed no differences in how males from different brain size selection regimes appraised information about the females offered (Appendix 2). In particular, we found no significant side bias in preference between the non-selected, large-brained and small-brained males (LMM side preference: brain size: $F_{2,2.76}$=0.21, P=0.825), or in their motivation to mate, as there were no differences between brain size treatments in the time spent outside the choice areas (LMM time of no choice: brain size: $F_{2,3.46}$=0.53, P=0.631). We did find a significant increase in time outside the choice areas in the second and third test for each male, although this pattern was not influenced by brain size of the males and on average males did not spend more than 16% of the time outside the left or right choice area (mean±s.e.m.: first test: 70.7±13.3 s; second test: 94.2±13.4 s; third test: 99.0±13.3 s; LMM time of no choice: test number×brain size: $F_{4,128.6}$=0.95, P=0.433).

Furthermore, we found no evidence that non-selected, large-brained and small-brained males gathered more information from one particular type of female as the ratio of visits to choice areas was not different between brain sizes (LMM visit ratio: brain size: $F_{2,3.11}$=0.15, P=0.870). The difference in size of the females offered to the males likewise did not influence any of the above-mentioned male behaviors (Appendix 2). In contrast, female body size difference
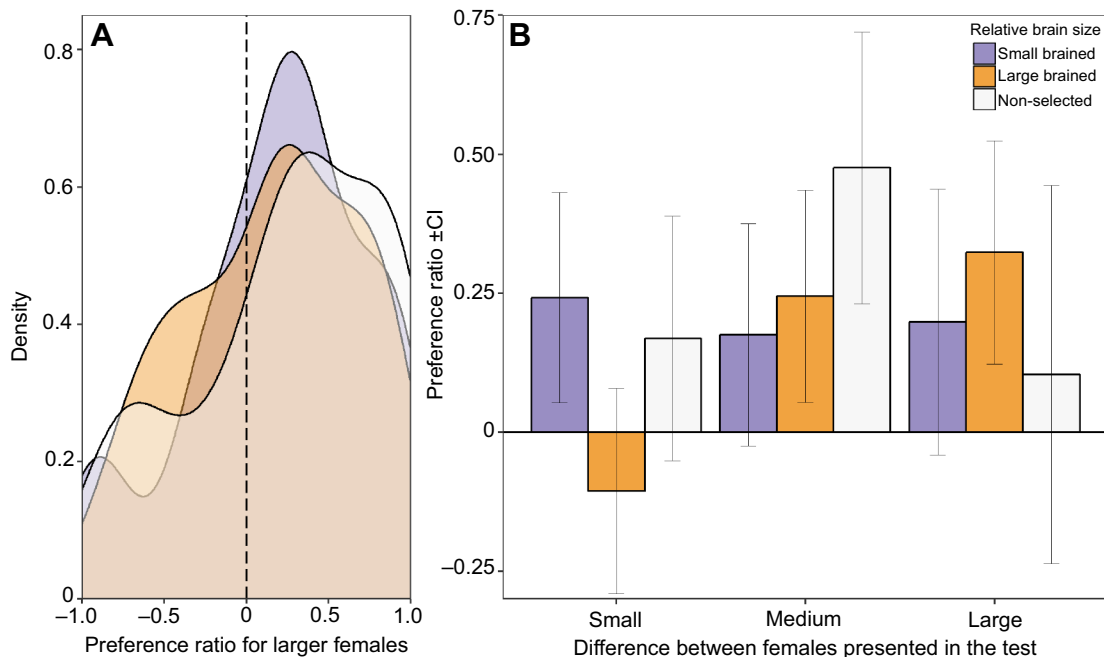
Fig. 1. Male preference for larger female guppies. Preference ratio for larger females was calculated as the difference in time spent with each female divided by the total amount of time in any of the choice areas. Preference ratios take values between −1 (all time spent with the smaller female) and 1 (all time spent with the larger female). (A) Kernel density plot showing the preference ratio distribution for larger females of large-brained, small-brained and non-selected males regardless of female body length differences of dyads presented in dichotomous choice tests. (B) Mean values and confidence intervals (CI) of the preference of large-brained, small-brained and non-selected males for larger females when presented with dyads of females that had small (1.6 mm, 6.25%), medium (3.4 mm, 12.5%) and large (7 mm, 25%) differences in body size. There were no differences between large-brained, small-brained and non-selected males in their preference for larger females (P=0.552). However, we found a significant interaction between relative brain size and female pair size difference treatments (P=0.043).

of the dyad influenced two activity proxy measurements, the total number of crossings between defined choice and no-choice areas (total movement) and the total number of visits that males paid to the two female choice areas (total visits; Appendix 2). In particular, we found that males paid significantly more visits to both female choice areas when the size difference between females was small (LMM number of visits: female difference: $F_{2,3.53}=8.00$, $P=0.048$; Fig. 2).

DISCUSSION

Our results show that brain size does not affect the discrimination of female body size in male guppies when associating with differently sized females using visual cues. In particular, no effect of brain size was observed in the preference for larger females when female body size differences presented were small (6.25%). Analyses combining the results for the different dyads of females while controlling for repeated measurements of each individual showed that all male groups, large-brained, small-brained and non-selected males, showed an overall preference for larger females. However, unlike small-brained males, large-brained males and to some extent also non-selected males biased their preference towards larger females as the difference in size between the females increased. Therefore, our results suggest that brain size and cognitive ability shape context-dependent preference in male mate choice.

The observed overall preference for larger females (when combining all results) is in accordance with what has been found in previous studies of visual male mate choice in guppies (Dosen and Montgomerie, 2004; Herdman et al., 2004; Godin and Auld, 2013; Auld and Godin, 2015; Auld et al., 2016). Furthermore, our results are consistent with these studies in that we found large individual variation in male preference for differently sized females. Female body size is a cue that conveys multiple pieces of information in this species; in addition to being more fecund, larger female guppies are often inseminated by more males, increasing the risk of sperm competition and reducing fitness benefits for individual males (Herdman et al., 2004). Yet, in our study, we tested males in a set-up without male–male competition and all males experienced similar social environments, with no previous experience with females. Under such circumstances, the observed overall preference by all male groups for larger females should provide important benefits to maximize reproductive success.

Which information-processing rules individuals follow to develop mating preferences remains a key question. Following the conceptual framework of animal decision making (Mendelson et al., 2016), our results suggest that brain size does not affect judgment based on the ability of males to discriminate between female body sizes. These results are in agreement with the previously demonstrated similar ability of large-brained and small-brained males to resolve spatial detail (Corral-López et al., 2017b). Taken together, these findings suggest that discriminating larger females in this species is a relatively easy task for which demanding cognitive processes might not be required, as previously demonstrated for proportional processing rules (Akre et al., 2011; Akre and Johnsen, 2014). Yet, we observed differences between large-brained, small-brained and non-selected individuals in their level of preference when exposed to pairs of females with small, medium and large body length differences. Surprisingly, it was in large-brained males that we found a lower preference for larger females when the task of discriminating between females was more difficult (small difference: 6.25%). However, preference levels of large-brained males in any of the female body size difference treatments did not differ from those of the small-brained and non-selected males. In contrast, unlike small-brained males, large-brained males seemed to bias their time more towards larger females as we increased the difference in female body size in the dyads. In our study, only three dyads of females were offered in binary choices for each treatment. Hence, we cannot rule out that the preference for particular females regardless of their body size might explain bias in the observed lack of preference for larger females in certain treatments. Another potential explanation for this pattern might be that large-brained males relied more on multiple traits to evaluate the quality of the females offered. Although females shown to males in this study were of equal age and raised in similar conditions to minimize differences among them (except for body size differences), it is possible that uncontrolled traits in our experiment, such as female condition and female response towards males, interacted with body size to shape male preference. In this scenario, our results would suggest that while the preference of small-brained males for larger females might be based on a single trait (female body size), large-brained males seemed to incorporate information from these other traits into their mating decisions but the relative importance of other traits was much lower when the difference in size became larger.
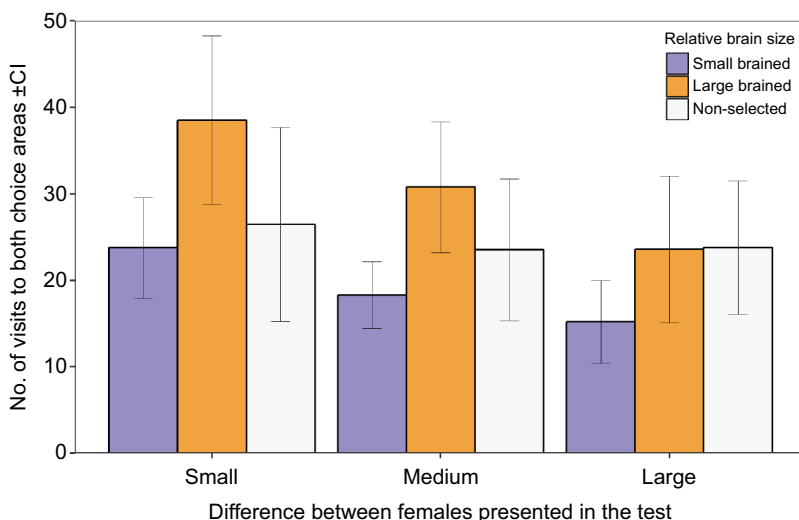
Fig. 2. Number of visits to choice areas during dichotomous choice preference tests. Mean (±CI) number of visits of large-brained, small-brained and non-selected male guppies when presented with dyads of females that had small (1.6 mm, 6.25%), medium (3.4 mm, 12.5%) and large (7 mm, 25%) differences in body size in dichotomous choice tests evaluating male preference for larger females. There was no significant difference between males of different brain sizes in the number of visits to the two choice areas ($P=0.273$). Overall, males performed more visits when presented with female dyads with a smaller size difference ($P=0.048$). Data were log transformed prior to statistical analyses.

Even though our experiment was not designed to test for evaluation and decision rules (Bateson and Healy, 2005; Kirkpatrick et al., 2006) in the preference for larger females, our results might be explained by differences in decision rules between small-brained and large-brained males. The fact that large-brained males associated most with the largest of all female stimuli offered across female dyads (i.e. with the largest female of 28.5 mm standard length) might be explained by large-brained males being more sensitive when making their decisions based on the absolute size of the larger females. Indeed, absolute decision rules have previously been suggested to be more cognitively demanding than simple proportional processing based on comparative evaluation between stimuli (Bateson and Healy, 2005). Our results suggest that incorporating the role of cognitive ability in future studies of mating decision rules might be important for solving inconsistencies in recent literature on rational and irrational mating decisions (e.g. Lea and Ryan, 2015; Hemingway et al., 2017).

Non-selected males likewise are more flexible in their preference towards larger females when presented with an intermediate difference in body size between them. But unlike in large-brained males, such a preference for the largest of all female stimuli was not observed in non-selected males. Previous studies have shown that male guppies decrease their preference towards larger females in situations of higher competition risk (Jeswiet et al., 2012; Auld and Godin, 2015; Auld et al., 2016). Our experimental design did not incorporate such environmental cues. Hence, innate behavioral differences in mating preference between selected and non-selected males potentially drove the strong reduction in preference for the largest of all female stimuli in the non-selected males. In the guppy, the largest females often attract the highest number of mates (Houde, 1997; Dosen and Montgomerie, 2004) and post-copulatory competition might decrease the fitness benefits of preferring such females (Herdman et al., 2004). How such social cues affect context-dependent preferences in our selection lines remains to be investigated. However, the similarities that we observed between large-brained and non-selected males in relation to small-brained males point mainly towards a decrease in the cognitive ability of small-brained males rather than an increase in the cognitive ability of large-brained lines. Interestingly, this finding matches our previous results on female choice where small-brained females showed a decrease in preference for colorful males while we found no increase in the preference of large-brained females in relation to non-selected females (Corral-López et al., 2017a).

Are intrinsic differences between the brain size selection regimes driving our results? Previous assays in these selection lines showed physiological, personality and behavioral differences between large-brained and small-brained individuals (Kotrschal et al.,

2013, 2014; van der Bijl et al., 2015). In the present study, such differences are unlikely to alter how much information males could gather on the presented females. This is because the time spent out of the choice areas and the ratio of visits between females did not differ between large-brained, small-brained and non-selected males. The fact that we did not find differences in the time spent outside the choice areas also suggests that there are no differences in motivation between males of different brain sizes. However, we found a significant effect of the female pair offered on the activity of the males, but this was not affected by brain size selection. Hence, we find it unlikely that personality differences drove the preference patterns, as male activity levels varied mostly depending on the female pair offered in the tests. As such, we think that these findings support the possibility that preference patterns were driven by mate quality assessment rather than by male ability to discriminate female body size across dyads.

The observed context-dependent mate choice for female size in large-brained males could have important evolutionary implications and potentially counteract the costs of evolving a larger brain under certain ecological circumstances. Previous studies have demonstrated the influence of the quality of potential mates encountered in shaping flexible mating decisions (e.g. Kvarnemo and Simmons, 1999; Shine et al., 2006). In addition, the ability to adapt to heterogeneous environments has been suggested as a key benefit of evolving a larger brain (Ratcliffe et al., 2006; Sol et al., 2008; Overington et al., 2009). In line with this, we speculate that our results provide experimental evidence that lower investment into the brain might be sufficient under more homogeneous social and physical environments where a consistent preference for higher quality mates might be adequate. Indeed, previous studies found correlations between neural substrate development and increased social complexity in voles (Fowler et al., 2002) and birds (e.g. Adar et al., 2008; see review by Gonda et al., 2013). In guppies, similar patterns might be expected as decreases in neural development have been found in captive-reared individuals, arguably a more homogeneous environment than natural habitats (Burns and Rodd, 2008; Burns et al., 2009). Likewise, our results stress the importance of incorporating intrinsic factors, such as cognitive ability, in context-dependent analysis of mate choice, as well as incorporating such intrinsic factors when evaluating optimal decision making in mate choice tests (Fawcett et al., 2014). Moreover, our results complement previous findings on how cognitive ability affects female preference when choosing between colorful and non-colorful males (Corral-López et al., 2017a). The combination of these findings highlights the role, in both sexes, that brain size and cognitive ability can play in the puzzling variation in mating preference and sexually selected traits observed across individuals.

Table A1. Backward elimination procedure for the full LMM with the preference ratio for larger females as the dependent variable

Fixed effect	SumSq	d.f.$_{num}$	d.f.$_{denom}$	F-value	Stepwise elimination	P-value
Size	0.069	1	73.07	0.271	1	0.604
Female pair difference:BS:test number	1.949	8	168.86	0.960	2	0.469
Female pair difference:test number	1.214	4	24.55	1.172	3	0.347
BS:test number	1.434	4	134.93	1.391	4	0.240
Female pair difference	0.652	2	5.91	1.252	Kept	0.352
BS	0.312	2	68.53	0.599	Kept	0.552
Test number	2.340	2	66.49	4.494	Kept	0.015*
Female pair difference:BS	2.633	4	138.70	2.528	Kept	0.043*

Female pair difference, difference in female body size in the test; BS, brain size selection regime; test number, number of tests previously performed by the male; size, male body size.
Asterisks indicate significant effects.

Appendix 1

To study the effect of female size differences and relative brain size in male mate choice, we used a LMM with preference for larger females as the dependent variable. Full models included the difference in female size in the test and brain size selection regime as fixed effects. We used the number of tests previously performed by the male and male body size as covariates in the models. The full model included all interactions between fixed effects and the order of presentation. In addition, all models included the identity of the male and the female pair used as random factors. In addition, we included a random intercept for each replicate selection line and a random slope for brain size within each replicate (Table A1).

Appendix 2

Based on the frequency and duration of visits to the left choice area, right choice area and no-choice area, quantified during the dichotomous choice tests using BORIS software (Friard and Gamba, 2016), we calculated the following behavioral responses for each male: (i) side bias ratio – the difference in time spent in the left choice area and right choice area, standardized by the total amount of time in any of the choice areas; (ii) time of no choice – the total time in seconds spent outside any of the two choice areas of the experimental tank; (iii) total movement – the total number of crossings between choice areas and no-choice areas or vice versa during the test; (iv) number of visits – the total number of crossings

from the no-choice area to either the left or right choice areas; (v) visits ratio – the difference in the number of visits to the larger female and the smaller female, standardized by the total amount of visits. We then assessed potential differences in the behavior of large-brained, small-brained and wild-type males during the dichotomous choice tests. For this, we used each behavioral response as the dependent variable in the model. All models included the interaction between brain size selection and the difference in female size as fixed effects, and the order of presentation as a covariate. Models also included the identity of the male and the female pair used as random factors, as well as a random intercept for each replicate selection line and a random slope for brain size within each replicate. When necessary, the dependent variable was log transformed to ensure that residual distributions were roughly normal with no signs of heteroscedasticity. All analyses were performed in R version 3.3 (http://www.R-project. org/). There were no significant differences in the response of large-brained, small-brained and wild-type males for any of the behaviors quantified (Table A2). In contrast, the difference in body size between females offered in the dichotomous choice test had a significant effect on two of the behaviors analyzed: the total movement of the males and the total number of visits to both choice areas during the test (Table A2).

Table A2. Results from LMM models used to quantify behavioral patterns

	d.f._num	d.f._denom	F-value	P-value
Behavior 1: side bias Response=left/right choice area ratio				
Female pair difference	2	5.024	0.515	0.626
BS	2	2.759	0.206	0.825
Test number	2	110.639	2.355	0.099
Female pair difference:BS	4	135.962	0.647	0.623
Behavior 2: time of no choice Response=log(time outside choice areas)				
Female pair difference	2	3.285	2.064	0.262
BS	2	3.466	0.526	0.631
Test number	2	23.754	6.854	0.004*
Female pair difference:BS	4	133.652	1.827	0.127
Behavior 3: total movement Response=log(no. of crossings between choice and no-choice areas)				
Female pair difference	2	3.574	7.826	0.049*
BS	2	3.232	1.926	0.281
Test number	2	30.119	3.306	0.051
Female pair difference:BS	4	135.558	1.237	0.297
Behavior 4: number of visits Response=log(no. of visits to both choice areas)				
Female pair difference	2	3.523	8.008	0.048*
BS	2	3.172	2.062	0.266
Test number	2	28.146	3.293	0.051
Female pair difference:BS	4	135.661	1.237	0.298
Behavior 5: visit ratio Response=ratio of visits to larger/smaller female				
Female pair difference	2	3.523	0.650	0.559
BS	2	3.110	0.145	0.870
Test number	2	100.741	1.852	0.162
Female pair difference:BS	4	138.974	0.794	0.531

Asterisks indicate significant effects.

Data availability
The dataset has been deposited in the Dryad Digital Repository (Corral-López et al., 2018): https://datadryad.org/resource/doi:10.5061/dryad.8kv341d

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.175240.supplemental

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