

Article

Sex differences in cognition and their relationship to male mate choice

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Abstract

Male cognition has gained recognition as an important potential player in sexual selection. A number of studies have found positive correlations between male sexual signals and cognitive performance and/or female preferences for males with better cognitive performance, although other studies have not found these relationships. Sex roles can differ dramatically, and sex differences in selection on cognition likely follow from the different tasks associated with these sex roles. Here, using threespine stickleback *Gasterosteus aculeatus*, a species with clearly divergent sex roles and mutual mate choice, we focus on the cognitive trait inhibitory control because males must differentially respond to reproductive females versus other sticklebacks while defending territories and refrain from eating eggs and fry while performing paternal care. We presented fish with a detour task four times over a period of 7 days, allowing us to assess initial inhibitory control and improvement over time. We ask 1) whether there are sex differences in inhibitory control and 2) whether male mate choice is associated with female inhibitory control. Although males outperformed females on three different measures of detour task performance across four trials, these differences were largely explained by males being less neophobic than females. Females took more trials to successfully solve the detour task, even after accounting for sex differences in neophobia. Female cognitive abilities, however, were unrelated to the vigor with which males courted them. The equivocal results regarding sex differences in cognitive ability suggest further study given the very different selection pressures each sex experiences.

Key words: cognition, detour task, mutual mate choice, sexual selection, threespine stickleback

Choosy females make mating decisions based on a wide variety of male traits (Andersson 1994; Rosenthal 2017). Recently, correlations between mating success and cognitive performance (Shohet and Watt 2009; Keagy et al. 2009, 2011; Minter et al. 2017) and correlations between cognitive performance and sexual display traits (Karino et al. 2007; Boogert et al. 2008; Boogert et al. 2011; Mateos-Gonzalez et al. 2011; Keagy et al. 2012; Fabre et al. 2014) have suggested that sexual selection can act on cognitive ability, although these relationships have not always been found (Boogert

et al. 2011; Sewall et al. 2013; Isden et al. 2013; Anderson et al. 2016). In many mating systems, sex roles can differ dramatically. Differences in how cognition is involved in divergent sex roles could result in differences in selection on cognition, generating sexual dimorphism in cognitive abilities (Galea et al. 1996; Jacobs 1996; Lindenfors et al. 2007). In addition, which sex(es) are choosy depends on the mating system (Johnstone et al. 1996; Edward and Chapman 2011). It is possible that males express preferences for females with superior cognitive abilities in mutual mate choice or

sex role-reversed species, although to our knowledge this question has not been studied.

Sexual dimorphism in cognitive ability has been demonstrated in a number of different species, often corresponding to differences in sex roles. For instance, in species such as meadow voles where males have large home ranges and reproductive success is directly related to finding females, spatial learning ability is enhanced compared with females (Gaulin and Fitzgerald 1986; Gaulin and Fitzgerald 1989; Galea et al. 1996). Conversely, female cowbirds must locate host nests in which to lay their eggs; and they have correspondingly better spatial learning abilities than males (Astié et al. 1998; Guigueno et al. 2014). Sex differences in cognition have been well studied in guppies (*Poecilia reticulata*, see review by Lucon-Xiccato and Bisazza 2017b). Novel foraging information spreads through subgroups of female guppies more quickly than subgroups of male guppies, perhaps because reproductive success is more tightly tied to resource acquisition for female guppies compared with male guppies (Reader and Laland 2000). Female guppies may also be more behaviorally flexible (Laland and Reader 1999; Lucon-Xiccato and Bisazza 2014; Lucon-Xiccato and Bisazza 2017a). In contrast, male guppies learned how to solve a maze whereas females did not, corresponding to males likely relying more on spatial learning because they disperse further than females and occupy vegetated areas more often (Lucon-Xiccato and Bisazza 2017a). These results highlight that sex differences can be very specific with respect to the cognitive ability involved.

Sexual selection on cognitive ability could occur through a direct route in which one sex selects the other based on a behavior strongly influenced by cognition (e.g., solving extractive food problems) or more indirectly through mate choice based on correlated traits (e.g., carotenoid coloration, body condition). Recently, evidence for the direct route was demonstrated with female parakeets changing their social preference after they observed that the previously unattractive males could solve an extractive food task, but the previously attractive males could not (Chen et al. 2019). However, even in this case, it cannot be known with certainty that it was cognition *per se* the females based their choice on; for example, the females may have interpreted differences in male ability to open petri dishes and puzzle boxes as a difference in male strength (Striedter and Burley 2019). The indirect route is feasible across a larger array of systems because it does not require that cognitive performance is directly observed by the choosing sex. It is also consistent with standard good genes models of sexual selection (reviewed in Rosenthal 2017). The indirect route requires that cognition affects a trait and that trait affects preference. In any case, with both the direct and indirect routes, the prediction is that cognitive performance correlates with mate preference, and so this is a good place to start. Female cognition research has typically focused on cognition involved with the mating process itself (reviewed in Ryan et al. 2009), such as how females learn from mating experiences (Uy et al. 2001; Dukas 2005), and how female social experience alters later mating decisions (Hebets 2003; Godin et al. 2005; Bailey and Zuk 2008). However, in mutual mate choice or sex role-reversed species, males mating with females with superior cognition may gain benefits.

Our study system is the threespine stickleback *Gasterosteus aculeatus*, a small fish with male only parental care and mutual mate choice. Male sticklebacks compete with each other for access to territories where they build nests, and after receiving a clutch of eggs from females, provide parental care for eggs and fry (Wootton 1976). Parental care is energetically costly (Smith and Wootton 1995; 1999) and includes nest defense from predators and conspicuous parenting

behaviors (Stein and Bell 2014). Likely owing to their large parental contribution, male mate choice is well-established in this system (Rowland 1982, 1989; Sargent et al. 1986; Kraak and Bakker 1998), for example preferring females that are larger or more gravid. Females produce energetically expensive eggs and choose amongst nesting males (Milinski and Bakker 1992; Tinghitella et al. 2015), exhibiting strong preferences for male characteristics including color traits, behaviors, and nest characteristics (Sargent 1982; Milinski and Bakker 1990; Rowland 1994; Candolin and Voigt 1998; Vamosi and Schluter 1999; Östlund-Nilsson and Holmlund 2003; Tinghitella et al. 2013). Sex roles are thus clearly divergent.

Stickleback males have larger brains than females given their body size, consistent with the hypothesis that differences in sex roles have resulted in the evolution of cognitive differences (threespine: Kotschal et al. 2012; ninespine: Herczeg et al. 2014). Brain size has been associated with superior cognitive skills in some comparative studies (Reader and Laland 2002; MacLean et al. 2014; Benson-Amram et al. 2016) and an experimental evolution study in guppies (Kotschal et al. 2013, 2014; Buechel et al. 2018). Adding to the evidence that parental care itself is the selective force involved, the sexual brain dimorphism is reversed in closely related threespine stickleback populations that have recently evolved near complete loss of paternal care behaviors (Samuk et al. 2014). A cognitive trait likely critical to male reproductive success is inhibitory control, the ability to inhibit an ineffective prepotent behavior or ignore irrelevant stimuli when attempting to achieve a goal (Boogert et al. 2011; MacLean et al. 2014). For example, territorial males must reduce their normal aggressive behavior towards intruders to effectively court reproductive females, and once they have mated, they must not eat their eggs and fry which under other circumstances are preferred prey (Hynes 1950; Whoriskey and FitzGerald 1985; Foster et al. 1988). Both courtship and parental care also likely rely greatly on behavioral flexibility, and inhibitory control is an important component of that skill (Amici et al. 2008; Griffin and Guez 2014; MacLean et al. 2014; Chow et al. 2017). Inhibitory control is often assessed through a detour task in which an individual has to maneuver around a clear barrier to reach a reward, rather than run head first into the barrier (Lucon-Xiccato and Bisazza 2017a, Kabadayi et al. 2018).

We recently demonstrated that male sticklebacks who had better inhibitory control as assessed by a detour task were preferred by females as mates (Minter et al. 2017). However, male inhibitory control was not associated with any measured sexual signals (throat color, eye color, body size: Minter et al. 2017). In this study, we examined male and female performance on the detour task. We presented the task four times over a period of 7 days, allowing us to assess initial detour task performance and improvement over time. We made several predictions. First, given our hypothesis that selection has resulted in sexual dimorphism in inhibitory control, we predicted that males would initially outperform females on the detour task. It was unclear whether there would be a difference between males or females in their improvement over time, as learning is likely important for both sexes. Finally, we predicted that males would more vigorously court females who performed well on the detour task.

Materials and Methods

We collected reproductive threespine sticklebacks from the Chehalis River (46° 58' 42"N, 123° 28' 46"W) in SW Washington, USA, in April 2014 using minnow traps. We separated the fish by sex before transporting them to the University of Denver where they were

housed in 110-L ($77 \times 32 \times 48$ cm) and 284-L ($123 \times 47 \times 54$ cm) holding tanks at a density that did not exceed one fish per 5-L. We set the lab temperature to 17°C with a 15:9 h light: dark cycle in the beginning of the experiment and adjusted the light: dark cycle throughout the breeding season to replicate conditions in SW Washington. The room was illuminated by broad spectrum Sylvania Optron Eco 5000 K fluorescent lights. We fed all individuals a mixture of defrosted brine shrimp (*Artemia* sp) and defrosted bloodworms (chironomid larvae) and only brine shrimp on alternating days. We obtained collection and transport permits from the Washington Department of Fish and Wildlife (14-078) and the University of Denver's IACUC approved the research conducted (2013-0004).

At the start of cognitive testing (conducted from June to October of 2014) we relocated fish from their holding tanks to randomly assigned, visually isolated, 110-L ($77 \times 32 \times 48$ cm) experimental tanks where cognition trials and mating trials were conducted. We allowed males to build nests in these experimental tanks. To mimic natural settings, experimental tanks contained a green plastic plant, a gravel pack (crushed coral in a nylon casing that helps maintain water quality), a nesting tray ($17 \times 11 \times 3$ cm) filled with sand and covered by half a flower pot ($15 \times 9 \times 7$ cm), and 5 g of live plant material *Ceratophyllum demersum* used for nest building.

Detour task

We used a detour task to measure male and female initial inhibitory control and improvement over time as in Minter et al. (2017). Briefly, the task involved reaching a food reward suspended inside of a transparent plastic cylinder (11.5 cm diameter base, 7 cm tall, with a 9.5 cm diameter opening on the top). We suspended a small clear plastic bag ($3 \text{ cm} \times 2.5 \text{ cm}$) containing bloodworms and water inside of the cylinder and provided fish a food reward of three bloodworms attached to the outside of the bag via petroleum jelly. We allowed fish to acclimate to their experimental tanks for 24 h prior to testing. During this acclimation period, we deprived the fish of food to increase the incentive to reach the food reward. Immediately before each trial, we lowered an opaque divider to block the fish's view while the clear cylinder and reward were placed into the tank. The trial began when we removed the opaque divider. To obtain the food reward, the fish needed to swim above and into the clear cylinder, rather than swim directly into the side of the transparent cylinder. We observed each fish for 10 min, or until the fish retrieved the food reward, whichever came first. After the trial, we removed the cylinder and food reward. Fish that did not enter the cylinder to retrieve the food reward were provided 3 bloodworms at least 1 h after the trial ended to equalize feeding across animals. We presented the detour task four times over 7 days, on Days 1, 2, 3, and 7. During this 7-day period, fish were fed only brine shrimp (*ad libitum*) aside from the 3 bloodworms provided on each detour task day.

For each trial, we recorded whether the fish entered the cylinder, the number of attempts each fish made to access the food reward by touching the transparent cylinder, and the time elapsed before entering the cylinder using the event recorder JWatcher (<http://www.jwatcher.ucla.edu/>). For analyses, we used the inverse of attempts, yielding the variable "entries per attempts" that ranges from (nearly) 0 to 1. If an individual entered the cylinder without first making an unsuccessful attempt, s/he was given a score of 1 (the maximum score). Fish that did not enter the cylinder were assigned the maximum possible trial time (10 min = 600 s). We removed all fish that never attempted to retrieve the food reward (across all four trials)

from our analyses. A total of 58 males and 54 females completed detour tasks. Results of tests on males only were previously reported in Minter et al. (2017). Here, we compare the outcomes for males and females.

Mate choice

We used the vigor with which stickleback males courted females (number of male courtship behaviors per minute) as a measure of his interest in a female mate (male preference). Detailed description of our mate choice procedure is in Minter et al. (2017). Briefly, males were allowed to construct nests in their experimental tanks. We considered nests complete when an opening and exit were clearly visible (Wootton 1976). As soon as males completed nest-building, we assessed male courtship vigor and female mating decisions in standardized no-choice mating trials using methods commonly used by multiple labs (Nagel and Schluter 1998; Head et al. 2009; Tinghitella et al. 2013). Each male had two mating trials (with the exception of two males who did not maintain nests long enough to do so). However, not all the females used in mate choice trials completed the detour task. In the analysis presented here, 13 males had mate choice trials with two females that completed the detour task and 13 males had mate choice trials with one. Females were used in mate choice trials with multiple males (1–4 males). As in past research, we allowed at least 2 h of resting time between mating trials (Kozak et al. 2009; Tinghitella et al. 2013).

Each courtship trial proceeded as follows. We first acclimated a female to the male's tank in an opaque tube with a false floor for 2 min before releasing her into the male's tank. We then recorded all behaviors associated with mate choice in real time, again using JWatcher for 20 min or until the female entered the nest. We carefully prodded females to exit the nest before they could deposit their eggs. Following courtship trials, we photographed males and females under standardized conditions with a Canon Powershot G15 to allow measurement of length from photos and weighed them to the nearest tenth of a gram (Scout Pro SP202). Finally, we determined body condition of each individual female by calculating the residuals from a regression of weight against length (Jakob et al. 1996); this condition measure most likely reflects differences in gravidity (females that were heavier than expected for their weight would be expected to have more or heavier eggs). We tagged all fish with an individualized elastomer mark (Northwest Marine Technology Inc) to identify individuals after they were released back into their home tanks. We completed 39 mate choice trials with 26 males and 24 females that also completed the detour task.

Statistical analyses

All statistical analyses were done in R v3.4.4 (R Core Team 2018). To test for how variables changed over time, we used linear mixed-effects regression models. The model had either entering the cylinder (yes/no), time to enter (log transformed), or entries/attempts (arcsine square root transformed) as the response variable and included trial number as a continuous variable (1, 2, 3, 4), sex, and their interaction as fixed effects. We also allowed each fish to have its own intercept and slope for the relationship between time and the response variable (i.e., random slopes and intercepts for fish identity). We used a binomial generalized linear mixed-effects model for entering the cylinder using the "glmer" function in the R package *lme4* (Bates et al. 2015) and a linear mixed-effects model for the other two response variables (using the "lmer" function in the *lme4* package). We tested statistical significance by calculating degrees of

freedom using the Satterthwaite approximation with the R package *lmerTest* v.2.0-36 (Kuznetsova et al. 2017).

As in Minter et al. (2017), we reduced the number of variables overall by performing a principal components analysis (PCA) on the three standardized first trial performance measures (z-scores) using the “prcomp” function in the R package *stats*. On average, fish improved their performance on the detour task over time (Results, Figure 1). Therefore, we quantified learning with three different measures: the number of presentations until first entry of the cylinder (with 5 = never entered), the change in entries per attempts, and the change in time to enter the cylinder. To obtain the latter two measures of learning, we performed linear regressions of (arcsine square root transformed) entries per attempts and (log transformed) time to enter on trial number (1, 2, 3, and 4) and used the slopes from these regressions. Better learners would thus have positive slopes in the models with entries per attempts and negative slopes in the models with time to enter. Next, to be consistent with Minter et al. (2017) we performed PCA as a variable reduction technique on the two slope variables (change in entries per attempts and change in time to enter) and retained number of trials to enter as a separate variable.

In the models assessing whether there was a sex difference in cognitive ability, the cognitive measure was the response variable and sex and (log-transformed) neophobia (time to first approach the barrier within one body-length) were fixed effects. These models were run with the “lm” function in the R package *stats*. Models assessing whether males preferred females with better cognitive ability had (log transformed) male courtship vigor as the response variable and the cognition measure, female condition/gravidity, and mate choice trial (i.e., first or second) as fixed effects with female identity and male identity as random effects. These models were run using the “lmer” function in the R package *lme4* and we tested statistical significance by calculating degrees of freedom using the Satterthwaite approximation with the R package *lmerTest* v.2.0-36.

Results

Change in detour task performance over time

Each of the detour task performance measures differed between the sexes and changed over time (the four presentations of the detour

task). Frequency of entering the cylinder increased over time (main effect of trial number: $\chi^2 = 17.86$, $df = 1$, $P \ll 0.001$) and males were consistently more likely to enter than females (main effect of sex: $\chi^2 = 14.97$, $df = 1$, $P < 0.001$), with a nonsignificant trend for the sex difference to be larger after the initial trial (interaction effect of trial number and sex: $\chi^2 = 3.11$, $df = 1$, $P = 0.078$, Figure 1A). The number of entries per attempts also increased over time (main effect of trial number: $\chi^2 = 10.84$, $df = 1$, $P < 0.001$), males had more entries per attempts than females (main effect of sex: $\chi^2 = 6.97$, $df = 1$, $P = 0.008$), and this difference remained similar across all trials (interaction effect of trial number and sex: $\chi^2 = 0.42$, $df = 1$, $P = 0.519$, Figure 1B). Time to enter decreased over time (main effect of trial number: $\chi^2 = 52.72$, $df = 1$, $P \ll 0.001$) and males were consistently faster than females (main effect of sex: $\chi^2 = 14.33$, $df = 1$, $P < 0.001$), although this difference became larger over time (interaction effect of trial number and sex: $\chi^2 = 4.51$, $df = 1$, $P = 0.034$, Figure 1C).

However, it is possible that differences in neophobia are largely responsible for these sex differences. Females were indeed slower to approach the barrier during the first presentation (Welch’s *t*-test, $t = 5.74$, $df = 107.02$, $P \ll 0.001$). When accounting for this difference by including neophobia in our repeated measures analyses, there was no longer a sex effect for frequency of entering the cylinder ($\chi^2 = 2.06$, $df = 1$, $P = 0.151$), entries per attempts ($\chi^2 = 0.93$, $df = 1$, $P = 0.336$), or time to solve ($\chi^2 = 0.34$, $df = 1$, $P = 0.558$). There was still a significant interaction between trial number and sex on time to solve ($\chi^2 = 4.51$, $df = 1$, $P = 0.034$), reflecting that males became increasingly faster than females at solving the detour task, even after controlling for neophobia (pattern confirmed through *post hoc* contrasts). In all three of these analyses, trial number and neophobia were significant predictors of performance (all $P < 0.002$, Appendix).

Sex differences in initial detour task performance

We performed a principal components analysis of the three measures of performance during the first presentation of the detour task. This analysis resulted in a first principal component (PC1_{detour}) that explained 77% of the variation with even loadings of each variable, giving us an excellent summary variable (Table 1a). This PC1 from an analysis which included both males and females was very similar

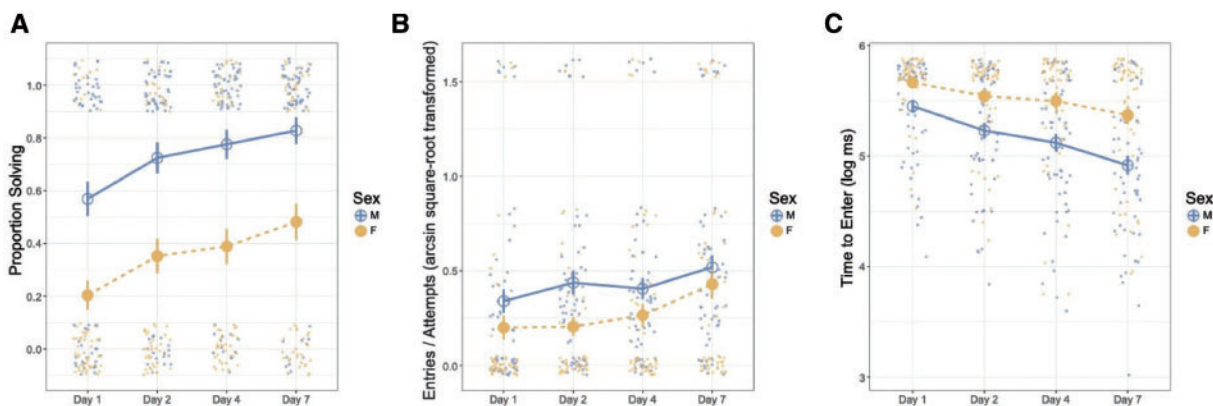


Figure 1. Change in detour task performance over time. Fish improved over time and males were consistently better than females on three measures of detour task performance: (A) entering the cylinder, (B) entries/attempts, and (C) time to enter the cylinder. Means for each sex for each day are indicated with large circles and error bars indicate standard errors. Each individual fish is represented with a small point; these points have been jittered slightly in the vertical and horizontal dimensions to improve visibility. In (A), fish scored as “0” are those who did not solve, and fish scored as “1” are those who did solve the detour task by entering the cylinder. Note that the male data are identical to Minter et al. (2017).

Table 1. Principal components analysis for variable reduction of (A) initial detour task performance variables and (B) learning slopes measures

(A)				(B)		
Trial 1 Variable (N = 112)	PC1 Eigenvector	PC2 Eigenvector	PC3 Eigenvector	Learning Slopes Variable (N = 112)	PC1 Eigenvector	PC2 Eigenvector
Enter (yes/no)	0.59	0.20	0.78	Change in Entries/ Attempts	0.71	-0.71
Entries/Attempts	0.58	0.57	-0.58	Change in Time to Enter	-0.71	-0.71
Time to Enter	-0.56	0.80	0.22	Eigenvalue	1.16	0.81
Eigenvalue	1.52	0.64	0.53	% Variance	67.5%	32.5%
% Variance	77.1%	13.6%	9.3%			

to the PC1 from our previous study which only included males (Minter et al. 2017). We did not find a sex difference in PC1_{detour} when we controlled for neophobia (neophobia: $F_{1, 109} = 44.08$, $P \ll 0.001$, sex: $F_{1, 109} = 0.08$, $P = 0.774$, Figure 2). An analysis that included only individuals that approached the cylinder provided similar results (neophobia: $F_{1, 64} = 4.93$, $P = 0.030$, sex: $F_{1, 64} = 0.72$, $P = 0.398$).

Sex differences related to learning the detour task

Females took significantly more trials to solve the detour task, even after accounting for the effect of neophobia (neophobia: $F_{1, 109} = 27.66$, $P \ll 0.001$, sex: $F_{1, 109} = 4.72$, $P = 0.032$, Figure 2). As in Minter et al. (2017), we took the two learning slopes variables and condensed them with a principal components analysis into a single variable (PC1_{learning}) describing 68% of the covariation in the learning slopes variables (Table 1b). There was a nonsignificant trend for males to have higher PC1_{learning} scores than females after accounting for the effect of neophobia (neophobia: $F_{1, 109} = 4.49$, $P = 0.036$, sex: $F_{1, 109} = 3.22$, $P = 0.076$, Figure 2).

Female cognitive performance and male courtship vigor

Because of the strong positive relationship between neophobia and PC1_{detour}, we regressed neophobia against PC1_{detour} and used the residuals, which we interpret as a measure of inhibitory control (see Minter et al. 2017). Inhibitory control did not predict male courtship vigor, although female gravidity/condition did (mate choice trial number: $F_{1, 30.40} = 0.02$, $P = 0.892$, gravidity/condition: $F_{1, 28.22} = 9.94$, $P = 0.004$, inhibitory control: $F_{1, 23.09} = 0.95$, $P = 0.340$). We found similar results with number to solve (mate choice trial number: $F_{1, 31.13} = 0.02$, $P = 0.733$, gravidity/condition: $F_{1, 29.40} = 8.72$, $P = 0.006$, number to solve: $F_{1, 23.41} = 1.61$, $P = 0.217$) and PC1_{learning} (mate choice trial number: $F_{1, 29.65} = 0.01$, $P = 0.912$, gravidity/condition: $F_{1, 29.00} = 9.18$, $P = 0.005$, PC1_{learning}: $F_{1, 24.09} = 1.14$, $P = 0.295$).

Discussion

We found dramatic differences in performance on the detour task between the sexes over time, with males generally outperforming females (Figure 1). However, these differences were largely explained by males being less neophobic (more likely to approach the barrier) than females. There was no difference between the sexes in the first principal component describing covariation in the three measures of initial detour task performance after accounting for neophobia (i.e., “inhibitory control”). However, females took more trials to solve the detour task even after accounting for differences in neophobia. In addition, after accounting for neophobia, there was a

non-significant trend for females to be poorer learners as quantified by the first principal component describing covariation in change in time to solve and change in entries/attempts. Our initial repeated-measures analyses also pointed to a potential difference between the sexes in learning, indicated by a nearly significant trial number x sex interaction in solving frequency and a significant trial number x sex interaction in time to solve. Taken together, these results give some evidence for sex differences in learning, although further testing should be done. In addition, disentangling inhibitory control performance from learning is not straight-forward, as learning occurs within a single trial in order for the detour task to be solved and inhibitory control could play a role in every trial, although its effect is expected to diminish over time. Finally, contrary to our predictions, we found that males did not preferentially court females that performed better on our detour task or learned faster.

Sex differences in initial inhibitory control were expected due to differences in selection pressures from different sex roles. Comparative brain studies have suggested that fish parental care is cognitively taxing (Gonzalez-Voyer et al. 2009; Kotrschal et al. 2012; Herczeg et al. 2014). Indeed, male sticklebacks typically have much larger brains compared with females after controlling for body size (threespine: Kotrschal et al. 2012; ninespine: Herczeg et al. 2014). Inhibitory control is an especially relevant cognitive skill for male sticklebacks because in order to court reproductive females, territorial males must reduce their normal aggressive behavior towards intruders. In addition, once parents, males must resist eating their eggs and fry which are otherwise preferred prey (Hynes 1950; Whoriskey and FitzGerald 1985; Foster et al. 1988). In fact, males will cannibalize their clutch if they detect low average paternity, indicating an ability to fine tune their behavior to different circumstances (Mehlis et al. 2010). However, we did not find any sex difference in initial performance on the detour task after controlling for neophobia, which we interpret as no sex difference in inhibitory control. Lucon-Xiccato and Bisazza (2017a) found that male guppies performed worse than females on a detour task and that this was driven by males persisting more at the barrier (i.e., lower inhibitory control). Male guppies also were poorer at a reversal learning task (Lucon-Xiccato and Bisazza 2014), persisting longer with the original reward contingencies. Lucon-Xiccato and Bisazza (2014, 2017a) suggest that male guppies may have been selected to have more persistence in general because increased reproductive success results from persistent harassment of females. As individual variation in inhibitory control is studied in a wider range of species, the proximate and ultimate drivers of this variation will become clearer.

The large sex difference in neophobia, and the effect it had explaining the sex difference in initial detour task performance, led us to consider how our experimental design may have affected these results. The sex difference in neophobia was largely caused by a

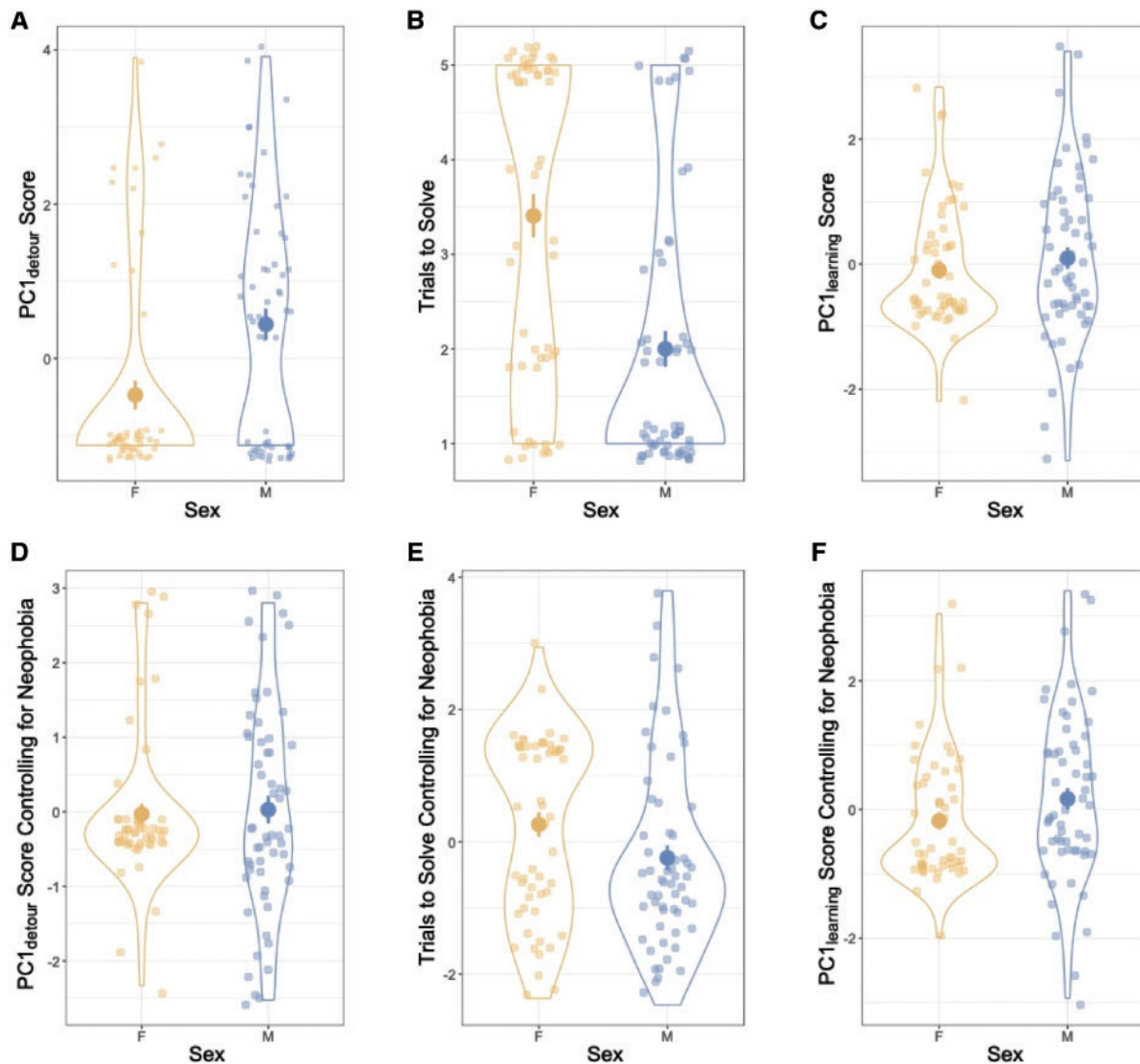


Figure 2. Sex differences in initial detour task performance and learning. Top panels (A-C) show unadjusted values and bottom panels (D-F) show values adjusted for neophobia (i.e., these are residuals from a regression of the cognitive performance measure against neophobia). The three cognitive performance measures shown are (A, D) PC1_{detour}, (B, E) trials to solve, and (C, F) PC1_{learning}. Means for each sex are indicated with large solid circles and error bars indicate standard errors. Each individual fish is represented with a small point; these points have been jittered slightly in the vertical and horizontal dimensions to improve visibility. The complete distribution is visualized with violin plots; the width corresponds to the probability of a sample being found at that value.

dramatic difference between the sexes in propensity to approach the barrier during the first presentation. While most males approached the barrier (50/58 = 86% approached), most females did not (17/54 = 31% approached). At least two non-mutually exclusive possibilities can explain this sex difference in behavior. First, although foraging behavior of fish from the population sampled has not been quantified during the breeding season, in other stickleback populations males are solitary foragers, whereas females forage in shoals (Hart and Gill 1994). In addition, non-breeding sticklebacks use social cues provided by conspecifics while foraging (Webster and Hart 2006). Since breeding females forage in groups, they may be more reliant on social cues, whereas males may be more reliant on personal information, although this has not been specifically tested. This potential sex difference could have generated differences in stress caused by foraging alone, resulting in differences in task performance (as shown in rats: Harris et al. 2008); future experiments could test this by measuring stress hormones or behaviors. Second, after

being added to an empty tank, reproductive males will display territorial behavior to intruders. It is possible that males are thus more likely to investigate novel objects because of this territorial behavior. Indeed, boldness (the inverse of neophobia) and aggressiveness are often part of the same behavioral syndrome (Huntingford 1976; Bell 2004). However, Bell (2004) found no difference between male and female sticklebacks in aggression towards an intruder after 1 day of being added to an empty tank. Future work could help mitigate these effects by first using behavioral shaping to train fish to feed at a specific location and then placing the barrier around the feeding location once a shaping criterion has been reached. Other strategies to diminish the effects of personality on task performance include adjustment of tank acclimation times or use of a simulated shoal.

After controlling for neophobia, we found that females took significantly more trials to first solve the detour task and we found additional support that females were poorer learners on the task (although sometimes these were only statistically nonsignificant

trends). We had not specifically predicted that males would be better learners than females, but these results raise that intriguing possibility. Given that males are solitary foragers during the breeding season and have to make brief and opportunistic foraging bouts compared with females (Webster and Laland 2010), it could be that there is selection on them to learn more quickly in foraging tasks. This intriguing possibility should be further studied. Females, on the other hand, might be expected to be more attentive to social cues and be more reliant on various forms of social learning (Webster and Laland 2010). In addition, female sticklebacks might perform better on spatial learning tasks because they commonly assess multiple male nests before relocating preferred males to mate with them (Tinghitella et al. 2015). It would be interesting to assess sex differences on multiple types of learning.

Male sticklebacks are the sole providers of costly parental care (Smith and Wootton 1995; 1999). We therefore predicted that males should be choosy, more vigorously courting females who have traits that could increase their fitness (Johnstone et al. 1996). Although females from the same population tested here prefer males with superior initial inhibitory control (Minter et al. 2017), males did not express a preference for females with better initial inhibitory control or who were better learners on the detour task. The asymmetry in preferences for cognition between the two sexes could be a product of the sexes experiencing different selection pressures. During the breeding season, males select optimal nesting sites (Sargent 1982; Candolin and Voigt 1998), forage alone (Hart and Gill 1994), build a nest and provide all parental care (Wootton 1976), including supplying adequate oxygen (van Iersel 1953; von Hippel 2000) and defending against predators (Wootton 1976; Stein and Bell 2014) and cannibalistic females (Whoriskey and FitzGerald 1985). Females, on the other hand, do not contribute to nest construction or parental care (Wootton 1976) and forage in shoals (Hart and Gill 1994). Females may prefer high performing males because a male's direct contribution to future offspring likely depends on his cognitive abilities. Males instead appear to prioritize female fecundity over cognitive ability. An alternative explanation for our null results is that males were unable to choose females with better cognitive performance because there were no female traits that covaried with females' cognition that males could assess.

In summary, we found that males consistently outperform females on a detour task, although neophobia differences between the sexes explain this difference. There is suggestive evidence that males were better than females at learning on this task. Although female sticklebacks consider male cognitive traits in their mating decisions (Minter et al. 2017), male sticklebacks do not preferentially court females that perform well on the same cognitive task. If males do have mating preferences related to female cognition, those preferences may be for an entirely different suite of cognitive abilities.

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Authors' Contributions

R.M. and R.M.T. conceived the project. R.M. conducted all behavior experiments and data collection. J.K. analyzed the data. J.K., R.M., and R.M.T. wrote the manuscript.

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Appendix. Effect of sex on cognitive performance

(a) Enter the cylinder (yes/no)

	χ^2	df	P
(log-transformed) Neophobia	17.60	1	<< 0.001
Trial Number (1, 2, 3, 4)	17.50	1	<< 0.001
Sex	2.06	1	0.151
Trial Number \times Sex	3.42	1	0.065

(b) Entries per attempts (arcsine square-root transformed)

	χ^2	df	P
(log-transformed) Neophobia	9.62	1	0.002
Trial Number (1, 2, 3, 4)	10.84	1	< 0.001
Sex	0.93	1	0.336
Trial Number \times Sex	0.42	1	0.519

(c) Time to enter cylinder (log-transformed)

	χ^2	df	P
(log-transformed) Neophobia	45.73	1	<< 0.001
Trial Number (1, 2, 3, 4)	52.72	1	<< 0.001
Sex	0.34	1	0.558
Trial Number \times Sex	4.51	1	0.034