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Mate assessment behavior is correlated to learning ability in female threespine sticklebacks

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Abstract

In many species, males signal quality with elaborate traits, but females often show inter-individual variation in preference for these traits. Choosing a mate requires multiple cognitive steps; therefore, cognitive style (how an individual processes information) likely influences the perception of sexual signals and ability to choose a high-quality mate. An important component of cognitive style is flexibility; cognitively flexible individuals are more perceptive to shifts in cues. We hypothesized that cognitively flexible individuals would acquire more information about potential mates, better discern between two quality-signaling traits, and thus be more discriminatory. Here, we show that mate assessment is correlated to other cognitive traits. Although we did not detect an effect of cognitive style on mate preference or discrimination, we found that female threespine sticklebacks *Gasterosteus aculeatus* that spent more time assessing potential mates (more responsive) in a dichotomous mate choice task reached both the initial and reversal learning criterion in a spatial learning task with fewer errors. However, these highly responsive females made more consecutive mistakes immediately at the beginning of the reversal phase, suggesting that they did not quickly adapt to the environmental change but instead rapidly formed strict routines during the learning task that were eventually reversible after repeated errors. Furthermore, we found evidence for condition-dependent mate preference, with larger females preferring the high-quality male. These are among the first results that illustrate how cognitive traits might influence mate choice, which has implications for the strength and direction of sexual selection.

Key words: cognition, cognitive flexibility, choosiness, computer animation, mate choice, sexual selection

Mate choice has resulted in the evolution of a vast array of sexual signals to attract the choosy sex (Bateson 1983). Females can gain direct fitness benefits or indirect benefits for their offspring by utilizing these signals to choose a high-quality mate (Kokko et al. 2003). However, rather than a clear population-level preference for the high-quality mate, there is often a large variation in what the choosy sex prefers, and this individual variation is likely to affect the strength and direction of sexual selection on these traits (Brooks and Endler 2001). Many studies have focused on these quality-indicating behavioral and physical traits

of the preferred mates (Andersson and Simmons 2006; Schuett et al. 2010), and recent research has started to explore the question of how the innate cognitive or behavioral characteristics of the choosy sex influence which mate is chosen. For instance, it has recently been shown that sensory configuration (Ronald et al. 2018) and brain size (Corral-López et al. 2017) in females influence mate choice and the ability to accurately assess the sexual signals of potential mates. Therefore, individual differences in cognition might explain some of the variation in preference for sexually selected traits that is often found in populations.

Cognition is defined as the way that individuals acquire, store, and use information (Shettleworth 2010). Cognitive ability is often measured by the ability to reach a learning criterion, and cognitive flexibility is usually measured by the ability to reverse or inhibit a previously learned cue or task (Coppens et al. 2010; Griffin et al. 2015). Cognitive style encompasses many aspects of cognition such as cognitive flexibility, decision speed, and information collection (Sih and Del Giudice 2012), and previous studies have found that individuals within populations show consistent differences in cognitive style (Matzel et al. 2003; Guillette et al. 2017; Matzel et al. 2017; Boogert et al. 2018). Individuals can vary in a plethora of cognitive traits such as information sampling, information storage, and cue dependence, resulting in differences in learning ability, memory, impulsiveness, and sensitivity to stimuli such as changing environmental conditions or sexual signals (Sih and Del Giudice 2012). Many of these aspects of cognition are hypothesized to be linked. For example, individuals that are relatively insensitive to new information tend to be more dependent on internal cues than environmental cues and thus less flexible when confronted with changing environmental cues, while individuals that are more sensitive to external cues are more flexible in response to environmental change (Benus et al. 1987; Benus et al. 1990; Koolhaas et al. 1999; Sih and Del Giudice 2012). It is likely that these individual differences in cognitive traits elicit different behaviors when assessing potential mates (David and Cézilly 2011).

Choosing a mate requires multiple cognitive steps; the choosy sex needs to perceive and learn these signals, remember this information, and use stored information to compare options and make a decision (Bateson and Healy 2005). Female mate choice decisions can differ in the preference for a certain mate and the strength of this preference in relation to other males (discrimination) along with the amount of time and energy invested in assessing mates to come to a decision (choosiness; Jennions and Petrie 1997). Assessing the cues of potential mates and making mating decisions based on this collected information therefore likely depends partially on individual cue sensitivity, as individuals that differ in cue sensitivity will perceive sexual ornaments and mate quality indicators differently. For example, more sensitive individuals may better discriminate between different values of the same trait and thus more accurately choose the higher quality mate (Edward 2015). Furthermore, sensitive individuals may be better able to assess multiple cues, collecting more information about a potential mate (Candolin 2003). Often, assortative or disassortative mate choice is advantageous, especially in monogamous species (Jiang et al. 2013), so individuals that are more accurate in self-referencing will make better mate choices. In nature, mate choice often occurs sequentially (Jennions and Petrie 1997). Females compare the current male to the previously encountered males and become less choosy with increased sampling (Bakker and Milinski 1991; Gabor and Halliday 1997), costs (Milinski and Bakker 1992), predation risk (Godin and Briggs 1996), and competition for mates (Fawcett and Johnstone 2003). To decrease sampling costs, social cues and experience are also important in mate choice (Westneat et al. 2000). Females have been shown to use social cues during mate choice (Dugatkin and Godin 1992; Goldschmidt et al. 1993; White 2004; Frommen et al. 2009), and there are individual differences in the use and perception of social information (Marchetti and Drent 2000; Nomakuchi et al. 2009; Kurvers et al. 2010; Trompf and Brown 2014). Overall there are many cues that need to be assessed and integrated during the mate choice process, and individual differences in these cognitive traits

might predict behavior and preference when evaluating traits signaling quality of potential mates.

Threespine sticklebacks are a model organism for behavioral studies (reviewed in Huntingford and Ruiz-Gomez 2009). This species is sexually dimorphic during the breeding season, which generally takes place from April to September. During the breeding season, males have blue eyes and red throats while females are drab with a swollen silver belly when gravid. There is a large body of research supporting the hypothesis that females prefer males with red throats (Milinski and Bakker 1990; Bakker and Milinski 1993; Bakker and Mundwiler 1994; Rowland 1994; Braithwaite and Barber 2000), however there is still individual variation in preference (Milinski and Bakker 1992; Bakker 1993; Bakker et al. 1999) despite the evidence that a red throat is an honest signal of quality (Candolin 2000). Red coloration can vary in hue and intensity, and both are important signals (Wedekind et al. 1998; Pike et al. 2011; Hiermes et al. 2016; Pike 2017). Males court females with a zig-zag dance, and when successful, females spawn in the nest of the courting male. This species has energetically costly paternal care (Rowland 1994; Östlund-Nilsson 2007), and both sexes are capable of reproducing several times per season with different mates (Wootton 1994), therefore females must assess the quality of many males throughout the breeding season. Since males care for the offspring, choosing a high-quality mate directly affects female fitness. Males broadcast their quality via multiple signals beyond throat coloration (i.e., blue eyes: Rowland 1994; spine symmetry: Mazzi et al. 2003; body size: Kraak et al. 1999; courtship behavior: Jamieson and Colgan 1989, Künzler and Bakker 2001; nest characteristics: Kraak et al. 1999) and thus selection should favor the evolution of cognitive mechanisms to discriminate between males of differing quality (Rowe et al. 2004).

We evaluated the mate choice behavior of female threespine sticklebacks with a dichotomous choice test using computer-animated males differing in breeding coloration and examined the spatial learning and reversal learning ability of the same individuals to look for correlations between spatial learning ability and mate assessment. In nature, female sticklebacks sequentially assess mates and some females might be better at remembering where the nests of high-quality males are located (Bakker and Milinski 1991; Milinski and Bakker 1992). Body size and fitness measures were also included as possible influences on mate choice behavior, as previous studies have shown an influence of female quality on mate choice preference, with high-quality females preferring high-quality males (Bakker et al. 1999; Hunt et al. 2005). We therefore expected that high-quality females would prefer the high-quality males. Furthermore, we hypothesized that there would be a correlation between cognitive traits and mate assessment behavior, specifically that females that learned the reversal learning task more quickly would also be more sensitive to the differences in presented sexual stimuli, resulting in a stronger preference for the high-quality male. However, since female sticklebacks show a variation in preference for bright orange or bright red males (Milinski and Bakker 1992; Bakker 1993; Bakker et al. 1999), the sensitive females might more strongly prefer one male over the other, resulting in a higher overall discrimination regardless of throat coloration of the preferred male.

Material and Methods

Experimental subjects
Experimental subjects were wild-caught *Gasterosteus aculeatus* (hereafter sticklebacks) from a freshwater population.

Approximately 1,200 sticklebacks were caught in February of 2017 from a pond in Derletal, Bonn-Duisdorf, Germany (50°42'30.1"N 7°02'29.4"E). Sticklebacks were transported to the Institute for Evolutionary Biology and Ecology at the University of Bonn and were held in a large outdoor tank (750 L, flow rate 3 L/min) for approximately 2–3 months, where they were fed daily (excluding weekends) in excess with *Chironomus* larvae (hereafter bloodworms). Experimental subjects were selected by netting a large group of the shoal and choosing individuals that appeared to be females, determined by an enlarged belly and the absence of blue eyes. All individuals selected exceeded a standard length of 4.0 cm (mean = 4.776 ± 0.325). Most individuals in the outdoor tank were not yet sexually dimorphic; males could not establish territories under these holding conditions and thus many of them did not have any breeding coloration and some females were not yet gravid. Therefore, some of the individuals selected started to show breeding coloration (red/orange throat) after being placed in individual tanks and these males were subsequently removed and replaced with fish from the outdoor tank, again waiting to see if the fish expressed male coloration or became gravid. Eventually, 53 females were kept as experimental subjects.

Housing conditions

All experimental subjects were kept in an air-conditioned room (18°C ± 1°C) under simulated summer conditions (16L:8D). Illumination was provided by natural daylight-simulating fluorescent lamps (True-Light lamp 58W/5500 T8, True-Light International GmbH, Germany). Fish were housed individually in tanks measuring 20 cm × 20 cm × 30 cm, filled to 15 cm with aged tap water and equipped with one air stone (Dohse Aquaristik GmbH and Co. KG, Germany). For all housing and experimental tanks, tap water was aged for 24 h to reduce trapped gas bubbles and allow the pH to stabilize. Tanks were visually isolated from one another with black opaque partitions. Sticklebacks were fed daily with defrosted bloodworms in excess in the afternoon after all experiments were finished. Individuals with learning experiments the next day were not fed. After 15 min for feeding, the excess food and fish excretions were removed and water refilled. Furthermore, water was exchanged in all tanks once weekly. All fish were briefly removed from the tank and examined visually for gravidity daily. Gravidity assessment was based on belly width and cloaca enlargement. If fully formed eggs were visible through the cloaca when gently squeezing the belly, the individual was determined to be gravid (Frommen et al. 2012).

Mate choice experiment

A dichotomous choice test using two computer-animated males that differed in throat coloration which is an important sexual signal was used to test female mate choice behavior. Mate choice experiments ran from May 22 to July 6, 2017, between 10:00 and 19:00. Experimental subjects were selected based on gravidity; when an individual was gravid it was immediately used in the mate choice experiment.

The experimental tank measured 20 cm × 20 cm × 30 cm and was situated between two identical computer monitors (Figure 1). The four walls were lined with gray plastic sheets with the exception of viewing windows on opposite ends of the tank, which measured 10 cm × 7 cm and were located 2.5 cm from the bottom of the tank. Preference zones (9 cm × 7 cm) were marked adjacent to the viewing windows on the underside of the tank. A transparent cylinder with a

diameter of 10 cm was positioned in the center of the tank and was attached with transparent fishing line to a pulley. During the experiments, aged tap water was filled to 11 cm depth. A Logitech QuickCam® Pro 9000 webcam was located 50 cm over the center of the tank for video recording of the trials. Opaque partitions surrounded the experimental tank to prevent external influences. There was a gap of 2.5 cm between the experimental tank and each monitor, and this was completely blocked around the viewing window to ensure that only the light emitted from the computer monitors was visible through the viewing windows. The tank and cylinder were cleaned using 3% hydrogen peroxide and rinsed with water to remove all odors between every trial.

The test fish was placed in the cylinder for an acclimatization period of 15 minutes, during which the empty background of the animation was displayed on each monitor. After 15 minutes, the animations were started, and females could observe the males performing the courtship zig-zag dance from within the cylinder for 30 s. After the 30 s, the cylinder was raised externally until the bottom rested within 1 cm of the surface of the water. Trials began when the cylinder was fully lifted and lasted 10 minutes.

The time that the test fish spent in each of the two preference zones and the total number of visits to each preference zone was determined. Responsiveness was calculated as the mean time spent in the preference zones of the two stimuli, meaning that more responsive females spent more time in the preference zones of the male animations, regardless of which animation was preferred. For simplicity in graphical presentation, preference index was calculated as the time spent in the preference zone of the red animated male, which predicts the probability of spawning (McLennan and McPhail 1990; Milinski et al. 2005), divided by the total time spent in both preference zones, so 0 indicates absolute orange preference, 0.5 indicates no preference, and 1 indicates absolute red preference. Discrimination was calculated as the standard deviation of the mean responsiveness (Brooks and Endler 2001).

After the experiment was finished, females were gently dried by blotting with a paper towel and their body mass (mg) and standard length (mm) was recorded. Gravid females can be easily stripped of their eggs without causing harm, and stripping is often used to justify gravidity (Baggerman 1957). It was important to justify gravidity in order to ensure that the behavior was valid in the context of assessing potential mates. Females were gently stripped before their body mass was determined again. Reproductive investment was calculated as the difference in body mass from before and after stripping divided by the body mass after stripping.
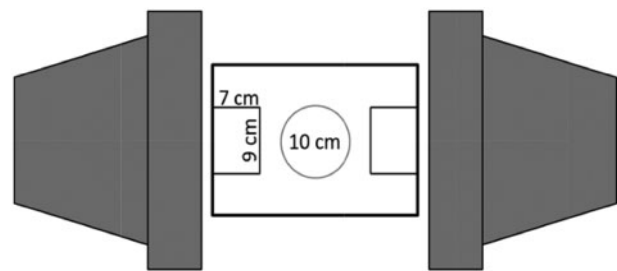

Figure 1. The mate choice experimental tank measured 20 cm × 30 cm × 30 cm and was situated between two identical computer monitors. A transparent cylinder (indicated by the circle, diameter of 10 cm) was located centrally and raised during the trial so that the bottom hovered 1 cm below the water line. Two preference zones (9 cm × 7 cm) were drawn on the underside of the tank adjacent to the animation viewing windows.

Use of animations

Animations are a powerful tool to study mate choice and allow for the manipulation of the focal trait while keeping all other variables constant (Künzler and Bakker 1998). The visual system of sticklebacks is considered to be well-suited for using animated stimuli, with certain restrictions (Mazzi et al. 2004). Although sticklebacks can see ultraviolet (UV) wavelengths between 300 and 400 nm (Rowe et al. 2004) and use UV visual cues during mate assessment (Rick et al. 2006; Rick and Bakker 2008), UV cannot be simulated by computer monitors. Therefore, any visual stimuli presented on a computer monitor will lack any UV signals that may be associated with the trait tested.

The computer animation used in this experiment was a modified version of that validated by Künzler and Bakker (1998) showing the courtship behavior of a computer-animated male stickleback. These animations have been successfully used in sticklebacks before (e.g., Bakker et al. 1999; Mazzi et al. 2003; Mehlis et al. 2008; Hiermes et al. 2015). The animation was constructed with a realistic virtual 3D model, its morphology was taken from a real male stickleback, and its courtship behavior was transferred from a real courtship sequence (Künzler and Bakker 1998). The animation was a repeated sequence beginning with a brief display of the background (5 s) followed by 28 s of courtship behavior, which included the zig-zag dance and fanning behavior. This sequence continued repeatedly for 150 s, and the video was repeated for the duration of the trial. The computer animations were displayed on a uniform black background on two identical Viewsonic Graphics Series G90fB CRT monitors. The size of the animation was calibrated to match the average size of males in this population. It was randomly determined for each trial which monitor displayed the orange male and which displayed the red male.

The animations were identical except for the male throat coloration, which had either a red or orange hue. The displayed colors of the animated stimuli were matched to the spectral properties of the "natural" red throat coloration of reproductively active males by taking perception through the stickleback visual system into account (Fleishman et al. 1998; Gomez et al. 2009; Richter 2012). The determined RGB values were based on spectrophotometric measurements from laboratory-bred males from an anadromous population whose diets differed in carotenoid composition (see Mehlis et al. 2015 for methods). The hue of the red animated male (RGB values: $R = 255$, $G = 31$, $B = 0$) was based on the coloration of males fed a high quantity of Astaxanthin, which is a high-quality carotenoid (Wedekind et al. 1998; Mehlis et al. 2015). The hue of the orange animated male (RGB values: $R = 255$, $G = 87$, $B = 0$) was based on the coloration of males fed a high quantity of Lutein, a low-quality carotenoid (Wedekind et al. 1998; Mehlis et al. 2015). The computer-animated males in this study therefore differed strongly in hue while the difference in chromaticity (saturation) was negligible (see Mehlis et al. 2015). Accordingly, Bakker et al. (1999) successfully used computer-animated male stimuli differing in hue (bright red, bright orange) to test condition-related female mating preferences in sticklebacks. Although the stimulus colors used in the present study were generated under somewhat artificial conditions in a different population, the coloration falls within the bounds of male stickleback coloration in nature, and the females were clearly responsive to the animations.

Learning experiment

A reversal learning experiment was used to measure the cognitive ability and flexibility. In discrimination learning, two cues are presented and only one signals a reward or threat (Griffin et al. 2015). After a criterion is met, reversal learning requires the inhibition of previously rewarded behavior and a redirection of that same behavior to a previously unrewarded cue (Griffin et al. 2015). Reversal learning ability is often used to measure cognitive flexibility (Coppens et al. 2010). Learning trials took place between June 6 and August 22, 2017, between the hours of 8:30 and 19:30. Individuals were stripped of eggs when they became gravid again after completing the mate choice experiment, and learning trials began the following day. The learning experiment began on average 42.625 ± 17.989 days after the mate choice experiment. Due to time constraints, 30 of the 53 females were used in the learning experiment.

A tank measuring 30 cm × 30 cm × 45 cm contained a T-maze (Figure 2). Previous studies have used a T-maze to test spatial learning in sticklebacks (Odling-Smee and Braithwaite 2003; Mamuneas et al. 2015). A natural daylight-simulating fluorescent lamp (True-Light lamp 58W/5500 T8, True-Light International GmbH, Germany) hung above the tank, and a Logitech QuickCam® Pro 9000 webcam was attached to the center of the light for video recording of the trials. Opaque partitions surrounded the experimental tank to exclude external influences.

Experimental subjects were placed in the start box for an acclimatization period of five minutes, after which the start box door was externally lifted. Each trial lasted ten minutes, regardless of how quickly the correct arm was chosen. Three bloodworms were consistently placed in the corner of one arm of the maze as a reward. The side was determined based on the fish identification number; individuals with an odd number were rewarded on the left side and even numbers were rewarded on the right side. Only the first decision in each trial was recorded; therefore in a correct trial the focal individual first entered the rewarded arm. When the learning criterion of eight correct trials out of ten trials was reached, the reversal learning trials began in which the reward was presented in the opposite arm. Some fish learned the opposite of what was intended ($N = 5$) and subsequently did not proceed to the reversal learning phase. The reversal learning criterion was again 8 out of 10 correct trials, and if an individual had not reached this criterion after thirty trials, the experiment for that individual was terminated ($N = 4$). The tank was rinsed and refilled with aged tap water after each trial. There were three trials per day with a pause of at least thirty minutes
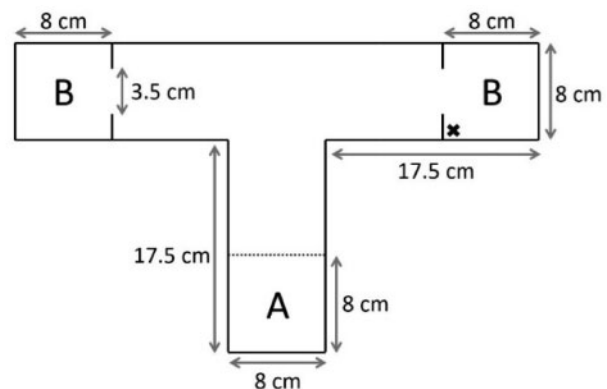

Figure 2. T-maze for learning experiment. Fish began in the start box (**A**). Trial began after a 5-min acclimatization period when the start box door (dotted line) was lifted externally. Each arm of the T-maze had a compartment (**B**) with an entrance hole of a diameter of 3.5 cm. A food reward of three bloodworms was located in the corner of the rewarded compartment, signified by the *x*.

between each trial for each individual. Two trials were run simultaneously in two tanks to optimize data yield, and there was no influence of tank on learning ability in the initial learning phase (Wilcoxon rank sum test; $N = 27$, $W = 103.5$, $P = 0.245$) and the reversal learning phase (Two-sample t-test; $N = 22$, $t = -0.800$, $P = 0.453$).

The number of errors (trials with an incorrect first decision) until the criterion was met during the initial learning phase (errors to criterion) and the reversal learning phase (errors to reversal criterion) were recorded. Persistence was used as another measure for cognitive flexibility and was determined as the number of consecutive trials at the beginning of the reversal phase which resulted in an inaccurate first decision. In these trials, the individual was still seeking the reward in the arm that was previously rewarded in the initial learning phase. The variables errors to criterion and errors to reversal criterion only applied to the individuals which successfully learned the respective task and persistence included all individuals which made it to the reversal phase, even if they did not reach the learning criterion in the reversal learning phase.

Ethical considerations

All applicable institutional and/or national guidelines for the care and use of animals were followed. This study conforms to the Animal Behavior Society guidelines for the use of animals in research. The experimental subjects were caught with permission and kept under optimal conditions. Holding and rearing conditions were approved by the City of Bonn Amt für Umwelt, Verbraucherschutz und Lokale Agenda, § 11 Abs. 1 TierSchG. After the experiment, fish were euthanized following standard procedures and frozen for future studies.

Data analysis

All videos were recorded using Windows Media Encoder (version 9.0). Trials were watched on VLC media player (version 2.2.2). The observer was blind to the location of the red male in the mate choice experiment and to the previous behavior of the test individual for the learning experiments. All statistical analyses were carried out using R 3.5.0 (R Core Team 2018). All given P-values are based on two-tailed tests, and the level of significance was set at 0.05.

Linear models (LMs; R Development Core Team 2018) and generalized linear models (GLMs; R Development Core Team 2018) were used to test the effect of cognitive abilities, body size, reproductive investment, and the date of the experiment on mate choice behaviors. However, due to the amount of missing data, the data set for each model comprised test individuals that completed all experiments necessary for the variables included. Therefore the sample size differs between the models. LMs were used when responsiveness or discrimination was the dependent variable. GLMs with a quasi-binomial error distribution were used with preference index as the dependent variable by using the function cbind with the time spent in the preference zones of the two stimulus animations to analyze the preference for the red stimulus animation. A backward stepwise model reduction was conducted by removing the explanatory variables in the order of statistical relevance (e.g. Engqvist 2005). Tests of significance were based on likelihood-ratio tests that follow a χ^2-distribution. First, models were constructed without the inclusion of any cognitive variables to determine whether body size, reproductive investment, or date had an effect on the mate choice behaviors with the full sample size (Table 1). Models were then constructed with one of the three mate choice experiment variables (preference index,

responsiveness, or discrimination) as the dependent variable, and one of the variables from the learning experiment (errors to criterion, errors to reversal criterion, or persistence) as a possible explanatory variable along with standard length and reproductive investment (Table 2). Date of mate choice experiment was used as a covariate in all models to control for any possible time effect since our initial models showed that the females became significantly less discriminatory later in the season (Table 1). The normality of residuals of the best explaining models was assessed visually and with the Shapiro-Wilk test.

Results

Responsiveness to the animations during the mate choice experiment was significantly correlated to several cognitive measurements. Females that learned the spatial learning task (Table 2, Model 2a; Figure 3A) and reversal learning task with fewer errors were more responsive in the mate choice experiment (Table 2, Model 2b; Figure 3B). Individuals that made more consecutive errors in the beginning of the reversal phase ("Persistence"; Table 2, Model 2c; Figure 3C) were also more responsive in the mate choice experiment. There was no overall preference for the red or orange male, instead there was variation in the population (Figure 4). Mate preference and discrimination were not significantly influenced by any of the measured cognitive traits, aside from a trend for females that preferred red males to be more persistent in making errors in the beginning of the reversal phase (Table 2, Model 1c). However, when looking at the full data set of all females that took part in the mate choice experiment, females that were larger significantly preferred the red male (Table 1, Figure 5A). Furthermore, females that had invested more in the current clutch also tended to prefer the red male (Table 1, Figure 5B).

Overall, the initial learning criterion was reached with significantly fewer errors than in the reversal learning task (Paired-samples Wilcoxon test; $V < 0.01$, $N = 22$, $P < 0.001$). However, no trade-off between initial learning ability and reversal learning ability was detected; there was no significant correlation between errors to initial criterion and errors to reversal criterion (Spearman's rank correlation; $r = 0.087$, $N = 22$, $P = 0.700$) or between errors to initial

Table 1. Results for models testing for the influence of date, body size, and reproductive investment on mate choice behaviors

Dependent variable	Explanatory variables	χ^2	P
Preference index	Date	0.555	0.460
	Standard length	4.077	**0.049**
	Reproductive investment	3.846	*0.055*
Responsiveness	Date	2.169	0.147
	Standard length	0.477	0.493
	Reproductive investment	0.180	0.674
Discrimination	Date	6.441	**0.014**
	Standard length	0.000	0.994
	Reproductive investment	0.532	0.469

$N = 53$ and degrees of freedom differed by 1 for all models. Preference index is a measure of which animation (orange or red male) was preferred, responsiveness is the mean time spent with both animated males, and discrimination is the standard deviation of the mean time spent with both animated males. A generalized linear model with quasi-binomial error structure was used for preference index. Linear models were used for dependent variables responsiveness and discrimination. Significant P-values are given in bold, tendencies in italic.

Table 2. Results for models testing the influence of cognitive variables, body size, and reproductive investment on mate choice behavior

Dependent variable		N	Explanatory variables	χ^2	P
1. Preference index	a)	26	Errors to criterion	1.834	0.189
			Standard length	1.736	0.202
			Reproductive investment	2.934	0.100
	b)	21	Errors to reversal criterion	0.481	0.498
			Standard length	2.810	0.112
			Reproductive investment	3.071	*0.097*
	c)	25	Persistence	3.829	*0.063*
			Standard length	2.325	0.143
			Reproductive investment	2.677	0.117
2. Responsiveness	a)	26	Errors to criterion	5.339	**0.031**
			Standard length	0.036	0.852
			Reproductive investment	3.001	*0.097*
	b)	21	Errors to reversal criterion	6.144	**0.023**
			Standard length	0.349	0.562
			Reproductive investment	0.068	0.731
	c)	25	Persistence	5.192	**0.033**
			Standard length	0.804	0.380
			Reproductive investment	0.119	0.734
3. Discrimination	a)	26	Errors to criterion	1.155	0.294
			Standard length	1.578	0.222
			Reproductive investment	0.203	0.657
	b)	21	Errors to reversal criterion	3.002	0.100
			Standard length	0.746	0.400
			Reproductive investment	0.185	0.673
	c)	25	Persistence	0.224	0.641
			Standard length	1.384	0.252
			Reproductive investment	0.024	0.879

Degrees of freedom differed by 1 for all models. Preference index is a measure of which animation (orange or red male) was preferred, responsiveness is the mean time spent with both animated males, and discrimination is the standard deviation of the mean time spent with both animated males. Generalized linear models with quasi-binomial error structure were used for preference index. Linear models were used for dependent variables responsiveness and discrimination. Significant P-values are given in bold, tendencies in italic.

criterion and persistence (Spearman's rank correlation; $r = -0.263$, $N = 26$, $P = 0.195$).

Discussion

This study found that the ability to learn a simple activity-based spatial learning task and inhibiting and reversing that learned behavior is correlated to the responsiveness during a mate choice task, specifically that females that learned a foraging task with fewer errors spent more time assessing potential mates. This suggests that spatial learning ability is not independent from cognition during the mate selection process. If females that spend more time assessing potential mates more accurately choose the higher quality male, impaired cognitive abilities might have fitness consequences. Females with
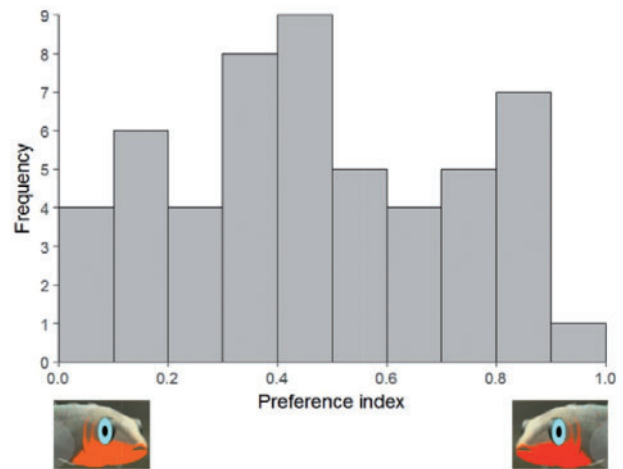

Figure 4. Histogram ($N = 53$) showing the variation in female preference for orange or red males from the 53 females tested in the mate choice experiment. A preference index of 0 indicates that all time was spent with the orange male while a preference index of 1 indicates that all time was spent with the red male.
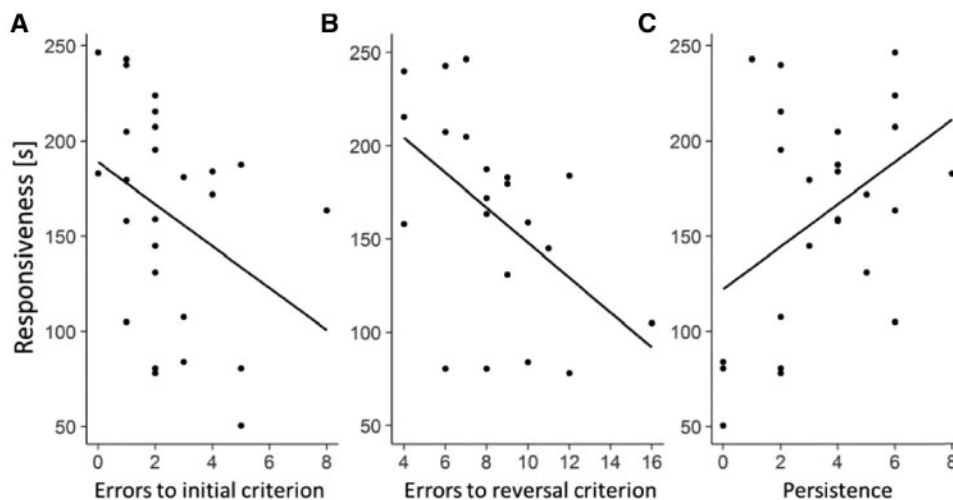

Figure 3. Females that were more responsive (spent more time in the preference zones of the animated males) during the mate assessment experiment reached the learning criterion in both the initial (**A**; Model 2a in Table 2) and reversal (**B**; Model 2b) phase with fewer errors. Within the reversal learning phase, although more responsive females made fewer errors overall (**B**; Model 2b), more of these errors were made directly at the beginning of the phase (Persistence: **C**; Model 2c). Regression lines are plotted from the predicted values from the corresponding linear model.
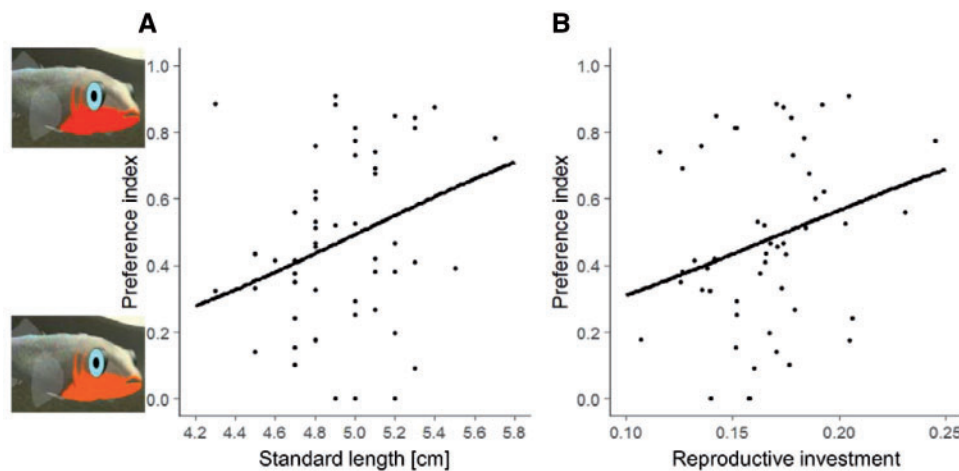
Figure 5. Individual condition influenced preference for red (Preference index = 1) or orange (Preference index = 0) stimuli animations. Standard length (**A**) significantly influenced preference index, with larger females preferring red males. Reproductive investment (**B**) non-significantly influenced preference index; females that had invested more in their current clutch tended to prefer red males. Regression lines are plotted from the predicted values from the corresponding generalized linear model with quasi-binomial distributed errors. Predicted values were obtained assuming a reproductive investment for (A) and standard length for (B) equal to the mean observed values (mean reproductive effort = 0.164 ± 0.028, mean standard length = 4.926 ± 0.292 cm).

impaired cognitive abilities may obtain less information from signals that indicate mate quality and suffer reduced fitness due to suboptimal mate choice. Alternatively, the less responsive females might have been able to make an equally optimal mate choice more quickly than the high responsive females. Taken together with the findings of Corral-López et al. (2017), in which guppy females selected for large brains had a higher cognitive ability and were better able to discriminate between males differing in quality, it appears that aspects of cognition are important for the mating decisions that drive sexual selection.

If cognitive flexibility is reflected by the amount of errors made until the learning criterion was reached in the reversal learning task, females that were highly responsive to the stimuli in the mate choice task were more cognitively flexible as they made fewer mistakes during the reversal learning task. However, we found contradicting results when looking at the immediate response to environmental change by using a count of consecutive errors at the beginning of the reversal phase as an additional measure of cognitive flexibility. Results from this measure suggested that females that were more responsive to the stimuli during the mate assessment task were less cognitively flexible since they required more trials before they were able to adjust their behavior to the reversed reward contingency. This measure of persistence might be a more precise measure of cognitive flexibility since it better captures the immediate response of an individual to a change in the environment, an important aspect of cognitive flexibility to assess that has been mentioned in previous studies (Bond et al. 2007; Bensky et al. 2017). Raine and Chittka (2012) found similar results in bumblebee colonies by utilizing blue and yellow flowers as an ecologically relevant learning task. Bumblebee colonies that learned the reversal task faster also initially probed more low-reward (previously high-reward) flowers before probing the first high-reward (previously low-reward) flower. If individuals with a low sensitivity to external cues form inflexible routines as suggested by Sih and Del Giudice (2012), insensitive females might have quickly learned the initial task and continued to follow their routine long after the reward contingency changed before forming an appropriately-adjusted inflexible routine. Furthermore, the learning task in our study was based heavily on

intuition, memory, and egocentric cues rather than sampling environmental cues, and insensitive individuals should accordingly have an advantage over sensitive individuals when tasks are based on internal cues (Sih and Del Giudice 2012), and our use of egocentric instead of environmental cues possibly explains why we did not detect a trade-off between initial learning ability and reversal learning ability. Numerous other studies have also failed to find this tradeoff (Raine and Chittka 2012; Brust et al. 2013; Bensky et al. 2017), and indeed initial and reversal learning tasks likely use different parts of the brain (Dalley et al. 2004), so it might not be necessary for these traits to be negatively correlated. These discrepancies highlight the importance of using multiple measures of cognitive traits to construct a better picture of how flexible and inflexible individuals differ in learning ability and use this strategically differently.

Total responsiveness to either animation in the mate choice experiment can be interpreted as a measure of energy and effort put into sampling potential mates or interest in mate assessment (Jennions and Petrie 1997). This measurement is an aspect of choosiness, as this study is restricted to mate preference, and females which gathered more information in the ten-minute trial by spending more time sampling might be choosier if allowed to mate with males. Furthermore, choosy individuals are predicted to invest more time in making a choice (Brooks and Endler 2001). Indeed, theoretical models have shown that mate searching time (albeit over the entire lifespan, not only a 10 minute trial) predicts choosiness (Etienne et al. 2014). Time and energy directed toward potential mates detracts from time and energy that could be spent foraging and inhibits predator vigilance, so sampling mates is considered a costly behavior (Pomiankowski 1987). However, responsiveness may not directly reflect mate assessment effort since we cannot determine the energy dedicated to the neurological processes in assessing mates (Edward 2015), and time spent sampling is not necessarily a direct measure of the information obtained. Overall, responsiveness serves as a good measure of the energy and time dedicated to assessing potential mates and is thus related to choosiness.

We failed to find an effect of cognitive abilities on mate preference and mate discrimination. This may be due to either the possibility that there is no effect of cognitive style on mate preference and

mate discrimination or that the relatively small sample size failed to identify patterns. The latter may be the case as the effects of body size and reproductive effort on mate preference that were found in the larger sample size failed to be statistically significant in the smaller sample size of females that completed the learning experiment. Furthermore, there are many male traits influencing female choice in sticklebacks, such as courtship behavior (Jamieson and Colgan 1989; Künzler and Bakker 2001), nest characteristics (Kraak et al. 1999), body size (Kraak et al. 1999), blue eye coloration (Rowland 1994), ultraviolet signaling (Rick et al. 2006), and spine symmetry (Mazzi et al. 2003). It has recently been suggested that intensity of coloration might be a more important signal to female sticklebacks than hue (Pike 2017). It could be that some of these are key traits that are missing or identical between the two presented males, resulting in preferences based on incomplete sensory data. Females might also differ in which sensory modality is preferred (Ronald et al. 2018), and this would result in a misrepresentation of preferences from individuals that favor chemical cues. Finally, it is important to consider that female sticklebacks sequentially sample males in nature, so there are limitations of using a dichotomous choice test and the ecological validity has been questioned (Wagner 1998). Dichotomous choice tests allow for an immediate comparison of males, and the sampling behavior measured in this test likely differs from that observed sequentially in nature. Nevertheless, dichotomous choice tests have been widely used to measure female preference in sticklebacks (e.g. Milinski and Bakker 1990; Bakker et al. 1999; Mehlis et al. 2008), and preferences are comparable to those obtained in sequential choice tests (Bakker and Milinski 1991; Milinski and Bakker 1992). We consider the immediate comparisons facilitated by dichotomous choice to be applicable for detecting cross-context individual differences in cognitive traits. Finally, the mate choice experiment was a novel environment and preceded by experimenter handling, and this might have elicited physiological and behavioral stress responses which may have influenced mate assessment behavior (Koolhaas et al. 1999), and previous studies have shown that stress negatively affects mate assessment (Davis and Leary 2015). Understanding how individual differences in cognitive traits influence mate choice decisions can benefit from future studies testing mate assessment and mate choice under a wider variety of conditions and by including direct measures of stress caused by the experimental procedure.

Cotton et al. (2006) predict that high-quality females should prefer high-quality males because they have more to gain and will experience greater fitness benefits than that of low-quality females, and indeed we did find evidence of condition-dependent mate choice. This echoes previous findings in sticklebacks (Bakker et al. 1999), crickets (*Teleogryllus commodus*; Hunt et al. 2005), wolf spiders (*Schizocosa*; Hebets et al. 2008), and peafowl (*Pavo cristatus*; Dakin and Montgomerie 2014); in all cases high-quality females preferred high-quality males. Previous studies also suggest that poor quality diminishes the preference for high-quality mates (Hingle et al. 2001; Lerch et al. 2013). Although we were unable to directly assess body condition in the reproductively active females, previous studies have shown that male sticklebacks prefer larger females, larger females produce more and bigger eggs, and egg size is generally constant across clutches (Wootton 1977; Baker 1994; Kraak and Bakker 1998). Therefore, there is mutual mate choice, and larger females can be considered higher quality. Furthermore, females that had invested more in their clutch tended to prefer the high-quality male, and it is likely that these females had more to gain from choosing a high-quality mate. Responsiveness should also be condition-dependent as mate assessment behavior is costly and best invested by high-quality females for high-quality offspring (Cotton et al. 2006), but this was not supported by our results aside from one weak positive correlation between responsiveness and reproductive investment.

In accordance with the theoretical framework offered by Sih and Del Giudice (2012), individuals that are more sensitive to environmental cues should be choosier, and indeed we observed that the choosier/more responsive individuals solved the reversal task with fewer errors. Furthermore, these choosier individuals also solved the initial learning task with fewer errors. Taken together, individuals that learned both tasks efficiently and quickly spent more time assessing potential mates. Thereby this study proposes a correlation between learning ability, cognitive flexibility, memory, and choosiness across foraging and mating contexts. Future studies could incorporate a more complex learning task that relies more on environmental cues, evaluate mate assessment behavior in response to different sexual signals, and include additional hormonal and behavioral measurements to better understand what other intrinsic traits contribute to mate preferences and how these individual differences are interconnected.

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Author contributions

T.L.R., T.C.M.B., and I.P.R. designed the study. T.L.R. carried out the experiments and analyzed the data with supervision from T.C.M.B. and I.P.R. T.L.R. and I.P.R. carried out the statistical analyses. T.L.R. wrote the manuscript in consultation with T.C.M.B. and I.P.R. All authors discussed the results and commented on the manuscript.

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