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Attractive males are cautious and better learners in the sailfin tetra

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A major component of Darwin's formulation of sexual selection theory is whether mate choice can contribute to the evolution of cognitive abilities. Although a correlation between cognition and attractive traits has commonly been reported, the processes that generate such associations remain elusive. Here, we investigated female preference, neophobia and spatial learning in the sailfin tetra, *Crenuchus spilurus*, a sexually dimorphic fish. Females chose the most ornamented males, which were also more neophobic. This is in line with the asset protection principle, which posits that attractive males should be more cautious because of their higher prospective fitness returns. After repeated exposure, more ornamented males learnt to navigate the complex maze faster, with chosen (and highest ornamented) males showing higher accuracy to solve the maze on the last day of trials. Because the asset protection principle stems from predation pressure, we propose that sexual selection through female mate choice creates a risk–reward trade-off, upon which natural selection acts by indirectly increasing learning abilities. As such, sexual selection forms the substrate, but natural selection drives enhanced cognitive abilities in attractive *C. spilurus* males.

Cognition refers to the neural mechanisms used to acquire, process, store and act upon information, allowing individuals to accomplish novel tasks in changing environments, and thus cognition can play a pivotal role in evolution (Dukas, 2004; Shettleworth, 2001, 2010). However, the mechanisms that drive the evolution of cognition are widely debated (Griffin, Guillette, & Healy, 2015). As originally proposed by Darwin (1871), cognition may evolve as a result of sexual selection through mate choice (Boogert, Fawcett, & Lefebvre, 2011; Miller & Todd, 1998), a process that has potentially contributed to human cognitive abilities (Miller, 2000). Nevertheless, few studies have tested many of the assumptions underlying the role cognition plays in mate choice, including the idea that choosers can select mates based on their cognitive prowess.

Mate choice that favours cognition could occur directly, via first-hand observation of a courter's cognitive performance (e.g. Chen, Zou, Sun, & ten Cate, 2019) or via assessment of a cognitive-based trait such as the song repertoire of a bird or the elaborate constructions of bowerbirds (Boogert, Anderson, Peters, Searcy, & Nowicki, 2011). Alternatively, choosers could indirectly select mates with greater cognitive abilities via preference for a conspicuous, nonperformance related trait, such as morphological ornamentation, that is correlated with cognitive ability. In this case, sexual selection can only indirectly favour cognitive abilities, which will be constrained by natural selection on the correlated traits. Still, evidence for the role of mate choice in either scenario is scarce.

Since the last decade, several studies have demonstrated that differences in behavioural types (i.e. ‘personalities’) play important roles in determining ecological and evolutionary patterns, from life history traits to population dynamics (Biro & Stamps, 2008; Dall, Bell, Bolnick, & Ratnieks, 2012; Munson, Jones, Schraft, & Sih, 2020; Sih, Bell, & Johnson, 2004). Recently, it has been suggested that certain behavioural types may be associated with individual variation in cognitive styles that carry different ecological implications (Sih & Del Giudice, 2012). One underlying assumption is that this association emerges from a speed–accuracy trade-off in which individuals that are faster at certain tasks commit more errors. Although some empirical evidence for a correlation between cognitive styles and behavioural types exists, the nature of these correlations is conflicting. For example, in brook trout, *Salvelinus fontinalis*, shy and less explorative individuals are better spatial learners (White, Wagner, Gowan, & Braithwaite, 2017), but in

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eastern water skinks, *Eulamprus quoyii*, both bold and shy individuals are better spatial learners than individuals with an intermediate behavioural type (Carazo, Noble, Chandrasoma, & Whiting, 2014). Furthermore, while studies have assessed the role of mate choice in the evolution of behavioural types and cognitive styles independently, the role of mate choice in developing or maintaining an association between these traits is unclear. Interestingly, many studies have documented sexual differences in cognitive skills (Gaulin & FitzGerald, 1986; Jonasson, 2005; Lucon-Xiccato & Bisazza, 2017a; Shaw, MacKinlay, Clayton, & Burns, 2019). Along with divergent home range size, these differences in cognitive performance are often attributed to sexual differences in foraging or reproductive tactics, which are assumed to be important observable traits for mate choice.

Here, we consider the asset protection principle (Clark, 1994) as a framework to further explore the association between cognitive styles and behavioural types in the context of mate choice. This principle posits that individuals with greater reproductive value will behave more cautiously, taking fewer risks to avoid predation. We present a study testing the relationship between neophobic behaviour and spatial cognition with respect to female mate preference in an Amazonian fish, the sailfin tetra, *Crenuchus spilurus*. The sailfin tetra is a sexually dimorphic, freshwater fish with conspicuous ornaments and courtship rituals (Pires, Farago, Campos, Cardoso, & Zuanon, 2016), making it a prime candidate for mate choice studies. We used neophobia assays to test whether more attractive *C. spilurus* males (those with a greater degree of ornamentation) behave according to the 'asset protection' principle by exhibiting more cautious behaviour. We hypothesized that less attractive males, on the other hand, would be less cautious and respond faster, but could commit more errors.

To test the hypothesis that behaviour type is correlated with cognitive decision-making style, we subjected the same *C. spilurus* males to neophobia trials and repeated maze experiments. For the latter, we measured both the latency to complete the task and the number of errors they committed. We then conducted mate preference trials to see whether females would accept courtship attempts from males with distinct behavioural types and cognitive styles. To our knowledge, this is the first study to relate behavioural types with cognitive styles and evaluate their potential roles in mate choice.

METHODS

Crenuchus spilurus Günther, 1863 (Characiformes: Crenuchidae) is a sexually dimorphic and dichromatic fish that inhabits Amazon forest streams. Males possess hypertrophied dorsal and anal fins with yellow and red ornaments (Fig. 1). Individuals of *C. spilurus* were collected from an urban forest fragment in central Amazon (3°6′22.94″S, 59°58′42.48″W) and transported to the laboratory, located 2 km away from the sampling site. Fish were separated by sex and maintained in 92-litre tanks for at least 2 months to acclimate to laboratory conditions. In total, 25 males were used, repeating the same males in each one of the experiments. A more detailed description of the methods can be found in the Ethical Note (see below). Experiments took place in the order described below.

Trait Measurements

To measure fin traits, we anaesthetized males in a eugenol solution (125 mg/litre), placed them on a moist white board and gently spread their fins using a wet, soft-bristle paintbrush. Pictures of fish were taken, along with a reference scale and a tag, using a Nikon D3300 camera positioned 30 cm away from the fish. A full-spectrum LED light source was positioned in front of the fish. Based on pictures of the males, we measured the standard length (SL) and the area of the dorsal and anal fins using the software ImageJ (Schneider, Rasband, & Eliceiri, 2012). To assign the degree of ornamentation in males, we took the residuals from the linear relationship of the sum of the areas of the dorsal and anal fins (square-root transformed to achieve linearity) against the standard length of the fish. Positive values thus represent a higher degree of ornamentation than expected for the size of the fish. Conversely, negative values represent a lower degree of ornamentation than expected for a given SL. Since the shape of the abdomen in fish often reflects body condition (see Greenway, Drexler, Arias-Rodriguez, & Tobler, 2016), we also conducted a geometric morphometrics analysis to assess whether variation in ornamentation, learning ability or mate preference outcomes could be condition dependent. To do so, we placed seven landmarks positioned along the ventral region of the fish (Supplementary Fig. S1) using ImageJ. We used the package 'geomorph' v.3.0.7 (Adams & Otárola-Castillo,

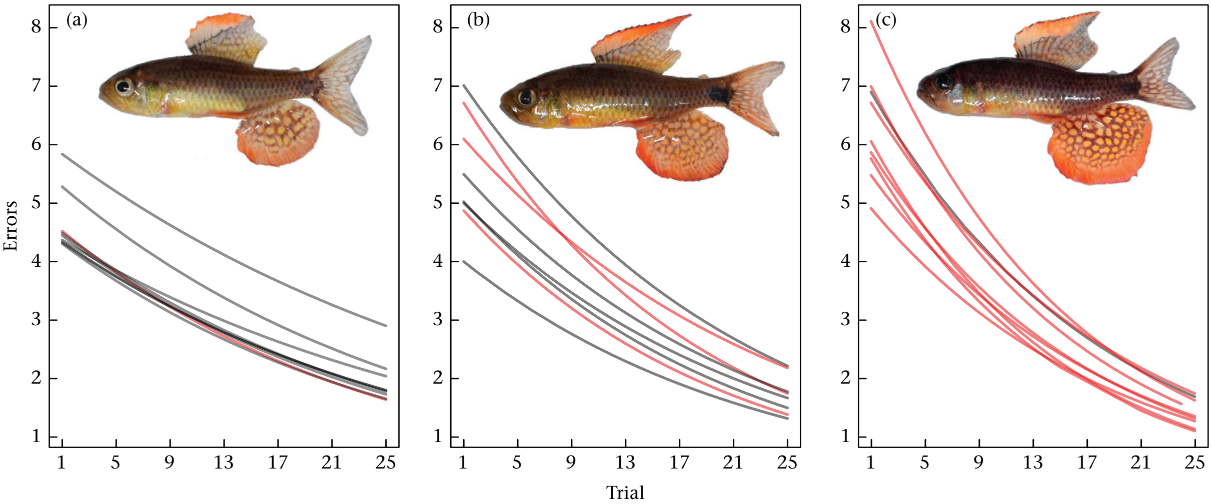

Figure 1. Spatial learning curves of male *C. spilurus* in a complex maze. Lines represent learning curves as modelled in a negative binomial GLMM. Red curves represent accepted males in female preferences tests ($N = 11$); grey curves represent rejected males ($N = 14$). Panels represent curves of males, divided by degree of ornamentation, into three intervals for visual simplicity: (a) from −0.177 to −0.056; (b) from −0.056 to 0.061; (c) from 0.061 to 0.176. Insets: pictures of studied fish representative of (a) low, (b) intermediate and (c) high degrees of ornamentation.

2013) to conduct a generalized Procrustes analysis (Rohlf, 1999) and a PCA on the resulting matrices, retaining the first axis (PC1) to represent body condition. Since the volume of females with developed oocytes is larger, we used the residuals of a linear regression between the volume of the females (cube-root transformed to approach linearity) against the SL as a measure of degree of spawning readiness of females. Volume was measured by placing the fish individually into a 50 ml graduated cylinder filled with 25 ml of water and subtracting the difference from the new volume. The degree of female spawning readiness was used to test whether female preference could be influenced by potential differences in sexual maturity.

After measurements, males were acclimated for at least 7 days in individual identical tanks (30 × 30 × 40 cm), each containing sandy substrate, a PVC pipe (10 cm long, 20 mm in diameter), an artificial plant for habitat enrichment and an individual identity (ID) badge. Individuals were prevented from observing each other by thin wooden panels positioned on the sides of the tanks.

Spatial Learning

The experimental tank (70 × 29 × 30 cm, filled with water to reach 15 cm of height, 30 litres) was surrounded by two sheets of black cloth to prevent visual contact between the fish and the experimenter during trials. We placed a 40 × 25 cm maze at a distance of 15 cm from each side wall of the tank. The 15 cm spaces on each side of the tank were used as the home sector, in which the fish was positioned before the trial, and the target sector, which the fish reached upon solving the maze. The maze was built using green plastic interlocking toy bricks (Lego Bricks, Billund, Denmark); the walls were 8.8 cm high and 3.2 cm wide. The narrow path works as an incentive for the fish to swim forward and solve the maze (Kellogg & Gavin, 1960; Lucon-Xiccato & Bisazza, 2017b). We built a narrow shelter with two open ends made of plastic bricks (1.7 × 9.5 × 2.7 cm) and placed it in the home sector. All males used this structure from the first day of acclimation. As rewards, we placed a PVC pipe identical to the one present in the housing tank and a food pellet in the target sector. Positions of the paths and walls followed Tolman (1948). A glass pane was used to close the upper portion of the maze (Supplementary Fig. S2). A video camera (Logitech C920) and a light source were positioned overhead to record fish movement.

A male was transferred from the housing tank to the home sector 24 h before the first day of trials. The entrance of the maze was blocked by a sliding glass pane. After the acclimation period, we removed the glass pane, moved the shelter containing the fish to the entrance of the maze and gently inserted a building block into the opposite end of the shelter, directing the fish to slowly swim into the maze. A piece of acrylic plate blocked the first 5 cm of the maze, creating an antechamber inside the maze. Fish were maintained in the anteroom for 2 min, at which point the acrylic plate was removed and the fish was recorded until it reached the target sector, or a maximum of 30 min had passed. Cases in which fish remained inside the maze for 30 min were not considered in the analyses. Fish were then returned to the home sector through a side corridor, taking care to minimize stress. Finally, we lifted the maze out of the water and placed it back in its original position, forcing the water to run through the paths, homogenizing the distribution of potential chemical cues. The experimental procedure was repeated five consecutive times each day, for five consecutive days. After the 25th trial, fish were transferred to their respective housing tanks to be used in female preference trials. The number of days and trials followed similar previous work (Lucon-Xiccato & Bisazza, 2017b; Wyss, Chambless, Kadish, & Van Groen, 2000). Based on the video recordings, we counted the number of errors, defined as the number of times that fish crossed into zones leading to a dead end within the maze (Burns & Rodd, 2008; Lucon-Xiccato & Bisazza, 2017b), and recorded the time to solve the task, defined as time in seconds between the moment the fish entered the maze until the fish reached the target sector.

Female Preference

We began female preference trials 7 days after all males had been tested in the spatial learning assay. Because both males and females reject mates much larger or smaller than themselves (Borghezan, Pinto, Zuanon, & Pires, 2019), we selected females that matched the size of males used in spatial learning (mean difference SL of male − SL of female = 0.71 mm). A male and a female were simultaneously placed into a previously unoccupied experimental tank that was identical to the individual housing tank. We recorded the interaction with a video camera (Sony HandyCam CX405) attached to a tripod positioned 60 cm away from the experimental tank. A black cloth that contained a small hole for the camera lens prevented fish from seeing the observer. All trials lasted 1 h and were conducted between 1600 and 1800 hours, to match the period when most courtship behaviour has been observed during direct field observations (Pires et al., 2016). A full-spectrum LED light (ADA, Japan) provided 250 lx of light. The experimental tank, light source and recording equipment were covered by a dark chamber to prevent any interference of external light on mating trials. Water was completely renewed after each trial to avoid courtship chemical cues from influencing subsequent trials.

In courtship, males display the dorsal and anal fins towards females and conduct bouts of circular movements around them. Female preference was assessed through acceptance of courtship behaviour by males. Females that reject courtship behaviour swim away from the males, whereas receptive females perform synchronized movements and darken the abdominal region (Pires et al., 2016). Males that refrained from starting courtship behaviour (not displaying the anal fin near the female, $N = 5$) were tested with another female the next day. Each male was scored only once (as chosen/rejected) and with a different female. After all fish had been tested in both spatial learning and mate preference tests, they were kept in their housing tanks for at least 7 days before starting neophobia trials.

Neophobia

We measured neophobia as the amount of time spent away from a novel object. Neophobia experimental tanks (60 × 15 × 15 cm) contained a cube made of brightly coloured Lego pieces on one side (novel object) and an artificial plant similar to the one present in the housing tank (familiar object, Supplementary Fig. S3) on the opposite side. All sides of the tank were covered with a black cloth to minimize disturbance from the experimental room. A video camera was placed above the tank and set to record for 1 h. We recorded two tanks simultaneously with the positioning of the novel objects flipped in each tank to control for possible side bias. Fish were netted from their individual housing tanks and gently placed on the side containing the familiar artificial plant. The position of the fish within each frame of the video was extracted using the open-source software SwisTrack (Lochmatter et al., 2008). For each video, we first extracted five frames using FFmpeg v.3.3, which were read into GIMP v.2.8 for the creation of background images. Background images consist of an image of the experimental set-up captured by the camera, excluding only the objects that would be tracked (in our case, the fish). We divided the tank into three equally sized zones (20 × 15 cm). Once the positions of the fish were extracted, we read the values in R (R Core Team, 2019) and used a custom script to automatically measure the time (in seconds) that the fish spent in each zone. We used 1 minus the time spent near the novel object divided by the total time as a measure of neophobia.

Statistical Analyses

All statistical procedures and graphical representation of data were in conducted in R v.3.5.2 (R Core Team, 2019).

Spatial learning

We modelled spatial learning as a generalized linear mixed model (GLMM) using the package 'lme4' (Bates, Mächler, Bolker, & Walker, 2014). The number of errors in a trial was used as the dependent variable. Our initial model included the following terms as fixed effects: trial number (representing the learning rate), degree of ornamentation, the interaction between these two, male neophobia scores, the interaction between neophobia score and trial number, body condition and the interaction between body condition and trial number. The identification codes of the individuals and trial number were included as random effects to specify a repeated measures design. We then used variance inflation factors (VIF, using the package 'car'; Fox & Weisberg, 2019) to identify multicollinearity issues and consequently removed the interaction term between neophobia score and trial number from the model. Thus, the influence of neophobia on learning was further assessed using an additional analytical approach (see below). Next, we used a backwards model selection procedure based on Akaike information criteria (AIC) to identify variables that did not contribute to the model. We compared models using Poisson, negative binomial and Gaussian error distributions. For the Gaussian distribution model, the data were transformed using the square root of the number of errors + 0.5 to approach normality. Model validation was conducted by assessing plots of Pearson's residuals against fitted values, normality of residuals and overdispersion statistics (Harrison, 2014) based on 1000 simulations (Harrison et al., 2018). The full analytical pipeline, model validation plots, R syntaxes and model statistics can be found in the Supplementary material.

To determine whether chosen and rejected males differed in accuracy on the last day of trials, we ran a *t* test to assess whether the number of errors (square-root transformed) differed according to the preference status of males (accepted or rejected).

Effect of neophobia on learning trials

The influence of neophobia on spatial learning was further investigated by regressing neophobia scores against the ratios of the learning curve of each male (relationship between errors and trial number, i.e. the rate of learning). Additionally, because neophobia would have the greatest influence on maze trials on the first day, we evaluated whether neophobia could explain the initial number of errors in the maze by regressing neophobia scores against the number of errors on the first day (from trial 1 to 5) of exposure to the maze. Also, we investigated the relationship between neophobic behaviour and degree of ornamentation in males using a simple linear regression of the neophobia score against the degree of ornamentation of the males.

Female mate preference and condition dependence

We modelled female mate preference (acceptance/rejection) in relation to the degree of ornamentation of males, female spawning readiness and male body condition using a logistic regression run as a generalized linear model (GLM).

We investigated whether degree of ornamentation in males was condition dependent by regressing degree of ornamentation against body condition (PC1; see Trait Measurements).

Speed–accuracy relationship

We modelled the relationship between accuracy and speed using the number of errors (square-root transformed) as the dependent variable. To obtain our independent variable, we extracted the residuals from a linear regression of the number of errors (square-root transformed) against the time (log), thus retaining a measurement of time to solve the maze that was not explained by the number of errors, since males entering dead ends naturally took longer to solve the maze. Errors and time were used as fixed effects. Fish ID and trial day were included as random effects to accommodate for repeated measures of the same fish and the variation that occurs due to learning.

Ethical Note

Fish were sampled using seines and clean hand-nets from a stream located in an urban forest fragment near Manaus, Amazonas, Brazil. During the dry season, it is possible to observe individuals of our study species (sailfin tetra) in very high densities, often in the thousands. Sampling of animals was conducted under permit SISBIO 10199-1, issued on 16 October 2007. This study has been approved by the Comissão de Ética no Uso de Animais (Animal Use Ethics Commission) (CEUA-INPA, process no. 046/2016), which follows the laws of the National Council for the Control of Animal Experimentation (CONCEA). Transportation from the field to the laboratory aquaria took less than 1 h. To minimize the possibility of injury, fish were carefully transported in plastic bags inside buckets using a large amount of water and tied off with a large air reservoir. Our laboratory is less than 5 km away from the sampling site, and most of this distance is covered by car. Once in the laboratory, males and females were kept in separate tanks at a maximum density of 50 fish per tank. Each tank measured 60 × 30 cm and was filled to 30 cm, resulting in a maximum of one fish per 1.08 litres of water. The majority of sailfin tetra individuals are between 3 and 4 cm long (standard length). To simulate the natural environment, natural and artificial plants were added to the tanks, as well as over 10 pieces of PVC pipes (10 cm long, 25 mm in diameter) to provide shelter. This species does not actively swim around the tanks, and its territory is only defended at a very close range near PVC pipes; thus, aggressive interactions were very rarely observed.

Each tank contained a filter and an air pump. Water changes were performed weekly to maintain water quality. Windows that covered over half of the wall of the laboratory provided indirect natural light and photoperiod (12:12 h light:dark cycle). We used dark cloth on the windows to control the amount of light that reached the laboratory, effectively simulating the natural canopy-shaded condition of an Amazon forest stream. An air conditioning system maintained the laboratory at a constant temperature of 24 °C, simulating natural temperature conditions of Amazon igarapés (forest streams located in nonflooded regions). All individuals were fed high-quality commercial fish food twice a day. We included only adult individuals in the study. The smallest individual measured 3.54 cm SL, 0.8 cm larger than the estimated size at maturity for this species (2.57 cm, Pires et al., 2016).

A major advantage of the proximity of our laboratory to the sampling site was our ability to maintain water quality similar to that of natural conditions. Our university water supply comes from groundwater, so the only distinction between water quality from the field and the laboratory was the lack of dissolved organic carbon. To account for this, we regularly collected dead leaves from the forest stream and added them to a 300-litre water reservoir, effectively simulating the natural dissolved organic carbon conditions found in black water streams. Water was maintained in this reservoir for at least 3 days before being transferred to tanks. After experiments were completed, most fish were returned to their site of origin. Fish that were not released back into the field were maintained in the laboratory for other experiments, none of which were invasive or noxious to the fish in any way.

RESULTS

Spatial Learning

We report the results of the learning model using the negative binomial error distribution as it showed lowest AIC scores and lowest overdispersion (Supplementary Table S4) when compared to the Poisson model. Results using Gaussian, Poisson and negative binomial error distributions were largely equivalent (see Supplementary material). The final (reduced) spatial learning model included only trial, degree of ornamentation and the interaction between the two as the fixed effects, and only fish ID as a random effect. The rate of learning (number of errors × trial number) differed among males with different degrees of ornamentation (GLMM interaction term: $z = -3.23$, $P < 0.001$), with more ornamented males having steeper learning curves in maze trials (Fig. 1). Preferred males in mate preference trials were more highly ornamented (Fig. 2) and were better able to navigate the maze, committing fewer errors on the last day of trials (last five trials: $t = -3.22$, $P = 0.001$).

The first axis of the PCA representing male body condition captured 45% of the total variation in the shape of the ventral region. We found no relationship between body condition and the degree of ornamentation ($R^2 < 0.001$, $P = 0.95$). Body condition was also unrelated to learning, as PC1 was removed during the model selection procedure. Chosen and rejected males did not differ in body condition ($t = -0.49$, $P = 0.62$).

Given the maze design, males that never backtracked (increasing the number of errors) could commit a maximum of six errors. On the first day, only highly ornamented males consistently swam to previously visited paths, resulting in more than six errors and indicating that highly ornamented males were reluctant to swim forward into the new environment (Appendix, Fig. A4). This is emphasized by the positive relationship between the neophobia scores and the number of errors on the first five trials ($R^2 = 0.23$, $P = 0.01$; Fig. 3a). One way to interpret this is that neophobic males sample a greater amount of information, allowing them to make more informed decisions with repeated exposure to the maze.

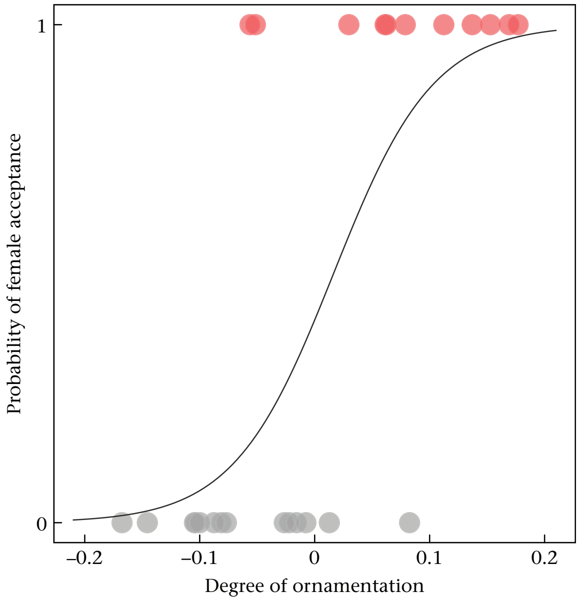

Figure 2. Relationship between the probability of female acceptance of male courtship behaviour and the degree of ornamentation in male *C. spilurus*. Red: prefered males ($N = 11$); grey: rejected males ($N = 14$).

Female Preference

Females accepted courtship behaviour (synchronizing courtship movements and darkening the abdominal region) when paired with highly ornamented males (11 of 25 males) but rejected males with lower-than-average ornamentation (GLM: $Z = 2.44$, $P = 0.014$; Fig. 2). Acceptance of courtship behaviour could not be attributed to differences in spawning readiness of females (GLM: $Z = 1.066$, $P = 0.28$) or male body condition (GLM: $Z = -1.231$, $P = 0.21$).

Speed–Accuracy Relationship

The negative relationship between the number of errors (inverse of accuracy) and time to solve the maze (LMM: $t = -3.01$, $P = 0.002$; Appendix, Fig. A5) is suggestive of a speed–accuracy trade-off.

DISCUSSION

Our results demonstrate that highly ornamented males were more neophobic and performed significantly better in a spatial learning task relative to less ornamented males (Fig. 1) and that neophobia and spatial learning were strongly correlated (Fig. 3b). Furthermore, our results show that females chose highly ornamented males (Fig. 2) independent of male body condition. Taken together, these results suggest that more cautious and attractive males are better at learning spatially complex tasks, and that by choosing the more ornamented males, female *C. spilurus* indirectly favour cautious males with increased spatial learning abilities. We propose that mate choice and natural selection work in conjunction to indirectly strengthen the association between cautious behaviour and spatial cognition, via increased ornamentation in males.

Our findings support predictions that a speed–accuracy trade-off underlies an association between behavioural type and individual variation in cognitive decision-making style (Fig. 3b, Appendix, Fig. A5) (Chittka, Skorupski, & Raine, 2009). Within this framework, bold individuals that are quicker to explore might obtain important resources faster, but they might also sample their environment less and perform poorer in spatially complex tasks. For example, a study on a wild population of great tits, *Parus major*, found that more aggressive birds were better competitors, but poor problem-solvers (Cole & Quinn, 2012). Still, conflicting evidence exists (Carazo et al., 2014; Mamuneas, Spence, Manica, & King, 2015), suggesting that the speed–accuracy trade-off and trait association may be taxon and context specific.

Extravagant ornamentation can increase susceptibility to predation by attracting the attention of predators (Godin & McDonough, 2003; Kotiaho, 2001; Magnhagen, 1991; Zuk & Kolluru, 1998) and by impairing locomotion (Basolo & Alcaraz, 2003). Our finding that highly ornamented *C. spilurus* males behaved more cautiously in both the neophobia (Fig. 3c) and maze (Appendix, Fig. A4) assays corroborates the theory on life-history trade-offs and the asset protection principle, which suggests that individuals with expectations of increased fitness will behave more cautiously (Clark, 1994). This principle also posits that associations between behavioural and conspicuous morphological traits are

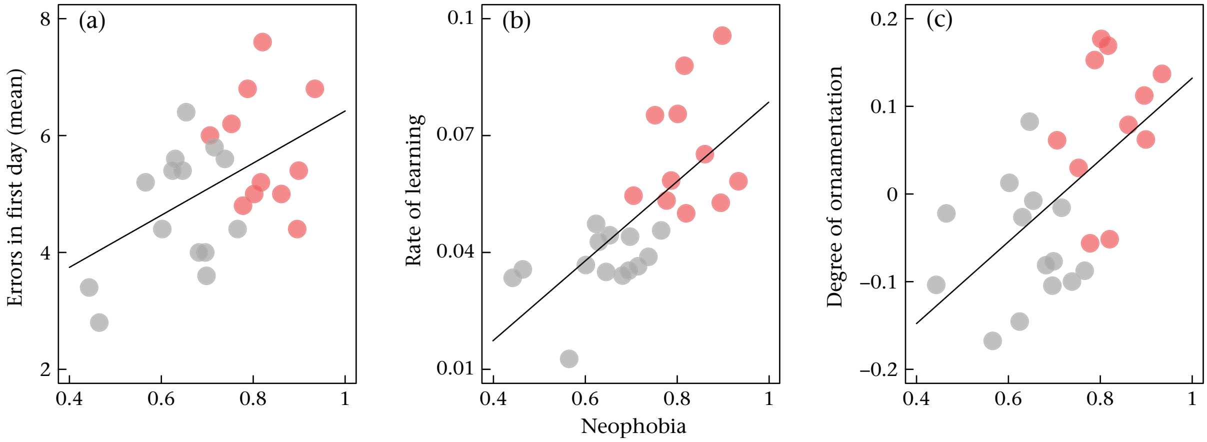

Figure 3. (a) Relationship between neophobia and the number of errors committed on the first day of trials in the spatial learning assay (complex maze). Males that scored higher in neophobia trials were initially more likely to swim back towards previously explored areas of the maze. (b) Relationship between the overall rate of learning (including all trials; regression slopes of errors × trial for each fish, in absolute values) and neophobia scores. (c) Relationship between neophobia and degree of ornamentation in males ($R^2 = 0.33$, $P = 0.002$). In all three panels, red circles denote accepted males in female preference tests, and grey circles denote rejected males.

expected if these associations lead to increased fitness (Wolf, van Doorn, Leimar, & Weissing, 2007). Further support for such associations has been found in field studies with crickets and fairy-wrens, showing that individuals with conspicuous mating displays will behave more cautiously so as not to jeopardize potential fitness gains by predation (McQueen et al., 2017; Wolf et al., 2007). However, cautious behaviour and a disinclination to explore novel environments could diminish an individual's ability to compete for limited resources such as food or mating opportunities. A study measuring spatial cognition and decision latency in populations of guppies, *Poecilia reticulata*, exposed to different predation regimes found that individuals from low-predation populations made faster decisions and had smaller telencephalons, a brain region crucial for spatial memory (Burns & Rodd, 2008). Because the cost of navigating through novel routes is expected to be lower for individuals that are less susceptible to predation, this can generate different risk-taking strategies, with some individuals sacrificing shorter decision latency to favour accuracy.

Given that mate choice seems to select for an increased degree of ornamentation and that predation can favour cautious behaviour in attractive males, natural selection seems to represent the most direct driver of increased spatial cognitive abilities. The lower spatial learning ability of some males can be compensated for by faster access to nutrients and mating opportunities afforded by their lesser ornamentation and bold behaviour. Because females did not observe male performance in the neophobia or maze trials, females most likely chose males based on ornamentation (Fig. 2), meaning that the other traits are indirectly selected for. In the *C. spilurus* model, while mate choice leads to selection for increased ornamentation, it is natural selection for neophobic behaviour that leads to an increase in spatial learning abilities as the by-product of longer decision latency and greater environmental sampling. It is possible this mechanism influences the evolution of spatial cognition and associated behaviours in other taxa with similar ecologies.

Continued female preference for greater ornamentation can reinforce the association between ornamentation and cognition as increased spatial cognition can provide males and females with further adaptive advantages. Because courtship often occurs away from nesting sites, spatial cognition might be important for males who need to safely swim back to their intended nesting sites during courtship and for the females following them. Still, the association is likely constrained by natural selection on the size of male ornaments due to predation pressures or limits imposed on swimming performance. This is in contrast to what is suggested to occur in species with notoriously high cognitive abilities, where individuals might select mates by directly assessing cognitive abilities (Chen et al., 2019) or traits that directly reflect cognitive abilities (Miller, 2000), leading to open-ended selection for cognition.

If female *C. spilurus* favour more ornamented, cautious males with increased spatial learning abilities, this raises two questions. Firstly, how do these traits influence the reproductive fitness of the female? Secondly, what is the heritability of these traits (increased ornamentation, cautious behaviour and spatial learning ability)? While measurements of reproductive success and the fitness consequences of these traits were not in the scope of this study, a study on rose bitterlings, *Rhodeus ocellatus*, found that sneaker males performed better in a spatial learning task and that learning accuracy was indeed heritable (Smith, Philips, & Reichard, 2015). We found no evidence that females preferred males based on body condition, and no relationship between body condition and degree of ornamentation was observed, indicating that the differences in learning ability represent among-individual variation in cognitive traits, not state-dependent variation. Lastly, while we suggest ultimate causes for linkages between behaviour, cognition and male ornamentation, the proximate mechanisms for this linkage remain unknown. Testosterone has been shown to play a role in regulating spatial cognitive abilities (Galea, Perrot-Sinal, Kavaliers, & Ossenkopp, 1999), the retention of carotenoids for ornamentation (Blas, Pérez-Rodríguez, Bortolotti, Viñuela, & Marchant, 2006) and neophobia (Tobler & Sandell, 2007), hinting at the possibility that sex hormone regulation may be a key factor in linking these traits.

To our knowledge, this is the first study to find support for an association between behavioural types, cognition and mate choice. Future studies with the sailfin tetra will address potential benefits that males with lesser degrees of ornamentation have, and whether the costs and benefits of higher ornamentation fluctuate according to environmental conditions. Additional studies could investigate the heritability of these traits and their potential fitness consequences, as well as the role of testosterone and its potential linkage between male ornamentation and spatial cognition.

Declarations of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2020.12.005.

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Appendix

Figure A1. Position of the landmarks used for geometric morphometrics analysis to represent body condition: (1) lower premaxilla; (3) posterior operculum; (5) pelvic fin insertion; (7) anal fin insertion. Landmarks (2), (4) and (6) represent midpoints between two other landmarks.

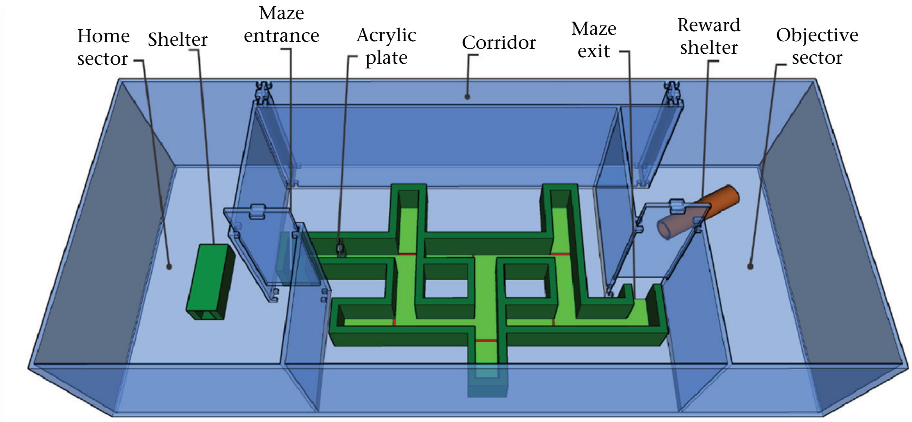

Figure A2. 3D sketch of the maze used for the spatial learning experiment. Red lines indicate imaginary limits used to score errors in path decisions. Paths were 3.2 cm wide, and hedges were 8.8 cm high.

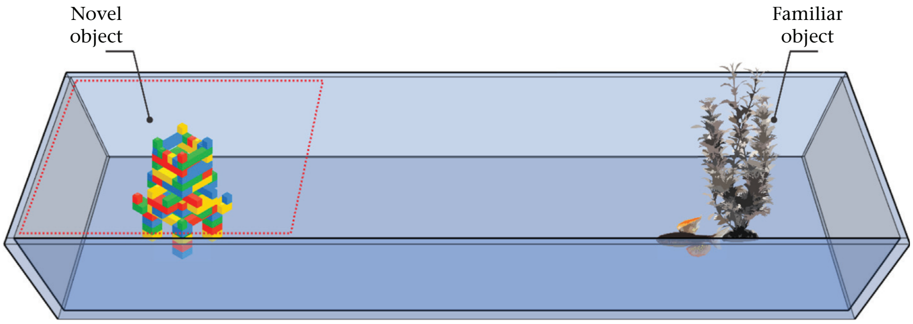

Figure A3. 3D sketch of the neophobia experiment. Red rectangle indicates the imaginary limits of the zone closest to the novel object.

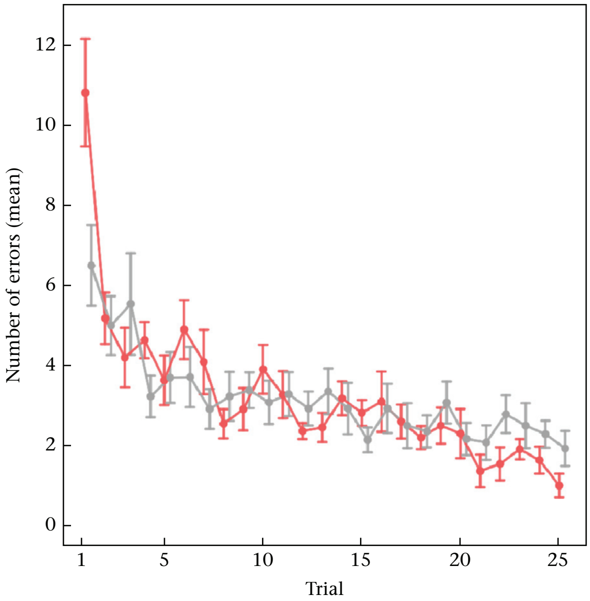

Figure A4. Spatial learning in male *C. spilurus* in a complex maze. (a) Number of errors (±SE) across the 20 trials. Red: chosen males in female choice tests ($N = 11$); grey: rejected males ($N = 14$).

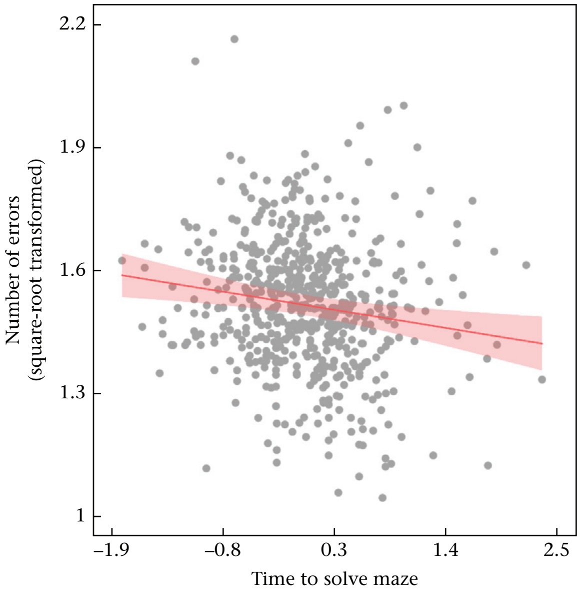

Figure A5. Effect plot representing the speed–accuracy trade-off.