

1 **Cognitive performance and stress responsiveness in the Trinidadian Guppy – a multivariate**  
2 **approach**

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19

20 Abstract

21 Among-individual variation in cognitive performance has been recently demonstrated across a range  
22 of animal taxa. While this variation is a prerequisite for contemporary natural selection, it is also true  
23 that selection does not act on traits in isolation. Thus, the extent to which cognitive traits covary with  
24 other aspects of phenotype (e.g. personality traits) is expected to be an important factor in shaping  
25 evolutionary dynamics. Here we adopt a multivariate approach to test for spatial learning ability in a  
26 captive population of male Trinidadian guppies (*Poecilia reticulata*), and ask whether differences in  
27 cognitive performance are associated with (repeatable) differences in stress response behaviour. We  
28 focus on stress response for two reasons. First, functional links between cognitive traits and ‘stress  
29 coping style’ have been hypothesised. Second, individual-level studies of cognitive performance  
30 typically rely on multiple testing paradigms that may themselves be a stressor. Thus, there is a risk  
31 that variation in stress responsiveness is itself a cause of apparent, but artefactual variance in  
32 cognitive ability. Using a set of fish exposed repeatedly to two distinct spatial learning tasks (maze  
33 layouts), and an acute stress response test (open field trial), we find differences among-individuals in  
34 task performance that are repeatable within- and across maze layouts. On average performance  
35 improves with experience in the first maze, consistent with spatial learning, but not the second. In  
36 both mazes there is among-individual variation in the trajectory of mean performance with trial  
37 number suggesting individuals differing in ‘learning rate’. Acute stress response behaviour is  
38 repeatable but predicts neither average time to solve the maze nor learning rate. We thus find no  
39 support for among-individual correlation between acute stress response and cognitive performance.  
40 However, we highlight the possibility that cumulative, chronic stress effects may nonetheless cause  
41 observed declines in performance across repeats for some individuals (leading to lack of improvement  
42 in mean time to solve the second maze). If so, this may represent a pervasive but difficult challenge  
43 for our ability to robustly estimate learning rates in studies of animal cognition.

44

## 45 Introduction

46 Cognition, or “information processing”, is defined as the set of mechanisms by which animals  
47 acquire, process, store and use information from the environment (Shettleworth, 2010), and is vital for  
48 carrying out day-to-day behaviours needed for survival and reproduction. While differences in  
49 cognitive performance among-species have long been studied in comparative psychology (for a  
50 review see Healy 2019) , a more recent focus in behavioural ecology has been the characterisation of  
51 among-individual variation within populations of non-human animals (Ashton et al., 2018; Boogert et  
52 al., 2018; Lucon-Xiccato & Bisazza, 2017a). This among-individual variation is interesting from an  
53 evolutionary perspective, as it is a pre-requisite for natural selection and genetic variation – both of  
54 which are fundamental for adaptive evolution to occur (Wilson et al. 2010). However, selection does  
55 not act on traits in isolation. Functional links between variation in cognitive performance and other  
56 aspects of behaviour (including, for example neophobia, boldness and stress responsiveness) have  
57 been hypothesised (Griffin et al. 2015; Medina-García et al. 2017; Quinn et al. 2012; Sweis et al.  
58 2013). Robustly testing these relationships is often challenging, requiring multivariate data collection  
59 and analyses to detect and describe patterns of variation between associated traits at the appropriate  
60 level (e.g., among-individual and/or among genotype; Dingemanse & Dochtermann, 2013).  
61 Nonetheless, such efforts are important if we hope to understand the adaptive evolution of cognition  
62 in the context of the wider phenotype (Thornton & Wilson, 2015). Here we address this broad goal in  
63 the more specific context of testing hypothesised links between cognitive performance and a stress-  
64 response (Gibelli et al., 2019; Øverli et al., 2007) in Trinidadian guppies (*Poecilia reticulata*).

65 Quantifying patterns of among-individual variation in cognitive traits is still in its infancy  
66 (Boogert et al., 2018; Rowe & Healy, 2014; Thornton et al., 2014), and empirical studies therefore  
67 remain somewhat limited (but see Ashton et al., 2018; Lucon-Xiccato & Bisazza, 2017b; Niemelä et  
68 al., 2013; Shaw et al., 2019; Sonnenberg et al., 2019 for examples). However it is now abundantly  
69 clear that populations typically harbour high levels of among-individual variation in behavioural traits  
70 more generally (Dingemanse & Réale, 2005). Individual differences in (mean) behaviours, commonly  
71 referred to as personality, can manifest as, for instance, variation in aggressiveness or sociability

72 towards conspecifics, or differences in response when faced with predators or other sources of  
73 perceived risk (Bridger et al. 2015; Réale et al. 2007). Since, strong directional or stabilising selection  
74 is usually predicted to erode variation (Roff, 2002), it is widely hypothesised that variation in  
75 personality traits is maintained by fitness trade-offs of some kind (Dingemanse et al., 2004; Quinn et  
76 al., 2016). For example, bolder individuals may be better at acquiring resources to invest in life  
77 history traits (e.g., growth, reproduction) but their behaviour may also expose them to greater  
78 predation risk. In this way personalities can themselves be viewed as components of life history  
79 strategies, leading to an expectation that they will be correlated with – and trade-off against - other  
80 aspects of physiological, reproductive, and behavioural phenotype (Réale et al. 2010; Sih, Bell, &  
81 Johnson 2004; Wolf et al. 2007). Certainly, arguments that trade-offs can maintain variation in  
82 cognitive performance parallel explanations made for widespread presence of personality. These  
83 could be trade-offs among cognitive domains, or between, for instance an overall cognitive  
84 performance trait ('general intelligence' (Burkart et al., 2017; Galsworthy et al., 2005; Plomin &  
85 Spinath, 2002)) or other aspects of phenotype.

86         Variation in stress response provides one putative source of among-individual differences in  
87 both personality traits and cognitive performance (Gibelli et al., 2019; Raoult et al., 2017). The  
88 widely used concept of stress coping style model predicts that individuals will vary - both  
89 behaviourally and physiologically- along a proactive/ reactive continuum (Coppens et al., 2010;  
90 Koolhaas et al., 1999; Sih, Bell, & Johnson 2004). As originally posited, the model predicts proactive  
91 coping styles will express more 'fight or flight' type behavioural responses induced by adrenaline-  
92 response to stressors. At the other extreme, reactive coping styles will be more behaviourally  
93 'passive' (e.g., freezing or hiding) and show high HPA(I) activity leading to cortisol response (Carere  
94 et al., 2014; Øverli et al., 2007). Various links to cognitive performance variation have been  
95 suggested. For instance, proactive styles are broadly thought to be associated with 'bold', exploratory,  
96 risk-taking personalities that may present with more opportunities to learn initially. Conversely,  
97 greater behaviourally flexibility associated with reactive coping styles (Coppens et al., 2010) may be  
98 important for tasks such as reversal learning, that require an ability to acquire (and use) new

99 information under changing environmental conditions (Griffin et al., 2015; Koolhaas et al., 1999; Sih  
100 & Del Giudice, 2012). More generally, sensitivity to external stressors or challenges could impact  
101 performance in cognitive assays if more stressed individuals are simply less motivated and/or are  
102 focused on sources of risk rather than environmental cues of rewards.

103         Although hypothesised links between stress responsiveness (or coping style) and cognitive  
104 performance seem intuitive, empirical evidence is still limited to a small number of studies (Bebus et  
105 al., 2016; Bensky et al., 2017; Brust & Guenther, 2017; Lukowiak et al., 2014; Mazza et al., 2018;  
106 Mesquita et al., 2015; van Horik et al., 2017). There are also contrasting studies in which either a  
107 weak or no relationship was detected (Carazo et al., 2014; Cole et al., 2011; Guillette et al., 2015). It  
108 is also possible that relationships are variable across different aspects of cognition. For instance in  
109 sailfin mollies (*Poecilia latipinna*), less anxious fish performed better in a discrimination learning task  
110 than highly anxious individuals, whereas the opposite was found in a reversal learning task. (Gibelli et  
111 al., 2019). Clearly, there is need for more empirical work before a clear picture of the complex  
112 relationship between variation in cognitive performance and stress responsiveness/coping style is  
113 understood. Here we address this broad goal by testing the hypothesis that individual differences in  
114 cognitive performance and stress responsiveness are correlated in male Trinidadian guppies (*Poecilia*  
115 *reticulata*).

116         The guppy is a freshwater poeciliid fish that is widely used as a model in behavioural and  
117 evolutionary ecology. Methods for assaying among-individual ‘personality’ variation are well  
118 established in this species generally (Burns & Rodd, 2008; White et al., 2016), while guppies have  
119 also been used in cognitive studies targeting colour and shape discrimination learning (Lucon-Xiccato  
120 & Bisazza, 2014, 2016), numerical learning (Kotrschal et al., 2013), and spatial learning (Kotrschal et  
121 al., 2015; Lucon-Xiccato & Bisazza, 2017b, 2017c). Here, we investigate the relationship between  
122 behavioural stress response and performance in a spatial learning task in which male guppies  
123 repeatedly navigated a maze to access females as a reward. The cognitive task was repeated using a  
124 second, differently structure maze in order that we could assess not just variation in learning within a  
125 single spatial context, but also ask whether – for instance – individuals displaying greater performance

126 in trials using the first maze subsequently also performed better in the second. In the wild, male  
127 guppies usually utilize large home ranges during mate search and foraging (Croft et al. 2003), and as  
128 such spatial learning is expected to be an ecologically relevant trait (Brown & Braithwaite, 2005). For  
129 our measure of stress responsiveness, we utilise ‘Open Field Trials’ (OFT). Widely used across  
130 species as a paradigm for characterising behavioural differences related to exploration, activity, and  
131 ‘shy-bold’ type variation (Bell et al., 2009; Gosling, 2001), previous studies on this captive population  
132 of guppies have highlighted its utility for assaying behavioural stress response (see e.g., Prentice et al  
133 2020). Observed behaviours expressed in the OFT are both repeatable and plastic with respect to  
134 experimentally-manipulated stressor severity (specifically perceived predation risk) (Houslay et al.,  
135 2018). We also know from pedigree-based quantitative genetic studies that individual (mean)  
136 behaviours and their predictability (defined as within-individual variance) are heritable (Prentice et  
137 al., 2020; White et al., 2019; White & Wilson, 2019). Furthermore, there is some evidence of genetic  
138 integration between OFT behaviour and cortisol expression, strengthening the view that the OFT  
139 provides an appropriate assay of behavioural stress response; (Houslay et al., 2019).

140 In what follows we: i) test for evidence of learning in naïve guppies repeatedly exposed to a  
141 spatial learning task (maze), ii) ask whether individuals differ in cognitive performance across  
142 repeated trials and if so; iii) whether performance in the first maze predicts performance in a second  
143 spatial context (i.e. reconfigured maze). We predict that time to complete the mazes (our proxy of  
144 cognitive performance) will, on average, improve with experience consistent with spatial “learning”,  
145 but that individuals will consistently differ in cognitive performance within each maze. We also  
146 predict that individual performance in the first maze will be positively correlated with performance in  
147 the second, consistent with stable differences in cognitive ability. Finally, iv) we test the hypothesis  
148 that individual differences in cognitive performance will be associated with differences in stress  
149 responsiveness. However, in the current absence of specific models, we make no *a priori* predictions  
150 about the sign of this relationship.

151

152 Methods

153 *Study site and housing*

154 All behavioural assays were carried out on guppies from a captive population (derived from  
155 wild fish collected in the Aripo River, Trinidad in 2008) housed at the University of Exeter's Penryn  
156 campus. Adult males ( $n = 64$ ) were randomly sampled from the stock population, and housed in  
157 groups of 8 in separate home tanks (15 l,  $18.5 \times 37 \times 22$  cm) maintained at 23–24°C on a 12:12  
158 light/dark cycle. The tanks shared a recirculating sump water supply which underwent a 25% water  
159 change once per week. All fish were fed to satiation twice daily on commercial flake food and live  
160 brine shrimp (*Artemia salina*) to control as much as possible for energetic and nutritional states prior  
161 to testing. We elected to focus on males only for several reasons. First, pilot studies showed a high  
162 occurrence of 'freezing' behaviour in females (relative to males) when introduced to the maze. While  
163 freezing can be a component of the behavioural stress response (Houslay et al., 2018), we considered  
164 that frequent occurrence during the cognitive assay would complicate data interpretation. Second,  
165 males show consistent sexual reproductive motivation towards females (Burns & Rodd, 2008),  
166 enabling the use of females as a 'reward' for males solving the maze (Kotrschal et al., 2015). Third,  
167 male guppies exhibit distinctive markings and colouration on body and fins. By recording and  
168 sketching these for each fish we were able identify individuals within groups without the need to  
169 subject individuals to invasive tagging.

170

171 *Ethics*

172 This work was conducted under the auspices of the Animals (Scientific Procedures Act) out  
173 with approval of the University of Exeter research ethics committee, under licence from the Home  
174 Office (UK) (Licence Number PPL30/3256). Experimental procedures and behavioural assays were  
175 developed in accordance with the principles of the three R's and ASAB guidelines (Buchanan et al.,  
176 2020) for use of animals. All periods of handling and emersion were kept to a minimum and only fish  
177 deemed healthy and exhibiting normal behaviour were used in trials. At the end of the experiment,

178 fish were returned to a designated ‘retirement’ tank (containing females as well as males) and not  
179 used in any further experiments.

180

### 181 *Overview of behavioural testing scheme*

182 We used a repeated measures approach to test for among-individual (co)variation in spatial  
183 learning performance and stress responsiveness. Spatial learning was first assessed by repeatedly  
184 trialling individuals in a maze apparatus (Maze A, Figure 1). Each individual fish was tested once per  
185 day for 11 consecutive days with improvement in time to complete the maze interpreted as ‘learning’.  
186 This is consistent with previous studies using either time to complete an objective or to perform a  
187 particular task to investigate variation in cognitive performance among-individuals (Guillette et al.,  
188 2015; Lucon-Xiccato & Bisazza, 2016; Mazza et al., 2018; Zidar et al., 2018). We acknowledge that  
189 this interpretation strictly requires the implicit assumption that the contribution of any other factors to  
190 among-individual variation (e.g., motivation, energetic state, experience previous to the experiment;  
191 Rowe & Healy 2014) is negligible relative to differential cognitive performance. We attempted to  
192 mitigate against other sources of among-individual variation as far as possible using standardised  
193 housing and husbandry conditions. Following completion of spatial learning trials using Maze A,  
194 individuals were tested for stress responsiveness three times each over a three-week period using  
195 Open Field Trials (OFT) with a mean (range) of 4 (1-5) days between successive trials. Finally, fish  
196 were retested in a second maze (Maze B) with a different layout, and repeat trials conducted (as  
197 before) one per day for 11 consecutive days. Thus, in total, the design called for all individuals to  
198 complete 22 spatial learning trials, 11 on each of two different maze layouts (distributed across two  
199 different mazes) and three OFT over a total testing period of 43 days. Note that the sample size  
200 declined slightly across the experiment as (i) a few mortalities occurred naturally within the testing  
201 period and, (ii) we proactively ‘retired’ any fish not deemed to be feeding well and behaving normally  
202 in their home tanks as a precaution against cumulative adverse effects. Thus 63 fish experienced Maze  
203 A, which declined to n=60 at trial 11 and OFT testing. Five fish were then removed prior to  
204 experiencing Maze B (n= 55 at trial 1 and n=53 at trial 11).



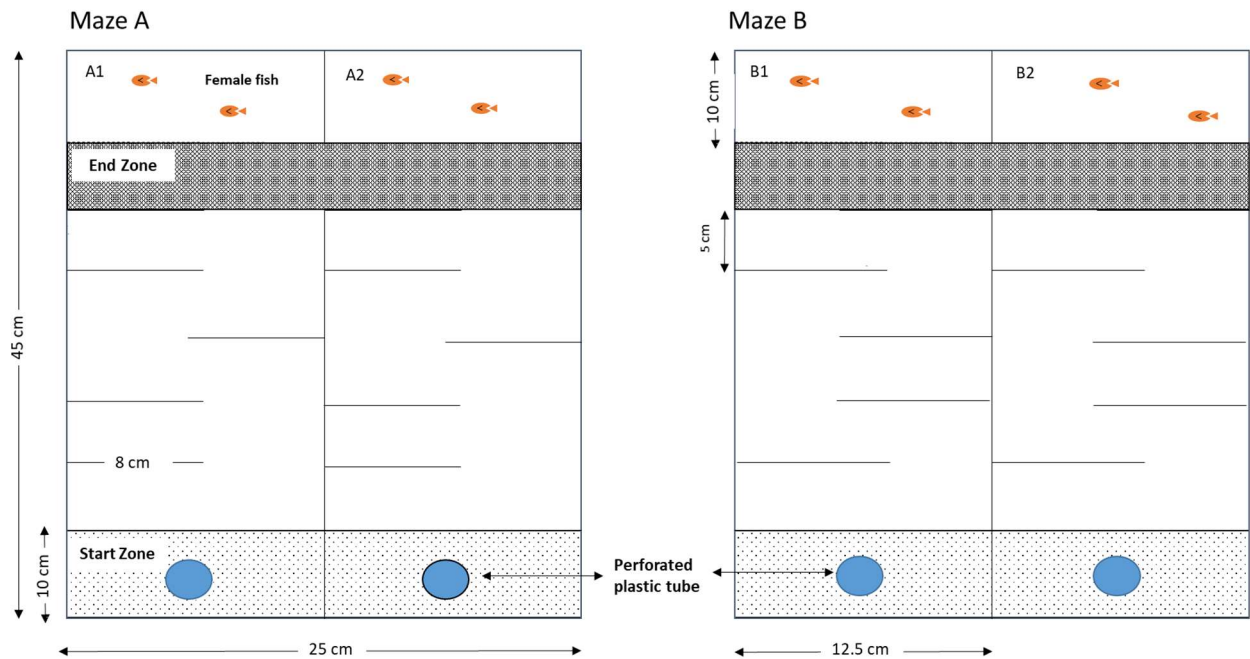
205

206 *Spatial Learning Trials*

207 In order to facilitate more rapid data collection, a single aquarium (25 x 45 x 25cm) was  
208 divided into two, with each half containing an identical version of maze A (A1, A2). Two replicates  
209 of maze B were similarly constructed (Figure 1). This allowed two fish to be tested concurrently  
210 during trials. Each maze consisted of 6 opaque Perspex panels (8 cm), spaced 5cm apart (Fig 1). A  
211 visually transparent perforated panel at one end of each maze was used to separate a small holding  
212 area (12.5 x 10 x 25 cm) contain two adult females selected haphazardly from stock. During trials the  
213 experimental maze tanks were lit from below by one fluorescent lamp and filled to a depth of 8 cm  
214 with room temperature water (approx. 23-24 °C). The water was taken from the same recirculating  
215 system used to house the male groups and was changed between each housing group (i.e. after every 4  
216 runs with two fish trialled per run). Stimulus females were also changed at the same time.

217 At each trial, two males were individually netted from their home tank and quickly identified  
218 from natural markings. Each was randomly allocated to one of the two maze replicates and carefully  
219 placed within a perforated plastic tube in the ‘start’ zone (Figure 1). They were given 60 s to  
220 acclimate before the plastic tubes were removed. A Sunkwang C160 video camera mounted above the  
221 tank allowed the fish to be observed without disturbance. Tracking software  
222 (<http://www.biobserve.com>) was then used to determine the *start latency* as the (post-acclimation)  
223 time taken before a fish started the maze by leaving the ‘start’ zone, and *maze time* as the latency from  
224 starting to completing the maze (with completion defined as reaching the ‘end’ zone; Figure 1). On  
225 reaching the ‘end’ zone individuals were given 60 s undisturbed visual access to the females before an  
226 opaque plastic sheet was inserted to obstruct females from view. Following the 60 s reward period,  
227 fish were netted and returned to the home tank. To ensure standardized exposure to the reward  
228 stimulus, individuals that did not complete the maze within 480 s post-acclimation period  
229 (irrespective of whether they had started) were gently guided through the maze to the end zone using a  
230 net behind them and then experienced 60 s visual access to the females. Following the 60 s reward

231 period, fish were netted and returned to the home tank. These fish were assigned a right censored  
232 value of 480 second for *maze time*.



233  
234 **Figure 1.** Aerial view of the maze designs used in the experiments (A and B), each tank was split into  
235 two identical mazes (1 and 2).

236

### 237 *Open Field Trial (OFT)*

238 OFTs to characterise stress responsiveness closely followed the protocol described in White  
239 et al. (2016). For each trial, a single individual was netted from the home tank, quickly identified and  
240 introduced gently into the centre of an open arena (a 30 × 20 cm tank filled to 5 cm water placed on a  
241 lightbox). A cardboard screen was around the tank prevented visual disturbance and a Sunkwang  
242 C160 video camera mounted above the arena again allowed movement to be tracked. Following a 30 s  
243 acclimation period, individuals' movements were tracked for 4 minutes and 30 s to determine *track*  
244 *length* (total distance swum (cm)) and *area covered* (percent of tank area covered). These two  
245 observed behaviours which are known to be repeatable and heritable in this population (Houslay et al.,  
246 2018; White et al., 2019; White & Wilson, 2019), were used to calculate the derived trait of *relative*

247 *area* following Houslay et al. (2019). *Relative area* is the observed area covered in the trial minus the  
248 expected area covered under a simulated ‘random swim’ of length equal to the observed track length  
249 (see Houslay et al. (2019) for further detail on simulations). Low values of *relative area* result from a  
250 ‘flight type’ behavioural stress response in which individuals swim rapidly (yielding a high track  
251 length) but exhibit thigmotaxis (staying close to the walls and seeking escape from the arena) and thus  
252 cover relatively little of the arena area. In contrast low values of *relative area* correspond to efficient  
253 exploration (i.e. a high proportion of the arena covered given distance swum), by putatively less  
254 stressed fish.

### 255 *Statistical Analysis*

256 Data from both types of behavioural assay were analysed using univariate and multivariate  
257 linear mixed effect models fitted by REML (restricted maximum likelihood) using ASReml within R  
258 (<http://www.vsni.com>) (Gilmour et al., 2009). By including individual identity as a random effect in  
259 these models we test for and characterise among-individual (co)variation. Traits were mean centred  
260 and scaled to standard deviation units to ease interpretation of results and facilitate convergence of  
261 multivariate models. For *maze time* we did this using the overall mean and standard deviation of  
262 observations from both mazes in order to preserve any meaningful differences in performance  
263 between A and B. With traits in standard deviation units (sdu), estimates of among-individual  
264 variance ( $V_{ind}$ ) can be interpreted as repeatabilities (i.e. proportion of the observed phenotypic  
265 variance explained by among-individual differences). However, we also calculate estimates of  
266 adjusted repeatability ( $R$ ), the proportion of phenotypic variance explained by consistent among-  
267 individual differences, after controlling for fixed effects on the mean (Nakagawa & Schielzeth, 2010).  
268 Thus  $R = V_{ind} / (V_{ind} + V_R)$  where  $V_R$  is the residual (within-individual) variance estimated from each  
269 model. The significance of random effects was tested using likelihood ratio tests (LRT), while fixed  
270 effects (included in the various models as described below) were tested using conditional F-statistics.  
271 All models assumed Gaussian error structures, an assumption that was deemed acceptable based on  
272 visual inspection of the model residuals.

273

274 *Univariate analyses of maze performance and spatial learning*

275 We use *maze time* as our observed measure of performance. Here we describe in full the  
276 univariate analysis of data collected in maze A (subsequently *maze time<sub>A</sub>*). Identical procedures were  
277 then applied to data from maze B. First, we visualised the distribution of *maze time<sub>A</sub>* across repeat  
278 using box plots and also plotted the proportion of mazes completed as a function of repeat to see if a  
279 pattern of increasing average performance (i.e. decreasing *maze time* and/or increasing proportion of  
280 successful completion) was immediately apparent. Next a series of three nested models with identical  
281 fixed effects but differing random effect structure were fitted to the centred and scaled *maze time<sub>A</sub>*  
282 data. All models included a fixed effect of *trial number* (the cumulative number of trials experienced  
283 by an individual, treated as a continuous variable), allowing us to test for improvement in the mean  
284 (indicative of learning). Additional fixed effects were included as statistical controls for potential  
285 sources of variance not relevant to hypotheses being tested here. These included time of day (in  
286 minutes after 9 am), maze replicate (as a factor denoting position 1 or 2 in maze tank), and order  
287 caught from the home tank. The latter was to account for any cumulative disturbance effect of  
288 removing fish sequentially from the home tank and/or build-up of chemical cues in the maze between  
289 water changes.

290 The first model contained no random effects, while the second contained a random intercept  
291 of individual identity. Likelihood ratio test (LRT) comparison of these models was conducted to test  
292 the hypothesis that individuals differ in their average performance (*maze time<sub>A</sub>*) across the 11 repeats,  
293 and we estimated the (adjusted) repeatability of performance under the second model. For the LRT we  
294 assume twice the difference in model log-likelihoods is distributed as a 50:50 mix of  $X^2_1$  and  $X^2_0$   
295 following Stram & Lee (1994). The third model was a first order random regression (i.e. a random  
296 slope and intercept model) in which each individual's deviation from the fixed effect mean *maze time*  
297 can change as a linear function of *trial number* (1-11). Variation in random slopes means that there is  
298 among-individual variation around the mean *maze time<sub>A</sub>* - *trial number* relationship. Thus, LRT

299 comparison of the second and third models thus provides a test for among-individual variation in  
300 learning rate. This comparison is conducted assuming the test statistics is distributed as  $X^2_2$  since the  
301 third model has two extra parameters (a slope variance and a slope-intercept covariance). Note that  
302 among-individual variance in slopes cannot be scaled to a repeatability as within individual variance  
303 in slope is not estimable (using data from a single maze; see below). Nor is its magnitude directly  
304 comparable to random intercept variance since slopes and intercepts are in different units. However,  
305 under the third model, among-individual variance in learning (slope) means that among-individual  
306 variance *maze time<sub>A</sub>* changes with *trial number* (Supplemental Materials Figure 1). Thus, to  
307 understand the biological effect size of estimated variance in slopes, we use the third model to predict  
308 among-individual variance ( $V_{\text{ind}}$ ) and adjusted repeatability (R) of *maze time<sub>A</sub>* at both initial (trial 1)  
309 and final (trial 11) performance (following e.g., Nussey et al. (2007); see Supplemental Materials  
310 Table 3 for didactic explanation and corresponding code). We note that among-individual variation at  
311 final performance has been used to infer differences in cognitive ability in studies adopting similar  
312 repeated measures designs (e.g. Langley et al. 2020) and so also has a useful biological interpretation  
313 here.

314

### 315 *Univariate analysis of relative area*

316 To verify our expectation that individuals would show consistent differences in stress  
317 responsiveness, we fit a simple random intercepts model to (scaled and centred) *relative area*. This  
318 model included fixed effects of trial number (1-3), and time of day (in minutes after 9 am in which  
319 each trial took place) as well as a random effect of individual identity as. Adjusted repeatability (R) of  
320 *relative area* was calculated and the significance of among individual variance tested by LRT  
321 comparison to a simplified model with no random effect (assuming the test statistic was distributed as  
322 a 50:50 mix of  $X^2_1$  and  $X^2_0$  as above).

323

324 *Multivariate modelling of Maze A, Maze B and OFT data combined*

325           Finally, to test the predicted correlation structure between cognitive performance and stress  
326 responsiveness, we formulated a trivariate mixed model in which the three response variables were  
327 *maze time<sub>A</sub>*, *maze time<sub>B</sub>* and *relative area*. Fixed effects were exactly as described above on all three  
328 traits. Random effects were also as described above (i.e. individual level random intercepts and  
329 slopes for *maze time<sub>A</sub>* and *maze time<sub>B</sub>* but a random intercept only for *relative area*) but the  
330 multivariate formulation allowed us to estimate the full 5x5 among-individual covariance matrix  
331 (**ID**) among these effects. Since each observation of a fish provided data on a single trait only,  
332 residual covariances among traits were fixed to zero. After fitting the model, we compared it to a  
333 simplified fit in which all among-trait covariance elements in **ID** were constrained to zero. This  
334 provides a global test of individual covariance between traits. We then scaled estimated pairwise  
335 covariances in **ID** to their corresponding correlations for easier interpretation (noting for a pair of  
336 effects *x,y* the correlation  $r_{xy} = \text{COV}_{xy}/(\text{V}_x\text{V}_y)^{0.5}$ ). This allowed us to scrutinise the correlation structure  
337 between stress responsiveness and cognitive performance in both mazes A and B, using both final  
338 performance and learning rate (i.e. random regression slope) as measures of cognition. Additionally, it  
339 allowed us to estimate the individual level correlation in cognitive performance measures (final *maze*  
340 *time* performance, learning) across mazes. These are not strictly equivalent to individual  
341 repeatabilities of cognitive performance measures across mazes (as opposed to individual repeatability  
342 of *maze time* across trials within mazes) because estimates could be negative. However, they can be  
343 readily interpreted in those terms; a strong positive correlation between, for example, individual  
344 *learning* in maze A and maze B means this latent variable is highly repeatable across mazes.  
345 Conversely, a negative correlation means that individuals learning faster in maze A tend to learn more  
346 slowly in maze B (and *vice versa*).

347

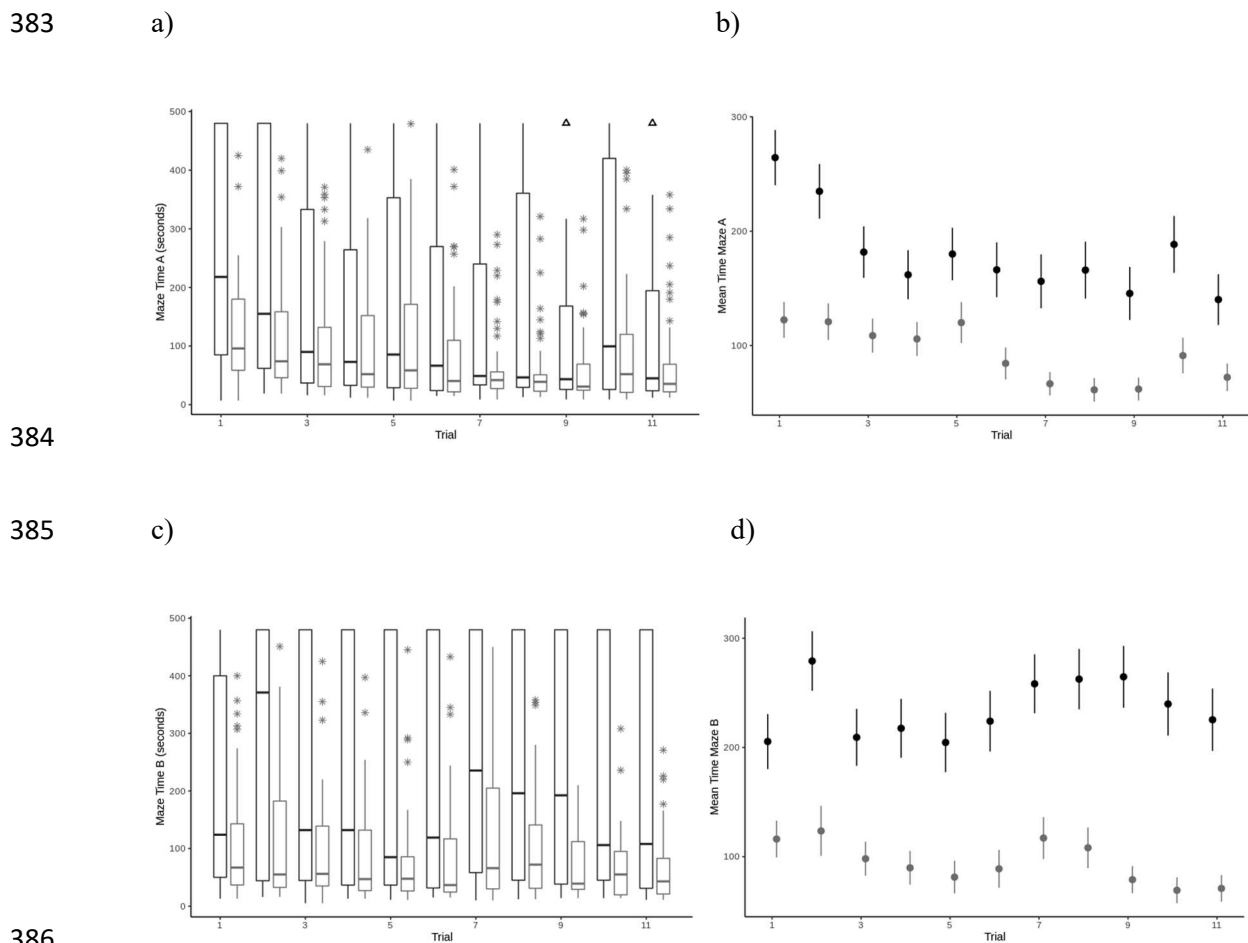
348 Results

349 *Performance in Maze A*

350 Plots of the raw data suggest that average time to complete Maze A decreases across trials,  
351 and that the success rate (proportion of individuals completing the tasks within the 480 s) tends to  
352 increase (Figure 2). These patterns are qualitatively consistent with expectations if (average)  
353 performance improves as a consequence of learning. The mixed model analysis of *maze time<sub>A</sub>*  
354 confirms statistical support for this with a significant negative effect of trial repeat number (based on  
355 the full random slope and intercept model; coefficient = -0.043 (0.014) sdu,  $F_{1,59,8} = 10.140$ ,  $P =$   
356 0.003). This effect size equates to an estimated decrease of 91.9 seconds in average *maze time* over  
357 the 11 trials. Other fixed effects of order caught and maze position were non-significant (see  
358 Supplementary Material Table S1). Likelihood ratio tests (LRT) confirmed among-individual  
359 variation in *maze time<sub>A</sub>* (comparison of null and random intercept models;  $\chi^2_{0,1} = 155$ ,  $P \leq 0.001$ ).  
360 Under the random intercept model, repeatability of *maze time<sub>A</sub>* conditional on fixed effects was  
361 estimated as  $R_A = 0.343$  (0.05).

362 LRT comparison of the random intercept and first order random regression models showed  
363 the latter to be a significantly better fit to the data ( $\chi^2_2 = 25.0$ ,  $P \leq 0.001$ ). This comparison provides  
364 evidence for among-individual variance in the rate of change of *maze time<sub>A</sub>* across repeated trials  
365 (interpretable, with caveats discussed below, as variation in rate of learning). Among-individual  
366 variance in intercepts (int) and slope (slp) were estimated as  $V_{ind_{int}} = 0.394$  (0.102) and  $V_{ind_{slp}} =$   
367 0.006 (0.002) respectively while the among-individual intercept –slope correlation was estimated as  
368 ( $r_{ind_{int},ind_{slp}} = -0.489$  (0.147)). Biological interpretation of these parameters is not completely  
369 straightforward. Given the scaling of *trial number* in the random effect structure of the model (see  
370 Supplemental Materials Table S3)  $V_{ind_{int}}$  is interpretable as among individual variance in *maze time<sub>A</sub>*  
371 at first trial. While slope variance is in different units and thus not of directly comparable magnitude,  
372 variation in slopes actually means that among-individual variance in the observed trait ( $V_{ind}$  for *maze*  
373 *time<sub>A</sub>*) changes with trial repeat number. Here the random regression model predicts values of

374  $V_{ind_{A1}} = 0.394$  (0.102), and  $V_{ind_{A11}} = 0.542$  (0.131)) at first and last trial in maze A respectively,  
375 suggesting more among individual variation in performance at the end of trials than at the beginning.  
376 The corresponding predictions of repeatability at first and last observed trial are  $R_{A1} = 0.431$  (0.070)  
377 and  $R_{A11} = 0.511$  (0.067). The negative intercept-slope correlation ( $r_{ind_{A.int,A.slp}} = -0.489$  (0.147),  $\chi^2_2 =$   
378 6.182,  $P = 0.045$ ), means that individuals with higher intercepts (high *maze time<sub>A</sub>* at trial 1, tended to  
379 have lower slopes (i.e., more negative, indicative of faster learning). These patterns are represented  
380 visually in Figure 3, which shows the individual reaction norms predicted from the best linear  
381 unbiased predictions (BLUPs) of random intercept and slope for each fish (following e.g., Houslay &  
382 Wilson (2017)).



387 **Figure 2.** Plots of raw data of *maze time* across both maze designs. Boxplots (a) and (c) show the data  
388 distributions for time to complete Maze A and Maze B respectively across the 11 trials. Black boxes  
389 display data of all individuals and grey boxes represent only those individuals that successfully

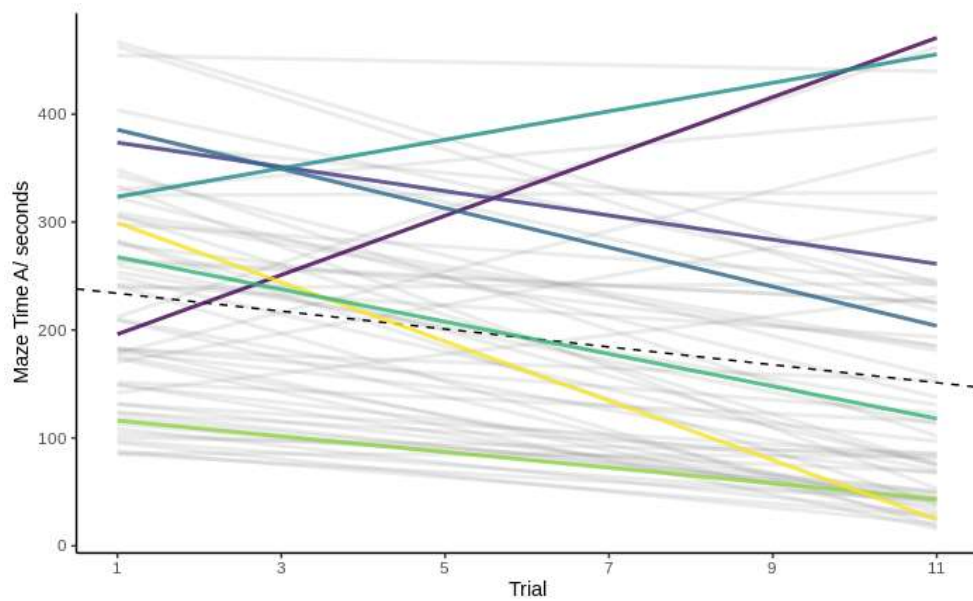


390 completed the task within 480 s. Horizontal lines within box correspond to behavioural medians, box  
391 boundaries correspond to first and third quartiles. When present, whiskers correspond to 10th and  
392 90th percentiles, and points correspond to outliers. Plots (b) and (c) represent mean and standard  
393 errors for time to complete Maze A and B respectively. Colours represent the same groups; black  
394 error bars represent mean and standard errors of *maze time* for all individuals, and grey represent only  
395 those individuals that successfully completed the maze in the allocated time.

### 396 *Performance in Maze B*

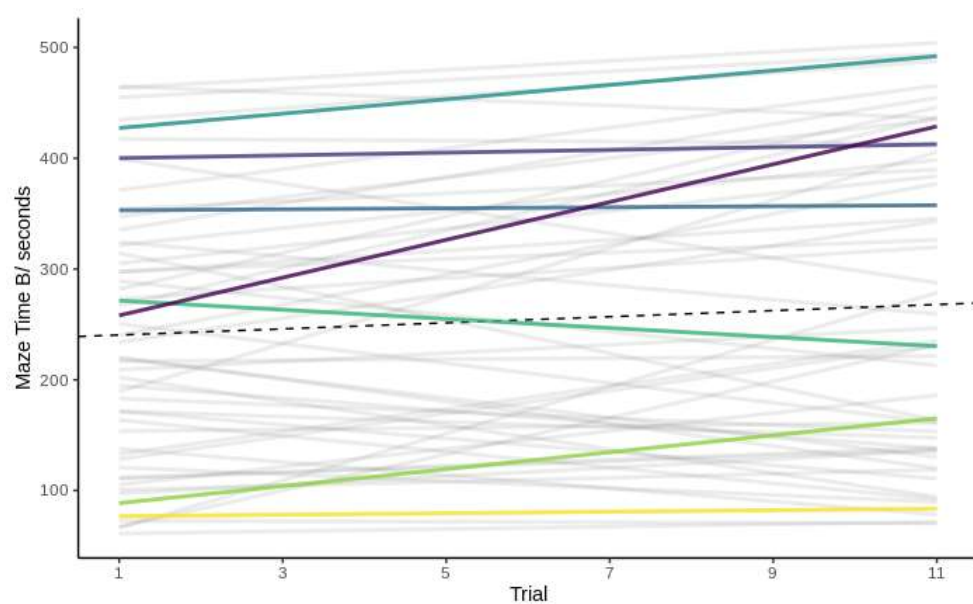
397 In contrast to Maze A, plotting *maze time<sub>B</sub>* data reveals no clear increase in performance (i.e.  
398 decrease in time) across trials. Furthermore, there is actually a trend towards fewer individuals  
399 successfully completing the task (Figure 2). However, we note that if the censored data points are  
400 excluded to leave only successfully complete trials, there is a decreasing trend in *maze time<sub>B</sub>* with trial  
401 number. The mixed model analysis (which uses data from all trials) confirms the lack of improvement  
402 in the mean *maze time<sub>B</sub>*, with a (non-significant) positive estimate of the trial repeat number effect (from  
403 random slope and intercept model; coefficient = 0.014 (0.014),  $F_{1,538,2} = 1.193$ ,  $P = 0.301$ ). Effects  
404 of order caught and maze position were not significant (Table S2). Likelihood ratio tests (LRT) between  
405 the univariate random intercept model and the null model with no random effect, shows the presence of  
406 significant among-individual variation for *maze time<sub>B</sub>* ( $\chi^2_{0,1} = 182.041$   $P \leq 0.001$ ), with a corresponding  
407 repeatability estimate of  $R_B = 0.401$  (0.055). The random slope model was a significantly better fit again  
408 ( $\chi^2_2 = 9.995$   $P = 0.007$ ) providing evidence of among-individual variation in the performance-trial  
409 number relationship. Among-individual variance in intercepts (int) and slope (slp) were estimated as  
410 0.472 (0.130) and 0.004 (0.002) respectively. These estimates mean predicted values of  $V_{ind_{B1}} =$   
411 0.472 (0.130) and  $V_{ind_{B11}} = 0.635$  (0.162)) which correspond to repeatabilities of  $R_{B1} = 0.439$  (0.074)  
412 and  $R_{B11} = 0.512$  (0.071). Given that there is no (significant) effect of trial number on mean *maze time<sub>B</sub>*  
413 the presence of among-individual variance in slope suggest that some individuals are improving  
414 (consistent with learning) while for others performance is tending to get worse across repeats in Maze  
415 B. Furthermore, the among-individual intercept–slope correlation was non-significant as ( $r_{ind_{B.int,B.slp}} =$

416  $-0.302 (0.214)$ ,  $\chi^2_2 = 1.476$ ,  $P = 0.478$ ). The predicted patterns are again represented visually by plotting  
417 the individual reaction norms (Figure 3).



418 a)

419



420 b)

421

422 **Figure 3.** Spatial learning traits across Maze A and Maze B as a function of trial number, *maze time<sub>A</sub>*

423 (a), and *maze time<sub>B</sub>* (b). Grey lines represent individual predicted reaction norms (BLUPs) from

424 univariate random slope models for each trait. Coloured lines are used to illustrate reaction norms for

425 a small random set of arbitrarily chosen individuals tested in both mazes. Black dashed line represents

426 the trend in fixed effect mean *maze time* across repeat trials.

427

428 *Among-individual differences in OFT behaviour*

429 We found evidence of significant among-individual variation in *relative area*,  
430 (*repeatability*(with SE),  $R = 0.465$  (0.089),  $\chi^2_{0,1} = 20.421$ ,  $P < 0.001$ ). This replicates previous  
431 findings in the same population (Prentice et al., 2020) though the current estimate of repeatability is  
432 somewhat higher, likely due to differences in study design (e.g. the current study used a shorter inter-  
433 observation interval and was limited to males only). Fixed effects from the OFT behaviour models are  
434 presented in the Supplementary Material (Table S2) for completeness, although are not directly  
435 relevant to our hypotheses in this study.

436 *Multivariate model*

437 The full multivariate model (**ID**) of *maze time<sub>A</sub>*, *maze time<sub>B</sub>* and *relative area* provides  
438 evidence of some significant among-individual covariance structure between observed traits  
439 (comparison of the full model to one in which all among-individual between trait covariances are  
440 fixed to zero;  $\chi^2_8 = 44.094$ ,  $P \leq 0.001$ ). Examination of the estimated covariances and correlations  
441 (Table 1) suggests this result is largely driven by a strong positive correlation between the individual  
442 intercepts for *maze time<sub>A</sub>* and *maze time<sub>B</sub>* ( $r_{ind_{A.int,B.int}} = 0.686$  (0.135)). In other words  
443 performance at first trial is positively correlated at the individual level across mazes (since  
444  $r_{ind_{A.int,B.int}} = r_{ind_{A1,B1}}$ ). Using the multivariate random regression model to predict the corresponding  
445 correlation at final trial (i.e. trial 11), performances across mazes yields an estimate (SE) of  
446  $r_{ind_{A11,B11}} = 0.602$  (0.131). Thus, our results suggest strong positive among-individual correlation  
447 of performance as measured by maze time across trials and mazes. This is not only the case for first  
448 and last performance, but also for intermediate trial numbers as can be shown by transforming the **ID**  
449 estimate from the random regression model (as shown in Table1) to a ‘character state’ correlation  
450 matrix among the full set of trials and maze specific observations, and *relative area* (see  
451 Supplementary Material Table S3 for this matrix and an explanation of the transformation).

452            However, returning to a reaction norm interpretation of results, we do not find evidence that  
 453 reaction norm slopes (i.e. putative rates of learning) are correlated across mazes. While the  
 454 multivariate model corroborates the presence of among-individual slope variance in mazes A and B,  
 455 the correlation between them was only weakly positive and non-significant ( $r_{ind_{A.slp,B.slp}} = 0.216$   
 456 (0.266); Table 1). Nor do we find statistical support for among-individual correlation between maze  
 457 performance intercepts or slopes (for either maze) and relative area.

458 **Table 1.** Among individual variance–covariance–correlation matrix from the final trivariate model of  
 459 *maze time<sub>A</sub>*, *relative area* and *maze time<sub>B</sub>*. Variances are shown on the diagonal (dark grey shading),  
 460 with covariances below and correlations above. Light grey shading denotes within trait  
 461 covariance/correlation estimates (i.e. between reaction norm intercepts and slopes). Standard errors  
 462 are shown in parentheses and bold font denotes nominally significant pairwise estimates assuming  
 463 approximate 95% CI of  $\pm 1.96SE$ ).

	<i>Maze time<sub>A</sub></i>		<i>Relative area</i>	<i>Maze time<sub>B</sub></i>	
	<i>intercept<sub>A</sub></i>	<i>slope<sub>A</sub></i>		<i>intercept<sub>B</sub></i>	<i>slope<sub>B</sub></i>
<i>intercept<sub>A</sub></i>	<b>0.436 (0.113)</b>	<b>-0.489 (0.147)</b>	0.286 (0.175)	<b>0.686 (0.135)</b>	-0.129 (0.254)
<i>slope<sub>A</sub></i>	<b>-0.027 (0.013)</b>	<b>0.007 (0.003)</b>	-0.075 (0.202)	-0.006 (0.209)	0.216 (0.266)
<i>Relative area</i>	0.127 (0.084)	-0.004 (0.011)	<b>0.451 (0.118)</b>	0.024 (0.125)	0.377 (0.231)
<i>intercept<sub>B</sub></i>	<b>0.299 (0.091)</b>	-0.003 (0.012)	0.011 (0.085)	<b>0.437 (0.119)</b>	-0.309 (0.212)
<i>slope<sub>B</sub></i>	-0.005 (0.010)	0.001 (0.001)	0.016 (0.011)	-0.013 (0.012)	<b>0.004 (0.002)</b>

464

465 Discussion

466 Here, we show evidence of among-individual differences in performance – measured as time to  
467 complete a maze – in guppies exposed to a spatial learning test paradigm. Performance of individuals  
468 is repeatable both within, and across, the two spatial learning tasks (i.e. mazes) presented. However,  
469 the question of whether there is robust evidence of learning, on average or by individual fish, is  
470 somewhat less clear cut. In particular, in the first maze used (A) we find evidence of improvement in  
471 mean performance consistent with learning (on average). We also find among-individual variation in  
472 this rate of improvement, and so – putatively their rate of learning. However, the same fish exposed to  
473 maze B show (on average), no increase in performance across successive trials. We found among-  
474 individual correlation structure between performances (i.e. time in the maze) but not learning (i.e. rate  
475 of improvement) across the 2 spatial learning tasks. We did not however find any significant  
476 association between individual differences in maze performance (or learning) and repeatable stress  
477 responsiveness as measured in the open field trials. In what follows we describe each of these  
478 findings in more detail and discuss them in the wider context of the cognitive literature.

479 The data from Maze A show that on average, time to complete the maze improves across repeated  
480 trials. This improvement suggests that spatial learning is occurring in the guppies, a finding consistent  
481 with previous studies of this species (Fong et al., 2019; Kotrschal et al., 2015; Lucon-Xiccato &  
482 Bisazza, 2017c). We also see evidence of consistent, repeatable differences among-individuals in  
483 performance in Maze A. This is shown in our reaction norm models as significant among-individual  
484 variance in intercept, which strictly represents performance at first trial. However, using among-  
485 individual variation in intercepts and slope to predict the corresponding variance at, and correlation  
486 among-, all trials (see Supplemental Materials Table 3 for derivation and presentation of these  
487 estimates) reveals that in fact individual performance is positively correlated across all trials from 1 to  
488 11. In simple terms, fish that are faster than average at completing Maze A in their first trial, tend to  
489 be faster than average across all subsequent trials too. Predicted repeatability of *maze time* is  
490 moderately high relative to many behavioural studies (e.g., 43% at trial 1, 51% at trial 11) but broadly  
491 comparable to estimates reported from similar assays designed to test cognitive variation; see

492 Cauchoix, Hermer, Chaine, & Morand-Ferron (2017) for an overview. We note that a contributing  
493 factor is likely to be short inter-observation period (here 24 hrs) typical of cognitive studies, since  
494 behavioural repeatabilities generally declines as this increases (Boulton et al., 2014).

495       Accepting that improvement across repeated trials can be interpreted as learning (caveats to this  
496 are discussed below), our random regression model also provides evidence for among-individual  
497 variation in spatial learning in Maze A. Usefully, our modelling strategy allowed all observations to  
498 contribute to estimating variance in the latent cognitive trait (learning) while avoiding statistically  
499 problematic ‘two-step’ analysis (Houslay & Wilson, 2017). Although this strategy is now widely used  
500 in studies of behavioural plasticity, it has not yet been widely adopted by researchers focussing  
501 specifically on animal cognition (but see e.g., Langley et al., 2020). In addition to finding variance in  
502 slopes (learning), we estimated a negative among-individual intercept-slope correlation using the  
503 Maze A data; individuals with higher intercepts (i.e. *maze time* at first trial) tend to have lower (more  
504 negative) slopes. While it is therefore the case that those fish performing poorly initially exhibit  
505 higher rates of learning, it is also true - as noted above - that individual performance (*maze time*) is  
506 positively correlated across trials 1-11. These two results are entirely compatible because differences  
507 in learning (slope) are not sufficiently pronounced that initially poor performing (but fast learning)  
508 fish will generally ‘overtake’ initially good performing (but slow learning) individuals in expected  
509 time to complete the maze by trial 11. We cannot comment on what fitness consequences, if any, the  
510 variation detected here would have in wild fish. Nonetheless, this finding does highlight a danger with  
511 the general presumption that cognitive abilities are under positive selection. Here, if we assumed that  
512 fitness benefits were accrued by rapidly achieving a spatial task (e.g. locating a resource) regardless of  
513 mechanism, it would be the slower learners that were advantaged. Thus, while it is tempting to  
514 assume fast learners will achieve better outcomes, they may sometimes simply be those with the  
515 ‘most room for improvement’.

516       Thus, findings from Maze A are consistent with our initial predictions that time to complete the  
517 maze would improve (on average) with experience due to spatial learning, but that individuals would  
518 also vary in both performance (*maze time*) and learning (rate of change in performance with

519 experience). We also found that individuals that were quicker (over all trials) to complete Maze A,  
520 tended to be quicker (over all trials) to complete Maze B. While this could be attributable to cognitive  
521 differences, there are certainly other possibilities. For instance more explorative and/or less neophobic  
522 individuals may be generally faster at solving tasks (Boogert et al., 2006; Bousquet et al., 2015; Zidar  
523 et al., 2018). Similarly there could be among-individual variation in perceived cue salience (Meyer et  
524 al., 2012), individual physiology (Bókony et al., 2014), or motivation (van Horik & Madden, 2016).  
525 Regardless, of these unknowns, an important difference between Maze A and Maze B was that we  
526 found no evidence of learning on average in the latter. In fact, for Maze B the mean *maze time*  
527 actually increased slightly, though not significantly, across trials. Despite this, patterns of individual  
528 variation around the mean trajectory were largely similar to those found in Maze A. Thus, there is  
529 among-individual variation in intercept (*maze time* at trial 1) and also in slope. Given that there is no  
530 (significant) change in mean performance, but there is significant variation in slopes, we conclude that  
531 some individuals are improving (learning) in Maze B while others are getting worse with experience.  
532 We also note that, as in Maze A, slope variance is present, but not sufficiently high to break down the  
533 positive correlation structure of individual performance (*maze time*) across trials 1-11.

534 Although we did not formally test for differences in average slope between maze A and B, we  
535 note that approximate 95% confidence intervals do not overlap (estimated as  $\text{coefficient} \pm 1.96\text{SE}$ ).  
536 Several possibilities may explain the finding of spatial learning on average in A but not B. First, the  
537 results from maze A may be a false positive (Fraser et al., 2018; Sterne & Smith, 2001). However  
538 coinciding with previous studies which show this species is capable of learning an initial spatial  
539 learning task (Fong et al., 2019; Kotrschal et al., 2015; Lucon-Xiccato & Bisazza, 2017b), we assume  
540 this unlikely. Second, it may be that the layout of maze B was, in some unknown way, more  
541 challenging to learn. This could certainly be true if, for instance learning to navigate a new maze  
542 following the acquisition of a previously learnt layout, poses a more challenging task such that more  
543 trials would be required to detect improvement. There is some evidence for such effects in guppies.  
544 For instance, Lucon-Xiccato & Bisazza (2014) found that on average guppies took 14.61 trials to



545 learn a reversed colour cue association, while Fong et al., (2019) found that on average, 15.30 trials  
546 were required for guppies to learn a reversed maze layout.

547 A third, possible explanation is that learning does lead to gains in maze B performance, but that  
548 these are being masked at the level of the sample mean by concurrent changes in aspects of average  
549 individual ‘state’ that reduces cognitive performance and/or motivation. One plausible hypothesis is  
550 that chronic stress responses arise cumulatively from repeated capture and handling necessitated by  
551 the experimental design (Huntingford et al., 2006; Warren & Callaghan, 1976; Wong, Dykstra,  
552 Campbell, & Earley, 2008). If so, this could negatively impact affected individuals and offset  
553 expected improvements in mean performance across trial number. Presently we cannot directly test  
554 this possibility, and variation in susceptibility to chronic stress response is not well understood.  
555 Nonetheless, our experiment does confirm repeatable among-individual variation ( $R= 0.465 (0.089)$ )  
556 in *relative area* covered in the OFT, used here as a measure of acute behavioural stress response. This  
557 replicates previous results using independent data sets of fish from the same captive population  
558 (Houslay et al., 2019; Prentice et al., 2020; White et al., 2016). Acute stressor exposure has been  
559 shown to affect cognitive performance in spatial learning tasks in both mammals and fish (Gaikwad et  
560 al., 2011; R. Y. Wong et al., 2019). At the individual level, there is also evidence to suggest short-  
561 term measures of acute stress responses can predict longer term organismal performance under  
562 chronic and/or repeated stressor exposure (Øverli et al., 2007; Salak-Johnson & Mcglone, 2007;  
563 Segerstrom & Miller, 2004).

564 Here, our modelling approach did not provide compelling statistical support for strong  
565 relationships between *relative area* and either initial *maze time*, or learning (i.e. improvement in *maze*  
566 *time*) in either Maze A or B. However, the estimated correlation between *relative area* and *maze time*  
567 in Maze B actually rises to  $r_{ind}=0.336 (0.169)$  by trial 11 and thus approaching nominal significance at  
568  $\alpha=0.05$  (assuming a lower 95% CI of  $r_{ind} - 1.96SE$ ). To explore this further we conducted a *post hoc*  
569 likelihood ratio test comparison of a bivariate model of *maze time<sub>B</sub>* and *relative area*; all effects as  
570 described for the trivariate model earlier) to the corresponding model fit where among-individual  
571 covariances between *relative area* and *maze time<sub>B</sub>* (intercept and slope) were constrained to zero. This



572 confirmed no significant covariance between *relative area* and *maze time<sub>B</sub>* ( $\chi^2_2 = 3.098$ ,  $P = 0.212$ ).  
573 Thus, we do not find statistical support for the prediction, made under the stress coping style model,  
574 that (acute) stress responsiveness will (co)vary with cognitive performance (Coppens et al., 2010;  
575 Griffin et al., 2015; Sih & Del Giudice, 2012). Nonetheless, the possibility that chronic stress  
576 negatively impacts apparent learning cannot be completely excluded here. Empiricists rightly seek to  
577 minimise the possibility of stress confounding conclusions from cognitive studies. However, we  
578 suggest the assumption that individuals remain (equally) ‘unstressed’ over experimental periods  
579 requiring repeated observations (and often repeated capture and or social isolation) is difficult to  
580 validate in practice.

581         In summary, here we have evidence of consistent differences among-individuals in spatial  
582 task performance in the guppy *P. reticulata*. Individual performance is repeatable across trials within-  
583 and between two different spatial tasks (i.e. maze layouts). This among-individual variation in  
584 performance may well be mediated by cognitive factors but differences in ‘personality’ (e.g.  
585 neophobia, exploratory tendency) may also contribute. We also find evidence of improved  
586 performance with experience, consistent with spatial learning. In both tasks variation around the  
587 trajectory of mean performance across trial number was present. While this means individuals can be  
588 considered as differing in ‘spatial learning rate’ it is important to note that performance declines for  
589 some individuals, especially in the second maze where there was no improvement in average time  
590 across 11 trials. We show here that an individual’s (repeatable) behavioural response to an acute stress  
591 stimulus does not predict either average performance in the maze or learning rate. However, we  
592 suggest the possibility that cumulative, chronic stress effects may contribute to declining performance  
593 (or reduced improvement) in our study. If individuals generally differ in susceptibility to chronic  
594 stress, this may represent a widespread but currently poorly acknowledged challenge for  
595 characterisation of cognitive variation in animal studies.

596

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