A multivariate view of cognitive differences reveals domain-general correlation structure in the Trinidadian Guppy (*Poecilia reticulata*)

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Abstract

Cognitive variation is common among-individuals within populations, and this variation can be consistent across time and context. From an evolutionary perspective, among-individual variation is important and required for natural selection. Selection has been hypothesised to favour high cognitive performance, however directional selection would be expected to erode variation over time. Additionally, while variation is a prerequisite for natural selection, it is also true that selection does not act on traits in isolation. Thus, the extent to which performance covaries among specific cognitive domains, and other aspects of phenotype (e.g. personality traits) is expected to be an important factor in shaping evolutionary dynamics. Fitness trade-offs could shape patterns of variation in performance across different cognitive domains, however positive correlations between cognitive domains and personality traits are also known to occur. Here we aimed to test this idea using a multivariate approach to characterise and test hypothesised relationships of cognitive performance across multiple domains and personality, in the Trinidadian guppy (*Poecilia reticulata*). We estimate the among-individual correlation matrix (**ID**) in performance across three cognitive domains; association learning in a colour discrimination task; motor cognition in a novel motor task and cognitive flexibility in a reversal learning task, and the personality trait 'boldness' measured as time to emerge. We found no support for trade-offs occurring, but the presence of strong positive domain-general correlations in **ID,** where 57% of the variation is explained by the leading eigen vector. While highlighting caveats of how non-cognitive factors and assay composition may affect the structure of the **ID**-matrix, we suggest that our findings are consistent with a domain-general axis of cognitive variation in this population, adding to the growing body of support for domain-general variation among-individuals in animal cognitive ability.

Introduction

Interest in the cognitive mechanisms by which animals acquire, process, store and use information from the environment (Healy et al., 2010; Shettleworth, 2010), has grown substantially in recent years. Differences in cognitive abilities among-species have long been recognised (Shettleworth, 2009; Wasserman et al., 2006), but we now know that variation among-individuals that is consistent across time and context is common in non-human animals (for a review, see Cauchoix et al., 2018). From an evolutionary perspective, variation at this level is required for natural selection and is thus central to our understanding of adaptive evolutionary dynamics (Roff, 2002). However, how or why this variation is maintained within populations is not always clear. For instance, while we might intuitively expect selection to favour high cognitive performance, directional selection of this form is generally expected to erode variation over time. One possibility is that fitness trade-offs could shape patterns of variation in cognition, just as they do in other aspects of phenotype (e.g. life history; Stearns, 1992). If so, do trade-offs arise among different cognitive 'domains' or traits, with variation maintained because individuals (or genotypes) that perform better than average in some respects, perform worse in others? Here we test this idea using a multivariate approach to characterise and test hypothesised relationships of cognitive performance across multiple domains in the Trinidadian guppy (*Poecilia reticulata*). We ask whether there is support for domain-specific correlation structure, where performance is negatively correlated as expected under the trade-off hypothesis. Or whether in fact domain-general correlation structure is present and uniformly positive – a pattern predicted if multivariate cognitive performance variation is explained by a single latent "general intelligence factor" (*g*) (Nisbett et al., 2012).

Many empirical studies have now shown that animal populations can harbour high levels of variation in cognitive performance among individuals (Boogert et al., 2018). This has been shown across taxonomic groups including insects (Li et al., 2017), fish (Lucon-Xiccato & Bisazza, 2017), birds (Quinn et al., 2016) and mammals (Mazza et al., 2019). Among-individual variation is also found across different cognitive domains (e.g. spatial memory (Sonnenberg et al., 2019); association learning (Kniel et al., 2020), problem solving (van Horik et al., 2019)), though relatively few studies have characterised the among-individual covariance (or correlation) structure between these. This is important to do because trade-offs between domains have been hypothesised to maintain cognitive variation (Del Giudice et al., 2018). This hypothesis leads to an

expectation of domain-specific structure of variation, where negative correlation structure is exemplified by predictions of 'speed-accuracy trade-offs' (Biro et al., 2008; Sih et al., 2012). Faster decision making should provide a competitive advantage (e.g. by increasing the potential rate of resource acquisition), but by allowing less time to assess environmental cues, error rates may be increased. In contrast, slower decisions may be more accurate, but being slow to act can mean resources are lost to competitors. A number of empirical studies have provided support for speed-accuracy trade-offs in animals. For example, individual archerfish (*Toxotes chatareus*) that tended to make slower decisions within a colour discrimination task also had greater accuracy (Jones et al., 2020). A similar result was found in zebrafish (*Danio rerio*) given a visual discrimination task (Wang et al., 2015), and in wild-caught great tits (*Parus major*) given a foraging task (Moiron et al., 2016). However, counter examples also exist. For example, a prior study of guppies found no support for a speed-accuracy trade-off using a shape and a colour discrimination task (Lucon-Xiccato, Dadda, et al., 2016), and three-spined sticklebacks (*Gasterosteus aculeatus*) making fast decisions in a spatial leaning task did not show reduced accuracy (Mamuneas et al., 2015).

Another widely hypothesised cognitive trade-off that might maintain variation is between learning and cognitive 'flexibility' (Del Giudice et al., 2018). Flexibility is broadly defined as the ability to adapt when environmental stimuli or information cues change. It is often tested by reversal learning experimental paradigms in which individuals must be flexible to override old cue-reward associations and form new ones (Bitterman, 1965; Buechel et al., 2018; Kehagia et al., 2010). For example, in Florida scrub-jays (*Aphelocoma coerulescens*) individuals that were quick to learn an initial colour-reward cue (high associative learning performance), were slower to adjust when the cue signal was reversed (Bebus et al., 2016). The implication of such patterns is that some individuals are more 'intrinsically driven' than others; they learn initial associations quickly but, being less sensitive to external stimuli, struggle to adapt when cues are altered. However, again counter-examples can be found. For instance, those individual bumblebees (*Bombus terrestris*) that quickly learned to discriminate between two colours (where one was associated with a floral reward), were also faster to learn a new association when the cues were reversed (Raine et al., 2012).

Thus, while trade-off among components of 'multivariate' cognitive ability are intuitive and evidenced in many cases, they may not be inevitable and positive correlations between specific domains are

88 sometimes found (Guenther et al., 2017; Wallace et al., 2021). If correlation structure among cognitive
89 performance traits is universally positive (with respect to expected fitness consequences), then variation
90 among individuals can be explained by a domain-general structure that invokes a single latent general
91 intelligence factor, sometimes denoted '*g*' (Deaner et al. 2006; Lefebvre and Sol 2008). While there is
92 evidence for this in humans (Burkart et al., 2017; Deary et al., 2010), support for the *g*-model in non-human
93 animals systems remains limited (but see Arden et al., 2016; Galsworthy et al., 2005; Hopkins et al., 2014;
94 Shaw et al., 2015). Note that, under this model, trade-offs may still be important for maintaining cognitive
95 variation, but if so they must operate between general intelligence and other (non-cognitive) aspects of
96 phenotype. This possibility is mirrored elsewhere in the behavioural literature since for example, individual
97 personality can be viewed as a component of an extended 'life history' (Sih et al., 2004; Wolf et al., 2007).
98 Indeed, given that personality traits and cognitive performance are frequently correlated (Guenther et al.,
99 2014; Nawroth et al., 2017; White et al., 2017), and both thought to drive variation in resource acquisition,
100 then trade-offs between them are plausible (Dougherty et al., 2018; Sih et al., 2012).

101 Here, we investigate among-individual (co)variation between cognitive performance across three
102 cognitive domains (associative learning, motor cognition and cognitive flexibility) in a captive population of
103 wild-type guppies (*Poecilia reticulata*). Guppies have been widely used as a model in behavioural and
104 evolutionary ecology, and methods for assaying among-individual variation in cognitive performance are well
105 established (Laland et al., 1999; Miletto Petrazzini et al., 2016). This species is known to perform well (on
106 average) in tests of associative learning (Kniel et al., 2020; Lucon-Xiccato & Bisazza, 2016), motor cognition
107 (Lucon-Xiccato, Gatto, et al., 2017; Lucon-Xiccato & Bisazza, 2016), and cognitive flexibility (Cauchoix et al.,
108 2018; Fong et al., 2019). However we know little about if and how these traits may covary among individuals
109 within populations. Broadly stated, our goal is to estimate the structure of this multivariate variation to
110 evaluate whether trade-offs among cognitive traits are evident, or whether among-fish variation is consistent
111 with a domain-general intelligence model (*g*).

112 We note that the extent to which among-trait associations shape, and in the particular context of
113 trade-offs, constrain evolutionary adaptation strictly depends not on the phenotypic correlation structure,
114 but on the genetic contribution to this. In particular, evolutionary constraint arises from the genetic

115 (co)variance structure (**G**) and its alignment (of lack thereof) with selection (A. G. Jones et al., 2004; Lande,
116 1979; Walsh et al., 2009). Unfortunately estimation of **G** is challenging in general (requiring large volumes of
117 data from related individuals; Wilson et al., 2010), and particularly so for cognitive traits. This is because high-
118 throughput phenotyping of cognitive performance across multiple domains is notoriously laborious and
119 challenging. Consequently, very few studies have estimated **G** for sets of cognitive traits in non-human
120 animals (but see Langley et al., 2020). Thus most multivariate studies of cognition, and behavioural
121 phenotypes more generally, rely on Cheverud's conjecture (Cheverud, 1988) that phenotypic patterns of
122 covariation can be used to infer evolutionarily important relationships between traits. Accepting this view
123 uncritically implies that the (co)variance structure of the phenotypic matrix **P** (historically referred to as the
124 phenotypic gambit by Grafen (1984)), which can be readily estimated in a set of individuals observed once
125 only for each of the target traits, can yield robust insights into the structure of **G**. However, behavioural traits
126 are typically very plastic and often subject to high levels of measurement error (e.g. relative to morphological
127 traits), in addition to sources of environmental variation. These phenomena lead to high levels of within-
128 individual variation such that a single observation may tell us relatively little about an individual's phenotype
129 (and so genotype) (Brommer, 2013). In other words, the extent to which **P** is a good proxy for **G** will decline
130 if **P** is dominated by within-individual variation (plasticity, measurement error) versus among-individual
131 variation (which includes genetic factors).

132 In the present study we therefore adopt an intermediate approach in which we estimate the among-
133 individual (co)variance matrix (**ID**) rather than either **G** or **P**. We do this by obtaining repeated measures of
134 performance on individual fish. Since **G** is a component of **ID** while **ID** is a component of **P**, all else being equal
135 we expect the among-individual covariance matrix to be better proxy of the genetic matrix than the total
136 phenotypic matrix. We target multiple domains of cognitive performance allowing us to 1) test whether
137 individuals differ in their ability to discriminate between rewarded and unrewarded colours in an association
138 learning task; 2) ask whether speed accuracy trade- offs mediate variation in performance in the association
139 task; 3) ask if individuals differ in performance in a novel motor task to access a reward; and 4) test whether
140 individuals differ in their ability to learn a reversal learning task when the colour-reward cue from the
141 association task is reversed. We predict that individuals will differ in average performance within all three

142 tasks; the association task, the novel motor task, and the reversal learning task as well as in their rates of
143 improvement with experience (interpretable as learning). Finally, we 5) estimate the **ID**-matrix among all
144 cognitive performance traits and a shy-bold type personality trait (henceforth referred to as 'boldness') and
145 ask whether it provides evidence for trade-offs among cognitive domains or whether it is dominated by
146 positive correlations consistent with the *g*-model of domain-general intelligence.

147 **Methods**

148

149 *Ethics*

150 This work was conducted under the auspices of the Animals (Scientific Procedures Act) with approval of the
151 University of Exeter research ethics committee, under licence from the Home Office (UK) (Licence Number
152 PPL30/3256). Experimental procedures and behavioural assays were developed in accordance with the
153 principles of the three R's and ASAB guidelines (Buchanan et al., 2020) for use of animals. All periods of
154 handling and emersion were kept to a minimum and only fish deemed healthy and exhibiting normal
155 behaviour were used in trials. At the end of the experiment, fish were returned to a designated 'retirement'
156 tank (containing females as well as males) and not used in any further experiments.

157

158 *Husbandry*

159 All behavioural assays were carried out during the months between October 2019 and January 2020. Data
160 was collected from captive-bred guppies bred and housed at the fish laboratory at the University of Exeter's
161 Penryn campus. The population is descended from wild fish caught in February 2017 from the lower Aripo
162 River, Trinidad and has been subsequently maintained with no deliberate selection or inbreeding. All fish
163 housed in the laboratory were fed to satiation twice daily (0800 – 1000h and again at 1600 – 1800h) using
164 commercial flake food and live *Artemia nauplii*. Water temperature was maintained at 23-24°C in well-
165 aerated closed system tank stacks that undergo 25% water changes each week and with weekly tests for
166 ammonia, nitrate and nitrite levels. Lighting was kept at a 12:12 light/dark cycle.

167

168 *Experimental apparatus*

169 Adult males (n = 43) and females (n = 37) were sampled from the stock population. Sampling was haphazard
170 but we approximately size matched fish within each sex (e.g. by avoiding very large females). Fish were then
171 housed singly in separate tanks (15 l, 18.5 × 37 × 22cm) for the duration of behavioural testing. The tank set
172 up closely followed that used by Lucon-Xiccato & Bisazza (2014), each being divided equally into a 'home'
173 compartment at the rear of the tank, and a 'test' compartment at the front of the tank, separated into two

174 compartments (using white plastic) by a guillotine door (Figure 3.1). The rear 'home' compartment (20 x 18.5
175 cm) allowed individuals visual access to fish in neighbouring tanks. Conversely, the 'test' compartment (17 x
176 18.5 cm) was screened from neighbours (using white plastic) to prevent any possibility of social learning (i.e.
177 by observation of neighbours) influencing cognitive task performance. The 'test' compartment contained a
178 white plastic plate (4 x 10 cm) placed on the gravel substratum, perforated with 2 equally spaced wells (Figure
179 3.1). A total of 48 experimental tanks were used. These were contained within two 'stacks', each comprising
180 24 tanks (8 tanks per row, 3 rows high) on a shared recirculating water supply. As the testing protocol
181 (described below) took 18 days per fish, data were in practice collected in 3 'blocks' over a total testing period
182 spanning 12 weeks. Before cognitive testing all fish were allowed to acclimate to experimental tanks for 48
183 hours. During this period they were fed twice daily with bloodworm (*Chironomidae* larvae) pipetted into one
184 (randomly chosen) well of the white plastic plate and the guillotine door was left open allowing unrestricted
185 use of both compartments.
186
187 *Cognitive assay*
188 We used a repeated measures design to test performance across multiple cognitive domains within a single,
189 extended, testing paradigm. Each fish was observed up to 63 times as it emerged from the home
190 compartment to obtain a food item that had been placed in one of the two wells in the test compartment.
191 Individual fish were trained to discriminate between a rewarded and an unrewarded colour cue, indicating
192 which well the reward could be obtained from. In all trials, food items (bloodworms) were actually placed in
193 both wells, but access was restricted by a small plastic disc for the well with the unrewarded colour cue. This
194 was to ensure that olfactory cues would be insufficient to locate available food, instead fish were required
195 to learn to associate a specific colour with reward access. The rewarded colour (either blue or green) was
196 randomly determined for each fish prior to testing, ensuring balance across subjects to control for any innate
197 colour bias. The relative position of the rewarded well (left versus right) for each trial was randomised and
198 we also controlled for any effect this could have in our statistical modelling (described later).
199 The 63 observations per individual were grouped into 7 'sets' of 9 'trials' (observations). Each set
200 spanned a 2 day period which was followed by a rest day before the next set. Test condition were altered

201 between trial sets, by adjusting the position of green and blue coloured plastic counters. Specifically, after
202 each set, the association task increased in difficulty as the coloured counter covered the holes to an
203 increasing extent. This also allowed extraction of information on different cognitive traits as we now describe.
204 In set 1, the coloured counters covered 0% of the wells, in set 2 we increased this to 25%, then subsequently
205 this was increased to 50% (set 3), 75% (set 4) and 100% (set 5). Once the counters covered 75% of the wells
206 (set 4), guppies had to dislodge the counters in order to reach the reward in the well underneath. We consider
207 this a novel motor task, as fish had to learn to dislodge the counter by physical manipulation. The difficulty
208 of this task is increased with 100% coverage (set 5). In the final two sets (set 6 and 7) of 9 trials we tested
209 reversal learning task, by reversing the colour cue -food reward association previously learnt in the first 5
210 sets.

211 Prior to each trial, fish were guided into the 'home' compartment of the tank with a net, and the
212 guillotine door was closed. The experimenter set up the test plate which was situated in 'test' compartment,
213 by pipetting bloodworm into the wells in the plate (the food in the unrewarded hole was then covered by a
214 small plastic disc), and the two coloured counters placed either to the side of (set 1), or covering the well
215 (partially or fully depending on set number as described). The trial started once the door to the experimental
216 compartment was opened and continued until the fish ate the bloodworm from the rewarded well, or after
217 10 minutes, whichever occurred first (see the electronic Supplementary Material, video S1, Appendix 1). All
218 trials were recorded with a GoPro Hero 6 camera, mounted in front of the tank and behavioural scoring of
219 videos was quantified using the software BORIS (Friard et al., 2016). We imposed a deliberately weak learning
220 criterion, removing any fish that failed to achieve a minimum of 5/9 successes (defined as locating and/or
221 eating the food reward) at the end of each set. In fact, we wished to avoid selective removal of fish as far as
222 possible such that, for example, among-individual variation seen in later sets can be interpreted as
223 representative of the initial population. However, correlations between task performance may be
224 confounded if the ability to solve each task is closely associated with the number of learning opportunities
225 (Guez et al., 2016; Shaw et al., 2017). Differences, for example in motivation or neophobia, could mean some
226 individuals engage with and solve the task each trial, while others do not (despite persistently trying to find
227 a solution or because they do not engage with the task at all). In this way, individual participation directly

228 influences the number of learning opportunities. Removal of fish that did not complete the task (by locating
229 and eating the food reward) ensured data was collected in subsequent set of trials, only from individuals that
230 had the same number of learning opportunities, thus reducing the possibility of confounding correlations in
231 performance caused by differences in e.g. motivation or neophobia for example. Furthermore, since
232 additional food (beyond the reward items) was not provided during the behavioural testing, the learning
233 criterion also ensured that individuals not engaging with the task were not deprived of food for any longer
234 than 2 days before being removed from the study. Over the course of the data collection, 16 individuals were
235 removed before the end of set 6.
236
237 *Trait definition*
238 Data obtained from the trial sets were used to define observed proxies of one personality trait (*boldness*)
239 and 6 measures of cognitive performance that are collectively informative for 3 cognitive domains
240 (*association learning, motor cognition, and cognitive flexibility*). The specific measures derived are described
241 below and also summarised for reference in Table 3.1.
242
243 <u>Boldness</u>
244 During the first nine trials (set 1), time taken to emerge from the home compartment into the experimental
245 compartment was recorded (*emergence*), as a proxy of consistent differences in personality trait 'boldness'
246 (White et al., 2016; White et al., 2020).
247
248 <u>Association learning</u>
249 We also focused on set 1 trials to test for speed-accuracy trade-offs, expecting that (on average) fish would
250 have effectively learnt the association in later sets making the speed accuracy trade-offs less relevant to
251 observed outcome. We recorded three behavioural variables. The first was whether the first counter
252 explored was the correct (1) or incorrect (0) choice for obtaining the reward ($AL_{accuracy}$). A choice was deemed
253 to have been made if individual fish swam within 1 body length of, and was actively exploring a counter. The
254 second variable was time taken to make this first choice (AL_{speed}), measured in seconds from emergence into

255 the test compartment. To evaluate overall performance in association learning, we used total time taken
256 from emergence to find and eat the food reward. We did this using all observations from all trials in sets 2
257 and 3 (AL_{time}). During these sets of trials, the counters covered 25% and 50% respectively, a level of coverage
258 that still allowed fish to access the reward easily without any physical manipulation of the counter required.
259
260 Motor Cognition
261 To assess performance in the novel motor task, we used observations from trials insets 4 and 5 (where the
262 counter covered 75% and 100% of the well area respectively). Note that at 75% coverage fish were required
263 to physically manipulate the counter in order to reach the food reward. We used time taken by each
264 individual in all trials to obtain and eat the food reward (MC_{time}). Note this was measured as time taken to
265 obtain the food reward after they had made the correct choice of counter in each trial.
266
267 Cognitive flexibility
268 This was assessed using observations from all trials in set 6 and 7, during which the reward colour was
269 reversed. Note that counter coverage of the wells remained at 100% so fish needed to dislodge the counter
270 in order to access the reward. For this reversal learning task we recorded the accuracy of each individuals'
271 first choice, ($RL_{accuracy}$) as well as the time taken, from emergence into the test compartment, to locate and
272 eat the food reward (RL_{time}).
273
274 *Statistical analysis*
275 We used univariate and multivariate linear mixed effect models to characterise among-individual variation
276 in and covariation among the traits defined. For analysis, the observed (censored) time traits from the
277 cognitive tasks were natural log-transformed (AL_{speed}, AL_{time}, MC_{time} and RL_{time}), and then all continuous time
278 traits were multiplied by -1 (*boldness*, AL_{speed}, AL_{time}, MC_{time} and RL_{time}). Following this, all response variables
279 were mean centred and scaled to standard deviation units. The log transformation was to improve the
280 assumption of Gaussian error structure, multiplication by -1 for ease of interpretation of multivariate analysis
281 (so that larger values equate to higher performance in continuous traits), and scaling to standard deviation

units was to ease interpretation of estimated variance components. All models were fit by REML (restricted maximum likelihood) using ASReml-R 4.1 (Butler et al., 2018; Gilmour et al., 2009) within R version 3.6.1 (R Core Team, 2017). We make the standard assumptions that random effects and residuals are normally distributed with means of zero and variances to be estimated. We acknowledge that these assumptions are necessarily violated since the two accuracy traits are recorded as binary variables, while time data are censored (at 10 minutes). Consequently, we consider this strategy justifiable given that Gaussian mixed models are generally robust to violations of distributional assumptions (Schielzeth et al., 2020). Pragmatically, we also note that the obvious alternative of fitting Bayesian multivariate generalised mixed models poses its own challenges.

Univariate analysis

First we fitted separate univariate mixed models to test for and characterise among-individual variation in each of our 7 traits (*boldness*, AL_{speed}, $AL_{accuracy}$, AL_{time}, MC_{time}, RL_{time} and $RL_{accuracy}$). All models included a fixed effect of the mean, as well as fixed factors of *sex*, *stack* (denoting which of two aquaria stacks the fish was tested in), *colour* (denoting the colour of counter individual fish were trained to associate with the rewarded cue; green or blue), and *reward side* (denoting which side the rewarded counter was placed on; left or right). We also included *trial number* (i.e. the repeat number of trial, fitted as a factor to avoid assuming a linear functional form for any change in the mean across repeats). For each trait, we firstly fit this 'null' model without random effects, and then refitted with *individual identity* as a random intercept. For each trait we compared the full (i.e. with *individual identity* included) and null models by likelihood ratio tests (LRT) to obtain a statistical test of the among-individual variance (V_I). To test a single variance component (which cannot be less than zero) we assume twice the difference in log-likelihood between the full and reduced models is distributed as a 50:50 mix of $\chi^2_{0,1}$ and χ^2_1 as recommended by Visscher (2006). Since transformed traits are analysed in standard deviation units, total observed variance is 1 and V_I can actually be interpreted as an estimate of repeatability. However, we also calculated estimates of the adjusted repeatability (R) which is the proportion of phenotypic variance conditional on fixed effects that is explained by among-individual differences (Nakagawa et al., 2010). Thus $R = V_I / V_P$ where V_I is the among-individual variance and V_P is sum

309 of V_I and V_R, the residual or within-individual variance. Conditional F-statistics were used to determine the
310 significance of fixed effects in each (full) model, and we elected not to perform model simplification, as we
311 wanted repeatability estimates to be conditioned on a common set of fixed effects and thus comparable
312 across abilities.
313
314 Multivariate analysis
315 To test for the presence of, and investigate the structure of, the (co)variance **ID**-matrix, we built a
316 multivariate mixed model among all cognitive performance traits and 'boldness'. All response variables were
317 transformed and scaled as per the univariate modelling procedure above, and we note that multiplication by
318 -1 of all the observed (censored) time traits simplified interpretation of the correlation structure (as larger
319 values equate to higher performance in continuous traits). Fixed and random effects were fitted on each trait
320 as specified for the univariate models. Fixed effects estimates are reported in the Supplementary Information
321 Table S3.1, Appendix 3. We specified the among-individual (V_I) covariance structure as an unstructured
322 matrix to be estimated. Note that R partitions observation-level covariances that are not statistically
323 identifiable if traits are not measured at the same time (i.e., all covariances between traits measured in
324 distinct 'sets' of trials). Where this was the case we constrained specific covariance terms in the residual (V_R)
325 matrix to equal zero. We tested for overall among-individual covariance among the traits by comparing this
326 model against a reduced one in which **ID** was specified as a diagonal matrix (i.e., among-individual variances
327 are estimated but covariances are assumed to equal zero).
328 To aid biological interpretation of the **ID**-matrix, we rescaled our estimate to the corresponding
329 correlation matrix in which off diagonal elements are the among-individual correlations (r_I) between each
330 pair of traits. For any pair of traits (x,y), $r_{I(x,y)} = COV_{I(x,y)} / (V_{I(x)}V_{I(y)})^{0.5}$). We then further scrutinised the
331 correlation structure among the cognitive traits only by dropping the row/column corresponding to boldness,
332 and subjecting the resulting 6x6 submatrix, henceforth denoted $\mathbf{ID_{rc}}$ (using rc to denote correlation scale (r)
333 and cognitive traits (c)) to eigen vector decomposition. This simply provides a descriptive view of the major
334 axes (or principle components) of variation in $\mathbf{ID_{rc}}$ allowing us to determine the proportion of among-
335 individual correlations captured by each principal component. Under the *g* model, we would expect

336 uniformly positive correlation structure in $\mathbf{ID_{rc}}$ with a single major axis of variation on which all traits loaded
337 with the same signs. Conversely, if trade-offs dominate the structure of among-individual variation in the
338 multivariate cognitive phenotype $\mathbf{ID_{rc}}$ should contain at least some negative correlations and the one or more
339 important principle component should have loadings that are antagonistic in sign between traits that trade-
340 off with each other. We estimated approximate 95% confidence intervals on the eigen values (scaled to
341 proportions of variation in the matrix) and on the trait loadings associated with each principal component
342 using a parametric bootstrap approach described in Boulton et al (2014).
343

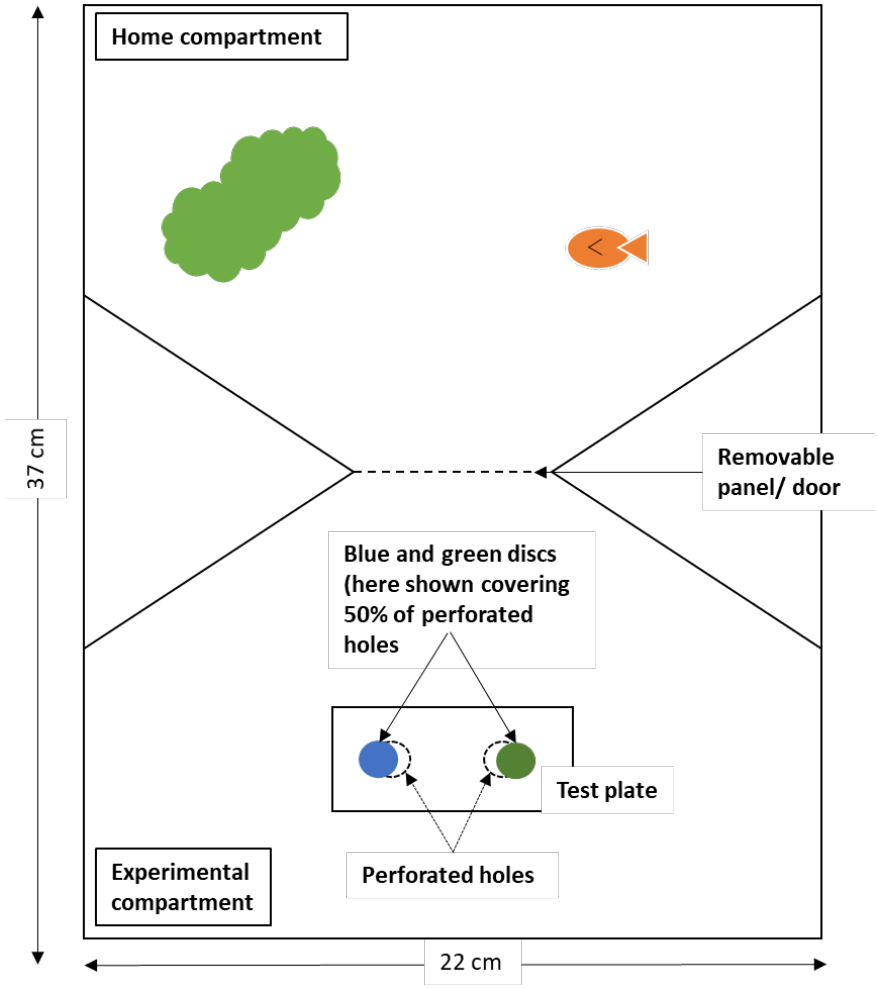

Figure 1. Aerial view of the home tank used to house individual fish, showing the experimental compartment and test plate used during each task.

348 **Table 1**. Outline of behaviours used to assess performance within each putative cognitive domain,
349 including details of corresponding set number at which each trait was measured and corresponding
350 acronyms used within the text.
351

Set Number	Cognitive/ Behavioural Domain	Trait	Acronym
1	**Boldness**	Time to emerge (Time taken to emerge into the test compartment once the compartment door is opened)	*emergence*
1 – 3	**Association learning**		
(*1*)	Speed accuracy trade-offs	Decision speed (After emergence into test compartment, time taken to make first choice, measured as swimming within 1 body length of, and actively exploring correct counter.)	AL_{speed}
		Decision accuracy (Decision of first choice, choice measured as swimming within 1 body length of, and actively exploring correct counter. Either correct or incorrect)	$AL_{accuracy}$
(*2,3*)	Performance	Time to eat (After emergence into test compartment, time taken to eat reward from the correct well)	AL_{time}
4, 5	**Motor cognition**	Time to eat (After correct choice made (i.e. swimming within 1 body length of, and actively exploring correct counter), time taken to dislodge counter and eat the food reward)	MC_{time}
6, 7	**Cognitive flexibility**	Time to eat (After emergence into test compartment, time taken to dislodge disc and eat reward from the correct well)	RL_{time}
		Decision accuracy (Decision of first choice, choice measured as swimming within 1 body length of, and actively exploring correct counter. Either correct or incorrect)	$RL_{accuracy}$

352

353

354 **Results**

355

356 Visualisation of the raw data shows a varied effect of trial number on performance across traits and cognitive
357 tasks (Figure 3.2; see Supplemental Information Figure S3.1 *a–g* of raw data across all sets of trials). Average
358 time to *emergence* (boldness) decreased over the first 9 trials but time-based measures of cognitive
359 performance did not uniformly improve over the sets of trials used to assay them, as might intuitively be
360 expected (Figure 3.2). Note however that for AL_{time} and MC_{time} the sets of 18 informative trials include an
361 increase in task difficulty (between trials 9 and 10). There was no increase in task difficulty over the 18
362 informative trials for the trait RL_{time} anda negative (albeit weak) trend is seen, indicative of improving
363 performance. In the association learning task, AL_{speed} and $AL_{accuracy}$ increased over the first set of trials, similar
364 to $RL_{accuracy}$ in the reversal learning task which also increased with trial number over the set of trials used to
365 assay this trait. The univariate mixed models confirmed the statistical significance of qualitative patterns seen
366 in the raw data with respect to changes across trials (see Supplementary Information Table S3.1 *a–g)*. Noting
367 that models were run on transformed traits such that positive effects correspond to increasing performance
368 (i.e. decreasing time) and that *trial number* was fitted as a factor to avoid assuming linear trends, we found
369 effects on *emergence* ($F_{8, 555.7}$=9.24, P< 0.001; with coefficients becoming more positive as *trial number*
370 increased; Table S2.1)*,* AL_{time} ($F_{17, 801.9}$=2.246, P=0.002; with coefficients becoming more negative)*,* AL_{speed} ($F_{8,}$
371 $_{555.0}$=7.380, P< 0.001; with coefficients becoming more positive)*,* $AL_{accuracy}$ ($F_{8, 555.0}$=4.602, P< 0.001; with
372 coefficients becoming more positive), MC_{time} ($F_{17, 692.6}$=1.174, P< 0.001; coefficients becoming more negative).
373 The effect of *trial number* on (mean) performance was not significant in RL_{time} ($F_{17, 581.2}$=1.565, P= 0.060) and
374 $RL_{accuracy}$ ($F_{17, 584.2}$=1.085, P= 0.271). The significance and magnitude of all other fixed effects included varied
375 across trait performances. These effects are not directly relevant to hypotheses being tested and we do not
376 discuss them further, but they are reported in full in the supplemental information (see Supplementary
377 Information Table S3.1). Likelihood ratio tests (LRT) provided strong statistical support for the presence of
378 among-individual variance in all seven traits tested (LRT of model 1 vs. model 0; all P < 0.001; Table 3.2).
379 Repeatabilies (R) estimated conditional on fixed effects (i.e. as $R = V_I/V_P = V_I/(V_I+V_R)$) were low to moderate
380 ranging from 20-46% with a median across the seven traits of 33.5% (Table 3.2).

381 The multivariate mixed model provided strong support for significant among-individual covariance
382 in the **ID**-matrix. Likelihood ratio comparison of the full model to a reduced fit in which all cross-trait
383 covariances in **ID** were set to zero showed the former was a significantly better to fit to the data
384 ($\chi 2_{21}$=242.756, P<0.001). Among traits, the estimated covariances/correlations were positive between all
385 trait pairs (Table 3.3). Boldness, as captured by *emergence* was strongly (and significantly; based on assuming
386 approximate 95% CI of r_I ±1.96 SE) correlated with cognitive performance as measured by all traits in the
387 association learning task ((r ± (SE)), AL_{time} = 0.663 (0.095), ALspeed = 0.818 (0.046), ALaccuracy = 0.788
388 (0.062); Table 3.2), and to decision accuracy within the reversal learning task ($RL_{accuracy}$ = 0.412 (0.171)).
389 Among the subset of 6 cognitive traits all estimated among-individual correlations (r_I) were positive
390 (Table 3.3). Among-individual correlations were strongly positive among all traits in the association task
391 ($r_{ALtime.\ ALspeed}$ = 0.758 (0.074); $r_{ALtime.\ ALaccuracy}$ = 0.729 (0.092); $r_{ALspeed.\ ALaccuracy}$ = 0.894 (0.039)) providing no
392 support for a speed accuracy trade-off. Similarly both traits in the reversal learning task ($r_{RLtime.\ RLaccuracy}$ =
393 0.473 (0.144)) were positively correlated, and this same pattern of positive correlations was also found across
394 traits putatively indicative of different cognitive domains. There was thus no evidence of negative
395 correlations as predicted by domain-specific trade-offs and rather the structure of **ID** is consistent with the
396 domain-general intelligence model (Table 3.3).
397 Eigen decomposition of $\mathbf{ID_{rc}}$ reflects this, with the first major axis (first principle component, PC1,
398 with 95% confidence intervals from 5000 bootstrap replicates) explaining 57.1% (42.7%, 69.8%) of the
399 among-individual variation in multivariate phenotype on a correlation scale. Subsequent vectors necessarily
400 explain sequentially diminishing amounts of variation (PC2 = 25.4% [12.6, 30.9]; PC3 = 12.1% [7.4, 15.6]; PC4
401 = 3.7% [4.7, 9.9]; PC5 = 1.6% [0.8, 5.5]; PC6 > 0.001% [0, 0]). All 6 cognitive traits load with the same sign on
402 PC1 and these loadings are statistically significant based on bootstrapped confidence intervals not
403 overlapping zero (Figure 3.3; Supplementary Information Table S3.2). Thus the eigen decomposition
404 reiterates the view that the correlation structure is consistent with a dominant axis of among-individual
405 variation in cognitive phenotype caused by differences in underlying domain-general intelligence *g*. On this
406 axis, individuals at one end of the axis can be considered to have 'higher/better' performance in all tasks (i.e.
407 are faster and more accurate in the association task, faster to solve the motor cognition task, and faster and

more accurate in the reversal learning task when the cue is reversed), while individuals at the other end perform relatively poorly in all respects.

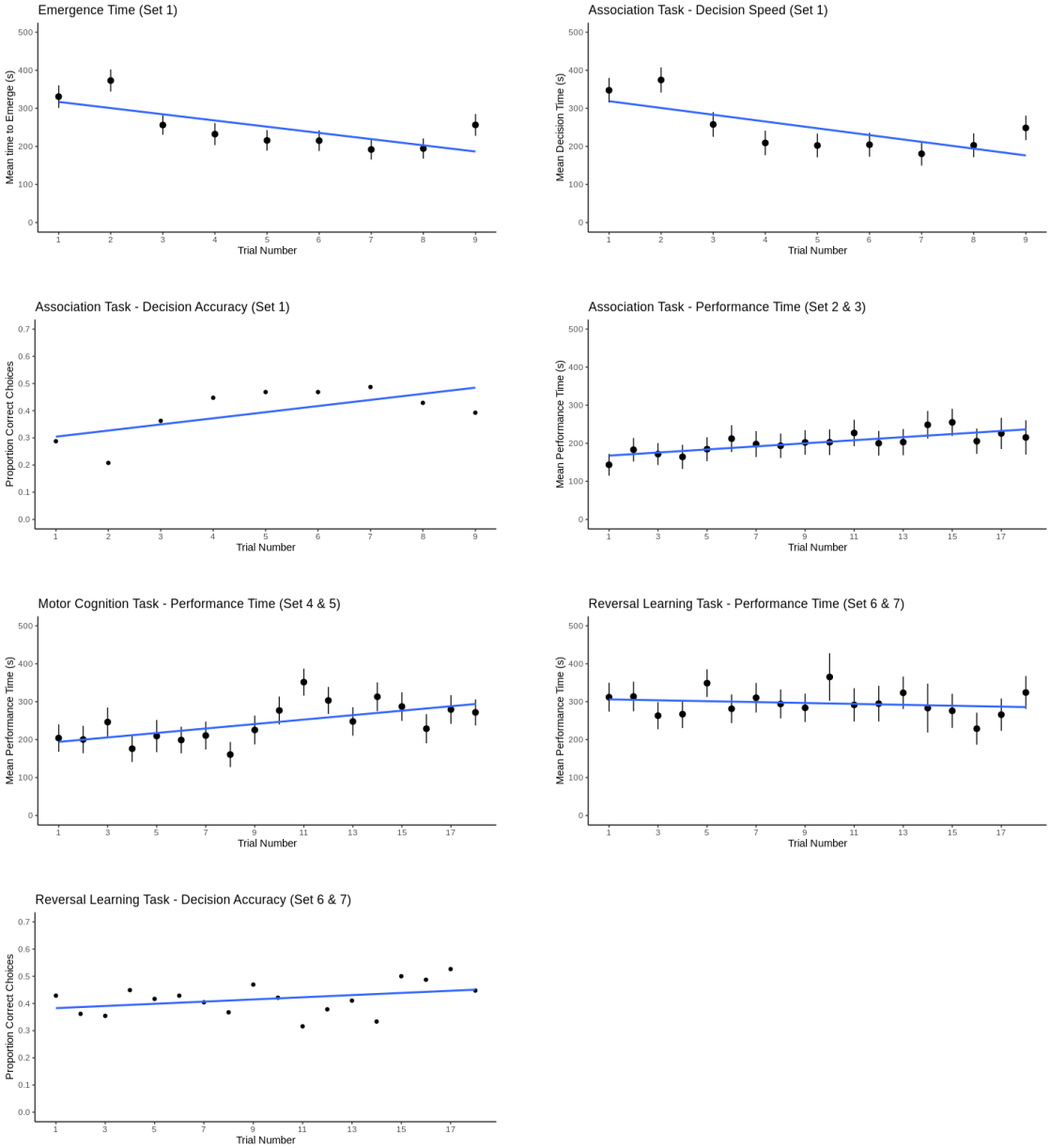

Figure 2: Plots of raw data of total performance time across outlined sets and trials used to assay each trait. Emergence time (*emergence)*, association learning task performance time *(*AL_{time}), association learning decision speed (AL_{speed}) and accuracy ($AL_{accuracy}$), motor cognition task performance time (MC_{time}), reversal learning task performance time (RL_{time}) and accuracy ($RL_{accuracy}$). Error bars represent mean and standard errors of performance time for individuals. Blue line represents regression line through mean performances at each trial.

423 **Table 2:** Estimated among-individual variance (V_I) and adjusted repeatability (R) from univariate models of
424 all traits. Standard errors are shown in parentheses. Also shown are likelihood ratio tests of V_I.
425

Cognitive Domain	Trait	V_I	R	$X^2_{0,1}$	P
Personality - Boldness	*emergence*	0.415 (0.077)	0.439 (0.049)	206.004	<0.001
Associative Learning	AL_{speed}	0.442 (0.081)	0.460 (0.049)	220.393	<0.001
	$AL_{accuracy}$	0.202 (0.045)	0.264 (0.046)	79.989	<0.001
	AL_{time}	0.341 (0.074)	0.335 (0.050)	186.345	<0.001
Motor Cognition	MC_{time}	0.275 (0.065)	0.329 (0.054)	171.462	<0.001
Reversal Learning	RL_{time}	0.372 (0.088)	0.375 (0.058)	178.426	<0.001
	$RL_{accuracy}$	0.182 (0.050)	0.203 (0.047)	65.327	<0.001

426

Table 3. ID variance–covariance–correlation matrix from the multivariate mixed model. Estimated variances are shown on the diagonal (dark grey shading), with correlations above and covariances below. Standard errors are shown in parentheses, and bold font denotes nominally significant estimates assuming approximate 95% CI of ± 1.96SE.

ID Matrix	*emergence*	AL_{speed}	$AL_{accuracy}$	AL_{time}	MC_{time}	RL_{time}	$RL_{accuracy}$
emergence	**0.426 (0.0773)**	**0.818 (0.046)**	**0.788 (0.062)**	**0.663 (0.095)**	0.239 (0.164)	0.166 (0.176)	**0.412 (0.171)**
AL_{speed}	**0.361 (0.072)**	**0.458 (0.082)**	**0.894 (0.039)**	**0.758 (0.074)**	0.271 (0.155)	0.228 (0.169)	**0.397 (0.168)**
$AL_{accuracy}$	**0.242 (0.052)**	**0.285 (0.056)**	**0.221 (0.046)**	**0.729 (0.092)**	0.124 (0.175)	0.090 (0.184)	0.258 (0.190)
AL_{time}	**0.286 (0.072)**	**0.340 (0.076)**	**0.227 (0.055)**	**0.437 (0.092)**	**0.747 (0.082)**	**0.540 (0.129)**	**0.423 (0.161)**
MC_{time}	0.092 (0.067)	0.108 (0.067)	0.034 (0.049)	**0.291 (0.075)**	**0.346 (0.078)**	**0.817 (0.067)**	**0.340 (0.167)**
RL_{time}	0.074 (0.082)	0.106 (0.083)	0.029 (0.060)	**0.246 (0.085)**	**0.331 (0.083)**	**0.474 (0.112)**	**0.473 (0.144)**
$RL_{accuracy}$	**0.122 (0.060)**	0.122 (0.061)	0.055 (0.043)	**0.127 (0.059)**	0.091 (0.051)	**0.148 (0.062)**	**0.205 (0.056)**

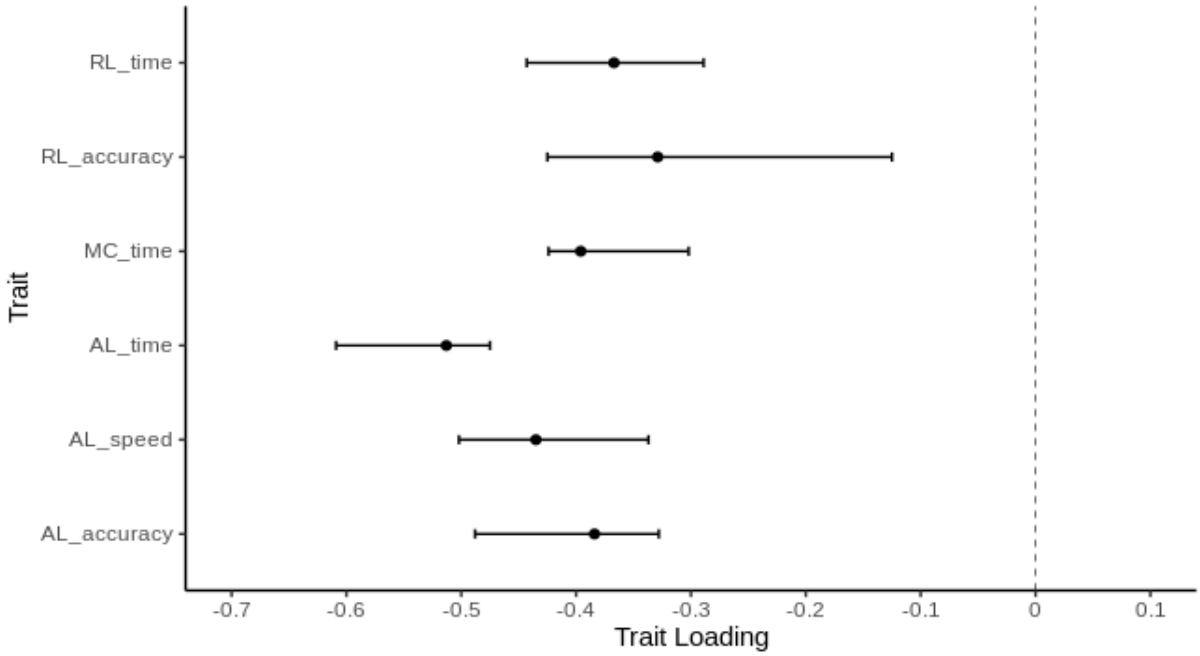

Figure 3: Trait loadings from the first eigen vector (principal component, PC1) of the **ID**-matrix. This axis explains 57.1% of the among-individual (co)variation found in the components of the cognitive phenotype in our guppy population. Points show trait loadings from the first eigen vector of our estimate of **ID**, with bars representing 95% confidence intervals on each loading (calculated from 5000 bootstrapped replicates of the model)

Discussion

In this study we sought to determine whether – and to what extent – there exists among-individual variation for cognitive performance in a captive population of recently wild-derived guppies. Adopting a multivariate approach allowed us to test for covariation among multiple cognitive domains, as well as between cognitive performance and a shy-bold type axis of personality variation. Our study yields three main findings. First, there is among-individual variation underpinning all cognitive traits. Second, there is strong among-individual correlation structure among cognitive traits and between cognition and bold type personality. Thirdly, the structure of **ID**-matrix provides no support for the presence of important performance trade-offs among specific traits or cognitive domains tested. Rather we suggest that it is consistent with a single axis of domain-general variation that causes positively correlated performance across cognitive tasks, such that individuals at one end of the axis can be considered to have relatively low 'general intelligence' compared to those at the other end of the axis. The structure of **ID**-matrix is therefore consistent with expectations under the *g*-model, although it is important to acknowledge that other latent factors could exist that create similar expectations of covariation among observed behaviours. In what follows, we discuss these findings in the context of understanding variation in, and evolution of, animal cognition, while also drawing attention to important assumptions and caveats underpinning our conclusions.

Among-individual variation was found in each of the behavioural traits and tasks examined. That guppies show consistent among-individual differences in 'boldness', as measured here by time to emerge into the test compartment over the first set of 9 trials (with a conditional repeatability of 43.9%) was expected given earlier studies of this population (e.g. Houslay et al., 2019) and guppies more generally (Brown et al., 2014; O'Neill et al., 2018; Gasparini et al., 2019). Indeed similar findings are common across a wide range of fish models used in behavioural studies (Boulton et al., 2018; White et al., 2020). We also find among-individual variation in performance in all cognitive traits across each task. Thus, we conclude that individuals differ in: ability to discriminate between rewarded and unrewarded colours in an association learning task; ability to learn a novel motor task; and, in cognitive flexibility as tested by a reversal learning task. The estimated repeatabilities of our observed behavioural proxies are moderate relative to behavioural traits generally (Bell et al., 2009), but generally consistent with reports for cognitive assays in animals

466 (Cauchoix et al., (2018)). A contributing factor is likely to be the short inter-observation period used. Here
467 this was usually less than 24hrs and in fact up to 9 observations were made in any single 48hr period. This
468 sampling frequency is quite typical for cognitive studies, and the short intervals between trails may explain a
469 decrease in performance due to reduced motivation. Furthermore, since behavioural repeatabilities
470 generally decline as inter-observation period increases (Boulton et al., 2014), this may also partially explain
471 the strong signal of repeatability.

472 Our multivariate modelling provides no support for trade-offs among cognitive traits. This conclusion
473 stems from the finding that the correlation structure in **ID** is universally positive. Thus, for example, speed-
474 accuracy trade-offs are not detected in our association learning trials. Speed-accuracy trade-offs are widely
475 predicted to arise where behavioural outcomes depend on cognitive decision making (Briffa, 2013), although
476 this prediction assumes that faster decisions are better (all else being equal). They have been detected in
477 some animal studies, for instance in Carib grackels (*Quiscalus lugubris*) where individuals that solve novel
478 problems faster also make more errors in discrimination learning tasks (Ducatez et al., 2019). Here we
479 actually find the opposite pattern, faster individuals are more accurate, a result that seems counterintuitive
480 but is consistent with reports in song sparrows (*Melospiza melodia*; (Boogert et al., 2011), and bumblebees
481 (*Bombus terrestris;* Raine, 2012). We note that the correlation structure of behavioural **ID**-matrices can be
482 sensitive to environmental context (Houslay et al., 2018) as a consequence of IxE interactions (among-
483 individual differences in plasticity; Nussey et al., 2007). It is therefore possible trade-offs could be apparent
484 only under specific conditions and/or assays. This scenario is suggested by a recent study of archerfish in
485 which a speed-accuracy trade-off was only statistically significant under the more challenging of two
486 cognitive testing treatments applied (Jones et al., 2020). Plastic responses to social context could also be
487 important since, for instance, in less competitive scenarios (including the single housing used here) slow
488 decisions may carry minimal costs removing motivation to be fast (Sih et al., 2012).

489 More broadly, we also find positive correlations in performance across traits picked as proxies of
490 different cognitive domains. This is counter to predictions under hypothesised trade-off models for
491 maintaining variation. For instance, it has been hypothesised that individuals more reactive to changes in
492 environmental cues will perform relatively poorly in association learning but –being cognitively flexible – will

493 do well in reversal learning tasks (Bebus et al., 2016; Sih et al., 2012). Here we find a strong positive among-
494 individual correlation between our measures of performance in association and reversal learning (r_I=0.54).
495 Again we note the absence of apparent trade-offs has precedent in the animal cognition literature. For
496 example, positive correlations have been reported between discrimination acquisition and reversal learning
497 in sparrows (Boogert et al., 2011), social learning and innovative problem solving in pigeons (*Columba livia*;
498 Bouchard et al., 2007), motor skill learning and reversal learning in pheasants (van Horik et al., 2018).

499 If positive correlations in the **ID**-matrix provide no support for trade-offs, then the corollary is that
500 they are consistent with a domain-general axis of cognitive variation among-individuals in this population.
501 Thus, excluding the boldness proxy of emergence time and focusing on cognitive traits only, we found that
502 57% of the variation in correlation matrix was explained by the leading principle component (or eigen vector).
503 By comparison in tests of the general intelligence model of cognition using human psychometric test
504 batteries, an underlying *g*-factor is typically found to account for about 40–50% of the multivariate variation
505 (Carroll, 1993; Deary, 2001). Under the *g*-model, trait performance in cognitive assays across multiple
506 domains are expected to load strongly (and in the same direction) on a dominant first principle component
507 (Plomin, 2001; Plomin et al., 2002). This is the pattern we found. Our results thus add to a small, but growing
508 body of empirical literature finding support for domain-general variation among-individuals in animal
509 cognitive ability (Ashton et al., 2018; Shaw et al., 2015).

510 Our conclusion that (multivariate) cognitive variation in guppies is consistent with an underlying
511 general intelligence factor requires some caveats. These largely arise because latent variables are, by
512 definition, unmeasurable. Thus, all inferences about (latent) cognitive traits from (observed) behavioural
513 performance measures are inevitably subject to assumptions. First, we are limited by the set of traits assayed.
514 Inclusion of more cognitive domains, different assays, and/or different contexts, would provide more robust
515 insight into the biological extent and evolutionary potential of general intelligence (Poirier et al., 2020). Thus,
516 for instance, we detect no evidence of domain-specific cognitive trade-offs, but they could occur among a
517 wider set of traits (or contexts) not examined. Here we targeted the domains of association learning, motor
518 cognition and reversal learning, but did so using a single testing paradigm in which performance measures
519 share a requirement for individuals to discriminate between two coloured cues. This strategy may be

predisposed towards finding positive correlation structure. Second, the eigen vector decomposition provides only a statistical description of the estimated correlation structure among observed traits; that **ID** is consistent with an axis of variation in an underlying general intelligence factor does not prove such a factor exists. Third, the positive correlation structure could be explained, at least in part, by shared dependence of the observed traits on some other parameter that varies among individuals such as metabolic state (Biro et al., 2010; Mathot et al., 2013; McKenzie et al., 2016), satiety (Ben-Shahar et al., 2001; Shettleworth, 1972), or other drivers of motivation (van Horik et al., 2016). For example, the increase in mean performance time in the association task could be confounded by changes in motivation due to trial fatigue (reduced motivation), at least for some individuals, even if some individuals clearly did perform better over time. Experimental conditions can have important consequences for robust interpretation of studies targeting cognitive traits (Boogert et al., 2018; Griffin et al., 2015; Rowe et al., 2014) and while we attempted to minimise 'non-target' sources of among-individual variation (e.g. by standardising food rations, housing and water chemistry) we cannot exclude the possibility that these contribute to the structure of **ID**. Finally, we acknowledge the potential for bias in our findings caused by selective removal of individuals due to our imposed learning criterion. Failure to participate in a cognitive test may result in sampling biases when measuring among-individual variation in cognitive performances (Thornton et al., 2012; van Horik et al., 2017). Our learning criterion was specifically weak so that all included individuals represented, as far as possible, among-individual variation of the initial population.

We also found that all six cognitive performance traits were positively correlated with 'boldness', measured here as an individual's tendency to consistently emerge rapidly from the home compartment during trial observations. Pairwise correlations were nominally significant in four of the six cases. Our finding that bolder individuals perform better in cognitive tasks mirrors results reported from several other studies. For instance, boldness has been positively linked with associative learning in rainbow trout (*Oncorhynchus mykiss*; Sneddon, 2003), shape discrimination in Cavies (*Cavia aperea*; Guenther et al., 2014a), and reversal learning in the Chimango Caracara, (*Milvago chimango;* Guido et al., 2017). While shy-bold type behavioural variation can have important fitness consequences (Ariyomo et al., 2012; Ballew et al., 2017; A. D. M. Wilson et al., 2010), estimates of contemporary selection on boldness in wild guppies are lacking. Nonetheless,

547 multiple studies have reported among-population differences in boldness mapping to differences in
548 predation, a link that is consistent with the hypothesis that variable levels of risk could impose balancing
549 selection that maintains variation in boldness. Very speculatively, if this is true, and if correlations in **ID** are
550 recapitulated in **G,** the link between boldness and cognitive performance could help maintain variation in the
551 latter. This is because selection on any one trait (e.g. boldness) has consequences for the evolutionary
552 dynamics of genetically correlated traits (Roff, 2002). We do know that shy-bold type personality variation is
553 heritable in the population of guppies under lab conditions, (White & Wilson, 2019; White, Houslay, et al.,
554 2019; Prentice, Houslay, et al., 2020) but not how selection is acting in the field.

555 In summary, we find evidence that individual guppies do differ in cognitive performance as
556 measured by a testing protocol that targets association leaning, motor cognition and cognitive flexibility
557 (reversal learning). We find no support for trade-offs occurring either between speed and accuracy (e.g.
558 within the association learning trials) or between overall performance across cognitive domains. Subject to
559 the caveats highlighted above, the absence of domain-specific trade-offs and the presence of strong
560 positive domain-general correlations in **ID** mean that the general intelligence model provides a good
561 description of the structure of multivariate variation. Our results also suggest that, to the extent that
562 directional natural selection favours higher performance in any single cognitive domain, it would lead to
563 positively correlated evolutionary responses across all domains. However, this inference is dependent on **ID**
564 being a reliable proxy for the **G** matrix (Brommer, 2013). Greater efforts to quantify **G** is thus an obvious, if
565 challenging, next step towards understanding the maintenance of variation in and evolutionary dynamics of
566 animal cognition.

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