

1 **Predation as a driver of behavioural variation and trait**  
2 **integration: effects on personality, plasticity, and**  
3 **predictability**

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15

16 **Abstract**

17 Predation is increasingly viewed as an important driver in maintaining ecological and  
18 phenotypic diversity. In contrast to classic evolutionary theory which predicts that predation  
19 will shift trait means and erode variance within prey species, several studies indicate higher  
20 behavioural trait variance and integration in high predation populations. These results come  
21 predominately from field-sampled animals that cannot isolate the role of predation from  
22 other ecological factors such as density. Here, we study the role of predation on behavioural  
23 trait (co-)variation in density-controlled populations of guppies (*Poecilia reticulata*) living  
24 with and without a benthic ambush predator. At 2.5yrs post introduction of the predators  
25 (up to 10 overlapping generations), 40 males were sampled from each of the six populations  
26 and extensively assayed for activity rates, water-column use and voracity. Individual  
27 variation was pronounced in both treatments, with substantial individual variation means,  
28 temporal plasticity and predictability. However, the effects of predation were subtle.  
29 Predators had little effect on mean behaviour, though predator-exposed fish spent more  
30 time at the surface in early trials, which decreased to the same as controls with time.  
31 Predators did however affect the integration of behavioural traits. Fish that were higher in  
32 the water-column fed slower and had a reduced positive correlation with activity in  
33 treatment populations, relative to control populations. Predators also affected the  
34 integration of personality and plasticity – leading to changes in among-individual variances  
35 through time in water-column use and activity – which was absent in controls. Our results  
36 contrast with the extensive guppy literature showing rapid evolution in trait means, and  
37 shows maintenance of behavioural variance under predation.

38 **Key words:** Behavioural syndromes, animal personality, predator-prey interactions,  
39 temporal plasticity, residual model, behavioural reaction norms

## 40 **Introduction**

41 Predators play a vital role in regulating prey communities, both by shaping the ecology of  
42 the environment (Estes et al. 2011) and exacting directional selection on a broad range of  
43 traits (Endler 1980; Lapiedra et al. 2018; Reznick et al. 1990). By modulating the relative  
44 abundance of prey species (Crooks and Soulé 1999), age and sex demographics (Reznick et  
45 al. 2001) and habitat usage (Ripple and Beschta 2004), predators promote ecosystem  
46 stability with effects that cascade down trophic levels (Mooney et al. 2010). An extension of  
47 these well studied effects of predation is the potential that predators may encourage trait  
48 variation in prey species (Bolnick et al. 2011).

49 While evidence for directional selection on traits such as life-history (Reznick et al. 1990;  
50 Spitze 1991), colouration (Endler 1980) and behaviour (Lapiedra et al. 2018; Magurran et al.  
51 1992) are plentiful, the effect of predation on trait variance has received less attention.  
52 While long-standing theory suggests that strong selective pressures like predation should  
53 shift the population mean and reduce variance (e.g. Hoffmann and Merilä 1999; Levene  
54 1953), a handful of more recent studies have suggested prey may exhibit greater levels of  
55 phenotypic variance in populations exposed to high- versus low-predation (Dhellemmes et  
56 al. 2020; Dingemanse et al. 2009). This increased variance may result from a couple of  
57 factors; negative frequency-dependent selection between predators and prey (Belgrad and  
58 Griffen 2016) or learned foraging strategies to target common prey phenotypes (Clarke  
59 1969) may selectively remove the common phenotype and lead to diversifying selection.  
60 Alternatively, predators may open niches in the ecological and social environment, leading  
61 to increased variance in the prey populations to occupy these niches (Ioannou et al. 2017).

62 The possibility that predation might increase trait variance is most apparent at the  
63 developmental level, where exposure to predation cues in early ontogeny can increase  
64 expressed behavioural variation later in life (Edenbrow and Croft 2013; Tariel et al. 2019;  
65 Urszán Tamás et al. 2018). For instance, tadpoles exposed to olfactory alarm cues showed  
66 greater among-individual variance in activity rates as adults (Urszán Tamás et al. 2018) and  
67 similar results have been found in the boldness of aquatic snails (Tariel et al. 2019). While  
68 these studies do not speak directly to the role of predation in promoting variation across  
69 generations, they do point to a gene-by-environment architecture that promotes variance  
70 when exposed to risk, a pattern consistent with the general increase in phenotypic variance

71 when animals are exposed to environmental stress (Rowiński and Rogell 2017). Further,  
72 these effects of predation extend to promoting phenotypic integration across traits  
73 (Adriaenssens and Johnsson 2013; Bell and Sih 2007; Dhellemmes et al. 2020; Spitze et al.  
74 1991). In sticklebacks (*Gasterosteus aculeatus*), boldness and aggression were not  
75 correlated prior to exposure to predation, but were correlated after exposure to predation  
76 that included predation selection (Bell and Sih 2007).

77 While these examples point to an inflation of among-individual variance in mean  
78 behaviour (i.e. 'personality'), predation history can also affect individual variation in  
79 plasticity (Urszán Tamás et al. 2018). The existence of variance in plasticity implies that  
80 personality differences are not fully maintained across environmental gradients or through  
81 time (Biro et al. 2010; Brommer 2013) and further imply that trait covariances may be  
82 context dependent (Class and Brommer 2015; Stearns et al. 1991). This is particularly apt in  
83 an acclimation or habituation context, where the conditions which initially induced a stress  
84 response subside with continued exposure. When in high predation environments,  
85 habituation rates are reduced due to the increased potential costs of any errors (Brown et  
86 al. 2013). At the individual level, this may also change alter the costs and benefits underlying  
87 traits, and thus ultimately effect how these traits covary with other traits.

88 Predation might also favour greater variance within individuals, to reduce the  
89 predictability of an individual's behaviour by predators (Briffa 2013; Domenici et al. 2008).  
90 Individuals commonly vary in their residual intraindividual variance (rIIV) (Stamps et al.  
91 2012), often termed 'behavioural predictability'. This unpredictability could be particularly  
92 advantageous for individuals with a high-risk personality (Highcock and Carter 2014), leading  
93 to correlations between personality and predictability when exposed to risk. While variation  
94 in personality, plasticity and predictability have different biological causes and  
95 consequences, they can also conflate the estimation and interpretation of the other factors.  
96 As such, it is important to take a hierarchical and integrated approach to study the effect of  
97 predation on behavioural variance.

98 The evolutionary ecology of predator-prey interactions has been particularly well studied  
99 in the guppy (*Poecilia reticulata*). In the native Trinidadian range, guppies live either side of  
100 waterfall barriers that confine predators to downstream regions (Endler 1978; Magurran  
101 2005). This natural variation is replicated across multiple, parallel flowing streams. This has

102 led to a rich body of comparative work, where samples of the high predation (downstream)  
103 populations are compared to the low predation (upstream) populations, yielding insights  
104 into the evolution of life-history traits (Reznick and Endler 1982), behaviour (Harris et al.  
105 2010; Seghers 1974), colouration (Endler 1978) and anatomy (Kotrschal et al. 2017; Reddon  
106 et al. 2018). The use of translocation experiments has effectively complemented this work  
107 to demonstrate evolution, where high predation guppies were moved to previously guppy-  
108 free low predation locations (Endler 1980; Magurran et al. 1992; Reznick et al. 1990).

109 However, these two methods of study are limited in their ability to control for the  
110 secondary effects of predation, which may help to explain the low predation phenotype.  
111 Low predation guppies grow slower, reproduce later and give birth to fewer fry (Reznick et  
112 al. 1990), while also senescing faster (Reznick et al. 2004). These traits all seem detrimental,  
113 raising the question of what maintains the low predation phenotype? Recent insights have  
114 been gleaned from a long-term introduction experiment, where low predation populations  
115 were monitored with high temporal resolution (Travis et al. 2014). This allowed the  
116 researchers to track temporal change in selection pressures resulting from natural density  
117 regulation (Reznick et al. 2019). What this work has made clear is the important role of  
118 density in the evolution of the low predation phenotype, with populations at carrying  
119 capacity favouring slower growth and fecundity (Reznick et al. 2019). Such dynamics also  
120 affect behavioural traits, as high density stimulates dispersal in these same populations (De  
121 Bona et al. 2019).

122 While secondary effects of predation – such as density regulation – may be important in  
123 promoting trait variance, these factors make it hard to distinguish the direct effects of  
124 predation from the secondary effects. Here, we report results from an experimental study  
125 where replicated populations of guppies were established and exposed to predators over  
126 the course of up to 10 overlapping generations in six semi-natural mesocosms. During this  
127 time, the density of control ponds was culled every 6 months to negate the effect of density.  
128 After 2.5yrs post-introduction of the predators, we sampled a total of 240 male guppies and  
129 repeatedly assayed activity, water-column use and voracity of fish, to better understand  
130 how predators affect the mean behaviour, phenotypic variance and phenotypic integration  
131 of behavioural traits in their prey. We expected to see predator exposed fish to have  
132 reduced activity rates, spend more time high in the water-column and acclimate to the

133 novel conditions slower. Further, we predicted predation to promote trait variances and  
134 covariances in the three traits.

## 135 **Methods**

### 136 **Populations and husbandry**

137 Guppies (*Poecilia reticulata*) used in this experiment were descendants of wild-caught  
138 fish collected in 2009 from Alligator Creek, Queensland (Guevara-Fiore 2012). Laboratory  
139 stock fish were used to create six populations, which were placed in six replicate ponds (3m  
140 × 1.5m × 0.6m deep). Each pond was progressively seeded with a total of 54 mature  
141 females, 42-43 mature males, and 22-24 unsexed juvenile guppies from May to August of  
142 2015. Populations were allowed to breed naturally until the 26<sup>th</sup> of October 2015, when a  
143 subset of fish were shuffled between all ponds to further reduce the potential for founder  
144 effects. Fifty fish were haphazardly collected from each pond and divided into groups of 10  
145 (five males and five females). Each pond then received one group of 10 from each of the  
146 other ponds, for a total of 50 additional fish per pond. Jaguar guapotes (*Parachromis*  
147 *managuensis*) were then added to three ponds (i.e. treatment ponds) on November 26  
148 2015, while the other three remained predator free controls. Cichlids were rotated between  
149 the 3 treatment ponds once a month, to control for effects of predator identity. As use of  
150 the native Trinidadian pike cichlid (*Crenicichla frenata*) is not permitted in Australia due to  
151 quarantine restrictions, we used the jaguar guapote, a cichlid native to Nicaragua where  
152 they cooccur with other *Poeciliids*. This is an ambush predator with a large gape that  
153 facilitates hunting of evasive prey (Hulsey and García de León 2005). The cichlids were highly  
154 cryptic during the day, and became more active during periods of reduced light, while  
155 background light went off each evening.

156 Guppies in each pond were provided a complete refuge, whereby one third of the tank  
157 was partitioned off with 16mm plastic mesh that allowed guppies to pass but not the cichlid.  
158 Late in the day prior to lights out, guppies increasingly used the refuge, and at night few fish  
159 were outside the refuge (D.J.M & P.A.B, *pers obs.*). Cichlids readily fed on guppies as  
160 evidenced from 60% increases in mass over the first year. Further, biomass of guppies was  
161 lower as a result of predation (see below for details). Guppies were also provided live plants  
162 (Java moss) and plastic plants for refuge throughout the mesocosm. All replicates contained

163 a cannister filter (Sicce Whale 500: 1200L/hr), a heater set to 25°C, and gravel substrate.  
164 Ponds were illuminated with plant growth spectrum light to stimulate plant growth, natural  
165 primary production and foraging resources, and were kept in 12:12 hr light:dark  
166 photoperiod (7am-7pm day). Water quality and temperature checks were conducted weekly  
167 to ensure all replicates were kept under the same stable conditions. Food was also provided  
168 to supplement natural foraging, controlled by automatic feeders that dispensed  
169 approximately 0.5 g of a combination of crushed commercial fish flake and dried shrimp into  
170 the ponds in the region outside the refuge. All populations were fed three times daily,  
171 though treatment populations were reduced to twice daily from August 2016 on due to a  
172 decrease in guppy biomass and voracity.

173 In order to maintain similar population densities between the two treatments, we  
174 reduced densities by wet mass in the control ponds every 6 months by culling a random  
175 sample of fish (see sampling section below for details). Guppy total biomass was nearly two-  
176 fold greater in control than in predator ponds prior to each cull; this, in combination with  
177 substantial growth of the predators indicated substantial predation. The measures  
178 employed to standardise food availability and density thus allowed us to better focus on the  
179 effect of predation, controlling for other density-related factors which are known to  
180 contribute to the evolved changes between high and low predation populations in the  
181 natural Trinidadian streams (Travis et al. 2014).

## 182 **Sampling**

183 Ponds were sampled in pairs of control and treatment, with 40 individual males sampled  
184 from each pond. To sample, we first caught all fish in each pond (to the best of our ability),  
185 while standardising sampling effort between the ponds. Filtration, and heaters were turned  
186 off and the cichlids, plants and any other obstacles removed prior to sampling. A fine mesh  
187 divide was introduced to the far end of the predator exposed section and was slowly  
188 shuffled across to coerce all fish into the refuge area. To standardise sampling effort, we  
189 performed three passes of the section with a custom-built seine net, which was the width of  
190 the tank, then two more passes using two large square-shaped dip nets.

191 To select fish for trials, the large tub containing the fish was gently stirred by hand, then a  
192 random scoop of fish was taken, the wet mass of the group recorded and then temporarily

193 placed in a holding tank. This was done exhaustively until all fish were caught. Holding tanks  
194 were then chosen at random to be a) sampled from, b) culled to reduce density, or c)  
195 returned to the pond. Males were sampled exhaustively from the tanks allocated for  
196 sampling.

197 Fish were moved to 1.25L home tanks (length: 25cm, width: 6cm, height: 15cm) in which  
198 they resided for housing and for all behavioural assays. Once on the recirculation system, all  
199 fish were fed to help them recover from handling and left overnight undisturbed to  
200 acclimate. The tanks were placed on a recirculation system, which was held under stable  
201 conditions (Temperature =  $24.7 \pm 0.2$  °C, pH = 7.9–8.1, kH = 100– 120 ppm, salinity = 1.1–  
202 1.35 ppt) that were the same as in the ponds.

## 203 **Behavioural observations**

### 204 ***Latency to feed***

205 Latency to feed trials, a measure of voracity, were recorded daily for 20 days and began  
206 the day after relocation to the lab. Each fish was provided 0.5mL of brine *nauplii* and the  
207 latency to commence feeding was recorded to a maximum latency of 150 seconds. This  
208 maximum latency was recorded in only 4.5% of observations, and was spread across many  
209 individuals and through time. Trials were conducted daily in the afternoons. Due to poor  
210 yields in hatching brine, trials were not conducted on some days, and fish instead received a  
211 standard ration of flake. In total, 4188 trials were conducted.

### 212 ***Activity and water-column use***

213 Video recorded trials began after fish had acclimated for one week and were designed to  
214 create minimal disturbance. Each individual's home tank was moved from the  
215 biorecirculation system to the vertical filming stage (located in the same small constant  
216 temperature room) for activity and water-column use assays. The 12-arena stage was backlit  
217 with infrared lighting. Once all individuals for a trial had been moved onto the stage, the  
218 next set of 12 individuals were fed flake rations in preparation for their trial and to  
219 standardise hunger. The experimenter then left the room, and a camera located 2.6m from  
220 the stage was set to record remotely. Trials lasted for 22mins, and were live-tracked with  
221 EthoVision XT9. The first 2mins were discarded to negate residual effects of movement of  
222 the experimenter in the room. From the tracks, we extracted the cumulative distance

223 moved in the 20min tracking period (activity) and the proportion of time in the top half of  
224 the tank (water-column use). As tanks were thin (6cm), movement occurred predominately  
225 in 2-dimensions. At the conclusion of each trial housing tanks were returned to the  
226 recirculation system. Trials were run between 9am and 1pm, began after one week of  
227 acclimation post-sampling, and were conducted daily for 14 consecutive days. One day was  
228 not run due to a power outage, so a handling effect control (where fish were moved on/off  
229 the stage to simulate the protocol) was run in the afternoon.

230 At the conclusion of all behavioural trials, fish were culled with an overdose of MS-222,  
231 dabbed dry with a KimWipe, and weighed to the nearest 0.001g. Due to a small amount of  
232 mortality, the final sample size was 237 fish, with 3239 video trials and 4188 latency to feed  
233 trials. Activity data from control fish has been used previously by Mitchell et al. (2020) as an  
234 example data set to illustrate statistical methods.

235 All procedures conformed to the standard for animal ethics at Deakin University (B39-  
236 2014).

## 237 **Statistical methods**

238 Data was analysed using double-hierarchical generalised linear models (DHGLM) (Cleasby  
239 et al. 2015). These models allow for the simultaneous analysis of a mean and residual  
240 model, the latter in log-linked standard deviations. Both are linear models, allowing for fixed  
241 and random effects. Full descriptions of these models and formulas can be seen elsewhere  
242 (Cleasby et al. 2015; Mitchell et al. 2016; Westneat et al. 2013), so we will not go into great  
243 detail here. In contrast to previous models however, we ran these models in a multivariate  
244 framework, to assess among-individual correlations between traits. Analyses were  
245 implemented through the Bayesian software 'brms' (Bürkner 2017).

246 Distance moved (in 2 dimensions) was square-root transformed and latency to feed was  
247 log-transformed to achieve normality of residuals. Proportion of time spent in the top half  
248 of the tank was left raw. After transformation to normality, the three response variables  
249 were Z-transformed to simplify prior specification and avoid large variance differences  
250 which can cause problems when estimating covariance matrices. Fish mass was also log-  
251 transformed, then z-transformed to aid specification of priors.

252 To aid linearity, number of days post-sampling (hereafter just ‘time’) was log-  
253 transformed for latency to feed and left-centred time was log-transformed for water-  
254 column use. No transformation to time was required for activity. As we were primarily  
255 interested in pre-acclimation scores, we left all predictors left-centred.

256 Both the mean and residual models for all three traits were fit with the fixed effects of  
257 treatment, batch, fish mass and time, with interactions between treatment and time, and  
258 treatment by batch (see Table 1a in results for full list of terms). The batch variable is a 3-  
259 level factor, denoting the pair of treatment and control ponds which were concurrently  
260 sampled. Together, the treatment by replicate interaction uses the 5 degrees of freedom  
261 required to separate each of the six populations.

262 Mean models were additionally fit with random intercepts and slopes of time, to assess  
263 individual variance in mean behaviour and acclimation rates. A random intercept was  
264 specified in the residual model to account for individual differences in rIIV (i.e. individual  
265 variation in predictability). As there was a modest ceiling effect in latency to feed trials  
266 (150secs, 4.5% of observations), we suggest some caution in interpretation of these results  
267 as this may truncate variance slightly (Stamps et al. 2012).

268 To assess covariances among traits, random effects were fit to an unstructured variance-  
269 covariance matrix, which calculates the correlation of all combinations of mean intercepts  
270 and slopes, and residual intercepts (rIIV) across the three traits. As we were interested in  
271 the effect of predation on trait variances and the integration of traits, we separated random  
272 effect (co)variances by treatment. Variance in random slopes indicates that individuals vary  
273 in the change of behaviour through time, meaning individual differences in behaviour are  
274 not fully maintained through time (Brommer 2013). Therefore, among-individual variances  
275 in predicted trait scores and covariances between traits also change with time (Brommer  
276 and Class 2015; Stearns et al. 1991).

277 Repeatability was calculated at the intercept through the standard equation;  $R = \frac{\sigma_{int}^2}{\sigma_{int}^2 + \sigma_{\epsilon}^2}$ ,  
278 though here the residual variance ( $\sigma_{\epsilon}^2$ ) is estimated at the midpoint between batches and  
279 calculated for each treatment using the residual side model (see supplementary material for  
280 more detail). Together, the random effect variance-covariance matrix infers changes in

281 among-individual variances (Eq. 1), cross-time covariances within a behavioural trait (Eq. 2)  
282 and covariances between traits (Eq. 3):

$$283 \sigma_{Pred1}^2[x_1] = \sigma_{int1}^2 + 2cov_{int1,slp1}x_1 + \sigma_{slp1}^2x_1^2 \quad (1)$$

$$284 cov_{Pred1[x1],Pred1[x2]} = \sigma_{int1}^2 + cov_{int1,slp1}x_1 + cov_{int1,slp1}x_2 + \sigma_{slp1}^2x_1x_2 \quad (2)$$

$$285 cov_{Pred1,Pred2}[x_1, x_2] = cov_{int1,int2} + cov_{int1,slp2}x_2 + cov_{int2,slp1}x_1 + cov_{slp1,slp2}x_1x_2$$

286 (3)

287 Where numbers in the subscript denote trait 1 or 2, 'Pred' refers to predicted values, 'int'  
288 to intercepts and 'slp' to slopes. The predictor 'x' refers to time, and can be specified  
289 separately for the two traits, to account for the differing transformations. These calculations  
290 are done for each iteration of the MCMC chain, yielding the credible distribution of the  
291 estimate. The implementation of these equations can be found in the supplements,  
292 including functions allowing easy generalisation to other datasets analysed with brms. Due  
293 to heterogeneous residual variances and that latency to feed trials were separated by 1-8hrs  
294 from the video trials, we did not deem it appropriate to try to assess residual covariances.

295 Models were fit with uninformative priors and ran across 6 chains for 3000 iterations,  
296 with a warmup of 500 iterations. Rhats for all parameters were within  $1 \pm 0.01$  indicating  
297 convergence. We quote mean effect sizes as the best estimate and confidence intervals  
298 based on quartiles for the estimations of 95% credible intervals.

## 299 Results

### 300 Population effects

301 As expected, there was evidence of acclimation effects in activity (increase over time)  
302 and in latency to feed (decrease over time), but acclimation rates did not differ between  
303 treatments (treatment\*time effect, NS; Table 1). Treatments also did not differ in mean  
304 activity or latency to feed. Predator exposed fish were initially higher in the water-column,  
305 and decreased with time to converge with control fish, indicated by the interaction effect  
306 (Table 1a, Fig. 1). Larger fish were more sedentary and spent more time towards the  
307 bottom. There was also an effect of batch in the three behaviours, which likely results from  
308 either population differences among the ponds, or small differences in conditions.

309 Residual variance in activity decreased over time, meaning fish became more predictable,  
 310 however the opposite was observed for latency to feed (Table 1b). Residual variance was  
 311 largely unaffected by other predictors, although again there were some population effects  
 312 on latency to feed indicated by the batch, and batch-by-treatment interactions.

		Activity			Water-column Use			Latency to Feed					
		Est.	Q2.5	Q97.5	Est.	Q2.5	Q97.5	Est.	Q2.5	Q97.5			
Mean model	Intercept	-0.148	-0.415	0.114	-0.112	-0.352	0.128	1.184	0.965	1.405			
	Batch 2	-0.167	-0.499	0.163	0.159	-0.150	0.468	<b>-0.549</b>	<b>-0.809</b>	<b>-0.288</b>			
	Batch 3	0.251	-0.096	0.591	0.206	-0.107	0.527	<b>-0.285</b>	<b>-0.555</b>	<b>-0.013</b>			
	Treatment	-0.079	-0.445	0.287	<b>0.488</b>	<b>0.117</b>	<b>0.856</b>	0.218	-0.069	0.507			
	Mass	<b>-0.247</b>	<b>-0.348</b>	<b>-0.145</b>	<b>-0.185</b>	<b>-0.281</b>	<b>-0.090</b>	0.030	-0.041	0.100			
	Time	<b>0.030</b>	<b>0.017</b>	<b>0.043</b>	-0.006	-0.082	0.071	<b>-0.447</b>	<b>-0.505</b>	<b>-0.390</b>			
	Batch 2*Trt	-0.049	-0.536	0.444	-0.189	-0.658	0.281	-0.135	-0.486	0.218			
	Batch 3*Trt	-0.393	-0.904	0.111	<b>-0.573</b>	<b>-1.055</b>	<b>-0.089</b>	-0.071	-0.432	0.289			
	Trt*Time	0.012	-0.006	0.031	<b>-0.138</b>	<b>-0.250</b>	<b>-0.026</b>	-0.019	-0.095	0.059			
Residual model	Intercept	-0.728	-0.866	-0.589	-0.522	-0.691	-0.354	-0.499	-0.621	-0.375			
	Batch 2	-0.063	-0.231	0.104	-0.034	-0.200	0.130	<b>-0.107</b>	<b>-0.206</b>	<b>-0.007</b>			
	Batch 3	-0.067	-0.240	0.105	0.001	-0.174	0.177	-0.002	-0.104	0.097			
	Treatment	-0.107	-0.306	0.095	0.021	-0.210	0.251	<b>-0.188</b>	<b>-0.371</b>	<b>-0.007</b>			
	Mass	-0.020	-0.070	0.030	0.022	-0.026	0.072	-0.022	-0.053	0.010			
	Time	<b>-0.023</b>	<b>-0.034</b>	<b>-0.013</b>	-0.023	-0.083	0.037	<b>0.090</b>	<b>0.045</b>	<b>0.134</b>			
	Batch 2*Trt	0.220	-0.020	0.454	0.188	-0.044	0.421	<b>0.231</b>	<b>0.076</b>	<b>0.388</b>			
	Batch 3*Trt	0.076	-0.174	0.321	0.061	-0.184	0.302	0.062	-0.096	0.222			
	Trt*Time	0.004	-0.012	0.020	-0.024	-0.110	0.062	0.026	-0.037	0.089			
		N <sub>ID</sub> = 237			N <sub>obs</sub> = 3239			N <sub>obs</sub> = 3239			N <sub>obs</sub> = 4188		

313 **Table 1:** Displayed are parameter estimates of the fixed effects in the mean (a) and residual  
 314 (b) models, with the upper and lower bound of the confidence intervals. Parameters in bold  
 315 denote no overlap with 0, indicating significance in the traditional sense. The control  
 316 treatment and batch 1 are reference groups.

317

### 318 Among-individual variances

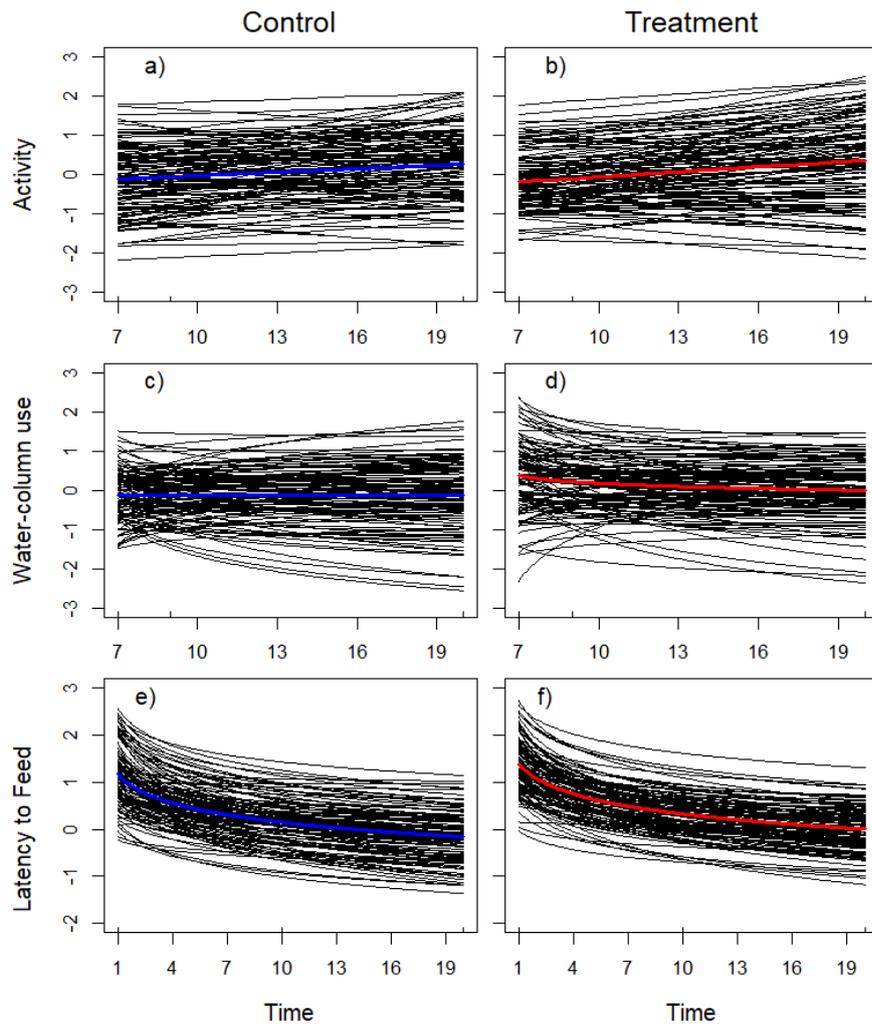
319 There was strong evidence for personality differences in all three behaviours. At the  
 320 intercepts there was very high repeatability for activity (control:  $R = 0.79$  [0.71, 0.85],  
 321 predation:  $R = 0.8$  [0.73, 0.86]). Repeatability was slightly lower for water-column use  
 322 (control:  $R = 0.64$  [0.51, 0.75], predation:  $R = 0.76$  [0.67, 0.84]), and latency to feed (control:  
 323  $R = 0.65$  [0.55, 0.74], predation:  $R = 0.68$  [0.57, 0.77]). Further, individuals differed in their  
 324 temporal plasticity, indicating differential responses during acclimation to experimental  
 325 conditions. Reaction norm variance in all traits lead to large changes in rank order, though

326 individual differences in means from the start of the trials were partially maintained for all  
327 traits. In activity rates, the correlation of predicted values of the first and last days were  
328 moderately high (control:  $r = 0.56$  [0.42, 0.69], predation:  $r = 0.59$  [0.44, 0.71]). In water-  
329 column use these were lower (control:  $r = 0.32$  [0.12, 0.52], predation:  $r = 0.4$  [0.21, 0.58]),  
330 as they were for latency to feed (control:  $r = 0.39$  [0.18, 0.58], predation:  $r = 0.41$  [0.18,  
331 0.62]). Finally, individuals also showed strong differences in predictability (coefficients of  
332 variance ranging from 0.13 to 0.34; see supplements), demonstrating that some individuals  
333 were more consistent in their behavioural scores than others (Table 2). However, these  
334 variances did not differ between treatments, with very similar variance estimates and large  
335 overlap in the credible distributions between the two treatments.

336

### 337 **Change in trait variances through time**

338 The effect of the treatment on trait variances appeared dependent on time. In activity,  
339 among-individual standard deviation did not change from the first day ( $\sigma = 0.9$  [0.79, 1.03])  
340 to the last day ( $\sigma = 0.92$  [0.81, 1.05]) in control fish (Fig. 1a), but the reaction norms fanned  
341 out in the predator exposed fish to expand variation from  $\sigma = 0.82$  [0.71, 0.94] to  $\sigma = 1.04$   
342 [0.91, 1.18] (Fig. 1d). In water-column use, among-individual variances increased from a low  
343 at the start of trials in controls ( $\sigma = 0.72$  [0.59, 0.86]) to a high at the end ( $\sigma = 0.89$  [0.77,  
344 1.03]; Fig. 1b); by contrast, predator exposed fish showed much higher variance initially ( $\sigma =$   
345  $0.99$  [0.83, 1.16]) and then converging to lower variance that was similar to the control ( $\sigma =$   
346  $0.83$  [0.72, 0.97]; Fig. 1e). By contrast, variance changes over time in latency did not differ  
347 among treatments. Reaction norms converged through time in latency to feed trials, from  $\sigma$   
348  $= 0.72$  [0.61, 0.84] to  $0.62$  [0.52, 0.72] in control, and from  $\sigma = 0.63$  [0.53, 0.75] to  $0.55$   
349 [0.47, 0.65] in treatment. This pattern was consistent across the two treatments (Fig. 1c,f),  
350 as indicated by the very similar intercept-slope correlations (Table 2).



351

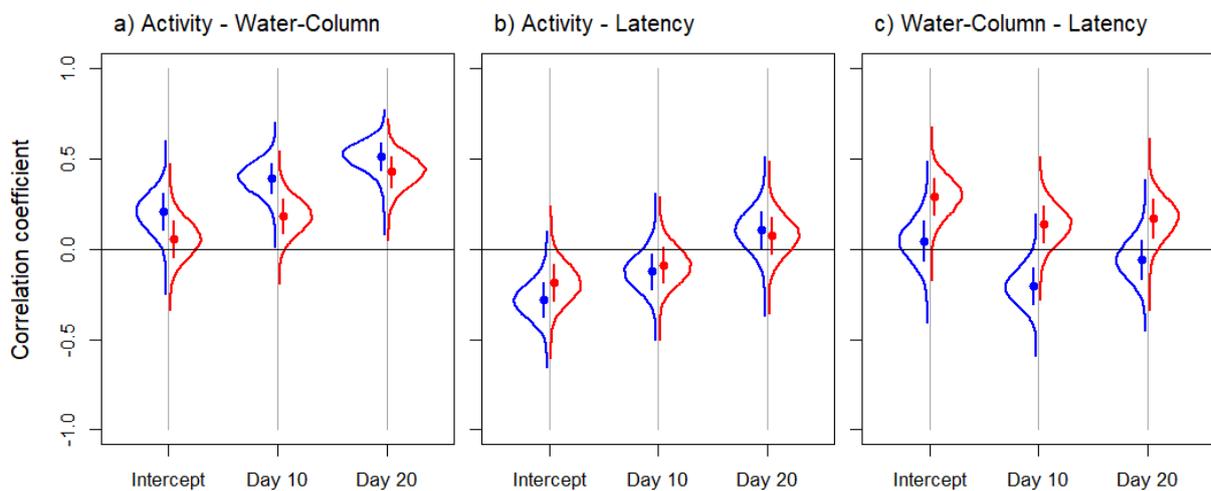
352 **Figure 1:** Displayed are reaction norm plots for individual activity (a,b), water-column use  
 353 (c,d) and latency to feed (e,f. Control are displayed on the left and predation on the right.  
 354 Coloured lines correspond to mean level trend, and black lines are individual level  
 355 predictions. Upward ticks correspond to centring in Fig. 2. Time is shown on the raw scale,  
 356 back transformed from the log-transformed data used in analysis in c through f, creating the  
 357 non-linear trends.  
 358

### 359 **Effects on covariances among traits**

360 There was some evidence that predators affected phenotypic integration of traits (Table  
 361 2). These differences appeared to centre on correlations with water-column use, with the  
 362 treatment fish that were previously exposed to the benthic jaguar guapote appearing to rest  
 363 near the surface. In both treatments, individuals that were more active were also more  
 364 likely to be higher in the water column, and this covariance increased with time (Fig.1a).  
 365 Control fish tended to be at the surface more when active, though effects were slight and  
 366 only appeared different around day 10 (Fig. 2a). Further, there appeared to be a consistent

367 difference in the correlations of water-column use and latency to feed between treatments,  
368 with top-dwelling fish having higher latency to feed in predation ponds, but not control (Fig.  
369 2c). Among-individual correlations between water-column use and latency were small in  
370 treatment populations and non-significant in control populations (fig 2c).

371 There was additionally strong temporal dependence of the trait covariances. Activity and  
372 water-column use started weakly or uncorrelated, but were relatively highly correlated in  
373 later trials (Fig. 2a). With activity and latency to feed, a small negative correlation  
374 disappeared with time (Fig. 2b), while water-column and latency to feed correlation seemed  
375 largely stable through time (Fig. 2c).



376  
377 **Figure 2:** Displayed are the 3 pairwise trait correlations at three different values of time.  
378 Density plots of the posterior estimate are displayed, with controls shown in blue and  
379 predator exposed fish in red. As latency to feed observations begun prior to the activity and  
380 water-column use assays, the 'left-centre' refers to a correlation of first assay of latency (1  
381 day after sampling) and first assay of the tracking trials (7 days after sampling). Other  
382 correlations are on matched days post sampling from ponds.  
383

### Control

Act[int]	0.903																				
ε	0.062																				
Act[time]	<b>-0.447</b>	0.066																			
ε	<b>0.077</b>	0.005																			
Act[rIIV]	-0.165	<b>0.471</b>	0.332																		
ε	0.105	0.095	0.032																		
WC[int]	<b>0.203</b>	<b>-0.408</b>	-0.074	<b>0.723</b>																	
ε	<b>0.101</b>	<b>0.095</b>	0.116	<b>0.067</b>																	
WC[time]	<b>0.288</b>	<b>0.363</b>	0.102	<b>-0.453</b>	0.359																
ε	<b>0.098</b>	<b>0.096</b>	0.118	<b>0.095</b>	0.033																
WC[rIIV]	<b>-0.475</b>	0.062	<b>0.482</b>	-0.066	<b>-0.255</b>	0.308															
ε	<b>0.092</b>	0.113	<b>0.105</b>	0.117	<b>0.118</b>	0.030															
Lat[int]	<b>-0.283</b>	0.156	<b>0.137</b>	0.043	<b>-0.222</b>	<b>0.240</b>	0.718														
ε	<b>0.094</b>	0.102	<b>0.113</b>	0.110	<b>0.110</b>	0.112	0.060														
Lat[time]	0.195	0.025	-0.182	-0.269	<b>0.343</b>	-0.201	<b>-0.642</b>	0.248													
ε	0.105	0.110	0.120	0.112	<b>0.110</b>	0.121	0.070	0.025													
Lat[rIIV]	0.119	0.156	0.007	0.099	0.069	-0.209	-0.210	<b>0.367</b>	0.124												
ε	0.150	0.152	0.161	0.158	0.163	0.166	0.157	0.157	0.027												

### Predation

Act[int]	0.819																				
ε	0.059																				
Act[time]	<b>-0.236</b>	0.066																			
ε	<b>0.094</b>	0.005																			
Act[rIIV]	0.074	0.332	0.317																		
ε	0.110	0.104	0.034																		
WC[int]	0.055	<b>-0.055</b>	-0.188	<b>0.985</b>																	
ε	0.101	<b>0.105</b>	0.112	<b>0.082</b>																	
WC[time]	0.179	<b>0.260</b>	0.235	<b>-0.646</b>	0.379																
ε	0.106	<b>0.104</b>	0.120	<b>0.068</b>	0.035																
WC[rIIV]	-0.268	0.002	<b>0.344</b>	-0.149	0.082	0.293															
ε	0.106	0.117	<b>0.121</b>	0.117	0.127	0.031															
Lat[int]	-0.188	0.142	<b>-0.202</b>	<b>0.289</b>	<b>-0.309</b>	0.097	0.634														
ε	0.101	0.107	<b>0.116</b>	<b>0.102</b>	<b>0.109</b>	0.120	0.058														
Lat[time]	0.104	0.011	0.138	<b>-0.262</b>	<b>0.401</b>	0.048	<b>-0.625</b>	0.216													
ε	0.114	0.120	0.130	<b>0.113</b>	<b>0.114</b>	0.131	<b>0.079</b>	0.025													
Lat[rIIV]	0.209	0.135	0.092	0.131	-0.038	-0.035	<b>-0.259</b>	<b>0.380</b>	0.189												
ε	0.120	0.125	0.140	0.129	0.138	0.141	<b>0.126</b>	<b>0.129</b>	0.026												

Cross-treatment difference  
P<sub>MCMC</sub> < 0.1 < 0.05

384

385 **Table 2:** Displayed are the best estimates with error estimates in parentheses of among-  
 386 individual correlation coefficients for all pairs of intercepts (personality), slopes (temporal  
 387 plasticity) and rIIV (predictability) across the three traits. On the diagonal is the standard

388 deviation. Correlations in bold denote no overlap of the 95%CRI with 0, while highlighted  
389 cells denote a significant difference of between treatments.

390

## 391 **Discussion**

392 Predators induce profound developmental and evolutionary change in the phenotypes of  
393 their prey species and this is particularly true in guppies. Previous work has shown guppies  
394 from high predation populations are more social (Seghers 1974), less bold (Harris et al.  
395 2010), higher in the water-column (Seghers 1973) and habituate slower (Brown et al. 2013)  
396 than the upstream low predation populations. Despite these strong and known effects of  
397 predators on guppies, we did not observe large differences between populations living  
398 under constant risk for 2.5yrs compared to those under predator-free conditions that were  
399 controlled for density. Fish from predator-exposed populations, exhibited no differences in  
400 activity rates and latency to feed, nor differed in acclimation rates to novel conditions than  
401 control populations. There was a subtle effect of predation history on water-column use –  
402 as predicted, predator exposed fish spent more time at the surface initially, and then  
403 decreased their use of surface areas over time. Further, as predicted there was greater  
404 among-individual variance in water-column use of predator exposed fish, with the effect  
405 also constrained to early trials.

406 Together, the results point to subtle effects of predation on the behaviours we  
407 measured, which contrasts with data from ecological comparisons and translocation  
408 experiments. There are however few comparisons for the effect of predation on trait  
409 variances in this species (but see Ioannou et al. 2017). We posit this contrast could be  
410 explained by a combination of three factors: 1) the standardisation of population density, 2)  
411 context dependence of behaviour and 3) the choice of predators.

### 412 **1) Population density**

413 Predators have a large impact on the ecological conditions of guppies, driving down  
414 population densities (Reznick and Endler 1982) and affecting size and age demographics  
415 (Travis et al. 2014). In contrast, low predation populations reach carrying capacity, and are  
416 therefore under greater intraspecific competition (and competition with *Rivulus hartii*) and  
417 reduced food availability when compared to high predation populations (Marshall et al.  
418 2012; Travis et al. 2014; Zandonà et al. 2017). This may help explain the limited effects we

419 saw in mean behaviour resulting from predator exposure. While it is intuitive and  
420 compelling to assume increased neophobia is due to increased benefit of being cautious in a  
421 high-risk environment, this could also occur due to decreases in costs associated with loss of  
422 foraging opportunity in a less resource-constrained environment (Brown et al. 2007).  
423 Consequently, as we were controlling densities and food availability, it is potentially  
424 unsurprising that we did not see differences in food motivation (latency to feed) and in the  
425 highly energetically costly behaviour (activity). By contrast, the traits where we did get a  
426 signal of an effect of predation was water-column use, which was likely the behaviour most  
427 directly tied to encounter rates with the benthic jaguar guapote.

## 428 **2) Context dependence**

429 There was strong evidence that context played an important role in behavioural trait  
430 expression. Behaviour is often measured under intensive handling protocols and novel  
431 conditions, leading to stress effects. If fish from contrasting predation regimes differ in  
432 stress coping styles (Koolhaas et al. 1999), this could exacerbate difference in population  
433 comparisons. In contrast, we tried to minimise handling time and performed all assays in  
434 home-tanks. Fish in our experiment were introduced to novel home-tank conditions, but  
435 were allowed to acclimate for 7 days before activity and water-column use assays begun.  
436 Supporting this explanation, in early trials predator exposed fish spent more time towards  
437 the surface, though with time and as fish continued to acclimate this difference between  
438 populations disappeared. Time also affected trait (co)variances, indicating the individual  
439 level expression of behaviour was highly context dependent.

440 Time of day effects could also explain the lack of differences between populations, the  
441 cichlids were most active at times associated with dawn and dusk, when lights were turned  
442 on and off. During this time, the cichlid was often observed out in the open and the majority  
443 of guppies occupied the predator refuge (D.J.M & P.A.B, *pers. obs.*). Predators are known to  
444 affect the diel patterns of guppy behaviour (Endler 1987) and behavioural assays taken at  
445 times associated with the increased activity of the predator may have resulted in larger  
446 effects. The data appears to indicate that activity and latency to feed during daytime hours  
447 were unlikely to have had large fitness consequences. However, water-column use may  
448 have been more important, given the observed differences in means, variances and  
449 covariances in water-column use.

### 450 **3) Differences in predation**

451 The final likely contributing factor to the lack of effects we found is the choice of  
452 predators. The most voracious natural guppy predator is the Pike cichlid (*Crenicichla*  
453 *frenata*). Pike cichlids are an active predator that preferentially preys on larger guppies  
454 (note sister species *C. saxatilis* used in citation) (Johansson et al. 2004), though due to  
455 quarantine legislation in Australia, we could not obtain *Crenicichla*. By contrast, Jaguar  
456 guapotes used here appeared to particularly prey on juveniles (fewer small fry and juveniles  
457 were seen in predator ponds), had a rounder body, and was likely ecologically closer to blue  
458 acara (*Aequidens pulcher*), which pose a more moderate risk to adult guppies (Deacon et al.  
459 2018; Endler 1980). Therefore, juveniles were likely at greater risk and the predators limited  
460 the rate of recruitment, while larger females were relatively safe. These females likely  
461 continued to give birth to offspring only a couple generations removed from the founders.  
462 Further, female guppies store sperm which they can continue to use for prolonged periods  
463 of time (López-Sepulcre et al. 2013), also increasing the effective generation time.  
464 Consequently, while the cichlids were clearly an effective guppy predator (see Methods),  
465 and guppies can exhibit large evolutionary change in shorter periods than examined here  
466 (e.g. large colour pattern divergence was observed within 14 months; Endler 1980), we may  
467 simply not have given sufficient time for the large phenotypic evolution observed in  
468 previous studies.

### 469 **Predation effects on trait variances**

470 While we did not see the evidence for strong directional selection that would erode trait  
471 variance (Levene 1953), this does not preclude the possibility that predation would promote  
472 trait variance. Predators could lead to niche specialisation (Ioannou et al. 2017) or  
473 diversifying selection through predators forming 'search images' (Clarke 1969). Similar to  
474 the effects on means, treatment differences in trait variances appeared transient and  
475 further point to the effects of predation history on behaviour being context dependent. As  
476 predicted, predation led to an inflation of among-individual variance in water-column use,  
477 although the reaction norms converged to similar levels of variance as the control. It is  
478 noteworthy that this inflation of variance occurred in the only trait to exhibit mean  
479 differences between treatments. It appears unlikely that the observed differences were due  
480 to selection induced by the predator as the effects were plastic and changed rapidly through

481 time. In the other traits, variances were largely maintained, which indicates that stabilising  
482 selection or other mechanisms that would erode variance were absent.

483 At the within-individual level, treatments (and the interaction with time) did not affect  
484 rIIV in any trait, though some population differences were detected in latency to feed trials.  
485 Predictions of decreased predictability (increased rIIV) are based on repeated interactions at  
486 the individual level of predators are prey. While this is feasible with emergence of hermit  
487 crabs from a shell within one attack bout (Briffa 2013), or escape trajectories of cockroaches  
488 (Domenici et al. 2008), predictions on the individual level are unlikely in the large population  
489 sizes of guppies over the time periods these behavioural traits were observed. A predator  
490 trying to make predictions in such a situation is more likely to make them based on  
491 experience of the population – where we did find some effects on variance.

#### 492 **Predation effects on trait covariances**

493 Predators did appear to affect the phenotypic integration of these behavioural traits.  
494 Previous work has demonstrated how predators may affect behavioural covariances  
495 (Adriaenssens and Johnsson 2013; Bell and Sih 2007), as the relative cost or benefit of a  
496 behaviour may be dependent on other aspects of the phenotype, leading to correlational  
497 selection (e.g. Calsbeek and Irschick 2007). In general, we observed evidence for a boldness  
498 syndrome in the control fish, with more active fish being higher in the water-column and (in  
499 early trials) fed quicker. By contrast, these effects were reduced in predator ponds and  
500 additionally, fish higher in the water-column were slower to begin feeding. Differences in  
501 these behavioural correlations appeared to centre on water-column use, a result likely  
502 driven by the benthic nature of the cichlid predator. This contradicted the *a priori*  
503 hypothesis of stronger trait correlations in guppies exposed to predators, though may be  
504 explained by the foraging strategy of the predators. Guppies in predation ponds were likely  
505 pushed towards the surface, away from where the predator resides. Predator fish appeared  
506 more willing to rest near the surface and results may indicate the surface was used as a  
507 refuge.

#### 508 **Temporal dependence of trait covariances**

509 In addition to the population comparisons, we quantified multivariate behavioural  
510 plasticity. Although quantifying individual differences in behavioural plasticity has become

511 common (Biro et al. 2010; Dingemanse et al. 2012; Martin and Réale 2008) few studies have  
512 assessed whether plasticity differences covary across multiple environmental gradients  
513 (Cornwell et al. 2018; Mitchell and Biro 2017; Saltz et al. 2017), or multiple behavioural  
514 traits (Stamps 2016). Through these cross-trait covariances in intercepts and slopes, we can  
515 assess how temporal plasticity shapes multivariate phenotypes (Brommer and Class 2015).  
516 What this analysis showed was “behavioural syndromes” were largely context dependent.  
517 Correlations of the same trait between the early trials and late trials were only moderate for  
518 all traits ( $r$  varied from 0.32 to 0.59), despite high intercept-specific repeatabilities. Further,  
519 in contrast to results on the movement behaviours of guppies which found stable  
520 behavioural covariances to contextual predation risk (Houslay et al. 2018), we found cross-  
521 trait covariances to be context dependent. In early trials, activity and water-column use  
522 were only weakly correlated, though in late trials the correlation was stronger. Between  
523 activity and latency to feed, a small negative correlation disappeared through time.

524 Further, no paper to our knowledge has examined whether behavioural predictability is  
525 correlated among individuals. Predictability is a measure of plasticity in response to  
526 endogenous factors or unaccounted for environmental stimuli (Stamps 2016; Stamps et al.  
527 2012; Westneat et al. 2015). In all three traits, individuals differed in their residual variance  
528 and thus their predictability. These effects were present despite highly standardised  
529 conditions between observations, with minimal variation in temperature or water-chemistry  
530 and standardisation of feeding. This effect was small in the latency to feed data, and more  
531 pronounced in the other two behaviours. Interestingly, there were positive among-  
532 individual correlations in rIIV between activity and water column use in both treatments,  
533 indicating that animals which were predictable for one trait were also predictable for the  
534 other. This indicates a degree of domain generality to predictability, and is consistent with  
535 evidence for correlations between predictability and other forms of contextual plasticity  
536 (Mitchell and Biro 2017). Predictability in latency to feed trials did not correlate with  
537 predictability of the other two traits, though estimates were imprecise due to the low  
538 among-individual variance.

539 Taken together, the data shows strong integration of personality, plasticity and  
540 predictability. While the effects of predation history were small in this case, the integration  
541 of behavioural traits was highly context dependent. Over the last decade, large theories

542 have gained a lot of traction purporting to predict broad correlations of behavioural traits  
543 across life-history continuums (Biro and Stamps 2008; Réale et al. 2010) or stress coping  
544 styles (Koolhaas et al. 1999), though available data fails to support this broad generality  
545 (Royauté et al. 2018). Understanding the stability of behavioural trait correlations to  
546 temporal or contextual change may prove highly informative in building predictions of  
547 under what conditions traits will covary.

548

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