

1 **Adaptive phenotypic plasticity induces individual variability along a**  
2 **cognitive trade-off**

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10 **Abstract**

11           Animal species, including humans, display patterns of individual variability in  
12 cognition that are difficult to explain. For instance, some individuals perform well in certain  
13 cognitive tasks but show difficulties in others. We experimentally analysed the contribution  
14 of cognitive plasticity to such variability. Theory suggests that diametrically opposed  
15 cognitive phenotypes increase individuals' fitness in environments with different conditions  
16 such as resource predictability. Therefore, if selection has generated plasticity that matches  
17 individuals' cognitive phenotypes to the environment, this might produce remarkable  
18 cognitive variability. We found that guppies, *Poecilia reticulata*, exposed to an environment  
19 with high resource predictability (i.e., food available at the same time and in the same  
20 location) developed enhanced learning abilities. Conversely, guppies exposed to an  
21 environment with low resource predictability (i.e., food available at a random time and  
22 location) developed enhanced cognitive flexibility and inhibitory control. These cognitive  
23 differences align along a trade-off between functions that favour the acquisition of  
24 regularities such as learning and functions that adjust behaviour to changing conditions  
25 (cognitive flexibility and inhibitory control). Therefore, adaptive cognitive plasticity in  
26 response to resource predictability and, potentially, similar factors, is a key determinant of  
27 cognitive individual differences.

28

29 **Keywords:** behavioural flexibility; cognitive ecology; cognitive plasticity; fish cognition;  
30 individual differences.

## 31 **Introduction**

32           That individuals display different cognitive abilities has been long acknowledged in  
33 human psychology (e.g., Gustafsson & Undheim, 1996; Humphreys, 1979), and evidence is  
34 now accumulating for many other animal taxa (e.g., mammals: Beran & Hopkins, 2018;  
35 birds: Langely et al., 2020; teleost fish: Lucon-Xiccato & Bisazza, 2017; insects: Mery et al.,  
36 2007). The pattern of this intraspecific cognitive variability is often quite complex, with  
37 individuals excelling at certain cognitive tasks but performing scarcely in others (e.g., Bebus  
38 et al., 2016; Bensky & Bell, 2020; Ferrari, 2014; Kim et al., 2018; Lucon-Xiccato & Dadda,  
39 2017; Mazza et al., 2018). Various hypotheses for this cognitive variability have been  
40 formulated and tested (e.g., covariation with personality traits: Carere & Locurto, 2012;  
41 energetic trade-offs: Kotrschal et al., 2013); however, we currently do not have a clear  
42 explanation.

43           Intriguingly, the cognitive variability has been observed often in functions that fall  
44 into two categories: 1) functions such as learning and memory that are advantageous in  
45 predictable environments, addressing consistent patterns and regularities (Carter et al., 2014;  
46 Ehlinger, 1989; Mery et al., 2007) and 2) functions, like the executive functions cognitive  
47 flexibility and inhibitory control (Bensky & Bell, 2020; Laschober et al., 2021; Lucon-  
48 Xiccato et al., 2020a) that allow individuals to change their behaviour rapidly and are likely  
49 advantageous in ever-changing situations (Diamond, 2013). Studies from other research  
50 fields have shown that the resource predictability in the environment affects a large number  
51 of non-cognitive traits, including foraging behaviour (Grand & Grant, 1994a; Sloat &  
52 Reeves, 2014; Stephens, 1993), aggressive behaviour (Goldberg et al., 2001; Grand & Grant,  
53 1994b), spatial behaviour (Cama et al., 2012; Eide et al., 2004; Lòpez-Lòpez et al., 2014;  
54 Riotte-Lambert & Matthiopoulos, 2020), metabolism (Sloat & Reeves, 2014), stress (Gottlieb  
55 et al., 2013), and reproductive and life history traits (Webb & Marcotte, 1984; Zammuto &

56 Millar, 1985). For instance, in predictable environments, individuals forage more efficiently  
57 (Grand & Grant, 1994a), are more aggressive (Goldberg et al., 2001), occupy smaller  
58 territories (Eide et al., 2004), and display lower levels of stress (Gottlieb et al., 2013). If  
59 environmental predictability also affects cognitive traits, it might generate interindividual  
60 variability along a trade-off between cognitive functions advantageous in highly predictable  
61 versus unpredictable environments (Tello-Ramos et al., 2019). Considering that individuals  
62 of a species may be subjected to different predictability levels across space and time (e.g.,  
63 Eide et al., 2004; Menge, 1972; Minckley et al., 1999), a probable mechanism for this effect  
64 is plasticity that permits individuals to match their cognitive phenotype to the predictability  
65 experienced. This cognitive plasticity would provide a critical contribution to intraspecific  
66 variability in cognition.

67         In our study, we tested the hypothesis that environmental predictability determines  
68 cognitive variability via cognitive plasticity. We manipulated the temporal (Bassett &  
69 Buchanan-Smith, 2007) and spatial predictability (Grand & Grant, 1994a) of foraging  
70 resources in experimental populations of guppies, *Poecilia reticulata*, a teleost fish with  
71 heightened cognitive variability (e.g., Lucon-Xiccato et al., 2020a). The treatment exposed  
72 guppies to simulated environments with either a predictable food source available each day in  
73 the same place and at the same time or to an unpredictable food source available at a pseudo-  
74 random location and time. We then compared guppies exposed to the two treatments using  
75 assays for learning, cognitive flexibility, and inhibitory control. Based on the aforementioned  
76 trade-off hypothesis (Tello-Ramos et al., 2019), we predicted a greater learning performance  
77 in guppies from the predictable treatment and a greater performance in the cognitive  
78 flexibility and inhibitory control tasks in guppies exposed to the unpredictable treatment.

79         We additionally administered two behavioural tests to the guppies because  
80 environmental predictability may affect various behavioural traits in fish (e.g., Sloat &

81 Reeves, 2014; Goldberg et al., 2001; Riotte-Lambert & Matthiopoulos, 2020), and the  
82 behavioural type of a fish often covaries with its cognitive abilities or affects the outcome of  
83 some cognitive tests (e.g., Savaşçı et al., 2021; Trompf & Brown, 2014). Therefore, eventual  
84 cognitive differences between the two predictability treatments could be at least in part due  
85 changes in guppies' behaviour. By simultaneously characterising the cognitive and  
86 behavioural phenotype of the experimental guppies, we tried to disentangle the mechanism  
87 with which predictability affects cognition. We focussed on two behavioural traits that have  
88 been consistently shown to covary with cognition in guppies: exploration and social  
89 behaviour (Lucon-Xiccato et al., 2017; Lucon-Xiccato et al., 2020b; Mair et al., 2021;  
90 Savaşçı et al., 2021). Both exploration and sociability are expected to be reduced in the  
91 predictable environment (Eide et al., 2004; Goldberg et al., 2001).

92

### 93 **Materials and methods**

#### 94 (a) Experimental manipulation of resource predictability

95 The experiments involved naïve, new-born guppies obtained from gravid females in  
96 our facility (electronic supplementary material, S1, section a). These subjects underwent  
97 exposure to environments with different levels of predictability for 20 consecutive days. We  
98 assigned a randomly chosen group of six individuals to each of 12 experimental aquaria (N =  
99 72 guppies overall). Six experimental aquaria were assigned the predictable environment  
100 treatment and the remaining six experimental aquaria to the unpredictable environment  
101 treatment (N = 6 replicates).

102 The experimental aquaria were rectangular and contained four separate foraging areas,  
103 one in each corner (Figure 1a). We administered food to the guppies once per day in one  
104 feeding area of the experimental aquarium, with a different schedule for the two treatments.  
105 For half of the aquaria assigned to the predictable environment treatment, we provided the

106 food at 11:00 h; for the remaining half in the aquaria of the predictable environment  
107 treatment, we provided the food at 15:00 h. Moreover, in the predictable environment  
108 treatment, the food was consistently administered in a predetermined foraging area per each  
109 aquarium. In the unpredictable environment treatment, we provided the food each day at a  
110 random time between 8:00 to 18:00 h and in a foraging area determined according to a  
111 pseudo-random scheme. Details of the treatment are provided in electronic supplementary  
112 material, S1, section b. At the end of the treatment, four subjects randomly collected from  
113 each experimental aquarium were used in the cognitive and behavioural assays, which were  
114 administered to a predetermined sequence (electronic supplementary material, S1, section c).  
115 We interrupted the testing of one subject because it showed signs of distress in the first assay.  
116 Therefore, the sample used in the study was N = 47 guppies, including 23 of the predictable  
117 environment treatment and 24 of the unpredictable environment treatment.

118

#### 119 (b) Learning assay

120 The learning assay was based on an established discrimination paradigm in which the  
121 guppies had to select a rewarded colour stimulus between two options (Lucon-Xiccato et al.,  
122 2022a; Montalbano et al., 2022). Briefly, each subject was tested in an experimental  
123 apparatus consisting of two chambers connected by a central corridor (Figure 1b). The  
124 apparatus was maintained under standard conditions and was provided with several  
125 enrichments (electronic supplementary material, S1, section d). After a pre-test procedure  
126 (electronic supplementary material, S1, section d), each subject underwent 12 colour  
127 discrimination trials per day. In each trial, the experimenter inserted two stimulus cards in  
128 one of the two chambers of the apparatus. Each card had a circle ( $\varnothing$  1.8 cm), either yellow or  
129 red. For each subject, one of the two colours was considered as the correct stimulus. The  
130 correct colour was counterbalanced between the experimental groups and the left-right

131 position of the correct colour was counterbalanced between trials. If the fish approached the  
132 correct colour within 15 min, it received a food reward; otherwise, the experimenter removed  
133 the cards. As the approach, we considered when the subject swam at 0.5 body length or less  
134 from the stimulus, oriented toward the stimulus. The testing of each guppy continued until it  
135 reached a criterion of less than 30% errors two consecutive days. In each day of testing, we  
136 recorded the number of errors and the number of correct responses of each subject.

137

#### 138 (c) Cognitive flexibility assay

139 After the learning task, we administered a reversal learning task to assess cognitive  
140 flexibility following the paradigm of previous studies in teleost fish (Lucon-Xiccato &  
141 Bisazza, 2014; Montalbano et al., 2022). The apparatus and the procedure were the same as  
142 for the test phase of the learning task. However, the experimenter rewarded the choice of the  
143 previously unrewarded colour. The reversal learning task started the day after the subject  
144 reached the criterion of the learning task. The testing continued until each subject reached a  
145 criterion less than 30% errors, and in each day, we collected the number of errors and correct  
146 responses, as previously described.

147

#### 148 (d) Inhibitory control assay

149 Following a paradigm implemented in this species (Lucon-Xiccato & Bertolucci,  
150 2019; Montalbano et al., 2020), we assessed inhibitory control as the ability to withhold  
151 attempts to capture an unreachable prey behind a transparent barrier. Guppies underwent the  
152 inhibitory control assay individually in 4-L experimental aquaria maintained under standard  
153 conditions (Figure 1c; electronic supplementary material, S1, section e). To perform the  
154 assay, the experimenter presented to the subject a laboratory glass tube ( $\varnothing$  1.2 cm) containing  
155 a solution of water and approximately 500 live *Artemia salina* nauplii. The tube was

156 suspended near one extremity of the apparatus. The guppies were accustomed to *A. salina*  
157 nauplii, as this prey was provided during the maintenance. Moreover, during a pre-test phase,  
158 the subjects were trained to feed in correspondence of the same extremity of the apparatus  
159 subsequently used to present the tube (electronic supplementary material, S1, section e).  
160 Therefore, most of the subjects rapidly approached the tube and attempted to capture the  
161 prey. Guppies' behaviour was videorecorded for 20 min, allowing the experimenter to record  
162 the capture attempts from the recordings played back at a reduced speed. The experimenter  
163 recorded as an error each event in which a guppy touched the glass tube with the snout in an  
164 attempt to capture a prey. Moreover, the experimenter recorded when the subject approached  
165 the stimuli for the first time. Because of an issue with the webcam software, we did not  
166 retrieve the recordings of 4 subjects. Therefore, the sample size of this assay was 43 guppies,  
167 22 of the predictable environment treatment and 21 of the unpredictable environment  
168 treatment.

169

#### 170 (e) Behavioural tests

171 First, we conducted a novel environment exploration test in an open-field arena  
172 (Brown et al., 2007; Burns, 2008; Burns et al., 2016). The guppies were observed  
173 individually in an unfamiliar, white, empty arena (Figure 1d) for 20 min. During this period,  
174 using an automatic tracking system (electronic supplementary material, S1, section f), we  
175 measured two variables. The first variable was the activity of the subject as the distance  
176 moved. The second variable was the time the subjects spent in the centre of the arena (10 cm  
177 from the edges). This latter variable is considered proxy for various behavioural traits. For  
178 instance, shy, more neophobic, and more anxious individuals tend to avoid the centre of the  
179 apparatus where they perceive to be more exposed to potential predators (thigmotaxis  
180 behaviour; Blaser et al., 2010; Kotrschal et al., 2014).



181 Second, we conducted a social behaviour test (Cattelan et al., 2019) in which the  
182 guppies were tested in the central compartment of a three-chamber apparatus (Figure 1e). The  
183 two lateral chambers were divided from the central one by a transparent partition. One lateral  
184 chamber contained a shoal of five guppies and the other was left empty. The experimenter  
185 released the fish in the apparatus and then recorded its behaviour for 20 min. From the video  
186 recordings, the experimenter obtained the time spent by the subject close to the social  
187 stimulus (i.e., within 5 cm) and the time spent close to the empty lateral chamber. From this  
188 data, we calculated an index of sociability for each subject considering that more social  
189 individuals were expected to spend more time close to the stimulus compared to the empty  
190 chamber. Further details of this procedure are reported in electronic supplementary material,  
191 S1, section g.

192

### 193 Research ethics

194 The experiments complied with ‘Directive 2010/63/EU of the European Parliament  
195 and of the Council of 22 September 2010 on the protection of animals used for scientific  
196 purposes’ and with Italian law ‘D. Lgs n. 26 4 marzo 2014 Attuazione della direttiva  
197 2010/63/UE sulla protezione degli animali utilizzati a fini scientifici’. The procedures were  
198 designed following the ASAB/ABS Guidelines for the Use of Animals in Research  
199 (<https://doi.org/10.1016/j.anbehav.2019.11.002>) and were approved by the Ethical committee  
200 (OPBA) of University of Ferrara (permit TLX-2022-1).

201

## 202 Results

### 203 (a) Predictable environment enhanced learning

204 All the subjects tested (N = 47) reached the criterion in the colour discrimination  
205 learning task in a relatively short period of time ( $4.43 \pm 2.58$  days, mean  $\pm$  standard

206 deviation). The analysis on the number of errors across testing days found a significant  
207 decrease (Generalised Linear Mixed-effects Model, GLMM:  $\chi^2_1 = 179.290$ ,  $P < 0.001$ ). This  
208 suggested that the subjects progressively learned to choose the correct colour. Critically, the  
209 decrease in number of errors was steeper for the guppies of the predictable environment  
210 comparing to the guppies of the unpredictable environment (GLMM:  $\chi^2_1 = 18.769$ ,  $P < 0.001$ ;  
211 Figure 2a). Therefore, learning was faster for the guppies of the predictable environment.

212

### 213 (b) Unpredictable environment enhanced cognitive flexibility

214 All the subjects tested ( $N = 47$ ) reached the criterion in the reversal learning assay.  
215 The number of days to the criterion in the reversal learning assay ( $8.36 \pm 4.06$  days) was  
216 approximately twice as that observed in the initial learning assay, suggesting greater  
217 difficulty of the cognitive flexibility assay for the guppies (paired-samples t test:  $t_{46} = 5.126$ ,  
218  $P < 0.001$ ).

219 The number of errors in the reversal learning assay significantly decreased across  
220 testing days (GLMM:  $\chi^2_1 = 564.565$ ,  $P < 0.001$ ), as expected due to subject's learning to  
221 handle the reversed reward contingency. Critically, the decrease in number of errors was  
222 steeper for the guppies of the unpredictable environment comparing to the guppies of the  
223 predictable environment (GLMM:  $\chi^2_1 = 17.198$ ,  $P < 0.001$ ; Figure 2b), suggesting greater  
224 cognitive flexibility in the guppies of the former treatment.

225

### 226 (c) Unpredictable environment enhanced inhibitory control

227 27 out of 43 guppies attempted to capture the stimulus prey, on average within the  
228 third minute ( $\pm 3.88$ , standard deviation) from the beginning of the test. The environment  
229 experienced by the subject did not affect whether it approached the prey (predictable  
230 environment: 16 out of 22 subjects; unpredictable environment: 11 out of 22 subjects; Fisher

231 exact test: = 0.215). Similarly, the environmental treatment experienced did not affect when  
232 the subjects approached the prey (two-samples t test:  $t_{25} = 0.099$ ,  $P = 0.922$ ; Figure 3a).

233 Overall, we observed 1661 attempts to capture the prey, with an average of  $61.52 \pm$   
234  $63.39$  (mean  $\pm$  standard deviation) attempts per subject. The number of attempts was higher  
235 at the beginning of the experiment and then, decreased over testing time (GLMM:  $\chi^2_1 =$   
236  $111.241$ ,  $P < 0.001$ ). Guppies from the predictable environment displayed a higher number of  
237 attempts (predictable environment:  $74.69 \pm 67.45$ ; unpredictable environment:  $42.36 \pm 62.87$ ;  
238 GLMM:  $\chi^2_1 = 5.413$ ,  $P = 0.020$ ; Figure 3b).

239

240 (d) Level of predictability did not affect variance within experimental group

241 The performance variance observed within each of the two experimental groups of  
242 guppies was not significantly different in any of the cognitive tasks (Bartlett tests: number of  
243 errors in the learning assay: Bartlett's  $K^2 = 0.273$ ,  $P = 0.601$ ; number of errors in the  
244 cognitive flexibility assay: Bartlett's  $K^2 = 0.033$ ,  $P = 0.856$ ; number of number of attempts in  
245 the inhibitory control assay: Bartlett's  $K^2 = 0.056$ ,  $P = 0.813$ ).

246

247 (e) Predictability affected guppies' activity but this did not explain cognitive plasticity

248 In the open-field test, the activity of the subjects decreased significantly across testing  
249 time (Linear Mixed-effects Model, LMM:  $\chi^2_1 = 239.026$ ,  $P < 0.001$ ). Moreover, guppies from  
250 the unpredictable environment showed greater activity (LMM:  $\chi^2_1 = 4.547$ ,  $P = 0.033$ ; Figure  
251 4a). The time spent in the centre of the arena in the open-field test was significantly affected  
252 only by the experimental time (LMM:  $\chi^2_1 = 7.055$ ,  $P = 0.008$ ), with no changes due to the  
253 treatment (Figure 4b). In the sociability test, none of the terms in the model, including the  
254 treatment, significantly explained the preference for the social stimulus (LMM: all P-values  $>$   
255  $0.5$ ; Figure 4c).

256 A regression analysis indicated that activity did not explain performance in the  
257 learning (linear regression:  $t = -0.740$ ,  $P = 0.463$ ,  $R^2 = 0.012$ ), cognitive flexibility (linear  
258 regression:  $t = -0.363$ ,  $P = 0.718$ ,  $R^2 = 0.003$ ), and inhibitory control task (linear regression:  $t$   
259  $= 0.207$ ,  $P = 0.838$ ,  $R^2 = 0.002$ ). Therefore, the effects of environmental predictability in the  
260 cognitive tasks are not explained by the change in behavioural activity detected in the  
261 exploration task.

262

## 263 **Discussion**

264 Our study revealed that guppies can develop a highly diversified cognitive phenotype  
265 that matches the resource predictability level experienced in the environment. When food was  
266 predictably found in the same spatial location and at the same time of the day, guppies  
267 developed greater learning performance. Conversely, when the location and timing of the  
268 food were unpredictable, guppies developed greater cognitive flexibility and greater  
269 inhibitory control.

270 We designed the study to investigate the effect of predictability experimentally and  
271 thus, we analysed populations of subjects exposed to very different levels of predictability. In  
272 nature, smaller fluctuations in the predictability levels experienced are likely to similarly  
273 determine plasticity-mediated cognitive variability between and within populations. The  
274 effect of predictability aligns with growing reports of cognitive plasticity in teleost fishes in  
275 response to other environmental factors (e.g., environment quality: Kotrschal & Taborsky,  
276 2010; social environment: Lucon-Xiccato et al., 2022b; enrichment: Montalbano et al., 2022;  
277 predation risk: Villa Pouca et al., 2021). All these forms of cognitive plasticity may interact  
278 in nature, thereby determining a broad spectrum of individual phenotypes. Concerning this, it  
279 will be important to ascertain whether the cognitive variability due to plasticity is stable  
280 across an individual's life or it can be altered if the environment changes. Some forms of

281 cognitive plasticity displayed by fish are likely malleable, such as those determined by factors  
282 that vary with the season (Carbia & Brown, 2020; López-Olmeda et al., 2021), further  
283 amplifying the potential of plasticity to produce individual differences in cognition. Notably,  
284 while the teleost's brain certainly displays a remarkable level of neural plasticity potential  
285 (reviewed in Ebbesson & Braithwaite, 2012), including extensive neurogenesis capacity in  
286 the adult (reviewed in Zupanc, 2006), cognitive plasticity might be also widespread in  
287 tetrapod vertebrates (e.g., Jankowsky et al., 2005; Tang et al., 2001).

288         The plasticity due to predictability level has differently affected the three cognitive  
289 functions investigated in this study, aligning with the trade-off hypothesis proposed by Tello-  
290 Ramos and colleagues (2019). This provides support for the idea that the observed cognitive  
291 plasticity is adaptive at least from two points of view. First, the trade-off hypothesis is based  
292 on the fact that enhancing functions such as learning and memory, should be advantageous  
293 when the environmental conditions are predictable because they permit to rapidly and reliably  
294 exploit resources that are available consistently with the same spatial and/or temporal pattern.  
295 Conversely, executive functions such as cognitive flexibility and inhibitory control are  
296 involved in modifying individuals' behaviour (Diamond, 2013), which should permit to  
297 adjust to resources that vary in space and time. Second, the function specificity *per se*  
298 supports the idea of an adaptive mechanism. A more general, non-adaptive mechanism is  
299 indeed expected to determine unidirectional changes (i.e., an increase or decrease) in all the  
300 cognitive abilities of an individual, a scenario that contrasts with what was observed in our  
301 study. Function specificity has also been reported for other forms of cognitive plasticity. For  
302 instance, guppies raised in the presence of biotic and abiotic stimuli developed greater  
303 learning ability compared to guppies raised in barren environments, but no differences were  
304 observed in inhibitory control and cognitive flexibility (Montalbano et al., 2022). Many  
305 earlier investigations on plasticity and adaptive selection have focussed on general proxies of

306 cognition, such as brain size (e.g., Burns et al., 2009; Reyes et al., 2022). The findings in  
307 relation to function-specific effects suggest the need of a more precise approach that  
308 investigates cognition at the level of single functions to depict cognitive adaptation fully.

309         The unpredictable treatment also increased guppies' activity (but did not affect our  
310 measures of boldness and social behaviour). Variability in behavioural traits has been linked  
311 to cognitive variability (Carere & Locurto, 2011), including in our study species (Budaev &  
312 Zhuikov, 1998; Lucon-Xiccato & Dadda, 2017; Savaşçı et al., 2021; Trompf & Brown,  
313 2014). However, in our correlation analysis, the observed effect on activity did not emerge as  
314 a potential explanation for the differences observed in the cognitive tasks. Unpredictable  
315 environmental conditions are also known to increase corticosteroid concentrations in all main  
316 vertebrate groups, including teleost fish (review by Wingfield & Ramenofsky, 1999) and  
317 these hormones may affect cognitive abilities in a range of tasks (Barreto et al., 2006; Endo et  
318 al., 1996; Saldanha et al., 2000). Therefore, corticosteroids are proximate mechanisms worth  
319 investigating for the effect observed in guppies.

320         In conclusion, we demonstrated a form of cognitive plasticity driven by the levels of  
321 predictability of resources in an environment. This plasticity determined cognitive variability  
322 along a trade-off line between functions useful to learn and fixate a specific behaviour and  
323 functions that permit changes in behaviour, highlighting that cognitive plasticity might have  
324 an important role in determining variance in cognitive phenotypes. To fully understand  
325 cognitive variability in animals, research efforts should be devoted to analyse other forms of  
326 cognitive plasticity and their interacting effects on individual's cognition. Altogether,  
327 multiple plasticity mechanisms might be responsible for individualities in cognitive abilities.

328

329 **Data accessibility**

330 The datasets supporting this article have been uploaded in electronic supplementary  
331 material S2. Details of the statical analysis are provided in electronic supplementary material,  
332 S1, section h.

333

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337

### 338 **Authors' contributions**

339 T.L.-X.: conceptualization, formal analysis, writing—original draft; G.M.:  
340 investigation, methodology, data curation, formal analysis, writing—review and editing;  
341 C.B.: conceptualization, writing—review and editing. All authors gave final approval for  
342 publication and agreed to be held accountable for the work performed therein.

343

### 344 **Competing interests**

345 We declare we have no competing interests.

346

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582 **Figure captions**

583 Figure 1. Diagram of the apparatuses used in the study. (a) Aquarium in which the subjects  
584 were exposed to the predictability treatments, details and lateral view. (b) Experimental  
585 apparatus for the learning and the cognitive flexibility assays, detail and top view. (c)  
586 Inhibitory control apparatus. Apparatuses used in the two behavioural assays, (d) exploration  
587 and (e) social behaviour.

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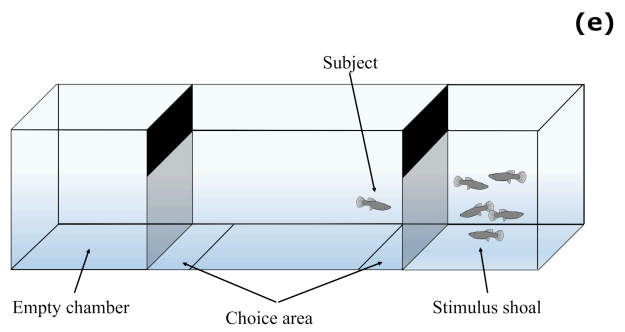
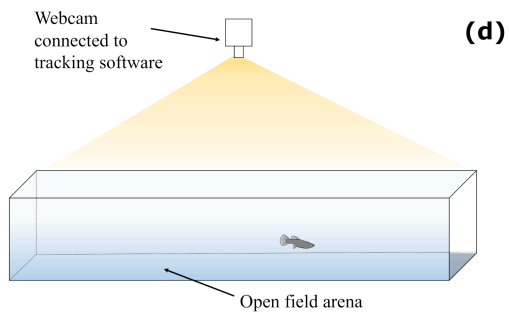
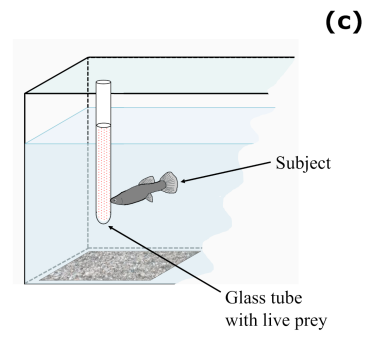
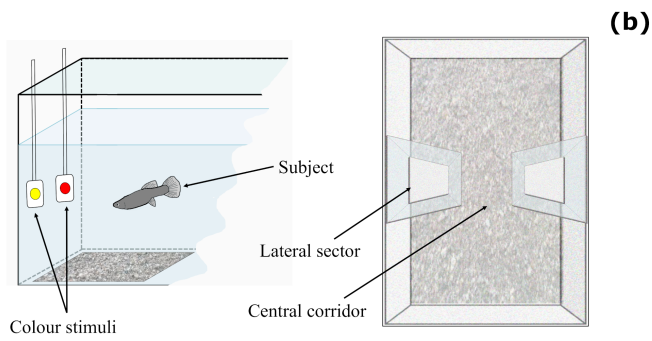
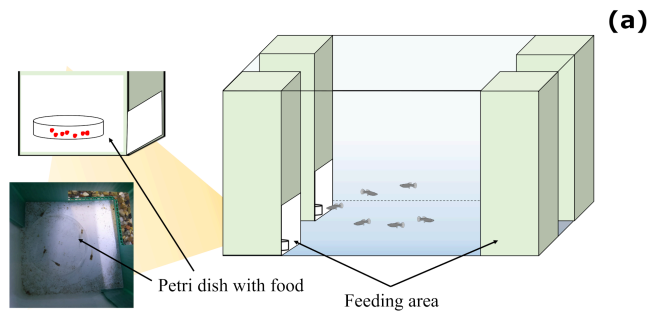
589 Figure 2. Results of the learning and the cognitive flexibility task. (a) Proportion of errors  
590 made by the subjects from the two treatments (predictable and unpredictable environment)  
591 when learning to discriminate between the two colours, divided per each day of the  
592 experiment. (a) Proportion of errors made by the subjects from the two treatments  
593 (predictable and unpredictable environment) when reversing the learned choice between the  
594 two colours, divided per each day of the experiment. In all the panels, points and shaded area  
595 represent mean and 95% confidence intervals estimated from the generalised linear mixed-  
596 effects model used in the analysis.

597

598 Figure 3. Results of the inhibitory control task. (a) Time taken by the subjects from the two  
599 treatments (predictable and unpredictable environment) to approach the stimulus prey; points  
600 and error bars represent means and standard errors, respectively. (b) Number of attempts to  
601 capture the prey performed by the subjects from the two treatments (predictable and  
602 unpredictable environment) in each minute of the test; points and shaded area represent mean  
603 and 95% confidence intervals estimated from the generalised linear mixed-effects model used  
604 in the analysis.

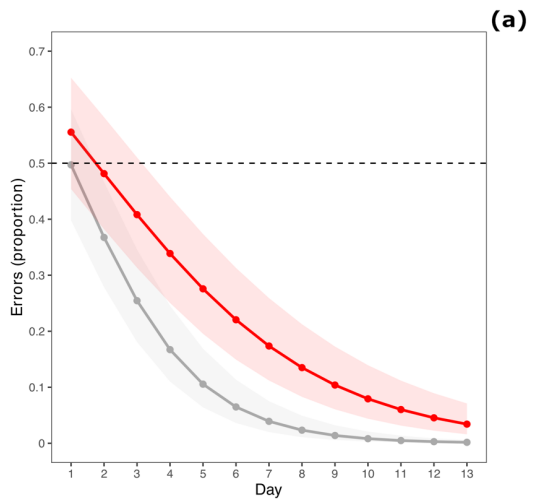
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606 Figure 4. Results of the behavioural tests. (a) Activity measured as distance moved in the  
607 exploration test. (b) Boldness measured as time spent in the centre of the arena in the  
608 exploration test. (c) Sociability as the proportion of time spent close to the social stimulus in  
609 the social behaviour test. In all the panels, points and error bars represent mean and 95%  
610 confidence intervals estimated from the linear mixed-effects models used in the analysis.  
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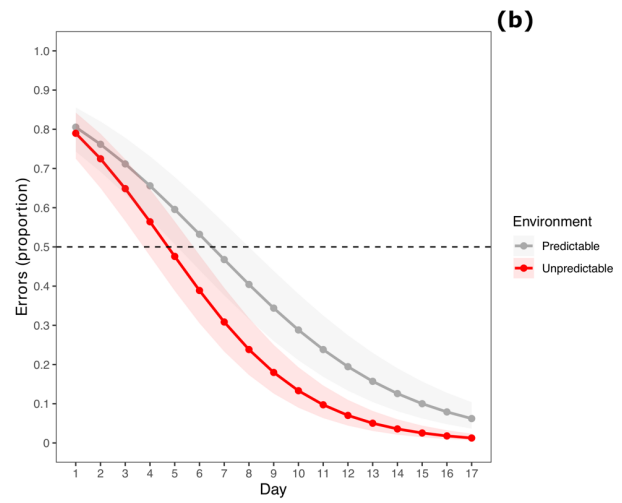
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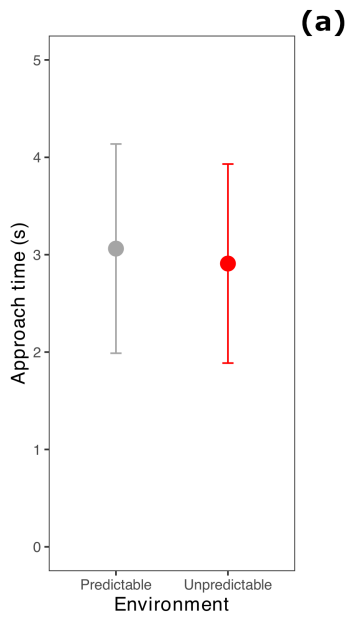


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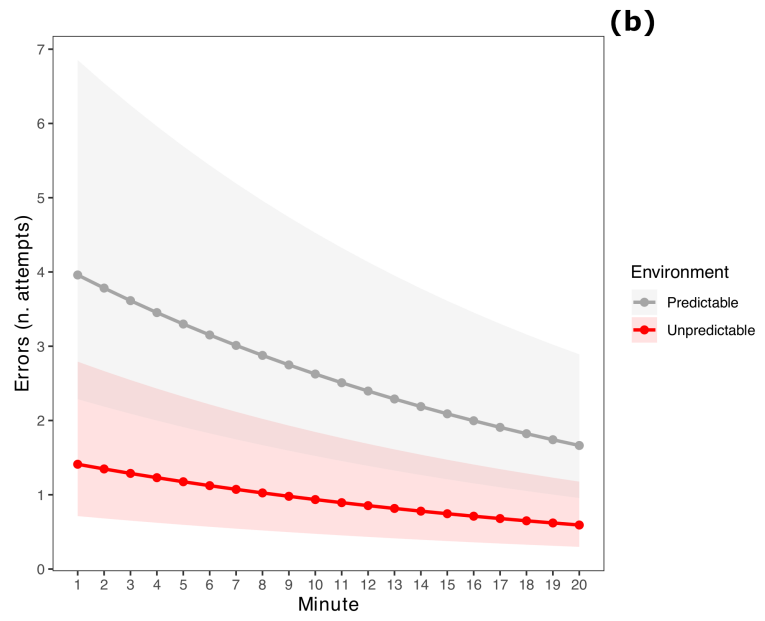


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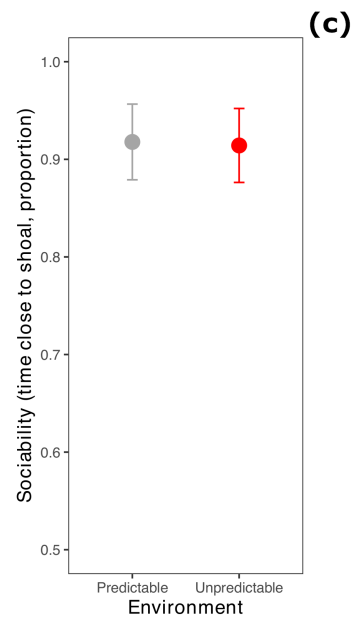
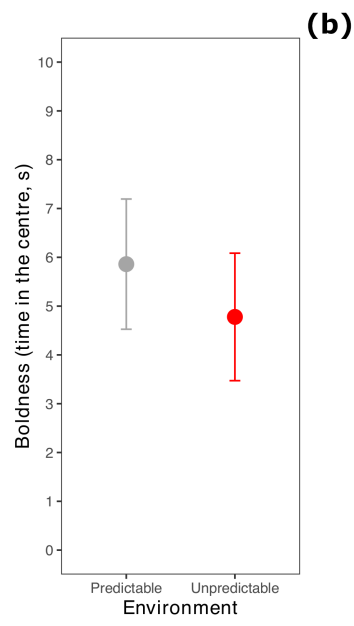
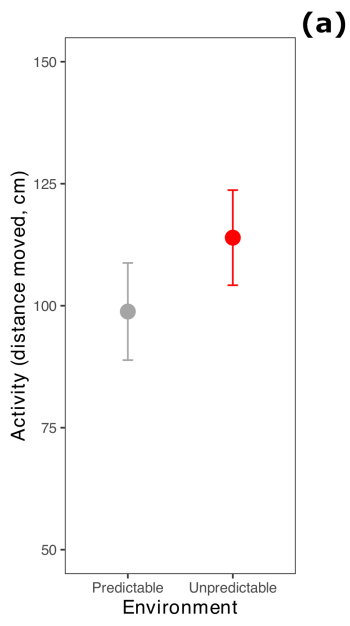


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