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Plasticity varies with boldness in a weakly-electric fish

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25 **ABSTRACT**

26 **Background:** The expression of animal personality is indicated by patterns of consistency in
27 individual behaviour. Often, the differences exhibited between individuals are consistent
28 across situations. However, between some situations, this can be biased by variable levels of
29 individual plasticity. The interaction between individual plasticity and animal personality can
30 be illustrated by examining situation-sensitive personality traits such as boldness (i.e. risk-
31 taking and exploration tendency). For the weakly electric fish *Gnathonemus petersii*, light
32 condition is a major factor influencing behaviour. Adapted to navigate in low-light
33 conditions, this species chooses to be more active in dark environments where risk from
34 visual predators is lower. However, *G. petersii* also exhibit individual differences in their
35 degree of behavioural change from light to dark. The present study, therefore, aims to
36 examine if an increase of motivation to explore in the safety of the dark, not only affects
37 mean levels of boldness, but also the variation between individuals, as a result of differences
38 in individual plasticity.

39 **Results:** Boldness was consistent between a novel-object and a novel-environment situation
40 in bright light. However, no consistency in boldness was noted between a bright (risky) and a
41 dark (safe) novel environment. Furthermore, there was a negative association between
42 boldness and the degree of change across novel environments, with shier individuals
43 exhibiting greater behavioural plasticity.

44 **Conclusions:** This study highlights that individual plasticity can vary with personality. In
45 addition, the effect of light suggests that variation in boldness is situation specific. Finally,
46 there appears to be a trade-off between personality and individual plasticity with shy but
47 plastic individuals minimizing costs when perceiving risk and bold but stable individuals
48 consistently maximizing rewards, which can be maladaptive.

49 **KEYWORDS:** boldness; behavioural plasticity; individual variation; weakly-electric fish

50 **BACKGROUND**

51 Variation in behaviour between individuals has been shown extensively in many
52 animal populations and linked to the way animals cope with their environment [1, 2]. Often,
53 the variation is indicated on a continuum ranging from the lowest to the highest level of
54 behavioural response within the population [3] and as such indicates the degree each
55 individual exhibits the behaviour in relation to the rest of the population. This variation can
56 be consistent across contexts (i.e. functional behavioural categories such as feeding),
57 situations (i.e. sets of current conditions such as feeding with and without predators) and time
58 [4, 5, 6]. Each behaviour that is consistently variable between individuals is termed an *animal*
59 *personality trait* and a number of such traits can be used to describe personality in animals
60 [7]. One of the most examined animal personality traits is *boldness*, which is indicated on a
61 shy–bold axis [8]. Human-derived terminology defines boldness as the consistent willingness
62 to take risks in unfamiliar situations [9]. This definition is often appropriated when studies
63 consider its evolutionary and ecological consequences [10]. However, 'ecologically-based'
64 approaches typically define bolder individuals as those that are the least affected by risk and
65 more willing to approach and explore novel objects or environments [11, 12].

66 Boldness, like all personality traits, remains consistent depending on the degree in
67 which behavioural plasticity varies between individuals [13]. On one hand, individuals can
68 adjust their behaviour, but the extent of adjustment may be relatively uniform within the
69 population. Thus, even if mean levels of behaviour change, between-individual variation is
70 maintained, i.e. all individuals show similar plasticity [14]. For example, the mean boldness
71 (propensity to exit shelter) of salamander larvae decreases in the presence of predators, but
72 the variation between individuals is maintained across situations with and without predators
73 [15]. On the other hand, environmental changes can affect the behaviour and physiology of
74 some individuals more than others [16, 17], e.g. rainbow trout that exhibit lower activity and

75 aggressiveness are affected more by increasing environmental stressors [18]. Consequently,
76 behavioural variability within populations can be biased by the variable degree in which
77 environmental changes affect individuals. Individuals may be more or less flexible over an
78 environmental gradient of changing conditions, i.e. they exhibit variable levels of *individual*
79 *plasticity* [19].

80 Links between personality and individual plasticity have been reported when testing
81 boldness across situations varying in their level of risk and familiarity [20]. Lima and
82 Bednekoff suggest that behavioural response depends on the level of perceived risk, which
83 can vary between individuals [21]. A greater response can thus be associated with a greater
84 perception of risk, even when uncertain about its presence, while the ability to adjust
85 response, depending on risk levels, can be overall more beneficial for surviving in the wild
86 [22]. This manifests in risk-taking behaviour, with individuals that respond more to risk (i.e.
87 those taking less risk) also showing greater changes across shifting levels of perceived risk.
88 For example, between situations that vary in perceived predatory risk (presence or absence of
89 sparrowhawk model), shy chaffinches (least active in a novel environment) show greater
90 behavioural plasticity than bold chaffinches (most active in a novel environment) [23].
91 Mortality, growth and fecundity can all be affected by an individual's response to changes in
92 risk [24], e.g. shier damselfish show lower mortality rates by being less active in unfamiliar
93 environments [25]. It is therefore imperative to examine how changes in levels of perceived
94 risk can affect boldness and individual plasticity.

95 For weakly-electric fish, the level of perceived risk in their environment is most
96 significantly affected by light conditions. Most species prefer lower light transmission, where
97 they can integrate their electric-sensing with other senses in the absence of light [26, 27]. One
98 example is the Central African mormyrid *Gnathonemus petersii*, which favours nocturnal
99 activity and turbid, vegetated waters [28,29]. This species can perceive spatial features,

100 navigate and explore objects and environments by using active electrolocation, i.e. the
101 sensing of changes to a self-produced electric discharge [30, 31]. Though often being prey to
102 bigger electric fish, it is argued that a function of electrolocation is avoiding risk from
103 visually-guided predators in darker environments [31, 32]. The lower predation risk would
104 increase their motivation to approach and explore objects and environments, hence their
105 preference to be active in the dark [26, 27]. However, the change in motivation can be greater
106 in some individuals, depending on how plastic they are, which can affect mean boldness
107 levels. This is supported by evidence of differences between individuals in the degree of
108 change in food searching times across light conditions [32]. The aim of the present study was
109 to examine boldness and changes in boldness across situations, with a particular interest in
110 the effect of light conditions on individuals.

111 Boldness was indicated by the willingness of *G. petersii* to approach (latency times)
112 and inspect (exploration times) novel objects and environments. First, fish were tested with a
113 different novel object on four occasions, to control for differences in object characteristics.
114 The tests were carried out in a bright, familiar environment. Then, individuals were tested in
115 two separate novel-environment situations differing in light condition, i.e. a dark and a bright
116 novel-environment. Finally, an intra-individual variance statistic was used to measure
117 individual plasticity across the environmental gradient between bright and dark [19, 33]. It
118 was tested whether boldness from the novel-object tests **1**) was consistent with boldness in
119 the bright and dark novel-environment situations and **2**) related to individual plasticity across
120 these novel-environment situations.

121

122 METHODS

123 *Animal maintenance and housing*

124 Twelve juvenile (70-100 mm length), wild-caught *G. petersii* of unknown gender
125 (external sexual dimorphism is lost in captivity) [34] were imported and commercially
126 supplied by Grosvenor's Tropicals, Lisburn, Northern Ireland. Fish were housed individually
127 in ~25L of water, fed 15-20 chironomid larvae daily and kept on a 12h:12h light to dark
128 photoperiod. Housing tanks were enriched with shelter (plastic pipes), sediment and plastic
129 plants, stones and ceramics. Housing and experimental tanks were fitted with filtering and
130 heating equipment and kept on same-level benches. Water quality in all tanks was tested
131 twice-weekly and maintained by partial water changes (mixed tap and reverse osmosis
132 water). The pH was kept at 7.2 ± 0.4 , temperature at $26 \pm 1^\circ$ and conductivity at a range
133 between 150-300 $\mu\text{S}/\text{cm}$.

134 ***Behavioural tests***

135 *Test conditions and procedures*

136 Light conditions varied between those within (*bright light* at 350-600 nm and 300 lux
137 at water surface) and those exceeding (*dark* in infra-red light >800 nm and 0 lux at water
138 surface) the visible spectrum of *G. petersii* [35]. Water conductivity in the test tanks was
139 150 ± 50 $\mu\text{S}/\text{cm}$. External cues were limited by attaching visual barriers (opaque blue plastic
140 sheets) around both the novel-environment test tanks and the housing tanks, during testing.
141 Behavioural variables were measured live during the novel-object test and from recordings of
142 the novel-environment test. This was carried out by a single observer (KK), with a response
143 latency of 1-2 seconds, using a stopwatch with a $\pm 0.2\text{s}$ measuring error.

144 *Novel-object tests*

145 Novel-object tests were in bright light. These were carried out following a two week
146 acclimatisation period to ensure that the objects were novel to the fish, but not the
147 environment (housing tank). Each individual received four separate novel-object tests, with a
148 5 minute interval between each test. The test was repeated with different novel objects in

149 order to control for variation in potential effects elicited by the differences in the
150 characteristics of novel objects. These effects could result from how each object is perceived
151 by individuals. *G. petersii* can sense multiple properties of objects, some of which are
152 typically not perceived by non-electrosensing fish, such as resistance and capacitance [29].
153 To that end, the novel objects not only differed in shape, colour and size, but also material.
154 Objects included: a ~ 5cm long black fishing weight (A), a ~7cm long stainless-steel fishing
155 lure without the hook (B), a ~15cm long yellow/green plastic dinosaur toy (C) and a 10cm³
156 multicolour wooden cubic toy attached to a small brass weight (D). Following
157 recommendations from Wilson et al. [36], objects were presented to each fish in the same
158 order (A-B-C-D) to control for carryover effects. The objects were lowered in housing tanks
159 at the furthest non enriched area from the individual's shelter using a monofilament-line
160 pulley-system. Fish were given up to five minutes to approach each object (within ~1.5 body-
161 lengths), which was measured as latency time [11]. Then a further 1 minute was allowed for
162 exploration (75% of individuals explored new objects under 55s in preliminary studies; see
163 additional material), during which the time spent performing electrosensing movements
164 (motor probing acts, e.g. lateral and chin probing) [37] within the 1.5 body-length distance
165 was measured as exploration time.

166 *Novel environment tests*

167 The recording of the novel-environment tests was carried out both under bright light
168 and in the dark and started a week after the novel-object tests (overall three weeks in the
169 laboratory), which allowed individuals to acclimatise to laboratory light conditions. Timers
170 switched between bright light and dark photoperiods every 12 hours (lights went on at 7am
171 and off at 7pm), daily. Novel-environment tests were carried out with a random light-
172 condition order between fish. Individuals randomly selected to be tested first in the dark,
173 were tested between 5am and 6am and then in bright light between 8am and 9am. Those

174 randomly selected for being tested first in bright light, were tested between 5pm and 6pm and
175 then in the dark between 8pm and 9pm. This procedure of recording during normal laboratory
176 photoperiods controlled for the risk of effects from circadian rhythms [31]. Each individual
177 was introduced to a segregated housing section (30cm Length by 30cm Width and 30cm
178 Height, ~27L) of the experimental tank with shelter and enrichments. Here, individuals were
179 allowed to habituate for ~12 hours prior to their first novel-environment test, and ~2 hours
180 during photoperiod changes between tests (~ an hour before and ~ an hour after lights turned
181 on or off). Tests began by lifting the plastic opaque divider creating the housing section via a
182 pulley system, allowing the fish entry to the rest of the tank (60cm Length by 30cm Width
183 and 30cm Height, ~54L). This area constituted the novel environment and included items that
184 were similar to enrichments in their housing tanks i.e. shelters (plastic pipes), ceramics,
185 stones and plastic plants of variable sizes. The items within the novel area were rearranged
186 and/or replaced between bright and dark tests for all fish. A wall-mounted infra-red camera
187 provided a live feed of the entire novel-environment test-tank from a birds-eye view. This
188 was relayed through a recorder to a computer placed out of view from the tank. During
189 recording, fish were allowed up to a maximum of 1 hour to enter the novel environment (i.e.
190 until an individual's tail passed the mark on the bottom of the tank) and a further 10 minutes
191 to explore. During the later viewing of the recordings, latency time was measured until an
192 individual entered the novel environment or until the hour-mark was reached, in which case
193 latency was recorded at 3600s and exploration at 0s (this was the case for only one individual
194 in the bright novel environment). Exploration was measured as the time actively moving in
195 the novel area and performing electrosensory probing acts.

196 *Analysis*

197 Calculations, statistical analyses and graphical representations were all produced in
198 Minitab[®] statistical software (version 17; Minitab Inc., State College, PA). Data from the

199 novel-object tests were either normally or approximately normally distributed. Only
200 exploration times from the novel-environment test data were normally distributed. Measures
201 were summed to produce composite, standardized boldness scores. This was carried out by
202 adding positive (time exploring) and subtracting negative (latency time to approach)
203 indicators and then standardising (*z*-scores).

204 In novel-object tests, some individuals were both less latent to approach and more
205 explorative than others (FIG 1 A). Preliminary analyses on the novel-object tests indicated a
206 strong linear relationship between latency and exploration ($R^2=0.500$, $F_{1,47}=47.32$, $P<0.01$).
207 Even though some differences were apparent between objects (FIG 1 A), these were not
208 significant ($R^2=0.065$, $F_{3,47}=2.04$, $P=0.122$). This suggested that boldness levels were
209 indicated by both measures with no effect from object characteristics. Measures from all four
210 novel-object tests were, thus, used to create boldness scores. Inter-individual differences in
211 latency and exploration were not similar between bright and dark novel environments (FIG
212 1B). Separate boldness scores were produced for each novel-environment situation, dark and
213 bright. Composite scores were used to test consistency in boldness across novel-environment
214 situations and between novel-environment and novel-object situations. For this, two Linear
215 Regression models (LR) were used. The first (LR1) tested the relationship between bright and
216 dark novel-environment scores. The second (LR2) tested if the effect of situation also
217 affected how novel-environment scores related to novel-object scores, i.e. were predicted by
218 situation, dark or bright, and its interaction with novel-object scores.

219 To calculate individual plasticity statistics, typically a measure of each individual's
220 variance between two situations is used [38]. Following Asendorpf's [33] suggestions, here,
221 this was measured as the intra-individual variance (*Var*) of each fish such that

$$Var_{xy} = \frac{(z_x - z_y)^2}{2}$$

222 where z is the standardized phenotypic score (here the novel-environment boldness score) at
223 situation x (bright) and y (dark). Higher intra-individual variance values designated greater
224 degree of change and therefore greater individual plasticity. In order to test if individual
225 plasticity varied with boldness, intra-individual variance statistics were then correlated with
226 novel-object boldness scores (Spearman's, r_s).

227

228 **RESULTS**

229 Individual scores were not consistent between novel-environment situations (LR1, $R^2=0.251$,
230 $F_{1,11}=3.35$, $P=0.097$) (FIG 2a). Boldness was significantly different between the bright and
231 dark novel environment (LR2, $R^2=0.211$, $F_{1,23}=6.85$, $P=0.016$), being on average greater and
232 less variable in the dark ($\bar{x}=0.45$, $s=0.09$) than in the bright ($\bar{x}= -0.45$, $s=1.28$) novel
233 environment (FIG 2a). However, the change between bright and dark was greater for some
234 fish (FIG 2b). Those with the greater change were also ones with below-median novel-object
235 boldness (FIG 3). The change between bright and dark affected the relationship between
236 novel-object and novel-environment scores (LR2, interaction: $R^2=0.143$, $F_{1,11}=4.65$,
237 $P=0.043$), which was stronger with the bright than the dark novel-environment scores (FIG
238 3). The intra-individual variance in boldness between the two novel-environment situations
239 was strongly negatively correlated with boldness score from the novel-object tests
240 (Spearman's, $r_s= -0.776$, $P=0.003$) (FIG 4).

241

242 **DISCUSSION**

243 This study provides compelling evidence supporting the hypothesis that the
244 degree of individual plasticity varies significantly with personality. Boldness was inconsistent
245 between bright and dark novel-environments (FIG 2a) and the intra-individual variance
246 exhibited across these environments depended on boldness (FIG 4). However, when

247 maintaining bright light conditions, changes in levels of familiarity/novelty (whether it is a
248 single unfamiliar object or a completely unfamiliar environment) seem to have little effect on
249 behavioral variability between individuals (FIG 3a). These findings emphasize the
250 overwhelming effect of light condition and indicate a boldness trait which is specific to
251 higher risk situations, given that bright light is naturally avoided by *G. petersii* [27].

252 An indirect effect of the environment can be seen when regularly changing conditions
253 (e.g. light, temperature and turbidity) influence the motivational state of individuals. For
254 example, small within-day increases in temperature relate to an increase in the tendency of
255 damselfish to exit a shelter (measure of boldness), but more so in some individuals than
256 others [39]. It is suggested that an increased motivation to exit shelter and look for food can
257 be associated with the need to compensate for the increased metabolic rates under elevated
258 temperatures [39;40]. The present study reaffirms that a similar effect is induced by perceived
259 risk through manipulations of light. The decrease in risk in the dark (lower predator threat)
260 increases the motivation to explore a novel environment in some individuals and as a result
261 impacts mean boldness in that situation. Notably, the results presented here also show that the
262 effect varies with boldness (FIG 3), i.e. perceived risk affects the motivation of shier
263 individuals more. Motivation levels can vary as a function of personality [41] and therefore
264 the impact on motivation by changing conditions may also vary depending on personality
265 traits like boldness.

266 The negative relation between boldness and individual plasticity (FIG 4) indicates
267 trade-offs that enable bolder individuals to out-compete shier ones (e.g. for food) in higher-
268 risk situations. However, maintaining bold behaviour in risky situations can be
269 disadvantageous and in the long-term maladaptive [42]. Shier individuals, which are more
270 responsive to change and more plastic [43], gain less when risks are high but compensate in
271 safer environments. This manifests in the behaviour of *G. petersii*, which is more variable in

272 situations with greater selective pressure (i.e. in bright light with high predatory risk) where
273 risk-aversion is elicited in shier fish, while in the safe dark situation boldness scores are
274 overall high (FIG 2).

275 The selection of plastic or consistent behaviour with changing conditions can depend
276 on both the physiological and cognitive state of individuals [44, 45]. Differences between
277 individuals in their physiological stress response [16, 17] and cognitive risk-assessment [22]
278 can explain the differences in strategy, i.e. plastic boldness vs. stable boldness [46]. For
279 example, recent evidence suggests that bolder fish make faster decisions [47]. There is
280 therefore a need to examine mechanisms further, including those used for sensing and
281 processing information, and test how they relate to individual plasticity and personality.

282

283 **CONCLUSIONS**

284 The current study highlights that individuals can vary in the degree of behavioural
285 plasticity exhibited between situations differing in risk level depending on their position
286 along an important animal personality axis, the shy-bold continuum. This strongly suggests
287 that the ability to cope with changing conditions, especially ones associated with the
288 perception of risk, vary between individuals as a function of their personality. Finally, it
289 accentuates that individual variation can be a significant predictor of behaviour and
290 behavioural change in wild populations.

291

292 **FIGURE LEGENDS:**

293 **Figure 1.** Latency and exploration times for each individual, as measured in all novel-object
294 tests (*a*) and each of the novel-environment situations (*b*). Individuals that were more
295 explorative, were also less latent to approach objects. Similarly, some individuals were more

296 explorative and less latent in the bright novel environment. However, in the dark novel
297 environment individuals were overall more explorative and less latent.

298 **Figure 2.** Comparisons between the bright and dark novel environment. The marginal plot
299 (*a*) shows an average increase in boldness and a decrease in variability in the dark novel
300 environment (box-plots), but also no significant linear relationship between boldness scores
301 from the two novel-environment situations (regression). The individual line plot (*b*) shows
302 some individuals changing more than others between bright and dark.

303 **Figure 3.** Linear relationships in boldness between the novel-object situation and each of the
304 novel-environment situations, bright and dark. Novel-object boldness scores were
305 significantly more consistent with those in the bright than those in the dark environment.
306 Those with novel-object boldness scores below the median (dotted line) showed more change
307 between light and dark.

308 **Figure 4.** Rank correlation between intra-individual variance and boldness scores from the
309 novel-object tests. Bolder individuals were less plastic between the bright and dark novel
310 environment.

311

312

313 **ETHICAL NOTE:** No animal was harmed. Strict procedures were followed [48] and sample
314 size was the minimum required. Procedures and laboratory conditions were inspected by the
315 Veterinary services of the DHSSPS Northern Ireland which deemed no need for licensing.
316 Fish were kept for separate experiments.

317

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321 Belfast.

322

323 **AVAILABILITY OF DATA AND MATERIAL:** The datasets supporting the conclusions
324 of this article are included within the article and its additional files.

325

326 **COMPETEING INTERESTS:** The authors have no competing interests.

327

328 **AUTHORS' CONTRIBUTIONS:** KK carried out the set-up, tests, recordings and data
329 collection, participated in the study conception and design, carried out statistical analysis,
330 results illustration and data interpretation, and drafted the manuscript; GA offered critical
331 revisions and input for the final version of the manuscript; RWE contributed significantly to
332 the design of the project, assisted with data analysis, interpretation and results illustration,
333 participated in the writing of the manuscript and carried out manuscript revisions; RAH
334 conceived and coordinated the study, participated in the design, data analysis and
335 interpretation of results, and revised the manuscript. All authors gave final approval for
336 publication and agreed to be accountable for all the aspects of the work.

337

338 **ADDITIONAL FILES:**

339 One additional file is submitted.

340 File name : 'Supplementary material'

341 File format: .xlsx

342 Title: 'Datasets and calculated statistics'

343 Description: The file includes: 1) datasets of recordings from preliminary and experimental
344 (novel object and novel environment) tests, and 2) tables with calculated boldness scores and
345 intra-individual variance statistics

346

347

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FIG 1

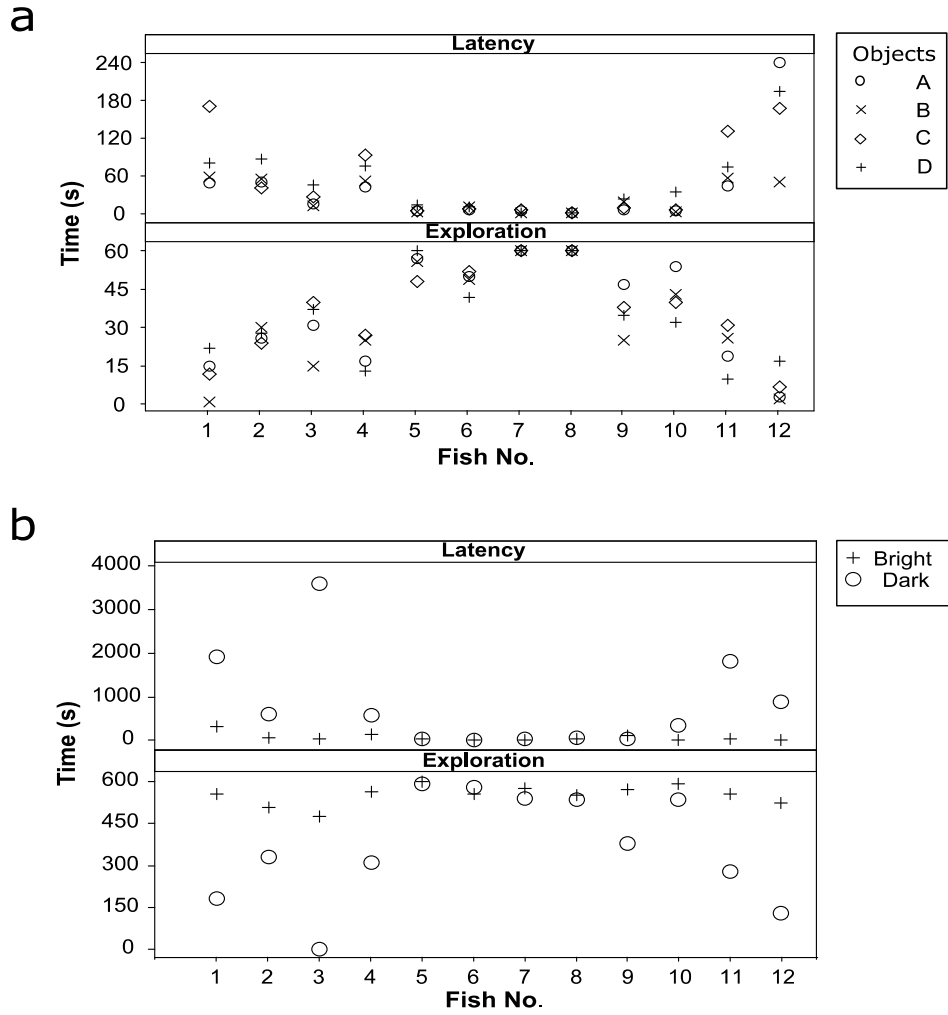
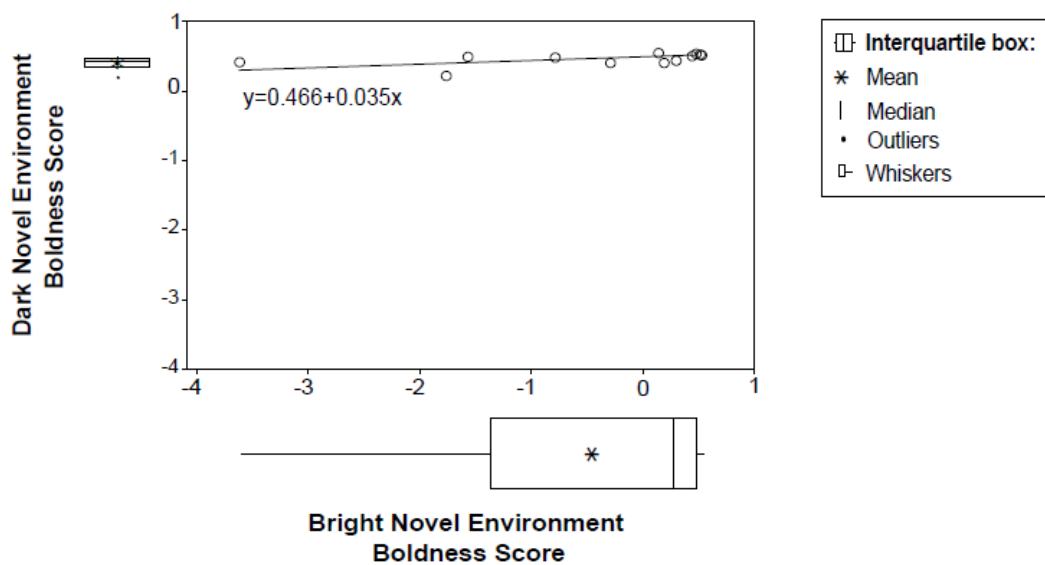


FIG 2

a



b

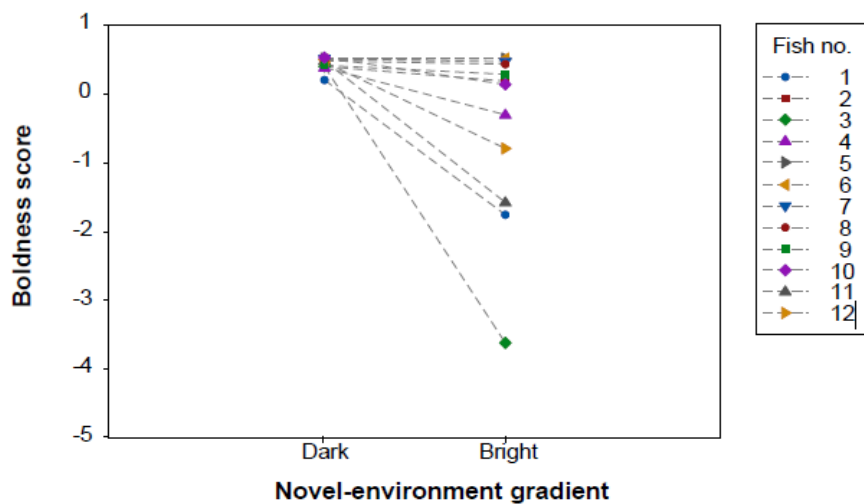


FIG 3

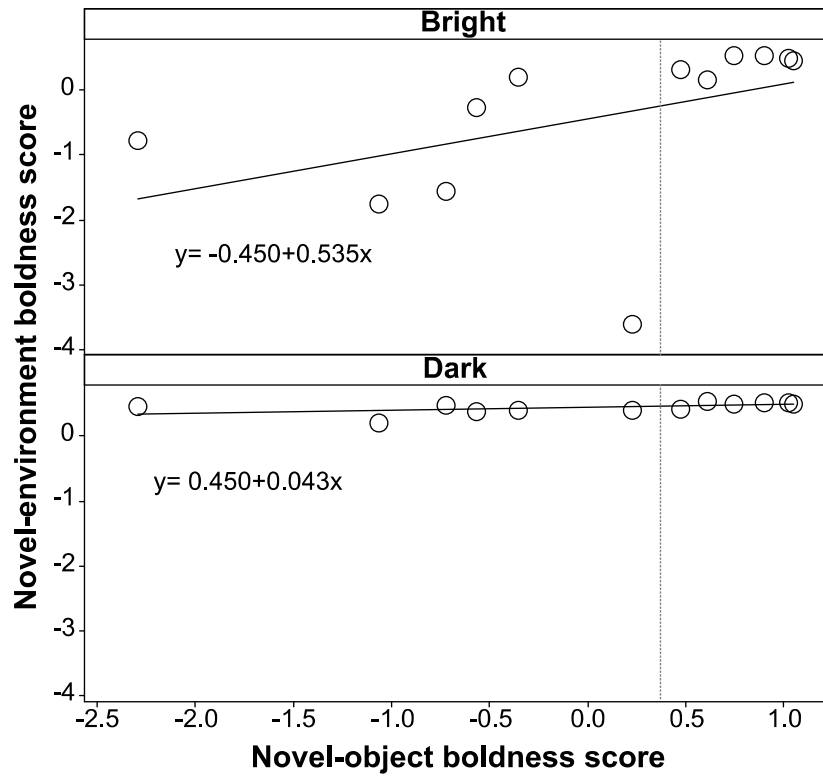


FIG 4

