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Fish learn collectively, but groups with differing personalities are slower to decide 1 and more likely to split

Kareklas, Kyriacos; Elwood, Robert W.; Holland, Richard

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1 *Title:* Fish learn collectively, but groups with differing personalities are slower to decide
2 and more likely to split.

3

4 *Authors:* Kyriacos Kareklas^{1*}, Robert W. Elwood¹ and Richard A. Holland²

5

6 *Affiliations:*

7 ¹School of Biological Sciences, Medical Biology Centre, Queen's University Belfast, 97
8 Lisburn Road, Belfast, Northern Ireland, BT9 7BL, UK

9 ²School of Biological Sciences, Bangor University, Deiniol Road, Bangor, Gwynedd, LL57
10 2UW, UK

11

12 *kkareklas01@qub.ac.uk (correspondence)

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16 **KEYWORDS:** collective cognition, decision-making, personality, spatial learning, shoaling

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23 **SUMMARY STATEMENT**

24 Zebrafish can be trained as a group to learn collective responses and memorise locations by
25 using cues. However, the speed of collective decisions when choosing between locations
26 can be limited by the splitting of groups comprising individuals of dissimilar personality.

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28

29 **ABSTRACT**

30 We tested zebrafish shoals to examine whether groups exhibit collective spatial
31 learning and whether this relates to the personality of group members. To do this we trained
32 shoals to associate a collective spatial decision to a reward and tested whether shoals could
33 reorient to the learned location from a new starting point. There were strong indications of
34 collective learning and collective reorienting, most likely by memorising distal cues, but
35 these processes were unrelated to personality differences within shoals. However, there was
36 evidence that group decisions require agreement between differing personalities. Notably,
37 shoals with more boldness variation were more likely to split during training trials and took
38 longer to reach a collective decision. Thus cognitive tasks, such as learning and cue
39 memorisation, may be exhibited collectively, but the ability to reach collective decisions is
40 affected by the personality composition of the group. A likely outcome of the splitting of
41 groups with very disparate personalities is the formation of groups with members more
42 similar in their personality.

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47 INTRODUCTION

48 Organised groups are characterised by cooperative and synchronised behaviour,
49 which allows for better resource acquisition and risk avoidance (Pitcher and Parrish, 1993).
50 However, collective behaviour varies depending on external and internal conditions, e.g.
51 environmental risk-levels and inter-group dynamics (Hoare et al., 2004; Sumpter, 2006). On
52 some occasions, such as during foraging, this may require that information about current
53 local conditions is disseminated between individuals within the group and presumably
54 processed collectively by the group (Laland and Williams, 1997). The collaborative use of
55 shared information to solve problems and make decisions is called collective cognition
56 (Couzin, 2009). Although collective cognition may be utilised for various group functions,
57 it is particularly useful for adjusting group behaviour in spatial contexts such as food
58 location or route choice (de Perera and Guilford, 1999; Conradt and Roper, 2005; Couzin et
59 al., 2005). Indeed, group living has been proposed to enhance navigation performance via
60 information-sharing (Simons, 2004). Navigation relies on several behavioural and cognitive
61 processes, such as exploration/sampling effort, decision-making, learning and cue
62 memorisation (Brown et al., 2006). The use of these processes by a group may be limited by
63 the extent to which cognitive or behavioural similarities between individuals facilitate
64 collective responses.

65 Most studies on group navigation have focused on collective decision-making as a
66 means of choosing between routes while maintaining group structure (Couzin, 2009; Couzin
67 et al., 2005; Conradt and Roper, 2005). Yet individual variation has been noted in important
68 cognitive processes: some individuals may be better at memorising information from their
69 environment (Croston et al., 2016), faster or more successful in their decisions (Chittka et
70 al., 2009) or faster learners (Trompf and Brown, 2014). Interestingly, individual variation in

71 many of these processes has been linked to animal personality (Griffin et al., 2015; Guillette
72 et al., 2016). Animal personality is often described by behavioural traits exhibiting
73 consistent inter-individual differences and intra-individual repeatability (Wolf and
74 Weissing, 2012). A well-studied trait, boldness, is indicated by exploration tendencies and
75 feeding motivation (Toms et al., 2010), making it a regular predictor of spatial associative
76 learning (e.g. Trompf and Brown, 2014; Mamuneas et al., 2015). Although a prominent
77 hypothesis is that bolder animals are faster but less accurate in their decisions (Chittka et al.,
78 2009), often effects manifest independently of these trade-offs. For example, bolder fish
79 may be faster at choosing between locations and faster learning rewarded responses, but not
80 less accurate in their choices than more timid animals (Trompf and Brown, 2014;
81 Mamuneas et al., 2015; Kareklas et al., 2017). Regardless of these trade-offs, the effects of
82 personality on cognitive performance may also influence how animals work collectively. In
83 particular, personality-differences between individuals may predict how they tackle
84 cognitive tasks collectively; the exploration tendencies and reward-motivation of group
85 members, could affect how they coordinate responses, how they decide, and how they
86 organise, share and utilise information when learning (Couzin, 2009).

87 To examine whether collective processes of decision-making and learning are
88 affected by the composition of groups, in terms of the individual boldness of their members,
89 we studied the zebrafish *Danio rerio*. Fish were first tested as individuals to determine their
90 levels of boldness (Figure 1) and were then trained as groups of five, referred to here as
91 shoals, in a spatial-associative learning task. During training, only spatial decisions made by
92 all individuals by reaching a location together were reinforced (reward or punishment), to
93 determine learning specific to a collective response. After reaching a learning criterion, we
94 tested the ability of shoals to reorient, examining their ability to memorise distal cues during

95 training. Animals may simply rely on the memorisation of a response, such as a turning
96 direction, or also on the memorisation of the relative positions of distal cues (Tolman et al.,
97 1946; Burgess, 2006). Associating a memorised response to a rewarded location relies on
98 orienting from a familiar starting point. In contrast, the additional memorisation of distal
99 cues can facilitate reorientation from novel starting points by attending to changes in the
100 relative position of these cues towards the correct arm (place learning; Rodriguez et al.,
101 1994). Therefore, reorienting can identify whether learning relies on composite strategies
102 that utilise the memorisation of the relative position of distal cues or simple associations of
103 location to directional-response.

104 First, we tested the hypothesis that collective decisions, learning and memorisation
105 are related to mean boldness levels, with shoals of bolder composition differing from those
106 with shier composition. Second, we tested the hypothesis that collective decisions, learning
107 and memorisation are predicted by the variance in boldness among shoal members, because
108 large differences in personality inhibit agreement or cooperation. Based on effects by
109 personality composition on group response-time in other shoaling species, we expected
110 decision times to be related to boldness, being generally faster for groups of bolder
111 individuals (Dyer et al., 2009). The learning of a collective response and memorisation-
112 strategies, such as place learning, have only recently been experimentally studied in fish
113 groups (McAroe et al., 2017), noting both the facilitation of visual-cue memorisation and
114 faster learning by zebrafish in groups. However, the effects of the personality composition
115 of groups on these group processes have not been examined. We predict that links to
116 personality may be indicated due to either differences between individuals in their response
117 tendency or their performance in particular cognitive tasks, with more variable groups
118 reaching lower agreement and cohesion (Ioannou and Dall, 2016), and overall bolder groups

119 being faster to decide and associate food reward to a location (such as in individuals, e.g.
120 Griffin et al., 2015; Guillette et al., 2016; Kareklas et al., 2017).

121

122 **RESULTS**

123 *Collective decisions*

124 All shoals reached collective decisions within the time limit (<5 min) in both the
125 initial and probe trial, but some tended to split before reaching a decision (supplementary
126 material). No significant differences were found between the initial trial (before training)
127 and the probe trial (after training) for either decision times ($R^2=0.017$; $P>0.05$) or the
128 probability of splitting ($R^2=0.02$; $P>0.05$), suggesting consistency in collective behaviour
129 and limited effects from differing individual learning during training. The mean boldness of
130 shoal members did not significantly contribute to the probability of splitting ($R^2=0.016$;
131 $P>0.05$; Figure 2a), and although shoals with members of greater mean boldness exhibited
132 shorter decision times ($R^2=-0.73$; Figure 2a) the relative effect was not significant ($P>0.05$).
133 The only significant predictor was variance in shoal-member boldness, which strongly
134 predicted both collective decision-times ($R^2=0.816$; $F_{1,20}=9.19$, $P=0.008$) and the probability
135 of splitting ($R^2=0.482$, $\chi^2_{1,20}=13.26$, $P<0.001$). Groups with greater variance in boldness
136 between their members were consistently more likely to split and took longer to collectively
137 reach an arm (Figure 2b and c). Further, collective decisions took longer when splitting
138 occurred than when not (Welch's $t=4.15$, $P=0.002$; Figure 2d).

139 Decision accuracy (number of erroneous decisions during training) was only weakly
140 predicted by the mean of shoal-member boldness ($R^2=0.127$; $\chi^2=8.19$, $P<0.05$), but was not
141 significantly predicted by the probability of splitting decision ($R^2<0.04$; $P>0.05$). Contrary
142 to predicted speed-accuracy trade-offs (Chittka et al., 2009), the number of erroneous

143 decisions during training did not significantly correlate with the time shoals needed to
144 decide in either the initial or the probe trial ($r_s < 0.2$, $P > 0.05$).

145 *Collective learning*

146 All shoals met the collective learning criterion of all fish being simultaneously in the
147 rewarded location for 8/10 trials over three consecutive days (Figure 3). The rate of learning
148 (number of days to reach criterion) was negatively related to the number of erroneous
149 choices during training (i.e. choosing the punished arm) ($R^2 = -0.945$, $\chi^2_{1,10} = 3.99$, $P = 0.046$;
150 Figure 3). However, learning rate was not significantly predicted by the variance and the
151 mean of shoal-member boldness, or the likelihood of splitting ($R^2 < 0.04$; $P > 0.05$).

152 At probe trials from the new starting point (i.e. the top arm which was blocked
153 during training) all shoals reached one of the arms collectively (i.e. were at the same arm
154 together before the 5 min), but the ability to reorient to the arm rewarded during training
155 was unrelated to the variance and the mean of shoal-member boldness or the likelihood of
156 splitting ($R^2 < 0.04$; $P > 0.05$). Indeed, the majority of shoals (8/10) showed preference for
157 reaching the rewarded arm significantly more than predicted by chance (proportion > 0.5 :
158 $z_{10} = 1.90$, $P = 0.029$; Figure 3).

159

160 **DISCUSSION**

161 To collectively reach one of two locations, groups must maintain cohesion and
162 structure. This relies on interactions between the individuals comprising the group, a
163 process known as self-organisation (Sumpter, 2006). The interactions facilitate information
164 sharing (Couzin, 2009; Ward et al., 2011) and in fish this can be in the form of changes in
165 swimming direction, where swimming towards a location by some individuals propagates
166 through the group (Croft et al., 2003). The extent of the propagation is indicated by the time

167 needed by all individuals to change direction together, which can be limited by individuals
168 deciding to act otherwise (Couzin, 2009; Ward et al., 2008). Here, our findings implicate
169 personality differences between group members in this process. Groups with greater
170 variance in boldness between its members were consistently more likely to split and took
171 longer to collectively reach an arm (Figure 3b and c). Given collective decisions took longer
172 when splitting occurred than when not (Figure 3d), we conclude that the splitting of groups
173 with members more dissimilar in their boldness results in collective decisions taking longer
174 to be reached. The involvement of personality on collective decision speed may reflect a
175 greater tendency by bolder individuals to reach food-rewarded locations (Kareklas et al.,
176 2017).

177 The relationship of personality differences with cohesion and collective-decision
178 speed proposes that high-variance groups might be disadvantaged when competing for
179 spatially distributed resources. A study on guppies *Poecilia reticulata* did not find mixed
180 groups more disadvantaged than bold groups, but faster at reaching food than shy groups
181 (Dyer et al., 2009). Differences in the effects of personality may depend on the species, but
182 the study in guppies also utilised a categorical separation of bold and shy to compose
183 groups. In contrast, here we measured the variance in boldness score within randomly
184 assembled groups. A higher variance in our shoals is most likely be due to the presence of
185 extremely shy individuals, based on their individual latency distributions (Figure 1). The
186 direct effects of high variance on splitting are unclear, as we did not track individuals, but
187 they are possibly driven by intra-group differences in exploration and approach tendency
188 between more greatly differing personalities (Toms et al., 2010) and possibly due to related
189 differences in sociality (Ward et al., 2004; McDonald et al., 2016). Another possibility is
190 that differences in boldness correspond to differences in decision-making strategy (Griffin

191 et al., 2015; Kareklas et al., 2017), which again would require identifying consistencies in
192 the position individuals occupy in a shoal. Further, different types of splitting may represent
193 different processes. Lateral fission may reflect individuals being less social and actively
194 seeking to split, but rear fission may be the result of either active splitting or passive
195 restraints (Croft et al., 2003), such as being more fearful and timid (Toms et al., 2010;
196 Kareklas et al., 2017). The splitting of groups with very high variance in personality could
197 possibly lead to the formation of groups with lower variance in personality. While this is yet
198 to be tested, it could be a way for groups to ensure that agreements are reached more easily.
199 Indeed, larger differences in personality can manifest effects on the way fish socialise,
200 cooperate and prioritise reward or risk (Ioannou et al., 2015). Alternatively, splitting might
201 be an effect of hierarchical dynamics, with leader initiations and follower delays relying on
202 similarities in personality aspects such as boldness and flexibility (Ioannou and Dall, 2016).

203 Contrary to expectations that personality differences have an effect on both speed
204 and accuracy due to trade-offs (Chittka et al., 2009), the number of erroneous decisions
205 during training was independent of how fast fish in a shoal reached a location together.
206 However, shoals that made fewer erroneous collective decisions during training reached the
207 learning criterion faster (Figure 3). This negative association between erroneous trials and
208 learning rate is consistent with learning by positive reinforcement, given less erroneous
209 shoals would collectively reach the rewarded arm more frequently during training (Brown et
210 al., 2006), but suggests a low effect from negative reinforcement by the mild punishment of
211 erroneous trials. Interestingly, the majority of shoals (8/10) re-oriented at probe trials to the
212 location rewarded during training (Figure 3). This indicates that most shoals did not simply
213 use a learned response for collectively reaching the rewarded arm, e.g. turn direction, but
214 learned the place of the reward. Place learning proposedly involves allocentric processes,

215 where positions of distant cues in relation to a target are memorised and reorientation is
216 possible (Tolman et al., 1946; Rodriguez et al., 1996). Although this may involve cognitive
217 mapping (mental representations of space using the relative positions of landmarks), other
218 cue-based strategies are difficult to exclude, e.g. beaconing to large cues near the goal
219 (Bennett, 1996). Most notably, *D. rerio* zebrafish individuals can take longer to learn and do
220 not prefer place over response learning (McAroe et al., 2016). Thus, being in a shoal can
221 facilitate both learning efficiency and the use of learning strategies that rely on the
222 memorisation of cues and not solely of simple directional responses. This has been
223 exemplified recently in a study comparing shoals to individual zebrafish, where only shoals
224 were able to exhibit place learning (McAroe et al., 2017). This is enabled in fish groups by
225 social learning (Laland and Williams, 1997; Trompf and Brown, 2014), cooperative
226 vigilance and information sharing (Pitcher and Parrish, 1993; Miller and Gerlai, 2011).

227 In contrast to models predicting that cohesion and individual differences in
228 behaviour may affect collective behaviour and learning (Couzin, 2009), we found no strong
229 evidence of personality or splitting having any significant influence on collective learning
230 or accuracy. Decision accuracy and learning may instead be influenced by inter-individual
231 differences in experience, attention, acquisition and cue perception (Couzin, 2009; Kao et
232 al., 2014). Indeed, in the absence of effects from individual behavioural phenotypes, based
233 on personality, differences in individual experience and a balancing between personal and
234 shared information in the group are both very likely alternative factors (Miller et al., 2013).
235 Otherwise, groups may rely on the leadership of more experienced or reward-driven
236 individuals (de Perera and Guilford, 1999; Krause et al., 2000). For memorisation strategies
237 in particular, there is evidence that individuals can use cue and response based strategies
238 together and often animals reverse between strategies over training times (Packard &

239 McGaugh, 1996; Burgess, 2006). These processes could carry over in collective learning
240 and this can be tested by repeated probe trials during collective training.

241 Although our study did not include analysis of any kinematic data, recent work has
242 increasingly shown the benefit of identifying behaviour-specific movement bouts (Marques
243 et al., 2018) and for assessing how the solitary movement patterns of group members affect
244 collective swimming patterns (Marras et al., 2015). This would provide more evidence for
245 the individual effects on collective decisions and learning, and could identify the extent to
246 which effects from individual motor behaviour are related to personality (e.g. bouts related
247 to risk-response or approach; Marques et al., 2018) or other phenotypic factors, such as
248 morphology (Conradsen and McGuigan, 2015). While these effects remain to be examined,
249 here we show that zebrafish can learn to reach collective spatial decisions for rewards and
250 utilise place memorisation strategies to do this, but that collective decisions are biased by
251 personality differences.

252

253

254 **MATERIALS AND METHODS**

255 **Animals and housing**

256 Naïve male zebrafish *D. rerio* (n=50) were acquired from a local supplier, Grosvenor Tropicals,
257 Lisburn, Northern Ireland. Given the supplier was not informed on strain variations in their stock, we used
258 only males that show no strain preferences for shoaling (Snekser et al., 2010), which also removed the chance
259 of mating during group-living and controlled for sex-related differences in boldness. Fish were housed in tanks
260 (26cm W x 36cm L x 30cm H; 26±2°C and 7.4±0.4pH dechlorinated tap-water) enriched with fine sediment,
261 plants and plastic-pipes. Photoperiods were 12h long (0700-1900) and feeding was daily (TetraMin® flakes).

262 **Behavioural tests for boldness**

263 Following a week-long acclimation to individual housing (tanks filled to 15 L with view of
264 neighbours to reduce isolation effects), the boldness of each fish was assessed in their housing tank by

265 measuring consistency in their approach latency towards novelty between two contexts often used to test
266 differences in boldness (see review by Toms et al., 2010). First, novel-object inspection was tested by the time
267 fish took to reach ~1.5 body-length distance from a 7cm toy after it was lowered by a pulley system to the
268 bottom of the tank, as estimated by viewing through a screen with a grid from above. Second, feeding
269 motivation towards an unusual food was tested by recording the time fish needed to initiate feeding on
270 chironomid larvae (released by forceps), which had not been previously offered to the fish in the laboratory.
271 Opaque sheets kept tanks invisible to neighbours and the observer during tests. Fish had not been fed for ~24h
272 prior to testing. Both tests were 5 minutes duration, carried out at 11:00-13.00, with a 48h interval between
273 them and in the same order for all fish to control carry-over effects (see Kareklas et al., 2017). As would be
274 expected for the expression of personality traits, like boldness (Toms et al., 2010; Wolf and Weissing, 2012),
275 latencies were found consistent between contexts (Chronbach's $\alpha= 0.803$; Pearson's $r=0.844$) and used to
276 calculate composite boldness scores. Greater latencies are linked to lower boldness (Toms et al., 2010), thus
277 the standardised sums of latencies from both tests were used as scores (z-values) and inversed in sign (positive
278 or negative) to rank by increasing boldness (Figure 1).

279 **Collective tests for learning**

280 Following individual behavioural tests, fish were randomly sorted in shoals of five (n=10) and housed
281 together (tanks filled to 25L tanks) for a further week and then trained in a plus maze (four-arm maze from
282 acrylic sheets; each arm measuring 15cm W x 30cm L). During training internal landmarks were unavailable,
283 but visual cues were available outside the maze, including white paper sheets on a distant wall, adjacent tank
284 tops and the camera arm above the tank. To control for inter-shoal differences by differing information, these
285 external cues and their location were kept constant during trials and for all shoals. Shoal trials started in the
286 bottom arm and the top arm was blocked during training. Trials commenced by removing an opaque divider
287 that kept shoals constrained in the starting arm for 2 minutes. Shoals were then presented the two remaining
288 arms, left or right, with 5 minutes to chose between them. A collective decision was indicated by all
289 individuals being in the same arm at the same time, training them to associate a collective decision towards
290 one arm to a reward and towards the other arm to a mild punishment. The choice of direction, left or right arm,
291 for the rewarded and mildly-punished arm was randomised across shoals. When reaching the arm randomly
292 assigned to be food rewarded, shoals were blocked in until each fish received 1-2 chironomid larvae
293 (individual feeding latency was <5s). However, in the unrewarded arm they were blocked in for 2 minutes and

294 not fed (mild-punishment; McAroe et al., 2016; Kareklas et al., 2017). Following their choice, fish were gently
295 guided by a net to the starting arm. After each trial, the tank-water was disturbed to minimise use of olfactory-
296 cues. Shoals had ten such trials daily until reaching a learning criterion of a minimum of 8/10 correct trials
297 (i.e. collectively choosing the rewarded arm) on 3 consecutive days. The learning criterion corresponds to a
298 learning plateau and success-rates exceeding 24/30 correct trials, which differ from chance (15/30) at the
299 0.1% level. Shoals were given a single probe trial 24h after reaching the learning criterion, which started from
300 the previously blocked top arm. This tested if fish were able to collectively reorient to the rewarded arm from
301 a novel starting point, via the memorisation of the relative positions of the distal cues during training
302 (Rodriguez et al., 1994). The probe trial was unrewarded to control for the use of olfactory cues.

303 Reaching the correct arm during probe trials showed the ability to reorient by using distal landmarks,
304 i.e. place learning. By contrast, a failure to reach the goal arm in the probe trial was considered the result of
305 learning to go left or right during training, i.e. response learning (McAroe et al., 2016; McAroe et al., 2017).
306 Collective decision speed, measured until the last fish of the group passed the mark to either arm (given all
307 other fish were already in the same arm to designate a collective choice), was recorded only for the first
308 training-trial (novel task) and the probe-trial (novel starting-point). The choice of using decision times only
309 from these two trials was because their novelty controlled possible effects of familiarity and experience of
310 making a particular decision; decisions from other trials during training could be biased by reinforcement from
311 previous trials and thus not representative of a novel decision. In addition, by measuring times at two
312 relatively novel trials, where one was before and one after training, allowed us to examine if novel decisions
313 are affected by the experience of training as a group. Comparisons before and after training further enabled us
314 to test consistency in the effects of intra-group boldness on decision making and to test for effects by
315 individual-level learning. Before reaching collective decisions in these trials, some shoals exhibited splitting:
316 individuals either stayed behind in the starting arm while others had chosen between left or right (rear fission)
317 or went in a different direction, reaching the opposite arm from the rest (lateral fission) (Croft et al., 2003).
318 The distance needed to travel between arms (centre to centre) was ~27cm or 5 zebrafish body-lengths (4-6
319 cm), and was thus considered sufficient to indicate splitting. We recorded the occurrence of any type of
320 splitting as an inverse measure of cohesion. If fish reached an arm together within the 5 minute recording time,
321 any splitting was noted and the collective decision was recorded as either correct (rewarded arm) or erroneous
322 (unrewarded arm). Alternatively, if no choice was reached, any splitting was again recorded, but we did not

323 count the trial as either correct or erroneous. Decision accuracy was measured by total number of erroneous
324 trials throughout training, because the number of correct trials can also be influenced by fish not choosing. The
325 number of training days to reach criterion indicated learning rate.

326 **Analysis**

327 The proportion of shoals reorienting at the probe trial was first tested against chance levels (0.5) by a
328 binomial-proportion test. Speed-accuracy trade-offs were tested by correlations between time to decide and the
329 number of erroneous trials during training (Spearman's r_s) (Chittka et al., 2009). Decision times from initial
330 and probe trials were compared between trials where any splitting occurred and trials where no splitting
331 occurred (Welch's t which does not assume equal variance and sample size). Individuals could not be
332 identified during collective tests because the week-long group-acclimation period prevented us from
333 continuously tracking them, and methods of tagging were unavailable. As a result, we could not identify
334 particular individuals with a known boldness score, but we could compare groups of differing composition in
335 terms of individual-member boldness. Therefore, regression models (linear for decision-times, Poisson for
336 number of days to learn and number of erroneous trials during training, and binary-logistic for splitting
337 probability) tested whether each measure was predicted by the mean (5% trimmed to limit bias by minority
338 fish with extreme phenotypes) or the mean absolute deviation of shoal-member boldness (variance across all
339 fish). Individuals with personality tendencies on the extreme ends of our distribution, mostly very shy
340 individuals (Figure 1), can skew both the mean and variance, making it impossible to assess them as having a
341 different effect, i.e. effects by the slowest individual would appear both in the mean and variance. However,
342 by removing the extreme ends of the group (5% trimmed) we extracted mean values for shoals that represent
343 the majority of their members and not biased by a single very timid fish. Conversely, the variance measure
344 includes these extreme personalities. This enabled differentiation between effects by the majority average
345 (trimmed mean) and the extremes (variance). Models testing decision-speed and splitting additionally tested
346 differences between initial and probe trial (categorical predictor; effect of learning) and included shoal number
347 as a random effects term to avoid pseudoreplication.

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351 **ETHICAL STATEMENT**

352 All applicable animal-welfare guidelines were followed (ASAB, 2016). Veterinary
353 inspections by DHSSPS, Northern Ireland, deemed no need for licensing. Animals were
354 kept for separate non-invasive tests.

355

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360

361

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463 **FIGUER LEGENDS**

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465 Figure 2: Shoal cohesion (probability of splitting) and consequent effects on collective
466 decision-times were influenced by individual boldness differences, but were not linked to
467 majority averages in boldness **(a)** The mean boldness of shoal-members (5% trimmed to
468 exclude biases by extremely bold or timid fish) had a negative, non-significant, effect on
469 mean decision times between initial and probe trial (black line and marks), but no effect on
470 splitting probability (grey curve and marks). **(b)** In contrast, the variance in boldness within
471 shoals (mean average deviation of all fish) positively predicted the probability of splitting at
472 probe and initial trials (grey curve and marks) and the mean decision times between initial
473 and probe trial (black line and marks). **(c)** Splitting was more consistent for shoals with the
474 most variance in boldness and **(d)** shoals took longer to reach a decision if they split.

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476 Figure 3: Shoals that made more erroneous trials during training (black bars) also took more
477 days to learn (grey bars), but a greater than chance majority of shoals was able to memorise
478 place (inset: proportion of shoals reorienting at probe trial, showing place learning). Shoals
479 are ordered by increasing number of error counts and marked (cross) if they showed place
480 learning. [$*P < 0.05$]

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487 Figure 1

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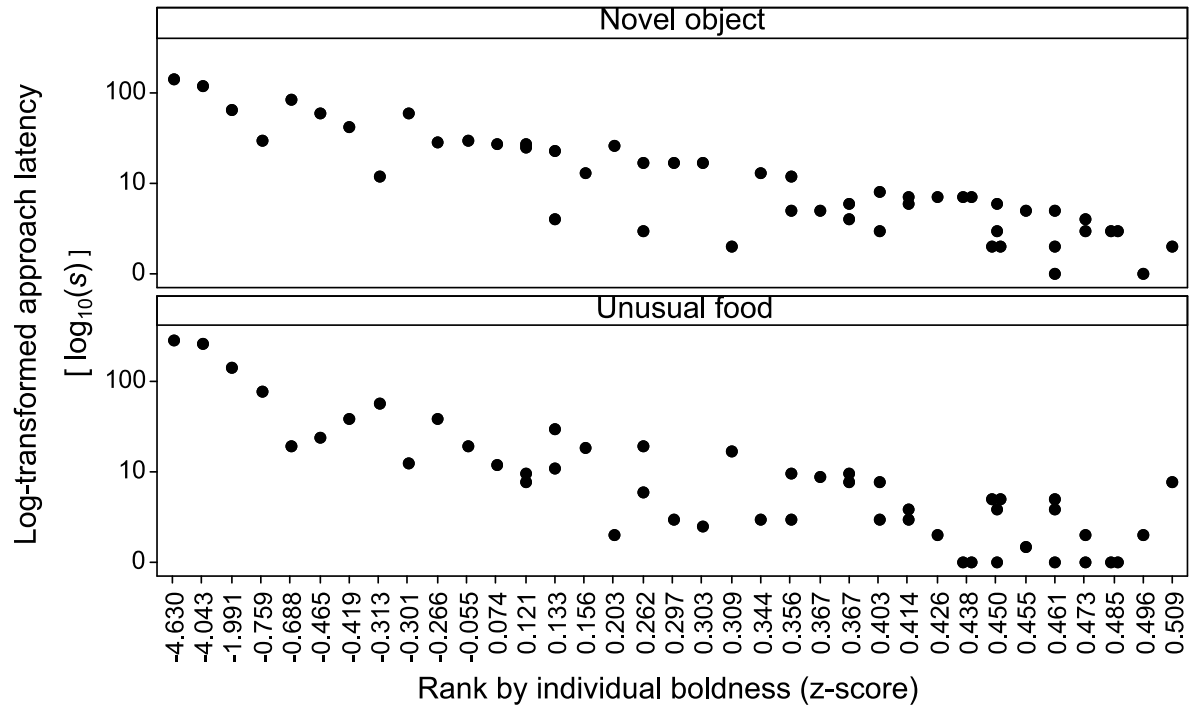
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505 Figure 2

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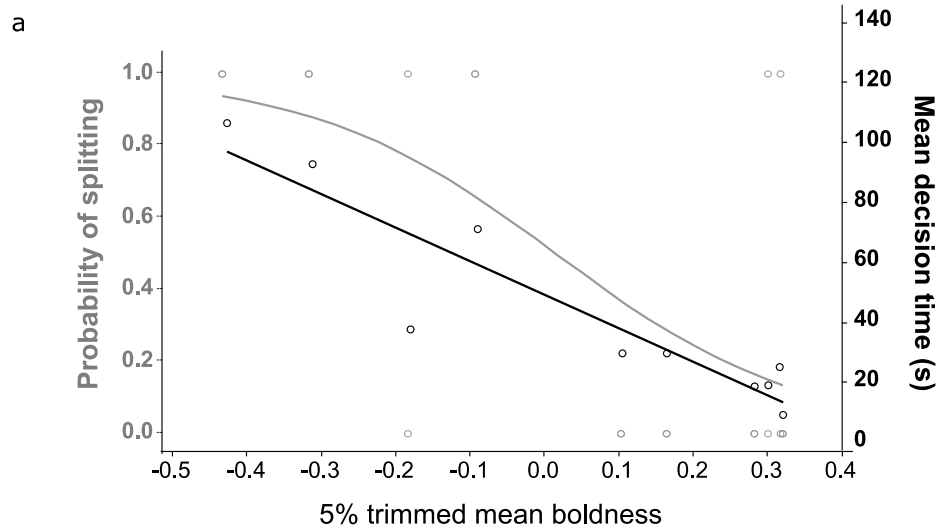
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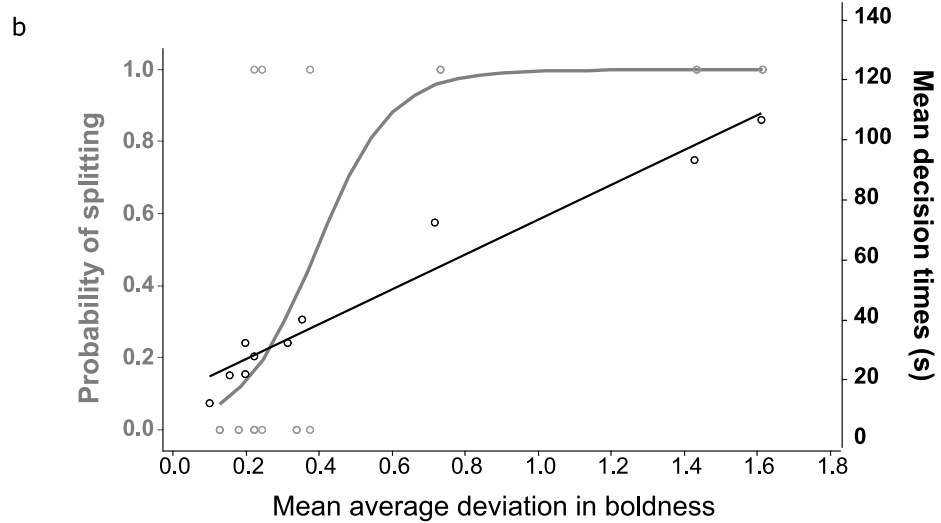
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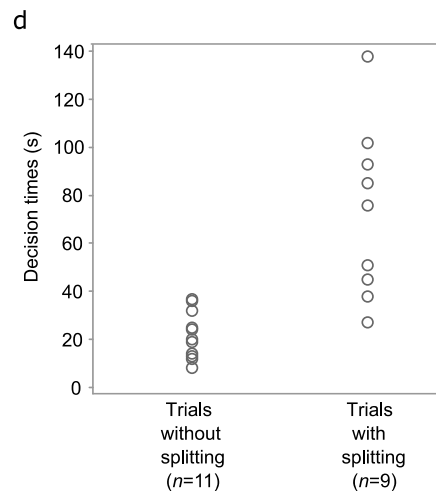
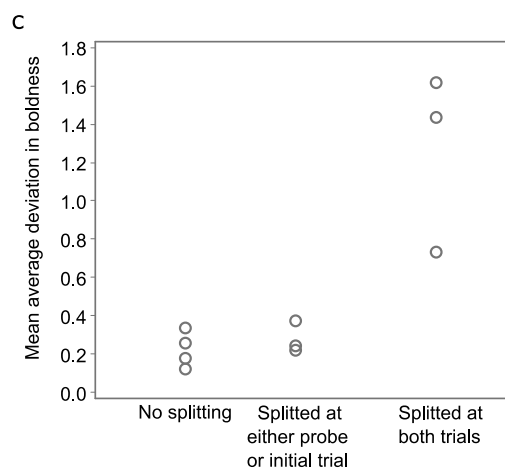


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522 Figure 3

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