

## Grouping promotes risk-taking in unfamiliar settings

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

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1                    **Grouping promotes risk-taking in unfamiliar settings**

2                                    Kyriacos Kareklas<sup>1\*</sup>,

3                                    Robert W. Elwood<sup>1</sup> and

4                                    Richard A. Holland<sup>2</sup>

5  
6                    *Affiliations:*

7                    <sup>1</sup>School of Biological Sciences, Queen's University Belfast, Medical Biology Centre, 97  
8                    Lisburn Road, BT9 7BL, UK

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

11  
12                    *\*Correspondence:* [kkareklas01@qub.ac.uk](mailto:kkareklas01@qub.ac.uk)

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27 **ABSTRACT**

28           Acting collectively in a group provides risk-reducing benefits. Yet individuals differ  
29 in how they take risks, with some being more willing than others to approach dangerous or  
30 unfamiliar settings. Therefore, individuals may need to adjust their behaviour when in  
31 groups, either as a result of perceiving greater safety or to coordinate collective responses, the  
32 latter of which may rely on within-group dynamics biased by group composition. In zebrafish  
33 we explored how these aspects of grouping affect risk-taking behaviour by comparing  
34 solitary to group conditions and testing the ability of group-member solitary responses to  
35 predict collective responses. We focused on approach-latency towards a novel object and an  
36 unusual food to test this, for shoals of five fish. There was no indication that collective  
37 latencies are predicted by how each fish responded when alone in terms of the extremes, the  
38 variance or the mean of group-member latency towards the unusual food and the novel-  
39 object. However, fish were overall faster and less variable in their approach when shoaling.  
40 This indicates lower risk aversion by individuals in groups, presumably as a result of group  
41 safety. An interesting consequence of the overall low risk-aversion in shoals is that more risk-  
42 averse fish adjust their behaviour more than less risk averse fish.

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45 **KEYWORDS:** social facilitation; risk-taking; zebrafish; shoal; collective behaviour

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## 53 1. INTRODUCTION

54           The benefits of being organised in groups have long been noted in many species  
55 (Scott, 1956). Threat detection and anti-predator functions are the most important examples,  
56 both of which depend on cooperation and synchronisation (Pitcher and Parrish, 1986). If  
57 information is successfully and rapidly distributed between group members then each  
58 member may spend less time on predator vigilance and more on feeding, while also  
59 improving efficiency when exploring areas for food (Magurran and Pitcher, 1983; Pitcher and  
60 Parrish, 1986; Laland and Williams, 1997). Further, the probability of an individual being  
61 attacked diminishes as group size increases because of dilution (Foster and Treherne, 1981)  
62 and the predator is less able to choose a specific target (Jeschke and Tollrian, 2007).  
63 Although these benefits should promote group formation, the tendency to group varies with  
64 local conditions (Magurran and Pitcher, 1983; Pitcher and Parrish, 1986). For example,  
65 killifish *Fundulus diaphanus* minimize competition by being individually spaced when  
66 sensing food odours and minimise risk by forming large aggregates when alarmed by cues  
67 from a dead conspecific. In more complex environments where both food and alarm cues are  
68 present, they average their response by forming smaller groups (Hoare et al., 2004).  
69 Therefore, group formation may depend on what is beneficial to individuals in each set of  
70 conditions.

71           Individuals of a range of species, however, exhibit consistent marked differences in  
72 their behavioural tendencies, including their willingness to take or avoid risk in unfamiliar or  
73 dangerous situations (Coleman and Wilson, 1998; Toms et al., 2010; Wolf and Weissing,  
74 2012). Individual differences in risk-taking suggest different strategies: those taking less risk  
75 typically benefit from reduced mortality, whereas those taking more risk may benefit from  
76 more rewards and increased growth (Stamps, 2007). If individuals retain at least some aspects  
77 of their own risk-taking tendencies when they are in groups then group cohesion and unified  
78 responses may be disrupted (Ward et al., 2004; Webster et al., 2007; Magnhagen and

79 Bunnefeld, 2009). Therefore, for the group to function, individuals should, at least partially,  
80 adjust their behavioural tendencies (Pitcher and Parish, 1986; Jeschke and Tollrian, 2007;  
81 Miler and Gerlai, 2012; McDonald et al., 2016).

82         The benefits offered by organising into groups suggest that, in identical situations,  
83 being alone is more risky than being in a group (Magurran and Pitcher, 1983; Webster and  
84 Ward, 2011; Ward, 2012). Therefore, being in a group may facilitate less risk-averse  
85 behaviour in all individuals. For example, individual fish become faster to approach food,  
86 more active and more explorative when in a group than when alone (Webster et al., 2007;  
87 Ward, 2012). This social facilitation of an increase in risk-taking behaviour is often attributed  
88 to the simple presence of others, and is arguably the result of the perceived safety offered by  
89 being organised in groups (Ryer and Olla, 1992; Guerin, 2010; Ward, 2012). Social  
90 facilitation of behavioural changes can be exhibited in both smaller and bigger groups, but  
91 the extent of the effect typically increases with group size (Ward et al., 2011; Ward, 2012)  
92 and may vary with individual tendencies, e.g. in risk-taking (Jolles et al., 2014).

93         Alternatively, changes to individual behaviour may simply be associated with the  
94 maintenance of group cohesion when responding collectively (Couzin and Krause, 2003).  
95 The collective responses of a group may arise from mechanisms of conformity, where  
96 individuals will progressively conform to the response of the majority or follow near-  
97 neighbours (Webster and Ward, 2011). However, majority responses may involve decisions  
98 made between individuals (Conradt and Roper, 2005; Sumpter et al., 2008; Couzin et al.,  
99 2011), which can be influenced by the nature of the individual differences between the  
100 animals comprising the group (Webster and Ward, 2011; Ioannou and Dall, 2016). On one  
101 hand, collective responses may reflect the mean behavioural tendency of individuals, but may  
102 also be limited by the extent to which differences between individuals affect the maintenance  
103 of group cohesion. For example, groups composed of bold fish are faster to approach food  
104 than if composed of shy fish (Dyer et al., 2009) and individual differences in feeding

105 motivation can drive differences in grouping tendency, with hungrier fish being less likely to  
106 keep close to group mates (Webster et al., 2004). On the other hand, the majority may choose  
107 to follow a leader, such as a more reward-motivated or less risk-averse individual (Krause  
108 et al., 1992; Krause et al., 2000; Ward et al., 2004). Consequently, collective (cohesive)  
109 responses would be largely determined by the behavioural response of leaders and the ability  
110 of followers to maintain short delays (Ioannou and Dall, 2016). Leadership can arise in larger  
111 and smaller groups (Couzin et al., 2005; Johnstone and Manica, 2011), but majority-decisions  
112 are generally facilitated in larger groups (Sumpter et al., 2008; Ward et al., 2008).

113         Fish groups are traditionally referred to as *schools* or *shoals*, with discriminations  
114 between the two relying on aspects of sociability and function; shoaling may refer generally  
115 to fish groups or those formed for social reasons, conversely schooling specifically refers to  
116 directed movement (Pitcher and Parrish, 1986). However, as Delcourt and Poncin (2012)  
117 point out, groups can be better characterised by precise metrics such as polarity (i.e. the level  
118 in which fish orient towards the same direction) and cohesion (i.e. the level in which fish stay  
119 close together). In zebrafish, larger shoals are less polarised and this could, arguably, be  
120 linked to the risk-reduction offered by more individuals staying together (Miller and Gerlai,  
121 2012). However, cohesion and polarisation generally fluctuate, which may affect information  
122 transfer during zebrafish collective responses (Miller and Gerlai, 2011). To elucidate what  
123 drives collective response in zebrafish shoals, we first examine effects of social facilitation by  
124 comparing shoaling and solitary risk-taking in *Danio rerio*. We then examine the ability of  
125 shoal-member solitary response in predicting collective response, as a process of inter-  
126 member interactions. We aimed to identify any changes in behaviour due to social conditions  
127 and whether the solitary behaviour of shoal members determines their collective response.

128         The approach latency of individuals and shoals was used to indicate levels of risk-  
129 taking in two contexts, novel-object exploration and feeding on unusual food (Toms et al.,  
130 2010). First, we compared the individual response in a solitary condition (slowest solitary

131 fish) to the individual response during shoaling (slowest shoal member). Based on the  
132 literature, we expected greater risk-taking by fish during shoaling, as compared to being  
133 alone (Webster et al., 2007; Ward, 2012). Second, the predictive power of shoal-member  
134 solitary behaviour was tested by examining whether collective latencies (i.e. until last fish,  
135 given cohesion was maintained) were: slower for shoals with members that have on average  
136 slower solitary responses (effect of general composition; Dyer et al., 2009), slower for shoals  
137 with members more dissimilar in their solitary response (degree of conformity; Ward et al.,  
138 2004), faster for shoals whose fastest member was particularly fast when alone (leadership by  
139 most reward-driven; Krause et al., 1992) and slower for shoals whose slowest member was  
140 particularly slow when alone (delay by most risk-averse; Ioannou and Dall, 2016).

141

## 142 **2. METHODS**

### 143 ***2.1. Animals and husbandry***

144 Male *D. rerio* zebrafish were acquired from a local supplier and first kept individually  
145 (n=50) in 15L tanks (30cmx25cmx20cm) and then as shoals of five (n=10) in 25L tanks  
146 (42cmx30cmx20cm). Given strain variations in the supplier's stock were unknown, we used  
147 only males that show no strain preferences during shoaling (Snekser et al., 2010), which also  
148 removed the chance of mating during group-living and controlled for sex-related differences  
149 in risk-taking. The different tank sizes used gave reasonable space for the individuals and  
150 shoals. During individual housing, neighbouring tanks on either side (two individuals) were  
151 kept visible to control effects from social isolation. Housing tanks were enriched with shelter  
152 (plastic pipes), plants and soft sediment. The water in the tanks was filtered, regularly tested,  
153 kept at  $25\pm 1^{\circ}\text{C}$  and maintained between 6.8-7.6pH. Photoperiods were kept at 12h light and  
154 12h dark (07.00-19.00) and food was provided daily (TetraMin® tropical flakes).

### 155 ***2.2. Behavioural tests***

156 Fish were left to acclimatise to individual housing for a week and then tested  
157 individually in their solitary housing tanks. A week following individual (solitary) testing, all  
158 fish were randomly arranged in sets of five and housed together for a further week. This  
159 provided time for individuals to experience group living before being tested for their  
160 collective response as a shoal, carried out in the housing tanks of shoals. Both individual and  
161 shoal testing was repeated in two contexts: when exploring/inspecting a novel object and  
162 when feeding on unusual food-items (not previously offered to them in the laboratory). When  
163 tested individually, fish were given brine shrimp at the feeding test and 48 hours later  
164 presented with a ~10cm long plastic soldier figurine for the novel-object test. When tested in  
165 shoals, fish were given bloodworm at the feeding test and 48 hours later presented with a  
166 ~12cm long plastic dinosaur toy for the novel-object test. The location and time (11.00-  
167 12.00) items were presented were kept constant, but a change in food and objects maintained  
168 novelty and controlled for episodic-like memorisation of familiar items (Hamilton et al.,  
169 2016). Objects were lowered at an uncovered part of the tank by a pulley system to the  
170 bottom of the tank, at which point recording started. Food was released with a pipette from  
171 the top-edge of the front-facing tank-wall and recording started after release in the water. The  
172 experimenter remained hidden behind opaque sheets surrounding the tanks during tests.  
173 Individuals and shoals were given 300s to approach the object or food and if no approach was  
174 noted within this period, latency was recorded as 300s. Latency to approach the food was  
175 measured until starting to feed and latency to approach the novel object was measured until  
176 fish were within a distance of ~1.5 body lengths from the object, estimated through a digital  
177 grid from recordings (Kinovea© version 8; J. Charmant & Co.). In keeping with other studies  
178 (Magnhagen and Bunnefeld, 2009; McDonald et al., 2016), all fish had the same order of  
179 testing, both for social-conditions and context. Further, all shoals received the same items in  
180 either social condition. The order of testing and of previously experiencing particular items  
181 could have effects on latency. Importantly, however, it ensures that any carry-over effects

182 from experience of previous items and from temporal order would be identical for all fish and  
183 therefore not contribute to inter-individual and inter-shoal variance (Wilson et al., 2012).

184 In order to validate responses as being collective we examined cohesion (ability to  
185 stay together) by identifying dispersal events and significant reductions in estimations of  
186 nearest-neighbour distances from video recordings of the tests. No dispersal events were  
187 observed during any of the shoal tests (i.e. no fish stayed behind or changed direction; Croft  
188 et al., 2003) and the distance from closest neighbours did not exceed average body-length  
189 (<5cm) as extrapolated from observing test-recordings through a digital grid (Kinovea©). The  
190 response of all shoals was fast (3-22 seconds), synchronous, in that individuals responded  
191 together, but not polarised (i.e. most individuals were not oriented towards the same  
192 direction). This made it difficult to record accurate times for all fish and calculate other  
193 indicators of cohesion, such as delays between initiator and follower response (Krause et al.,  
194 2000; Ioannou and Dall, 2016). We therefore recorded approach by the last fish to indicate  
195 collective latency times, i.e. time needed for the whole shoal to approach together. Note that  
196 although fish in the shoal were not individually marked, the use of the slowest fish as the  
197 collective measure is a conservative approach because all other fish were faster.

### 198 ***2.3. Calculations and Analysis***

199 Calculations and statistical tests were carried out in Minitab<sup>®</sup> statistical software  
200 (version 17; Minitab Inc., State College, PA). Latencies of individuals from the solitary tests  
201 were compared (*t*-test) and correlated (Pearson's *r*) between feeding and novel-object to  
202 examine consistency and order effects. To examine changes with social conditions (solitary  
203 or shoaling) we carried out discrete comparisons between the solitary latency time of the  
204 slowest fish from each set of five and the slowest fish when acting as a shoal, for both the  
205 novel-object exploration and the feeding context. We cannot guarantee that the slowest in  
206 each social condition was the same fish, but the slowest fish in the solitary condition was at  
207 most as latent as the slowest in the group condition. Thus, providing a conservative method to

208 assess change between the social conditions. For discrete comparisons we used Welch's  $t$ -test  
209 for mean changes (does not assume equal variances), Cohen's  $d$  for effect size and Levene's  
210  $W$  for equal variances. Then, using a linear mixed model (LMM), we tested if collective  
211 latencies differed between contexts and sets of fish (random factor to avoid  
212 pseudoreplication), and predicted by the mean (slower members promote slower collective  
213 response), standard deviation (more variable shoals are slower to collectively respond), minimum  
214 (leadership by a faster leader) or maximum (delay by a slower follower) of the solitary responses  
215 of group members.

216

### 217 3. RESULTS

218 The latencies of individuals when tested alone were strongly positively correlated  
219 between contexts (Pearson's;  $r=0.844$ ,  $P<0.001$ ), confirming that individual behaviour in  
220 either context is linked to consistent individual tendency and not a random effect. Mean  
221 latency did not differ between tests in either social condition ( $P>0.5$ ), indicating no order or  
222 context effects. Latencies of solitary individuals in the two contexts were varied and ranged  
223 between 1s and 300s, but collective latencies in the two contexts were relatively uniform  
224 between shoals, ranging between 3s to 22s (supplementary material). The slowest individuals  
225 from each set of five, when tested as solitary individuals, were significantly slower and more  
226 variable in their response than the response of the slowest group member when shoaling  
227 (Figure 1), both during novel-object exploration (Welch's  $t_{10}=-3.91$ ,  $P=0.004$ ; Levene's  
228  $W_{1,20}=7.78$ ,  $P=0.012$ ;  $d=1.749$ ) and feeding (Welch's  $t_{10}=-2.81$ ,  $P=0.020$ ; Levene's  
229  $W_{1,20}=6.04$ ,  $P=0.024$ ;  $d=1.257$ ). The overall decrease in latency when shoaling, as well as the  
230 low variance between shoals, indicated that differences in response between solitary and  
231 shoaling conditions were greater for individuals that were the most latent during the solitary  
232 tests (Figure 1). The solitary latency of shoal members had no effect, with the mean,  
233 variance, maximum and minimum failing to predict collective latency (LMM;  $P>0.5$ ,

234  $R^2 < 0.02$ ). In particular, sets of fish with lower mean solitary latency did not have lower  
235 collective latencies when shoaling, sets of fish with greater variability in solitary responses  
236 did not have slower shoaling responses and neither the slowest solitary latency of each set  
237 (follower delay) or the fastest solitary latency of each set (leader initiation) predicted  
238 collective latencies when shoaling .

239

#### 240 **4. DISCUSSION**

241         This study demonstrates the effects of being in a small group compared to being alone  
242 in different contexts. It revealed that fish were faster on average when tested as a group than  
243 individually, both during feeding and novel-object exploration. This was shown when the  
244 slowest solitary individuals were compared with the slowest in the shoal (Figure 1) and hence  
245 slower than all fish responding collectively as a shoal. Particularly slow solitary fish were the  
246 ones differing most from the collective response and hence the ones changing most between  
247 social conditions (Figure 1). This indicates that collective behaviour is skewed towards lower  
248 risk-aversion and, as a result, the most risk-averse individuals change the most. However,  
249 collective responses by shoals were not predicted by between-shoal differences in the solitary  
250 behavioural tendency of their members. This suggests that increases in risk-taking when  
251 shoaling and the ability to maintain fast collective responses is more likely a result of the  
252 effects of social conditions on individual behaviour, and not due to the individual tendencies  
253 of members affecting collective response. Although, the low predictive power of shoal-  
254 member solitary-tendency may also be due to the single collective latency measure not  
255 reflecting subtle inter-group dynamics.

256         Studies on fish show how collective responses can be driven by agreement between  
257 the members of a group (Sumpter et al., 2008; Couzin et al., 2011). Collective responses were  
258 confirmed for all shoals in the present study by the observed synchrony and the lack of  
259 instances where members of the group stayed behind or changed direction (Croft et al.,

260 2003). However, the mean and variance in the individual response of members did not predict  
261 the collective response, which suggests that the degree of similarity in the solitary tendency  
262 between members of a group does not affect how they act collectively during shoaling  
263 contexts. This may be due the small size of our shoals, where collective decisions may be  
264 infrequent, relying on quorum processes (Ward et al., 2008), and individual-differences may  
265 be greater, reducing agreement (Magurran and Pitcher, 1983; Herbert-Read et al., 2013).

266 An alternative explanation may be that some individuals take leading positions and  
267 others follow (Krause et al., 2000). Leadership can change dynamically and it has been linked  
268 to both individual risk-taking behaviour and reward motivation (Krause et al., 1992; Ioannou  
269 and Dall, 2016). Risk-taking individuals are typical contenders for leadership, such as in  
270 stickleback and mosquitofish (Ward et al., 2004; Burns et al., 2012), in that the other  
271 members of the group follow the highest risk-taking fish. Further, leadership during feeding  
272 may go to the hungriest fish, such as in the common roach (Krause et al., 1992). However,  
273 there was no indication that shoals whose fastest member was faster to feed and explore in  
274 solitary testing were faster during group testing. Hierarchical processes can also be evident  
275 via follower behaviour (Krause et al., 2000; Couzin et al., 2005; Ioannou and Dall, 2016).  
276 Although risk-averse individuals that are more reluctant to follow would be more likely to  
277 stay behind and reduce cohesion (Ward et al., 2004; Johnstone and Manica, 2011), a delay by  
278 individuals with the slowest solitary response was not indicated, with the slowest solitary-  
279 latency not predicting collective latency during group testing. We consider that this could be  
280 a limitation of being unable to track subtle interactions within shoals. Indeed, effects by  
281 individual risk-taking tendency on leader-follower interactions have been demonstrated for  
282 small groups in other fish, e.g. in pairs of three-spined sticklebacks *Gasterosteus aculeatus*  
283 (Jolles et al., 2014; Ioannou and Dall, 2016), and related to social feedback (Harcourt et al.,  
284 2009). Collective decisions that suppress individual-tendencies are preferred to hierarchies  
285 only in bigger groups of three-spined sticklebacks, e.g. 10-member shoals (McDonald et al.,

286 2016). But the most limiting factor to detecting leadership or agreement effects in our study,  
287 is that all shoals responded collectively and with limited differences between them. Indeed,  
288 the low variability in response between shoals in both contexts suggests that the changes  
289 exhibited by being in a group are consistently independent of differences between shoals in  
290 group composition.

291 Fish species with lower grouping tendencies have previously been shown to exhibit  
292 more inter-individual differences in risk-taking and foraging behaviour than fish with higher  
293 grouping tendencies (Magurran and Pitcher, 1983). Although, from our results it seems that  
294 even in species with significant shoaling tendencies, such as the one studied here (Miller and  
295 Gerlai, 2011; Suriyampola et al., 2016), individual behaviour depends on social conditions,  
296 whether solitary or shoaling. When fish are on their own, the inability to have both safety and  
297 resource abundance is resolved by phenotypic variability between individuals (Stamps et al.,  
298 2011). This is likely to optimise survival based on individual states, such as morphology (e.g.  
299 size) and physiology (e.g. stress hormone levels) (Wolf and Weissing, 2012). However,  
300 individual behaviour is adjusted during shoaling (Webster et al., 2007; Ward, 2012). These  
301 adjustments might rely on simple rules, such as individuals remaining close to others in order  
302 to optimise pay-offs (Ryer and Olla, 1991). The perceived benefits of group functions (e.g.  
303 increased growth and reduced mortality) also influence how individuals adjust behaviour, i.e.  
304 the reduced risk offered when in a group may facilitate shorter approach latencies in all  
305 group members (Ward, 2012). Effects of social facilitation on risk-taking, similar to the ones  
306 shown here, have also been shown in other fish, such as the three-spined stickleback and the  
307 mosquitofish (Ward et al., 2004; Webster et al., 2007; Ward et al., 2012). The facilitation of  
308 risk-taking and general faster approach could be attributed to the benefits of shoaling as in  
309 these other fish species, but also due to the reduction of stress-levels from being first housed  
310 individually and then in groups, something particularly relevant to zebrafish phenotypic  
311 expression (Kalueff et al., 2014). The consistently low variability in collective response

312 between shoals (Figure 1) and the inability of differences in composition predicting collective  
313 response, emphasise further the likelihood that the collective latencies recorded in our study  
314 are those of social facilitation. The pay-offs offered by a collective responses may suffice in  
315 driving individuals to stick together, while the perception of safety-in-numbers and the  
316 reduction of stress drives individuals in a group to be less aversive to risk.

317         Notably, since shoaling decreases risk-aversion to uniform levels, the most risk-  
318 aversive fish show the greatest behavioural change (Figure 1), a likely a result of shoaling  
319 being perceived as a lower-risk condition by all group members. Individuals often exhibit  
320 such differences in flexibility when encountering changes in perceived levels of risk, e.g.  
321 between high and low predation-risk levels (Quinn and Cresswell, 2005; Briffa, 2013;  
322 Kareklas et al., 2016). While flexibility is energetically costly (Dall et al., 2004), the  
323 maintenance of high levels of risk-taking can also be maladaptive when risks are extremely  
324 high (Johnson and Sih, 2005; Kareklas et al., 2016). These costs are resolved by variable  
325 levels of flexibility within a population and may be linked to life-history trade-offs, e.g. in  
326 growth/mortality or reproductive success (Wolf et al., 2008; Stamps, 2011). Comparisons  
327 across social conditions in other fish species show similar individual effects. For example,  
328 shoaling in perch also reduced risk-avoidance and variance between individuals, and it was  
329 also the most latent solitary fish that changed the most when in a group (Magnhagen and  
330 Bunnefeld, 2009). In a recent study on zebrafish pairs, individual differences in flexibility  
331 across social conditions were found to be consistent and linked to the exploratory tendency of  
332 partners (Guayasamin et al., 2017). The mechanisms mediating the dramatic shift between  
333 individual variability and group cohesion require further investigation. The current evidence  
334 argues for the need to understand better the effect of social conditions in facilitating  
335 collective responses and to examine the phenotypic transitions exhibited by individuals with  
336 changes in social conditions. This is particularly relevant for species like zebrafish that

337 exhibit dynamic changes in their level of social organisation depending on external factors  
338 (Suriyampola et al., 2016).

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340

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344

345 **ETHICAL APPROVAL:**

346 All applicable guidelines for the care and use of animals were followed (ASAB/ABS, 2016)  
347 and fish numbers were kept to the minimum required. Following inspection, the DHSSPS  
348 Northern Ireland deemed no need for licensing. Fish were kept for separate tests.

349

350 **DATA ACCESSIBILITY :**

351 Raw data were submitted as supplementary material with this article.

352

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356

357 **COMPETING INTERESTS:**

358 The authors have no competing interests.

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363 **REFERENCES:**

- 364 ASAB/ABS. (2016). Guidelines for the treatment of animals in behavioural research and teaching. *Animal*  
365 *Behaviour*, 111, I–IX .
- 366 Briffa, M., 2013. Plastic proteans: reduced predictability in the face of predation risk in hermit crabs. *Biol. Lett.*  
367 9, 20130592 (doi:10.1098/rsbl.2013.0592)
- 368 Burns, A.L, Herbert-Read, J.E., Morrell, L.J., Ward, A., 2012. Consistency of leadership in shoals of  
369 mosquitofish (*Gambusia holbrooki*) in novel and in familiar environments. *PLoS One* 7, e36567 (doi:  
370 10.1371/journal.pone.0036567 ).
- 371 Coleman, K., Wilson, D.S., 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are  
372 context-specific. *Anim. Behav.* 56, 927-936
- 373 Conradt, L., Roper, T. J. 2005. Consensus decision making in animals. *Trends Ecol. Evol.* 20, 449-456.
- 374 Couzin, I.D., Ioannou, C.C., Demirel, G., Gross, T., Torney, C.J., Hartnett, A., Conradt, L., Levin, S.A. and  
375 Leonard, N.E., 2011. Uninformed individuals promote democratic consensus in animal groups. *Science*  
376 334, 1578-1580.
- 377 Couzin, I.D., Krause, J., 2003. Self-organization and collective behavior in vertebrates. *Adv. Stud. Behav.* 32, 1-  
378 75.
- 379 Couzin, I.D., Krause, J., Franks, N.R., Levin, S.A., 2005. Effective leadership and decision-making in animal  
380 groups on the move. *Nature* 433, 513-516.
- 381 Croft, D.P., Arrowsmith, B.J., Bielby, J., Skinner, K., White, E., Couzin, I.D., Magurran, A.E., Ramnarine, I.  
382 and Krause, J., 2003. Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia*  
383 *reticulata*. *Oikos* 100, 429-438.
- 384 Dall, S.R, Houston, A.I., McNamara, J.M., 2004. The behavioural ecology of personality: consistent individual  
385 differences from an adaptive perspective. *Ecol. Lett.* 7, 734-739
- 386 Delcourt, J., & Poncin, P., 2012. Shoals and schools: back to the heuristic definitions and quantitative  
387 references. *Rev. Fish Biol. Fish.* 22, 595-619.
- 388 Dyer, J.R, Croft, D.P., Morrell, L.J., Krause, J., 2009. Shoal composition determines foraging success in the  
389 guppy. *Behav. Eco.* 20, 165-171.
- 390 Foster, W. A., Treherne, J. E., 1981. Evidence for the dilution effect in the selfish herd from fish predation on a  
391 marine insect. *Nature*, 293, 466-467.
- 392 Guayasamin, O. L., Couzin, I. D., & Miller, N. Y. (2017). Behavioural plasticity across social contexts is  
393 regulated by the directionality of inter-individual differences. *Behav. Proc.*, 141, 196-204.

- 394 Guerin, B., 2009. Social facilitation. Cambridge University Press, Cambridge
- 395 Hall, D., Suboski, M.D., 1995. Visual and olfactory stimuli in learned release of alarm reactions by zebra danio  
396 fish (*Brachydanio rerio*). *Neurobiol. Learn.Mem.* 63, 229-240.
- 397 Hamilton, T.J., Myggland, A., Duperreault, E., May, Z., Gallup, J., Powell, R.A., Schalomon, M., Digweed,  
398 S.M., 2016. Episodic-like memory in zebrafish. *Animal cognition*, 19(6), pp.1071-1079.
- 399 Harcourt, J. L., Ang, T. Z., Sweetman, G., Johnstone, R. A., Manica, A., 2009. Social feedback and the  
400 emergence of leaders and followers. *Curr.Biol.*, 19, 248-252.
- 401 Herbert-Read, J. E., Krause, S., Morrell, L. J., Schaerf, T. M., Krause, J., & Ward, A. J. W., 2013. The role of  
402 individuality in collective group movement. *Proc. R. Soc. B* 280, 20122564.
- 403 Hoare, D.J., Couzin, I.D., Godin, J.G., Krause, J. 2004. Context-dependent group size choice in fish. *Anim.*  
404 *Behav.* 67, 155-164.
- 405 Ioannou, C. C., & Dall, S. R., 2016. Individuals that are consistent in risk-taking benefit during collective  
406 foraging. *Sci. Rrep.* 6, 33991 (doi: 10.1038/srep33991)
- 407 Jeschke, J.M., Tollrian, R., 2007. Prey swarming: which predators become confused and why?. *Anim. Behav.*,  
408 74, 387-393
- 409 Johnson, J.C., Sih, A., 2005. Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for  
410 behavioral syndromes. *Behav. Ecol. Sociobiol.* 58, 390-396.
- 411 Johnstone, R.A., Manica, A., 2011. Evolution of personality differences in leadership. *Proc. Natl. Acad. Sci.*  
412 *USA* 108, 8373-8378.
- 413 Jolles, J. W., Fleetwood-Wilson, A., Nakayama, S., Stumpe, M. C., Johnstone, R. A., & Manica, A., 2014. The  
414 role of previous social experience on risk-taking and leadership in three-spined sticklebacks. *Behav.*  
415 *Ecol.*, 25, 1395-1401.
- 416 Kalueff, A. V., Stewart, A. M., & Gerlai, R., 2014. Zebrafish as an emerging model for studying complex brain  
417 disorders. *Trends Pharmacol. Sci.*, 35, 63-75.
- 418 Kareklas, K., Arnott, G., Elwood, R.W., Holland, R.A., 2016, Plasticity varies with boldness in a weakly-  
419 electric fish. *Front. Zool.* 13 (doi: 10.1186/s12983-016-0154-0)
- 420 Kareklas, K., Elwood, R.W. & Holland, R.A., 2017. Personality effects on spatial learning: comparisons  
421 between visual conditions in a weakly-electric fish. *Ethology* (doi: 10.1111/eth.12629)
- 422 Krause, J., Bumann, D., Todt, D., 1992. Relationship between the position preference and nutritional state of  
423 individuals in schools of juvenile roach (*Rutilus rutilus*). *Behav. Ecol. Sociobiol.*, 30, 177-180.

- 424 Krause, J., Hoare, D., Krause, S., Hemelrijk, C.K., Rubenstein, D.I., 2000. Leadership in fish shoals. *Fish Fish.*  
425 1, 82-89.
- 426 Laland, K.N. & Williams, K., 1997. Shoaling generates social learning of foraging information in guppies.  
427 *Anim. Behav.* 53, 1161-1169
- 428 Magnhagen, C. & Bunnefeld, N., 2009. Express your personality or go along with the group: what determines  
429 the behaviour of shoaling perch?. *Proc. R. Soc. B* 276, 3369-3375
- 430 Magurran, A.E, Pitcher, T.J., 1983. Foraging, timidity and shoal size in minnows and goldfish. *Behav. Ecol.*  
431 *Sociobiol.* 12, 147-152
- 432 McDonald, N.D, Rands, S.A., Hill, F., Elder, C., Ioannou, C. C., 2016. Consensus and experience trump  
433 leadership, suppressing individual personality during social foraging. *Sci. Adv.* 2, e1600892  
434 (doi:10.1126/sciadv.1600892)
- 435 Miller, N.Y, Gerlai, R., 2011. Shoaling in zebrafish: what we don't know. *Rev. Neuroscience.* 22, 17-25
- 436 Miller, N.Y, Gerlai, R., 2012. From schooling to shoaling: patterns of collective motion in zebrafish (*Danio*  
437 *rerio*). *PLoS One*, 7, e48865. (doi: 10.1371/journal.pone.0048865)
- 438 Pitcher, T.J., Parrish, J.K., 1993. Functions of shoaling behaviour in teleosts, in: Pitcher, T.J (Ed.), *Behaviour of*  
439 *teleost fishes*. Chapman and Hall, London , pp. 363-439.
- 440 Quinn, J. L., Cresswell, W., 2005. Personality, anti-predation behaviour and behavioural plasticity in the  
441 chaffinch *Fringilla coelebs*. *Behaviour* 142,1377-1402
- 442 Ryer, C.H., Olla, B.L., 1991. Information transfer and the facilitation and inhibition of feeding in a schooling  
443 fish. *Environ. Biol. Fish.* 30, 317-323.
- 444 Scott, J.P., 1956. The analysis of social organization in animals. *Ecology* 37, 213-221.
- 445 Sneksner, J. L., Ruhl, N., Bauer, K., & McRobert, S. P., 2010. The influence of sex and phenotype on shoaling  
446 decisions in zebrafish. *Int. J. of Comp. Psychol.* 23, 70-81.
- 447 Stamps, J.A., 2007. Growth-mortality tradeoffs and 'personality traits' in animals. *Ecol. Lett.* 10, 355-363
- 448 Sumpter, D.J., Krause, J., James, R., Couzin, I.D., Ward, A.J., 2008. Consensus decision making by fish. *Curr.*  
449 *Biol.* 18, 1773-1777.
- 450 Suriyampola, P.S., Shelton, D.S., Shukla, R., Roy, T., Bhat, A., Martins, E.P., 2016. Zebrafish social behavior in  
451 the wild. *Zebrafish*, 13, 1-8.
- 452 Toms, C.N., Echevarria, D. . & Jouandot, D.J., 2010. A methodological review of personality-related studies in  
453 fish: focus on the shy-bold axis of behavior. *Int J. Comp. Psychol.* 23, 1-25.

- 454 Ward, A. J., 2012. Social facilitation of exploration in mosquitofish (*Gambusia holbrooki*). *Behav. Ecol.*  
455 *Sociobiol.* 66, 223-230.
- 456 Ward, A.J., Herbert-Read, J.E., Sumpter, D.J., Krause, J., 2011. Fast and accurate decisions through collective  
457 vigilance in fish shoals. *Proc. Natl. Acad. Sci. USA* 108, 2312-2315.
- 458 Ward, A.J., Sumpter, D.J., Couzin, I.D., Hart, P.J., & Krause, J., 2008. Quorum decision-making facilitates  
459 information transfer in fish shoals. *Proc. Natl. Acad. Sci. USA* 105, 6948-6953.
- 460 Ward, A.J., Thomas, P., Hart, P.J., Krause, J., 2004. Correlates of boldness in three-spined sticklebacks  
461 (*Gasterosteus aculeatus*). *Behav. Ecol. Sociobiol.* 55, 561-568
- 462 Webster, M.M., Ward, A.J., 2011. Personality and social context. *Biol. Rev.* 86, 759-773.
- 463 Webster, M.M., Ward, A.J.W., Hart, P.J.B., 2007. Boldness is influenced by social context in threespine  
464 sticklebacks (*Gasterosteus aculeatus*). *Behaviour* 144, 351-371
- 465 Wilson, C.D., Arnott, G., Elwood, R.W., 2012. Freshwater pearl mussels show plasticity of responses to  
466 different predation risks but also show consistent individual differences in responsiveness. *Behav.*  
467 *Process.* 89(3), 299-303.
- 468 Wolf, M., Van Doorn, G.S., Weissing, F.J., 2008. Evolutionary emergence of responsive and unresponsive  
469 personalities. *Proc. Natl. Acad. Sci. USA* 105, 15825-15830 .
- 470 Wolf, M., Weissing, F.J., 2012. Animal personalities: consequences for ecology and evolution. *Trends Ecol.*  
471 *Evol.* 27, 452-461
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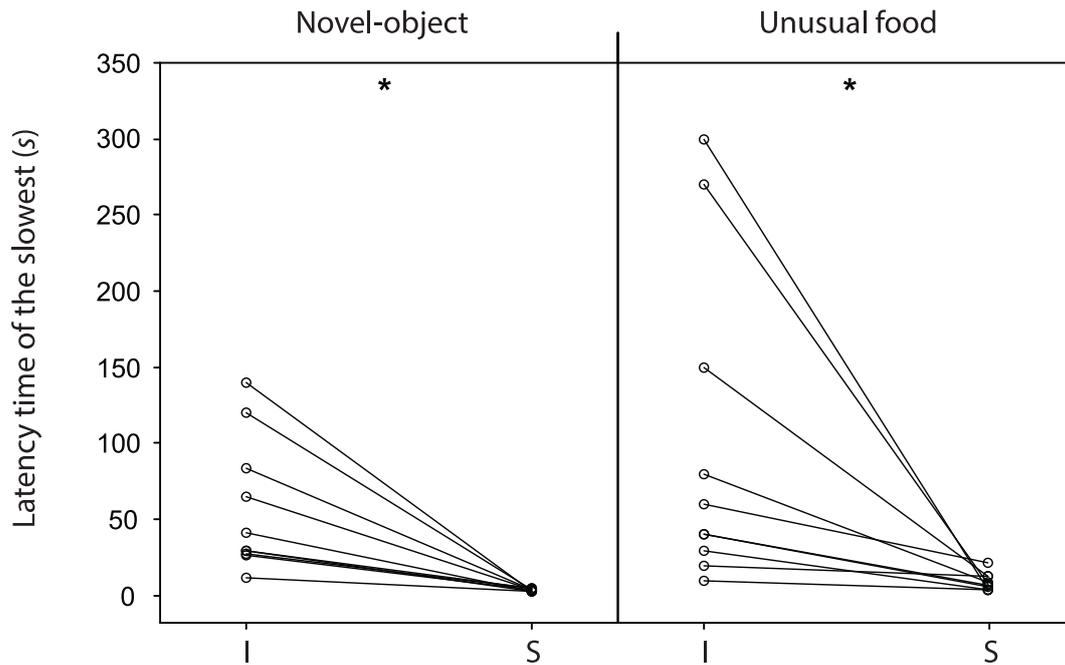
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493 **Figure 1: Differences in latency time between social conditions.** The slowest solitary  
 494 response from each set of five fish during the individual test (I) was significantly slower than  
 495 the response of the slowest fish during the shoaling test (S) in both the novel-object  
 496 inspection and the feeding context. Lines indicate change between social conditions [\*  
 497  $P < 0.05$ ].

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