Grouping promotes risk-taking in unfamiliar settings

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Behavioural Processes

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1 **<u>Grouping promotes risk-taking in unfamiliar settings</u>**

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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   aversive 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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1. INTRODUCTION

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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-aversive

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-aversive 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-aversive; Ioannou and Dall, 2016).

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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 $25\pm1^{O}C$ 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® 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=0844, 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-aversive 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-aversive 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-memeber 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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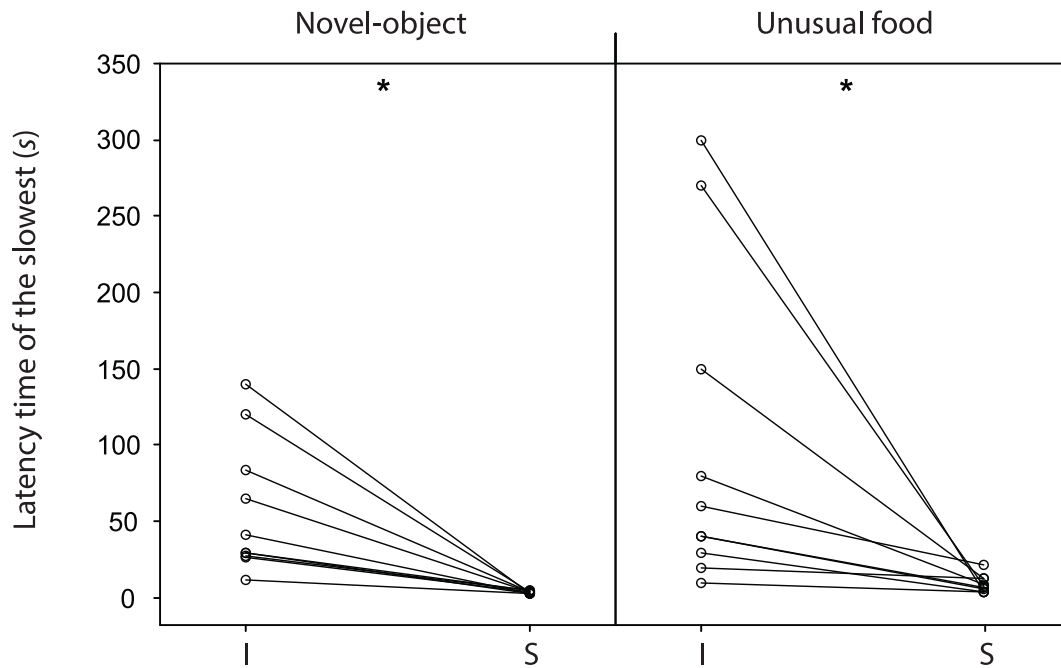
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Figure 1: Differences in latency time between social conditions. The slowest solitary response from each set of five fish during the individual test (I) was significantly slower than the response of the slowest fish during the shoaling test (S) in both the novel-object inspection and the feeding context. Lines indicate change between social conditions [* $P<0.05$].