

1 **Mid-sized groups perform best in a collective decision task in sticklebacks**

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13 Numerous studies have reported functional improvements in collective behaviour with increasing
14 group size, however the possibility that such improvements may saturate or even decline as group
15 size continues to grow have seldom been tested experimentally. Here, we tested the ability of
16 solitary three-spined sticklebacks and those in groups, ranging from 2 to 29 fish, to leave an
17 unfavourable patch of habitat. Our results replicate the findings of previous studies at low group
18 sizes, with the fish initially showing a reduction in their latency to leave the unfavourable habitat as
19 group size increased. As group size continued to increase, however, latency to leave the habitat
20 increased, so that the functional relationship between group size and latency to depart was U-
21 shaped. Our results suggest an optimum group size in this context of between 12 and 20 fish.
22 Underlying this group-level trend was a similar U-shaped relationship between group size and the
23 first fish to leave the habitat, suggesting that at larger group sizes, social conformity to the behaviour
24 of the majority can stifle the ability of fish to innovate - in this case, to induce a collective movement
25 from the unfavourable habitat.

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27 Keywords: Grouping; sociality; shoaling; schooling; swarm intelligence

28 Living in groups provides important and wide-ranging benefits to animals [1, 2]. These benefits have
29 often been demonstrated to scale with group size, so that individuals in larger groups are more
30 successful at evading predators or gain greater per capita foraging rewards [1, 3]. Underlying these
31 functional improvements are the tendencies of larger groups to acquire, integrate and use
32 information more effectively in collective decision-making [4-7]. In some systems, such as starling
33 flocks, the responsiveness of individual group members to near neighbours provides the basis for
34 scale-free correlation between behaviour of birds within the flock, meaning that irrespective of the
35 size of the flock, the movements of all group members remain highly coordinated [8, 9].
36 Nonetheless, initial improvements in collective function that accompany increases in group size may
37 eventually saturate and, if group size continues to grow, the possibility exists for collective function
38 to decline. One potential reason for this is social conformity and, in particular, the effect of
39 conformity to stifle innovation or transitions between different types of behaviour. For example, in a
40 study of the effect of conformity on foraging in guppies (*Poecilia reticulata*), Day et al. showed that
41 innovation was more likely to occur in smaller rather than in larger groups [10]. Similarly, moving
42 shoals of rummy-nose tetras (*Hemigrammus rhodostomus*) were less likely to change direction as
43 group size grew [11]. In these cases, the pressure to conform to established behaviour patterns
44 therefore appears to constrain the options available to members of large groups. Nonetheless, the
45 potential conflict between conformity on the one hand and facilitation on the other has received
46 relatively little attention in the study of experimental collective behaviour.

47

48 The extent and degree to which group performance declines is likely to vary with context (such as
49 predator detection, collective navigation or problem solving) and mechanism (such as pool of
50 competence, or collective sensing), and this is an interesting problem in itself. As a starting point,
51 here we focused upon one context, a collective decision to escape from an unfavourable
52 environment into a refuge. Except when basking, fish generally avoid shallows and prefer to move to
53 deeper water [6,12]. Using the three-spined stickleback (*Gasterosteus aculeatus*), an established
54 model for the study of social and collective behavior [13-17], we examined the effect of increasing
55 group size on the latency of fish to exit an area of shallow water and escape into a deeper area. We
56 predicted that measures of group performance would be a non-linear function of group size, rather
57 than the linear relationship that is most often tested. We further investigated potential mechanisms
58 underlying group-size related changes in behaviour: leadership/innovation, measured as the time
59 taken by the first fish to depart the arena as a function of group size, and group
60 coherence/fragmentation, measured as the variance among group members in the time taken to
61 exit the habitat.

62

63

64 **Methods**

65

66 Three-spine sticklebacks with a body length of 32.2 ± 4.1 mm (mean \pm SD) were caught using large
67 (1.2 x 1 m) hand nets at the Great Eau in Lincolnshire, UK (53° 24' 50 N, 0° 11' 3 E) in October 2017.
68 The fish were most likely young of the year and, since it was outside the breeding season, sex was
69 not assessed. The large size of the nets meant that we were able to capture entire shoals as they
70 passed. The fish were transported to nearby facilities, where they were kept for 2 days prior to
71 experiments in two 200L circular holding containers and fed with defrosted frozen bloodworm.

72

73 Experiments took place in a circular, black plastic arena, 1.1m in diameter, and filled to a depth of 45
74 cm. A second, opaque, rectangular plastic arena, measuring 64 x 35 cm was suspended within this.
75 The inner arena was placed on a platform, so that the water depth inside this was 6.5 cm. At one
76 end of this inner arena, we cut a door, 18.5 cm in width. This door could be lifted remotely to allow
77 the fish to exit.

78

79 For each trial, we haphazardly collected a group of fish and added them to the inner arena. These
80 fish were allowed to settle for two minutes before the door was raised allowing them the
81 opportunity to exit the inner arena and move into the deeper water. Five minutes after the door was
82 initially raised, we terminated each trial, then counted the number of fish as they were removed.
83 Used fish were placed in a different holding container to unused fish. Each individual fish was used
84 once.

85
86 All experiments were filmed from above using a Panasonic GH4 camera, filming at 24fps, and at a
87 resolution of 1080p. Subsequently, the videos were analysed blind by a research assistant who was
88 not aware of the hypotheses being tested. The time taken for each individual fish to exit the inner
89 arena was measured.

90
91 All analyses were conducted in R version 3.5.2. Data were inspected using quantile-quantile plots.
92 Since the time to exit the inner arena was positively skewed, we analysed the data using a
93 generalized linear mixed model, specifying gamma-distributed errors. Models met the required
94 assumptions and were not overdispersed. To account for the non-independence of individuals within
95 each trial, we included trial as a random effect in the model. To capture the relationship between
96 group size and time to exit, we included 1st and 2nd order polynomials in our model. To examine the
97 relationship between group size and the time taken for the first individual to exit the inner arena, we
98 used a generalized linear model, again specifying gamma-distributed errors and including 1st and 2nd
99 order polynomials. We used the MuMIn package to calculate the marginal and conditional r^2 values
100 for the models following [18]. Finally, to assess whether group cohesion was affected by increasing
101 group size, we examined the effect of group size on mean group standard deviation in time to exit,
102 and the mean difference in exit time between successive fish in each group using linear regression.
103

104 105 **Results**

106 In total, we tested 51 groups, ranging in size from singletons to groups of 29 fish. Of these, 3 groups
107 were excluded from the analysis due to the failure of the gate to open correctly. The remaining 48
108 groups comprised a total of 438 fish. Of these 5 fish failed to exit within 5 minutes and were given a
109 score of 300.

110
111 Time for all fish to exit was a quadratic function of group size ($\chi^2 = 9.938$, $p = 0.007$; trigamma
112 estimates: marginal $r^2 = 0.206$, conditional $r^2 = 0.605$; see Fig. 1). Applying Akaike's Information
113 Criterion, we established that the quadratic model (weight: 0.909) provided a better fit than the
114 linear model (weight: 0.091). In addition, the model including group as the random effect provided a
115 better fit (weight: 1) than a model without the random effect (weight: 0), meaning that the groups
116 had significantly different intercepts and suggesting within-group similarity in terms of their times to
117 exit.

118
119 Time for the first fish to exit was a quadratic function of group size ($\chi^2 = 63.604$, $p < 0.001$; trigamma
120 estimate of $r^2 = 0.472$; see Fig. 2). The quadratic model (weight: 1) provided a better fit than the
121 linear model (weight: 0).

122
123 Finally, there was no significant relationship between mean group standard deviation of time to exit
124 and group size (Adjusted $r^2 = 0.063$, $F_{1,39} = 3.703$, $p = 0.062$), nor was there a significant relationship
125 between the difference in exit time between successive fish in each group and group size (Adjusted
126 $r^2 = 0.006$, $F_{1,39} = 0.738$, $p = 0.396$)
127

128 129 **Discussion**

130

131 As group sizes of sticklebacks increased from low to medium group sizes, there was an improvement
132 in the collective ability of group members to exit the unfavourable habitat. This is in line with
133 previous studies, demonstrating often powerful benefits to augmenting group size, especially for
134 singletons and small groups [6]. However, as group size continued to increase, this collective ability
135 deteriorated. Negative effects of larger group sizes have been discussed in the context of optimal
136 group size, in relation to competition, greater visibility to predators and increased exposure to
137 parasites [1]. Most relevant to the present work is the suggestion made by previous studies that, in
138 larger groups, social conformity may limit the ability of innovative behaviour to establish and spread
139 and likely explains the greater latency to exit of larger groups.

140

141 As group size increases, their members derive benefits from improvements in both the acquisition
142 and use of information. For instance, larger groups have greater ability to detect relevant cues, for
143 example in the 'many eyes' effect [19, 20], or to track environmental gradients [7, 21]. Information
144 can then spread through repeated local interactions between individuals, to promote distributed,
145 self-organised decision-making [22, 23]. In addition, larger groups are simply more likely to contain
146 individuals who are more capable, more knowledgeable or more motivated. This 'pool of
147 competence' argument is thought to underpin group size-related improvements in decision-making
148 [24-26]. These and similar mechanisms are likely to at least partially explain the initial reductions in
149 latency to exit in the present study. A further explanation is offered by the social facilitation of
150 activity in larger groups, promoting greater exploration [27]. We saw some evidence for this within
151 trials, especially in comparing the singletons and pairs to larger groups, however this is difficult to
152 quantify and compare given the rapid exit times of many of the medium-sized groups.

153

154 The latency to exit the unfavourable habitat was lowest in groups comprising from 12 to 20
155 individuals. Beyond these group sizes, latency increased. Of the various potential explanations for
156 this, the one with the most support is that larger group sizes constrain innovation, such as
157 embarking on an alternative pattern of behaviour. The time taken for the first fish, which we term
158 the innovator, to leave followed a similar pattern to the analysis including all fish. Specifically, the
159 latency to exit for the innovator initially decreased with group size before subsequently increasing.
160 The tendency to conform to an established pattern of behaviour may increase with group size, or
161 alternatively to adopt behaviour in proportion to the number of individuals already performing that
162 behaviour, are established phenomena described in many species across a range of taxa [28-31]. The
163 challenge for individuals whose preferences conflict with that of the group is to decide whether to
164 act on their own information and behave independently, thus surrendering the benefits of group
165 membership, or to conform to the behaviour of the majority, thereby incurring the consensus cost of
166 foregoing opportunities [32, 33]. This has been described in groups of giant danios (*Devario*
167 *aequipinnatus*) [34] and likened to a 'school trap' whereby minorities in animal groups are unable to
168 exert their preferences in group decision-making [35].

169

170 Alternative explanations for the increased latency to exit in larger groups include reductions in the
171 perception of risk in larger groups [36, 37]. This might potentially reduce the urgency to exit the
172 habitat in larger groups, however it does not explain the initial decrease in latency to exit as group
173 size increased. Moreover, we note that in no case did a fish re-enter the unfavourable habitat having
174 previously left it, regardless of group size, indicating that fish had a strong preference to avoid the
175 shallower water. Another explanation for our results is that the larger groups may have been less
176 coherent than smaller ones, making the process of exiting longer and more drawn out. There was no
177 evidence to support this, however. Further, the improvement in model fit provided by including
178 group as a random effect suggests within-group consistency in latency to exit. Taken together with
179 our finding of clear parallels between the time to exit for all fish, and the time to exit for the first

180 fish, indicate that the increased latency to exit in larger groups was driven by what might be termed
181 group inertia rather than by group fragmentation.

182
183 In an earlier field study of this population [38], encompassing 77 shoals of free-ranging sticklebacks,
184 mean group size was 14.8. While acknowledging that there are many factors that influence group
185 size distributions, this observed mean elective group size in the wild comes close to that which
186 would maximise the advantages of collective decision-making, in this context at least. Our results
187 have parallels in models produced by Kao & Couzin [39] who found that medium-sized groups
188 maximized the efficiency of decision-making and by Mateo et al. [40] who demonstrated that the
189 number of connections in a network influenced the collective response of the system and that
190 limiting that number could improve the response under some circumstances. Most recently,
191 Toyokawa et al. [41] showed that conformity, or 'herding', increased with group size and the
192 difficulty of the task at hand. Useful future work would include examining group-size effects on
193 collective decision-making in other contexts, re-examining previous established patterns using larger
194 group sizes in order to investigate the functional collective responses of groups beyond the initial
195 and more widely-documented improvements seen in groups as they increase from small to medium
196 group sizes.

197
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202

203 **Figure Legends**

204

205 Figure 1: Time (in seconds) for all fish to exit the unfavourable habitat patch as a function of group
206 size. The quadratic model is plotted with shaded areas to represent 95% confidence intervals.

207

208 Figure 2: Time (in seconds) for the first fish in each group to exit the unfavourable habitat patch as a
209 function of group size. The quadratic model is plotted with shaded areas to represent 95%
210 confidence intervals.

211

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