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Animal behaviour

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

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

1. Introduction

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

The extent and degree to which group performance declines is likely to vary with context (such as predator detection, collective navigation or problem solving) and mechanism (such as a pool of competence, or collective sensing), and

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this is an interesting problem in itself. As a starting point, here we focused upon one context: a collective decision to escape from an unfavourable environment into a refuge. Except when basking, fish generally avoid shallows and prefer to move to deeper water [6,12]. Using the three-spined stickleback (*Gasterosteus aculeatus*), an established model for the study of social and collective behaviour [13–17], we examined the effect of increasing group size on the latency of fish to exit an area of shallow water and escape into a deeper area. We predicted that measures of group performance would be a nonlinear function of group size, rather than the linear relationship that is most often tested. We further investigated potential mechanisms underlying group size-related changes in behaviour: leadership/innovation, measured as the time taken by the first fish to depart the arena as a function of group size, and group coherence/fragmentation, measured as the variance among group members in the time taken to exit the habitat.

2. Material and methods

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

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

For each trial, we haphazardly collected a group of fish and added them to the inner arena. These fish were allowed to settle for 2 min before the door was raised, allowing them the opportunity to exit the inner arena and move into the deeper water. Five minutes after the door was initially raised, we terminated each trial, then counted the number of fish as they were removed. Used fish were placed in a different holding container from unused fish. Each individual fish was used once.

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

All analyses were conducted in R v. 3.5.2 [18]. Data were inspected using quantile–quantile plots. Since the time to exit the inner arena was positively skewed, we analysed the data using a generalized linear mixed model, specifying γ-distributed errors. Models met the required assumptions and were not overdispersed. To account for the non-independence of individuals within each trial, we included trial as a random effect in the model. To capture the relationship between group size and time to exit, we included first- and second-order polynomials in our model. To examine the relationship between group size and the time taken for the first individual to exit the inner arena, we used a generalized linear model, again specifying γ-distributed errors and including first- and second-order polynomials. We used the MuMIn package to calculate the marginal and conditional R^2 values for the models following [19]. Finally, to assess whether group cohesion was affected by increasing group size, we examined the effect of group size on mean group standard deviation in time to exit and the mean difference in exit time between successive fish in each group using linear regression.

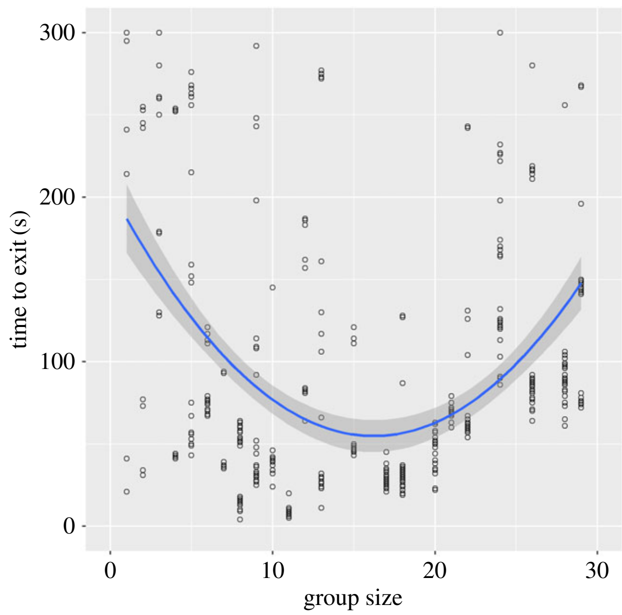

Figure 1. Time (in seconds) for all fish to exit the unfavourable habitat patch as a function of group size. The quadratic model is plotted with shaded areas to represent 95% confidence intervals. (Online version in colour.)

3. Results

In total, we tested 51 groups, ranging in size from singletons to groups of 29 fish. Of these, three groups were excluded from the analysis owing to the failure of the gate to open correctly. The remaining 48 groups comprised a total of 438 fish. Of these, five fish failed to exit within 5 min and were given a score of 300.

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

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

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

4. Discussion

As group sizes of sticklebacks increased from low to medium, there was an improvement in the collective ability of group members to exit the unfavourable habitat. This is in line with previous studies, demonstrating often powerful benefits to augmenting group size, especially for singletons and small groups

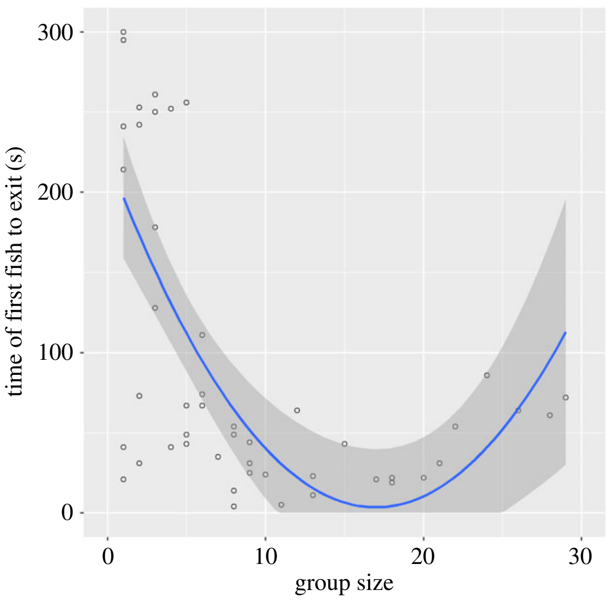

Figure 2. Time (in seconds) for the first fish in each group to exit the unfavourable habitat patch as a function of group size. The quadratic model is plotted with shaded areas to represent 95% confidence intervals. (Online version in colour.)

[6]. However, as group size continued to increase, this collective ability deteriorated. Negative effects of larger group sizes have been discussed in the context of optimal group size, in relation to competition, greater visibility to predators and increased exposure to parasites [1]. Most relevant to the present work is the suggestion made by previous studies that, in larger groups, social conformity may limit the ability of innovative behaviour to establish and spread and likely explains the greater latency to exit of larger groups.

As group size increases, their members derive benefits from improvements in both the acquisition and use of information. For instance, larger groups have greater ability to detect relevant cues, for example in the 'many eyes' effect [20,21], or to track environmental gradients [7,22]. Information can then spread through repeated local interactions between individuals, to promote distributed, self-organized decision-making [23,24]. In addition, larger groups are simply more likely to contain individuals that are more capable, more knowledgeable or more motivated. This 'pool of competence' argument is thought to underpin group size-related improvements in decision-making [25–27]. These and similar mechanisms are likely to at least partially explain the initial reductions in latency to exit in the present study. A further explanation is offered by the social facilitation of activity in larger groups, promoting greater exploration [28]. We saw some evidence for this within trials, especially in comparing the singletons and pairs with larger groups; however, this is difficult to quantify and compare given the rapid exit times of many of the medium-sized groups.

The latency to exit the unfavourable habitat was lowest in groups comprising from 12 to 20 individuals. Beyond these group sizes, latency increased. Of the various potential explanations for this, the one with the most support is that larger group sizes constrain innovation, such as embarking on an alternative pattern of behaviour. The time taken for the first fish, which we term the innovator, to leave followed a similar pattern to the analysis including all fish. Specifically, the latency to exit for the innovator initially decreased with group size, before subsequently increasing. Two related phenomena may explain the increased latency to leave in larger groups: first, the pressure on group members to conform to an established pattern of behaviour increases with group size, and second, the likelihood of adopting novel behaviour is proportional to the number of individuals already performing that behaviour [29–32]. The challenge for individuals whose preferences conflict with that of the group is to decide whether to act on their own information and behave independently, thus surrendering the benefits of group membership, or to conform to the behaviour of the majority, thereby incurring the consensus cost of foregoing opportunities [33,34]. This has been described in groups of giant danios (*Devario aequipinnatus*) [35] and likened to a 'school trap' whereby minorities in animal groups are unable to exert their preferences in group decision-making [36].

Alternative explanations for the increased latency to exit in larger groups include reductions in the perception of risk in larger groups [37,38]. This might potentially reduce the urgency to exit the habitat in larger groups; however, it does not explain the initial decrease in latency to exit as group size increased. Moreover, we note that in no case did a fish re-enter the unfavourable habitat having previously left it, regardless of group size, indicating that fish had a strong preference to avoid the shallower water. Another explanation for our results is that the larger groups may have been less coherent than smaller ones, making the process of exiting longer and more drawn out. There was no evidence to support this, however. Furthermore, the improvement in model fit provided by including group as a random effect suggests within-group consistency in latency to exit. This, in conjunction with the clear parallels in latency to leave across the range of group sizes for the first fish and for all fish, indicate that the increased latency of larger groups to leave was driven not by group fragmentation but by what might be termed group inertia.

In an earlier field study of this population [39] encompassing 77 shoals of free-ranging sticklebacks, mean group size was 14.8. While acknowledging that there are many factors that influence group size distributions, this observed mean elective group size in the wild comes close to the size that would maximize the advantages of collective decision-making, in this context at least. Our results have parallels in models produced by Kao & Couzin [40], who found that medium-sized groups maximized the efficiency of decision-making, and by Mateo *et al.* [41], who demonstrated that the number of connections in a network influenced the collective response of the system and that limiting that number could improve the response under some circumstances. Most recently, Toyokawa *et al.* [42] showed that conformity, or 'herding', increased with group size and the difficulty of the task at hand. Useful future work would include examining group-size effects on collective decision-making in other contexts, re-examining previously established patterns using larger group sizes in order to investigate the functional collective responses of groups beyond the initial and more widely documented improvements seen in groups as they increase from small to medium group sizes.

Ethics. All work was carried out in accordance with local guidelines and was approved by the University of Sydney's animal ethics committee, approval 2017/1160.

Data accessibility. Data package title: Data from: Mid-sized groups perform best in a collective decision task in sticklebacks. DOI: https://doi.org/10.5061/dryad.22c54m5. Data files: Saltfleet2017Data.

Authors' contributions. A.J.W.W. and M.M.W. designed and performed all experiments, analysed the data and wrote the manuscript. Both were involved in revizing the manuscript according to referees' comments. Both authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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