

Fast and accurate decisions through collective vigilance in fish shoals

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Although it has been suggested that large animal groups should make better decisions than smaller groups, there are few empirical demonstrations of this phenomenon and still fewer explanations of the how these improvements may be made. Here we show that both speed and accuracy of decision making increase with group size in fish shoals under predation threat. We examined two plausible mechanisms for this improvement: first, that groups are guided by a small proportion of high-quality decision makers and, second, that group members use self-organized division of vigilance. Repeated testing of individuals showed no evidence of different decision-making abilities between individual fish. Instead, we suggest that shoals achieve greater decision-making efficiencies through division of labor combined with social information transfer. Our results should prompt reconsideration of how we view cooperation in animal groups with fluid membership.

swarm intelligence | collective decision-making | sociality

Social animals are frequently required to make collective decisions about such things as the timing and direction of group travel, the detection and avoidance of predators, or the location of food (1). The decision-making accuracy of groups is typically predicted to be greater than that of component group members; accuracy of decision making initially increases with group size before leveling off (2, 3). This phenomenon is driven by the fact that larger groups of animals are more effective than smaller groups or solitary individuals at gathering information, whereas the integration of the information gathered by different group members allows more accurate decisions to be made by larger groups (4, 5). Furthermore, integration of information during the decision-making process need not incur a great cost in terms of speed if groups use some simple heuristic based on the behavior of group mates, such as a quorum response, which allows information to be integrated and filtered both rapidly and accurately (6–8).

The “many eyes” theory predicts that predators will be detected sooner by larger groups, increasing the probability of escape for the individual that first detects them, as well as for other group members as the information is transmitted across the group (9–13). Despite the fact that numerous studies have provided evidence in support of this functional benefit of larger group sizes, little is known about the decision-making mechanisms that underlie this key benefit of sociality. If we assume that members independently gather information and scan different parts of the environment, then the first individual to detect a given cue could initiate a response that proliferates rapidly throughout the group (14–17). Under this scenario, improvements in both speed and accuracy of collective decision making with group size can result because *a*) the probability that the group contains individuals that are better at scanning increases with group size and/or *b*) individuals do not need to scan as much of their environment when in groups, effectively focusing their information gathering to a smaller area of space.

Whereas previous studies have predicted increases in decision-making accuracy with group size (6), little is known about how group size interacts with the other critical parameter of decision making: speed. Hence we tested the decision making of fish on

their own as well as in groups of different sizes under simulated predation risk, predicting that, because animals should optimize both speed and accuracy in their decision-making process, larger groups would make faster as well as more accurate decisions than smaller groups or singletons.

Results

In a simple decision-making task (Fig. 1), solitary fish performed relatively poorly, avoiding a replica predator in 60 of 108 trials (55.6%). The proportion of fish making an accurate decision increased with group size with focal individuals in groups of 8 fish and of 16 fish being significantly more likely to make accurate decisions (i.e., to avoid the replica predator) than solitary ones (binomial test: group of 8, $P = 0.02$; group of 16, $P = 0.02$; Fig. 2A).

The theoretical “perfect many eyes” case, where the probability of all individuals avoiding the predator is equal to that of just one or more individuals detecting the predator, can be calculated from the single-fish experiments by noting that the probability that a single fish spots the predator is 0.11 (assuming that when they did not spot the predator they take a random fork of the Y-maze). Thus, the probability that at least one individual in a group of size n spots the predator is $1 - (1 - 0.11)^n$ and the probability that the group avoids the predator is then

$$1 - \frac{1}{2}(1 - 0.11)^n,$$

where the factor of 1/2 accounts for the fact that even if the group does not spot the predator it has a 50% chance of choosing the correct branch. This perfect many eyes model accurately predicts the experimental results as group sizes increase (regression: $r_4 = 0.92$, $P = 0.03$).

There was no difference in swimming speed between groups in the approach zone (speed in approach zone: ANOVA: $F_{4,157} = 1.54$, $P = 0.19$). However, in the decision-making zone, swimming speed increased with increasing group size (speed in the decision zone: ANOVA: $F_{4,157} = 9.93$, $P < 0.001$; Fig. 2B). Time spent in both zones decreased with increasing group size (time in approach zone, ANOVA, $F_{4,157} = 4.51$, $P = 0.002$; time in decision zone, ANOVA, $F_{4,157} = 5.45$, $P < 0.001$; Fig. 2C; group-level dynamics are plotted in Figs. S1 and S2). This discrepancy between speed and time in the zones is likely explained by path tortuosity, which decreased with increasing group size in both zones (tortuosity in approach zone, ANOVA, $F_{4,157} = 4.76$, $P = 0.001$; tortuosity in decision zone, ANOVA, $F_{4,157} = 5.33$, $P < 0.001$; Fig. 2D). Solitary focal fish and those in pairs decreased

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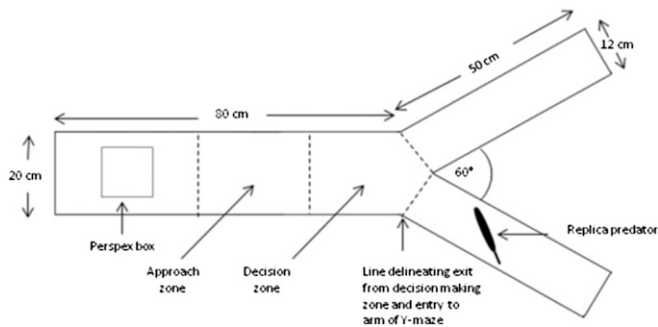


Fig. 1. Experimental apparatus.

their swimming speed in the decision zone compared with the approach zone, whereas those in larger groups did not (paired *t* test: solitary, $t_{107} = 5.1$, $P < 0.01$; group of 2, $t_{12} = 2.4$, $P = 0.03$; group of 4, $t_{12} = 1.5$, $P = 0.16$; group of 8, $t_{13} = 0.7$, $P = 0.49$; group of 16, $t_{13} = 1.1$, $P = 0.29$). Focal fish in all group sizes increased tortuosity in the decision zone compared with the approach zone (paired *t* test: solitary, $t_{107} = 12.9$, $P < 0.01$; group of 2, $t_{12} = 5$, $P < 0.01$; group of 4, $t_{12} = 3.4$, $P < 0.01$; group of 8, $t_{13} = 3.7$, $P < 0.01$; group of 16, $t_{13} = 3.7$, $P < 0.01$).

Can the improvement in decision-making ability in larger groups be explained by the presence of “expert” decision makers? Under this scenario, we envisage that there would be variation in decision-making ability between individuals and that, where groups are randomly composed, the probability of including high-quality decision makers in a group would increase with the number of individuals in that group. To test this hypothesis we measured the repeated decision-making performance of 44 individual fish in nine separate tests at weekly intervals. The observed distribution of accurate decisions across these trials did not differ from a null expectation of a binomial error probability distribution (χ^2 -test: $\chi^2_9 = 14.15$, $P = 0.11$). Furthermore, the performance of fish in the first four trials did not predict their performance in the subsequent five trials (regression: $r_{43} = 0.15$, $P = 0.3$). Finally, in the trials involving groups of fish, we found that fish in the front half of groups were not more accurate than fish in the back half of groups (paired *t* test: $t_{53} = 1.97$, $P = 0.08$).

An alternative explanation is that the improvement in decision making occurs not through diversity in individual ability, but through social facilitation of predator detection with increasing group size. One means by which this could be achieved is through a form of self-organized division of the task of vigilance. If group members divide up the task of vigilance between each other, then each individual can concentrate its attention on a smaller section of the environment. This being the case, we predict changes in individual scanning behavior as group size increases, including a reduction in the frequency of direction changes. In accordance with this prediction, we found that the frequency of direction changes by focal fish did decrease as group size increased (ANOVA: $F_{4,157} = 9.57$, $P < 0.001$).

Because self-organization is characterized by positive social feedback, we next investigated whether there was any social influence on decision making. For each individual focal fish we calculated whether the fish avoided the predator and measured the number of other fish in the decision zone at the same time as the focal fish. These decision zone “companions” were also classified as to whether they went on to avoid the predator (companions were defined as those fish that occupied the decision zone at the same time as the focal fish). Fig. 3 shows the frequency of correct choices by the focal fish as a function of the number of companions in the decision zone that went on to avoid the predator (denoted X_1) minus those companions that took the branch containing the predator (denoted X_2). We fit a logistic regression model to the probability of avoiding the replica predator:

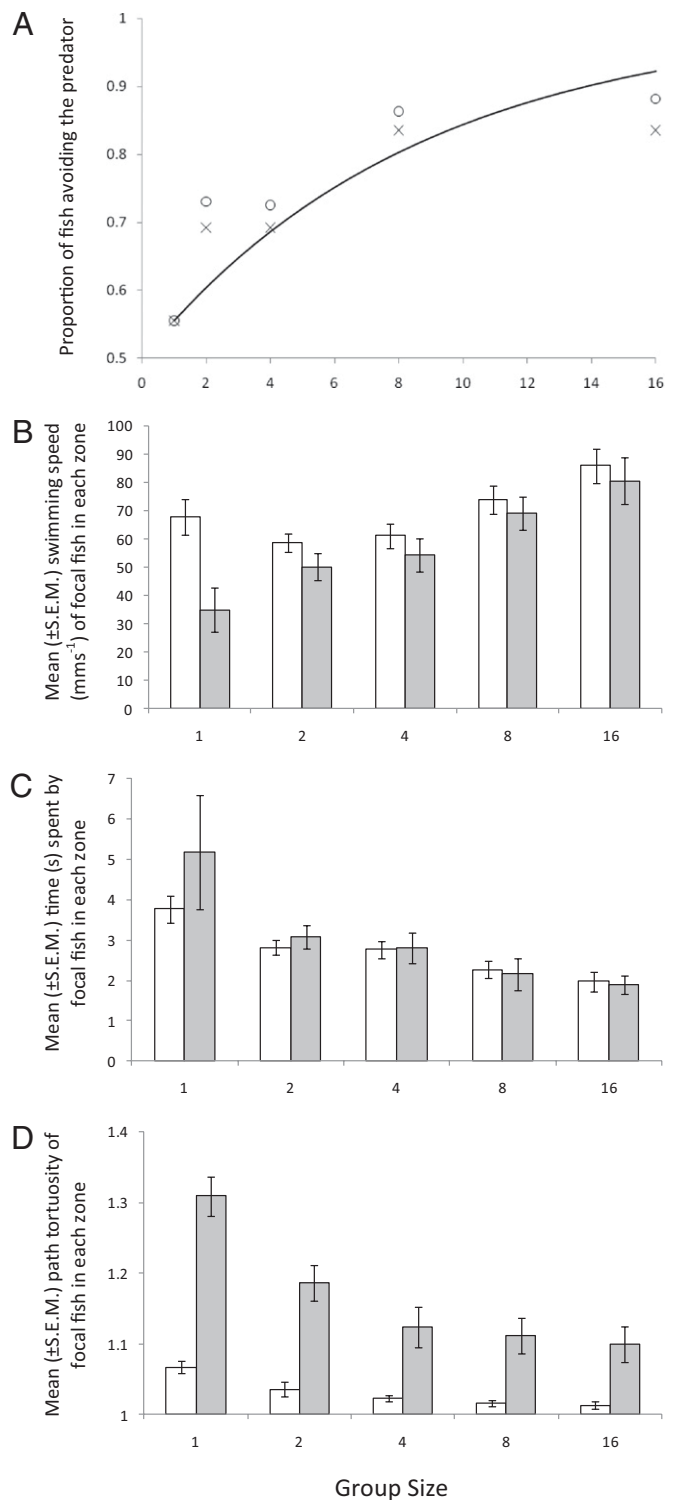


Fig. 2. (A) proportion of focal fish (x) and of all fish (o) avoiding the predator as a function of group size. (B) Mean swimming speed (\pm SEM) of focal fish in each group size. (C) Mean time (\pm SEM) spent in each zone by focal fish. (D) Mean path tortuosity (\pm SEM) of focal fish in each group size. In B–D, open bars refer to the approach zone, and shaded bars refer to the decision zone.

$$P = \frac{1}{1 + \exp(-0.24 - b_1X_1 + b_2X_2)}$$

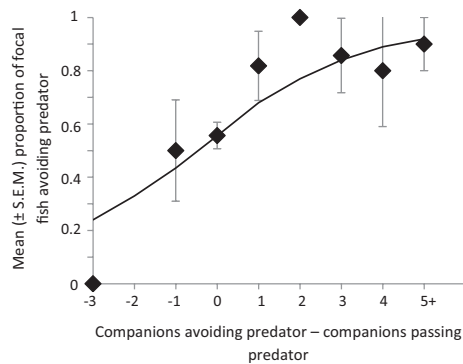


Fig. 3. Mean proportion (\pm SEM) of focal fish choosing the branch that avoids the predator as a function of the number of companions that avoid the predator minus the number that pass the predator. The fit of the logistic model $p = 1 / (1 + \exp(-0.24 - b_1X_1 + b_2X_2))$ is made assuming the probability of a single fish is equal to that over all our single-fish observations, i.e., 55.7%. The solid line shows the best fit of the model given this assumption.

The best fit of this model shows a significant positive effect of predator-avoiding companions ($b_1 = 0.512 \pm 0.162$; $z = 3.167$; $P = 0.001$) and negative effect of companions that swam past the predator ($b_2 = 1.753 \pm 0.751$; $z = -2.333$; $P = 0.019$). This result suggests a strong concordance of decision making between spatially close individuals. The solid line in Fig. 3 shows the fit of a model in which we assume that fish moving in either direction contribute equally to the probability of following (i.e., $b_1 = b_2$). The value for b_1 under this model is similar to that found when b_1 and b_2 are estimated separately ($b_1 = b_2 = 0.478 \pm 0.156$; $z = 3.065$; $P = 0.002$).

To better understand how interactions between fish led to the collective avoidance of the predator we analyzed the $(x(t), y(t))$ coordinates along with the direction of movement $(x(t+1) - x(t), y(t+1) - y(t))$ of the two fish at the front of the group over time, t (Fig. 4A). We chose the first two fish in this analysis because they were less likely to be correlated with other fish. The analyses of spatial and temporal directional correlation are provided in Fig. 4B and C. The directional heading of pairs in which the distance between fish was 2–6 cm was significantly correlated (2–4 cm, $P = 0.0004$; 4–6 cm, $P = 0.0008$) and not significantly correlated for distances >6 cm (6–8 cm, $P = 0.39$; ≥ 8 cm, $P = 0.85$; Fig. 4B). The distance between the pairs was seldom <2 cm and at this proximity the direction of the fish was not closely correlated ($P = 0.8$). Fish within 6 cm of each other showed significant temporal correlations in direction of only up to 0.5 s (Fig. 4C).

Discussion

Both speed and accuracy of collective decision making increase with group size. In comparison with single fish, groups of 8 and of 16 fish were significantly faster and more accurate. The improvements in accuracy were remarkably similar to a perfect many eyes prediction, where detection of the predator by a single individual equates to detection by the entire group.

Uncertainty in a novel environment is typically indicated by a high frequency of turning and a slower traveling speed (18–21). This was also the case here as focal fish in all groups showed increased tortuosity as they moved into the decision zone; however, only solitary individuals and those in smaller groups reduced their speed. Further, the reduction in path tortuosity and turning frequency with increasing group size suggests mutual reliance on the vigilance of others in our system (22). Single fish may experience greater uncertainty in a novel environment than grouping individuals because they have to gather all of the information they need to make a decision for themselves without access to social information. It appears that this self-reliance makes them prone to errors. Sensitivity to social information is likely to be increased in situations where private information is limited, which is pre-

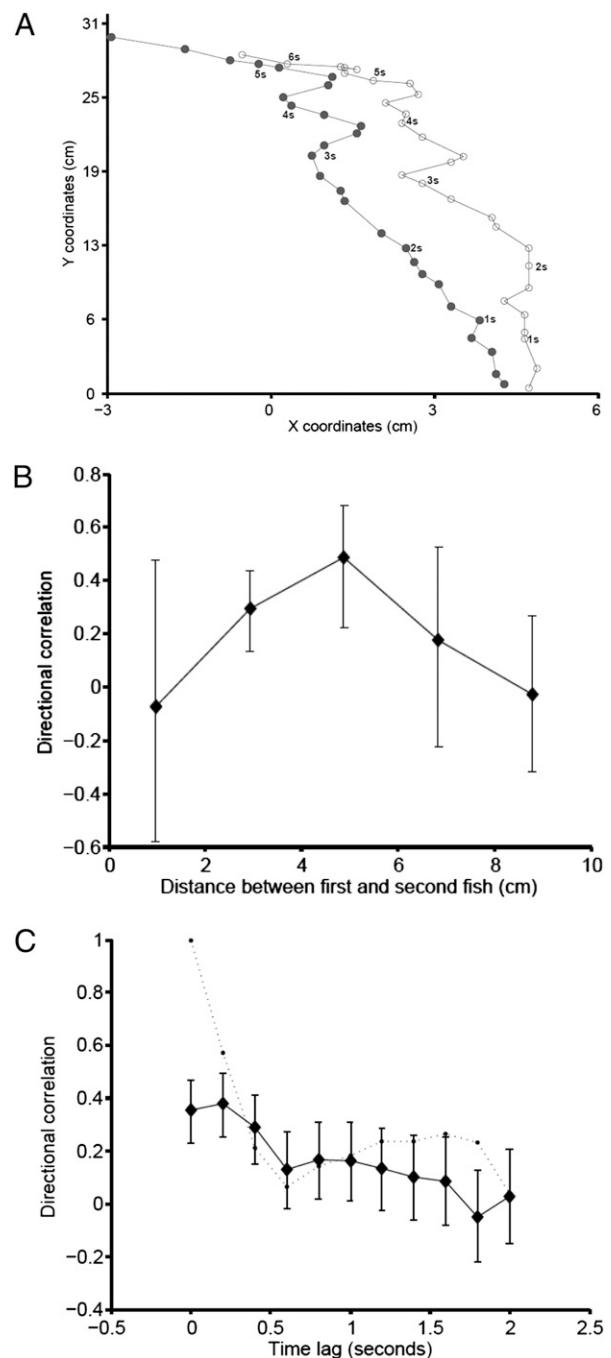


Fig. 4. Correlations between the leading pair of fish. (A) Example of fish positions through time from a 2-fish trial. Solid circles are the position of the leading fish, and open circles are the following fish. Labels “1s” and “2s” indicate the position of that fish at the time in seconds since the first fish entered the approach zone. (B) Spatial correlation of fish direction over the first 2 fish in all 2-, 4-, 8-, and 16-fish trials. The change in spatial position during each time step of 0.2 s was calculated for 2 leading fish at any point in time (note that the leading fish can change during a trial). The correlation coefficient was calculated between the direction of the leading and the second fish, with binning according to distance between the fish. Error bars show 95% confidence intervals. The number of observations varied between bins: 0–2 cm, $n = 14$; 2–4 cm, $n = 142$; 4–6 cm, $n = 49$; 6–8 cm, $n = 26$; ≥ 8 cm, $n = 48$. (C) Temporal correlation. For all leading pairs within 6 cm of each other, the correlation coefficient was calculated for time lags of 0 up to 2 s, in steps of 0.2 s. The solid line is the temporal correlation between the leader fish direction and the second fish direction at different time lags. Error bars show 95% confidence intervals. The dotted line gives the autocorrelation of the direction of the leader fish, i.e., correlation in the direction time-lagged for various times.

dicted in theory to lead to more cooperative vigilance behavior (23). A strong reliance on social information in the present experiments is suggested by the spatial and temporal correlations between leader fish. The similarity of the between-fish temporal correlation to the autocorrelation of the leader fish alone seems to contradict the idea that either of the fish is leading the other one. Rather, these observations are consistent with existence of a local interaction radius over which directional information is rapidly propagated backward and forward between both fish. At the level of the group, individuals can use the available social information while concentrating their vigilance efforts on a smaller portion of their immediate habitat and ultimately make more accurate decisions.

Clustering of decisions is indicative of positive feedback through social cues. This feedback may well involve quorum rules, where the probability of moving in a particular direction increases nonlinearly with group size (7, 8). These quorums allow errors by individual fish to be filtered out. However, what is most remarkable in the current experiment is that improvements in accuracy start even in groups of two and then accelerate rapidly.

Although the swarm intelligence literature predicts that interindividual diversity can produce benefits in terms of improved collective decision making (2, 24), we found no evidence for interindividual differences in predator-detection ability between fish. In addition to our finding that leading fish (those in the front half of shoals) were not more accurate than followers (in the rear half of shoals), this result suggests that diversity of the group members' abilities cannot effectively explain the observed increase in decision-making speed and accuracy with increasing group size (25). We propose that the many eyes response is facilitated by a form of self-organized vigilance, whereby information acquired by one individual is transmitted by positive feedback and communicated across the group (26).

Although there may be some debate about what mechanisms allow such accurate and fast decision making in groups, it is clear that our results are not consistent with the game-theoretic reasoning often applied when thinking about predator avoidance situations. For example, there is no evidence of individuals in larger groups slowing down to force another group member to take the risk of inspecting the two options. On the contrary, the efficiency of the fish shoal's many eyes suggests a high degree of cooperation in detection and avoidance of predators. The evolution of this cooperation can be understood only by identifying

the cues used by a fish that allow it to determine when another fish has spotted a predator (26).

Materials and Methods

Experimental Subjects. The study species used in this experiment was the mosquitofish, *Gambusia holbrooki*, obtained from Lake Northam, Sydney, Australia (33°53'6.14"S, 151°11'35.75"E). Individuals used in the experiments measured 26 ± 5 mm. We used both sexes and observed no difference in accuracy (male accuracy = 0.577; female accuracy = 0.549; binomial test, $P = 0.34$) or speed (independent t test: $t_{38} = 0.48$, $P = 0.63$) between the sexes. Before experiments, the fish were held in 180-L vats held at a temperature of 23.1 ± 1 °C in the animal holding rooms at the University of Sydney and were fed daily on Wardley aquarium flake food.

Experimental Protocol and Materials. Experiments took place in a Y-maze constructed from white Perspex (Fig. 1). The stem of the "Y" was raised so that the water gradually increased in depth from 1 cm at the foot of the Y to 12 cm at the tips of the arms. A replica predator, measuring 12 cm in length, was allocated to one of the arms of the Y-maze at random and suspended in midwater using fine monofilament line. In pilot trials, the fish showed a strong aversive response to the predator once they detected it.

Experimental fish were added to a clear container set in the stem of the Y. After 120 s the box was raised, releasing the fish. In all cases, the fish made their way down the Y and into one of the arms. All trials were filmed and the fish were subsequently tracked using ImageJ software. We used five different group sizes: 1, 2, 4, 8, and 16 fish. Each experiment was filmed using a Logitech Pro9000 webcam positioned directly above the experimental apparatus. The fish were then tracked using the manual tracking facility in ImageJ at a frequency of five frames/s.

We defined two zones for our analysis: The area immediately before the fork in the Y was designated the "decision zone." An area of the same size that the fish crossed before reaching the decision zone was designated the "approach zone." The use of zones allows us to compare the behavior of the experimental animals before and during the decision-making process. To analyze, we randomly preselected a single focal fish from each replicate group and calculated its speed, path tortuosity (defined as the ratio of the path taken by the fish to the straight line distance between the beginning and the end of that path), the number of direction changes that it made, and the accuracy of its decision. We defined accuracy as entry into the arm of the Y-maze that did not contain the replica predator. The positioning of the zones had little effect on our response variables (Table S1).

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Correction

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Correction for “Fast and accurate decisions through collective vigilance in fish shoals,” by Ashley J. W. Ward, James E. Herbert-Read, David J. T. Sumpter, and Jens Krause, which appeared in issue 6, February 8, 2011, of *Proc Natl Acad Sci USA* (108:2312–2315; first published January 24, 2011; 10.1073/pnas.1007102108).

The authors note that, due to a printer’s error, on page 2312, right column, fourth paragraph, fourth line, the word “decreased” was not changed to “increased.” The sentence should instead appear as “However, in the decision-making zone, swimming speed increased with increasing group size (speed in the decision zone: ANOVA: $F_{4,157} = 9.93$, $P < 0.001$; Fig. 2B).” This article has been corrected in print and online.

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