Fish pool their experience to solve problems collectively

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Access to information is a key advantage of grouping. Although experienced animals can lead others to solve problems, less is known about whether partially informed individuals can pool experiences to overcome challenges collectively. Here we provide evidence of such 'experience-pooling'. We presented shoals of sticklebacks (*Gasterosteus aculeatus*) with a two-stage foraging task requiring them to find and access hidden food. Individual fish were either inexperienced or had knowledge of just one of the stages. Shoals containing individuals trained in each of the stages pooled their expertise, allowing more fish to access the food, and to do so more rapidly, compared with other shoal compositions. Strong social effects were identified: the presence of experienced individuals increased the likelihood of untrained fish completing each stage. These findings demonstrate that animal groups can integrate individual experience to solve multi-stage problems, and have implications for our understanding of social foraging, migration and social systems.

Group-living provides animals with both ready access to valuable social information and the potential, by processing information through social interactions, to achieve solutions to cognitive problems that might lie beyond the reach of lone individuals[1–11]. Information processing by groups can occur through several different mechanisms, and distinguishing between these is a key challenge faced by researchers[10]. Such mechanisms include swarm intelligence, facilitation and pool-of-competence effects. Swarm intelligence refers to improved cognitive performance that stems from distributed, self-organized decision making, with decisions emerging from repeated local interactions between individuals[12,13]. The 'many-wrongs' principle of collective navigation is an example of swarm intelligence. Here, individuals' motivation to follow their varied and imperfect estimates of the correct travel direction interacts with their drive to remain in close proximity to their neighbours, resulting in a group-level compromise on preferred direction that is more accurate than the separate estimates of most individuals[14,15]. A second mechanism, facilitation, occurs when necessary costs such as vigilance for predators are shared among group members, allowing individuals to allocate more effort to other problems, such as searching for resources[11]. Finally, pool-of-competence describes effects arising from group size and diversity, with larger groups being statistically more likely to include more experienced, motivated, persistent or bold individuals that are more likely to solve problems and from which others in the group can acquire information[10,16].

Our study is concerned with one aspect of the pool-of-competence effect, specifically variation in experience amongst group members. It is often likely to be the case in nature that within a given group, members will hold different information about the environment, with some individuals possessing relevant experience in solving a particular challenge that other members lack. This may be especially so in populations with fission–fusion social structure and in those where group fidelity is low, resulting in high turnover of group membership and frequent disbandment and formation of groups. Research has demonstrated that minorities of experienced individuals can lead their uninformed groupmates[17–20]. Here, leadership may emerge as an outcome of the experienced individuals'

attraction to the target and the mutual social attraction between these and their naive groupmates[3,17,21], without any communication or direct transmission of information about the target from leader to follower. Often, different group members might have partial but complementary information about the component parts of a particular task that can be broken down into a number of 'stages' or elements. They might be familiar with different sections of a navigation route, for example, or some might know where to find food whereas others might know how to access it. Plausibly, groups of animals may be able to overcome such multi-stage problems through social interactions that combine the separately held information possessed by individuals, allowing them to reach integrative solutions that lie beyond the grasp of single individuals[5]. Here we set out to test whether groups of partially informed individuals could indeed pool their knowledge about the separate components of a task to solve complex problems in this manner.

We presented shoals of sticklebacks (*Gasterosteus aculeatus*) with a two-stage navigation and foraging task (see Methods) that required them first to locate a hidden patch of food within a mesh feeder box by swimming through a structured environment towards a light cue (stage 1), and then to access the box by swimming through a small hole to obtain the food (stage 2). Some subjects were given prior experience of solving the navigation component of the task, and others experience of accessing food from the food-box, but no single fish had prior experience of both components of the task. We varied the prior experience possessed by individual fish and arranged these into four different combinations, performing ten replicates per combination. One combination consisted solely of individuals with no prior training (knowledge of neither stage 1, nor stage 2). Two combinations consisted of a majority of untrained fish plus a minority of individuals that had been trained either to complete the navigation part of the task, or to access food from the feeder box (knowledge of either stage 1, or stage 2). Finally, one combination consisted of shoals containing equal numbers of untrained fish, navigation-trained fish and feeder-trained fish (knowledge of both stage 1 and stage 2). We predicted that fish in this latter group would access the food patch most rapidly and that more individuals overall would be successful.

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Results

The composition of the group (treatment) strongly influenced the number and rate of entries to both the goal area and the feeder (Supplementary Fig. 1).

Numbers of group members entering goal area and feeder. More fish entered the green-light goal area in groups that contained trained fish (light-trained, Wald test Z-score $= 7.37$, $P < 0.01$; feeder-trained, Wald $Z = 3.6$, $P < 0.01$; combined feeder-trained and light-trained, Wald $Z = 6.36$, $P < 0.01$) than in shoals of untrained fish. Fish in the combined and light-trained groups entered the goal area more often than those in the feeder-trained groups (light-trained compared with feeder-trained, Wald $Z = -4.63$, $P < 0.01$; combined compared with feeder-trained, Wald $Z = -4.9$, $P < 0.01$). More fish entered the feeder unit in groups with training (light-trained, Wald $Z = 3.17$, $P < 0.01$; feeder-trained, Wald $Z = 3.31$, $P < 0.01$; combined Wald $Z = 7.2$, $P < 0.01$) than in untrained groups. As predicted, we observed elevated rates of entry in the combined groups compared with other treatments (light-trained, Wald $Z = -5.07$, $P < 0.01$; feeder-trained, Wald $Z = -4.94$, $P < 0.01$, Fig. 1a).

When we focused only on the proportion of naive fish from each group that entered the goal area and the feeders, we saw a similar pattern of results. There was an increased number of entries by naive fish into the goal area for shoals containing fish with any type of training (light-trained, Wald $Z = 6.23$, $P < 0.01$; feeder-trained, Wald $Z = 3.07$, $P < 0.01$; combined, Wald $Z = 4.74$, $P < 0.01$) than for untrained groups. We also saw an increased rate of entry into the feeder by naive fish in treatments with training (light-trained, Wald $Z = 3.01$, $P < 0.01$; feeder-trained, Wald $Z = 1.96$, $P < 0.05$; combined, Wald $Z = 4.96$, $P < 0.01$).

Rate of entry. The time for the first fish in each group to enter the green-light goal area was lower in the combined and light-trained groups than it was in the feeder-trained and untrained groups (Cox regression: Wald $Z = 4.05$, $P < 0.001$ (combined versus feeder-trained), and Wald $Z = 4.39$, $P < 0.001$ (combined versus

untrained)). The entry times of the first fish in the combined group did not differ from that of the light-trained treatment groups (Wald $Z = 0.93$, $P = 0.35$). Regarding entry times into the feeder, as predicted, the first fish in the combined group were faster than for all of the other treatment groups (untrained, light-trained and feeder-trained: Wald $Z = 5.42$, $P < 0.001$; Wald $Z = 4.13$, $P < 0.001$; and Wald $Z = 4.16$, $P < 0.001$ respectively, Fig. 1b).

An identical pattern was seen when we only considered rates of entries by naive fish from each group into the goal area and the feeders. For goal area entries, there was no difference between the light-trained and combined groups in the rate at which untrained fish first entered the goal area (Wald $Z = 0.64$, $P = 0.52$). The first fish from the untrained and feeder-trained groups took longer to enter the goal area compared with the combined groups (Wald $Z = 2.60$, $P = 0.009$ and Wald $Z = 2.21$, $P = 0.027$). As predicted, the first naive fish from the combined groups to enter the feeder did so sooner than the first fish from the untrained, light-trained and feeder-trained groups (Wald $Z = 3.73$, $P < 0.001$; Wald $Z = 1.96$, $P = 0.049$ and Wald $Z = 2.72$, $P = 0.007$ respectively).

Hazard models. Following these analyses, we also ran two proportional hazard models to understand the factors that contributed to the fish entering each area (Fig. 2).

We first ran a set of models that analysed the rate of entry without explicit consideration of the effect of social information. We found that fish that had prior light-training entered the goal area faster than those without it (Wald $Z = 4.62$, $P < 0.01$), and that fish in the presence of conspecifics with light-training entered the goal area faster than those without (Wald $Z = 10.37$, $P < 0.01$). A similar, but weaker, effect on rate of entering the goal area was observed for feeder-trained fish (Wald $Z = 2.1$, $P = 0.04$), and fish in a group with feeder-trained fish (Wald $Z = 3.15$, $P < 0.01$). We also found that prior feeder-training (Wald $Z = 3.09$, $P < 0.01$), but not prior light-training (Wald $Z = 1.55$, $P = 0.12$), increased the rate at which fish entered the feeder, and that the presence of feeder-trained fish in the group significantly increased the rate at which all fish entered
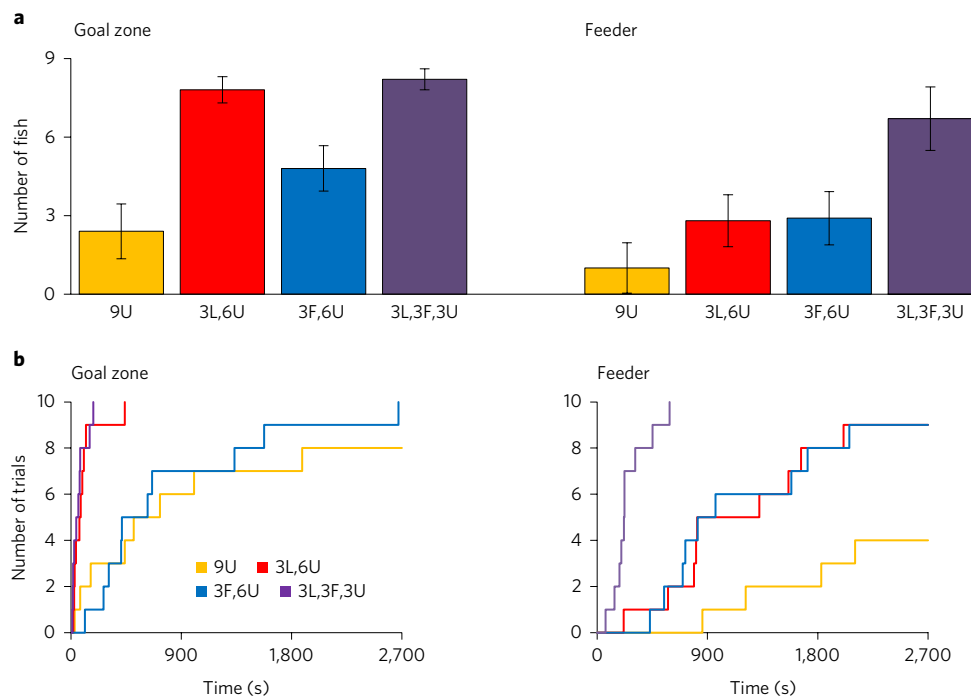

Figure 1 | Number and rate of goal zone and feeder entries. a, The number of fish in each group to enter the green-light goal area and the feeder (mean ±95% confidence interval, CI). **b**, Survival plots showing the time for the first fish in each group to enter the goal area and feeder. 9U: nine untrained fish; 3L,6U: three light-trained and six untrained fish; 3F,6U: three feeder-trained and six untrained fish; 3L,3F,3U, three feeder-trained, three light-trained and three untrained fish.
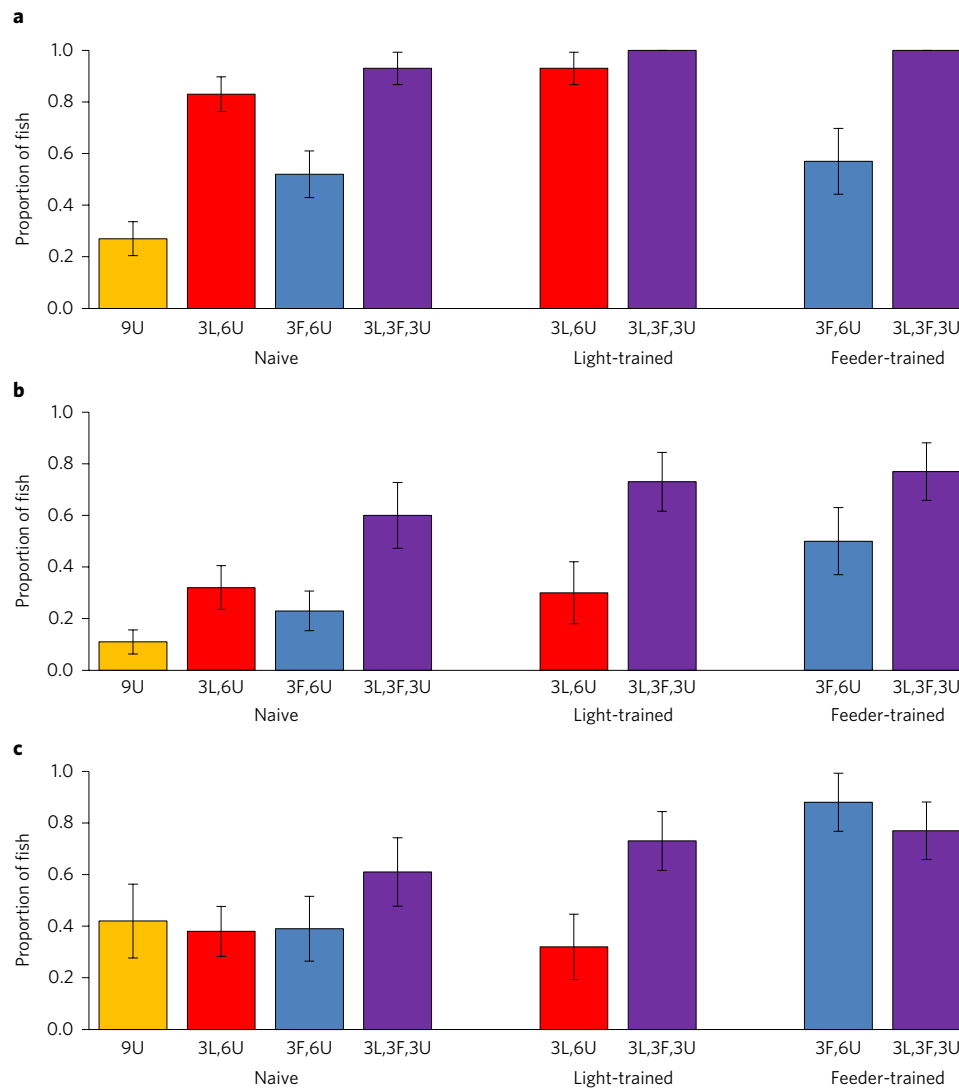
Figure 2 | Proportion of naive fish entering the goal and feeder areas. a, The proportion of fish for each level of training to enter the green-light goal area, broken down by treatment group. **b**, The proportion of fish for each level of training to enter the feeder area, broken down by treatment group. **c**, The proportion of fish for each level of training who entered the goal area and then entered the feeder area, broken down by treatment group. In each case, mean ±95% CI is shown. 9U: nine untrained fish; 3L,6U: three light-trained and six untrained fish; 3F,6U: three feeder-trained and six untrained fish; 3L,3F,3U, three feeder-trained, three light-trained and three untrained fish.

the feeder (Wald $Z = 2.81$, $P < 0.01$). Interestingly, the presence of light-trained fish significantly reduced the rate at which other fish entered the feeder (Wald $Z = -2.72$, $P < 0.01$).

Extended models that incorporated social information in more complex ways revealed that previous training to approach the green light (Wald $Z = 5.67$, $P < 0.01$), the number of light-trained fish (Wald $Z = 5.05$, $P < 0.01$) and the number of feeder-trained fish (Wald $Z = 3.19$, $P < 0.01$) all positively increased the rate at which fish entered the goal area. We also found a strong positive effect of having had a shoalmate enter the goal area in the previous 10 seconds (Wald $Z = 19.25$, $P < 0.01$), but no effect of having had a shoalmate leave in the previous 10 seconds (Wald $Z = 0.48$, $P = 0.63$). Overall, the number of fish in the goal area was associated with a decrease in the rate of entry for other fish to enter the goal area (Wald $Z = -2.79$, $P < 0.01$).

We found a similar pattern of results when analysing entry of the feeder. Prior feeder-training significantly increased the rate that fish entered the feeder (Wald $Z = 2.84$, $P < 0.01$), and fish were disproportionately more likely to enter the feeder within 10 seconds of a shoalmate doing so (Wald $Z = 12.83$, $P < 0.01$). We did not find

a significantly increased rate for fish entering the feeder within 10 seconds of another fish leaving it (Wald $Z = 1.53$, $P = 0.13$). Overall, the number of fish currently in the feeder was associated with a decrease in the rate at which other fish entered the feeder (Wald $Z = -5.39$, $P < 0.01$). Model coefficients for the goal area and the feeder hazard models can be found in Supplementary Tables 2 and 3.

Discussion

This experiment provides clear evidence of experience-pooling, with groups of partially informed fish integrating their experience to solve a two-stage foraging problem collectively. A greater proportion of group members gained access to the food patch, and did so sooner, in the mixed groups that contained some fish experienced in the navigation part and others in the feeder-access aspect of the task compared with fish in other treatments that contained members experienced in only one or in neither of the two components of the task. Moreover, naive fish in the mixed groups also benefited by accessing the food sooner than did naive fish in the other groups.

Both experience and social information were significant in affecting entries into the goal area, the first stage of the task. We saw

that light-trained fish entered the goal area at a greater rate than did untrained fish, as expected, but also that feeder-trained fish did too. This latter effect possibly arose because the fish were able to see the feeder as they came close to the goal area and, having learned an association between the feeder and food, were more motivated to approach it and enter the goal area than were fish untrained in either task. At the group level, fish in the light-trained, feeder-trained and combined groups were more likely to enter the goal area than were those in the untrained treatment group. Fish with prior feeder-training, and those that were grouped with feeder-trained fish, entered the feeder at a greater rate, but we also found a negative effect of the presence of light-trained fish on feeder entries. This may have resulted from the fact that light-trained fish were given experience of feeding beneath the green lights, but not in the feeder itself. They may therefore have anticipated finding food beneath the lights, causing them to remain in this area, where they attracted other group members, delaying their entry into the feeder.

Further analyses that incorporated social transmission in more nuanced ways revealed that a fish entering the feeder or goal area substantially increased the likelihood that other fish did so in the next 10 seconds. This is consistent with both past experimental findings analysing the following behaviour of fish[22,23] and theory predicting that individuals that are both motivated to move towards a particular location and socially attracted to their groupmates may be able to entrain the group and move them towards the target, a principle termed 'leading according to need'[17,18,20,21]. We found no evidence that the rate at which fish entered the goal area increased immediately after a fish left either the feeder or the goal area, suggesting that this effect is mediated by following rather than attention to cues or locations. Such following effects were also identified in a study of recruitment of naive fish to prey patches by experienced shoalmates[23], in which the effects were termed 'untransmitted social effects'.

Interestingly, in both hazard models, we saw that the number of fish in the goal and feeder areas was associated with a decrease in the rate of entry for other fish into those areas. The reason for this effect is unclear. One possibility is that it was due to trained individuals entering the goal or feeder areas sooner, with naive fish either entering quickly after this (fish were more likely to enter the goal and feeder areas if a group mate had entered within the past 10 seconds), or else taking much longer to find or access the patch because they had been left behind.

Taken together, our analyses, when considered alongside other studies[17,18,20,21], suggest that leadership arising from the balance between goal-orientedness and social attraction may be sufficient to generate collective problem-solving.

Several factors potentially contribute to the ability of groups to process information and solve problems, including facilitation, pool-of-competence effects and swarm intelligence, with these mechanisms potentially acting in concert[10,16]. For example, among flocks of songbirds, larger groups of naive birds were more likely to obtain food from novel feeding devices. The presence in the group of a knowledgeable bird further increased the likelihood of the group accessing food, and larger groups were more likely to contain such individuals than smaller ones[16]. Moreover, birds had more success when they were in larger groups and when the feeding devices were closer to cover than when they were further away, suggesting that facilitation through reduced predation risk might also affect problem-solving. In our study, we directly manipulated the experience of group members while holding group size constant, allowing us to show that information held by the group could be pooled. This approach also allowed us to rule out other mechanisms, although it does not discount the possibility that multiple effects might operate together under natural conditions, as was observed in previous work[16].

Our findings indicate that for groups of ecological generalists negotiating variable environments, diversity in experience and a distributed knowledge base across a group may be of critical importance, potentially more so than the presence of 'omniscient' individuals with full knowledge of the challenges[24]. Experience pooling might be especially important within populations that exhibit fission–fusion social structures, for which, at any point, current group members might be expected to possess a greater range of experience than those of more stable groups that have travelled and experienced the same conditions together. We anticipate that experience-pooling, underpinned by leader–follower interactions similar to those seen in our study, might be found in groups of animals facing challenges ranging from learning how to exploit new foods and avoid new predators, to navigating between ephemeral resources and tracing long migration routes.

Methods

Subjects. Threespine sticklebacks ($N = 360$) were collected with hand nets from the Kinnessburn steam in St Andrews, UK, in July 2012, and housed in the laboratory in groups of 40 in 90-l aquaria. Each aquarium contained a layer of sand and artificial plants, and was connected to an external filter. The temperature in the laboratory was held at 8 °C, and the lights were on for 12 hours per day. The fish were fed daily with frozen bloodworms, unless otherwise stated below. We used fish measuring 30–35 mm in length that showed no signs of being in reproductive condition. Fish were not sexed.

Overview. The experiment presented 40 groups of nine fish with a two-stage navigation task. To access a food reward, the fish first had to travel to the far end of a large structured arena, where a feeder box containing the food was hidden behind an opaque screen, and to gain access to the food in the feeder box by entering through one of two small holes. The end of the arena with the feeder box and food reward contained two green lights. We tested groups of fish that contained different combinations of individuals trained to approach green lights, trained to enter the feeder box through the target holes, or not trained in either task. Fish that were not trained to the green lights or to the feeder box were nevertheless exposed to these during training, so as to remove any neophobic responses to the stimuli that might otherwise have confounded their behaviour in the experiment proper. The training procedure and two pilot experiments designed to test the efficacy of the training are described in the Supplementary Material. All procedures were reviewed and approved by the departmental ethics committee.

Experimental arena. The arena (Supplementary Fig. 2) consisted of a black plastic box measuring 160 cm long, 100 cm wide and 40 cm tall. It contained a 2-cm-deep layer of fine sand, and was filled with water to a depth of 25 cm. The feeder box was placed 10 cm from one end of the arena, 40 cm from each long wall. It was suspended 10 cm above the sand substrate. The feeder box was 20 cm long by 10 cm tall and wide. It consisted of a 2-mm-wide plastic frame around which was stretched a fine nylon mesh. A square hole (2 cm × 2 cm) was cut in each end of the feeder box, which enabled fish to swim inside and access the food reward (20 dead bloodworms placed in the centre of the feeder box). The use of a mesh feeder had the advantage that olfactory cues emanating from the food would diffuse through the sides and would not provide an odour gradient leading to the entrance hole. The food was also visible through the mesh walls and floor of the feeder box, leaving the fish highly motivated to solve the task. However, the fish could not find the food simply by swimming towards the sight or smell of it, and previous experiments have shown that this arrangement makes finding the entrance a challenging task[25].

A white plastic screen measuring 40 cm × 40 cm was placed 10 cm in front of the feeder box and 30 cm from each of the long walls of the arena. This prevented the group of fish, which began the experiment at the other end of the arena, from being able to see the feeder box. To reach it, they had to swim either side of this barrier. On each side of the feeder box, we placed a green light-emitting diode (LED) unit (Trimble, Milton Keynes, UK). These consisted of a circle of 24 individual LEDs set within a case with a diameter of 5 cm. A green filter was taped over each LED unit. Each unit was suspended 10 cm above the surface of the water, 20 cm either side of the feeder box and 20 cm from each longwall of the arena. The light produced by the LED units was visible to the fish at the far end of the arena at the beginning of the experiment. A high-definition webcam (Logitech C920, Logitech International SA, Lausanne, Switzerland) was mounted 80 cm above the feeder box. This was used to film the end of the arena immediately behind the barrier, which was designated the 'green-light goal area'.

At the other end of the arena, we placed a holding unit constructed from colourless, perforated plastic. This measured 20 cm × 20 cm wide and 40 cm tall. The bottom and top of the holding unit were open. It was placed directly on the sand substrate, 5 cm from the back wall and 40 cm from each long side wall of the arena. This was used to house the fish at the beginning of the experiment.

In the middle section of the arena, we placed four artificial plants. These were approximately 10 cm tall and 10 cm in diameter. One pair of plants were placed

20 cm apart, 30 cm from each long wall of the arena and 40 cm from the end of the arena where the fish holding unit was placed. The second pair of plants were placed 20 cm from these and 50 cm from the white plastic barrier. The plants provided cover for the fish once they were released into the main arena at the beginning of the trial, and aided movement throughout the centre of the arena.

Experimental groups. Fish were allocated using a random number algorithm to replicate groups in four treatments that differed in the experience (that is, prior training) possessed by constituent members. Each group contained nine fish, and we ran ten replicates in each of the four treatments. The first treatment consisted of groups of nine naive (non-trained) fish. In the second, each group contained three fish that had been trained to approach the green light and six naive fish. The third treatment comprised shoals that contained three fish that had been trained to enter the feeder box and six naive fish, and the fourth contained shoals with three fish from each training regime plus three naive fish. Hereafter, these treatment groups respectively are referred to as 'untrained', 'light-trained', 'feeder-trained' and 'combined'. For clarity, individual fish that had not been trained are referred to as naive, while the treatment consisting entirely of naive fish is referred to as untrained. Because familiarity has been shown to affect social foraging interactions in this species[26], within each group each fish was drawn from a separate holding tank, ensuring that all were equally unfamiliar to one another. Within each group, every fish was fitted with a non-invasive, colour-coded circular tag on its first dorsal spine[27]. These were fitted on the last day of training, and the day before the experiments were performed. This allowed us to recognize each individual fish in the videos. Sample sizes were informed by an earlier social foraging experiment conducted in our laboratory[26].

Experimental procedure. For each trial, the experimental arena was established as above, and food items (20 dead bloodworms) added to the feeder box. The experimental group was added to the holding unit and allowed to acclimate for 15 minutes, before the holding unit was raised 15 cm using a pulley, releasing the fish and beginning the trial. The trial ran for a further 45 minutes. From the webcam footage, we recorded the identity of each fish as it entered the green-light goal area. For every second of the trial, we recorded whether each fish was inside or outside the goal area, and inside or outside the feeder box. We performed five such trials each day (see Supplementary Table 1 for schedule). Following each trial, we replaced the water, sand substrate and feeder box prey in the arena. The experimenter was not blind with respect to treatment group.

Statistical analysis. We analysed the total proportion of fish and the proportion of untrained fish that entered the green-light goal area and the feeder box during the trial using a binomial model. We examined the time at which the first fish entered each area for different groups using Cox regressions, focusing on the entry times of the first fish (irrespective of training) and the first naive fish from each group. We then used Cox proportional hazard models to model all entries in the group and gain a finer temporal resolution of the factors that predict whether and when fish enter either the goal area or the feeder, and the frequency at which they enter the areas. We examined the rate at which fish entered the feeder and goal area predicted by their previous training, previous time spent in the goal area during the trial, the number of light-trained fish, the number of feeder-trained fish, and three social cues: the number of fish that had entered the goal/feeder area in the previous 10 s, the number of fish that had exited the goal/feeder area in the previous 10 s and the total number of fish in the goal/feeder area. Our data met the assumption of proportional hazards expected by these tests. All proportional hazard models were run in the R programming environment[28] using the 'survival' package[29].

Data availability. The datasets analysed during the current study are available from the corresponding author on request.

References

1. Krause, J. & Ruxton, G. D. *Living in Groups* (Oxford Univ. Press, 2002).
2. Danchin, É. *et al.* Public information: from nosy neighbors to cultural evolution. *Science* **305**, 487–491 (2004).
3. Couzin, I. D. *et al.* Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516 (2005).
4. Couzin, I. D. Collective cognition in animal groups. *Trends Cogn. Sci.* **13**, 36–43 (2009).
5. Krause, J., Ruxton, G. D. & Krause, S. Swarm intelligence in animals and humans. *Trends Ecol. Evol.* **25**, 28–34 (2010).
6. Sumpter, D. J. *Collective Animal Behavior* (Princeton Univ. Press, 2010).
7. Laland, K. N., Atton, N. & Webster, M. M. From fish to fashion: experimental and theoretical insights into the evolution of culture. *Phil. Trans. R. Soc. Lond. B* **366**, 958–968 (2011).
8. Ward, A. J. *et al.* Fast and accurate decisions through collective vigilance in fish shoals. *Proc. Natl Acad. Sci. USA* **108**, 2312–2315 (2011).
9. Berdahl, A. *et al.* Emergent sensing of complex environments by mobile animal groups. *Science* **339**, 574–576 (2013).
10. Ioannou, C. C. Swarm intelligence in fish? The difficulty in demonstrating distributed and self-organised collective intelligence in (some) animal groups. *Behav. Process.* http://dx.doi.org/10.1016/j.beproc.2016.10.005 (2016).
11. Ward, A. J. W. & Webster, M. M. *Sociality: The Behaviour of Group Living Animals* (Springer, 2016).
12. Bonabeau, E., Dorigo, M. & Theraulaz, G. *Swarm Intelligence: From Natural to Artificial Systems* (Oxford Univ. Press, 1999).
13. Garnier, S., Gautrais, J. & Theraulaz, G. The biological principles of swarm intelligence. *Swarm Intel.* **1**, 3–31 (2007).
14. Codling, E. A., Pitchford, J. W. & Simpson, S. D. Group navigation and the 'many-wrongs principle' in models of animal movement. *Ecology* **88**, 1864–1870 (2007).
15. Codling, E. A. & Bode, N. W. Balancing direct and indirect sources of navigational information in a leaderless model of collective animal movement. *J. Theor. Biol.* **394**, 32–42 (2016).
16. Morand-Ferron, J. & Quinn, J. L. Larger groups of passerines are more efficient problem solvers in the wild. *Proc. Natl Acad. Sci. USA* **108**, 15898–15903 (2011).
17. Dyer, J. R. *et al.* Leadership, consensus decision making and collective behaviour in humans. *Phil. Trans. R. Soc. Lond. B* **364**, 781–789 (2009).
18. Ioannou, C. C., Singh, M. & Couzin, I. D. Potential leaders trade off goal-oriented and socially oriented behavior in mobile animal groups. *Am. Nat.* **186**, 284–293 (2015).
19. Jolles, J. W. *et al.* The role of social attraction and its link with boldness in the collective movements of three-spined sticklebacks. *Anim. Behav.* **99**, 147–153 (2015).
20. Webster, M. M. Experience and motivation shape leader–follower interactions in fish shoals. *Behav. Ecol.* **28**, 77–84 (2017).
21. Conradt, L. *et al.* 'Leading according to need' in self-organizing groups. *Am. Nat.* **173**, 304–312 (2009).
22. Day, R. L. *et al.* Interactions between shoal size and conformity in guppy social foraging. *Anim. Behav.* **62**, 917–925 (2001).
23. Atton, N. *et al.* Information flow through threespine stickleback networks without social transmission. *Proc. R. Soc. Lond. B* **279**, 4272–4278 (2012).
24. Krause, S. *et al.* Swarm intelligence in humans: diversity can trump ability. *Anim. Behav.* **81**, 941–948 (2011).
25. Reader, S. M. & Laland, K. N. Diffusion of foraging innovations in the guppy. *Anim. Behav.* **60**, 175–180 (2000).
26. Atton, N. *et al.* Familiarity affects social network structure and discovery of prey patch locations in foraging stickleback shoals. *Proc. R. Soc. Lond. B* **281**, 20140579 (2014).
27. Webster, M. M. & Laland, K. N. Evaluation of a non-invasive tagging system for laboratory studies using three-spined sticklebacks (*Gasterosteus aculeatus*). *J. Fish Biol.* **75**, 1868–1873 (2009).
28. R Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2013).
29. Therneau, T. M. & Lumley, T. survival: Survival analysis v. 2.41-2. https://cran.r-project.org/web/packages/survival/index.html (2015).

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Author contributions

M.M.W. designed and performed the experiments. M.M.W., A.W. and K.N.L. analysed the data and co-authored the paper.

Additional information

Competing interests

The authors declare no competing financial interests.