

Social information, conformity and the opportunity costs paid by foraging fish

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Abstract Animals pay opportunity costs when pursuing one of several mutually exclusive courses of action. We quantified the opportunity costs of conforming to the behaviour of others in foraging sticklebacks (*Pungitius pungitius*), using an arena in which they were given the option of shoaling in one area or searching for food in another. Fish foraging in the absence of stimulus conspecifics found the prey patch sooner and spent longer exploiting it than those in trials where a stimulus shoal was present. Furthermore, in trials where the stimulus shoal exhibited feeding cues, subjects approached them sooner and spent more time shoaling with them, exploring less of the arena than in trials where the stimulus shoal exhibited no such cues. This suggests sensitivity not only to the mere presence of conspecifics, but also to the social information that they produce. We also saw that groups of focal fish, compared to single individuals, were less influenced by the stimulus shoal and explored more of the arena, a behaviour that may be attributed to facilitation, competition or both. Such opportunity costs are likely to be offset by benefits such as reduced predation risk, and we discuss this in terms of the trade-offs associated with living in groups.

Keywords Costly information · Diffusion · Public information · Social cue · Social facilitation · Social learning

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Introduction

An opportunity cost is the price of foregoing the next best alternative when choosing between multiple mutually exclusive options or courses of action (Hoskin 1983). Selection has equipped many species with the ability to use information from multiple sources, allowing them to increase the efficiency with which they exploit their surroundings, in so far as doing so maximises their fitness. In processing and acting upon different sources of information, however, animals are faced with opportunity costs. These sources may include privately held information based upon previous experience, potential information that could be gained from sampling the environment, or social information from one or more sources. The costs and benefits in terms of fitness of using information from different sources, such as private versus social, and the strategies governing relative reliance upon them, have generated much attention from theoreticians (Boyd and Richerson 1985; Coussi-Korbel and Fragaszy 1995; Baron et al. 1996; Feldman et al. 1996; Laland 2004; Kendal et al. 2005; Galef 2009; Rendell et al. 2010, 2011) and inspired a number of experimental investigations (e.g. Briggs et al. 1996; Galef and Whiskin 2006; Galef 2009; Kendal et al. 2009; Pike et al. 2010; Pike and Laland 2010; Webster and Laland 2008; 2011) in recent years. This work has given rise to a branch of research that attempts to predict the conditions under which individuals should prioritise collecting or using information from different sources.

Despite this, many social animals do not optimally switch between different sources of information, probably because they have evolved heuristic behavioural rules that bias them

in favour of responding to socially transmitted cues. Such rules might tend to lead individuals to move towards conspecifics, or to attend to and respond to information that they produce, even when doing so conflicts with private information that they hold. For example nutmeg mannikins (*Lonchura punctulata*) will use conflicting social information when selecting between artificial feeders, even when this conflicts with highly reliable private information (Rieucan and Giraldeau 2009). Similarly, threespine sticklebacks (*Gasterosteus aculeatus*) trained to expect food on one type of substrate but not on another will switch from preferentially searching for food on the substrate to which they have been trained to foraging on the non-preferred substrate, if provided with social information which conflicts with their previous experience (Webster and Hart 2006).

In this study we sought to determine the costs of responding to social information, in terms of lost foraging opportunities, in a facultatively social species. Furthermore, we investigated how the behaviour of a stimulus group and the previous experience of the focal individuals interacted to affect the rate at which the focal individual discovered and exploited hidden prey. We used the facultatively social ninespine stickleback (*Pungitius pungitius*) as our study species. This species has previously been shown to be adept at using social information in a foraging context, to be able to learn asocially about the distribution and relative quality of prey resources and to discriminate between these two sources of information when they conflict, in an apparently adaptive manner (reviewed by Laland et al. 2011).

In our first experiment we established an arena containing a hidden prey patch, and, in a separate location, a fixed enclosure holding a stimulus shoal of conspecifics. We varied the behaviour of the conspecifics, so that they were either not feeding, attacking prey (that was hidden from the focal fish) or were seen to be attacking prey before being removed, simulating a shoal that had arrived at a prey patch and exploited it, in the view of the observing focal fish, but that had subsequently moved on before the focal fish could join them. The latter condition tests for social learning via delayed local enhancement (Coolen et al. 2003). This social learning process has been widely investigated in this species using a public information binary choice paradigm (Laland et al. 2011). The behaviour of the focal fish in these three treatments was compared against that of focal fish tested in the absence of a stimulus shoal. Further, we tested focal fish that were either naïve to the layout of the arena, or which had previous experience of its layout and the location of the prey patch (but in the absence of the stimulus shoal). We predicted that fish tested in the absence of any social influence would find the prey patch faster than those tested in the presence of conspecifics. We further predicted that fish tested in the presence of stimulus conspecifics that were exhibiting feeding behaviour would

spend more time in the vicinity of the stimulus group and would therefore spend less time exploiting the hidden prey patch, since the two behaviour patterns are mutually exclusive. We expected too to see an effect of delayed local enhancement, specifically that fish would approach the area where they had seen others feeding sooner than they would in the trials where no stimulus shoal was present. We made these predictions based upon observations from multiple studies in which ninespines have been reported to approach areas where they have seen others feeding at the greatest rate (reviewed by Laland et al. 2011). We also predicted that fish that were familiar with the experimental arena would approach the prey patch sooner than those that had no previous experience of it. We compared the proportion of time that the focal fish spent in proximity to the edge of the arena, a measure of thigmotaxis. Thigmotaxis is commonly regarded as a risk averse behaviour (Uryu et al. 1996; Mashoodh et al. 2009). Here we predicted that fish that had previous experience of the arena would be less thigmotactic. Finally, we hypothesized that we might see an interaction between stimulus shoal behaviour and focal fish experience; we expected that experienced fish tested in the absence of stimulus conspecifics should locate the prey patch sooner and spend longer exploiting it compared to naïve fish tested in the presence of feeding conspecifics.

In addition to this main experiment we performed two further investigations, looking at stimulus shoal size and focal fish group size. In the former, we predicted that the focal fish's tendency to approach and shoal with the stimulus group would increase with increasing stimulus group size (Hager and Helfman 1991). In the latter, we predicted that larger groups of focal fish would be influenced by the stimulus shoal to a lesser extent, spending less time shoaling with them, due to facilitation brought about by reduced per capita predation risk (Day et al. 2001; Ward 2011). We also predicted that larger groups would find the prey patch sooner and spend longer exploiting it, an effect that has previously been reported (Pitcher et al. 1982; Day et al. 2001; Ward 2011), probably arising from the greater probability of any one individual finding the food and inadvertently disclosing its location to others via cues associated with feeding, and through greater individual search rates brought about by facilitation, competition or both of these factors (Morgan and Colgan 1987; Grand and Dill 1999; Ward 2011).

By comparing the foraging efficiency, in terms of latency to find prey and time spent exploiting it, between fish tested in the absence of conspecifics and those tested in the presence of conspecifics performing different behaviours, we can identify the opportunity costs of conformity (grouping with others in a fixed location) and using social information. Our two follow-up experiments elaborate on this by allowing us to explore the effect of variable social context.

Methods

Subjects

Ninespine sticklebacks were collected from Melton Brook, Leicestershire, UK (GRID REF: SP 602075) in October 2010 and taken to our laboratory where they were held in groups of 30 in 90-L aquaria. Each aquarium contained a layer of coarse sand, an external filter and artificial vegetation for cover. The light:dark regime was held at 14:10 hours, and the temperature was maintained at 8°C. The experiments described later in the article were performed between March and June 2011. Only fish showing no signs of reproductive state were used, since this is known to influence social behaviour (Webster and Laland 2011). We used a pool of around 120 fish as stimulus fish. Stimulus fish were drawn from this pool haphazardly, though we ensured that no individuals were used more than once in any 72-h period. Test subjects were only used once. We used fish measuring 38–45-mm standard length. Within trials all stimulus and focal fish were size-matched to within 2-mm standard length.

Experimental arena

The experiments were performed in a test arena (Fig. 1) consisting of a grid of 16×16 4-cm wide and 4-cm deep square pits (see Webster and Laland 2011). The whole apparatus was constructed from black plastic and was enclosed by 40-cm tall black plastic walls. The arena was not water tight, and so was placed within a larger, 120-cm-diameter plastic pool. The pits were filled with 1 cm of coarse sand. The surface of the water in the test tank was 5 cm above the base of the pits. This meant that the test fish had to pass over each pit to see inside it. The apparatus was designed to represent a structurally complex natural substrate. In one corner of the arena, four pits were covered by an 8-cm square plastic base, forming a platform. This held a removable colourless plastic holding unit, measuring 7×7 cm and 10 cm tall. The test fish was held in this area at the start of the trial. Another set of four pits, located in another corner of the arena, off the same wall as the starting platform contained a stimulus shoal chamber. This consisted of a colourless Perspex box, with an 8×8-cm base and 7 cm tall, filled to a depth of 5 cm. This contained between zero and five stimulus conspecifics, depending upon the experimental treatment, as described later in the article. Finally, one pit, located four squares from either edge of the grid in the corner diagonally opposite the stimulus shoal chamber, contained a prey patch of 25 dead chironomid larvae. The whole apparatus was surrounded by black plastic screening to minimise outside disturbance and was filmed from above with a Logitech C600 webcam linked to a laptop computer. Water and prey were changed after each trial.

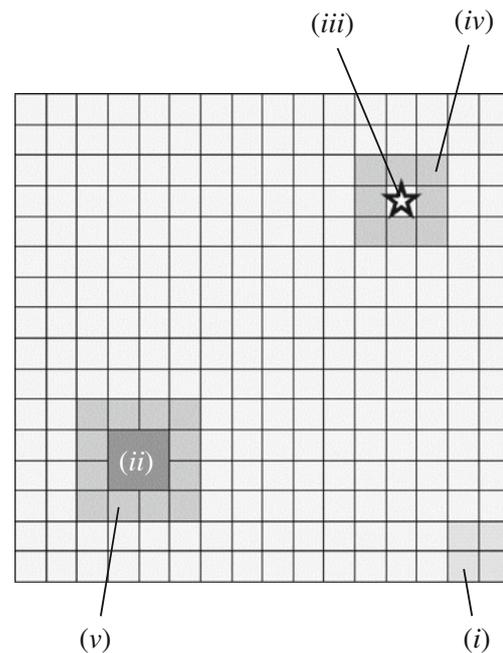


Fig. 1 The test arena, consisting of a grid of 16×16 4-cm wide and 4-cm deep squares, filled with 1 cm of coarse sand. In one corner of the arena, four pits were covered by an 8-cm square plastic base, forming a starting platform (i). Another set of four pits were covered by a stimulus shoal chamber (ii). A further pit contained a prey patch of 25 dead chironomid larvae (iii). Goal zones one grid square wide surrounded both the stimulus chamber (iv) and the prey patch (v). See main text for more information

Experimental procedure

Subjects were deprived of food for 24 h before the trial began in order to generate motivation to forage (Webster and Hart 2004). Prior to the start of each trial, 25 prey items were added to the designated prey patch grid square. This represented more food than the fish could eat during the trial, ensuring that the prey patch could not be depleted. At the beginning of each trial, the test fish was added to the holding unit in the starting corner of the test arena and allowed to settle for 10 min. Following this, a black plastic screen was placed diagonally across the front of the holding unit for 1 min, after which both the screen and the holding unit were raised and removed, beginning the trial. The purpose of the screen was to avoid startling the focal fish in treatment (d), where the stimulus shoal was removed after the settling period, described later in the article. This procedure was adopted in all treatments, however, in order to standardise any effect it may have had on the focal fish. The arena was filmed for 20 further min. We recorded the following behaviours: the location of the test fish to the nearest grid square every 10 s; the latency of the test fish to enter the prey patch goal zone, designated as the prey patch grid square and the eight squares immediately surrounding it (Fig. 1); the latency of the test fish to enter the stimulus shoal association

zone, defined as the 16 squares immediately surrounding the stimulus shoal holding unit, corresponding to around 1.5 body lengths (Webster et al. (2007a) reported inter-individual distances of 0.9–1.5 body lengths in shoals of the closely related and ecologically similar threespine stickleback (*G. aculeatus*)); the number of unique squares entered during the trial; and finally the proportion of movements that took place in the outermost grid squares, a measure of thigmotaxis (Webster and Laland 2011).

Experiment 1. Stimulus shoal behaviour and focal fish experience

Here we sought to determine the effect of the focal fish's naïvety with or experience of the test arena and location of the prey patch, the effect of the presence and behaviour of a stimulus shoal, and the interaction of these variables upon the behaviour of the focal fish. We used a two-by-four factorial design in which focal fish were either naïve or experienced with the test arena, and in which stimulus fish were either (a) absent, (b) present but not feeding, (c) present and performing feeding-like behaviour or (d) made visible to the focal fish during the settling period, in which they performed feeding-like behaviours, and then absent during the testing period. We termed the latter treatment 'delayed local enhancement' (*sensu* Coolen et al. 2003). We performed 15 replicates within each treatment, giving 120 trials in total.

Focal fish experience Naïve test fish were held in groups of three in 45-L aquaria for 3 days prior to being tested. Each aquarium contained a layer of coarse sand, an external filter and artificial vegetation for cover. They were fed three times per day for the first 2 days and deprived of food for the remaining 24 h prior to being tested. Experienced fish were placed in groups of three in a test arena identical to the one described previously in the article for 3 days prior to being tested. They too were fed three times per day during the first 2 days, with the food being placed in the location of the experimental prey patch (Fig. 1), before being deprived of food for the remaining 24 h prior to being tested.

Stimulus shoal behaviour

a) Absent

No stimulus fish were present in the stimulus chamber during either the settling period or the test period. The focal fish was tested in the absence of any social influence.

b) Present but not feeding

Three stimulus fish were added to the stimulus chamber at the same time as the focal fish was added to the holding

unit. No prey were present in the stimulus chamber. The stimulus fish had been deprived of food for 24 h.

c) Present and performing feeding-like behaviour

Three 24-h-food deprived stimulus fish were added to the stimulus chamber at the same time as the focal fish was added to the holding unit, as described previously in the article. In this trial prey (15 dead bloodworms) were present in a 1×2×4-cm transparent water tight box placed within the central grid square beneath the stimulus chamber (Fig. 1). The stimulus fish were able to see and attack the prey, but could not eat it. This served to prevent the stimulus fish from becoming satiated, but also prevented them from redistributing the prey around the stimulus chamber. This, along with placing the prey container within the grid square ensured that the focal fish could not see the prey itself, but could acquire social information by watching the stimulus fish attack it. Attacks took the form of rapid strikes, performed with the body angled 45–90° off-vertical, and directed against the base of the holding unit above the prey container. We recorded the number of strikes made by the stimulus fish during the final 5 min of the settling period and as well as during the experimental phase of the trial.

d) Delayed local enhancement

This treatment was similar to treatment (c), described previously, except that the stimulus fish were only present during the 10-min settling period. Following this the entire stimulus chamber and prey container were carefully removed and replaced with an identical, empty stimulus chamber. This took around 10 s. The black plastic screen, described previously, prevented the focal fish from seeing this procedure. We recorded the number of strikes made by the stimulus fish during the settling period.

Statistical analyses We used censored Cox regression survival analyses (Crawley 2007) to investigate the effects of focal fish experience (naïve or experienced in relation to the test arena), stimulus shoal behaviour (absent, present but not feeding, present and feeding, delayed local enhancement) and the interaction between these factors upon the latency of the focal fish to stimulus shoal association zone and the prey patch goal zone. Survival analysis models, such as Cox models, can be used for any time-to-event data. Using Cox regressions has the advantage that it allows a ceiling value to be applied, allowing those animals that did not enter the zone to be included in the analyses as 'censored' data points, without distorting the results, as would occur if ceiling values were included in a standard regression analysis. We used simple contrasts to compare the latency scores obtained for the 'present but not feeding', 'present and performing feeding-like behaviour' and 'delayed local enhancement' treatments to those obtained in the 'stimulus conspecifics absent' treatment. We used two-way

ANOVAs with Tukey HSD post-hoc analyses to compare the effects of focal fish experience, stimulus shoal behaviour and the interaction between these factors upon the following behaviours: time spent in the stimulus shoal association zone, in the prey patch goal zone, the total number of unique squares entered and the thigmotaxis index, which is proportion of movements that took place in the outermost grid squares.

Experiment 2. Stimulus shoal size

Here we varied the number of stimulus fish over three treatments, with either one, three or five stimulus fish present in the stimulus trainer. The procedure was otherwise identical to that described in treatment (b), “Present but not feeding”, described in “Experiment 1”. We performed ten replicates within each treatment group.

Statistical analyses We used censored Mantel–Cox log rank survival analysis to compare the latency to enter the stimulus shoal association zone and the prey patch goal zone, and pairwise Mantel–Cox log rank comparisons to make post-hoc comparisons between treatment groups. One-way ANOVAs with Tukey HSD post-hoc analyses were used to make the following between-treatment comparisons: time spent in the stimulus shoal association zone, in the prey patch goal zone, the total number of unique squares entered and the thigmotaxis index, which is proportion of movements that took place in the outermost grid squares.

Experiment 3. Focal fish group size

Here we varied the number of focal fish, with either one, three or five present. There were three stimulus fish present in all treatments, with the procedure being otherwise identical to that described in treatment (b) in “Experiment 1”. We only collected data on one target focal individual per trial. Thus, in the three and five focal fish treatments, the target individual was randomly selected at the moment of the removal of the holding unit, and its behaviour followed for the duration of the trial. We performed ten replicates within each treatment group.

Statistical analyses The statistical analyses performed were identical to those described for “Experiment 2”.

Results

Stimulus fish feeding strike rate

We compared the feeding strike rate of the stimulus fish for the final 5 min of the settling phase and the four sequential

5-min blocks of the test phase in the ‘conspecifics present and performing feeding-like behaviour’ using a repeated measure ANOVA, finding no changes in strike rate over time ($F_{(4, 56)}=1.95$, $P=0.11$). We saw no differences in strike rate during the final 5 min of the settling phase between stimulus fish in the conspecifics present and performing feeding-like behaviour and delayed local enhancement treatments (one-way ANOVA: $F_{(1, 28)}=0.34$, $P=0.56$).

Experiment 1. Stimulus shoal behaviour and focal fish experience

Stimulus shoal

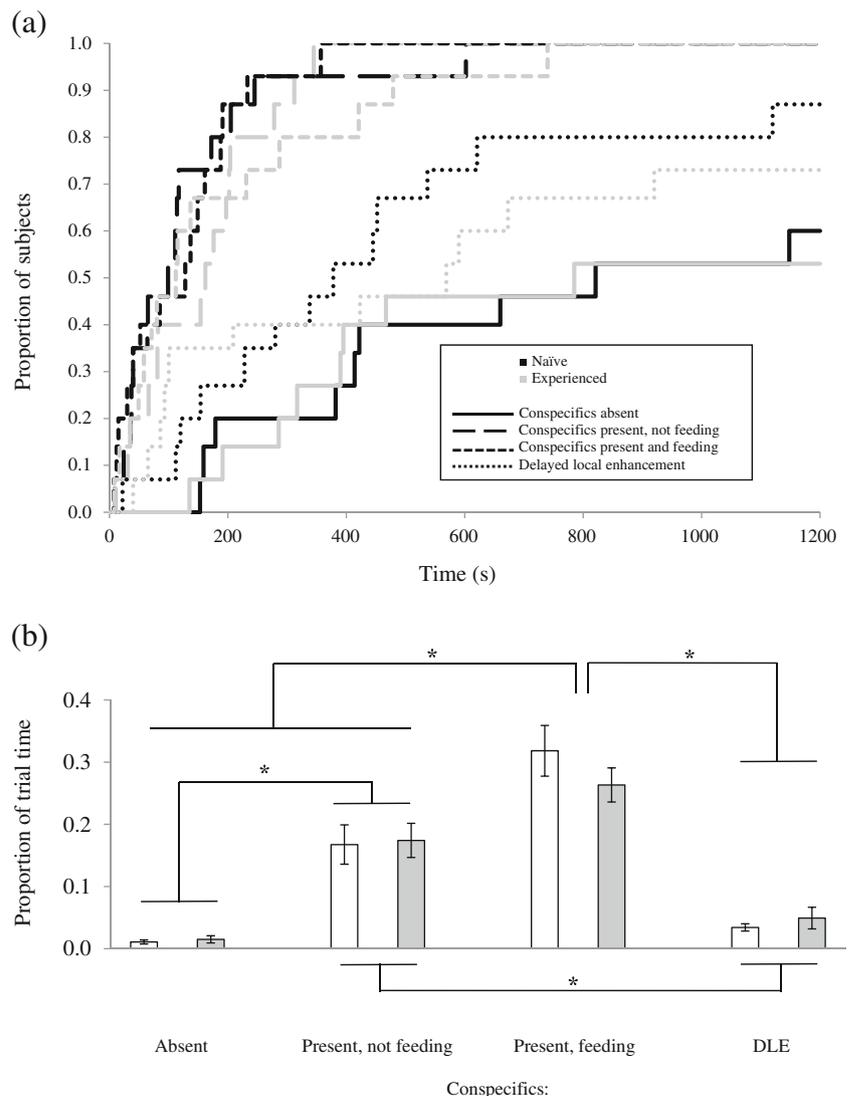
A Cox regression revealed a significant effect of stimulus shoal behaviour upon the latency of focal fish to arrive in the stimulus shoal association zone ($\chi^2=28.25$, $df=3$, $P<0.001$, Fig. 2a), but no effect of focal fish experience ($\chi^2=0.56$, $df=1$, $P=0.45$) and no interaction between these factors ($\chi^2=0.57$, $df=3$, $P=0.90$). Simple contrasts revealed that focal fish in the conspecifics present but not feeding, conspecifics present and performing feeding-like behaviour and delayed local enhancement treatments entered the stimulus shoal association zone significantly sooner than those tested in the absence of stimulus conspecifics ($B=2.07$, $\chi^2=38.90$, $P<0.001$; $B=1.98$, $\chi^2=37.53$, $P<0.001$; and $B=0.66$, $\chi^2=4.30$, $P=0.038$ respectively).

We also saw that the proportion of trial time spent in the stimulus shoal association zone was significantly affected by the stimulus shoal behaviour (two-way ANOVA: $F_{(3, 112)}=56.35$, $P<0.001$), but not by either focal fish experience ($F_{(1, 112)}=0.19$, $P=0.66$) or the interaction between the two ($F_{(3, 112)}=0.88$, $P=0.45$, Fig. 2b). Tukey post-hoc analyses identified that fish in the conspecifics present but not feeding and conspecifics present and performing feeding-like behaviour, but not those tested in the delayed local enhancement treatments spent significantly more time in the stimulus shoal association zone than those tested in the absence of stimulus conspecifics ($P<0.001$; $P<0.001$ and $P=0.64$ respectively). Fish tested in the conspecifics present and performing feeding-like behaviour treatment spent more time in the association zone than those in the conspecifics present but not feeding treatment ($P<0.001$), while fish in both of these treatments both spent more time in the association zone than those in the delayed local enhancement treatment ($P<0.001$ in both cases).

Prey patch

A Cox regression revealed significant effects of both stimulus shoal behaviour ($\chi^2=35.98$, $df=3$, $P<0.001$) and focal fish experience ($\chi^2=7.22$, $df=1$, $P=0.007$) upon the latency

Fig. 2 a Survival plot of latency to enter the stimulus shoal association zone. We saw no effect of focal fish experience (experienced versus naïve), but there was a significant effect of experimental treatment: latencies for ‘conspecifics present, not feeding’, ‘conspecifics present and feeding’ and ‘delayed local enhancement’ were significantly different from ‘conspecifics absent’. See main text for details. **b** Bar chart (means \pm SE) of proportion of trial time spent in the stimulus shoal association zone. We saw no effect of focal fish experience (naïve, \square , versus experienced, \blacksquare). * P <0.05. DLE delayed local enhancement



of focal fish to enter the prey patch but no interaction between these factors ($\chi^2=0.12$, $df=3$, $P=0.98$, Fig. 3a). Fish in the conspecifics present but not feeding, conspecifics present and performing feeding-like behaviour and delayed local enhancement treatments all took significantly longer to enter the prey patch than fish that were tested alone (Simple contrasts, $B=-2.15$, $\chi^2=36.92$, $P<0.001$; $B=-2.36$, $\chi^2=43.17$, $P<0.001$; and $B=-1.26$, $\chi^2=18.15$, $P<0.001$ respectively).

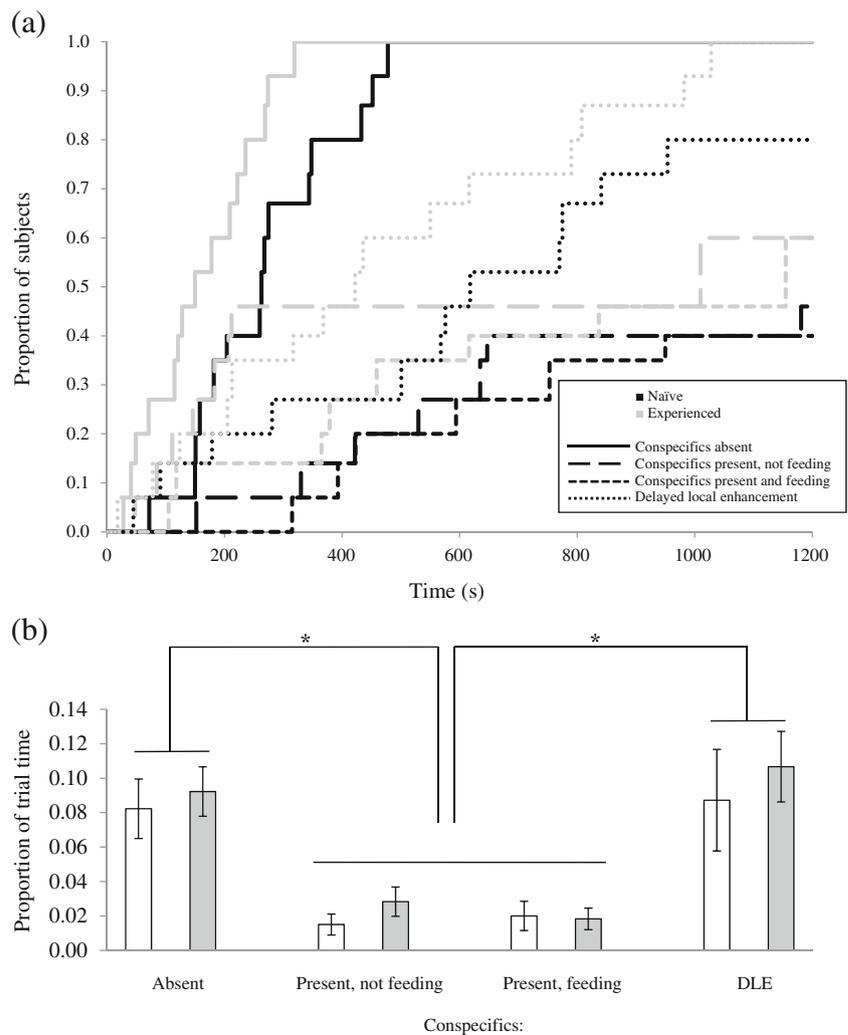
The proportion of trial time spent in the prey patch was significantly affected by the stimulus shoal behaviour (two-way ANOVA: $F_{(3, 112)}=13.74$, $P<0.001$), but not by either focal fish experience ($F_{(1, 112)}=0.84$, $P=0.36$) or the interaction between the two ($F_{(3, 112)}=0.15$, $P=0.92$, Fig. 3b). Tukey post-hoc analyses identified that fish in the conspecifics present but not feeding and conspecifics present and performing feeding-like behaviour, but not those tested in the delayed local enhancement treatments spent significantly less time in the prey patch than those tested in the absence

of stimulus conspecifics ($P<0.001$; $P<0.001$ and $P=0.92$ respectively). Fish tested in the conspecifics present and performing feeding-like behaviour and conspecifics present but not feeding treatments did not differ ($P=0.99$), while fish in both of these treatments both spent less time in the association zone than those in the delayed local enhancement treatment ($P<0.001$ in both cases).

Unique squares entered

We saw significant effects of experimental treatment (two-way ANOVA: $F_{(3, 112)}=6.76$, $P<0.001$, Fig. 4a), but not focal fish experience ($F_{(1, 112)}=2.66$, $P=0.11$) upon the number of unique grid squares entered during the trial. There was no interaction effect between treatment or experience ($F_{(3, 112)}=0.25$, $P=0.89$). Tukey post-hoc analyses revealed that fish in the conspecifics present and performing feeding-like behaviour entered fewer unique squares than those in the conspecifics

Fig. 3 a Survival plot of latency to enter the prey patch goal zone. We saw no effect of focal fish experience (experienced versus naïve), but there was a significant effect of experimental treatment: fish in the ‘conspecifics present, not feeding’, ‘conspecifics present and feeding’ and ‘delayed local enhancement’ treatments all took significantly longer to enter the prey patch than fish that were tested alone. See main text for details. **b** Bar chart (means \pm SE) of proportion of trial time spent in the prey patch goal zone. We saw no effect of focal fish experience (naïve, \square , versus experienced, \blacksquare). * $P < 0.05$. DLE delayed local enhancement



absent ($P < 0.001$) or the conspecifics present but not feeding treatments ($P = 0.003$).

Thigmotaxis

We saw significant effects of both experimental treatment (two-way ANOVA: $F_{(3, 112)} = 7.74$, $P < 0.001$, Fig. 4b) and focal fish experience ($F_{(1, 112)} = 27.70$, $P < 0.001$) upon thigmotactic behaviour, as well as a weak interaction between these factors ($F_{(3, 112)} = 2.56$, $P = 0.058$).

Fish tested in the conspecifics absent treatment performed more movements in the squares at the arenas edges than did those in the conspecifics present but not feeding and conspecifics present and performing feeding-like behaviour treatments (Tukey post-hoc tests: $P = 0.015$ and $P < 0.001$). Fish tested in the delayed local enhancement treatment were also more thigmotactic than those tested in the conspecifics present and performing feeding-like behaviour treatment ($P = 0.004$). Finally, fish that had previously experienced the experimental arena were less thigmotactic than those that were naïve to it.

Experiment 2. Stimulus shoal size

Stimulus shoal

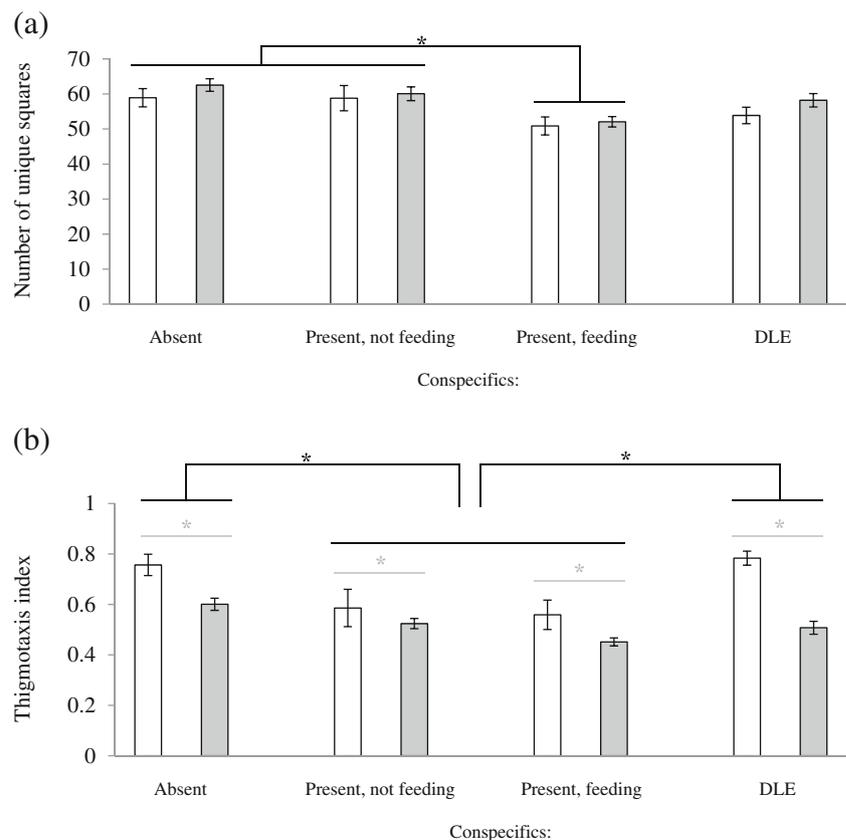
Pairwise Mantel–Cox log rank survival analyses revealed that the focal fish took longer to approach a single stimulus fish than they did a group of five ($\chi^2 = 4.81$, $P = 0.028$, Fig. 5a). We saw no differences in approach latencies when we compared stimulus shoal group sizes of one versus three ($\chi^2 = 2.51$, $P = 0.11$) or three versus five ($\chi^2 = 0.04$, $P = 0.84$).

A one-way ANOVA revealed significant differences in the time spent in the stimulus chamber association zone ($F_{(2, 29)} = 5.48$, $P = 0.010$, Fig. 5b). Tukey post-hoc analyses revealed that focal fish spent significantly longer in the association zone when five stimulus fish were present compared to one ($P = 0.008$) or three ($P = 0.043$).

Prey patch

Pairwise Mantel–Cox log rank survival analyses revealed that focal fish took longer to approach the prey patch when

Fig. 4 Bar charts (means \pm SE) showing **a** the number of unique grid squares entered and **b** the thigmotaxis index (the proportion of grid squares entered that were in the outer edge of the arena). \square naïve, \blacksquare experienced, * $P < 0.05$



five stimulus fish were present than they did when only one was present ($\chi^2=4.39$, $P=0.036$, Fig. 5c). There were no differences in approach latencies when we compared stimulus shoal group sizes of one versus three ($\chi^2=1.41$, $P=0.23$) or three versus five ($\chi^2=1.31$, $P=0.25$).

One-way ANOVA revealed significant differences in the time spent in the stimulus chamber between treatments goal zone ($F_{(2, 29)}=6.89$, $P=0.004$, Fig. 5d). Here, Tukey post-hoc analyses showed that focal fish tested in the presence of only one stimulus conspecific spent longer in the prey patch goal zone than did those tested in the presence of three ($P=0.013$) or five ($P=0.007$) stimulus conspecifics.

Unique squares entered

We saw no differences in the total number of unique grid squares entered by focal fish tested in the different treatments (ANOVA: $F_{(2, 29)}=0.92$, $P=0.41$, Fig. 5e).

Thigmotaxis

We saw a weak trend for fish tested in the presence of three stimulus conspecifics to perform a greater proportion of movements in the grid squares at the edge of the arena (one-way ANOVA ($F_{(2, 29)}=2.66$, $P=0.09$, Fig. 5f).

Experiment 3. Focal fish group size

Stimulus shoal

Pairwise Mantel–Cox log rank survival analyses revealed no differences between focal fish group sizes in time to enter the stimulus shoal goal zone (one versus three $\chi^2=2.87$, $P=0.10$; one versus five $\chi^2=1.99$, $P=0.16$; three versus five $\chi^2=0.41$, $P=0.52$, Fig. 6a).

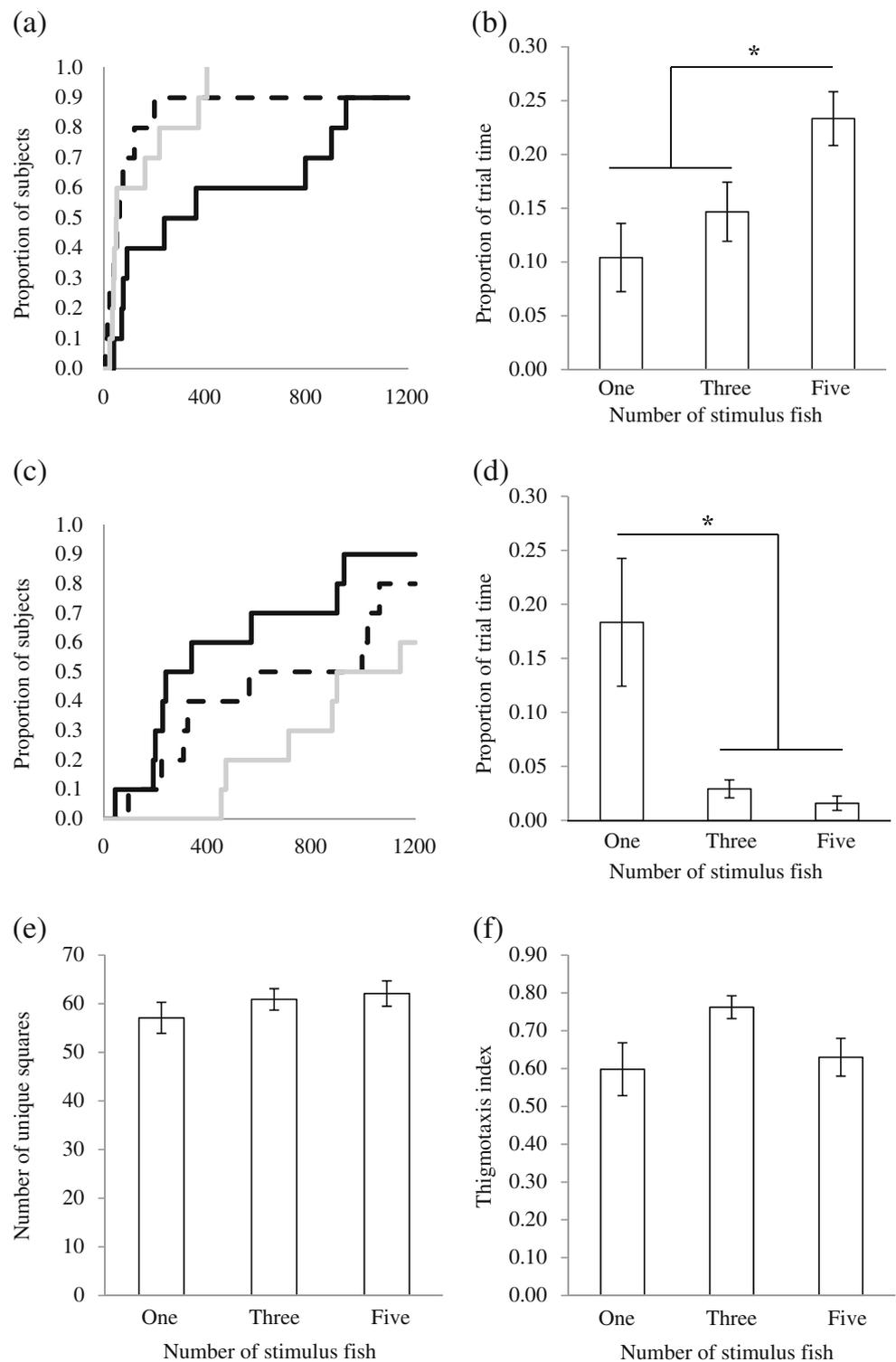
A one-way ANOVA revealed significant differences in the time spent in the stimulus chamber association zone by focal fish in different group size treatments ($F_{(2, 29)}=24.20$, $P < 0.001$, Fig. 6b). Tukey post-hoc analyses indicated that focal fish tested alone spent more time in the stimulus chamber association zone than did fish tested within groups of three or five ($P < 0.001$ in both cases).

Prey patch

Pairwise Mantel–Cox log rank survival analysis revealed that focal fish in groups of three or five approached the prey patch sooner than did single fish (one versus three: $\chi^2=15.14$, $P < 0.001$; one versus five: $\chi^2=15.13$, $P < 0.001$; three versus five: $\chi^2=1.75$, $P=0.19$, Fig. 6c).

Fig. 5 Experiment 2, number of stimulus conspecifics. **a** Survival plot of latency to enter the stimulus shoal association zone. We saw a significant difference between latencies for fish tested with one versus five conspecifics present (*solid black line* = one stimulus conspecific present, *broken black line* = three present, *solid grey line* = five present). **b** Bar chart (means \pm SE) of proportion of trial time spent in the stimulus shoal association zone. **c** Survival plot of latency to enter the prey patch goal zone. We saw a significant difference between latencies for fish tested with one versus five conspecifics present (*solid black line* = one stimulus conspecific present, *broken black line* = three present, *solid grey line* = five present). **d** Bar chart (means \pm SE) of proportion of trial time spent in the prey patch goal zone. **e** Bar chart (means \pm SE) showing the number of unique grid squares entered. **f** Bar chart (means \pm SE) showing the thigmotaxis index (the proportion of grid squares entered that were in the outer edge of the arena).

* $P < 0.05$

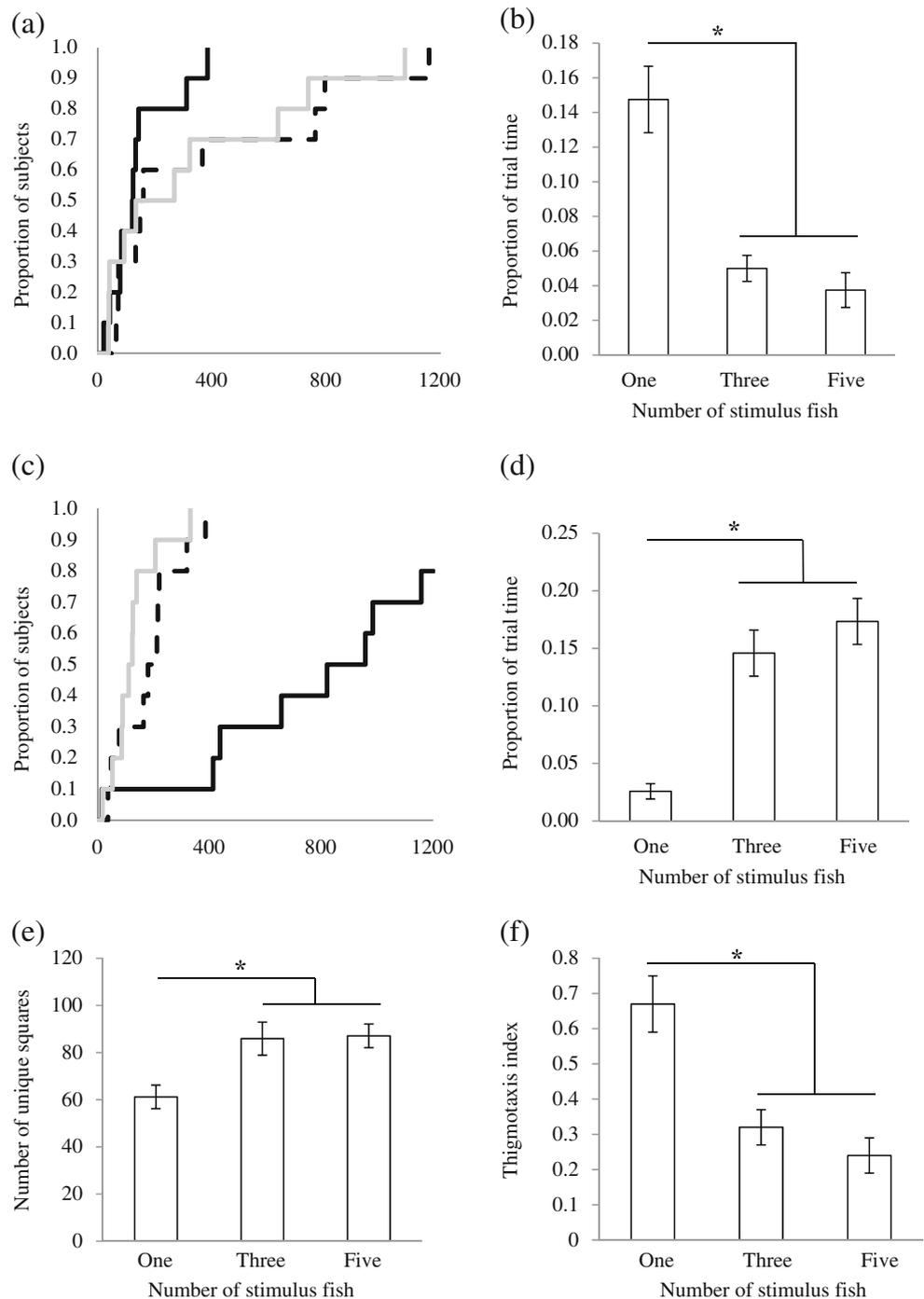


A one-way ANOVA revealed significant differences in the time spent in the prey patch goal zone between group size treatments ($F_{(2, 29)} = 22.75$, $P < 0.001$, Fig. 6d), with fish tested alone spending less time there compared to fish tested in groups of three or five (Tukey post-hoc: $P < 0.001$ in both cases).

Unique squares entered

Single focal fish entered fewer unique grid squares than did focal fish in groups of three or five (one-way ANOVA: $F_{(2, 29)} = 35.19$, $P < 0.001$; Tukey post-hoc: $P < 0.001$ in both cases, Fig. 6e).

Fig. 6 Experiment 3, focal fish group size. **a** Survival plot of latency to enter the stimulus shoal association zone. We saw no differences between focal fish group sizes in time to enter the stimulus shoal goal zone (*solid black line* = single focal fish, *broken black line* = focal fish among group of three, *solid grey line* = focal fish among group of five). **b** Bar chart (means \pm SE) of proportion of trial time spent in the stimulus shoal association zone. **c** Survival plot of latency to enter the prey patch goal zone. We saw that focal fish in groups of three or five approached the prey patch sooner than did single fish (*solid black line* = single focal fish, *broken black line* = focal fish among group of three, *solid grey line* = focal fish among group of five). **d** Bar chart (means \pm SE) of proportion of trial time spent in the prey patch goal zone. **e** Bar chart (means \pm SE) showing the number of unique grid squares entered. **f** Bar chart (means \pm SE) showing the thigmotaxis index (the proportion of grid squares entered that were in the outer edge of the arena). * $P < 0.05$



Thigmotaxis

Single focal fish performed a greater proportion of their movement in the grid squares around the arena edge compared to focal fish in groups of three or five ($F_{(2, 29)} = 28.18$, $P < 0.001$, Tukey post-hoc: $P < 0.001$ in both cases, Fig. 6f).

Discussion

We carried out three experiments designed to quantify the opportunity costs of social conformity in ninespine sticklebacks. We have shown that they respond to the presence and behaviour of conspecifics, both in real time while they are present and after having observed them feeding before they

are removed, and that they are attracted to the location where they are or were. In doing so, they pay opportunity costs in terms of delayed foraging opportunities. The extent of these costs is determined both by the number of stimulus conspecifics and by the number of groupmates accompanying the focal fish.

In our first experiment we saw that fish tested in the absence of conspecifics arrived at the prey patch sooner than did fish tested in the presence of a stimulus shoal. In trials where the stimulus shoal was present, focal fish quickly approached them and spent a significantly greater proportion of the trial in close proximity to the stimulus shoal holding unit, compared to fish tested in the absence of conspecifics. While this observation is unsurprising, we also saw that focal fish tested in the presence of conspecifics that were feeding spent significantly more time shoaling with them compared to those tested with conspecifics that were not feeding. This suggests that focal fish are sensitive not only to the presence of conspecifics, but also to their behaviour. In the delayed local enhancement treatment we observed that focal fish that had previously seen a now absent stimulus shoal feeding approached their former location sooner than did fish tested alone and without having been exposed to conspecifics. This finding is consistent with experiments on public information use in this species (Laland et al. 2011), which have shown that ninespine sticklebacks tend to approach locations where they have seen one of two groups feeding at the greatest rate, and is indicative of social learning. It is also worth noting that while no food was present at the location of the stimulus shoal in our experimental design, fish tested in the delayed local enhancement treatment did not differ from fish tested alone in the proportion of trial time that they went on to spend at the hidden prey patch. This suggests that the costs of using misleading public information may not always be severe, at least on the spatial and temporal scale employed in this study.

Previous experience of the experimental arena had surprisingly little effect upon the behaviour of the focal fish, nor did it interact with experimental treatment in the way we had anticipated. Experienced fish tended to arrive at the prey patch sooner than did naïve fish, but did not differ from them in the amount of time they spent there. Experienced fish were less thigmotaxic than naïve fish, suggesting a degree of habituation to the arena (thigmotaxis is commonly regarded as being consistent with risk-aversion or stress, Uryu et al. 1996; Mashoodh et al. 2009), but both groups were equally responsive to the stimulus shoal, with experienced and naïve fish joining them at similar rates and shoaling with them for a similar proportion of trial time.

The finding that hunger-motivated focal fish responded strongly to the presence and behaviour of conspecifics, even when doing so conflicted with their previous experience of

finding food elsewhere in the arena, is consistent with those of previous studies (e.g. Rieucan and Giraldeau 2009; Webster and Hart 2006). The opportunity costs of doing so included taking longer to find a prey patch, spending less time exploiting it and exploring less of the arena. We suggest that such behaviour might be underpinned by heuristic rules of social attraction, such as ‘approach others’, ‘approach larger groups over smaller groups’ and ‘approach groups that are producing cues that are consistent with feeding, or feeding at the greatest rate’ (e.g. Coolen et al. 2005). A tendency to approach others that are feeding, as well as the capacity to attend to cues indicative of feeding, is likely to benefit animals foraging in patchy environments by allowing them to detect food without having to pay the costs of sampling the environment directly. That no food could actually be detected directly by the focal fish at the location of the feeding stimulus shoals in our study was an experimental contrivance, employed to remove the possibility that focal fish might use cues emanating from the prey itself, rather than the focal fish. In reality, numerous studies have shown that it can pay to join others that have discovered food, depending upon factors such as forager density and rates of patch depletion (Giraldeau and Caraco 2000).

Such rules of social attraction might ultimately be explained in terms of adaptation to predation pressure. Our experimental design set up a dichotomy between shoaling in one restricted area of the tank, where no food resources are to be found, or exploring, alone, the rest of the tank, and with the possibility of finding and exploiting the food patch. In reality, predation risk is likely to have significant influence upon the advantages of pursuing either of these options, in that individuals within groups are subject to lower per capita risk of being preyed upon, and may benefit through other effects such as the disproportionately greater ability of groups to detect predators. In contrast, predation risk is greater, along with the necessary investment in vigilance (often at the cost of effort invested in foraging) for individuals travelling alone (Krause and Ruxton 2002). For this reason, while there is a demonstrable short-term cost to grouping with others and responding to their behaviour in terms of lost foraging opportunities, as well as longer term growth costs (e.g. Gonda et al. 2009; Herczeg et al. 2009), these may be offset by reduced predation risk. The opportunity cost of grouping rather than exploring alone may be reduced (or even absent) if the risk from predators or other environmental hazards is greater for single individuals. This speculation should be subject to further investigation. Such work might rerun these experiments in the presence of predators or simulated predation risk, or could adopt a comparative approach, focusing upon the behaviour of individuals from multiple high and low predation environments.

Our second and third experiments investigated the effects of group size upon focal fish behaviour. In “Experiment 2” we varied the number of fish in the stimulus shoal, finding that individual focal fish were drawn to larger shoals and spent less time in the prey patch compared to when only a single stimulus fish was present. This finding is consistent with those of previous studies; while group size is strongly context dependant (Pitcher et al. 1996; Hoare et al. 2004), larger groups have a greater ability to recruit individuals under certain conditions (e.g. Hager and Helfman 1991; Day et al. 2001; Buckingham et al. 2007; Pike and Laland 2010). The third experiment found that focal fish embedded in groups behaved differently compared to focal fish tested alone. They were less thigmotaxic and explored more of the arena. They were also found to be less susceptible to influence from the stimulus shoal, spending significantly less time shoaling with it. They also found the prey patch sooner and spent significantly more time exploiting it. The greater rate of exploration and lower degree of thigmotaxis may be due to facilitation effects (Ward 2011), whereby fish in groups are subject to lower per capita predation risk and are able to invest less effort or time into vigilance, allowing them to engage in behaviours that may be mutually exclusive with vigilance, such as traveling or foraging. Such behaviour could also be brought about through resource competition, which may cause individuals to alter the way that they trade-off between food intake rate and vigilance or other risk averse behaviours (Grand and Dill 1999). These processes may operate in tandem; individuals must change their behaviour in the presence of increasing numbers of competitors if they are to maintain a minimum level of prey intake and are able to do so because increasing group size leads to decreased predation risk. The lower latency to arrive at the prey patch seen in focal fish in groups compared to fish tested alone could be not only due to enhanced rates of individual searching brought about by the facilitation, competition or both but also due to the greater probability of any one individual finding the food and inadvertently disclosing its location to others via cues associated with feeding (Pitcher et al. 1982; Day et al. 2001), and the fact that larger groups have been shown to process information faster and with greater accuracy, through self-organised division of vigilance (Ward et al. 2011).

That the focal fish that were tested in groups were less responsive to the stimulus shoal has implications for the directed transmission and diffusion of information. It is recognised that animals typically do not use social information indiscriminately and that they do not attend to the behaviour of all members of the population equally (Coussi-Korbel and Fragaszy 1995). Research has focussed upon strategic social learning and the evolved rules that determined when and who individuals should copy (Laland 2004; Galef 2009; Rendell et al. 2011). It may be that for some species, particularly those

living in relatively large or dense free-entry groups, as do many fishes and birds for example, potential models for social learning are limited by the number of conspecifics that an individual can monitor at any given time. This may render individuals receptive to information from only some individuals within their group or make them less likely to monitor or use information from individuals that are not in their immediate vicinity, even if those individuals are physically detectable. Theoretical and empirical work exploring the collective behaviour of large groups of animals has identified metric and topological response rules which govern which groupmates an individual monitors and responds to, such as all those within x body lengths (e.g. Couzin et al. 2002) or the nearest x individuals (e.g. Ballerini et al. 2008). Such behavioural rules may be born out of expediency, when faced with a large number of groupmates to attend to or else they could reflect sensory or cognitive limitations which cap the number of groupmates that can effectively be tracked. While such local rules are attracting much interest in the fields of collective behaviour and social organisation, they have received less attention in the social learning literature and could form the basis of useful future research.

We have already alluded to further work that could add to this research by exploring the potentially mitigating role of predation risk upon the trade-offs associated with grouping versus acting alone in facultatively social species. We have also highlighted the scope for integrating metric and topological response rules into research on social learning strategies. A final area worthy of further research is the relationship between personality, sociality and the use of social information (reviewed by Webster and Ward 2011). Stable individual-level behavioural variation is thought to be widespread (Reale et al. 2007), but the relationship between personality and social information use has only been investigated in a few studies to date (e.g. Webster et al. 2007b; Harcourt et al. 2010; Kurvers et al. 2010). Potential therefore exists for work focusing upon integrating the effects of personality and social context in order to determine not only when individuals are more likely to use information from different sources but also whether some individuals are predisposed to do so more than others.

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