Boldness is influenced by social context in threespine sticklebacks (*Gasterosteus aculeatus*)

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Summary

Boldness refers to the extent to which animals balance risk against benefits when engaging in such behaviors as foraging, exploration or resource competition. Evidence suggests that individuals can behave strategically, acting boldly in situations when doing so is adaptive, whilst avoiding risk when the rewards are correspondingly lower. In this study we sought to determine the effects of social context upon the boldness of threespine sticklebacks (*Gasterosteus aculeatus*). We found that when individuals were tested alone, those that were more active were more likely to resume foraging sooner when subjected to a simulated predator attack in a separate test, and also consumed more prey in foraging competition trials. We found no effect of group size upon the relative ability of individuals to effectively compete for prey. Group size did affect other behaviours however: focal fish were more active and resumed foraging more rapidly when tested in groups that they did when tested alone. Finally, individual social information use was not correlated with behaviour in other contexts. Two competing hypotheses, the adaptation and the constraint hypotheses have been posited to explain the presence and prevalence of individual variation in boldness; our findings offer partial support for the former of these.

Keywords: Social foraging, competition, social facilitation, social conformity, bold-shy axis, behavioural syndromes, shoal, flock.

Introduction

The bold-shy axis describes the degree to which animals balance fundamental trade-offs between returns and risk when undertaking such tasks as

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foraging, inspecting predators and competing for resources (Wilson et al., 1994; Wilson, 1998; Sih et al., 2004). Studies have revealed that in numerous species, individuals that behave boldly in one context also behave boldly in other, separate contexts and that within a given population, individual variation in boldness can be substantial (Verbeek et al., 1996; Dugatkin & Alfieri, 2003; Bell & Stamps, 2004; Ward et al., 2004; Bell, 2005; Quinn & Cresswell, 2005). On the other hand, behaving in a consistently bold or shy manner in all situations is potentially maladaptive, since it may prevent animals from producing optimal responses to different stimuli. Accordingly, there is also evidence to suggest that some animals modify their responses, behaving boldly only when it is adaptive to do so (Coleman & Wilson, 1998; Reale et al., 2000; Lopez et al., 2005).

Little is known of how social context relates to the boldness of individuals however. Aspects of sociality such as social facilitation and the use of social information clearly affect the way individuals exploit resources, interact with their environment, and the extent to which they take risks when doing so (Krause & Ruxton, 2002). This is important since many previous studies of boldness have focused upon the bold/shy responses of single animals only, often restoring the social context only to look at aggressive or competitive interactions. The impact of many of the day-to-day costs such as predation risk and resource sampling can be less severe for animals that live in groups than it would be if they were living alone. This is because in groups there are likely to be at any given time certain members that are engaged in sampling resources, or watching for predators, and who actively or passively transmit information derived from these activities throughout the group. To the individual group member this can reduce the required minimum investment of time and energy into meeting these costs, allowing them to spend more time engaged in other often non compatible activities, such as searching for and consuming prey (Galef, 1988; Baird et al., 1991; Day et al., 2001; Krause & Ruxton, 2002). Related to this, social animals can assimilate and use public information about their surroundings. Public information is specialized form of social information, one that specifically conveys to the receiver information about the quality of a resource (Valone, 1989; Valone & Templeton, 2002). If we are to further our understanding of the role of boldness in determining the behaviour of members of free-ranging populations we need to know how such behaviour is expressed under naturally realistic conditions when social cues are available.

In this study we examined the influence of social context upon the expression of bold/shy behavioural responses by individual threespine sticklebacks (*Gasterosteus aculeatus*). We measured the behaviour of focal fish in two separate contexts, activity levels in novel surroundings and foraging when under simulated predation risk, predicting that individuals that are more active should also resume foraging more rapidly following a simulated attack from a predator. Previous studies have shown that these behaviours can be correlated in this way in this species (Bell & Stamps, 2004). Using these and further assays we performed a series of three experiments designed to determine the relationship between social context and individual bold/shy behavioural tendencies. The first of these experiments considered prey competition and group size. Prey competition is costly, and it can potentially increase the risk of predation of those individuals taking part (Jakobsson et al., 1995; Slotow & Paxinos, 1997). For this reason we predicted that the prey share of a focal fish would be correlated with its behaviour in other contexts when the size group of competitors was low, in accordance with previous findings (Ward et al., 2004), but not when the group size was larger. We reasoned that in numerically larger groups where the per capita predation risk was lower it would be adaptive to behave boldly by competing more vigorously and that an individual's prey share would no longer correlate with its behaviour in other contexts. In the second experiment we tested the prediction that an individual's behaviour would be correlated between the two behavioural contexts, activity in novel surroundings and foraging behaviour under simulated predation risk when it was tested alone in each but not when it was tested within a group of conspecifics in one or other of these contexts. Again we reasoned that social facilitation through the presence of shoal mates should allow individual group members to behave more boldly than they would if they were alone. In our third experiment, we considered the use of public information by threespine sticklebacks. Previous research has revealed that threespine sticklebacks can obtain public information about prey patch quality by observing the foraging success of attendant conspecifics, and that they use this information to discriminate between patches, preferentially foraging at patches where prey yield is higher (Webster & Hart, 2006a). Though privately collected information is generally thought to be more accurate than information gathered second hand through the observation of the foraging successes of others, collecting it is riskier, since the forager must expose itself to predation risk by sampling multiple patches itself. Given this, we

predicted that individuals that were less active and which took longer to resume foraging following a failed attack by a simulated predator would use social information to a greater extent.

Materials and methods

Fish Collection and Housing

Threespine sticklebacks (30-35 mm standard length) were collected from the Great Eau river, Lincolnshire, UK in June 2006. They were housed in the laboratory in groups of 20 with each group assigned to its own holding tank ($40 \times 25 \times 25$ cm, water depth 20 cm, sand substrate, and artificial vegetation for cover). The water temperature and light: dark regimes were held at 10°C and 12:12 hours. Fish were fed frozen chironomid larvae once per day, unless otherwise stated below. They were held under these conditions for three months before the experiments began. Over the course of the study no fish was used more than once.

Part 1. Does boldness predict prey share and is this affected by group size?

The aim of Part 1 was to determine (a) whether the competitive ability of an individual, determined by its share of a finite prey resource, was related to its behaviour in other contexts and (b) whether this relationship was affected by the size of the group in which it was competing. Fourteen groups of two and fourteen groups of six fish were established with each housed in its own chemically and visually isolated tank ($40 \times 25 \times 25$ cm, water depth 20 cm, sand substrate). All fish were size matched to within <1 mm standard length. One focal fish was randomly selected from each group. This fish was identified by the pigmentation patterns along its flanks and a digital photograph of each focal fish was taken whilst it was still within its tank, along with a written record describing its markings, to ensure that each focal fish could be quickly and accurately identified. Fish were held under these conditions for 24 hours before experiments began. Each group/focal fish was subjected to three experiments according to the following schedule:
   Day 1: the experimental groups were established
   Day 2: prey share competition trial 1
   Day 4: prey share competition trial 2

Day 6: prey share competition trial 3
Day 8: focal fish activity level test
Day 10: latency to resume foraging under simulated predation risk test
These assays are described below.

Part 2. Is individual boldness affected by social facilitation?

Individual animals can benefit from reduced predator vigilance costs by being a member of a group, potentially allowing them to engage in certain other behaviours to a greater extent than they could if they were alone (Krause & Ruxton, 2002). In this part of the study we sought to determine (a) if focal fish would be more active and resume foraging more rapidly under predation risk when they were in groups compared to others tested alone and (b) whether behavioural responses were correlated within individuals when they were tested alone in one context but not in the other.

Thirty-six focal threespine sticklebacks were used, with each housed in its own chemically and visually isolated tank ($40 \times 25 \times 25$ cm, water depth 20 cm, with a 1 cm deep fine sand substrate). In addition to the focal fish, each tank contained two companion fish. These individuals were included to minimize stress in the focal fish, and were not used in any of the experiments. As described above, focal fish were identified by their flank pigmentation patterns. Three experimental groups of 12 focal fish each were established, and tested according to the following schedule:
Day 1: focal and companion fish assigned to holding tanks
Day 3: activity level test
Day 5: latency to resume foraging under simulated predation risk test

The first experimental group was used in a control treatment. Individuals were tested alone in the activity level test on day 3, and then alone again in the foraging under simulated predation risk test on day 5 according to the assays detailed below. Individuals from the second experimental group were tested in a modified version of the activity level test on day 3, described below. They were then tested alone on day 5 in the foraging under simulated predation risk test, also described below. Finally, individuals from the third experimental group were tested alone in the activity level test on day 3. They were then tested in a modified version of the simulated predation risk test on day 5, described below.

Part 3. Is boldness correlated with the use of public information?

The aim of this part of the study was to determine whether the use of public information by individuals was related to their behaviour in other contexts. Thirty focal fish were used and each was housed in its own chemically and visually isolated tank (40 × 25 × 25 cm, water depth 20 cm, with a 1 cm deep fine sand substrate). In addition to the focal fish, each tank contained two companion fish as described in Part 2. Experiments were performed according to the following schedule:

    Day 1: focal and companion fish assigned to holding tanks
    Day 3: activity level test
    Day 5: latency to resume foraging under simulated predation risk test
    Day 7: use of public information test
    These assays are described below.

Experimental behaviour assays

These behavioural assays were used to measure intra-individual behavioural correlations across different contexts. They were selected because they have previously been used in studies of boldness in this species. Previous studies have revealed that behavioural tendencies in these contexts are relatively stable within individuals (Ward et al., 2004; Bell, 2005) and for this reason, with the exception of the prey competition test, each was only performed once.

Prey competition test (Part 1)

Fish were tested within their own holding tank so as to minimize stress. Each group was provided with single, sequentially delivered 3 mm long sections of chironomid larvae, a natural prey type that fish had been fed during their time in captivity. Prey items suspended in 2 ml of tank water were added via a 5 ml syringe through one of five holes, spaced 2 cm apart at the water line of each aquarium. The order in which each hole was used was randomly pre-selected to prevent fish from predicting and monopolizing the feeding position and pre-selected to avoid experimenter bias. In the trials where the group contained two fish a total of six prey items were introduced, and in the trials where the group size consisted of six fish a total of 10 prey items were added. The ratio of prey items to group members was therefore lower

in the trials where the group size was six. This approach was adopted in order to minimize the chance that superior competitors might consume many prey items and become satiated before the experimental trial was completed. Prey were delivered sequentially, with a 30 s period between the ingestion of one item by a fish and the introduction of the next. In each trial the prey share of the focal fish was recorded. Prey competition took the form of both scramble competition, whereby multiple foragers were able to detect prey items directly and sought to be the first to reach, handle and consume them, and also contest competition, whereby individuals actively and aggressively contested ownership of the resource (Ward et al., 2006; Webster & Hart, 2006b). This test was performed three times according to the above schedule, and was used to calculate the mean proportional prey intake of the focal fish. Immediately after testing excess chironomid larvae were added to the tank, so that all fish could feed until satiated. This served to standardize hunger levels between trials. Fish were fed again the following day, after which all uneaten prey were removed, and the fish were deprived of food for 24 hours until the next feeding trial. It is unlikely that familiarity could have had any influence upon individual prey share over such a short timeframe and previous research has shown that although levels of agonistic competition for prey items may decrease within groups of this species over a 28 day period, levels of individual prey share remain stable (Webster & Hart, 2006b).

Activity level test (Parts 1-3)

When animals enter new surroundings they face a trade-off between increasing their activity in order to gather information about their new environment, something that which may also increase their likelihood of being detected by a predator, or remaining inactive, at the cost of a potentially reduced prey intake. In this test we recorded the activity rates of focal fish in a previously unexplored test tank. Testing took place in a tank measuring $60 \times 30 \times 30$ cm, with a water depth of 27 cm and a 2 cm deep layer of 5 mm gravel. The tank was otherwise unfurnished, and was covered externally with black screening on the sides and rear. The focal fish was introduced to the centre of the tank within a 7×7 cm, 27 cm tall holding unit. This was constructed of clear, perforated plastic, allowing the fish to assimilate visual and chemical cues from the test tank. The fish was held in the unit and allowed to settle for 5 minutes, before this was removed, releasing the fish, and beginning the trial.

The trial ran for 5 minutes and point sampling (Lehner, 1996) was used at 15 s intervals (giving $N = 20$ measurements) to record whether the fish was active or whether it was stationary on the substrate. Observations were made via a slit in a black screen in order to remove observer effects. Following each trial the fish was returned to its respective tank and the water in the test tank was replaced.

Modified version of the activity level test (Part 2)

In Part 2 we used a modified version of this test, in that four additional fish were present in the test tank. These were size matched to within <1 mm standard length of the focal fish. They were obtained from a different stock tank to the focal fish and, therefore, were unfamiliar with it. They were added five minutes before the focal fish was added, and were allowed to move around the tank whilst the focal fish acclimatized for five further within the holding tower. Following the release of the focal fish its movement rate was determined using point sampling, as above. Following the completion of a trial the tank water and four additional fish were replaced.

Latency to resume foraging under simulated predation risk test (Parts 1-3)

Foraging animals are compelled to cease feeding and seek refuge or take evasive action when predators attack. Foragers face a trade-off regarding when to resume feeding following a failed attack; too soon and the predator may still be close by, too late and their rate of prey intake decreases. In this test we measured the latency of focal fish to resume foraging following a simulated attack from a fish-eating bird.

We used a test tank dived into three chambers. At one end of the tank were two 15 × 12 cm chambers situated side by side, leaving a larger 30 × 48 cm chamber in the remainder of the tank. The left-hand chamber held the focal fish, whilst the right-hand chamber received the simulated predator attack. The walls of the two smaller chambers that faced into the larger chamber were made from one-way glass, aligned so that the focal fish within the left-hand chamber could see into the larger chamber. All of the other walls were constructed from clear, regular glass and the focal fish was therefore able to see both into the right-hand chamber as well as into the larger chamber. All of the chambers contained a 2 cm layer of 5 mm gravel and were filled with water to a depth of 27 cm. The larger section was otherwise empty except in

the modified version of this test used in Part 2 and described further below. Three 10 cm strands of artificial vegetation were floated on the surface of the left-hand chamber in order to minimize stress to the focal fish.

Ten 3 mm long sections of chironomid larvae were placed across the bottom of the left-hand chamber and 5 minutes later the focal fish was added. A 100 g weight was suspended 20 cm above the container on the right. The focal fish was added to the container on the left and allowed to begin to feed. After the focal fish had consumed one prey item the weight was released and allowed to drop into the right-hand container. This caused a disturbance designed to simulate a failed attack from a fish-eating bird, and was sufficient to induce a fright response in all of the focal fish. The latency of the focal fish to resume foraging was recorded, and taken as a second measure of boldness. Following each trial the water and prey were replaced in the container on the left, and 5 minutes were allowed to elapse before the next trial was carried out (versions of this assay have been used successfully in a number of previous studies (Bell & Stamps, 2004; Ward et al., 2004; Bell, 2005).

Modified version of the foraging under simulated predation risk test (Part 2)

In Part 2 we used a modified version of this test, in that four additional fish were present in the larger chamber of the test tank. The focal fish, held in the left-hand chamber was able to see these additional fish. The additional fish were unable to see either the focal fish or the disturbance caused by the falling weight because of the one way glass. They were also unable to see the reaction of the focal fish to the falling weight, preventing them too from displaying any fright responses that might in turn have affected the behaviour of the focal fish. As above, the focal fish was allowed to begin to feed before the weight was dropped, eliciting a fright response, and we recorded its latency to resume feeding.

Use of public information test (Part 3)

In this test we quantified the use of public information of focal fish by measured the proportion of time that they spent shoaling with each of two stimulus shoals, one feeding from a high yield feeder and one from a low yield feeder. A binary choice arena was established in an experimental tank ($39 \times 17 \times 18$ cm deep, water depth 15 cm). At each end of the tank along its longest axis was an 8 cm wide stimulus chamber, separated from the central

section of the tank by screens of colourless perforated plastic (perforation diameter 0.1 cm, 5 ± 1 perforations/cm^2). This allowed the exchange of both visual and chemical cues. A 2 cm deep substrate of 0.5 cm gravel was provided in the central section of the tank and in the two stimulus chambers. Three 10 cm lengths of artificial plastic vegetation were floated on the surface in each of the stimulus chambers. These served to keep the stimulus fish from becoming stressed by providing overhead cover. On the outside of the glass two association zones were marked by vertical black lines, 2 cm from each of the stimulus chambers. This distance falls well within the range of inter-individual distances seen in free-ranging fish shoals (Pitcher & Parrish, 1993). In the centre of each stimulus chamber was a vertically positioned 2 cm diameter, 30 cm long white plastic tube. Each tube was cut diagonally across the last 3 cm of its length at a 45° angle, and positioned so that this end rested on the substrate, with the longest side of the tube facing into the test tank towards the focal fish. These served as prey delivery tubes. Positioning them in this way prevented the focal fish from seeing the uneaten prey as it was delivered to the chamber. Instead the focal fish could gauge only patch quality by observing the prey capture success of either stimulus shoal.

Three stimulus fish were added to each stimulus chamber. These were size matched to within <1 mm of each other and to the focal fish. Stimulus fish were drawn from different stock tanks to the focal fish, and were therefore unfamiliar to it. The focal fish was introduced to the centre of the tank within a 7×7 cm, 27 cm tall holding unit. This was constructed of clear, perforated plastic, allowing the fish to assimilate visual and chemical cues from the test tank. The focal and stimulus fish were then allowed to settle for five minutes. After this period prey was added to the stimulus chambers. One chamber was randomly assigned to be a high quality prey patch and the other a low quality prey patch. A single prey item was added every 10 seconds to the high quality prey patch, whilst the low quality patch received a prey item every 30 seconds. Prey consisted of a 3 mm long section of chironomid larvae. These were delivered via the prey delivery tube in 1 ml of prey conditioned water, obtained by crushing 1.5 g (wet mass) of frozen Chironomid larvae in 10 ml of tank water. In order to control for prey odour effects at the intervals when no prey was being delivered to the low quality patch, 1 ml of prey condition water alone was added at the same time as the high quality patch was receiving a prey item. These prey items were added whilst the focal fish was still being held in the holding unit. Prey cues were provided in this way

for 2 minutes before the removal of the holding unit and the release of the focal fish, which marked the beginning the trial. The trial ran for 5 further minutes, during which time prey and/or prey odour cue provision to the two stimulus chambers continued. In all trials the stimulus fish were seen to seize the prey as soon as it emerged from the delivery tube. The amount of time that the focal fish spent within the 2 cm association zone in front of the high or low quality prey patch group was recorded and used as an indicator of its use of public information (Coolen et al., 2003, 2005; van Bergen et al., 2004; Webster & Hart, 2006a).

Statistical analysis for part 1

We calculated the mean proportional prey share of the focal fish, and its movement rate as a proportion of the total trial time. These data were not normally distributed therefore non parametric statistics were used. The data collected were each used in two separate analyses. Performing multiple analyses requires that the alpha level had to be corrected in order to reduce the likelihood of making type-I errors. We therefore performed a Sidak's adjustment, reducing the alpha level for each test to 0.025. We performed Spearman Rank correlations to investigate relationships between individual activity levels and latency to resume foraging, activity levels and prey share, and latency to resume foraging, and prey share. We did this for each group size treatment, performing a total of six correlations.

Statistical analysis for part 2

Data were not normally distributed and we used non parametric statistics for the following analyses. We compared firstly the movement rates and secondly the latency to resume foraging of the focal fish from the three experimental groups using Kruskal-Wallis test with Langley post-hoc analyses Langley (1979). We then performed Spearman Rank correlations to investigate relationships between individual activity levels and latency to resume foraging within each of these groups performing a total of three correlations.

Statistical analysis for part 3

We sought firstly to determine whether the focal fish had used public information. We subtracted the proportion of trial time spent by the focal fish

shoaling with the stimulus group housed at the poor quality feeder from that spent shoaling with the stimulus group housed at the high quality feeder. We compared these values to a null value of zero using a Wilcoxon signed rank test. We then used three Spearman Rank correlations to look for correlations between these values and individual activity levels and latency to resume foraging. As in part 1, these data sets were each used in two separate analyses, so we carried out a Sidak's adjustment, reducing the alpha level for each test to 0.025.

Results

Part 1. Does boldness predict prey share and is this affected by group size?

We saw that individuals that were more active also tended to resume foraging sooner under predation risk. Spearman Rank correlations revealed that individual activity levels were negatively correlated with latency to resume foraging in both group size treatments (group size two: $N = 14, r = -0.72, p = 0.004$; group six: $N = 14, r = -0.62, p = 0.014$). Movement rate was positively correlated with prey share when the group size was two ($N = 14, r = 0.69, p = 0.007$). When the group size was six we saw a positive trend; however, this was marginally non-significant at our corrected alpha level of 0.025 ($N = 14, r = 0.60, p = 0.027$). Latency to resume foraging was related to prey share by a negative, but marginally non-significant trend when group size numbered two, due to the adjusted alpha level ($N = 14, r = -0.55, p = 0.040$). Latency to resume foraging was negatively correlated with prey share when group size numbered six ($N = 14, r = -0.76, p = 0.001$, Figure 1).

Part 2. Is individual boldness affected by social facilitation?

Focal fish in experimental group 2 where conspecifics were present in the activity level test were more active than those in groups 1 and 3, where the focal fish were tested alone (Kruskal-Wallis test: $H = 10.84; df = 2, p = 0.004$, Langley post-hoc: $p \leqslant 0.001$ in both cases). Similarly, focal fish in experimental group 3 where conspecifics were present in the latency to resume foraging test tended to resume feeding more rapidly than did those in groups 1 and 2 ($H = 12.41; df = 2, p = 0.003$, Langley post-hoc: $p \leqslant 0.001$ in both cases).
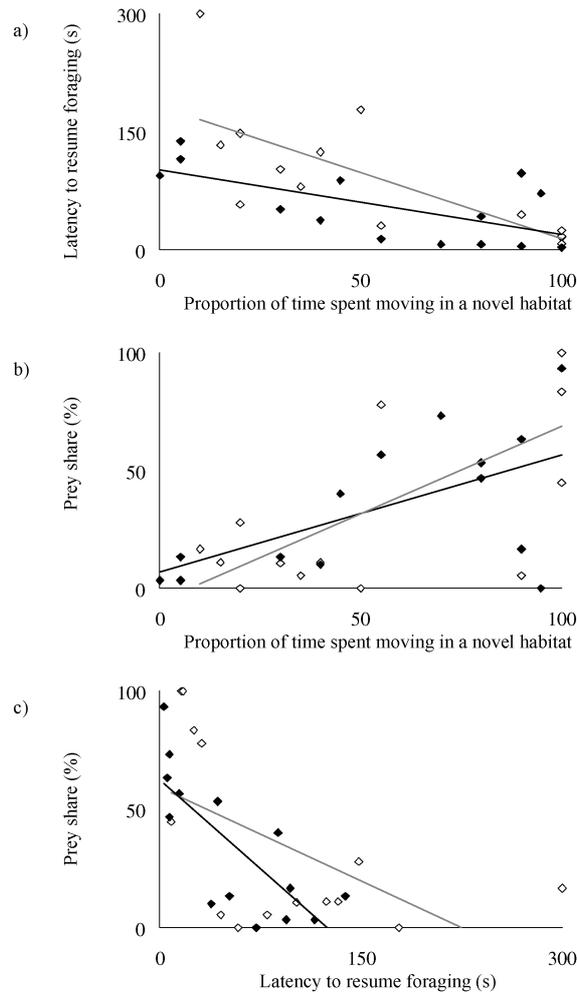
Figure 1. Scatterplots showing correlations between activity levels, latency to resume foraging following a simulated attack by a predator and proportional prey share when foraging in a group. Plot (a) shows that individuals that were more active also resumed foraging more rapidly following an attack. Plot (b) shows that individuals that were more active also consumed more prey in group competition trials. Plot (c) shows that individuals that resumed foraging more rapidly following an attack also consumed more prey in group competition trials. Focal fish that were tested in prey competition trials of group size two are shown by white points and a grey line, and focal fish that were subsequently tested in prey competition trials of group size six are shown by black points and a black line. Each data point represents one individual fish.
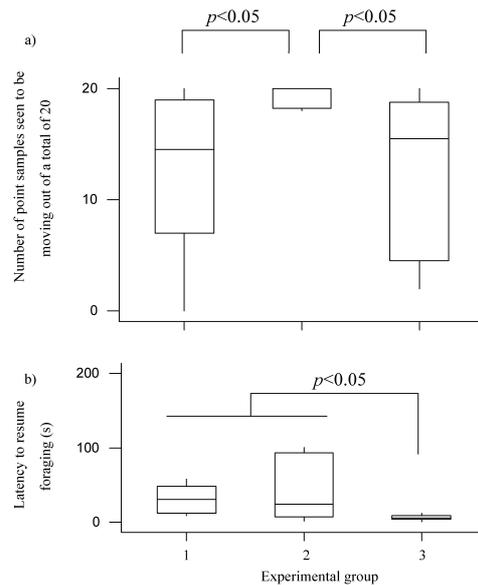
Figure 2. Boxplots showing the number of sampling instances out of a maximum of 20 spent moving (a) and the latency to resume foraging following a simulated predator attack of fish in three treatment groups (b). In each case the plot shows the median values, inter-quartile range and the 95% confidence intervals. Fish in group 1 were tested alone in both the activity level and the latency to resume foraging tests. Fish in group 2 were tested in the presence of conspecifics in the activity level test and alone in the latency to resume foraging test. Fish in group 3 were tested alone in the activity level test and in the presence of conspecifics in the latency to resume foraging test. Please note that in the plot for group 2 on graph (a) the values representing the median, upper quartile and upper confidence interval were identical.

Individual activity levels were negatively correlated with latency to resume foraging in the first experimental group where individuals were tested alone in both tests (Spearman Rank correlation: $N = 12, r = -0.60, p = 0.038$). We saw no correlations in the second ($N = 12, r = 0.10, p = 0.73$) or third experimental groups ($N = 12, r = 0.21, p = 0.35$) where conspecifics were present in the activity level or latency to resume foraging test, respectively (Figure 2).

Part 3. Is boldness correlated with the use of public information?

A Wilcoxon signed rank test revealed that focal fish spent significantly more time with the stimulus group housed next to the rich feeder ($N = 30, Z = 2.50, p = 0.012$) suggesting that they were using public information. As

in Parts 1 and 2, individual activity levels were negatively correlated with latency to resume foraging (Spearman Rank correlation: $N = 12, r = -0.81, p < 0.001$). There were no relationships however between use of public information and either activity levels or the latency to resume foraging ($N = 30, r = -0.04, p = 0.83$ and $N = 30, r = 0.05, p = 0.79$, respectively, Figure 3).

Discussion

In each of our three experiments we saw that individual fish that were more active were also more likely to resume foraging sooner following a simulated predator attack. This robust result is consistent with previous findings in the threespine stickleback and in other species (Bell & Stamps, 2004; Ward et al., 2004; Bell, 2005).

In Part 1 we saw that individual prey share was positively correlated with activity levels when group size was two, whist when group size was six this relationship was marginally non-significant.

Prey share was negatively correlated with the latency to resume foraging, both when the group size numbered six, with the relationship being marginally non-significant when group sizes were two.

This finding does not offer substantial support for our initial prediction that boldness should become uncoupled from prey share in larger groups because of social facilitation effects. Previous research has revealed that individual bold/shy behaviour directly influences prey share in social foraging situations, and that this can have long term effects upon growth rates (Ward et al., 2004). It is possible that though the boldness of individual fish might be enhanced by increasing group size, the rank order of differences in boldness between individuals might remain unchanged. If this is the case, then although individuals might exhibit behavioural plasticity in response to social context, we would expect to see persistent correlations between behavioural responses in different contexts. Another potential explanation relates to winner and loser effects, which allow individuals to assess their chances of winning or losing contests based respectively upon their past record of victories or losses (Barnard & Burk, 1979; Hollis et al., 1995). Work by Hollis et al. (1995) on aggressive interactions between blue gouramis (*Trichogaster trichopterus*) revealed that previously successful fish went on to win more
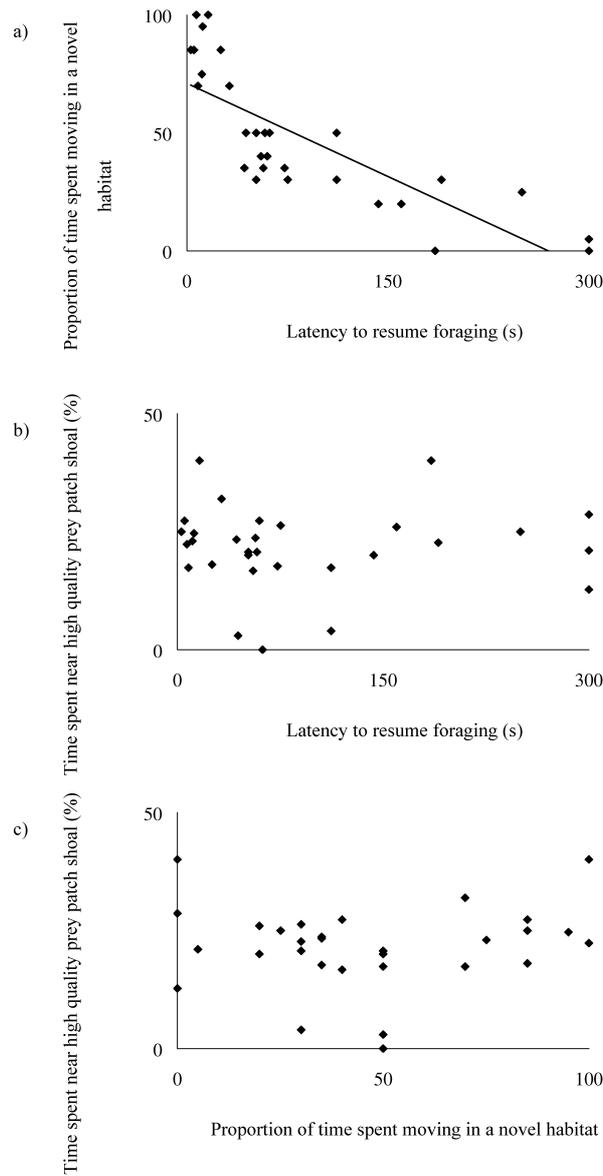
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Figure 3. Scatterplot (a) shows that individuals that were more active also resumed foraging more rapidly following an attack. Scatterplots (b) and (c) reveal no correlation between the use of public information and either the latency to resume foraging following an attack or activity levels. Public information use was inferred from the net proportion of time that the focal fish spent shoaling with a stimulus group that was feeding from a rich prey patch in a binary choice test. Each data point represents one individual fish.

contests whilst unsuccessful fish persisted in losing contests. It is conceivable that winner and loser effects could be associated with boldness since bolder individuals frequently out-compete shyer ones in prey contests (Ward et al., 2004; Webster et al., unpublished data). Further research in this area would be useful. Finally, engaging in competition has also been shown to increase the risk of predation to participants (Jakobsson et al., 1995; Slotow & Paxinos, 1997), for example, by increasing their conspicuousness to, and by reducing their capacity to detect nearby predators. In this context competition could be viewed as a trade-off between potentially receiving a greater share of a contested resource versus exposure to greater risk of predation. The avoidance of such risk, at the cost of reduced prey share, is consistent with the shy behavioural disposition. The results of this part of our study may go some way towards explaining how significant disparity in prey share can persist within stable groups of animals (e.g., Metcalfe & Thomson, 1995; Webster & Hart, 2006b).

In Part 2 of our study we found significant effects of group size upon boldness. Here we saw that the correlation between individual activity levels and latency to resume foraging, readily apparent in the control treatment when focal fish were tested alone in both contexts, was absent when additional conspecifics were present in either one of the two tests. The links between larger group size and greater social facilitation effects are broadly understood and the theory is well supported by numerous empirical studies (reviewed in Krause & Ruxton, 2002). In any given situation, individuals may make assessments of the levels of risk that they are prepared to incur. Per capita risk is lower when in a larger group and this potentially allows individuals in such groups to engage in risky behaviours to a greater extent before unacceptable thresholds of risk are reached. Accordingly, in our study we saw that focal fish were more active, and resumed foraging more rapidly in the presence of conspecifics, relative to others that were tested alone. Few studies have made the link between boldness and social facilitation effects however, and indeed many previous studies have focused on the bold/shy responses of single animals, often restoring the social context only to look at aggressive or competitive interactions. One study to consider the social aspect in relation to boldness, that of Magnhagen & Staffan (2005), showed that shy Eurasian perch (*Perca fluviatilis*) behaved more boldly when they were embedded within shoals consisting only of other shy individuals, compared to when they were initially held in shoals containing a mixture of bold

and shy conspecifics. Their finding suggests that there may be an influence not only of the presence of other individuals upon the behaviour of a given animal, but also a more subtle effect of group composition.

Part 3 of our study revealed that although test fish were using public information, there was no correlation between boldness and public information use, in disagreement with our initial prediction. Research by Coolen et al. (2003) found that ninespine sticklebacks (*Pungitius pungitius*) used public information to a greater extent than did sympatric threespine sticklebacks. Godin & Clark (1997) reported that ninespine formed more cohesive shoals and inspected predators to a lesser extent than did threespine from the same population. Of these two closely related species, threespines generally possesses longer dorsal and pelvic spines and more robust bodily armour than do ninespines, and this is seen as an adaptive countermeasure to predation risk. It has been suggested that the less armoured and therefore more vulnerable ninespine stickleback should minimise predation risk through the adoption of shy-type behavioural strategies, such as greater reliance upon social information, whilst the armoured threespine stickleback is better equipped to gather and use private information. Interestingly, research by Webster & Hart (2006a) revealed that threespine sticklebacks gathered from a different population both to that studied by Coolen et al. (2003), and to that used in this study, also used public information. Further research by these authors (unpublished data) has shown that threespine and ninespine sticklebacks from a sympatric population did not differ in their mean behavioural responses in a range of contexts, despite obvious differences in armour morphology. These results suggest that intra- and interspecific patterns of social information use vary between populations under the influence of as yet undetermined pressures, most likely including predation risk and environmental instability. Clearly, further research in these areas is required.

Two hypotheses, the constraint and the adaptation hypotheses, have been developed to explain the presence and prevalence of bold/shy behavioural variation within and between populations. The constraint hypothesis argues that certain behavioural responses are controlled by the same underlying hormones or genes and are therefore correlated with one another. As a consequence, individuals should exhibit similar levels of boldness across different contexts, since the uncoupling of behaviours would require substantial mutation or evolution of the underlying genetic or endocrinal architecture. The adaptation hypothesis states that behaviours should become correlated only

when it is adaptive for them to do so, whilst associations between behaviours that lead to a decrease in fitness should be selected against (Cheverud, 1996; Bell & Stamps, 2004; Bell, 2005). As such, correlation between behaviours should vary between different populations, under the influence of the prevailing selective pressures acting upon each. These two theories oppose one another, since the former assumes the restriction of selection, whilst the latter is a consequence of it. The results of our study demonstrate that at least some bold/shy behavioural responses are context specific, in that individuals that behave shyly when alone in one situation may act more boldly when in the presence of conspecifics, a more naturally realistic situation for social species. This is consistent with the predictions of the adaptation hypothesis and contrary to those of the constraint hypothesis. Related to this, if social context influences boldness then making inferences about the bold/shy behaviour of social animals in nature using data derived from tests of single individuals may be misleading. Context specificity as a determining influence upon bold/shy behaviours and behavioural correlations has previously been demonstrated in species from a range of taxonomic groups including mammals (Reale et al., 2000), reptiles (Lopez et al., 2005), fish (Coleman & Wilson, 1998) and cephalopods (Sinn & Moltschaniwskyj, 2005). Furthermore, individual variation in boldness has been seen to be correlated with body size (Brown et al., 2005; Lopez et al., 2005), morphology and health (Lopez et al., 2005) suggesting that physiology may play a role. As of yet neither of the constraint or the adaptation hypothesis has been rigorously tested. Future work should aim to definitively test these hypotheses by targeting multiple populations of a given study species that together are subject to a range of quantifiable selection pressures. By accounting for rates of mutation and genetic drift, such a study could confirm or refute either of these hypotheses, and would give us greater insight into how bold/shy axes come to exist, and into those selective agents that determine how the members of a population are distributed along it.

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