



Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks

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The grouping behaviour of fish is a widespread phenomenon of high biological significance but little is known as to how consistent individual behavioural differences may affect group joining preferences. When given the option to join either a shy or a bold shoal of three-spined sticklebacks, *Gasterosteus aculeatus*, both shy and bold individuals showed a strong preference for associating with bold fish. Personality type interacted with individual hunger levels to affect the extent of association, suggesting important strategy variation by focal fish in a competitive foraging environment. Furthermore, shoals modified their behaviour in relation to the focal individual. Individual behavioural differences were shown to have a complex role in influencing association preferences as well as driving previously unrecognized behavioural modifications in foraging groups.

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The shy–bold continuum is a fundamental axis for human behaviour and also a relatively stable behavioural component for many other species (Wilson et al. 1994), leading to boldness becoming one of the most commonly studied personality traits in animals (Bell 2007). Differences in boldness, which defines the propensity of individuals to take risks (Reale et al. 2007), seem to reflect a trade-off between growth and mortality (Stamps 2007) and, since boldness levels have also been shown to vary between populations experiencing different rates of predation (Brown et al. 2005), may have fitness consequences depending on environmental context (Brown et al. 2007). Until recently, most work on animal personality considered the individual in isolation, but over the last couple of years the focus has shifted towards the potential role of personality in shaping group behaviour. Personality has been suggested to influence the degree of interactions within social networks (Pike et al. 2008), and boldness differences may affect leadership potential (Leblond & Reeb 2006; Harcourt et al. 2009).

Whether to join a group or not depends on the balance of the costs and benefits of synchronizing one's activities with other

individuals. Group living can bring advantages in terms of reduced predation risk, mostly through dilution and confusion, as well as an increase in foraging efficiency. At the same time, being different from other individuals (the 'oddy effect') might increase the likelihood of an individual being targeted by a predator or increase competition with other group members which can be costly (Krause & Ruxton 2002). It may also force individuals to adopt behavioural rhythms that are suboptimal (Ruckstuhl et al. 2006) and thus it is important to select the appropriate group to join. Work on fish has indeed shown that individuals take into account a multitude of factors when selecting a group to join. Fish tend to prefer larger shoals that provide more safety from predators (Krause et al. 1997, 1998; Buckingham et al. 2007), tend to match their own phenotype with the phenotype of other group members (e.g. Rosenthal & Ryan 2005) and can be influenced by activity levels (Pritchard et al. 2001). Hunger levels can also play a role, with hungrier fish spending less time in a large group (Krause 1993), preferring to associate with better fed individuals (Krause et al. 1999) or being willing to risk greater levels of oddity when foraging (Reeb & Saulnier 1997). Given that these various individual characteristics can affect group joining decisions, we would expect personality to be a potential factor that would influence shoal choice. Evidence suggests that boldness may be associated with fitness characteristics such as exploration, activity and body weight (Brown et al. 2007). However, it is not known whether boldness

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influences the decision to join a social group and what impact additional variation in hunger may have.

Individual boldness differences in three-spined sticklebacks, *Gasterosteus aculeatus*, have been recognized for many years (Huntingford 1976) and are known to correlate across contexts (Ward et al. 2004), making this group-living species a particularly useful model system to investigate the effects of behavioural differences on shoal joining preferences. In this study, we used a laboratory-based population of three-spined sticklebacks to examine how boldness affects shoaling preferences. We created stimuli shoals of either four bold or four shy fish and tested focal individuals, both bold and shy, for a tendency to join either group. Since an individual's nutritional state can affect its perception of the costs and benefits of joining a shoal of potential competitors (e.g. Krause 1993; Reeb & Saulnier 1997; Krause et al. 1999), we tested both fed and hungry fish of both personality types to see whether state interacted with personality.

METHODS

Study Organism and Equipment

Stocks of three-spined sticklebacks were collected with sweep nets from the Histon and Swaffham Bulbeck areas of the River Cam, U.K. during 2007. They were transported to the laboratory in large buckets and immediately transferred to large glass aquaria where they were kept at 17 ± 1 °C on a 10:14 h light:dark regime for at least 1 month before being used in experiments. This study is part of a series of experiments that were approved under a non-regulatory procedures framework by the Animal Users Management Committee of the University of Cambridge. Fish became part of a laboratory population and will be released at their collection location at the end of the project.

To avoid familiarity affecting shoaling decisions (Griffiths & Magurran 1997), sticklebacks used in stimuli shoals were taken from wild populations that were different from those used to obtain focal individuals. The two populations were kept in separate aquaria which were lined with gravel, contained a number of plastic plants (Hagen, Montreal, Canada) and used dual filtration systems (under-gravel and external Hagen filters). Sticklebacks were not sexed, but the standard laboratory temperature used prevented them from coming into breeding condition (Borg et al.

2004). Fish used in experiments were of similar length (45 ± 5 mm from tip of snout to caudal peduncle) to remove size as a potentially confounding variable (Ranta et al. 1992). All sticklebacks were fed to satiation daily on frozen bloodworms (chironomid larvae).

Boldness Assessments

In the first part of this study, we moved fish to be tested for boldness into individual holding tank compartments (10×40 cm and 30 cm high). Each holding tank contained six such compartments, separated by transparent plastic partitions that allowed individual fish identification but minimized any stress caused by isolation. Under-gravel filtration operated over the whole system and each compartment had a plastic plant at one end and a white plastic tile (approximately 1.5 cm²) on which we delivered food at the other. Fish to be used in shoals were tested first (see below for details), assigned to groups according to boldness, and placed back in the larger aquaria before focal individuals were tested.

During training and observation, we transferred fish to experimental tanks (30×90 cm and 30 cm high). The walls of these were covered with black opaque plastic to prevent external movement from being seen by the fish. Each tank was partitioned lengthwise with an opaque barrier to form two long compartments so that fish had a narrower lane within which to move. The tanks were lined with white gravel in such a way that a slope was created from a deep end with water depth of 12 cm to a shallow feeding end with water depth of 2 cm. We placed two plastic plants (Hagen) in the deep end of each compartment and a feeding tile similar to those used in the holding tanks at the other end. A small vertical white plastic screen (8×8 cm visible above the gravel) was put in front of each feeding tile to prevent fish at the deep end of the tank from seeing food at the shallow end (Fig. 1a). Water was aerated when fish were not present in the tank. We recorded fish behaviour using a Sony DCR-35E digital video camera mounted directly above each tank and aligned to give a full view of the whole tank.

We collected data in cycles of 5 days, with fish spending 1 h each weekday in the experimental tanks. The first 3 days of a cycle were used for training purposes. Before any hour-long session, a single medium-sized bloodworm was placed onto the feeding tile in each tank. We then moved fish individually from a holding tank to the

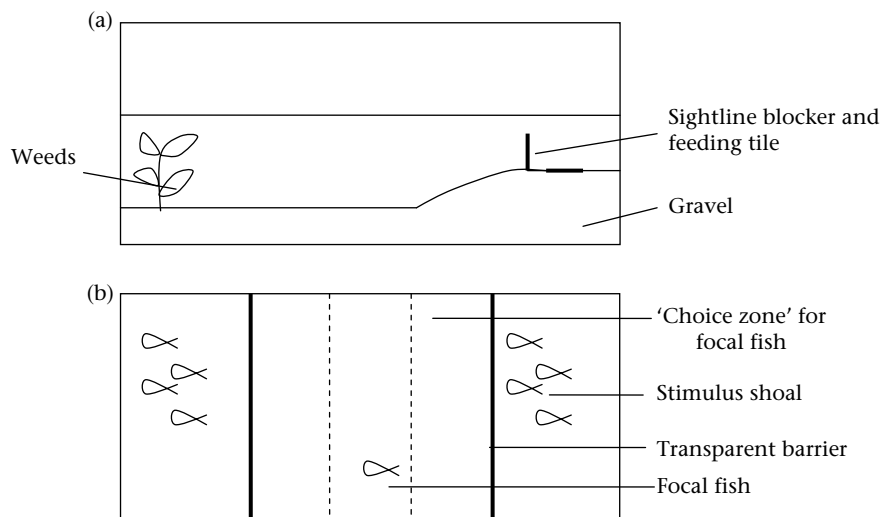


Figure 1. Schematic representation of the experimental tanks: (a) lateral view of boldness assessment tank; (b) view from above of shoal choice assessment tank.

deep end of an experimental tank. After 30 min we inspected the tank and a second bloodworm was placed on the tile to encourage further foraging if the first had been consumed. Any fish that failed to consume two bloodworms on any given day was fed in the holding tanks after training to ensure that all received and ate two bloodworms each day during the cycle.

After 3 days, fish that had failed to eat any bloodworms during training were excluded from the experiment and the rest then underwent boldness assessments. For 1 h on each of the following 2 days, we videoed fish in the experimental tank without any food (since feeding could reduce further foraging incentive during the trials) and scored the amount of time a fish spent out of the safe resting area (i.e. full body out of the artificial weed) using a custom-designed data logger. For the purpose of this experiment we defined fish as being 'bold' if they were seen to forage for at least 40% of the observation time and 'shy' if found to forage for less than 5% of the time. Although boldness scores follow a continuum and fish spent anything between 1% and 82% of time out of cover, the definitions we used here gave the most sensible distribution to look at contrasting behaviours; owing to the spread of scores obtained when testing our populations, shy fish represent the lower 37% of the total distribution, and bold the upper 24%. Fish were fed a single bloodworm per day upon being returned to the holding tank.

Shoal Choice Tests

Having assessed boldness levels for all test fish, we were able to create stimuli shoals containing either four shy or four bold fish; these shoals were allowed to settle at either end of an experimental choice tank (40 × 60 cm and 30 cm high) for 10 min (Fig. 1b). Tank sides were again covered in black opaque plastic to prevent the fish from seeing external movement. We used two transparent barriers to divide the tank into three sections with a central compartment of width 30 cm and two equal end compartments of width 15 cm. We then introduced a focal fish, either shy or bold, to the central compartment of the tank via a transparent cylinder (8 cm diameter) and allowed it to observe the shoals for 5 min. We then gently removed the cylinder to leave the focal fish in the central tank compartment. The focal fish was able to swim freely between the shy and bold shoals for 10 min. We recorded the initial direction choice made by the fish as well as the total amount of time spent in a 'choice zone' near either shoal. These zones referred to the two 10 cm end sections of the central compartment nearest to either shoal. The central third of the middle compartment was left as a 'neutral zone' and time spent here was not considered to reflect an active preference for either shoal (a similar method for indicating shoal preferences to that used by Evans et al. 2007). We also measured the activity levels of both groups and individuals. For stimuli shoals, we picked a fish from the group at random every 2 min during the observation period and recorded the number of times it crossed the centre of the shoal compartment. For focal individuals, we noted the number of times the fish crossed the centre line of the tank.

We repeated the test when stimuli shoals were on opposite sides of the tank to control for any directional bias and then repeated the whole experiment when focal fish were hungry, having not been fed for the previous 24 h. Fish for stimuli shoals were taken at random in each trial from a larger stock of 20 bold or 20 shy fish and the position of the shy shoal (left or right) was randomized across all tests. None of the shoal fish were used as test fish. In total, we tested 32 shy and 21 bold focal fish in the choice tanks, each being observed when fed on a normal routine and also following a 24 h period of food deprivation.

Data Analysis

For all our analyses, we used generalized linear mixed models which accounted for the fact that individual fish were tested more than once. As the random effects were not significant in any of the models (estimated variance component < 0.01, $P > 0.2$), we dropped it and ran a generalized linear model (GLM, Crawley 2002). In such cases, the results from the latter are presented, but we also checked that keeping the random factor in the model would not qualitatively affect the results.

We first tested for a preference in associating with either shoal. The proportion of time spent with the bold shoal out of the time spent with either shoal (i.e. excluding time spent in the neutral zone) was used as a response in a model with the interaction of personality and hunger status as predictors. Proportion data were arcsine square-root transformed. We tested for preferential association with bold shoals overall by checking whether the intercept differed significantly from arcsine ($\sqrt{0.5}$), that is equal time spent with either shoal, when the reference levels of the factors were set to the ones that gave the lowest proportion of time spent with the bold shoal. We also investigated the initial choice made by focal fish by building a model with first choice (bold/shy) as a binary response using a binomial error structure and the interaction between boldness and hunger status as predictors.

We were also interested in whether personality and hunger status might affect the focal fish's tendency to shoal. To test this, we fitted a model with the proportion of time spent shoaling with either shoal out of the total experimental observation time (arcsine square-root transformed) as a response and the interaction between personality and hunger status as predictors. We built similar models with the time taken by a fish to make its first choice and the total amount of time spent shoaling as response variables.

Finally, we investigated activity levels by building models (for both focal fish and stimulus shoals) with the number of crossings as a response with a Poisson error structure and the interaction between personality and hunger status as predictors. We also looked for an effect of focal fish presence on the shoals by testing time spent with a shoal against shoal activity.

RESULTS

Focal fish, irrespective of their personality and hunger status, showed a preference for spending time with the bold shoal (test for intercept of GLM being different from the expected value for no

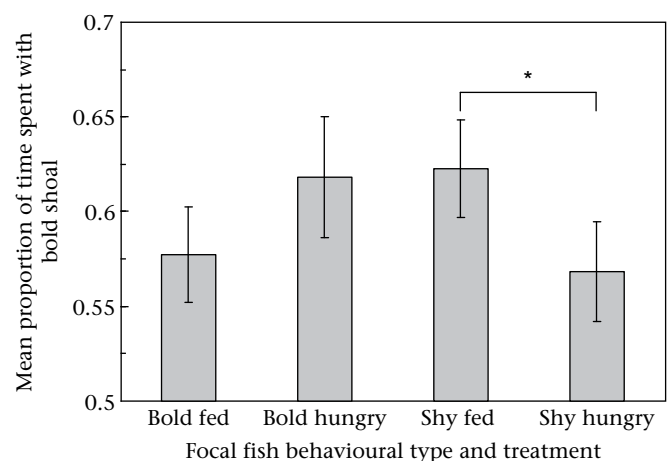


Figure 2. Mean proportion of time \pm SE spent by hungry or fed focal fish with the bold shoal. * $P < 0.05$.

preference, that is, $c \neq \arcsin(\sqrt{0.5})$: $t_{208} = 2.459$, $P = 0.015$). There was also a significant interaction between personality of focal fish and hunger level influencing the amount of time spent in the zone nearest the bold shoal (GLM: $F_{1,208} = 4.81$, $P = 0.029$; Fig. 2), mostly caused by a decrease in the preference for the bold shoal by shy focal fish when hungry compared to when fed (significant posthoc comparison, $P = 0.042$; all other pairwise comparisons were nonsignificant). While fish preferred to spend time with the bold shoal overall, they did not show any preference for which shoal they first joined at the beginning of the experiment (GLM: $F_{1,211} = 1.23$, $P = 0.22$). Personality and hunger did not predict the total time spent shoaling rather than remaining in the middle 'neutral' zone (personality: $F_{1,211} = 0.72$, $P = 0.396$; hunger: $F_{1,211} = 0.03$, $P = 0.86$) or affect the speed at which an initial decision was made (personality: $F_{1,211} = 2.22$, $P = 0.137$; hunger: $F_{1,211} = 0.78$, $P = 0.38$).

Analysis of focal fish movement showed that, while all fish swam freely between shoals, bold fish were more active than shy fish, crossing the middle line significantly more often (mean activity of bold fish \pm SE = 17.7 ± 0.9 ; mean activity of shy fish \pm SE = 13.7 ± 0.6 ; $F_{1,211} = 14.45$, $P < 0.001$); hunger had no such effect ($F_{1,211} = 0.94$, $P = 0.33$). Similarly, fish in bold shoals were more active than individuals in shy shoals (mean activity of bold shoal \pm SE = 15.8 ± 0.5 ; mean activity of shy shoal \pm SE = 10.6 ± 0.3 ; $F_{1,422} = 101.22$, $P < 0.001$). We found that not only were bold shoals significantly more active ($F_{1,422} = 101.22$, $P < 0.001$) but, as illustrated in Fig. 3, activity level of shoals also varied in relation to the focal individual with which they were interacting ($F_{1,422} = 7.38$, $P = 0.007$). Shoal activity level was not affected by the interaction between shoal personality and focal fish personality ($F_{1,422} = 0.62$, $P = 0.431$) nor by the time spent by focal fish with the shoal ($F_{1,422} = 2.17$, $P = 0.14$).

DISCUSSION

Regardless of personality or hunger state, focal fish preferred to associate with groups of bold individuals rather than shy shoals. This result is somewhat surprising, as it suggests that matching one's own phenotype is not a major factor in choosing with which shoal to associate. On the other hand, recent work on guppies, *Poecilia reticulata*, by Dyer et al. (2009) found that bold shoals have higher foraging success than shy shoals, so focal fish might be trying to associate with the shoal most likely to find food. The main visible difference between the bold and the shy shoal was in their activity levels, which were significantly higher for the former, and fish have been suggested repeatedly to prefer more active shoals (Reebs & Saulnier 1997; Pritchard et al. 2001; Gomez-Laplaza

2006). However, none of these studies explicitly considered the possibility that the measured preference for activity levels might have been the result of phenotype matching. For example, Pritchard et al. (2001) 'created' a low-activity shoal by cooling down one of the tank compartments, while the focal fish was kept at room temperature together with the high-activity shoal. In our experiments, in which focal fish differed in their activity levels, bold shoals also consistently showed higher activity levels than shy shoals and it is not possible to disentangle these two variables fully; it has been suggested that activity level may even be a behavioural syndrome in its own right (Moretz et al. 2007). More active shoals may provide a stronger visual stimulus for a solitary fish seeking a shoal with which to associate. This explanation would also suggest that a fish's first choice should be to associate preferentially with the more active, bold shoal which was not the case in our experiments. However, the first choice in our set-up might be a somewhat artificial response, as the focal fish was forced to be on its own, and might have simply joined any shoal as long as it meant not being alone. All fish spent most of the observation period associating with a shoal rather than swimming by themselves, suggesting perceived predation pressure was an important determinant of their behaviour (Magurran 1990).

More active shoals have also been argued to be attractive because activity levels can indicate anticipation of food (Reebs & Gallant 1997). While in some species swimming speed has been shown to be correlated with hunger (Mikheev et al. 1992), we failed to find such an effect in sticklebacks suggesting activity is inherently related to boldness (at least in our set-up). Furthermore, hungry shy fish showed a significantly lower preference for shoals composed of bold individuals than their fed counterparts, suggesting that activity levels are unlikely to be used as a signal of food availability. The difference in preference between hungry and fed shy fish suggests that the individuals in the bold shoal are seen as potential competitors by shy individuals. If the focal fish were well fed, this was not an issue, but when the shy fish were hungry, they started spending more time with the shy shoal, members of which were less likely to be aggressive, superior competitors. No significant difference in preference was observed between bold fish with different hunger states, supporting the interpretation that fish modify shoaling preferences based on the level of competition for gaining food (Hensor et al. 2003).

Observations of shoal activity showed that groups modified their behaviour in relation to that of the focal individual; previous work has indicated that fish are capable of varying their shoaling behaviour in relation to environmental context (Sogard & Olla 1997; Hoare et al. 2004). While one may argue that this provides each focal individual with a slightly different choice to make, the difference between the two shoals appears to stay distinct as both groups modified their activity levels by similar amounts (Fig. 3). The stimulus for such behavioural modification in our set-up seems to be provided by fish simply being in the same tank, as time spent by the fish in close proximity to the shoal did not affect activity levels. Bold shoals were intrinsically more active but both groups showed higher activity levels when joined by a bold fish than when joined by a shy individual. One possibility is that the shoal responded to the addition of a new individual by finding a 'compromise' level that avoided the 'oddity' effect (Theodorakis 1989). However, this might predict that being joined by a bold fish would have a greater impact on a shy shoal and we found no significant interaction between personalities in relation to shoal activity level; both shoal types increased activity in a more uniform manner when joined by a bold fish (Fig. 3). Alternatively, the change might be seen as a competitive response; fast-moving individuals can cover the foraging area more quickly which may stimulate greater group activity when joined by a bold fish but

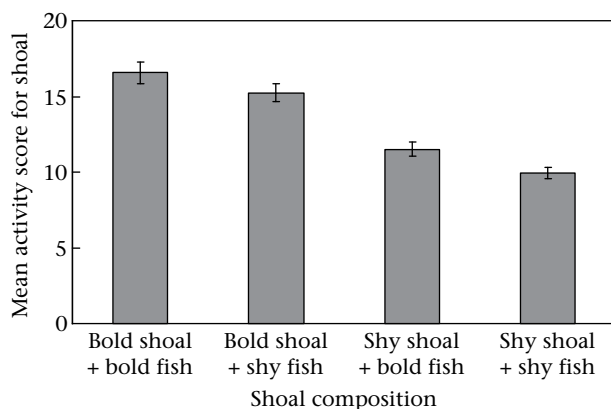


Figure 3. Mean activity \pm SE of bold and shy shoals in trials with both bold and shy focal fish.

result in lower activity and less need to compete in terms of energy expenditure when the group is joined by a shy fish.

We have shown that personality traits can influence association preferences based on individual needs as well as drive behavioural modification by foraging groups. While boldness levels have a clear effect on shoal joining preferences, it is also a complex one, and the interaction with hunger illustrates nicely trade-offs that individuals with different behavioural characteristics face when considering competitive foraging and predation risk. Our results show that individual behavioural differences may play an important but previously unrecognized role in group behaviour; with so many group-living species showing evidence of a shy–bold behavioural continuum (Wilson et al. 1993; Verbeek et al. 1994; Cote & Clobert 2007), understanding the influence of such variation across aggregations is a key area for further study.

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