Shoal composition determines foraging success in the guppy

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The composition of an animal group can impact greatly on the survival and success of its individual members. Much recent work has concentrated on behavioral variation within animal populations along the bold/shy continuum. Here, we screened individual guppies, *Poecilia reticulata*, for boldness using an overhead fright stimulus. We created groups consisting of 4 bold individuals (bold shoals), 4 shy individuals (shy shoals), or 2 bold and 2 shy individuals (mixed shoals). The performance of these different shoal types was then tested in a novel foraging scenario. We found that both bold and mixed shoals approached a novel feeder in less time than shy shoals. Interestingly, we found that more fish from mixed shoals fed than in either bold or shy shoals. We suggest that this can be explained by the fact that nearly all the cases where one fish was followed into the feeder by another occurred within mixed shoals and that it was almost always a shy fish following a bold one. These results suggest clear foraging benefits to shy individuals through associating with bold ones. Surprisingly, our results also suggest potential foraging benefits to bold individuals through associating with shy individuals. This study highlights a possible mechanism by which interindividual variation in behavioral types is maintained in a population. *Key words:* behavioral variation, boldness, foraging, personality, producer–scrounger, social environment. *[Behav Ecol 20:165–171 (2009)]*

Τhe composition of an animal group may impact greatly on the survival and success of its members. It is generally believed that the benefits of grouping are greater where individuals are phenotypically and behaviorally similar (Landeau and Terborgh 1986; Ranta et al. 1994; Ward et al. 2002). Consequently, groups are often assorted by factors such as body length, coloration, sex, or parasite status (see Krause and Ruxton 2002); however, considerable variation can exist within single-species groups (Wilson 1998), particularly in behavior. Individuals may show consistent variation through time or across contexts for a variety of important behaviors, such as boldness, aggressiveness, activity levels under predation risk, and exploratory behavior. This has been referred in many ways including behavioral type (BT) (Sih and Watters 2005), personality (vanOers et al. 2005), and coping style (Koolhaas et al. 1999).

Behavioral variation along the bold/shy continuum is receiving an increasing amount of attention. This behavioral axis has been identified for a wide range of taxa including mammals (Svartberg 2002; Armitage and Van Vuren 2003), birds (Dingemanse et al. 2004; de Azevedo and Young 2006), fish (Huntingford 1976; Wilson et al. 1993; Coleman and Wilson 1998; Sneddon 2003; Brown et al. 2005), cephalopods (Sinn 2006), and crustaceans (Rochette et al. 2001). Boldness can be broadly defined as a willingness to accept a higher degree of risk in return for potentially greater returns in terms of foraging or mating (Ward et al. 2004), with bold individuals characterized by more risk-prone behaviors such as being quicker to approach novel objects (Wilson et al. 1993; Frost et al. 2007) or consume novel food items (Wilson et al. 1993; Magnhagen and Staffan 2003), being more likely to inspect potential predators (Dugatkin and Alfieri 2003), spending more time in open habitats (Sneddon 2003; Westerberg et al. 2004; Magnhagen and Staffan 2005), and having a greater tendency to explore

(Magnhagen 2007). Consequently, it is reasonable to assume that bold individuals are more likely to find patchy or ephemeral food patches. There must, however, also be costs associated with being bold otherwise shyness would not persist (Wilson et al. 1993, 1994). Bolder individuals are likely to suffer an increased risk of predation through taking more risks than shyer individuals (Ward et al. 2004; Bell and Sih 2007). It is also possible that the food discoveries of bold individuals may be exploited by shy individuals.

The fitness of a BT is known to be influenced by environmental conditions (Sih et al. 2003; Dingemanse et al. 2004). Centrally to game theory, however, the mix of BTs within a group will also influence the fitness of each type (Maynard Smith 1982). Previous studies have found an influence of the social composition of a group (in terms of the mix of BTs) on the expression of individual behavior within the group (Magnhagen and Staffan 2005; Sih and Watters 2005). Sih and Watters (2005) demonstrated that the mix of BTs in groups of water striders, *Aquarius remigis*, in terms of aggression and activity levels influenced the mating success of males. Thus, it is reasonable to predict that the mix of bold and shy individuals could affect other aspects of individual fitness such as foraging success.

In this study, we investigate the effects of individual boldness and social environment on foraging success in the guppy. Budaev (1997) studied personality in the guppy, finding variation in individual behavior that was consistent over time and between contexts. First, we screened individual guppies for boldness by measuring their time to resume moving after a simulated aerial predation event. Second, we constructed shoals consisting of 4 individuals, differing in the proportion of bold and shy fish. Finally, we looked at the performance of the different shoals in a novel foraging task. We predict that bold individuals will show an increased propensity to explore and innovate, and thus, groups of bold individuals should show enhanced foraging success. In mixed groups, containing both BTs, shy individuals may be able to exploit the enhanced food-finding ability of bold individuals, or alternatively, their presence may constrain the behavior of the bold individuals.

MATERIALS AND METHODS

Study site and holding conditions

Guppies were captured from the lower stretches of the Aripo River in the Northern Mountain Range of Trinidad (grid reference: 10°40′ N, 61°14′ W) during June 2006 between 0900 and 1600 h using a 2-m seine net. The lower Aripo is considered to be a high predation site for the guppy as it coexists here with high numbers of its main fish predators, including the Pike Cichlid, *Crenicichla* spp. (Magurran 2005; Croft et al. 2006). All fish were caught from pools within the same 3-km stretch of the lower Aripo on 4 separate occasions each separated by approximately 1 week. On each catching trip, we walked down the same section of the river, seining each suitable pool that was encountered until at least 60 females between 23 and 35 mm in length (standard length) had been captured. This always required seining at least 20 different pools. Consequently, although there may have been prior associations between a small number of our fish, we consider this to be negligible and highly unlikely to affect our results. The fish were taken back to the laboratory (at the University of the West Indies, St Augustine, Trinidad), and females of 23–35 mm length (standard length) were selected. All other fish were returned to the river close to the location of capture after the investigation. In total, 257 females (mean length ± standard deviation: 28.80 ± 2.82) were used in the study. To standardize the time period between the fish arriving in the laboratory and being used in the experiment, 60–70 individuals were kept at any one time, and the experiment was repeated 4 times with approximately 1 week between each repeat. After capture and sorting, females were placed into a large holding tank (length [l] × height [h] × width [w] = 76 × 46 × 46 cm, water depth = 14 cm) and fed at the surface twice daily on freeze-dried bloodworm, *Chironomus* spp.

Marking

All individuals (60–70 fish each time) were anesthetized using tricane methanesulfonate and given individual identity marks using a visible implant elastomer injected in the dorsal epidermis (for details, see Croft et al. 2003). Standard length was also measured and recorded for each individual. After marking, the fish were returned to their holding tank and allowed to acclimatize for 12–16 h before being screened for boldness.

Boldness screening

Two test fish were screened for boldness simultaneously in 2 separate sections of the same tank (l × h × w = 90 × 30 × 30 cm, water depth = 14 cm; Figure 1 inset). The test tank was split into 3 equal sections (l × h × w = 30 × 30 × 30 cm) using 2 opaque plastic partitions (l × h × w = 30 × 18 × 0.1 cm). The 2 outside sections were used for boldness screening. A cylindrical glass container (height × diameter = 16.5 × 8.5 cm) was placed at the edge of each of the 2 test compartments. Each container held a stimulus shoal consisting of 3 females, each from different size categories (1 fish of 23–27 mm body length, 1 of 28–31 mm, and 1 of 32–35 mm), to minimize any potential effects of size differences between test fish and stimulus shoals. As guppies are a highly social species in the wild, we included a stimulus shoal to more closely reflect natural conditions and to minimize stress. Before each day of screening, the stimulus shoals were habituated to the fright stimulus through repeated exposure (at least 30 times at 1-min intervals) until they all resumed movement almost immediately (less than 1 s) after an exposure. Each stimulus shoal was used for half of the fish tested in any one day (ca., 2 h of testing) and then placed in a holding tank and not used again.
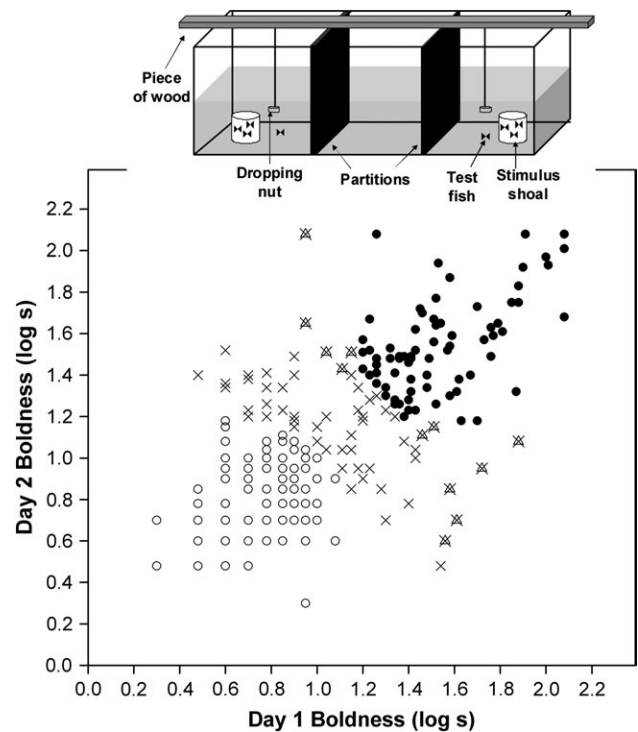

Figure 1
Relationship between the time taken to recover after the fright stimulus by each individual (log s) on day 1 and day 2 of testing. Hollow circles represent fish that were defined as bold. Crosses represent fish defined as intermediate and therefore not used in further testing. Filled circles represent individuals defined as shy. Crossed triangles represent those individuals which qualified as bold or shy by their mean boldness score but whose boldness scores were very inconsistent over the 2 days of testing and so were not used in further testing. (Inset) Setup used for boldness screening.

Two test fish were captured at a time from their holding tank using a dip net and placed into individual glass beakers containing water also taken from the holding tank (h × depth [d] = 12 × 9 cm). The identities of the 2 individuals were recorded, and they were simultaneously released, one into each compartment of the test tank by gently tipping their beakers.

A single observer (J.R.G.D.) was seated a distance of approximately 1.5 m from the test tank with the tank at eye level. The test fish were allowed a 3-min recovery and acclimatization period, following the disturbance of being moved and released into a new tank. At the end of the 3-min period, the majority (254/257 fish) of test fish were swimming freely and shoaling with the stimulus shoals. Occasionally (3/257 fish), the test fish would be frozen or behaving erratically (fast bursts of movement) after the 3-min period, in which case they were removed from the test tank, returned to a separate tank, and excluded from further testing.

At the end of the 3-min acclimatization period, the test fish were subjected to a simulated aerial predation event. Two metal nuts (diameter = 11 mm) attached to each end of a piece of wood (l × w × h = 120 × 7 × 1 cm) with 26-cm lengths of string were rested on the top surface of the same piece of wood above the tank. Another identical piece of wood was pulled using 2 lengths of string (from below the level of the bottom of the tank) across the surface of first piece of wood knocking the nuts into the water at an approximately central point in each of the compartments. Once the nuts had dropped into the water, the test fish would almost always freeze instantly or after a very short burst of movement. The time taken for them to

begin moving again (defined as any movement from the place of freezing) was recorded. On the very few occasions (5 out of the 254 fish tested) that the fish did not freeze almost instantaneously, they were excluded from future testing. On the few occasions (3 fish on day 1 of and 4 fish on day 2 of testing), the test fish took longer than 120 s to resume movement; their recovery time was recorded as 120 s. After being tested, each fish was returned to their holding tank and all fish were fed freeze-dried bloodworm at the surface and left overnight.

Each fish was retested approximately 24 h after the first screening to ensure the repeatability of the screening method and consistency of recovery times. There was a strong significant positive correlation between the log of the time taken to recover from the fright stimulus on the first and second days of boldness screening (Pearson correlation: $n = 249$, $r^2 = 0.666$, $P < 0.001$; Figure 1). This is important as it shows that the results for each individual are constant over time. After the second screening day, each fish was returned to the test tank, fed freeze-dried bloodworm at the surface, and left overnight.

A "mean recovery time" was calculated for each individual fish from their recovery times over the 2 screening days. Thus, the lower the mean recovery time the more bold the fish. There was a significant positive correlation between body size and mean recovery time, suggesting that smaller fish are bolder (Pearson correlation: $n = 249$, $r^2 = 0.202$, $P = 0.001$). We therefore include body length as a variable in all relevant analyses (see statistical analyses). The fish were ranked according to their mean boldness score, and the individuals with the 20 lowest values (fastest to recover of the 60–70 fish) were categorized as bold and the individuals with the 20 highest values (slowest to recover of the 60–70 fish) were categorized as shy. This gave a total of 80 bold and 80 shy fish for the whole experiment. All bold fish also had a mean boldness score of <10 s, whereas all shy fish had a mean boldness score of >20 s. Some fish had very inconsistent scores over the 2 days of testing. These individuals were not used in the shoals for the foraging trial if one of their boldness scores was more than 5 s above the boundary of 10 s for bold fish and more than 5 s below the boundary of 20 s for shy fish, for example, if a fish recovered in 3 s on the first day and 16 s on the second, its mean would be 9.5, which under our criteria would make it a bold fish, but it would be excluded because its score on the second day is >5 s above the 10-s threshold for bold fish. Likewise, if a fish scored 60 s on the first day and then 10 s on the second day, its mean would be 35 s qualifying it as shy, but it would be excluded because its score on the second day is >5 s below the 20 s threshold for shy fish (see Figure 1).

Approximately 14–16 h after the second day of boldness screening, we grouped the fish into shoals of 4 individuals. The shoals differed in the number of bold and shy fish they contained, creating 3 treatment groups. "Bold" shoals contained 4 fish categorized as bold, "shy" shoals contained 4 fish categorized as shy, and "mixed" shoals contained 2 fish categorized as bold and 2 fish categorized as shy. From each original group of 60–70 females, we created 10 test shoals, with 3 or 4 shoals in each treatment. In total, we tested 40 shoals (13 bold, 14 mixed, and 13 shy), but data were excluded for 6 of the shoals. In 4 of these cases, a light bulb above the tank failed shortly before they were due to be tested, and in the other 2 cases, the partitions in the test tank (see below) did not lift smoothly and scared the fish which then remained frozen throughout the foraging trial. This gave us data for a total of 34 shoals (11 bold, 12 mixed, and 11 shy).

Each shoal was placed into a separate tank (identical in size to the test tank used to screen the fish: $l \times h \times w = 90 \times 30 \times 30$ cm, water depth = 14 cm) and confined (using a removable, opaque plastic partition, attached to a length of string which passed over the end of the tank) to a section (a third of the tank: $l \times w \times h = 30 \times 30 \times 30$ cm) at one end of the tank. We alternated the side of the tank to which the fish were confined to remove any side biases in the experiment. The fish were then fed a small pinch of freeze-dried bloodworm and allowed to acclimatize to the tank for 20–24 h before the foraging trial began.

Foraging trial

Novel feeding device
The following day, each shoal was presented with a novel feeding device. This consisted of an upturned clear cylindrical plastic jar with its yellow lid facing down in the water (Figure 3a inset). A circular hole cut in the center of the lid (4 cm diameter) provided the only route by which fish could enter the feeder. The bottom of the jar (the uppermost part once the jar was placed in the tank) was removed so that food could be added once the feeder was in position. The feeder was introduced to the test tanks and was positioned centrally 8 cm from the end of the tank furthest from the section where the fish were confined and held in place by firm wires hooked over each side of the tank. It hung in the water with the entrance hole 2 cm above the bottom of the tank and the top 4 cm above the surface of the water. Freeze-dried bloodworm was sprinkled into the feeder and floated on the surface, visible from outside the feeder.

Procedure
After the introduction of the feeder, a single observer (J.R.G.D.) sat at a distance of approximately 1.5 m from the test tank with the tank at approximately eye level, and the fish were given 3 min to recover from the disturbance, after which all fish had resumed normal swimming behavior. The partition was then raised very slowly by pulling the length of string from behind the end of the tank (out of view of the fish). After the partition was fully raised, a stopwatch was started. The time taken for the first fish to approach the feeder (defined as moving to a position 4 body lengths or less from the wall of the feeder) was recorded. Each trial lasted for 20 min after the first approach. The time and identity of each fish entering and feeding from the surface inside the feeder were recorded during this period.

After the trial, the feeder was removed and washed in clean water, and the fish were once again confined to a third of the tank and left overnight before being screened as a group for boldness.

Shoaling associations
During the foraging trials, shoaling associations were recorded every minute for the 20-min period after the first approach. We defined an association between 2 fish as occurring when the fish were positioned within 4 body lengths of each other, a distance that falls within the range of interindividual distances most commonly observed in shoaling fishes in nature (Pitcher and Parrish 1993). From these data, we could observe the number of separate groups at 1-min intervals (during the 20-min period), for each shoal. This enabled us to calculate a mean number of groups for each individual shoal (from the 20 readings).

Following events
Occasionally, one fish would follow close behind another as it entered the feeder and fed at the surface. More commonly though, the following fish would remain around the entrance of the feeder after another fish had entered and then enter after a period of time. For this reason, we present the number of following events in each shoal type after different time

periods following the entrance of the first fish. These time periods are 10, 20, and 30 s after the initial entrance.

Group boldness

16–20 h after the foraging trial, the shoals were subjected to the same simulated aerial predation event used in the boldness screening. The 2 lengths of wood and the nuts and strings were set up above each of the tanks, and the same observer (J.R.G.D.) sat at a distance of approximately 1.5 m from the test tank with the tank at approximately eye level. The fish remained confined to a single compartment as in the original screening and were given 3 min, after the observer was in place, to recover from the disturbance. The shoal was then exposed to the fright stimulus as before, and the time for each fish to begin moving again was recorded.

Statistical analyses

Statistical analysis was carried out in R, version 2.3.1, and SPSS, version 14.0. Parametric analyses were used throughout where the assumptions of normality and homogeneity of variance were met. In the event that transformation failed to meet the assumptions of parametric analysis, nonparametric statistics were used.

Pearson correlations were used to look at the relationship between boldness scores on day 1 and day 2 and also at the relationship between individual body length and mean boldness (see above). An analysis of variance (ANOVA) was used to compare the log mean body length of shoals (calculated from the body lengths of the 4 individual shoal members) in the 3 different experimental treatments.

We used general linear models (LMs) to analyze the effect of treatment (shoal composition) and the mean body length of shoals and their 2-way interaction term, on the time taken for both the first fish and the last fish in the shoal to approach the novel feeder. Both approach time measures were logged to meet parametric assumptions and were treated separately as the response variables in the LM analyses. General LMs were also used to analyze the effect of treatment and the mean body length of shoals and their 2-way interaction term, on log mean time taken for fish to resume swimming after being subjected (as a group) to the aerial fright stimulus and on log mean number of groups formed by shoals within the 20-min period following first approach. Following any significant results from LM analyses, Tukey honest significant difference (HSD) post hoc tests were used to make multiple comparisons between individual treatments.

A generalized LM (GLM) was used to analyze the effect of treatment, mean shoal body length, and mean number of groups and their 2- and 3-way interaction term on the number of fish feeding from the novel feeder. The number of fish feeding was treated as the response variable in the GLM analysis, with a Poisson distributed error variance. Following a significant result from a GLM, a sequential Bonferroni procedure (see Holm 1979) is used to correct the P values of multiple comparisons between individual treatments.

A binomial test was used to compare the likelihood of bold and shy fish entering the feeder in different positions (first, second, third, and fourth). A Spearman correlation was used to look at the relationship between number of fish entering and number of fish feeding from the feeder.

RESULTS

Body length of shoal types

The log mean body length of shoals did not differ significantly between treatments (ANOVA: $F_{2,31} = 0.428$, $P = 0.655$).

Group recovery time

Neither mean shoal body length nor its 2-way interaction with treatment had a significant effect on group recovery time and so was discarded from the model. The treatments differed significantly in the log mean time taken for fish to resume swimming after being subjected (as a group) to the aerial fright stimulus (LM: $F_{2,31} = 8.420$, $P = 0.001$). Both bold and mixed shoals resumed swimming in significantly less time than shy shoals, but there was no difference between bold and mixed shoals (Figure 2).

Novel foraging task

Time to approach
Neither mean shoal body length nor its 2-way interaction with treatment had a significant effect on log time for either first or last fish to approach and so was discarded from both models. There was a significant difference between the treatments in the time taken to approach the novel feeding device both in terms of the time taken for the first fish (LM: $F_{2,31} = 8.304$, $P = 0.001$) and last fish to approach (LM: $F_{2,31} = 7.592$, $P = 0.002$). In both cases, fish from both all bold and mixed shoals approached the feeder significantly faster than those from all shy shoals, but there was no significant difference between bold and mixed shoals (Figure 3a).

Entry and feeding
The number of fish entering the feeder and the number of fish feeding at the surface were highly correlated (Spearman correlation: $r_s = 0.947$, $N = 34$, $P < 0.001$), and so number of fish feeding rather than number of fish entering was used in further analysis. Neither mean shoal body length, mean number of groups, or their 2- and 3-way interactions with treatment had a significant effect on the number of fish feeding and so were sequentially discarded from the model. Treatment had a significant effect on the number of fish feeding (GLM: $\chi^2 = 17.227$, degrees of freedom $= 2$, $P < 0.001$). Significantly more fish fed in mixed shoals than either bold or shy shoals. No significant difference was found between bold and shy shoals (Figure 3b).

Number of groups
Neither mean shoal body length nor its 2-way interaction with treatment had a significant effect on the log mean number of groups and so were discarded from the model. There was
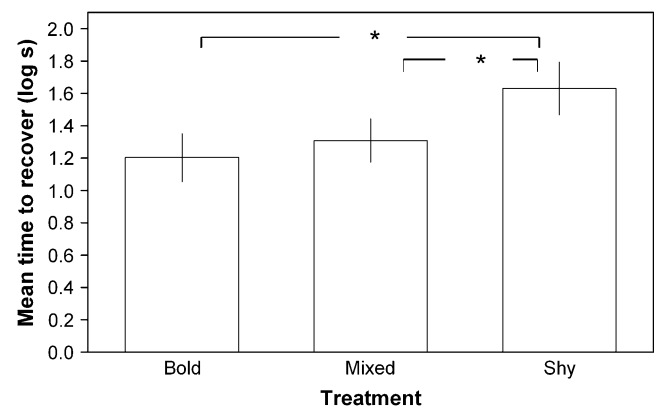
Figure 2
The mean (± 2 standard error) time taken to recover (log s) by shoals in each treatment when exposed to the fright stimulus as a shoal. Treatment differences are indicated by Tukey HSD post hoc tests: *, 0.05.
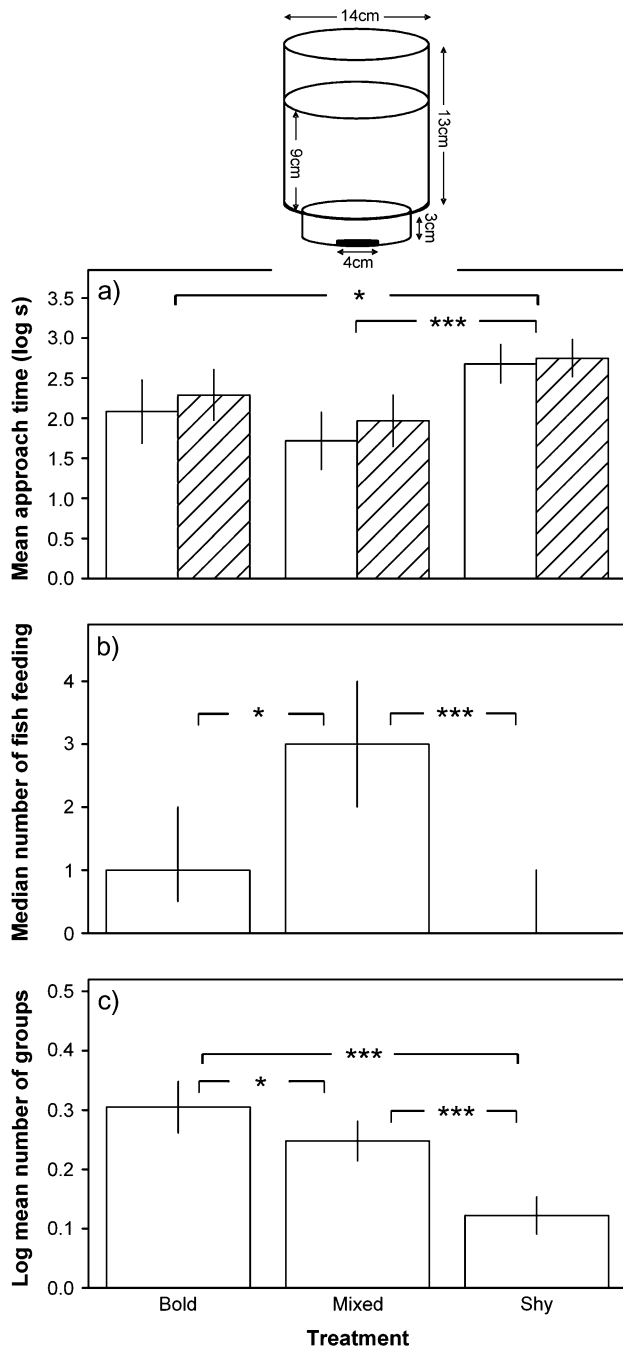
Figure 3
(a) Mean (±2 standard error) time to approach the feeder (log s) in each treatment. Hollow bars represent time taken for the first fish to approach, and striped bars represent time taken for the last member of the shoal to approach. Treatment differences were the same for both approach times and are indicated by Tukey HSD post hoc tests: ***, 0.001; **, 0.01; *, 0.05. (b) Median (±interquartile range) number of fish feeding in each treatment. Treatment differences are indicated by sequential Bonferroni post hoc tests: ***, 0.001; **, 0.01; *, 0.05. (c) Mean (±2 standard error) number of separate groups formed in each treatment, taken from the median number of groups formed by each shoal over the 20-min period after the first approach. Treatment differences are indicated by Tukey HSD post hoc tests: ***, 0.001; **, 0.01; *, 0.05. (Inset) Novel foraging device with dimensions.

a significant difference between the treatments in terms of the mean number of groups observed in the 20 min following the first approach (LM: $F_{2,28} = 26.886$, $P < 0.001$). Bold shoals were observed to form more separate groups than mixed shoals or shy shoals, and mixed shoals formed more groups than shy shoals (Figure 3c).

Mixed shoals
Within mixed shoals, we looked at the order with which the fish entered and fed from the feeder. The first fish to enter and feed was almost always one of the bold individuals (bold:shy = 11:1, binomial test: $n = 12$, $P = 0.006$), and the second fish to enter and feed was usually one of the shy individuals (bold:shy = 2:10, binomial test: $n = 12$, $P = 0.039$). There was no significant difference between the number of bold and shy fish feeding third (bold:shy = 4:3, binomial test: $n = 7$, $P = 1.000$) or fourth (bold:shy = 1:3, binomial test: $n = 4$, $P = 0.625$; Figure 4), although sample sizes here are small.

Following events
We also looked at the occasions on which a fish was followed into the feeder. Every following event occurred within a mixed shoal regardless of whether we defined following as one fish entering the feeder within 10, 20, or 30 s of another (see Table 1). Also on every occasion a following event occurred within a mixed shoal, it was a shy fish following a bold one.

DISCUSSION

Shoal composition not only affected individual behavior but also generated potential foraging benefits to both bold and shy fish through associating together in mixed groups, with significantly more fish feeding in mixed than in either bold or shy shoals. Our results strongly suggest that boldness and shyness represents a producer–scrounger situation in shoals of guppies. We found that in mixed shoals, the first fish to feed was significantly more likely to be bold than shy (on 11 out of 12 occasions), the second was significantly more likely to be shy than bold (on 10 out of 12 occasions), all following events occurred within mixed shoals (Table 1), and on every occasion it was a shy fish following a bold one. Furthermore, bold shoals formed significantly more separate groups than mixed shoals, which in turn formed more than shy shoals, suggesting that the more shy fish present the more
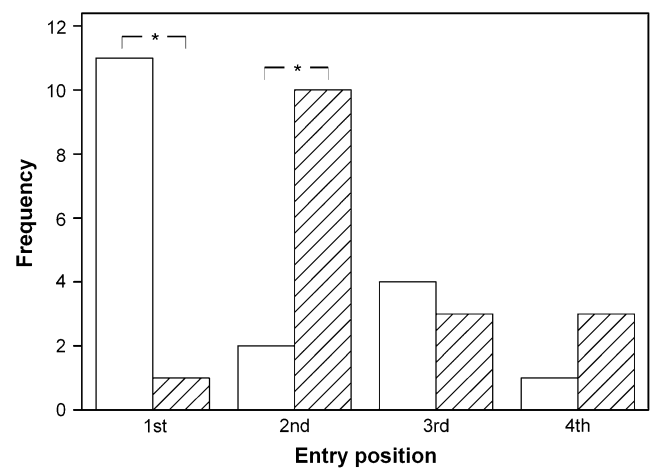

Figure 4
The number of times bold and shy fish entered the feeder in the 4 different entry positions (first, second, third, or fourth). Treatment differences are indicated by binomial tests: *, 0.05.

Table 1

Number of shoals, number of fish, and number and percentage of fish entering, feeding, and following another into the feeder for each treatment type

	Bold	Mixed	Shy
Number of shoals	11	12	11
Number of fish	44	48	44
Total number and percentage of fish entering	16 (36%)	35 (73%) 18 bold (75%) 17 shy (71%)	8 (18%)
Total number and percentage of fish feeding	14 (32%)	33 (69%) 17 bold (71%) 16 shy (67%)	7 (16%)
Following events (10 s)	0	5	0
Following events (20 s)	0	8	0
Following events (30 s)	0	9	0

tightly associated the shoal. Previous work has shown that bold individuals explore more (Magnhagen 2007) and are more likely to discover and feed on novel food sources (Wilson et al. 1993, Magnhagen and Staffan 2003; Sneddon 2003; Frost et al. 2007), whereas shy individuals have a higher shoaling tendency (Budaev 1997; Ward et al. 2004) and so are probably more likely to be close by when a discovery is made. Barnard and Sibly (1981) suggested that many inter- and intraspecific relationships between animals are likely to be based on scrounger individuals exploiting the efforts of producers. They found that within captive flocks of house sparrows, *Passer domesticus*, some individuals (producers) obtained food by actively foraging and others (scroungers) obtained most of their food by interaction. Unsurprisingly, scroungers did much better when at least one producer was present. Our results are in agreement as more than 4 times the proportion of shy fish fed in mixed shoals when compared with shoals consisting of only shy individuals (Table 1). In reality though, individuals do not fit into such discrete categories as bold and shy. Rather, boldness is very much a continuum with some individuals we categorize as bold being very much bolder than other bold individuals (see Figure 1). In natural shoals, it is likely that many individuals fall somewhere toward the center of this continuum, yet, will be able to exploit the discoveries of those bolder than themselves and may be exploited by those that are shyer.

Similar to previous work (Magnhagen and Staffan 2005; Sih and Watters 2005), we find that the behavioral composition of a group can impact on the behavior and fitness of individual BTs. Like Magnhagen and Staffan (2005), we find evidence that shy fish are bolder in the presence of bold individuals. Mixed shoals resumed swimming after a fright and also approached the novel feeder significantly more quickly than shy shoals and no slower than bold shoals. For approach time, this was not just in terms of the first fish to approach but also the last fish to approach showing that shy fish approach the novel feeder more quickly in the presence of bold fish. However, although it appears that shy fish are acting more boldly, it is also possible that they are simply showing a greater tendency to stay with the group, as found in previous studies (e.g., Budaev 1997; Ward et al. 2004).

Surprisingly, within mixed shoals, not only was the proportion of shy fish feeding far greater than in all shy shoals but also was the proportion of bold fish feeding compared with all bold shoals (more than twice the proportion of bold fish fed in mixed shoals; Table 1). This suggests that not only do shy fish gain foraging benefits from associating with bold fish but also that there are benefits to bold fish too. It is plausible that shy fish confer potential antipredator benefits to bold individuals through their increased caution and vigilance. Therefore, within mixed shoals, bold fish may have been able to explore the novel foraging task more thoroughly through relying to some extent on the vigilance of the shy fish who were often close by. Alternatively, it is possible that less aggression occurred within mixed shoals. Recently, interest has grown in the proactive–reactive syndrome, in which proactive individuals are both bold and aggressive (Benus et al. 1991; Hessing et al. 1993; Malmkvist and Hansen 2002; van Hierden et al. 2002; Schjolden et al. 2005). The increased number of bold fish in bold shoals compared with mixed ones may have meant that more aggression and potentially exclusion from the feeder occurred in bold shoals. However, this did not appear to be the case as aggression was rarely observed and incidences were fairly evenly spread between the treatments.

Similar to Brown and Braithwaite (2004), we find a positive relationship between body length and time to resume swimming, suggesting that smaller fish are bolder. This may be due to the greater metabolic requirements of smaller fish (Brown and Braithwaite 2004). In fish, age is correlated with standard length, suggesting that younger individuals are bolder (Brown and Braithwaite 2004). Age and experience are likely to be important influences on boldness, and it is possible that older fish have learnt to be shyer through past experience or that bolder fish are more likely to be predated (Brown and Braithwaite 2004). Bell and Sih (2007) found that bolder three-spined sticklebacks, *Gasterosteus aculeatus*, were less likely to survive in the face of real predation and also that exposure to predation could generate a correlation between boldness and aggressiveness. Recent theoretical work has demonstrated how life-history trade-offs can favor the evolution of animal personalities (Wolf et al. 2007).

Our results may have implications in terms of composing groups of animals for release after captive breeding, suggesting that success may be increased through having a mix of BTs, though more research in this area is necessary. These results may also help explain the maintenance of interindividual variation in BTs. A number of studies have looked at the variation in success of BTs through time and fluctuating environments (e.g., Dall 2004; Dingemanse et al. 2004; Both et al. 2005). Both et al. (2005) found that pairs of great tits, *Parus major*, with extreme personalities in terms of speed to explore (e.g., bold–bold and shy–shy pairs) enjoyed the highest reproductive success. Here we show that foraging success is maximized when there is variation in BTs in a group. Metcalfe and Thomson (1995) found that fish (European minnows, *Phoxinus phoxinus*) can recognize and prefer to shoal with poor competitors even without obvious cues such as differences in size, levels of aggression, or instantaneous feeding rate. It is possible that guppies too may be able to assess competitive ability or associated personality traits, resulting in bolder individuals choosing to shoal with shyer individuals or vice versa.

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