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Association patterns and foraging behaviour in natural and artificial guppy shoals

LESLEY J. MORRELL*, DARREN P. CROFT*†, JOHN R. G. DYER*, BEN B. CHAPMAN*,
JENNIFER L. KELLEY‡, KEVIN N. LALAND§ & JENS KRAUSE*

*Institute of Integrative and Comparative Biology, University of Leeds
†College of Natural Sciences, School of Biological Sciences, Bangor University
‡School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney
§School of Biology, University of St Andrews

Animal groups are often nonrandom assemblages of individuals that tend to be assorted by factors such as sex, body size, relatedness and familiarity. Laboratory studies using fish have shown that familiarity among shoal members confers a number of benefits to individuals, such as increased foraging success. However, it is unclear whether fish in natural shoals obtain these benefits through association with familiars. We investigated whether naturally occurring shoals of guppies, *Poecilia reticulata*, are more adept at learning a novel foraging task than artificial (in which we selected shoal members randomly) shoals. We used social network analysis to compare the structures of natural and artificial shoals and examined whether shoal organization predicts patterns of foraging behaviour. Fish in natural shoals benefited from increased success in the novel foraging task compared with fish in artificial shoals. Individuals in natural shoals showed a reduced latency to approach the novel feeder, followed more and formed smaller subgroups compared to artificial shoals. Our findings show that fish in natural shoals do gain foraging benefits and that this may be facilitated by a reduced perception of risk among familiarized individuals and/or enhanced social learning mediated by following other individuals and small group sizes. Although the structure of shoals was stable over time, we found no direct relationship between shoal social structure and patterns of foraging behaviour.

Wild animal groups commonly display nonrandom patterns of social structure. Within a species, individuals are known to associate on the basis of kinship (Ward & Hart 2003; Silk et al. 2006), body size (Ward & Krause 2001), parasite load (Krause & Godin 1994), disease status

Correspondence: D. P. Croft, College of Natural Sciences, School of Biological Sciences, Bangor University, Brambell Building, Deiniol Road, Bangor, Gwynedd LL57 2UW, U.K. (email: darren_croft@hotmail.co.uk). L. J. Morrell, J. R. G. Dyer, B. B. Chapman & J. Krause are at the Institute of Integrative and Comparative Biology, LC Miall Building, University of Leeds, Leeds LS2 9JT, U.K. J. L. Kelley is at the Centre for Evolutionary Biology, Zoology Building, School of Animal Biology (M092), The University of Western Australia, Nedlands, WA 6009, Australia. K. N. Laland is at the School of Biology, University of St Andrews, Bute Medical Building, Queen's Terrace, St Andrews, Fife, Scotland KY16 9TS.

(Behringer et al. 2006) and colour (McRobert & Bradner 1998), resulting in groups that are assorted by phenotypic characteristics. These association patterns are thought to confer antipredator benefits, such as a reduction in risk through predator confusion, and foraging benefits, such as reduced competition for resources (Krause & Ruxton 2002). A further level of social organization can arise when individuals preferentially associate with, or avoid, conspecifics based on previous interactions (Griffiths 2003).

Preferences for associating with familiars have been reported in a number of animal groups (e.g. mammals: Porter et al. 2001; birds: Senar et al. 1990; reptiles: Bull et al. 2000; insects: Clarke et al. 1995), but have been particularly well studied in shoaling fishes. These studies have revealed that associations based on familiarity occur both

in the laboratory (e.g. Barber & Ruxton 2000; Barber & Wright 2001) and in the field (Griffiths & Magurran 1997a; reviewed in Griffiths 2003). A number of benefits to associating with familiars have been shown, including enhanced predator escape responses (Chivers et al. 1995), reduced levels of aggression (fishes: Utne-Palm & Hart 2000; birds: Temeles 1994), increased foraging success (reviewed in Krause & Ruxton 2002; Griffiths 2003; Ward & Hart 2003) and an elevated performance in learning tasks (Swaney et al. 2001; Galef & Giraldeau 2001).

Previous work has shown that animal groups contain pairs or small groups of individuals that are linked by stable interactions (Croft et al. 2004, 2006; Gero et al. 2005). However, the majority of work investigating the benefits of familiarity has focused on groups of fish that are artificially familiarized in the laboratory (by holding fish together in small groups for a period of 2 weeks or more), and it is unclear whether wild (i.e. naturally assorted) shoals would gain the same benefits. Wild shoals of fathead minnows, *Pimephales promelas*, show more cohesive antipredator behaviour than unfamiliar, laboratory-assembled shoals (Chivers et al. 1995), but other putative benefits of familiarity have not yet been studied in natural groups. Here, we investigate whether natural shoals of guppies, *Poecilia reticulata*, benefit from enhanced foraging success compared to artificial (laboratory-assembled) shoals. We used female guppies, as they display greater within-shoal fidelity than males (Griffiths & Magurran 1998), are more likely than males to exploit novel foods (Laland & Reader 1999a) and learn new foraging tasks more rapidly than males (Laland & Reader 1999b). We presented the shoals with a novel foraging task, consisting of a novel foodstuff hidden within a feeder, and investigated the success of shoal members in completing the task.

Previous work with fishes has shown that foraging success and performance in a novel learning task are influenced by social structure, specifically group size. For example, individuals in larger groups are generally more successful at locating food patches (e.g. Pitcher et al. 1982) and learning to escape from a moving net (Brown & Warburton 1999) than individuals in smaller groups, but individuals in smaller groups can locate food more quickly when the food is hidden (the conformity effect; Day et al. 2001). The influence of familiarity on learning has been well studied: in fish, individuals learn more successfully from familiar demonstrators than from unfamiliar conspecifics (where familiar groups are created by holding individuals together in the laboratory over a period of time; Swaney et al. 2001; Ward & Hart 2005), and in birds, the young learn how to handle a new food source more effectively from familiar adults than from unfamiliar ones (Cadieu & Cadieu 2004).

One method that is becoming increasingly useful for understanding associations and structure in animal populations is social network analysis (e.g. Croft et al. 2004; Lusseau & Newman 2004; Wolf 2005). Previous work on guppies using this approach has shown that individuals have preferred associations (i.e. associations are nonrandom), even within small shoals of fish (Croft et al. 2004, 2006). We used a social networks approach to investigate the influence of social structure on the performance of guppies in a novel foraging task. To our knowledge, this is the first time these techniques have been used in this way. First, we investigated differences in social structure between natural and newly created artificial shoals and success in the foraging task. Second, we investigated whether social association patterns are linked to patterns of foraging and information transfer within groups. We predicted that the social structure of natural shoals would reflect the nonrandom associations occurring within them (Croft et al. 2006) and thus would differ from association patterns in artificial shoals, in which individuals would be unfamiliar and preferred associations would not have been established. We also predicted that individuals in natural shoals would forage more successfully (Swaney et al. 2001; Ward & Hart 2005) and that within shoals, individuals would be more likely to forage with and obtain social information from those shoal members with whom they had close associations.

METHODS

Study Site and Holding Conditions

We captured fish from the Arima River in the Northern mountain range of Trinidad (within 500 m of Verdant Vale Village, 10°41′N, 61°17′W) during May 2005, between 0900 and 1600 hours, using a 2-m beach seine. In our investigation we used natural and artificial shoals of fish, each containing eight adult females. We chose shoals of eight as being representative of natural shoal sizes (2−20 individuals; Croft et al. 2003a). Natural shoals ($N = 10$) consisted of groups captured together in the wild, and artificial shoals ($N = 10$) were groups assembled in the laboratory from over 300 fish (see below).

We captured natural shoals, consisting of at least 10 individuals, from the river in their entirety, releasing any males back into the river and selecting eight females of similar body size (size of females in natural shoals: mean ± SD = 27.99 ± 2.97 mm) from each shoal. We returned the remaining fish to the river. We defined a shoal of guppies as individuals that were within four body lengths of one another (Pitcher & Parrish 1993). We kept the eight fish together, isolated from other shoals, and took them to the laboratory, where we placed each shoal in a large artificial pool (diameter 120 cm, water depth 5 cm, water temperature 26 °C) and allowed them to acclimatize for 24 h.

We created the 10 artificial shoals by collecting over 300 females using 36 seine hauls from a 500-m stretch of river. We took the fish to the laboratory and placed them in an artificial pool (as above) for 24 h to allow complete mixing. From this population we selected 80 individuals of similar body size (size of females in artificial shoals: mean ± SD = 28.09 ± 4.07 mm) and assigned them haphazardly to 10 shoals. We then placed each shoal in a visually isolated pool for 24 h, as above. Body size did not differ significantly between the fish in natural and artificial shoals (independent samples *t* test: $t_{1,158} = -0.178$, $P = 0.859$), and there was no significant difference in

within-shoal standard deviation between natural and artificial shoals ($t_{1,18} = -1.437$, $P = 0.168$). We placed unused fish in two large outdoor pools and maintained all test shoals on a diet of commercially available flake food, given twice per day.

Female guppies do not have any natural markings that can be used for identification purposes and thus we anaesthetized individuals from all shoals using tricane methane sulfonate (MS222) and gave them individual identity marks using a visible implant elastomer injected into the dorsal epidermis (a standard procedure for marking fish: see Croft et al. 2003b). All fish recovered quickly from the anaesthetic, normal swimming behaviour was quickly resumed and we observed no mortality as a result of the marking process. Previous work has shown that the procedure does not affect shoaling decisions in guppies (Croft et al. 2004). After marking, we allowed the shoals to acclimatize for 12−16 h before beginning experimental procedures. The experimental protocol for each shoal consisted of (1) quantifying the social structure and shoaling associations (see below), (2) introducing a novel foraging task to the pool and observing the success of fish in completing the task and (3) requantifying the social structure. For each shoal, we carried out the three elements of the experimental protocol sequentially, separated by periods of 10 min.

Quantifying Social Structure

We quantified patterns of association by visually observing and recording the membership of subgroups within the shoal once per minute over a 30-min period (Croft et al. 2004; Thomas et al. 2008). Previous work has shown this to be a sufficient time period to quantify the nonrandom social network structure of guppy shoals (see Croft et al. 2004 online supplementary material). We defined an association between two fish as occurring when the fish positioned themselves within four body lengths of each other, a distance that falls within the range of interindividual distances most commonly observed in shoaling fishes in nature (Pitcher & Parrish 1993). All fish in a subgroup were within four body lengths of at least one other member of the group (thus, if fish A and fish C were six body lengths apart, but fish B was positioned between them, then all were considered members of a single subgroup). One observer sat motionless, close to the edge of the pool, and a second person was positioned farther back from the pool to record the observations relayed to him or her by the observer.

Novel Foraging Task

Ten minutes after quantifying association patterns, we introduced a novel foraging task into the experimental arena. The task consisted of a white, opaque, plastic cylinder (the 'feeder', height 85 mm, diameter at base 75 mm, diameter at top 68 mm) with a 20×20 mm entrance hole located in the lower wall. We placed the feeder with its centre 30 cm from the edge of the pool closest to the observer, with the entrance hole facing the observer.

At the beginning of the trial, we placed a pinch of freeze-dried bloodworm (*Chironomus* spp.) in the feeder, where it floated on the surface of the water, but was constrained within the feeder. Any odour cues from the bloodworm were likely to be well contained within the feeder (K. N. Laland, unpublished data). Bloodworm represents a high-protein food source, readily consumed by the fish, and similar food items are likely to make up part of their natural diet (Magurran 2005). As the bloodworm floated on the water surface, fish feeding at the surface inside the feeder were not visible to fish outside the feeder.

Following the introduction of the feeder, we recorded the time taken and the identity of the first fish to approach the feeder within four body lengths. After this initial approach we continued observing for a 30-min period. The delay before commencing the observation period ensured that the fish were settled following the introduction of the feeder into the pool and that they had identified the presence of this novel object. Each time a fish entered the feeder, or fed on the bloodworm at the surface, we recorded the time since the start of the observation period and the identity of the fish.

After 30 min, we removed the feeder and any remaining bloodworm from the pool using a fine-mesh dip net, and after a 10-min settling period, we requantified social structure and association patterns using the same procedure as above. This allowed us to check whether social structure was stable over the time period of the experiment. Previous work has shown that in the wild guppies can move between shoals very rapidly, changing shoals up to once per minute (Croft et al. 2003a), and that associations quantified using this method are based on active preferences (Croft et al. 2004). The 30-min interval between the two measures of (pre- and post-foraging task) social stability is therefore sufficient to allow ample opportunity for individuals to move among groups. At the end of the experiment, we removed the fish from the experimental arena and placed them in large artificial outdoor pools, isolated from the river system.

Data Analysis

Group sizes and social stability

From our observations of association patterns prior to the foraging task (see Quantifying Social Structure) we calculated the number and size of subgroups occurring at each time interval (i.e. every minute for 30 min, yielding 30 observations of group size for each shoal). From these data, we calculated the mean group size for every time interval and the median value for each shoal independently. We compared the median group sizes of natural and artificial shoals using a Mann−Whitney U test. For each shoal, we also calculated the mean percentage of individuals that were present in groups of sizes 1 to 8, over the 30 observations, to give frequency distributions of group sizes for natural and artificial shoals.

To test whether shoal associations are stable over time (i.e. before and after the foraging task), we created association matrices for each shoal, describing association patterns before and after the foraging trial. We compared

the two association matrices (before and after the foraging task) for each shoal using Mantel tests for matrix correlations. Where appropriate, P values were combined using Fisher's omnibus test to examine patterns across shoals. Throughout, 'shoal' refers to all eight individuals in a pool, and 'group' is used when the shoal divides into subunits.

For each shoal, we calculated the proportion of times that each individual fish was observed with each other fish (i.e. the proportion of times all possible pairs were associated) during the observation period (association strength, AS). The mean of these values gives an overall AS for each shoal, which is an additional measure of shoal cohesion. To investigate the variation in association scores, we calculated the coefficient of variation of the association strengths for each shoal. In each shoal, we observed all fish together one or more times over the 30-min observation period, giving fully interconnected social networks. As such, measures of social network structure based on the presence or absence of interactions between individuals (such as mean degree, path length and clustering coefficients; e.g. Newman 2003; Croft et al. 2004) are not informative and therefore were not calculated.

Patterns of foraging

If individuals learn socially from one another, we predicted that they are likely to follow one another into the feeder. To investigate whether individuals solved the task by following another individual, or entering the feeder alone, we identified events in which an individual first entered the feeder shortly after another individual. We used three definitions of following, 5, 10 and 20 s, and included all following events. Thus, an individual that entered the feeder 4 s behind another would be included in all three analyses, whereas an individual entering 14 s behind another would be included only in the 20-s analysis. A definition of following within 5 s represents a situation in which individuals enter closely behind another individual (within about four body lengths) and therefore could be considered members of the same shoal (Pitcher & Parrish 1993). A definition of following within 20 s, on the other hand, allows for the possibility that individuals can observe another entering the feeder from some distance away, then approach and enter the feeder themselves. In the most successful shoal, the total number of feeder entries over the 30 min was 59. This means that on average, one fish fed every 30.5 s, a greater time interval than our longest following definition of 20 s. Within a shoal type (natural or artificial) we corrected P values using Benjamini & Hochberg's (1995) method for false discovery rate control. Adjusted P values are presented.

If individuals do follow one another into the feeder, rather than foraging independently, we would predict that entries to the feeder would be more closely clustered in time than would be expected by chance (i.e. the null hypothesis would be that foraging events are independent of one another). To investigate whether this was the case, we performed a randomization test. We used only foraging events occurring within the interquartile range of foraging times (i.e. the 'middle half' of the each trial) to control for

differences in response towards the feeder after it was placed in the pool and any effect of satiation or food depletion on foraging towards the end of the trial. For each shoal, we calculated the total number of observed feeder entries and the number of occasions on which the difference between one entry time and the preceding one (the entry lag) was less than 5, 10 or 20 s (possible following events). We then generated a random set of feeder entry times (within the time available in the interquartile range), containing the observed number of feeder entries, and calculated the number of times the entry lags were less than 5, 10 or 20 s. This was repeated 999 times. We calculated the total number of randomizations in which the predicted number of following events was greater than or equal to the number observed in the shoal, to give a conservative probability that entries were more clustered in time in the observed shoal than expected by chance (one-tailed test). We repeated this for all 10 natural shoals and the six artificial shoals for which entry events were observed.

We used a further randomization technique to investigate whether individuals that first entered the feeder by following a leader ('lead−follow pairs') were significantly more highly associated with that individual than would be expected if they learnt the task by following another individual at random. To control for differences between shoals in overall levels of association, we calculated the total of the association strengths of all lead−follow pairs for each shoal. We defined lead−follow pairs as two fish that entered the feeder within 20 s of each other, assuming that individuals followed the immediately preceding fish (i.e. if three individuals enter closely in time, in the order A, B and C, we assume that B follows A, and C follows B). The 20 s rule was used only because of low numbers of following events for other rules in some shoals. For each shoal, we then randomly selected the same number of pairs as were observed in lead−follow events and summed their association strengths. We repeated this randomization 999 times for each shoal. We then calculated how many of the randomly generated pairs had a higher sum of association indexes than the observed pairs, generating a probability (P) that the observed pairs were significantly more associated than random pairs (one-tailed test).

RESULTS

Are There Differences in Social Structure and Foraging Success between Natural and Artificial Shoals?

Grouping behaviour differed between natural and artificial shoals. The median group size was significantly larger in artificial shoals than in natural shoals (Mann−Whitney U: $Z = -3.659$, $N_{natural} = N_{artificial} = 10$, $P < 0.001$), and small groups were common in shoals of naturally co-occurring fish, whereas larger groups were most common in artificial shoals (Fig. 1).

Natural shoals had a significantly smaller mean shoal AS than artificial shoals (Mann−Whitney U: $Z = -3.628$, $N_{natural} = N_{artificial} = 10$, $P < 0.001$; Fig. 2a). Associations
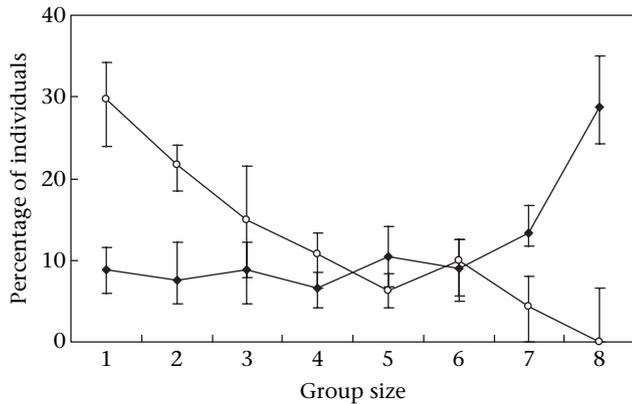
Figure 1. Percentage frequency distributions of guppy groups in natural (open circles) and artificial (filled circles) shoals. Values are the median percentage frequency of individuals in groups of each size across all replicate trials. Error bars represent interquartile range. Solid lines are used as a visual aid only, linking values for each shoal type.

in natural shoals were also more variable than in artificial shoals: the coefficient of variation in AS was higher in natural than in artificial shoals (Mann−Whitney U: $Z = -3.175$, $N_{natural} = N_{artificial} = 10$, $P = 0.001$; Fig. 2b). Both natural and artificial shoals thus showed variation in AS between pairs of individuals within a shoal, giving us the opportunity to investigate patterns of learning in relation to patterns of social structure.

After the feeder had been placed in the pool, fish from natural shoals approached it significantly more rapidly than fish from artificial shoals (Mann−Whitney U: $Z = -2.117$, $N_{natural} = N_{artificial} = 10$, $P = 0.035$; Fig. 3a), and more fish from natural than from artificial shoals entered and fed from the feeder (Mann−Whitney U: entering the feeder: $Z = -2.701$, $N_{natural} = N_{artificial} = 10$, $P = 0.007$; not shown, feeding: $Z = -3.752$, $N_{natural} = N_{artificial} = 10$, $P < 0.001$; Fig. 3b). In all 10 of the natural shoals at least three fish fed, successfully completing the task. In one shoal, all fish fed. In comparison, we observed feeding in only five of the artificial shoals, from which a maximum of three individuals fed.

Can Patterns of Association Predict Patterns of Foraging?

Patterns of association in the pre-foraging trial (first) social network were significant predictors of association patterns in the post-foraging trial (second) social network (network correlations analysed using Mantel test for matrix correlations, P values combined using Fisher's omnibus test: wild shoals: $F_{20} = 63.45$, $P < 0.001$, Table 1; random shoals: $F_{20} = 35.64$, $P = 0.02$). This suggests that associations are stable over the time of the experiment, and all further analysis is based on pre-foraging trial associations only.

Do individuals follow others?

We found strong evidence that entries to the feeder were more closely clustered in time than would be expected by
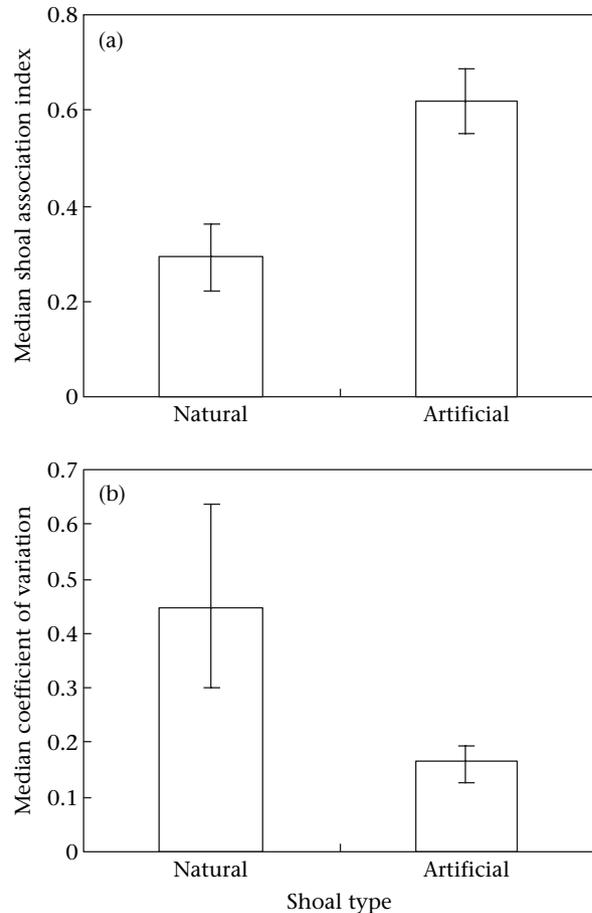

Figure 2. Comparison of median values for network measures (association strength; AS) between natural and artificial shoals. (a) Shoal AS ($Z = -3.628$, $N_{natural} = N_{artificial} = 10$, $P < 0.001$) and (b) coefficient of variation in AS ($Z = -3.175$, $N_{natural} = N_{artificial} = 10$, $P = 0.001$). Error bars indicate the interquartile range.

chance in both natural and artificial shoals, regardless of the definition of following used (natural shoals: 5 s, $F_{20} = 83.989$, $P < 0.001$; 10 s, $F_{20} = 84.011$, $P < 0.001$; 20 s, $F_{20} = 54.200$, $P < 0.001$; artificial shoals: 5 s, $F_{12} = 27.522$, $P = 0.006$; 10 s, $F_{12} = 44.190$, $P < 0.001$; 20 s, $F_{12} = 46.207$, $P < 0.001$). Fish in both natural and artificial shoals are therefore more likely to enter the feeder together than might be expected if each individual was foraging independently, suggesting that the guppies were foraging socially.

In natural shoals, the majority of fish first entered the feeder alone (using a rule that individuals followed only if they entered the feeder within 5 s of another fish), rather than following closely behind another fish (Wilcoxon signed ranks test: $Z = -2.501$, $N = 10$, $P = 0.036$; Fig. 4), but this was not the case in artificial shoals ($Z = -2.014$, $N = 10$, $P = 0.123$; Fig. 4). Using a 10- or 20-s rule, however, there was no difference in the number of individuals that first entered the feeder alone and the number that first entered the feeder by following another individual (Wilcoxon signed ranks test: 10 s: natural shoals, $Z = -1.869$, $N = 10$, $P = 0.093$; artificial shoals, $Z = -1.841$, $N = 10$, $P = 0.099$; 20 s: natural shoals, $Z = -1.279$, $N = 10$, $P = 0.201$; artificial shoals, $Z = -1.236$,
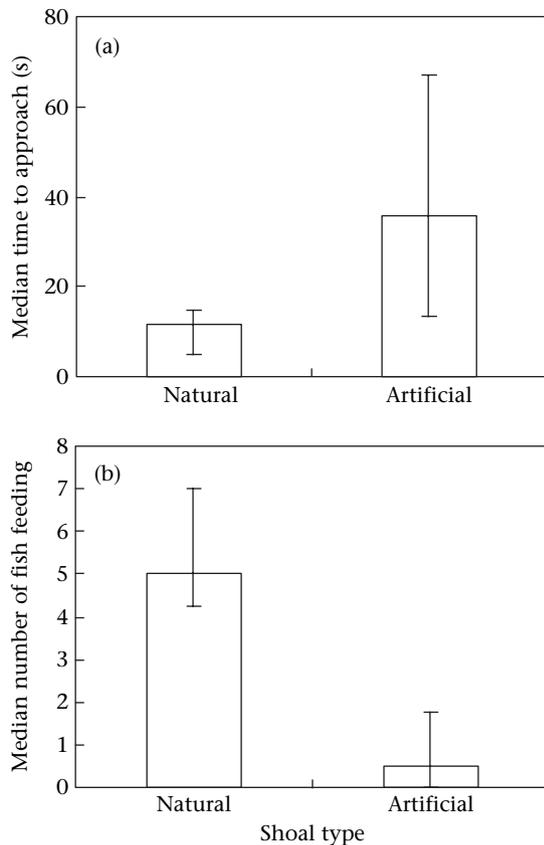
Figure 3. Results of the foraging trial comparing natural and artificial shoals. (a) Median time to approach the feeder ($Z = -2.117$, $N_{natural} = N_{artificial} = 10$, $P = 0.035$) and (b) the median number of fish feeding in each shoal ($Z = -3.752$, $N_{natural} = N_{artificial} = 10$, $P < 0.001$). Error bars indicate the interquartile range.

$N = 10$, $P = 0.216$; Fig. 4). Using all rules, there were elevated numbers of individuals that solved the task by following in the natural compared to the artificial shoals (Mann−Whitney U: 5 s: $Z = -2.282$, $N_{natural} = N_{artificial} = 10$, $P = 0.039$; 10 s: $Z = -2.868$, $N_{natural} = N_{artificial} = 10$,

$P = 0.008$; 20 s: $Z = -3.032$, $N_{natural} = N_{artificial} = 10$, $P = 0.008$). As a proportion of the total number of individuals that successfully solved the task, there was a nonsignificant trend towards a higher proportion of individuals following in natural shoals (Mann−Whitney U: 20 s: $Z = -1.810$, $N_{natural} = 10$, $N_{artificial} = 6$, $P = 0.073$).

Do individuals follow close associates when first entering the feeder?

We confined our analysis of within-shoal following patterns to natural shoals for two reasons. First, in natural shoals, individuals may be predicted to follow familiar associates, and second, successful foraging (and thus the opportunity to learn by following) occurred in only half of the artificial shoals. We found no evidence for higher associations in observed lead−follow pairs (using the 20 s rule, see Methods for definition) than would be expected if individuals followed others at random (Table 1; Fisher's omnibus test to combine P values across shoals: $F_{20} = 17.205$, $P = 0.639$).

Do individuals forage with close associates?

Previous work has suggested that individual guppies that associate in one context may also associate in another (Croft et al. 2006). We investigated whether social associations before the foraging trial were significant predictors of associations during the 30-min foraging period. We again defined a pair of fish as being associated during foraging when they entered the feeder within 20 s of one another. If individuals forage with close associates more frequently than with distant associates, we would predict a positive correlation between the social associations and the foraging associations. We used Mantel tests for matrix correlations and found no evidence to suggest that associations during foraging could be predicted by the social structure before the task (Table 1, P values combined using Fisher's omnibus test: $F_{20} = 27.93$, $P = 0.111$).

Table 1. Results of the Mantel tests for matrix comparisons and within-shoal foraging events for the 10 natural shoals only

| Shoal | Is social structure stable over time? | | Do individuals follow close associates? | Does social structure predict foraging associations? | |
	CC	P		CC	P
1	0.751	**0.003**	0.828	−0.17421	0.746
2	−0.092	0.683	0.848	−0.19205	0.827
3	0.075	0.357	0.852	−0.23796	0.919
4	0.221	0.123	0.811	−0.32566	0.960*
5	0.018	0.462	0.432	0.188126	0.220
6	0.088	0.336	0.243	0.305839	0.108
7	0.606	**0.017**	0.195	−0.00192	0.517
8	0.627	**0.002**	0.249	0.495813	**0.003**
9	0.696	**0.007**	0.211	−0.03941	0.548
10	0.530	**0.005**	0.352	0.429002	0.078
Combined P		**<0.001**	0.639		0.111

Correlations between social structure before and after the foraging trial, whether individuals first enter the feeder by following a close associate and correlations between social network structure and associations during the foraging trial are shown. P values for significant positive correlations are highlighted in bold, significant negative correlations are marked with an asterisk. Combined P values are the result of Fisher's omnibus tests (see text for details). CC: correlation coefficient.
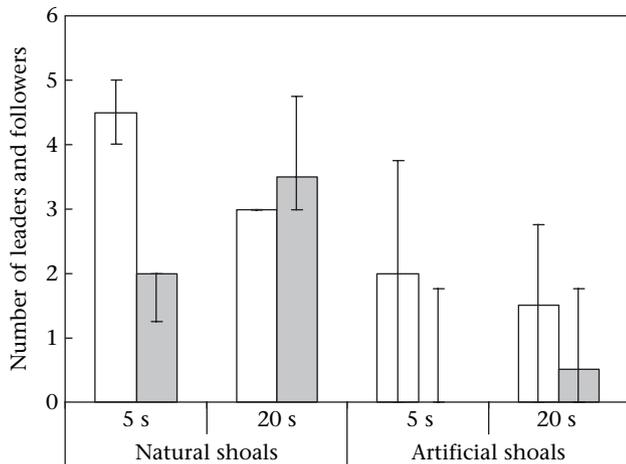
Figure 4. Median number of fish in a shoal that first entered the feeder alone (open bars) as opposed to following a demonstrator (closed bars), for both a 5- and 20-s following rule, in natural (5 s: $Z = -2.501$, $N = 10$, $P = 0.036$; 20 s: $Z = -1.279$, $N = 10$, $P = 0.201$) and artificial (5 s: $Z = -2.041$, $N = 10$, $P = 0.123$; 20 s: $Z = -1.236$, $N = 10$, $P = 0.216$) shoals. Error bars indicate the interquartile range.

DISCUSSION

Foraging Success, Boldness, Familiarity and Social Conformity

This study shows for the first time that naturally occurring fish have a foraging advantage over randomly composed shoals. In natural shoals, more individuals successfully fed from the feeder than in artificial shoals, thus benefiting from enhanced foraging success. Whereas a number of factors may have influenced the success of natural shoals, our results suggest three plausible explanations: (1) a risk perception hypothesis—differences in the perception of danger, resulting in greater risk-prone or bold behaviour in the natural shoals and more risk-averse or shy behaviour in the artificial shoals; (2) a social learning hypothesis—elevated levels of following and reduced effects of conformity in natural compared to artificial shoals; (3) a time trade-off hypothesis—differences in the prioritization of foraging and establishing social ties, resulting in reduced foraging motivation in artificial compared to natural shoals.

Several researchers have suggested that the perception of danger (resulting in risk-averse or shy behaviour) may reduce foraging motivation (Warburton 2003), information transmission and learning (Dall et al. 1999) among animals. In our study, fish in natural shoals approached the feeder more rapidly after it was placed in the experimental pool and showed a lower overall shoaling tendency (illustrated by the predominance of smaller groups and lower association strength) than fish in artificial shoals. A short latency to approach a novel object and low shoaling tendency are often used as indicators of boldness when assessing behavioural syndromes in fish (e.g. Budaev 1997; Ward et al. 2004; Brown et al. 2007). The ability (Sneddon 2003) and opportunity (Dugatkin & Alfieri 2003) for fish to learn a novel task

has previously been shown to be enhanced by increased boldness: bold fish tend to be more successful, learning more rapidly compared with shy fish. Although we cannot distinguish between behavioural types (e.g. differences in boldness or innovativeness; Sih et al. 2004) or differences in anxiety, motivational state or curiosity, our findings are consistent with the idea that associating with natural groupmates generates a reduced perception of danger.

Familiarity with the physical environment (i.e. the habitat) has been shown to influence risk perception in fishes (Brown 2001). However, this is unlikely to have played a role in the current experiment as both natural and artificial shoals had spent equal amounts of time in captivity and in the test arenas. The reduced perception of danger may instead stem from the familiar social environment experienced by the natural shoals during the experiment. In contrast, individuals in artificial shoals experience an unfamiliar social environment, in addition to the unfamiliar physical environment of the experimental pool. This may cause them to behave in a more risk-averse manner, resulting in lower foraging success compared to fish in natural shoals. It takes 12 days for familiarity to develop among members of guppy shoals (Griffiths & Magurran 1997b) and individuals in the artificial shoals (composed 36–40 h before the experiment commenced) may have moved between groups frequently to begin the process of familiarization, resulting in the observed higher and less variable levels of association in artificial compared to natural shoals. The effect of the social environment is one factor that has previously been shown to influence individual performance in tests of boldness (Griffiths et al. 2004; Sih & Watters 2005). Bhat & Magurran (2006) found that individual guppies emerged more quickly from a refuge in the presence of a familiar partner than they did when paired with an unfamiliar partner, suggesting a role for familiarity in determining perception of risk or levels of boldness. Enhanced foraging success and improved learning performance are also linked to familiarity (Swaney et al. 2001; Griffiths 2003; Ward & Hart 2003, 2005; Griffiths et al. 2004). Our work suggests that one underlying mechanism for the increased foraging success of familiar shoals may be reduced perception of risk.

A second potential explanation for the relative success of natural shoals is that they showed higher levels of social learning of the route to the food source. This hypothesis is supported by the observation that entries into the feeder were clustered in time and that levels of following in natural shoals were somewhat elevated in comparison to artificial shoals. However, clustering was evident in both natural and artificial shoals, and the proportions of individuals first entering the feeder by following were similar. One factor known to influence the level of social learning is the 'conformity effect' (positive frequency-dependent social learning) mediated by shoaling patterns (Day et al. 2001; Brown & Laland 2001). We found that in natural shoals, groups within the shoal were smaller than those in artificial shoals. Day et al. (2001) found that although individuals in larger groups are on average generally more successful at locating food than individuals in smaller groups, individuals in smaller groups can find

a resource more quickly when the resource is hidden. Day et al. (2001) attributed this to a greater reluctance on the part of individuals to leave larger compared to smaller groups. In our study, the feeder was opaque, thus, for a fish to enter and feed it needed to break visual contact with the rest of the shoal. Therefore, individuals in artificial shoals may have been more reluctant to leave their larger groups and enter the feeder than individuals in natural shoals. Alternatively, the more a shoal subdivides into smaller groups, the greater the chance that any single individual will find a hidden resource. This high level of subdivision may be due to lower levels of risk aversion linked to the familiar social environment.

A further hypothesis to explain the relative success of natural shoals is related to the prioritization of different activities in the different shoal types. Individuals in artificial shoals may prioritize learning about each other (i.e. the process of familiarization) over immediate foraging, given the benefits associated with familiarity (Griffiths 2003; Ward & Hart 2003). Larger group sizes, higher association strengths and lower variation in associations in artificial shoals compared to natural shoals support the idea that individuals are switching associations rapidly as part of this process.

Information Transmission within Shoals

Previous work has suggested that individuals benefit by learning more rapidly from familiar than from unfamiliar shoalmates (Lachlan et al. 1998; Swaney et al. 2001), as fish in familiar groups are more likely to follow one another, leading to an increase in social learning of novel tasks (Swaney et al. 2001). We found evidence that fish followed one another into the feeder and that association patterns were consistent over time, allowing us to investigate the links between associations and following patterns. However, despite our finding that association patterns before the foraging trial could be used to predict associations after the foraging trial, associations during foraging could not be predicted by previous association patterns. Neither could we find any evidence that individuals specifically followed close associates. Thus, we were unable to find any evidence that information was transmitted along strong ties in natural shoals. However, to our knowledge this is the first time a social networks approach has been used to study patterns of potential information transmission.

There may be several explanations for our findings. First, individuals may choose their social partners different from the way they choose their foraging partners. Individuals may, for example, benefit by foraging with those that they know to be poor foragers (Metcalfe & Thompson 1995), rather than with those that are preferred associates in other contexts (e.g. predator inspection; Croft et al. 2006). Second, our method of establishing the social and foraging ties may have been inadequate, although it has been previously found to be sufficient to quantify the nonrandom structure of such groups (Croft et al. 2004 online supplementary material). Third, our power to detect an effect may be reduced by the presence of random interactions creating 'noise' around the nonrandom preferred interactions.

A fourth possibility is that information may spread via local (Thorpe 1956) or stimulus (Spence 1937) enhancement, by which the activity of an individual draws the attention of an observer towards a particular location or object. Information is therefore scrounged by naïve individuals at distance, rather than acquired through close dyadic transmission. Although individuals were unable to see shoalmates while they were foraging, they may have been able to detect successful foragers after they emerged from the feeder (Lachlan et al. 1998), or the presence of individuals near the feeder may have facilitated movement towards it by naïve individuals. Individuals may therefore have learnt the task from any other individual in the shoal, rather than those with which they were strongly associated. Such exploitation of social information has been shown experimentally in fish (Ward & Hart 2003). However, information is more likely to be scrounged from close by than from farther away, and one might still expect patterns of foraging to be linked to association patterns.

Finally, we cannot rule out the possibility that the task used in this experiment was easily learned asocially by individual fish and consequently did not require social information for its solution. The movement of odour cues may have facilitated this, although they are likely to have been well contained (K. N. Laland, unpublished data), particularly without water movement to disperse them (Vogel 1994). Experiments using similar tasks, in which individuals learn the route to a foraging resource, have provided evidence for social learning (Reader et al. 2003), and we found evidence that individuals entered the feeder in small groups, suggesting foraging was a social activity. Studies in which inexperienced individuals are unlikely to learn the task themselves provide the most compelling evidence for social learning (Lefebvre & Palameta 1988); thus individuals within a shoal could be trained in a more complex task (e.g. Reader & Laland 2000; Stanley et al. 2008) and the links between social structure and foraging patterns investigated.

Further work is clearly needed to show whether reduced risk perception, social learning or a further explanation underlies the improved foraging success of natural groups. Evidence is growing for variation in behavioural types across animal species (Sih et al. 2004), and the methodology available for assessing boldness and other traits is increasing, providing the opportunity to assess individual behavioural types in relation to social environment and performance in novel tasks.

Social network techniques provide the ideal opportunity for investigating the relationship between group structure, innovation and the diffusion of information or learned behaviours (Latora & Marchiori 2001). We show that differences exist between natural and artificial shoals in terms of their social structure, but although these differences may have influenced the effectiveness of information transmission, our investigation found no direct links between social structure and patterns of learning within shoals. Further investigation may reveal a more subtle relationship between social structure and patterns

of information transfer, and we hope our study encourages this.

Acknowledgments

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