Animal Behaviour 90 (2014) 287–295

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Strong personalities, not social niches, drive individual differences in social behaviours in sticklebacks

Kate L. Laskowski [a,b,*], Alison M. Bell [b]

[a] Department of Biology & Ecology of Fishes, Leibniz Institute of Freshwater Ecology & Inland Fisheries, Berlin, Germany
[b] School of Integrative Biology, University of Illinois, Urbana, IL, U.S.A.

ARTICLE INFO

Article history:
Received 11 November 2013
Initial acceptance 17 December 2013
Final acceptance 27 January 2014
Published online
MS. number: 13-00951R

Keywords:
behavioural type
consistent individual differences
Gasterosteus aculeatus
repeatability
social niche
social specialization
threespine stickleback

Understanding the mechanisms responsible for consistent individual differences in behaviour is a recent challenge for behavioural ecology. Although theory is rapidly developing in this area, there are few empirical tests. There are at least two hypotheses to explain why individuals behave differently from one another in a dynamic social environment. The social niche specialization hypothesis proposes that repeated social interactions generate consistent individual differences in social behaviour. The behavioural type hypothesis proposes that an individual's social behaviour reflects its behavioural type. We tested these two hypotheses by manipulating the opportunity for repeated social interactions in groups of threespine stickleback, *Gasterosteus aculeatus*, and by measuring the behavioural types of the same individuals in three contexts: when in a novel environment, when presented with an opportunity to associate with conspecifics and when confronted by an intruder. We found no evidence that repeated social interactions increased between-individual variation in social foraging behaviour. Instead, individuals' social foraging behaviour was related to their behavioural type, specifically their shoaling behaviour. In addition, the behavioural types of the members of a group strongly influenced a group's average foraging behaviour. Together, these results do not support the hypothesis that social dynamics within groups generates individual differences in behaviour. Instead, they suggest the reverse: individual differences in behaviour drive group-level dynamics.

While there is growing empirical evidence for consistent individual differences in behaviour (reviewed in Bell, Hankison, & Laskowski, 2009), there are few explicit empirical tests of hypotheses explaining the potential adaptive significance of personality (but see Laskowski & Bell, 2013; Mathot et al., 2011). Social behaviour can be particularly plastic in response to the biotic and abiotic environment (reviewed in: Bergmüller, Schürch, & Hamilton, 2010; Webster & Ward, 2011), therefore emerging evidence for consistent individual differences in behaviour within social groups is especially intriguing (e.g. Pruitt, Riechert, & Jones, 2008; Sih & Watters, 2005). Some studies have found that individuals dramatically alter their behaviour in response to social stimuli, such as in groups of foraging birds (David, Cezilly, & Giraldeau, 2011; Morand-Ferron, Varennes, & Giraldeau, 2011). However, other work finds that individual differences persist despite changes in the social environment. For example, the way individual perch, *Perca fluviatilis*, behave while alone is related to their behaviour in a group (Magnhagen & Bunnefeld, 2009), and individuals maintain their behavioural type regardless of the social group (Staffan, Magnhagen, & Alanärä, 2002).

There are at least two hypotheses to explain why individuals within social groups consistently vary in behaviour. One possibility is that the social interactions themselves drive individual differences (the social niche specialization hypothesis; Bergmüller & Taborsky, 2010; Montiglio, Ferrari, & Reale, 2013). This hypothesis proposes that the presence of other individuals causes individuals to behave differently from each other to reduce direct competition, thereby generating between-individual variation in behaviour (Wolf, van Doorn, & Weissing, 2008). Once individuals behave differently from each other, the presence of others increases the benefits of behaving predictably, thereby maintaining individual differences through positive feedback mechanisms (Wolf, van Doorn, & Weissing, 2011). This process can lead to 'social niches' for each individual within a group (Bergmüller & Taborsky, 2010; Montiglio et al., 2013). These social niches can be the result of evolutionary forces, but it is also possible that ecological processes may drive the generation of social niches within the lifetime of an individual. For example, in a patchy foraging environment, individuals generally arrange themselves among patches to

* Correspondence: K. L. Laskowski, Department of Biology & Ecology of Fishes, Leibniz Institute of Freshwater Ecology & Inland Fisheries, Berlin, Germany.
E-mail address: kate.laskowski@gmail.com (K. L. Laskowski).

http://dx.doi.org/10.1016/j.anbehav.2014.02.010
0003-3472/

maximize their own food intake (i.e. the ideal free distribution, Fretwell & Lucas, 1970). The presence of other individuals can favour between-individual variation in patch use behaviour; that is, some individuals should use one patch, whereas other individuals use a different patch. If individuals forage in a predictable way, then the individuals within the group should be able to achieve the ideal free distribution more quickly in repeated encounters by reliably distributing themselves among patches. Predictable patch use behaviour could therefore increase individual payoffs by reducing competition. However, if group membership changes, then the behaviour of the individuals might change, requiring individuals to resample patches to determine their profitability. If the construction of social niches is a key driver of consistent individual differences in behaviour, then individuals within groups that have repeatedly interacted with each other should show greater between-individual differences in behaviour (for example, patch use behaviour) compared to individuals within groups that have not had the opportunity for repeated social interactions.

Another potential, nonexclusive explanation for why individuals within social groups might behave differently from one another is because their social behaviour reflects their behaviour in other contexts (i.e. their behavioural type, Sih, Bell, & Johnson, 2004). The recent interest in consistent individual differences in behaviour is in part due to the observation that individuals do not always alter their behaviour in response to changes in external cues, such as the social environment (Sih et al., 2004). The behavioural type hypothesis therefore suggests that individuals behave according to their behavioural type even within a dynamic social environment. In foraging groups, individual patch use behaviour might be a result of their behaviour in other, seemingly unrelated contexts. For example, individuals that are more exploratory might be more likely to discover a new, previously unexploited food patch (e.g. Herborn et al., 2010). Alternatively, or in addition, an individual's social tolerance might predict its foraging strategy: individuals that are more social might be less likely to exploit a new foraging opportunity if it requires that they leave the group (e.g. Cote & Clobert, 2007; Cote, Forgarty, & Sih, 2012). Finally, individuals that are more dominant and/or aggressive generally might move less between patches, excluding other less aggressive individuals from those patches (e.g. despots; Fretwell, 1972; Godin & Keenleyside, 1984; Milinski, 1984). Importantly, if an individual's social behaviour is determined by its behavioural type, then the extent of between-individual variation should not differ between groups of individuals that have and have not repeatedly interacted. In addition, individual behavioural types should act additively on the group's phenotype as a whole (Bleakley, Parker, & Brodie, 2007; Krause & Ruxton, 2002): that is, the average behaviour expressed by a group should be explained by the behavioural types of its constituent members.

We tested these two hypotheses using threespine sticklebacks, *Gasterosteus aculeatus*, a species known for its extensive behavioural variation (Bell, 2005; Dingemanse et al., 2007) and its social behaviour (reviewed in Croft et al., 2005). Sticklebacks prefer to associate with familiar individuals in the laboratory and field (Barber & Ruxton, 2000; Croft et al., 2005), suggesting that repeated social interactions among individual sticklebacks are common. We experimentally manipulated the amount of time that individual sticklebacks were housed together and then measured their social foraging behaviour while in a group. For our measure of social foraging behaviour we used latency to utilize a new food patch in a two-patch environment while in the presence of other sticklebacks (e.g. Laskowski & Bell, 2013). Prior to measuring social foraging behaviour, we also repeatedly measured the behaviour of those same individuals in three contexts that could plausibly influence their patch use behaviour. This allowed us to assess each individual's behavioural type prior to experiencing (or not experiencing) repeated social interactions with other individuals. We predicted that highly exploratory individuals would be more likely to utilize a new food patch, as has been found in wild blue tits, *Cyanistes caeruleus* (Herborn et al., 2010), that less social (low-shoaling) individuals would be more willing to leave a social group and therefore more likely to find a new food patch (Cote & Clobert, 2007; Cote et al., 2012) and that less aggressive individuals would be excluded from a food patch, making them more likely to switch patches (e.g. Fretwell, 1972; Milinski, 1984).

METHODS

Overview

We created eight groups of six size-matched, nonreproductive sticklebacks and assigned four of the groups to a 'familiar' treatment and four groups to a 'nonfamiliar' treatment (Fig. 1). After becoming familiar (or not) with other individuals within their group for 3 weeks, individuals within each group were repeatedly measured for their social foraging behaviour, where we kept track of each individual's social foraging behaviour. These data allowed us to test whether the individuals in the familiar treatment showed greater between-individual variation in social foraging behaviour, compared to individuals in the nonfamiliar treatment. In addition, prior to assigning them to their familiarity treatment groups, we repeatedly measured the behaviour of individuals while alone in three standardized assays designed to measure exploratory, shoaling and aggressive behaviour. Individuals were randomly assigned to groups (i.e. blind to their behaviour in other contexts). These data allowed us to test whether social foraging behaviour could be predicted by exploratory, shoaling or aggressive behaviour.

Animal Care and Maintenance

All individuals were wild-caught, nonreproductive individuals from the Navarro River in northern California, U.S.A. We captured 100 individuals by hand net and transported them by FedEx via overnight special delivery to our laboratory at the University of Illinois. Fish were kept in the laboratory for 3 months prior to testing and fed a daily ab libitum diet of bloodworms, *Mysis* and brine shrimp and kept on a 12:12 h light:dark cycle at a maintained temperature of 20 °C for the entirety of the experiment. One month prior to experimentation all fish were permanently individually marked with four small subcutaneous UV elastomer marks on their dorsal side with a fine-gauge needle (Northwest Marine Technologies, Inc., Shaw Island, WA, U.S.A.) while anaesthetized (5 mg/litre solution MS-222). The marking procedure took less than 30 s, and fish were restrained in the hand while marking. Fish were then allowed to recover in a well-aerated aquarium. All fish were housed in 38-litre glass aquaria with six fish (both sexes) per aquarium containing a biofilter, gravel and several plastic plants for enrichment. Opaque dividers were placed between aquaria to prevent visual interactions. There was no evidence of overt dominance or aggression in the tanks beyond what is typically observed in natural populations (K. L. Laskowski, personal observation). After completion of the experiment, animals remained housed in the laboratory until their natural deaths in the laboratory as captive animals were not allowed to be returned to the wild. All experimental protocols abide by U.S. federal and state laws and were approved by the University of Illinois' Institutional Animal Care and Use Committee protocol number 11128.

Creating Familiar and Nonfamiliar Groups

We generated groups of individual fish that differed in the amount of time they had spent together prior to being measured

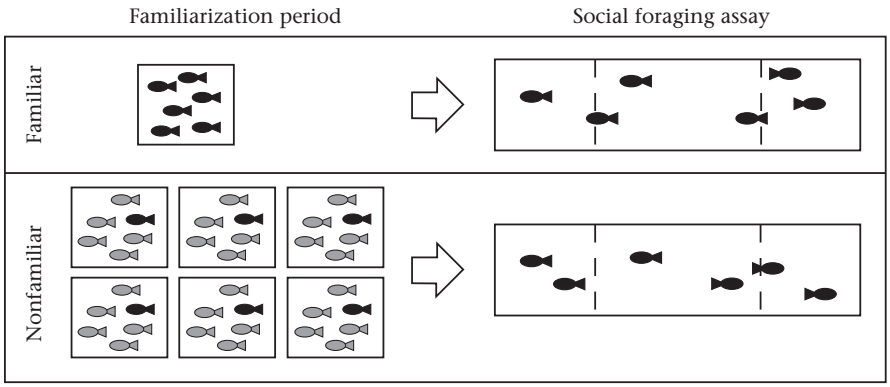

Figure 1. Schematic depicting the experimental design used to create familiar and nonfamiliar groups of fish. Each group contained six familiar or unfamiliar individuals, and we generated four groups ($N = 24$ individuals) per treatment. All individuals were housed in these treatments for 3 weeks prior to being measured for their social foraging behaviour (latency to utilize a new food patch).

for their social foraging behaviour. To create groups of familiar fish (familiar treatment), four groups of six focal individual fish were housed together for 3 weeks prior to the social foraging behaviour test. Previous work has shown that sticklebacks prefer to shoal with familiar individuals (Barber & Ruxton, 2000) and preference for familiar individuals in fishes can occur anywhere between 24 h to 3 weeks (Griffiths & Magurran, 1997; Ward, Holbrook, Krause, & Hart, 2005). We choose a 3-week familiarization period to maximize the chances that all fish would be highly familiar with others within their group. To create groups of nonfamiliar fish (the nonfamiliar treatment), focal individuals were housed with five other 'background' individual sticklebacks for 3 weeks, then measured for social foraging behaviour with five other focal individuals that were unfamiliar (Fig. 1). Therefore, in this experimental design, all fish, regardless of treatment, experienced a similar social environment in terms of group density throughout the experiment; the only difference was whether the group members were familiar or unfamiliar during the social foraging behaviour assay. As all fish were caught from a large wild population (Navarro River, CA), it is possible that individuals in the nonfamiliar groups might have previously interacted in the field. However, 3 months elapsed between capture and testing, and thus we assumed that any previous social interactions in the field should not have influenced behaviour during the time of testing.

The social foraging behaviour assay was carried out in a two-patch foraging environment. To allow individuals to become familiar with their group members' foraging behaviour, during feeding in the familiarization period we simultaneously dropped food into the aquarium via two pipettes at either end of the long axis of the aquarium.

Measuring Social Foraging Behaviour

After the familiarization period, we marked fish with small plastic tags on their pelvic spines to ensure visual identification (Webster & Laland, 2009) in the social foraging behaviour trials. These tags were cut from plastic coloured tape (3M PVC insulation tape); two pieces of approximately 4 mm square pieces were placed together by their adhesive sides. A hole was poked through the tag with a needle, and the tag was placed over the individual's pelvic spine. The tag was held in place by the spine's serrations without the need for adhesives. One group of fish was then gently netted into a water-filled cup and transferred to the social foraging behaviour arena where it remained until trials were complete. The group was allowed to acclimate for 2 days and then tested in two social foraging trials per day for 5 days. Trials performed on the same day were separated by 1 h. Therefore we had 10 observations of each individual's social foraging behaviour. Fish generally consumed all the bloodworms during a trial, and we observed no overt aggression (biting, chasing) during the trials. Fish were only fed during the trials to limit the development of individual patch preferences and increase motivation for foraging during the trials.

The social foraging behaviour arena was a long aquarium (113×30 cm and 35.5 cm deep; 120 litres) with a food patch at either end and a neutral area in between. Food could be dropped independently into either patch. The experimental protocol for the trials is a modification of previously published methods (Laskowski & Bell, 2013). Briefly, each trial consisted of two 5 min periods. In the first 5 min period, bloodworms were added at a rate of 10 bloodworms/min to only one patch of the arena. The patch that received food first was randomly chosen. In the second 5 min period, bloodworms were then added at a reduced rate (five bloodworms/min) to both patches. This meant that a second food patch became available in the second part of the trial. We measured how quickly each individual moved into the second, newly available food patch during the second part of the trial (latency to utilize a new food patch) as our measure of social foraging behaviour (Laskowski & Bell, 2013). Therefore, an individual that quickly utilized the new food patch had a short latency. Individuals that did not move into the new food patch within the 5 min of the second part of the trial were given a maximum latency of 300 s. If an individual was already in the second patch when the patch began receiving bloodworms, we could not assign a latency score to that individual for that trial. In total, for the 38 individuals that completed the experiment we recorded 339 observations of latencies to utilize the new food patch.

Measuring Exploratory, Shoaling and Aggressive Behaviours

To determine whether behaviour in the social foraging assay reflected an individual's behavioural type, we measured all individuals in three contexts designed to measure exploratory, shoaling and aggressive behaviour. To ensure that behaviour in these contexts was not influenced by the familiarity treatment, these assays were carried out 2 weeks prior to the familiarization period. Each fish was measured in each context twice to determine whether individuals behaved consistently within each context. Twelve fish were measured per observation day and all behavioural observations were conducted in a fixed order (exploratory, then shoaling, then aggressive behaviour; Bell, 2013), but each fish was observed in a random order. Individuals were then assigned to their familiarity treatment group blind of their behaviour in these assays.

Fish were remeasured in all three behavioural contexts 1 week later to determine whether individuals differed consistently in behaviour. We tested a total of 48 individuals; however, 10 fish died of natural causes before they could be tested in the social foraging assay, resulting in a total sample size of 38 ($N = 19$ per treatment; mortality was even across the treatments). This mortality rate was similar to that experienced by other fish kept in the laboratory that were not part of the study. Fish that died were replaced with other (nonphenotyped) fish in the social foraging trials to maintain the same density ($N = 6$) within each group, but we excluded data on the social foraging behaviour of the replacement fish. We captured an individual from its home tank and quickly checked its UV elastomer marking and, if it was an experimental fish, it was placed into a water-filled cup and transferred to a small opaque cylinder in the centre of the exploratory arena. The exploratory arena consisted of a 1.8 m diameter blue plastic kiddie pool divided into nine equal sections: one circular centre section and eight sections around the outside. The centre section contained a small plastic plant next to the acclimating cylinder, and each of the outside sections contained a small rock pile for cover.

The individual was allowed to acclimate in the cylinder for 3 min, after which the cylinder was raised remotely from behind a blind exposing the focal fish. We then removed the cylinder from the arena and measured the time it took for the individual to begin freely swimming. The purpose of this assay was to assess the exploratory behaviour of the focal individual in response to an open field environment (as in Bell, 2005). After the individual began swimming, we measured its behaviour for an additional 5 min. As our measure of exploratory behaviour we measured the total number of sections that an individual swam between. Individuals that did not begin swimming within 5 min were given a score of '1' for the total number of sections explored (28 out of 76 trials) and the trial was terminated. After the trial was complete we noted the section where the focal individual was located and began the shoaling behaviour assay.

The shoaling behaviour assay was performed immediately after the exploratory assay. The purpose of this assay was to assess an individual's tendency to remain close to a small group of conspecifics (modified from Ward, Thomas, Hart, & Krause, 2004). We haphazardly selected two conspecific sticklebacks to act as stimuli from a large group of about 30 sticklebacks and placed them in a water-filled glass flask. We confined the stimulus fish to a flask as preliminary observations showed they would otherwise hide among the rocks in the arena. The stimulus fish were all given time to settle after being placed in the flask and before being used in a trial to reduce any stress-related behaviour. The flask was placed in the section directly next to the focal individual. The conspecifics were from the same population and were not used for any other part of this experiment. After the stimulus fish were added to the arena, we recorded the behaviour of the focal individual. Orienting behaviour occurred when the focal individual turned directly towards the flask. After the focal individual oriented towards the flask, we measured the total time spent within one body length of the flask for 5 min as our measure of shoaling behaviour. If a focal individual did not orient towards the flask within 5 min, the trial was terminated and the individual received a score of '0' for the total time spent within one body length of the flask (30 of 76 trials). After completion of the shoaling behaviour trial, the focal individual was gently netted out of the arena and placed in an aggression observation arena ($35.5 \times 35.5 \times 35.5$ cm; 42 litres) by itself where it remained until the next morning. Preliminary observations indicated that overnight acclimation promoted dominance and aggression in the focal individuals.

The purpose of the aggression assay was to assess the behaviour of the focal individual in response to a simulated intrusion by a single conspecific (as in Bell, 2005). Preliminary observations demonstrated that maximal aggression by the focal fish was elicited when confronted by a free-swimming intruder that was slightly smaller than the focal fish. Therefore, we presented the focal fish with an intruder that was 10% smaller, selected from a large pool of nonexperimental individuals. The intruder was placed into a small opaque cylinder within the aggression observation arena and allowed to acclimate for 3 min. After 3 min, the cylinder was lifted remotely and removed from the arena, allowing the intruder to swim freely. We measured the total number of bites directed towards the intruder by the focal individual for 5 min after the first orient. Note that these 'bites' were superficial in nature. The intruder was not bodily injured; rather the focal fish 'pecked' at the intruder. If the focal individual did not orient towards the intruder within 5 min, the trial was terminated and the focal individual was given a score of '0' for the total number of bites directed towards the intruder (9 out of 76 trials). After the trial was completed, the intruder was removed and the focal individual was gently netted and placed back into its home tank.

Ethical Note

All collected individuals were transported in specially approved plastic bags, one-third filled with oxygenated water (8–10 individuals per bag), and placed inside an insulated cooler in a large box. All fish were received at the University of Illinois the next day; there was no mortality during transport. Of these 100 fish, we used only healthy nonreproductive individuals for the study. Previous work (Laskowski & Bell, 2013) has shown that a sample size of 18 individuals is adequate to detect consistent individual differences in behaviour in threespine sticklebacks, but we increased this to 24 individuals per treatment to account for the expected normal mortality rates over the course of the experiment.

All fish were marked with subcutaneous UV elastomer while anaesthetized. This marking was necessary to identify permanently all experimental fish (i.e. external tags occasionally fall off). Each fish was marked at four sites on its dorsal side with up to three different colours which provided enough unique markings to identify individually all experimental animals. No fish suffered detrimental effects from the elastomer markings. All fish were also tagged with a small plastic tag on their pelvic spine that was necessary for visual identification on the videos of the social foraging assays (elastomer markings are not visible on camera). The tags were removed at the completion of the assays. Three fish developed small fungal infections at the site of the plastic tag when it was removed at the end of the experiment. These fish were treated with standard antifungals (tea tree oil) for 1 week and all recovered with no detectable detrimental effects.

Although sticklebacks are a social species, it was necessary to measure the focal individuals' exploratory behaviour while in isolation to minimize the confounding effects of other individuals; in the shoaling and aggression assays, individuals were measured in the presence of other individuals as was necessary to characterize these inherently social behaviours. We opted to use live encounters between the focal fish and a free-swimming intruder to measure aggressive behaviour as preliminary observations showed that the focal fish did not act aggressively towards an intruder that was confined to a flask. The intruder could seek refuge from the focal fish by hiding in the plastic plant, which caused the focal fish to ignore the intruder (K. L. Laskowski, personal observation). Prior to the experiments we determined that we would stop any observation that resulted in bodily injury or exhaustion to the intruder. However, the biting behaviour by the focal fish towards the intruder was superficial and never resulted in any injury to the intruder. We limited observations to 5 min as preliminary

observations demonstrated this interval was adequate to characterize the variation in aggressive behaviour without injuring or exhausting the focal or intruder fish.

Data Analysis

We first tested for differences in latency to utilize the new food patch between the familiarity treatments using a linear mixed model with treatment as a fixed effect. We also included trial and its interaction with treatment as fixed effects to test whether foraging behaviour changed with repeated testing. Group and individual (nested within group) were included as random effects. To test whether familiarity among group members increased consistent individual differences in behaviour, we compared the repeatability and variance components of latency to utilize a new food patch between the two familiarity treatments. Repeatability (r) is the proportion of total variation that can be attributed to between-individual differences in repeated measures data. We ran a separate model for each treatment with the 10 observations of latency to utilize the new food patch as the response variable and individual and group as random effects. We included no fixed effects as we wished to provide a conservative measure of between- and within-individual variation (Dingemanse & Dochtermann, 2013). We used a Gaussian error distribution as preliminary analyses showed a Poisson or other error distribution worsened the fit (as assessed by the deviance information criterion; data not shown). As variance estimates are inherently tied to the total variation present in the response variable, to enable comparison across models, we first mean-centred and scaled the variance of our response variable to 1 within each treatment. We used Markov-chain Monte Carlo simulations to estimate the variance components as this is an especially powerful method to estimate the variance associated with different random factors (Dingemanse & Dochtermann, 2013). We used MCMCglmm in R version 2.14.0 (Hadfield, 2010) to partition the variation into its components, which we then used to estimate repeatability (Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010). Bayesian methods such as MCMC are useful for variance component comparison as they return 95% credibility intervals, which are used to test whether a component estimate differs significantly from zero and whether it differs significantly from other estimates. For each simulation, we used weakly informative inverse-gamma distribution priors (Hadfield, 2010), although changing the priors had little to no effect on the repeatability estimates (data not shown). We ran a total 500 000 iterations with a 1000 burn-in and thinning every 100 iterations for each model. We checked for proper model mixing and convergence by running five independent chains for each model and inspecting the autocorrelation and posterior distributions of the model effects.

We also tested whether an individual's exploratory, shoaling and/or aggressive behaviour predicted its social foraging behaviour. We first tested whether individuals showed behavioural types by estimating the repeatability of behaviour across the two test periods using the same methods as described above. We ran a separate model for each behaviour (exploratory, shoaling or aggressive behaviour), with the two observations of each behaviour as the response variable, and included individual as a random effect. All behaviours were best approximated by a Gaussian error distribution as preliminary analyses showed model fit was worsened by using a Poisson or other error distribution (data not shown). We also estimated Pearson correlations among the individual averages of each behaviour to determine whether there were between-individual correlations in exploratory, shoaling and aggressive behaviour, which would be indicative of a larger behavioural syndrome. We measured each individual's exploratory, shoaling and aggressive behaviour prior to the familiarity treatment and social foraging behaviour assays, and we wished to test whether variation in these behaviours could predict an individual's social foraging behaviour. To do this, we regressed each individual's average latency to utilize a new food patch (average of 10 observations) on its average exploratory, shoaling and aggressive behaviour (average of two observations). Finally, we also tested whether the behavioural types of the members of a group influenced that group's average social foraging behaviour. To do this, we regressed each group's average latency to utilize a new food patch on each group's average exploratory, shoaling or aggressive behaviour.

RESULTS

Variation Between and Within Groups

Fish in the nonfamiliar treatment took a mean ± SE of 105.7 8 s to utilize a new food patch, and fish in the familiar treatment took a mean of 92.0 ± 7 s. The difference in average latency to utilize a new food patch did not differ between familiarity treatments ($F_{1,6} = 0.72$, $P = 0.43$) or change over time (trial: $F_{1,299} = 0.14$, $P = 0.70$; treatment*trial: $F_{1,299} = 0.10$, $P = 0.75$).

Within each treatment, there was extensive variation between individuals in latency to utilize a new food patch: variation spanned the entire range (0.5–300 s) in both treatments. The repeatability of latency to utilize a new food patch was significantly greater than zero in both familiarity treatments (Table 1). However, contrary to the social niche specialization hypothesis, we did not detect greater between-individual variation in latency to utilize a new food patch in the familiar fish, compared to the nonfamiliar fish, as evidenced by repeatability estimates (familiar: $R = 0.09$, 95% CI: 0.02, 0.22; nonfamiliar: $R = 0.16$, 95% CI: 0.04, 0.35) and the individual variance components in the two treatments (Table 1).

Although the two familiarity treatments did not differ in the extent of variation between individuals, they did differ in the extent of variation between groups within the treatments: between-group variation accounted for a significant portion of the variation in the familiar treatment (group variance estimate = 0.19, 95% CI: 0.03, 0.46; Table 1, Fig. 2), whereas there was essentially zero variation between groups in the nonfamiliar treatment (group variance estimate = $6.9e^{-9}$, 95% CI: $5.7e^{-10}$, $1.1e^{-8}$; Table 1, Fig. 2).

Variation in Exploratory, Shoaling, and Aggressive Behaviours

There was consistent individual variation in exploratory, shoaling and aggressive behaviour. Individuals explored 1–59 sections during the 5 min exploratory trial (mean ± SE = 7.8 ± 1.2 sections), and this variation was consistent over time ($R = 0.43$, 95% CI: 0.21, 0.66). Individuals also showed consistent individual differences in the total time spent shoaling with conspecifics ($R = 0.22$, 95% CI: 0.07, 0.38), with some individuals shoaling not at all and others shoaling for nearly the entire 5 min trial (279 s).

Table 1
Variance component estimates of latency to utilize to a new food patch in the familiar and nonfamiliar treatments

Estimate	Familiar	Nonfamiliar
Group	0.19 (0.03, 0.46)	$6.9e^{-9}$ ($5.7e^{-10}$, $1.1e^{-8}$)
Individual	0.11 (0.02, 0.28)	0.20 (0.04, 0.49)
Residual	0.95 (0.75, 1.16)	0.95 (0.76, 1.15)
Repeatability	0.09 (0.02, 0.22)	0.16 (0.04, 0.35)

Each linear mixed model included the random effects of group and individual and was estimated using Markov-chain Monte Carlo simulations. Repeatability of the latency to utilize a new food patch was calculated as the individual variance component divided by the total variance. The 95% credibility intervals are given in parentheses.

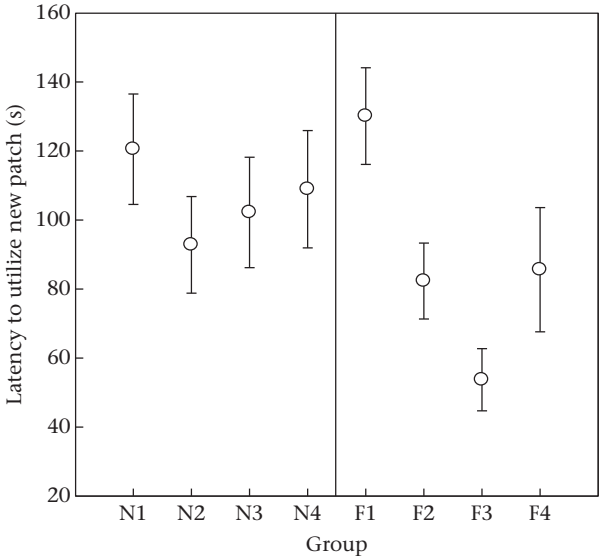

Figure 2. Between-group differences in social foraging behaviour. Average latency to utilize a new food patch in each treatment group. Each data point shows the group mean ± SE. N1–N4: nonfamiliar treatment groups; F1–F4: familiar treatment groups.

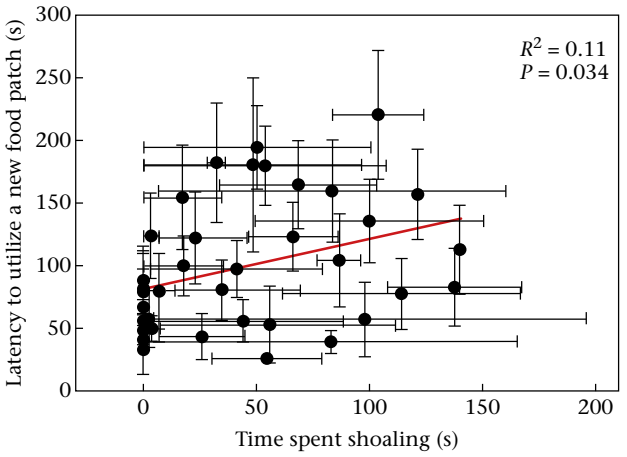

Figure 3. Between-individual relationship between shoaling behaviour (averaged across two trials) and social foraging behaviour (averaged across 10 trials). Data points represent individual means ± SE ($N = 38$).

Finally, there was also dramatic individual variation in aggressive behaviour, some individuals never bit the intruder while others bit 151 times during the 5 min trial (average = 25 times). Individual variation in aggressiveness was also consistent over time ($R = 0.62$, 95% CI: 0.42, 0.80). There was evidence of a behavioural syndrome as individuals that were highly aggressive were also highly exploratory and also showed high shoaling behaviour (Table 2). Individuals that were highly exploratory also tended to shoal more, but this difference was nonsignificant after correcting for multiple comparisons (Table 2).

We tested whether individual variation in exploratory, shoaling and aggressive behaviour could explain the individual differences in latency to utilize a new food patch, as predicted by the behavioural type hypothesis. There was no evidence that individuals that were less aggressive showed faster latencies to utilize a new food patch (aggression: $R^2 = 0.01$, $P = 0.52$). Individuals that were more exploratory tended to utilize the food patch more quickly, although this was not strictly statistically significant (exploration: $R^2 = 0.07$, $P = 0.10$). Individuals that spent less time associating with conspecifics in the shoaling assay were more likely to utilize a new food patch quickly while in a group ($R^2 = 0.11$, $P = 0.034$; Fig. 3).

The behavioural type hypothesis also predicts that the average behaviour of a group can be explained by the behavioural types of its members. Consistent with this hypothesis, individual differences in the shoaling behaviour assay translated into group-level differences in social foraging behaviour (Fig. 4): the average shoaling behaviour of the individuals that composed a group significantly predicted the group's average latency to utilize a new food patch ($R^2 = 0.73$, $P = 0.007$; Fig. 4b). Specifically, groups composed of fish that showed low shoaling behaviour quickly utilized a new food patch while in a group (Fig. 4b). There was no detectable relationship between a group's average latency to utilize a new food patch and its average exploratory ($R^2 = 0.06$, $P = 0.56$; Fig. 4a) or aggressive ($R^2 = 0.08$, $P = 0.51$; Fig. 4c) behaviour.

Table 2
Pearson correlations between each individual's average behaviour in each context

	Exploration	Shoaling	Aggression
Exploratory	—	0.38 (P=0.02)	0.57 (P=0.002*)
Shoaling		—	0.48 (P=0.002*)
Aggression			—

* Remained significant after Bonferroni correction for multiple testing.

DISCUSSION

Contrary to the social niche specialization hypothesis, we found no evidence that repeated social interactions among group members resulted in greater between-individual variation in social foraging behaviour in sticklebacks. Instead, between-individual variation in social foraging behaviour was related to variation in behavioural types. In particular, the individuals that shoaled less with conspecifics were also the individuals that were more likely to utilize a new food patch quickly in the social foraging assay. In addition, the behavioural types of constituent individuals within a group had a dramatic impact on the average social foraging behaviour of that group.

Understanding the mechanisms responsible for between-individual variation in behaviour is a primary goal for the study of animal personality. Recent theoretical models predict that individuals within groups may differentiate and specialize on certain behaviours in an effort to reduce competition with group members (Wolf et al., 2008; Wolf et al., 2011). Individual diet specializations are known to be strongly driven by intraspecific competition (Bolnick et al., 2003), and recently this idea has been expanded to the social context (i.e. 'social niche specialization'; Bergmüller & Taborsky, 2010; Montiglio et al., 2013), making this a plausible mechanism driving between-individual variation in social foraging behaviours. A previous study in sticklebacks (Laskowski & Bell, 2013) found that between-individual variation in a social foraging behaviour increased the longer the group had been together, which suggested that positive feedback mechanisms enhanced between-individual variation through repeated social interactions. Here we explicitly tested this hypothesis, and our results suggest that the pattern found previously was not likely to be caused by repeated social interactions. An alternative explanation for Laskowski and Bell's (2013) finding is that the change in individuals' behaviour was due to learning, without the need for repeated social interactions: with repeated testing some individuals learned how to exploit a new food patch quickly, whereas others learned to remain

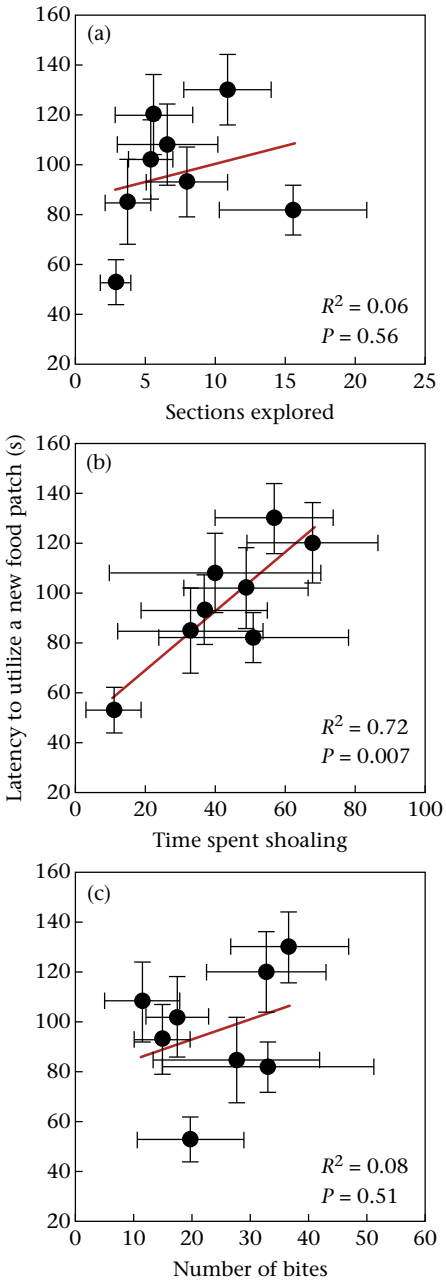

Figure 4. Between-group relationships between social foraging and other behaviours. Relationship between a group's average latency to utilize a new food patch and its average (a) exploratory, (b) shoaling and (c) aggressive behaviour. Data points represent group means ± SE ($N = 8$).

in the old patch. In our current experiment, individuals were trained in the two-patch feeding design during the familiarization period. Therefore, once the individuals were placed in the social foraging assay they had already learned to exploit two patches.

It is possible that familiarity does not promote individual variation in sticklebacks because their social structure is fairly fluid, marked by fission–fusion dynamics (Croft et al., 2005; Ward et al., 2002). Individual sticklebacks leave and join shoals throughout the day (Ward et al., 2002), and while certain pairs of individual sticklebacks are found together more often than predicted by random chance, pairs are still frequently found within larger groups of (potentially nonfamiliar) sticklebacks (Croft et al., 2005), which might mask any effect of repeated social interactions within the pair. Evidence that group member interactions promote personality variation might be more likely to be found in species with more stable social groups (e.g. cichlids, *Neolamprologus pulcher*: Schürch, Rothenberger, & Heg, 2010; social spiders, *Anelosimus studiosus*: Pruitt et al., 2008; marmots, *Marmota flaviventris*: Armitage, 1986).

It is still possible that repeated social interactions might generate between-individual variation in behaviour in sticklebacks, but our experiment failed to capture it effectively. We might be more likely to detect effects of repeated social interactions on the behaviour of juveniles, when behaviour might be especially susceptible to social influences (Chapman, Ward, & Krause, 2008; Sundström, Lohmus, & Johnsson, 2003). Another possibility is that 3 weeks of familiarization is not adequate for individuals to develop social niches, although this seems unlikely given that sticklebacks are known to prefer familiar individuals after only 24 h (Ward et al., 2005). Another potential explanation is that social dynamics might actually suppress between-individual variation in behaviour via social conformity (Day, MacDonald, Brown, Laland, & Reader, 2001; Kendal, Coolen, & Laland, 2004). It also seems likely that both social niche specializations and behavioural types may influence individual behaviour in other contexts and/or other systems. An individual's behavioural type may determine how it first behaves within a group, but then repeated social interactions may act to reinforce or potentially change that behaviour. For example, a study on cichlids found that juvenile aggression predicted adult aggression under some circumstances, but this changed with time spent in a social group (Schürch & Heg, 2010). More studies are needed to investigate further the potential interactions and feedbacks between an individual's behavioural type and its social role.

Although our results are not consistent with the social niche specialization hypothesis, they are consistent with the hypothesis that an individual's behaviour while in a social group reflects its behaviour while alone. Individuals showed stable individual differences in exploratory, shoaling and aggressive behaviour, and there was evidence of a larger behavioural syndrome linking these behaviours. Specifically, an individual's shoaling behavioural type was related to its latency to utilize a new food source. This suggests that an individual's tendency to associate with other individuals might be an important determinant of its foraging behaviour: low-shoaling individuals might be especially willing to leave the safety of the group (e.g. Herborn et al., 2010). While social foraging behaviour was related to individual differences in shoaling behaviour, it was not related to exploratory or aggressive behaviour. One possible explanation for the failure to find a relationship with exploratory behaviour is that the sticklebacks might not have perceived the social foraging arena as novel and potentially risky because they were allowed to acclimate to the arena for 2 days prior to testing. Moreover, while an earlier study found that more dominant sticklebacks excluded less aggressive sticklebacks from a food patch (Milinski, 1984), it is possible that aggressiveness was not related to social foraging behaviour in our study because we never observed overt aggressive interactions among any individuals during the social foraging trials.

In support of the behavioural type hypothesis, individuals maintained their behavioural types despite the experience of repeated social interactions, and individual differences in behaviour translated into group-level differences in average social foraging behaviour. This result demonstrates that the average behaviour of a group can vary depending upon the group's behavioural composition. Other studies on this population have also found evidence of strong behavioural types and behavioural syndromes (Bell, 2005; Laskowski & Bell, 2013). Differences between groups in average foraging behaviour could have important consequences in the wild, such as differences in the ability to find

and consume resources. Important between-group variation in behaviour has been found in several other studies, such as water striders and social spiders, where the behaviour of the constituent group members can influence a group's behaviour and fitness (Pruitt, 2012; Sih & Watters, 2005). If individuals show strong behavioural types, then there may be pressure for individuals to choose the most appropriate group given their own behavioural type (e.g. Saltz, 2011; Sih & Bell, 2008). This sort of social selection is an exciting area for future research. We attempted to standardize group composition by sorting individuals into treatment groups blind to their behaviour, but the most likely explanation for the between-group differences we observed is that we incidentally nonrandomly assigned individuals with somewhat similar behavioural types to the same group. Given the small number of treatment groups in total (eight groups), this possibility is not unrealistic.

Altogether, our results provide strong support for the hypothesis that individuals can retain their distinctive personalities even in a dynamic social situation. We also show that the behavioural types of individuals can result in differences between groups that may have functional importance (e.g. food intake). These findings are in direct contrast to other studies that have suggested that individual behaviour is socially contingent: the behaviour of zebra finches, *Taeniopygia guttata* (David et al., 2011), nutmeg mannikins, *Lonchura punctulata* (Morand-Ferron et al., 2011) and sticklebacks (Webster, Ward, & Hart, 2007) changes dramatically when placed in a new social context. There is growing interest in interactions between an individual's behavioural type and its social context, and a need for theory and data to explain why individual behaviour is socially contingent in some species, or in some situations, but not others.

Acknowledgments

We thank Kelly Hogan and Nick Yohanna for help with the behavioural observations and video coding. Pierre-Oliver Montiglio and two anonymous referees provided valuable comments that improved the manuscript. This work was supported by the National Institutes of Health (R01 GM082937), the National Science Foundation (DDIG 1110791 and IOS 1121980) and a Sigma Delta Epsilon (SDE)//Graduate Women in Science (Eloise Gerry Fellowship).

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