



Stable social groups foster conformity and among-group differences

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The social niche hypothesis theorizes that repeated social interactions between group members is an important mechanism for generating consistent individual differences in behaviour. However, such frequent interactions also have the potential to mask or suppress behavioural differences if individuals conform towards a group behavioural norm (i.e. the social conformity hypothesis) by either synchronizing their behaviour or shifting their behaviour towards that of influential group members. Both of these predictions hinge on the notion that social feedback among group members plays a key role in modulating consistent behavioural variation; thus, in the absence of such feedback, it could be expected that such consistent variation will be reduced. Here, we investigated how a 1-month housing with a stable social group, as opposed to being socially isolated, affected consistent individual differences in the shoaling tendencies of threespine stickleback, *Gasterosteus aculeatus*. Specifically, we repeatedly tested the tendency of individual sticklebacks to shoal with conspecifics before and after their social experience. In support of the social conformity hypothesis, we observed a four-fold increase in among-group differences, but no change in among-individual differences, in the shoaling tendencies of sticklebacks housed in groups. A post hoc analysis revealed that the increase in among-group differences may have been driven by the most 'social' pretreatment group member. Conversely, fish that were housed in isolation, expressed a notable, albeit nonsignificant, decrease in individual shoaling variation and repeatability. This decrease in shoaling variation corresponded with an increase in the average shoaling tendencies of solitary fish post-treatment, suggesting that solitary fish converged towards a similarly high level of shoaling tendencies post-treatment. For both treatment groups, however, we found among-individual positive correlations in pre- and post-treatment shoaling tendencies, suggesting that individuals may inherently differ in their shoaling tendencies, but that the social environment plays an important role in mediating the expression of these differences.

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Across the animal kingdom, individuals often exhibit both between-individual differences and within-individual consistency in their behaviour (Bell, Hankison, & Laskowski, 2009). Consistent individual differences in behaviour, sometimes referred to as behavioural types or animal personality (Réale et al. 2007; Sih, Bell, & Johnson, 2004), have important ecological consequences (Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2012) and persist despite sometimes leading to suboptimal responses (e.g. Johnson & Sih, 2005). Evidence for consistent individual differences in behaviour in many species continues to grow, but empirical evidence of the mechanisms that generate consistent individual variation remain in question (Sih et al., 2015).

Early work on consistent behavioural variation studied animals in isolation but quickly expanded to consider the role of the individual's behavioural type in shaping group behaviour (Brown & Irving, 2014; Harcourt, Sweetman, Johnstone, & Manica, 2009; Pike, Samanta, Lindström, & Royle, 2008) and the effect that the group has on the individual's behavioural expression (Michelangeli, Smith, Wong, & Chapple, 2017; Montiglio, Ferrari, & Réale, 2013; Niemelä & Santostefano, 2015). While in some instances behavioural types seem to remain inflexible to social experience (Laskowski & Bell, 2014), the social context has been proposed as an important factor for generating and maintaining consistent individual differences in behaviour (Bergmüller & Taborsky, 2010; Montiglio et al., 2013; Wolf, Van Doorn, & Weissing, 2011). In particular, the social niche hypothesis builds on seminal ecological niche theory to explain patterns of both among-individual differences and within-individual consistency in behaviour (Bergmüller & Taborsky, 2010; Montiglio et al., 2013). Repeated social interactions among individuals in a social group can lead to character

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displacement. Positive feedbacks then keep individuals in a consistent social role (or niche) due to the benefits of specialization for the individual and group, and the associated costs of switching between behavioural strategies (e.g. increased conflict). Indeed, variation among social members has been shown to improve group coordination (Nakayama, Stumpe, Manica, & Johnstone, 2013), reduce competition (Laskowski & Bell, 2014), potentially foster the division of tasks (Dall, Bell, Bolnick, & Ratnieks, 2012; Loftus, Perez, & Sih, 2020; Modlmeier, Liebmann, & Foitzik, 2012) and improve network stability (Dakin & Ryder, 2020), all of which can ultimately lead to greater individual and/or group success. The key prediction is that repeated social interactions should lead to stronger consistent differences among individuals in behaviour.

Social living also has the potential to mask or suppress behavioural differences if individuals conform towards a group behavioural norm (i.e. the social conformity hypothesis; King, Williams, & Mettke-Hofmann, 2015; Fürtbauer & Fry, 2018; McCune, Jablonski, Lee, & Ha, 2018; Webster & Ward, 2011). Social conformity can occur via two processes; individuals within groups can either synchronize their behaviour (i.e. meet in the middle) or shift their behaviour towards that of influential or extreme group members (Brown & Irving, 2014; Fürtbauer & Fry, 2018; Jolles, Boogert, Sridhar, Couzin, & Manica, 2017). Importantly, both forms of social conformity can have similar, but also different, effects on the expression of consistent individual differences. If individuals converge towards a behavioural middle ground, among-individual differences should become less pronounced. For instance, eastern mosquitofish, *Gambusia holbrooki*, exhibit individuality in locomotory behaviour when tested in isolation, but when in groups, locomotion converges towards the mean of the group, and as a result, among-individual variation in locomotory behaviour is lost (Herbert-Read et al., 2013). On the other hand, if individuals shift their behaviour to more closely match influential or 'extreme' individuals in the group, then conformity can occur with or without the loss of among-individual variation (e.g. if all individuals in the group equally shift their behaviour dependent on a key individual). However, regardless of how social conformity occurs, as individuals conform towards the behavioural rules of the group, a key prediction is that groups will become more distinct and that consistent among-group differences will emerge (Webster & Ward, 2011).

Theoretically, the emergence of social niches and social conforms are more likely to arise and be maintained when group membership is also relatively stable through time. This is because long-term interactions between familiar individuals should become more predictable, allowing social learning to occur and social constructs to stabilize (Webster & Ward, 2011). Another shared assumption of both hypotheses is that social feedback from group members modulates the consistency of behavioural expression. If this is true, then individuals that are isolated from social interactions should exhibit less consistency in their behavioural expression due to the absence of social information and/or competitive feedback from conspecifics.

Here, we investigated how social experience affects consistent individual differences in shoaling tendencies of threespine sticklebacks, *Gasterosteus aculeatus*. This was achieved by testing how a relatively long-term exposure to a stable social group, as opposed to being socially isolated, affected both among-individual differences and within-individual consistency in shoaling tendencies. We first tested the shoaling tendency of sticklebacks twice, after which they were either housed in stable groups or in isolation for 1 month. Following 1 month in their social treatment, we retested each individual's shoaling tendencies twice. Given that long-term social experience is expected to strengthen consistent individual differences in behaviour (i.e. the social niche hypothesis), we predicted that fish that were housed in groups would exhibit increased

among-individual variation and hence, repeatability in shoaling tendencies, whereas fish that were housed in isolation would exhibit reduced individual differences. Alternatively, if fish housed in social groups conform towards a group behavioural norm (i.e. the social conformity hypothesis), then we should expect to see an increase in among-group variation and/or a decrease in among-individual variation in shoaling tendencies.

METHODS

Animal Collection and Husbandry

Sticklebacks were wild-caught over 3 days in June 2019 using minnow traps and seine netting from Beaver Pond, Davis, California, U.S.A. (38°31'39.3"N, 121°48'41.5"W). We used two different capture methods, seine netting and minnow traps, to minimize any behaviour-dependent trapping bias in our sample population (Michelangeli, Wong, & Chapple, 2016). Only young-of-the-year, nonreproductive individuals were retained. Following collection, fish were immediately transported to the Center for Aquatic Biology and Aquaculture, University of California, Davis.

Focal fish were housed in 75.7-litre tanks in groups of 15, and additional stimulus fish were housed in groups of 10 in 37.8-litre stock tanks. Tanks were kept in a temperature-controlled room that was maintained at a temperature of 18 °C, on a 12:12 h light:dark cycle, for the entirety of the experiment. All tanks contained a biofilter, gravel, and plastic plants and PVC pipes for enrichment, and were wrapped in black plastic on three sides to visually separate all tanks. Fish were fed ad libitum a diet of frozen bloodworms, *Daphnia* and spirulina brine shrimp. Fish were housed in the laboratory for 2–3 weeks prior to testing. A week before starting the experiment, focal fish were individually tagged with a minimally invasive, unique, permanent identification code using visible implant elastomer (VIE; Northwest Marine Technology, Anacortes, WA, U.S.A.). All fish were anaesthetized using 150 mg/litre MS-222 before being injected with two colour tags, one above and one below the dorsal line. Fish were then weighed and photographed for total length. The marking procedure took less than 30 s per fish. Fish were allowed to recover in a well-aerated 18.9-litre tank prior to being returned to home tanks.

Experimental Procedure

Sticklebacks were randomly assigned to one of two social treatments: solitary ($N = 41$) or group ($N = 80$). There was no difference in body length (mean \pm SD: solitary: 40.59 \pm 5.98 mm; group: 41. \pm 5.1940 mm) or weight (mean \pm SD: solitary: 0.55 \pm 0.25 g; group: 0.58 \pm 0.24 g) of fish in each treatment. Each treatment experienced the following experimental procedure (also see Appendix, Fig. A1).

Stage 1: pretreatment shoaling tendency assays

Before social treatments were applied, we first measured the individual shoaling tendency of each stickleback (assay details are outlined below). Individuals were tested twice, with each retest occurring 3 days apart to assess short-term repeatability (Bell et al., 2009). Shoaling tendency assays were conducted between 0900 and 1400 hours within temperature-controlled rooms that matched the fish housing temperature (18 °C). All assays were videorecorded and later played back using Jwatcher (Blumstein, Evans, & Daniels, 2006).

Stage 2: application of social treatment

Once the pretreatment shoaling tendency assays were completed, focal fish were placed into their social treatment for 4

weeks. Specifically, fish assigned the group treatment were placed into a 75.7-litre tank housing 10 fish. Group tanks contained roughly size-matched fish (average within-tank body length deviation 1.72 ± 0.63 mm). We also ensured that fish were placed in group tanks with unfamiliar individuals, those who they did not experience during the initial housing period, to avoid any carryover familiarity effects. We could not control for potential familiarity effects arising from the time fish spent together in the wild prior to capture. Fish assigned to the solitary treatment were placed into one half of an 18.9-litre tank that was split halfway by netting preventing fish from using the entire tank. This was done in order to hold fish at similar densities in the two treatments. We did not place another fish in the other half of the solitary tank (i.e. fish had the entire tank to themselves). All tanks contained a biofilter, gravel and plastic plants and PVC pipes, and were held under the same light and temperature conditions as during pretreatment period. We also wrapped the outside of all tanks with black opaque plastic to avoid any outside visual cues from surrounding tanks. During the treatment period, fish were fed ad libitum a diet of frozen bloodworms, *Daphnia* and spirulina brine shrimp. Fish in the social treatment were allowed to interact and swim freely together in the tank, as well as compete for food. Note, however, that while we did not try to spread food equally among fish, fish were fed regularly and food was distributed around the tank (rather than at a single source point), thus any competition for food was likely limited. Any fish that died in the group tanks during the treatment period ($N = 19$) was replaced by a similarly sized fish from a stock tank to maintain treatment densities, but replacement fish were not used in shoaling tendency assays. Two solitary fish also died during the treatment phase but were not replaced. After accounting for fish mortality, final sample sizes were $N = 61$ for the group treatment and $N = 39$ for the solitary treatment.

Stage 3: post-treatment shoaling tendency assays

Following the 4-week treatment period, we again tested the shoaling tendencies of sticklebacks twice using the same experimental procedure outlined in stage 1. Overall this three-stage protocol allowed us to test the effects of social experience on individual shoaling tendencies and behavioural variation.

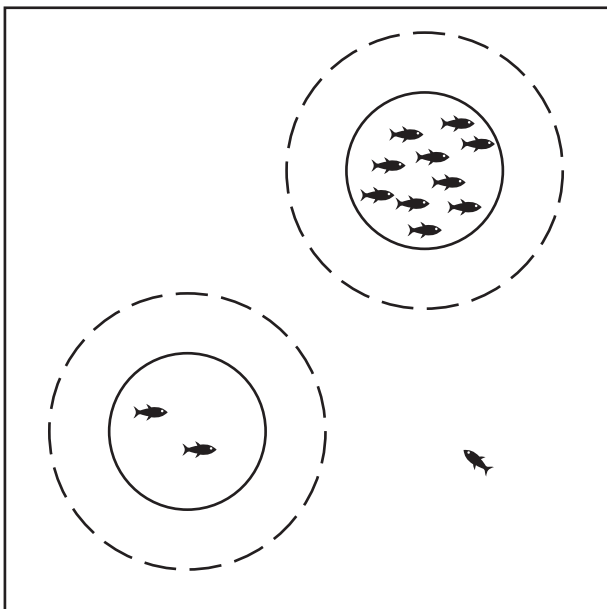


Figure 1. Diagram of the shoaling tendency assay.

Shoaling Tendency Assay

The shoaling tendency assay was conducted in six large square arenas (50×50 cm at the base with water to a depth of 10 cm) with sloped sides, surrounded with white curtains to limit glare and visual disturbances. There were two marked 23 cm circles; one in the front left and one in the back right corner of the arena. These two circles marked out two shoaling zones: a large shoal zone and a small shoal zone. The large shoal zone contained 10 stimulus fish within a 3.78-litre glass jar, whereas the small shoal zone contained two stimulus fish also within a 3.78-litre glass jar (see Fig. 1 for an illustration of the experimental set-up). We gave focal fish the choice between two different shoal sizes, as opposed to a choice between a shoal and no shoal zone, as such a design has previously been shown to reveal greater variability in shoaling behaviour of sticklebacks (Wark, Wark, Lageson, & Peichel, 2011). Jars were placed in the centre of the marked circles such that there was a 5 cm border surrounding the jar. Stimulus fish were haphazardly selected from stock tanks and gently transferred via nets to the glass jars and allowed to settle for approximately 15 min so as to limit any stress-related behaviours prior to the start of the assay. The positions of the small and large shoals were switched after every trial with all stimulus fish being exchanged every two trials to minimize the amount of time stimulus shoals were in jars but also to reduce handling time between trials.

Focal fish were then netted from home tanks and placed in a stiff net tube in the front right corner of the arena and allowed to acclimate to test conditions for 5 min. After the acclimation period, the net tube was gently removed and the individual fish was allowed to explore the arena for 10 min. During this 10 min period, we recorded the time the fish spent within the large and small shoaling zones. We also measured the average duration per visit that a focal fish spent in each zone to account for fish that were highly active and regularly moving in and out of the zones rather than spending continuous time within the zones. At the end of the trials, focal fish were netted and returned to their home tank.

Ethical Note

All procedures were in accordance with U.S. federal and state laws and were approved by the University of California, Davis Institutional Animal Care and Use Committee protocol number 21086. After the experiment, all fish were maintained in the laboratory for future experiments pending ethical approval.

Fish handling, tagging and identification

To generally minimize stress in fish, handling time was restricted to experimental periods only. Fish were also provided with large aquaria space containing vegetation and shelter to provide a safe environment and minimize any stress related to the presence of humans. Visible implant elastomer (VIE) is a commonly used tagging method in small animals. Tagging with VIE involves injecting two biological inert colour tags into the fish's dorsal fin (one above and one below the dorsal line). All fish were anaesthetized using 150 mg/litre MS-222 before the injection to minimize any discomfort. The marking procedure took less than 30 s per fish. Fish were allowed to recover in a well-aerated 18.9-litre tank prior to being returned to home tanks. Stimulus fish were allowed 15 min to settle in jars before the commencement of shoaling assays to minimize stress. Any fish that appeared distressed during this 15 min acclimation period were immediately removed and placed back into their housing tanks. Furthermore, stimulus fish were exchanged every two trials to minimize the amount of time stimulus shoals were in jars but also to reduce handling time between trials.

Sample size justification

A key aim of our research was to quantify intraspecific behavioural variation, both within and between treatment groups. Based on past research working on the sticklebacks (e.g. [Laskowski & Bell, 2014](#)), and in light of the inherent variation normally associated with behavioural data, we used the minimally required sample sizes (solitary treatment, $N = 41$; group treatment, $N = 70$) for adequate statistical power to fulfil our aim.

Statistical Analysis

Data analysis was conducted in R v.3.3.2 (R Core Team, <http://www.r-project.org>). All variables were first square-root transformed and entered into a principal component analysis (PCA) to reduce the behavioural metrics taken from the shoaling tendency assay (i.e. total time and mean duration per visit with the large shoal, time spent with neither the large shoal nor the small shoal) into a single standardized shoaling tendency score. We used a PCA to capture a more complete behavioural profile of the shoaling tendency assay than the alternative approach of using a single measured behavioural metric (e.g. time spent in the large shoaling zone). Principal components were chosen based on the 'broken-stick criterion' in which components are retained if their eigenvalues exceed those expected by random chance ([Tabachnick & Fidell, 2013](#)). We used the resulting PC1 score, which explained 84% of the variation, as our response variable for the rest of the analysis, with larger scores corresponding to greater shoaling tendencies (i.e. more time spent shoaling, on average, but particularly with the large shoal; see [Appendix](#), Table A1). Because our PCA combined data from each trial and treatment (i.e. did not consider repeated measures and within-treatment variation), we also cross-checked our resulting PCA scores to PCA scores derived from PCAs that only contained data from each treatment and trial separately, but we found no differences (see [Appendix](#) for details).

We used the Bayesian packages MCMCglmm ([Hadfield, 2010](#)), brms ([Bürkner, 2017](#)) and rethinking ([McElreath, 2016](#)) for mixed effects modelling. Data were modelled with a Gaussian distribution, and models were checked for adequate mixing, autocorrelation and convergence. Models with different priors were compared to ensure that our final choice of prior did not heavily influence our results (results not shown here). We report posterior modes for all estimated parameters (fixed and random effects), and inference is based on the overlap of 89% credibility intervals ([McElreath, 2016](#)).

Effect of social treatment on average shoaling tendency

We used a Bayesian univariate mixed effects model to determine how social treatment influenced mean shoaling tendency. The model contained treatment, stage (pre- and post-treatment), treatment*stage interaction, test arena, trial number (T1 or T2), position of the large shoal during testing (i.e. front or back of arena) and body length as predictors. Fish identity (ID) was included as a random effect. We also initially included a stage*trial number interaction but found it had little influence on the model and thus removed this term from the final model. Test arena was included as fixed factor because two of the arenas (arenas 5 and 6) were slightly larger than the others. We were primarily interested in testing for a significant treatment*stage interaction, which would suggest that social treatment had an effect on average shoaling tendency.

Effect of social treatment on shoaling variance and repeatability

To determine whether variation in shoaling tendency changed as a result of social treatment, we first compared models where the variance components (among-individual variation, V_{ind} , within-individual variation, V_{res} , and both V_{ind} and V_{res}) were allowed to vary between treatments to a null model where the

variances were set to be equal between treatments ([Royauté & Dochtermann, 2020](#)). This was done separately for both pre- and post-treatment social tendency scores. This model comparison allowed us to assess whether social treatment had an effect on the variance components. Models contained treatment, trial number, arena, location of the large shoal and body length as fixed factors. Model comparisons were performed using the deviance information criterion (DIC), where smaller DIC values are preferred, and values >5 indicate substantial differences between models ([Barnett, Koper, Dobson, Schmiegelow, & Manseau, 2010](#)). DIC is a generalization of the Akaike information criterion (or AIC) for Bayesian analysis and is similarly a measure of model fit that penalizes for model complexity ([Spiegelhalter, Best, Carlin, & Van Der Linde, 2002](#)).

We then used separate Bayesian bivariate mixed models for each treatment to calculate and compare repeatability and the associated variance components of shoaling tendencies before and after the social treatment was applied. Bivariate models for each treatment contained both the pre- and post-treatment shoaling tendency scores as response variables and trial number, test arena and position of the large shoal during testing as predictors. Fish ID was included as a random factor. We also included group ID as a random factor in the group treatment model to account for possible variation arising among group tanks. Large among-group variation would suggest that groups differed in their average shoaling tendencies. Using the variance components extracted from the bivariate models, we then calculated individual repeatability (R_{ind}). We also calculated a group repeatability for the group treatment (R_{Group}). Individual repeatability was calculated as the proportion of variation attributed to among-individual (or group) differences relative to the total phenotypic variance. A repeatability with a value higher than 0.5 indicates that most of the observed behavioural variation is due to differences among individuals ([Nakagawa & Schielzeth, 2010](#)), but on average, behavioural repeatability tends to be around 0.37 (i.e. 37% of variation is explained by among-individual differences in behaviour; [Bell et al., 2009](#)). By including predictors in our bivariate models, our repeatability estimates control for the variation potentially arising from experimental deviations among shoaling trials ([Nakagawa & Schielzeth, 2010](#)). These models also allowed us to estimate the individual behavioural variance components separately for pre- and post-treatment measurements, as well as the among-individual covariance (which we standardized to correlations) between pre- and post-treatment scores. We report R_{ind} , R_{Group} , V_{ind} , V_{Group} and V_{res} , as well as the differences in repeatability and variance components between pre- and post-treatment scores (ΔR , ΔV_{ind} , ΔV_{Group} and ΔV_{res}). The latter measurements provide an estimation of the effect size for the differences in variances between pre- and post-treatment scores, whereby positive values indicate greater variances post-treatment. If the social niche hypothesis is true, and social interactions between group members lead to the divergence and consistency in individual shoaling behaviour, then we should expect to see a significant increase in V_{ind} and a significant decrease in V_{res} post-treatment in socially housed fish. Alternatively, if the social conformity hypothesis is true, and social interactions between group members lead to individuals shifting their behaviour towards a group behavioural norm, then we should expect to see either an increase in V_{Group} and/or a decrease in V_{ind} post-treatment in socially housed fish.

Finally, we conducted a post hoc analysis on the group treatment data to test whether observed among-group differences in post-treatment shoaling tendencies were driven by individuals within each tank with the highest or lowest pretreatment shoaling tendency scores (i.e. the most behaviourally 'extreme' individuals in each group). Mixed effects models contained individual post-

treatment shoaling tendency scores as the response variable and the average maximum and minimum pretreatment individual shoaling score within each tank as a fixed factor. We also included group and individual ID nested within group as random factors.

RESULTS

Effect of Social Treatment on Average Shoaling Tendency

We found evidence of a treatment*stage interaction in our model, suggesting that social treatment had an effect on average shoaling tendency (Table 1). To disentangle the interaction, we explored each treatment separately. Sticklebacks exhibited a higher shoaling tendency after being housed in isolation for 1 month (mode of posterior distribution [89% CIs]: 0.73 [0.57, 0.90]; Fig. 2). Sticklebacks that were housed in groups for 1 month also exhibited an increase in shoaling tendency following treatment, but this difference was smaller and nonsignificant (0.18 [-0.02, 0.37]; Fig. 2). Overall, larger fish spent less time shoaling than smaller fish (Table 1), and fish, regardless of treatment and stage, spent less time shoaling in the second trial, suggesting a consistent habituation effect to the assay (Table 1). There were also experimental effects. Fish tended to shoal more when the location of the large shoal was located at the front of the arena (Table 1). Second, there was an effect of test arena, which is likely result of slight variations in the size of the test arenas (Table 1), but this did not influence our main results of interest. Summary statistics for shoaling tendency scores are provided in the Appendix, Table A2.

Effect of Social Treatment on Shoaling Repeatability and Variance

We found evidence of changes in the variation underlying shoaling behaviour following social treatment. All pretreatment models had similar support to the null model ($\Delta\text{DIC} < 2.3$; Table 2), suggesting that there were no clear differences in shoaling variation between solitary and group fish prior to the social treatment. However, for the post-treatment model comparison, the model allowing differences at the among-individual level and the model allowing differences at both the among- and within-individual levels had similar support, with the remaining models, including the null model, being strongly rejected ($\Delta\text{DIC} > 10$; Table 2). This suggests that social treatment had an effect on shoaling behavioural variation.

We found a substantial increase in shoaling variation following the treatment period in socially housed fish (see Table 3), but this increase was mostly driven at the among-group level (ΔV_{Group} : 0.42

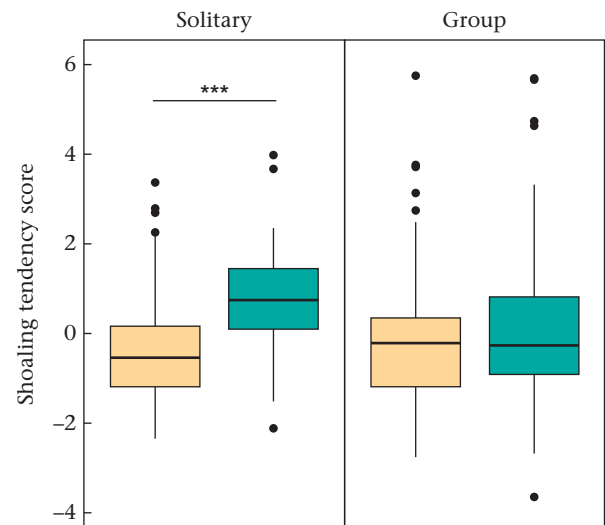


Figure 2. Shoaling tendency scores of sticklebacks pre (yellow box plots) and post (green box plots) social treatment. Box plots show 25th, 50th (median) and 75th percentiles with horizontal lines. Outliers are represented by filled circles.

Table 2

Model comparison for testing the effects of social treatment on variance components (V_{ind} : among-individual variance; V_{res} : within-individual variance) pre- and post-treatment

	Pretreatment		Post-treatment	
	DIC	ΔDIC	DIC	ΔDIC
Null model	505.78	2.27	515.73	18.46
V_{ind} -only model	505.65	2.14	501.70	4.43
V_{res} -only model	504.10	0.59	509.55	12.28
$V_{\text{ind+res}}$ model	503.51	0.00	497.27	0.00

The null model constrained V_{ind} and V_{res} to be equal between social treatments. V_{ind} -only model allowed V_{ind} to differ between treatments. V_{res} -only model allowed V_{res} to differ between treatments. $V_{\text{ind+res}}$ model allowed both variances to differ between treatments. Bold scores indicate the best model based on the deviance information criterion (DIC), and italicized scores indicate models with equal support to the best model ($\Delta\text{DIC} < 5$).

[0.07–1.59]; Fig. 3). This suggests that social groups diverged in their average shoaling tendencies following the treatment period (Fig. 3). Our post hoc analysis revealed that the observed group divergence in average shoaling tendencies post-treatment may have been driven by the individuals in each tank that had the

Table 1

Effect of social treatment (solitary or group), stage (pre- and post-treatment), position of the large shoal in arena during testing (front or back), trial number (T1 or T2) test arena (1–6) and body length on average shoaling tendencies

Random effect	Fixed effect	Estimate [89% CI]
Individual ID	Intercept: Treatment (solitary)	-0.09 [-0.38, 0.20]
$V_{\text{ind}} = 0.47$ [0.35, 0.60]	Treatment (group)	0.25 [0.01, 0.50]
$V_{\text{res}} = 0.81$ [0.75, 0.88]	Stage (post-treatment)	0.73 [0.51, 0.94]
	Large shoal arena position (front)	0.24 [0.09, 0.39]
	Arena 2	-0.24 [-0.52, 0.05]
	Arena 3	0.01 [-0.27, 0.29]
	Arena 4	-0.19 [-0.47, 0.09]
	Arena 5	-0.52 [-0.80, -0.24]
	Arena 6	-0.33 [-0.61, -0.05]
	Trial (T2)	-0.32 [-0.45, -0.19]
	Body length	-0.20 [-0.30, -0.10]
	Treatment (group) × stage (post)	-0.56 [-0.84, -0.28]

Significance of fixed effects was based on the overlap of 89% credibility intervals [CI] with zero (highlighted in bold). V_{ind} and V_{res} indicate the variance for the among-individual and within-individual components of the phenotypic variance estimated through the random effect of individual identity (ID).

highest shoaling tendency scores in the pretreatment assays (0.79 [0.34, 1.24]), and not by the individuals with the lowest pretreatment shoaling tendency scores (-0.51 [-1.27, 0.30]; Fig. 4, Appendix, Fig. A1). We also found no clear change in shoaling variation at the among-individual level (<0.01 [-0.27, 0.35]) or the within-individual level (0.05 [-0.25, 0.32]) in socially housed fish post-treatment. Fish housed in isolation exhibited a nonsignificant decrease in among-individual (-0.12 [-0.40, 0.12]) and within-individual (-0.09 [-0.29, 0.11]) variation after the social treatment (Fig. 3, Table 3).

Shoaling tendencies were repeatable pretreatment for both solitary (R_{ind} : 0.38 [0.13, 0.62]) and group fish (0.25 [0.08, 0.43]; Table 3, Fig. 3), with an overall repeatability of 0.25 [0.16, 0.34]. We found no group level repeatability in socially housed fish pretreatment (<0.01 [0, 0.10]). However, given the substantial increase in among-group level variation post-treatment, group repeatability also increased significantly following the social treatment (ΔR_{group} : 0.44 [0.18, 0.71]). In contrast, individual shoaling repeatability slightly decreased for socially housed fish (ΔR_{ind} = -0.08 [<0.01, 0.52]). Shoaling tendencies were no longer repeatable in solitary housed fish post-treatment ($R < 0.01$ [0, 0.45]), although the decrease in repeatability between pre- and post-treatment shoaling tendency scores was nonsignificant (ΔR_{ind} = -0.12 [-0.45, 0.22]). These results suggest that consistent individual differences in shoaling tendencies did not substantially change in fish that were housed in groups or for fish that were housed in isolation. Instead, we found nearly a four-fold increase in consistent among-group differences post-treatment. Thus, our results do not provide support for the social niche hypothesis, but instead are more aligned with the social conformity hypothesis.

Finally, we also found significant, positive among-individual correlations in social tendency scores pre- versus post-treatment in both solitary and group fish, although there was large uncertainty around the estimates (Fig. 5, Table 3). The correlation was also strong when considering all fish together ($r = 0.72$ [0.32, 0.97]). These results suggest that fish that had the highest shoaling tendencies pretreatment also tended to have the highest shoaling tendencies post-treatment, regardless of social experience. However, we did not find among-group correlations in social tendency scores pre- versus post-treatment in socially housed fish. This further suggests that consistent group level shoaling tendencies emerged only after a period of familiarization among group members.

DISCUSSION

The social niche hypothesis predicts that consistent among-individual differences in behaviour arise when individuals frequently interact, allowing social roles or niches to emerge (Bergmüller & Taborsky, 2010; Montiglio et al., 2013). Based on this hypothesis,

Table 3
Variance components, individual repeatability, tank repeatability and among-individual correlation estimates for pre- and post-treatment shoaling tendency assays (posterior mode [89% credible intervals])

	Solitary				Group			
	Pretreatment	Post-treatment	$\Delta\text{Post-Pre}$	Correlation	Pretreatment	Post-treatment	$\Delta\text{Post-Pre}$	Correlation
V_{ind}	0.213 [0.03, 0.48]	0.002 [0, 0.23]	-0.121 [-0.40, 0.12]	0.63 [0.05, 0.97]	0.245 [0.05, 0.47]	0.257 [0.06, 0.54]	-0.004 [-0.27, 0.35]	0.866 [0.47, 0.99]
V_{tank}	—	—	—	—	0.001 [0, 0.08]	0.393 [0.11, 1.59]	0.419 [0.07, 1.59]	-0.034 [-0.67, 0.89]
V_{res}	0.403 [0.26, 0.57]	0.297 [0.21, 0.44]	-0.094 [-0.29, 0.11]	—	0.687 [0.55, 0.94]	0.718 [0.56, 0.97]	0.05 [-0.25, 0.32]	—
V_{total}	0.497 [0.31, 0.84]	0.413 [0.30, 0.58]	-0.068 [-0.43, 0.20]	—	0.930 [0.64, 1.20]	2.105 [1.49, 3.33]	1.288 [0.48, 2.45]	—
R_{ind}	0.376 [0.13, 0.62]	0.003 [0, 0.45]	-0.12 [-0.45, 0.22]	—	0.25 [0.08, 0.43]	0.15 [0.02, 0.65]	-0.08 [-0.304, 0.12]	—
R_{tank}	—	—	—	—	0.001 [0, 0.10]	0.443 [0.22, 0.73]	0.439 [0.18, 0.71]	—

V_{ind} : among-individual variation; V_{tank} : among-tank variation; V_{res} : within-individual variation; V_{total} : total phenotypic variation; R_{ind} : individual repeatability; R_{tank} : tank repeatability. The difference between pre- and post-treatment variances and repeatability ($\Delta\text{Post-Pre}$) was calculated such that positive values indicate an increase in variation post-treatment. Bold scores represent significant difference between pre- and post-treatment estimates.

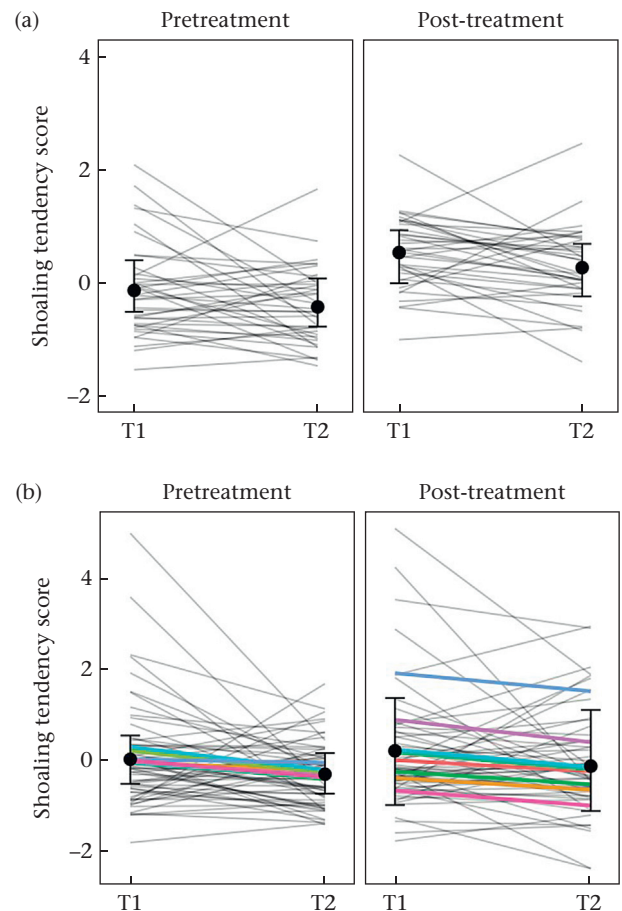


Figure 3. Shoaling tendency scores for (a) solitary fish and (b) group fish in trial 1 (T1) and trial 2 (T2) during pre- and post-treatment shoaling tendency assays. Points represent model predicted trial means with 89% credibility intervals. Coloured lines in (b) represent group random intercepts to illustrate differences in among-group shoaling variation between pre- and post-treatment shoaling tendency assays.

we predicted that sticklebacks would exhibit a substantial increase in among-individual variation and repeatability in their shoaling tendencies following a 1-month period of being housed in stable social groups. However, our results did not support this prediction. Instead, we found a four-fold increase in among-group variation and no change in among-individual variation in shoaling tendencies of group-housed fish following the 1-month social treatment. These results suggest that groups became consistently more different in their average shoaling tendencies, but that individuals within these groups did not. Moreover, among-group divergence in

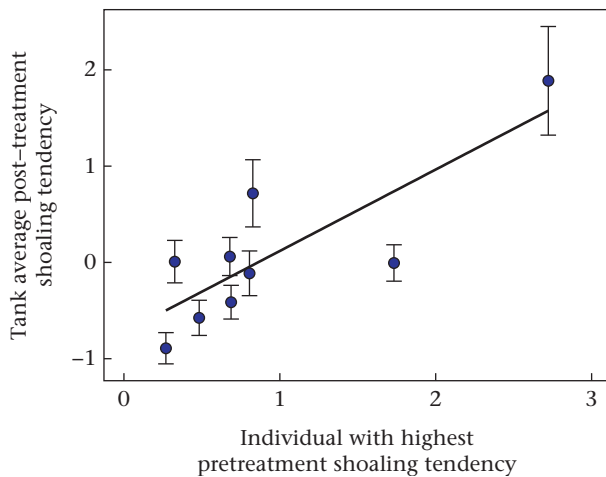


Figure 4. Positive correlation between mean (\pm SE) group post-treatment shoaling tendency scores and the individual with the highest pretreatment shoaling tendency scores (i.e. the most ‘social’ pretreatment individual in each group).

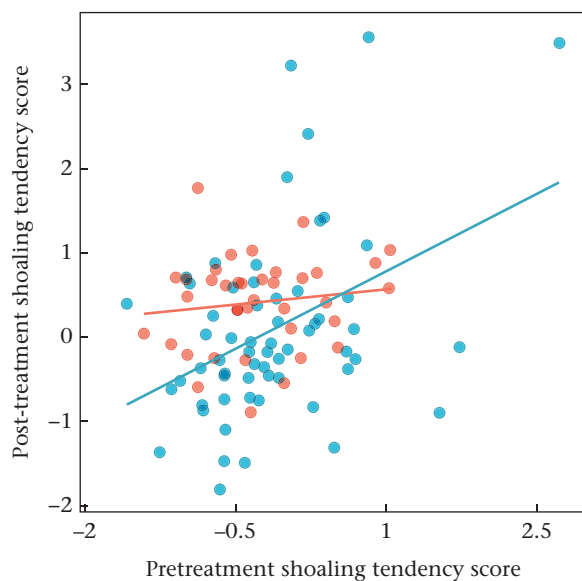


Figure 5. Correlation between the average pre- and post-treatment shoaling tendency scores for each individual. Red = solitary fish; blue = group fish.

shoaling tendencies appears to have been driven by the most ‘social’ pretreatment individual in each tank, rather than by individuals in each tank converging towards a group mean. Together, these results provide support for the social conformity hypothesis, as opposed to the social niche hypothesis (Webster & Ward, 2011). Furthermore, prior to treatment, fish housed alone initially exhibited significant differences among individuals ($V_{ind} > 0$) and significant repeatability in shoaling tendency, but after being held in isolation for 1 month, they no longer exhibited significant differences among individuals (V_{ind} close to zero) or significant repeatability in shoaling tendency. Broadly, these results suggest that social interactions play a pivotal role in generating variation at the group level and modulating variation at the individual level, and that when such social feedback is absent, consistent variation does not arise.

The results of our study also support a previous study on sticklebacks showing that an individual's behavioural type in a nonsocial context is a better predictor of within-group variation in

social foraging behaviour than are repeated social interactions between group members (the social niche hypothesis) (Laskowski & Bell, 2014). While we did not test other behaviours in our sticklebacks, we did find that regardless of treatment, fish that had the highest shoaling tendency scores pretreatment also had the highest shoaling tendency scores post-treatment (i.e. significant among-individual correlations). This finding concurs with a number of other studies that have also found the presence of consistent shoaling types in sticklebacks (Bevan, Gosetto, Jenkins, Barnes, & Ioannou, 2018; Jolles et al., 2017; Laskowski & Bell, 2014; Ward et al., 2002; Wark et al., 2011). Together, these results suggest that sticklebacks may inherently differ in their shoaling tendencies due to some proximate mechanism (e.g. genes, hormones), but that the degree to which these differences are expressed is modulated by the social environment.

Social behaviours like shoaling tendencies may be more likely to change and persist across contexts as a result of social conformity, compared to other behaviours like exploration or boldness that are less inherently social (Koski & Burkart, 2015). Because many social behaviours typically require two or more actors, learning and positive reinforcement over time may lead groups to behave more similarly to match the effort invested by other group members. Social species, in particular, that benefit more strongly from group cohesiveness may be more likely to elicit behavioural uniformity among group members particularly in behaviours related to shoaling (e.g. average distance to nearest neighbours; Jolles, Laskowski, Boogert, & Manica, 2018; McDonald, Rands, Hill, Elder, & Ioannou, 2016; Webster & Ward, 2011). Indeed, a previous study on sticklebacks showed that differences in group shoaling dynamics primarily emerged as a result of group members (followers) conforming to the fastest-moving individual in the group (the leader) (Jolles et al., 2017). The authors also found that swimming speed and shoaling proximity to group members were negatively correlated traits, suggesting that the post-treatment differences in among-group shoaling tendencies that we observed in our study may be the result of individuals conforming towards the shoaling tendencies of the most extreme individual in the group. Accordingly, after performing a post hoc analysis, we found that among-group divergence in shoaling tendencies may have been driven by the individuals with the highest pretreatment shoaling tendency scores within each tank (Fig. 4, Appendix, Fig. A2). This seems to be particularly true for one tank (G7) that contained a particularly social pretreatment individual. Given that this result was not part of our initial hypothesis, we only treat it as supplementary here, but nevertheless, it provides a potentially interesting example that warrants further study of how behaviourally ‘extreme’ individuals can serve as key ‘influencers’ that govern social group outcomes.

Evidence for the social conformity hypothesis has typically come from studies showing that changes in consistent individual behavioural tendencies are dependent upon whether the individual is tested in a social or asocial (solitary) context. For example, Gouldian finches, *Erythrura gouldiae*, alter their behaviour from an asocial context to more closely match the behaviour of their social partner in a social context (King et al., 2015). In the current study, however, we found that socially housed fish altered their consistent shoaling tendencies after the treatment period despite having their shoaling tendencies tested with unfamiliar individuals. This suggests that social conformity could have potential lasting effects on the expression of individual behavioural tendencies even across contexts, as long as social conforms are provided enough time to emerge and stabilize. The long-term effects of social conformity might be dependent on the number of factors including the length of time social groups are together, the stability of group membership, group size and the behaviour in question.

In contrast to sticklebacks housed in groups, sticklebacks housed in isolation were deprived of the opportunity for social interaction. Sticklebacks in the solitary treatment also experienced the greatest alteration in housing conditions during the experimental period as they were initially housed in social conditions prior to the beginning of the experiment. Consequently, it appears that the shoaling tendencies of solitary fish post-treatment may have been primarily driven by a desire for social contact, as on average, individuals significantly increased the time they spent shoaling after being isolated for 1 month. Sticklebacks use conspecifics to acquire information about the environment, such as the location of food resources, and to lower predation risk (i.e. dilution effect; [Harcourt, Biau, Johnstone, & Manica, 2010](#)). Thus, solitary sticklebacks potentially increased their shoaling tendencies following isolation due to being deprived of group safety and social information for an extended period.

Shoaling tendencies were also no longer repeatable in solitary fish after their social isolation. This may have occurred because solitary fish in general exhibited similarly high social tendencies post-treatment, hence reducing among-individual variance in this behaviour. Previous studies have shown that isolation of social species can induce greater social behaviour ([Gómez-Laplaza & Morgan, 2000](#); [Riley et al., 2018](#)), as well as hinder behavioural variation and consistency ([Han & Brooks, 2014](#)). For instance, tree skinks (*Egernia striolata*) reared in isolation were initially more social than skinks reared in groups but also became more homogeneous in their social associations over time ([Riley et al., 2018](#)). The effects of social isolation on behavioural variation may also be behaviour dependent ([Gómez-Laplaza & Morgan, 2000](#)). A previous study on sticklebacks, for example, found that individual variation in boldness was higher in fish that had been isolated for 3 days compared to fish housed in groups ([Jolles, Taylor, & Manica, 2016](#)). Indeed, when sticklebacks are alone, consistent individual differences in boldness emerge, but when tested in groups, shy individuals become bolder likely due to the antipredator benefits of shoaling, potentially leading to lower among-individual variation in risk-taking behaviour ([Bevan et al., 2018](#); [Jolles et al., 2018](#); [Webster, Ward, & Hart, 2007](#)). Because of the relatively low number of individual repeats of the shoaling tendency assay in our study, we were unable to determine how different social behavioural types responded to changes in social conditions (i.e. behavioural type-dependent plasticity or reaction norms; [Dingemanse, Kazem, Réale, & Wright, 2010](#)), but this would be an interesting follow-up study.

Our research also adds to a growing number of studies demonstrating the effect of social housing conditions on behavioural expression and repeatability (e.g. [Bevan et al., 2018](#); [Han & Brooks, 2014](#); [Jäger, Han, & Dingemanse, 2019](#); [Jolles et al., 2016](#)). Biologists interested in studying consistent individual differences in behaviour, particularly in laboratory settings, need to carefully consider housing social conditions when designing their experiments. As work on sticklebacks has shown, including the current study, the appropriate choice of social housing conditions is not only dependent on the study species being used, but also on the behaviour being tested ([Jolles et al., 2016](#); [Laskowski & Bell, 2014](#)). For example, in our study, we found that social isolation can dampen among-individual variation in shoaling tendencies, whereas other work has shown that isolation can increase individual differentiation in boldness ([Jolles et al., 2016](#)). Our results suggest that social species should not be left in isolation for long periods, as their behaviour in the wild is likely mediated by

information received within the social environment, and thus social isolation might lead to biased and erroneous biological interpretations regarding individual differences in behaviour.

To conclude, we did not find evidence for the social niche hypothesis, but instead found some evidence of social conformity. Sticklebacks housed in stable social groups for 1 month experienced a four-fold increase in among-group variation in shoaling tendencies and no clear change in among-individual variation. Divergence in group mean shoaling tendencies may have been mediated by the most 'social' individuals in the group as determined by their pretreatment shoaling tendency scores. On the other hand, sticklebacks housed in isolation for 1 month experienced an overall decrease in shoaling variation and were no longer repeatable in their shoaling tendencies. Our results broadly suggest that behaviours related to group cohesiveness and performance are more likely to be mediated by social conformity. Furthermore, we also found among-individual correlations in shoaling tendencies between pre- and post-treatment assays, suggesting that social behavioural types in sticklebacks can persist over time (at least over 1 month) and are relatively robust to changing social conditions. It appears that sticklebacks inherently differ in their shoaling tendencies, but that the social environment plays an important role in mediating the expression of these differences. Why sticklebacks inherently differ in their shoaling tendencies and what the consequences of this diversity are for the ecology of aquatic systems remains an interesting avenue for future research.

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Appendix

Table A1

Principal component analysis on behavioural metrics taken from the shoaling tendency assay

	PC1	PC2	PC3
Time with large shoal	0.94	-0.26	0.24
Time not shoaling	-0.95	0.20	0.26
Mean time with large shoal	0.87	0.50	0.02
Eigenvalue	2.52	0.36	0.12
Proportion of variance explained	84%	12%	4%

Table A2

Summary statistics of pre- and post-treatment shoaling tendency scores for solitary and group housed fish

Treatment	Stage	Mean	SD	Min.	Max.
Solitary	Pretreatment	-0.275	0.753	-1.53	2.08
Solitary	Post-treatment	0.415	0.674	-1.38	2.47
Group	Pretreatment	-0.132	0.975	-1.80	4.99
Group	Post-treatment	0.053	1.23	-2.36	5.09

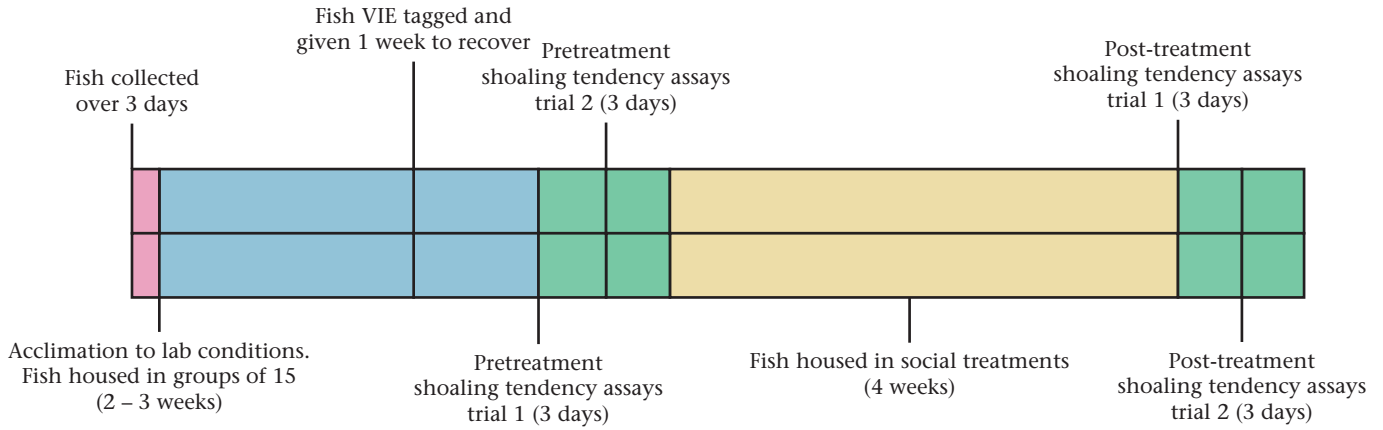


Figure A1. Diagram of experimental timeline. VIE = visible implant elastomer tag.

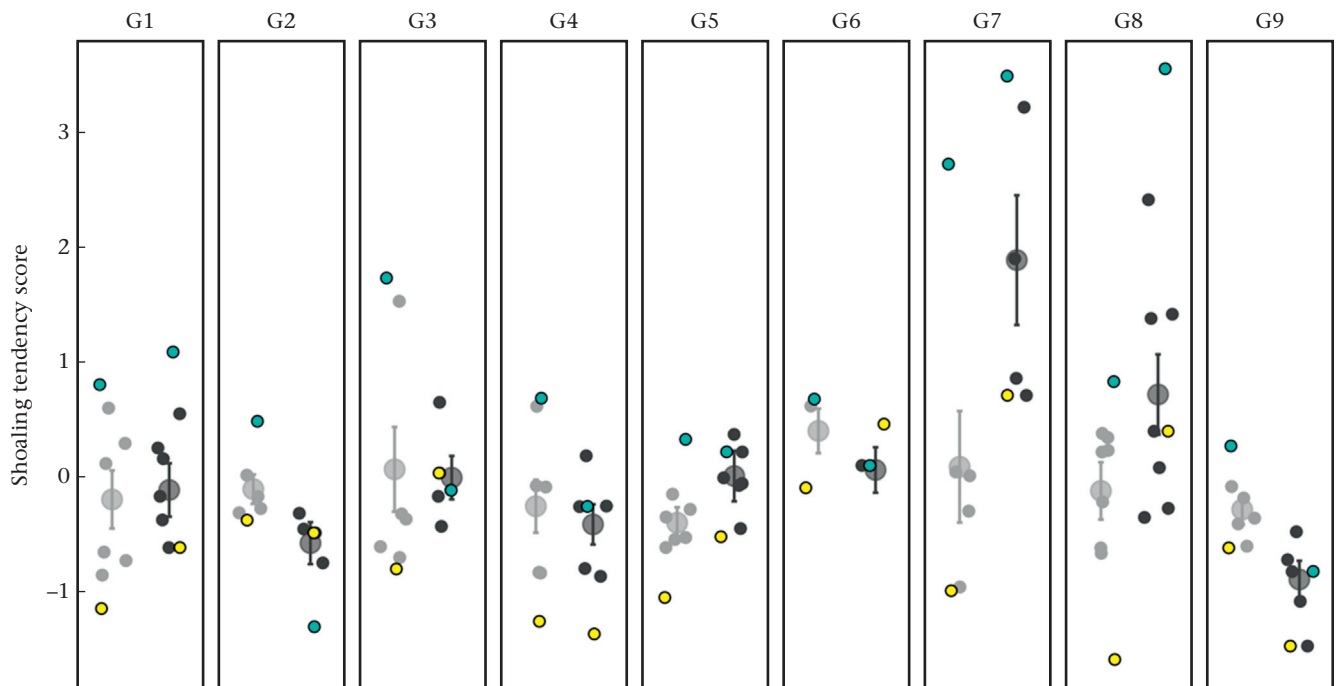


Figure A2. Group mean (\pm SE) shoaling tendency scores pretreatment (grey) and post-treatment (black). Smaller points represent individual mean shoaling tendencies within groups. Highlighted points represent the individuals within each group with the maximum pretreatment average shoaling tendency score (blue) and the minimum pretreatment average shoaling tendency score (yellow).