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Assortative interactions revealed by sorting of animal groups

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26

Abstract

28

Animals living in groups can show substantial variation in social traits and this affects their social organisation. However, as the specific mechanisms driving this organisation are difficult to identify in already-organised groups typically found in the wild, the contribution of inter-individual variation to group-level behaviour remains enigmatic. Here, we present results of an experiment to create and compare groups that vary in social organisation, and study how individual behaviour varies between these groups. We iteratively sorted individuals between groups of guppies (*Poecilia reticulata*) by ranking the groups

35 according to their directional alignment and then mixing similar groups. Over the rounds of sorting the
36 consistency of the group rankings increased, producing groups that varied significantly in key social
37 behaviours such as collective activity and group cohesion. The repeatability of the underlying individual
38 behaviour was then estimated by comparing the experimental data to simulations. At the level of basic
39 locomotion, individuals in more coordinated groups displayed stronger interactions with the centre of the
40 group, and weaker interactions with their nearest neighbours. We propose that this provides the basis for a
41 passive phenotypic assortment mechanism that may explain the structures of social networks in the wild.

42 Keywords: collective behaviour, repeatability, sociability

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45 Group living can reduce predation risk (Hamilton, 1971; Seghers, 1974; Foster & Treherne, 1981;
46 Magurran & Seghers, 1994), improve reproductive opportunities (Krause & Ruxton, 2002; Silk,
47 2007) and provide access to social information about the location of food and shelter (Sumpter &
48 Pratt, 2009; Sumpter, 2010; Pike & Laland, 2010; Miller, Garnier, Hartnett, & Couzin, 2013).

49 However, groups of animals are typically not behaviourally uniform. Individuals of the same
50 species commonly differ in repeatable inter-individual behaviour, also known as behavioural
51 phenotypes, for traits such as boldness, aggression and sociability (Réale, Reader, Sol, McDougall,
52 & Dingemanse, 2007; Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Wolf & Weissing, 2012).

53 How these traits affect social organisation and therefore impact group behaviour is still not
54 completely understood. Behavioural phenotypes can affect the function and organisation of groups
55 in at least three ways. First, properties of the group that emerge from many inter-individual
56 interactions can be affected by the presence or absence of different behavioural types in the group,
57 that is, on its “group phenotypic composition” (Farine, Montiglio, & Spiegel, 2015). For instance,
58 more variation in boldness affects the shape of animal groups (Couzin, Krause, James, Ruxton, &
59 Franks, 2002; Killen, Marras, Nadler, & Domenici, 2017) and their spatial distribution (Michelena,
60 Jeanson, Deneubourg & Sibbald 2010). On longer time scales, the composition of behavioural types
61 affects the survival of groups, and hence this may be subject to selection (Pruitt & Goodnight,

2014). Second, behaviour of the individuals within the group may also depend on the behavioural phenotypic composition of the group (Webster & Ward, 2011; Dingemanse & Araya-Ajoy, 2015). For example, conformity to the average group behaviour is widely observed (Herbert-Read et al, 2013; King, Williams, & Mettke-Hofmann, 2015), and the resulting similarity across group members can reduce risk of predation (Landeau & Terborgh, 1986). Certain behaviours may also be expressed to compensate for a lack of variation in a group, for instance by modulating aggression in order to reduce risk in conflict (Sih & Watters, 2005). Third, it has been shown that individuals can actively associate with other individuals depending on their phenotypes (Krause, Butlin, Peuhkuri, & Pritchard, 2000). For example, associating with dissimilar behavioural phenotypes may confer an advantage for competitive foragers (Metcalf & Thomson, 1995).

These three mechanisms (which we will refer to respectively as emergence, behavioural plasticity and active self-assortment) are functionally distinct, but can all lead to animal groups being structured according to behaviour, which poses a challenge for inferring which mechanism applies. In addition, it is often difficult to analyse consistent differences between groups in the wild, such as when group membership is constantly changing. One fruitful mode of observational study has been social network analysis, in which the strength of social ties between pairs of individuals may be quantified by propensity to co-occur in the same groups (Croft et al., 2005; Sundaresan, Fischhoff, Dushoff, & Rubenstein, 2007; Farine & Whitehead 2015). These can be used to infer that, for example, individuals self-assort by shoaling tendency, as reflected in the structure of the network (Croft et al., 2005). However, using such methods, the role of inter-individual influence on individual social behaviour still cannot be ruled out (Shalizi & Thomas, 2011). To determine the role of social context, laboratory methods may be used, such as analysing responses to specific phenotypic compositions (Magnhagen & Staffan, 2005; Pike, Samanta, Lindström, & Royle, 2008; Dyer, Croft, Morrell, & Krause, 2009).

Here we use a novel method in a laboratory setting to maximise the variation in shoaling tendency between groups of guppies (*Poecilia reticulata*) that resembles the variation between self-assorted

88 groups in the wild. By creating groups with consistent differences in individual behaviour, we can
89 investigate the traits underlying the properties of shoals, and hence obtain insights into how specific
90 group behaviours may evolve under selection (Ioannou, Guttal, & Couzin 2012). Guppies are a
91 model species in the study of anti-predator shoaling behaviour (Farr, 1975; Dugatkin & Godin,
92 1992; van der Bijl, Thyselius, Kotrschal, & Kolm, 2015; Herbert-Read et al., 2017), known for
93 fission-fusion dynamics and self-assortment according to sociability (Croft et al., 2005). We
94 investigate the differences between these sorted groups' shoaling behaviours, to identify possible
95 mechanisms for self-assortment. We divide three independent collections of 128 guppies each into
96 16 groups of 8. We subject each of these groups repeatedly to open field assays to quantify their
97 directional 'alignment' — that is, the degree to which the eight guppies are moving in the same
98 direction. This measurement combines cohesiveness, crucial in the 'selfish herd' response to
99 predation (Hamilton, 1971), and co-ordination, which facilitates information transfer (Strandburg-
100 Peshkin et al., 2013; Rosenthal, Twomey, Hartnett, Wu, & Couzin, 2015). In subsequent iterations,
101 we manipulate the membership of the groups based on the results of the previous round (i.e. we
102 switch individuals between groups that show similar social scores).

103 Assuming that variation in group alignment is primarily driven by behavioural phenotype, we
104 predict that groups keep consistent rankings between rounds. We further predict that with an
105 increasing number of iterations, this consistency will increase as the traits become sorted according
106 to phenotype, and hence, within-individual variation becomes relatively less important. By fitting
107 our experimental results to a simulated model of the sorting process, we estimate the trait
108 repeatability R . Finding R from purely group-level data may seem counter-intuitive, but maximum-
109 likelihood fitting is possible due to the fact that the sorting dynamics depend heavily on the
110 underlying variation between individuals (Szorkovszky et al., 2017). We then analyse differences
111 between the sorted groups at three scales: at the group level, at the level of subgroups (local
112 aggregations) and at the level of basic locomotion and interactions. Using this data, we then
113 demonstrate how variation at all levels may provide a mechanism for self-assortment as seen in the

114 wild.

115 **Methods**

116 **Sorting**

117 The laboratory population of guppies used for this study originated from a down-stream population
118 of the Quare river in Trinidad, subject to high predation levels. The original collection was made in
119 1998 (Pélabon et al., 2014) and the lab population has since been kept in several large (>500 litre)
120 tanks of >500 individuals each to avoid inbreeding. All described experiments here were performed
121 in a sub-set of this original collection at the Stockholm University aquatic facilities. The laboratory
122 was maintained at 26°C with a 12:12 light:dark schedule. Fish were fed a diet of flake food and
123 freshly hatched brine shrimp six days per week.

124 [FIGURE 1 AROUND HERE]

125 On the first day of filming, mature, unmarked female guppies were allocated into 16 groups of eight
126 fish such that all conspecifics within each group were unfamiliar to each other. Each group was kept
127 in a seven litre tank containing two cm of gravel and a biological filter. We allowed for visual
128 contact between the tanks. After this initial allocation, we used an iterative procedure of mixing
129 groups to sort the guppies. In each round of the experiment, 16 new groups were created and
130 immediately filmed in a shoaling assay. These videos were then tracked and each group was
131 evaluated before the following round. The first round was filmed without sorting and, from the
132 second round onwards, the groups were paired and mixed according to their rankings in the
133 previous round. For instance, if a group was ranked 8th in the previous round we would exchange
134 four fish from this group with four fish from the group ranked 7th. An illustration of the procedure
135 used for each pair of groups can be seen in Figure 1. To control for catching bias (Biro & Post,
136 2008), we caught all fish in one tank with a single sweep of the net and then split the individuals
137 randomly between two arenas. This was repeated for a second tank to make up two new groups of
138 eight. The 16 new groups were filmed in a random order, two pairs of groups at a time, in four

139 identical 550mm diameter circular white arenas filled to 3cm water depth. Care was taken to ensure
140 uniform lighting across all arenas. Each group was initially placed in the middle of the arena in a
141 white ring with 12cm diameter for two minutes, which was lifted as filming started, and was then
142 filmed for 10 minutes at 25 frames per second. Videos were tracked in IDTracker (Pérez-Escudero,
143 Vicente-Page, Hinz, Arganda, & de Polavieja, 2014) from the one minute mark until the end, and
144 the median global alignment over this time period was used as each group's score (see below).
145 These ranks were then used to pair the groups in the next round.

146 The sorting continued for 12 rounds, and was repeated for a total of three times (each instance
147 referred to from here as a 'replicate'), each with an independent collection of 128 guppies. The time
148 between rounds varied between one and 10 days, with a mean of 2.1 days (see Supplementary
149 Information A).

150 [FIGURE 2 AROUND HERE]

151 The median of the global alignment over time was used as the sorting measure. This is a standard
152 measure for characterising the directional co-ordination of animals (Kotrschal et al., 2018), also
153 known as polarisation (Couzin et al., 2002) or the order parameter (Vicsek & Zafeiris, 2012). The
154 global alignment is defined as the normalised sum of the eight unit vectors that characterise the
155 directions of motion. This measure is equal to one if all fish have the same orientation, and
156 decreases as they become less aligned. It has recently been shown that familiar groups of guppies
157 are slightly more aligned than non-familiar groups in open field tests, an effect attributed to the
158 attention required to assess unfamiliar conspecifics (Davis, Lukeman, Schaerf, & Ward, 2017). We
159 believe that with our method, this effect should be uniform across all groups, as all guppies would
160 need to assess four unfamiliar or semi-familiar conspecifics each round. In addition, the average
161 time between rounds was much shorter than the approximate 12 days required in guppies for
162 developing familiarity (Griffiths & Magurran, 1997).

163 As illustrated in Figure 2, the global alignment measure is affected by both alignment and cohesion,
164 which are in general difficult to separate (Perna, Grégoire, & Mann, 2014). To independently

165 measure the cohesion of the groups, we identified the fish that were exploring the arena together in
166 a ‘subgroup’ for each frame of the video. Any pair of fish that were within 100mm of each other
167 (approx. four body lengths) was counted as part of the same subgroup. On each frame, we identified
168 the number of fish in the largest subgroup, and took the mean of this number over the trial as a
169 measure of cohesion (group size). The median speed over all data points, using one data point per
170 fish per frame, was used to measure the activity of the group.

171 **Finding repeatability from group consistency**

172 The group consistency for a given global measure is defined here as the Spearman rank correlation
173 of the measure between rounds. For example, the group consistency of global alignment is the rank
174 correlation between the 16 global alignments in the current round and the 16 global alignments in
175 the previous round. This quantifies how similar the rankings of the groups are before and after
176 exchanging half of their members. Because this is based on rankings, it is not influenced by factors
177 affecting the behaviour of all groups over time in the same direction (e.g. reduced activity due to
178 habituation). Note that when adjacently ranked groups are paired to form two new groups, the new
179 groups are assigned the identities of the two old groups randomly, since both are composed in an
180 identical way. Under a null hypothesis in which the 16 group rankings are entirely randomised (i.e.
181 if there is no consistency in group-level behaviour over time) the group consistency lies between
182 -0.50 and 0.50 with a probability of 95% for a single round. Trends in group consistency were
183 tested with a linear mixed-effect model, with the square root of the round number and the number of
184 days since the previous round as fixed effects, and replicate as a random effect. Trends in the
185 measures themselves were tested in the same way, with the rank of the group as an additional fixed
186 effect.

187 It is reasonable to assume that consistent differences between groups are due to consistent
188 differences in some individual trait, usually quantified by repeatability (Bell, Hankison, &
189 Laskowski, 2009). The group consistency of global alignment was therefore fitted to a theoretical
190 model (Szorkovszky et al., 2017), in order to estimate the repeatability of the underlying individual

191 trait. The expected trend in the group consistency depends on the within-individual variation
192 relative to the between-individual variation, as well as on how the group's outcome is related to its
193 phenotypic composition. In the model, the repeatability R is tuned by adjusting the ratio of the
194 among-individual variance to the within-individual variance. In the limit that R is zero (i.e. there are
195 no consistent differences between individuals), then the group rankings are expected to change
196 randomly at each round and hence the group consistency varies around zero. For small but non-zero
197 R , the group consistency is expected to be above zero on average. For larger R , the group
198 consistency increases to larger values over successive rounds. In the limit that R approaches one
199 (i.e. differences between individuals account for all variation), the consistency of the rankings
200 rapidly approaches one as sorting progresses. Using maximum-likelihood estimation, the simulated
201 R that best fits the outcome can therefore be chosen (Szorkovszky et al., 2017).

202 We modelled the global alignment of a group separately as a function of the mean, maximum, or
203 variation of phenotypes in the group. For each model, and for each value of R , we performed 1000
204 simulations of the experiment. The log-likelihood for a given round was then calculated by
205 comparing the experimental group consistency to a histogram of group consistency from the
206 simulations. This was then summed for all rounds of the experiment for the total likelihood of the
207 combination of model and repeatability (see Supplementary Information B).

208 **Subgroup properties**

209 The global measurements above characterise the average alignment, cohesion and activity of all
210 eight individuals. To get a more detailed picture of how the guppies shoal, we define more
211 measurements limited to subgroups (i.e. ≤ 8 guppies in close proximity). The mode of the main
212 subgroup size was recorded in every two-second period (50 frames) to create a coarse-grained time
213 series for each trial. By analysing this time series, probabilities of this main subgroup increasing or
214 decreasing in size were calculated (see Supplementary Information C). We also calculated
215 properties of the subgroups depending on their size. The mean distance from the centre of the
216 subgroup (subgroup radius) was used as a local aggregation measure. Subgroup alignment was

217 defined within subgroups similarly to the global alignment, and subgroup speed was defined as the
218 median speed of the centre of the subgroup.

219 **Locomotion and interactions**

220 Ultimately, the group level properties of animal groups emerge from differences in the locomotion
221 of individuals within them. Using the fine-detailed tracking data, we can measure how their
222 locomotion varied according to whether they formed part of a higher ranked aligned group, versus a
223 lower ranked aligned group. Guppies swim with intermittent locomotion, with burst and glides
224 motion typical of many species of fish (Weihs, 1974). Many of these bursts are accompanied by a
225 change in angle prior to the increase in speed (Herbert-Read et al., 2017). The discrete nature of
226 these bursts allows us to measure the timings, magnitudes of speed change, and turning angles
227 during this intermittent locomotion (see Supplementary Information F). We can also ascertain the
228 influence of the social environment on this motion by assessing how these decisions are affected by
229 the location or direction of near neighbours.

230 Turning angles were compared against four potential directional influences. The heading of a fish's
231 nearest neighbour and the mean heading of the group were used as alignment influences. Similarly,
232 the direction to the nearest neighbour and to the centre of the group were used as attraction
233 influences. For each of these four influences, the correlation between the turning angle and the
234 angle of this influence was used as a measure of its strength within each trial.

235 Body sizes were also obtained from the videos using IDTracker, and adjusted for small differences
236 in lighting between and within arenas (see Supplementary Information G). The sizes were then
237 tested against group ranking, controlling for differences between replicates, to test whether body
238 size influenced the sorting procedure.

239 **Statistics**

240 Trends in the behaviours that were quantified for each group were tested using a linear mixed-effect
241 model (LMM). Group ranking, round number, and the number of days since the previous round

were used as fixed effects. Replicate was used as a random effect. All measures were checked for normality of residuals. Effect sizes are reported as t-statistics. All analysis was performed in MATLAB R2014b.

Results

[TABLE 1 AROUND HERE]

Group-level measures

After 12 rounds of sorting, the top 8 sorted groups, as well as being more aligned, formed tighter groups and moved faster than the bottom 8 groups. Sample videos of top, middle and bottom-ranking groups after the end of sorting are available (see Supplementary Information H). Table 1 shows that group rank had a significant effect on all of our measurements of collective behaviour (see Supplementary Information I for full details of statistics). Figure 3 (a-c) shows the changes in the per-trial mean global alignment, the mean size of the largest group and the median speed over the course of the sorting procedure, averaged over all three replicates. The clearest pattern is a decrease in all three measures over time. During the early rounds of sorting, the guppies are unfamiliar with the test arena, and group tightly while actively exploring the novel environment, leading to a high global alignment, group size and speed. In subsequent rounds, the guppies dispersed more widely around the arena and moved more slowly in both the top and bottom eight groups. The group rankings according to global alignment were highly positively correlated with the rankings according to mean group size and speed. The mean Spearman rank correlation coefficient between mean global alignment and mean size of the largest group was $\rho = 0.72$ ($P < 0.001$), while the mean Spearman rank correlation coefficient between mean global alignment and median speed was $\rho = 0.52$ ($P = 0.02$).

[FIGURE 3 AROUND HERE]

Finding repeatability from group consistency

266 Even though the groups were mixed every round, groups showed high positive consistency for their
267 global alignment, group size and speed between rounds (Figure 3 d-f). The group consistency of
268 global alignment increased over subsequent rounds (LMM: $t = 3.1$, $P = 0.006$, $df = 30$), but was not
269 influenced by the time between rounds ($t = 0.1$, $P = 0.9$, $df = 30$). However, when a longer time had
270 passed since the previous round, the group consistency of the average speed decreased ($t = -2.0$, P
271 $= 0.05$, $df = 30$).

272 Another way of showing that the sorting procedure increased the group consistency of the global
273 alignment is by considering the average change in group ranking. For a null hypothesis of the
274 groups changing randomly between rounds, the average change is 5.25 for a 16-group experiment.
275 In our experiment, the average change in ranking according to global alignment, after fitting to a
276 linear trend, decreased from 4.1 to 3.2 between the second and 12th rounds (Figure 4, $t = -2.4$, $P =$
277 0.02 , $df = 30$). Therefore, as adjacent groups became more similar in their phenotypic composition,
278 mixing adjacent groups had a smaller effect on behaviour over time.

279 [FIGURE 4 AROUND HERE]

280 By comparing the observed changes in rank to simulations based on simple models that relate group
281 composition to performance (Szorkovszky et al., 2017), we estimated the repeatability of the
282 individual behaviour governing the global alignment. A conservative estimate was obtained using a
283 model in which individuals' contributions to the global alignment were additive and each varied
284 around its respective phenotype. This gave an estimate of $R = 0.43 \pm 0.03$ (S.E.) for the
285 repeatability (see Supplementary Information B). This is close to the figures previously found for
286 sociability ($R = 0.46$) and activity ($R = 0.38$) in female guppies (Brown & Irving, 2014). If we
287 instead assumed in the simulations that global alignment depends on leader/follower relationships,
288 where one or a small number of individuals lead the rest of the group, the best fit to the
289 experimental data was obtained using a higher value of R . The limiting case, where the global
290 alignment depends on the maximum or minimum individual phenotype, led to an estimate for R
291 above 0.7 (see Supplementary Information B).

292 **Subgroup properties**

293 As sorting progressed, subgroups became more likely to break up and, when containing at least six
294 members, became less likely to increase in size (see Supplementary Information D). Higher ranked
295 groups were more likely to increase in size, and less likely to break apart (LMM: $P < 0.001$ for all
296 group sizes larger than 2).

297 [FIGURE 5 AROUND HERE]

298 By separating all of the data into subgroups and comparing subgroups of the same number of fish,
299 we could control for differences in average subgroup size. Larger groups moved slower, were less
300 aligned and occupied larger areas (Fig. 5). Higher ranked groups were faster, more aligned and
301 more compact across all subgroup sizes. We found a negative correlation between subgroup speed
302 and subgroup radius when using the average of each trial ($N=8$, Spearman $\rho = -0.31$, $P < 0.001$),
303 despite the fact that subgroup radius increased with higher subgroup speed within a trial (see
304 Supplementary Information E).

305 **Locomotion and interactions**

306 The burst patterns of the guppies depended on the position of the nearest neighbour, as shown in
307 Figure 6 (a-c), and on round number, time between rounds and group ranking as shown in Table 1.
308 A guppy's speed over time was mainly regulated by the speed 'minima' at which the bursts were
309 made, and the acceleration during these bursts. On average, guppies retained a higher speed when
310 their nearest neighbours were at moderate distances ($\approx 40 - 100\text{mm}$). Individuals in higher ranked
311 groups had higher average burst speeds and higher accelerations. While the mean time between
312 bursts was also dependent on nearest neighbour distance as shown, and increased over the
313 experiment, there was no discernible difference between differently-ranked groups.

314 [FIGURE 6 AROUND HERE]

315 Another component of burst-and-glide motion is the directional change before bursts. The average
316 turning angles as a function of the four potential directional influences are shown in Figure 6 (d-g).

317 In each case, the average turning angle was maximal when the direction of influence (ϕ) was close
318 to 90 degrees. Hence, for each of these four influences, the correlation between the turning angle
319 and $\sin(\phi)$ provided a useful measurement of the strength of that influence within each trial. The
320 linear mixed-effect models for these measures are shown in Table 1, alongside the four global-level
321 measures. Alignment-based correlations decreased significantly over subsequent rounds, while
322 attraction-based correlations increased. The top ranking groups showed an increased response to the
323 average position and the average orientation of all fish in the trial, as well as the orientation of the
324 nearest neighbour. The direction to the nearest neighbour, however, had a reduced influence in
325 higher-ranked groups. Notably, for only one measure (attraction to the group centre) is the effect of
326 group ranking in the same direction as the effect of round number.

327 The mean, maximum, minimum and standard deviation in body sizes were also ranked across
328 groups for each round. None of these ranks were significantly correlated with the global alignment
329 rank. Therefore, body size did not significantly influence the sorting procedure (see Supplementary
330 Information G).

331 Discussion

332 The consistency of the group rankings increased over the sorting process, clearly supporting our
333 prediction of repeatable variation in shoaling behaviour across groups. The mixing of similar groups
334 did not influence behaviour enough to substantially alter the group rankings, compared to mixing of
335 dissimilar groups. This implies that the alignment of a guppy shoal is driven by a repeatable
336 behavioural phenotype rather than temporal factors such as familiarity.

337 The differences between groups with high and low alignment can be explained by a combination of
338 differences in activity and attraction to conspecifics, or sociability, both of which are well-
339 established repeatable traits in guppies (Budaev, 1997; Burns, 2008; Brown & Irving, 2014). This is
340 reflected in measurements at all three of the levels we examined. Individuals in top ranked groups
341 were more active, as shown by a higher average speed as well as higher speed at bursting times.

342 Individuals in top-ranked groups also formed larger and more stable subgroups and were more
343 likely to stay close to the centre of these, as shown by the smaller spatial spread of subgroups,
344 increased turning responses to the group centre and lower likelihood of groups breaking up.
345 Interestingly, individuals in low-ranking groups, rather than showing a reduced response to all
346 social stimulus, instead showed a relative increase in responses to their nearest neighbours'
347 positions. This could indicate that sociability differences may be not in the strength, but in the
348 selectivity of interactions (Strandburg-Peshkin et al., 2013; Jiang et al., 2017). Although top-ranked
349 groups show increased alignment with the nearest neighbour, this may be a side-effect of higher
350 activity (i.e. both individuals closely following the group trajectory) rather than from a direct social
351 response to the neighbour. Our analysis of shoaling groups provides a more natural quantification of
352 shoaling tendency than standard sociability assays, in which individuals are assessed in how they
353 approach a shoal, generally situated behind a barrier (Budaev, 1997; Brown & Irving, 2014).
354 Notably, such individual assays evaluate the tendency to join a group, whereas from studying the
355 changes in subgroup sizes we can conclude that there is even greater variation in the tendency to
356 leave groups. With our method, individuals can be assigned scores based on the rank of their final
357 group, although this limits the number of possible levels to the number of groups.

358 For most measurements we analysed, the effect of group ranking (i.e. increased group alignment) is
359 opposite to the effect of round number (Table 1). A potential explanation for this observation is that
360 higher ranked groups habituate slower to the repeated assays. Individual differences in habituation
361 have been found in threespine sticklebacks (*Gasterosteus aculeatus*), separate from other personality
362 differences (Bell & Peake, 2012). Notably, in our experiment the turning response to the centre of
363 the group, which has been found to be a relatively accurate predictor of anti-predator responses in
364 guppies (Kimbell & Morrell, 2015), increased with both time and group ranking. This indicates that
365 potential habituation differences cannot explain the observed social differences between low-ranked
366 and high-ranked groups. To fully investigate the habituation effect, additional control replicates are
367 needed in which groups are either kept unsorted or shuffled randomly for the same number of

368 rounds.

369 We also quantified the repeatability R of behaviour by fitting a simulated experiment to the data.
370 Although R is generally quantified by multiple assays on individuals (Réale et al., 2007; Bell,
371 Hankison & Laskowski, 2009), we were able to estimate R using the changes in group rankings
372 (Szorkovszky et al., 2017). Our conservative repeatability estimate was similar to what has been
373 reported for repeatability of activity and sociability as measured in assays on individual female
374 guppies (Brown & Irving, 2014). This result is consistent with the conclusion that sociability and
375 activity are the main contributors to variation in shoaling behaviour as tested here. Additionally we
376 find a positive correlation between activity and sociability. This may contrast with what has
377 recently been shown in threespine sticklebacks, where more social fish were found to be less active
378 in both individual and collective settings (Jolles, Boogert, Sridhar, Couzin, & Manica, 2017). The
379 variation in sociability is consistent with that found between guppies from high and low-predation
380 environments respectively (Herbert-Read et al., 2017). This predation study used a similar open
381 field test in groups of eight, but found no effect of predation on overall activity. This suggests that
382 activity and sociability do not form a syndrome in guppies, and our choice of alignment as the
383 sorting measure introduced the positive correlation.

384 Guppies in the wild self-assort by social tendency, although whether this is due to active decisions
385 to associate with similar conspecifics or due to a passive mechanism is still an open question (Croft
386 et al., 2005). Our results suggest that this self-assortment can emerge passively from the simple
387 differences we have identified. In an open environment, the individuals with high sociability could
388 maintain links with each other (as observed in networks) by staying as close as possible to the
389 centre of the group, while individuals with low sociability form smaller and more numerous cliques,
390 by staying close to their nearest neighbours. Such predictions can be verified by using simulated
391 models of collective motion (Eriksson, Jacobi, Nyström, & Tunström, 2010; Sumpter, 2010).

392 The method that we have devised is a novel way of analysing the variation in behaviours, such as
393 shoaling, that are difficult to quantify with individual assays. Results on the underlying quantitative

394 structure of the trait rely on simulations, which may require strong assumptions in some cases.
395 However, work can be done to extend the validity of our approach to more general situations. For
396 instance, in the simulations we have assumed various functions for how the group-level property
397 emerges from individual behaviours (Farine, Montiglio & Spiegel 2015), and then fitted a single
398 parameter to estimate the repeatability. For cases in which the group-level measurement is (either
399 explicitly or equivalently) a sum of individual behaviours, it is also possible to adopt an indirect
400 genetic effects formalism (Moore, Brodie & Wolf 1997) in the simulated model. For example,
401 interactions between phenotypes may be modelled by a single interaction coefficient (Bijma 2014)
402 which is expected to affect the sorting dynamics. Hence, this parameter may also be estimated in
403 addition to the repeatability. As interactions between multiple conspecifics are difficult to decouple
404 using regression methods (Bijma 2014), our approach may provide a fruitful alternative.

405 We have demonstrated strong and repeatable variation in shoaling behaviour that persists during
406 repeated mixing of groups, and which may explain common patterns of self-assortment. This
407 laboratory setup provides the opportunity for a number of follow-up experiments uncovering
408 collective behaviour. For instance, directed breeding of sorted individuals will allow the heritability
409 of the sorted traits to be determined (Drent, van Oers, & van Noordwijk, 2003), and if heritable,
410 assays of subsequent generations will reveal which traits coevolve with these aspects of social
411 behaviour. Such further tests will provide experimental data on the ecological function and
412 evolution of variation in shoaling behaviour.

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582 Appendix A: Time between rounds

583 [Figure A1 HERE]

584

585 Appendix B: Model fitting

586 To fit the empirical rank transitions to simulations, we used maximum-likelihood estimation. In the
587 sorting simulations, the between-individual variation was kept constant and the within-individual
588 variation σ was varied. This was done for three prototypical models of group behaviour, where the
589 group feature (i.e. the global alignment) depends on the mean, maximum or standard deviation of
590 the individual phenotypes comprising the group (Szorkovszky et al., 2017). For a given
591 experimental round t , the group repeatability $C(t)$ was compared against likelihood histograms from
592 1000 iterations of each model and σ parameter. This was done for every round after the second,
593 treating each as independent. For a single replicate, the likelihood for a value of σ over the twelve
594 rounds was then calculated as

$$595 \quad L(\sigma) = \sum_{t=2}^{12} \log l_{\sigma}(t, C(t))$$

596 where $l_{\sigma}(t, c)$ is the likelihood of the correlation in round t being c , based on histograms obtained
597 from performing several simulations with within-individual variation parameter σ . The replicates
598 were then combined by adding the log-likelihood for all three.

599 [FIGURE A2 AROUND HERE]

600 The between-individual variation was set to one, so the individual repeatability R was then defined
601 as (Bell, Hankison, & Laskowski, 2009)

$$602 \quad R = \frac{1}{1 + \sigma^2}$$

603 This resulted in a curve for each of the three models, showing the relative likelihoods of the

604 parameter R , as shown in Figure A2. The lowest estimate was for the ‘mean’ model with $R \approx 0.43$.
 605 A standard error of 0.03 was determined using the asymptotic normal approximation, by fitting a
 606 fourth-order polynomial to the combined log-likelihood function and calculating the second
 607 derivative from the fitted coefficients.

608 Appendix C: Subgroups

609 For each point in time, subgroups were defined by counting any pair of fish < 100mm apart as part
 610 of the same subgroup. We denote the position vector of a fish with label i as $\vec{r}_i(t)$ and define its
 611 instantaneous velocity as

$$612 \quad \vec{v}_i(t) = \vec{r}_i(t) - \vec{r}_i(t-1)$$

613 where $t > 1$ denotes the frame of the video. The centroid of the subgroup G with n members is
 614 defined simply as

$$615 \quad \vec{r}_G(t) = \sum_{i \in G} \vec{r}_i(t)$$

616 If the membership of subgroup G was kept constant from the previous frame, the instantaneous
 617 speed of subgroup G was then defined as the speed of its centroid

$$618 \quad S_G(t) = |\vec{r}_G(t) - \vec{r}_G(t-1)|$$

619 The radius of subgroup G is defined as the average distance from the centre

$$620 \quad R_G(t) = \sum_{i \in G} |\vec{r}_i(t) - \vec{r}_G(t)|$$

621 The subgroup alignment was given by the length of the sum of the normalised velocities of the
 622 members, divided by the number of members n_G

$$623 \quad A_G(t) = \frac{1}{n_G} \left| \sum_{i \in G} \frac{\vec{v}_i(t)}{|\vec{v}_i(t)|} \right|$$

624

625 Appendix D: Subgroup size transitions

626 The mode of the main subgroup size was recorded in every two second period (50 frames) to create
627 a coarse-grained time series for each trial. These time series were collated according to group
628 ranking and sorting round. Figure A3 shows the transition probabilities calculated from these time
629 series, for groups in the top 8 and bottom 8 of the ranking. The more aligned groups are less likely
630 to decrease in main subgroup size, and more likely to increase. The effect sizes for group size
631 decreases are consistently larger (Table A1).

632 [FIGURE A3 AROUND HERE]

633

634 Appendix E: Subgroup speed and radius

635 Within each trial, the Spearman rank correlation was calculated between sub- group speed and
636 radius (mean distance from group centroid) for all frames where all fish were in the same subgroup.
637 This correlation averaged $\rho = 0.18$ with a standard deviation of 0.18 ($\rho > 0 : t = 26.2, P < 0.001$).
638 The correlation between the per-trial medians of these measures took the opposite sign ($\rho = -0.31$,
639 $P < 0.001$). This can also be seen the two-dimensional frequency distributions, separated according
640 to rank and time, as shown in Figure A4.

641 [FIGURE A4 AROUND HERE]

642

643 Appendix F: Burst and glide analysis

644 Speeds were calculated from the first derivatives of the x and y time series, then smoothed using a
645 third-order Savitzky-Golay filter. A peak-finding algorithm was then used to find local maxima and
646 minima, with each set constrained to be at least one third of a second apart. The maxima and
647 minima were then paired to determine accelerations during each burst (speed at maximum minus

648 speed at prior minimum), as well as subsequent glide times (time of minimum minus time of prior
649 maximum, limited to four seconds to control for inactive periods).

650 The heading angles of the fish were also calculated from the first derivatives of the x and y time
651 series, then unwrapped. An L1-Potts functional was used to detect jumps upward or downward in
652 this angle (Weinmann, Storath, & Demaret, 2015), which were recorded as turning decisions.

653

654 Appendix G: Body sizes

655 Eight body sizes were estimated for each trial, accounting for changes in apparent size between the
656 middle and edge of the arena. Sizes were then corrected using a linear mixed-effect model. The
657 fixed effect of time accounted for growth of the fish over the experiment, and a fixed effect of
658 group ranking was used to test for a body size effect on sorting. Random effects were replicate and
659 arena, accounting for different ages and lighting conditions, respectively. The resulting corrected
660 body sizes are shown in Figure A5. After correction, the body sizes are approximately normally
661 distributed, with no discernible difference in the distribution between the top and bottom four
662 groups. From the model, the fitted size difference between the top and bottom group is 4.7% of the
663 residual standard deviation (group rank effect $P = 0.20$). From this, we can conclude that the sorting
664 did not operate on the body size.

665 [FIGURE A5 AROUND HERE]

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667 Appendix H: Videos

668 Three one-minute videos of sorted groups in the open field arena are available in the Online
669 Supplementary Information. These are taken from the 7th minute of trials, taken 7 days after the
670 final sorting round in replicate 2. Corresponding smoothed plots of global alignment vs time are
671 shown in Figure A6. The shaded regions correspond to the location of the videos.

672 [FIGURE A6 AROUND HERE]

673

674 Appendix I: Full statistics

675 For the measures presented in the main text, full statistics including intercepts, estimates and
676 standard errors (SE) are contained in Table A2. Refer to main text for full description of each
677 measure. The number in parentheses denotes the degrees of freedom of the error (DFE). Residuals
678 are plotted in Figure A7.

679 [FIGURE A7 AROUND HERE]

680

681 Appendix J: Single-group plots

682 An alternative version of Figure 3(a-c) from the main text, where measures are plotted against
683 group rank instead of round, can be seen in Figure A8. To see the consistency between the last two
684 rounds of sorting at the group level, we show changes in global alignment after exchanging
685 members as a reaction norm plot (Dingemanse, Kazem, Réale, & Wright, 2010) in Figure A9.

686 [FIGURE A8 AROUND HERE]

687 [FIGURE A9 AROUND HERE]

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Tables and Figures

Table 1: Summary of fixed effect sizes for all measured variables

Measure	Round		Days		Rank	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Global align	-27.1	<0.001	5.4	<0.001	39.5	<0.001
Speed	-6.9	<0.001	3.7	<0.001	13.1	<0.001
Group size	-11.3	<0.001	2.6	0.010	21.9	<0.001
Radius (N=8)	3.4	0.001	-1.0	0.331	-7.7	<0.001
Speed minimum	-6.8	<0.001	4.9	<0.001	12.6	<0.001
Acceleration	-0.6	0.518	-2.2	0.025	7.5	<0.001
Glide time	9.1	<0.001	-3.5	0.001	0.1	0.910
Group align	-14.8	<0.001	1.0	0.310	21.5	<0.001
Group attract	3.3	0.001	0.5	0.637	11.7	<0.001
N.n. Align	-13.3	<0.001	1.0	0.339	19.3	<0.001
N.n. Attract	12.2	<0.001	-2.7	0.008	-6.8	<0.001

Fixed effect sizes for round number, days between rounds and group rank are shown as t-statistics with associated P-values. For all tests above the error degree of freedom $df = 524$. Group-level measures are Global align: median global alignment; Speed: median speed; Group size: mean size of largest subgroup; Radius: median average distance to global centroid when all eight are in the same subgroup. Individual-level measures are Speed minimum: mean speed at beginning of burst; Acceleration: mean minimum to maximum speed change during burst; Glide time: mean time between maximum and next minimum. The final four measures are correlations of individuals' turning angles with the sine of angular influences. Group align: mean heading of the group; Group attract: direction of the centre of the group; N.N. align: heading of the nearest neighbour; N.N. attract: direction to the nearest neighbour. See Supplementary Information I for full details.

712

713

714 Table A1: Effect sizes for subgroup transitions

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716

Measure	<i>df</i>	Round <i>t</i>	Round <i>P</i>	Day <i>t</i>	Day <i>P</i>	Rank <i>t</i>	Rank <i>P</i>	Ratio
Pup (N=2)	412	-0.70	0.485	-2.54	0.011	2.89	0.004	-0.24
Pup (N=3)	517	-1.17	0.242	0.75	0.454	7.45	<0.001	-0.16
Pup (N=4)	523	0.33	0.744	0.20	0.842	6.01	<0.001	0.05
Pup (N=5)	523	0.04	0.967	0.01	0.995	7.15	<0.001	0.01
Pup (N=6)	523	-2.34	0.019	0.98	0.328	4.96	<0.001	-0.47
Pup (N=7)	523	-5.34	<0.001	0.99	0.324	7.32	<0.001	-0.73
Pdn (N=3)	517	2.43	0.016	-0.39	0.698	-8.02	<0.001	-0.30
Pdn (N=4)	523	4.96	<0.001	-1.60	0.110	-9.66	<0.001	-0.51
Pdn (N=5)	523	5.09	<0.001	-0.42	0.675	-11.25	<0.001	-0.45
Pdn (N=6)	523	5.47	<0.001	-2.38	0.018	-9.25	<0.001	-0.59
Pdn (N=7)	523	8.64	<0.001	-2.64	0.009	-14.08	<0.001	-0.61
Pdn (N=8)	523	9.61	<0.001	-3.09	0.002	-12.05	<0.001	-0.80

717

718 Fixed effect sizes for round number, days between rounds and group rank, shown as t-statistics,

719 and associated P-values, for the probabilities of transitions up (Pup) and down (Pdn) in the main

720 subgroup size. The right-most column shows the round number effect size (*t*) divided by the group

721 rank effect size. If this is greater than zero, both effects are in the same direction.

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732 Table A2: Full statistics of measures presented in the main text.

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	Estimate	SE	<i>t</i>	<i>P</i>
Global align				
Intercept	0.872	0.022	40.305	<0.001
Round	-0.076	0.003	-27.075	<0.001
Rank	-0.015	0.000	-39.513	<0.001
Day	0.005	0.001	5.398	<0.001
Speed				
Intercept	59.209	3.614	16.385	<0.001
Round	-2.864	0.415	-6.894	<0.001
Rank	-0.726	0.055	-13.124	<0.001
Day	0.503	0.135	3.711	0.000
Group size				
Intercept	7.407	0.125	59.390	<0.001
Round	-0.313	0.028	-11.264	<0.001
Rank	-0.081	0.004	-21.900	<0.001
Day	0.023	0.009	2.602	0.010
Radius (N=8)				
Intercept	54.425	2.598	20.948	<0.001
Round	1.963	0.578	3.396	0.001
Rank	0.592	0.077	7.659	<0.001
Day	-0.182	0.187	-0.973	0.331
Group align				
Intercept	0.410	0.020	20.638	<0.001
Round	-0.044	0.003	-14.790	<0.001
Rank	-0.008	0.000	-21.467	<0.001
Day	0.001	0.001	1.017	0.310
Group angle				
Intercept	0.398	0.029	13.706	<0.001
Round	0.013	0.004	3.323	0.001
Rank	-0.006	0.001	-11.723	<0.001
Day	0.001	0.001	0.472	0.637

N.n. Align

Intercept	0.398	0.024	16.471	<0.001
Round	-0.045	0.003	-13.267	<0.001
Rank	-0.009	0.000	-19.257	<0.001
Day	0.001	0.001	0.957	0.339

N.n. Angle

Intercept	0.179	0.023	7.651	<0.001
Round	0.037	0.003	12.235	<0.001
Rank	0.003	0.000	6.757	<0.001
Day	-0.003	0.001	-2.675	0.008

Speed min

Intercept	32.608	2.226	14.646	<0.001
Round	-1.838	0.272	-6.767	<0.001
Rank	-0.456	0.036	-12.614	<0.001
Day	0.433	0.089	4.881	<0.001

Acceleration

Intercept	68.164	2.803	24.316	<0.001
Round	-0.189	0.292	-0.647	0.518
Rank	-0.290	0.039	-7.451	<0.001
Day	-0.214	0.095	-2.247	0.025

Glide time

Intercept	11.616	0.365	31.813	<0.001
Round	0.496	0.055	9.108	<0.001
Rank	-0.001	0.007	-0.114	0.910
Day	-0.062	0.018	-3.461	0.001

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737 Figure 1: Mixing the first pair of groups in a sorting round. The groups are initially paired according
738 to the previous round's rankings. 1. A random adjacent pair of groups is chosen. 2. Each group is
739 separated into groups of four, and the groups are mixed. 3. The new groups are filmed in two
740 arenas. 4. The new groups are put into tanks, re-numbered in order of filming. Steps 1-4 are
741 repeated until all 16 groups have been mixed and filmed. The videos are then tracked and ranked
742 according to the global alignment.

743

Figure 2: Examples of low and high global alignment. At a given point in time, the eight fish have positions and orientations denoted by arrows. They form, in arena (a) a large subgroup with low local alignment, in (b) two small subgroups with high local alignment, and in (c) a large subgroup with high local alignment. Only example (c) shows high global alignment.

Figure 3: Changes in group-level measures and group rank consistency during sorting. In panels (a)-(c) the measurements are separated into the top 8 and bottom 8 groups, ranked by the global alignment. In each case, the median (lines) and interquartile range (error bars) of the 24 observations (8 groups, 3 replicates) are shown for each round. Panels (d)-(f) show the group rank consistency of the given measure for each replicate. The dotted line at zero represents the average group consistency for the null hypothesis of random group rankings. Alternative representations of the data in panels (a-c) are available in Supplementary Information J.

Figure 4: Changes in rank over time. Shown is the mean absolute change in rank per round of experiment (red circles) and a linear fit (red line). For comparison is the expected mean absolute change in rank if groups change rank randomly (dotted black line).

Figure 5: Properties of subgroups of different sizes during final round of sorting. (a) Frequency of a fish being a member of a subgroup of a given size for (red) top eight and (blue) bottom eight groups, averaged over time and replicate. The other panels display the (b) speed of the group centre, (c) alignment, and (d) average distance from group centre, for different group sizes. The markers represent the median values, and error bars represent the interquartile range.

768 Figure 6: Characterisation of observed burst-and-glide motion of individuals as a function of the
769 social environment. Solid lines indicate (a) the mean speed at beginning of burst, defined as a local
770 minimum; and (b) the mean glide time, defined as the time between a local maximum in speed and
771 the next minimum, as a function of the distance to the nearest neighbour. (c) Frequency of nearest
772 neighbour distance over all burst events. (d-e) Mean turning angle as a function of the direction to
773 the nearest neighbour and its relative orientation, when the nearest neighbour is 25-100mm away.
774 (f-g) Mean turning angle as a function of the direction to the average position of all eight
775 individuals, and their average relative orientation, when the average position is < 100mm away.
776 Data is from the final six rounds of sorting, averaged over all replicates. Shaded areas represent ± 1
777 standard error.

778

779 Figure A1: Histogram of the number of days between rounds in the experiment.

780

781 Figure A2: Log-likelihood estimates of the individual repeatability for each model.

782

783 Figure A3: Main subgroup size and transitions. (a) Probability distribution of the main subgroup
784 size N for the top 8 and bottom 8 ranked groups in the first six rounds. (b-c) Box plots of the
785 probability per trial of transitions (b) up and (c) down in group size, for all trials in the first six
786 rounds of sorting. Probabilities are calculated from the average likelihood of the main subgroup size
787 either increasing or decreasing in the following two second period, given a current main subgroup
788 size N. Panels (d-f) are as above but for the final six rounds of sorting.

789

790 Figure A4: Two-dimensional histograms of group speed versus group radius when all eight fish
791 were in the same subgroup. Lighter colour indicates higher likelihood. The vertical and horizontal
792 position of the markers denote the mean values for the respective measures.

793

794 Figure A5: Histogram of all estimated body sizes in the top and bottom four of the group rankings,
795 in the final four rounds of sorting, after correcting for time, arena and replicate.

796

797 Figure A6: Global alignment vs time for the highest, 8th highest and lowest ranked groups
798 (replicate 2). Each point is the median of the surrounding two- second period (51 frames). The
799 shaded regions correspond to the videos in the Online Supplementary Information.

800

801 Figure A7: Residuals (vertical axis) plotted against fitted values (horizontal axis) for the linear
802 mixed-effect models.

803

804 Figure A8: Group-level measures plotted against group ranking for the first round (grey) and the
805 final round (black) for each replicate.

806

807 Figure A9: Behavioural reaction norms for the final two rounds of assays. The vertical axis is the
808 global alignment. Each line connects the group measure before and after exchanging four group
809 members. Darker shade indicates higher ranking (by global alignment) before exchanging members.

1.

Rank	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Tank	5	7	11	2	1	16	14	3	9	4	8	15	12	6	13	10

2.

3.

4.

(a)

low

(b)

low

(c)

high