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10 **Association patterns and foraging behaviour in natural and artificial**
11 **guppy shoals**

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13 LESLEY J. MORRELL¹, DARREN P. CROFT^{1,2}, JOHN R.G. DYER¹, BEN B.
14 CHAPMAN¹, JENNIFER L. KELLEY³, KEVIN N. LALAND⁴ & JENS KRAUSE¹
15

16 ¹Institute of Integrative and Comparative Biology, University of Leeds

17 ² College of Natural Sciences, School of Biological Sciences, University of Wales

18 Bangor

19 ³School of Biological, Earth and Environmental Sciences, University of New South

20 Wales, Sydney

21 ⁴School of Biology, University of St Andrews

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23 **Correspondence:**

24 Darren Croft
25 College of Natural Sciences
26 School of Biological Sciences
27 Bangor University
28 Brambell Building
29 Deiniol Road
30 Bangor, Gwynedd
31 LL57 2UW
32 Email: darren_croft@hotmail.co.uk
33

34 **Postal addresses:**

35 LJ Morrell, JRG Dyer, BB Chapman, & J Krause: Institute of Integrative and
36 Comparative Biology, LC Miall Building, University of Leeds, Leeds, LS2 9JT, UK
37 JL Kelley: Centre for Evolutionary Biology, Zoology Building, School of Animal
38 Biology (M092), The University of Western Australia, Nedlands, WA 6009, Australia
39 KN Laland: School of Biology, University of St Andrews, Bute Medical Building,
40 Queen's Terrace, St. Andrews, Fife, Scotland KY16 9TS
41

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43

ABSTRACT

44
45 Animal groups are often non-random assemblages of individuals that tend to be
46 assorted by factors such as sex, body size, relatedness and familiarity. Laboratory
47 studies using fish have demonstrated that familiarity among shoal members confers a
48 number of benefits to individuals such as increased foraging success. However, it is
49 unclear whether fish in natural shoals obtain these benefits through association with
50 familiars. Here, we investigate whether naturally occurring shoals of guppies
51 (*Poecilia reticulata*) are more adept at learning a novel foraging task than artificial
52 (where shoal members were selected randomly by the authors) shoals. We used social
53 network analysis to compare the structure of natural and artificial shoals and examine
54 whether shoal organisation predicts patterns of foraging behaviour. We found that fish
55 in natural shoals benefited from increased success in the novel foraging task
56 compared with fish in artificial shoals. Individuals in natural shoals showed a reduced
57 latency to approach the novel feeder, followed more, and formed smaller sub-groups
58 compared to artificial shoals. Our findings show that fish in natural shoals do gain
59 foraging benefits, and that this may be facilitated by a reduced perception of risk
60 among familiarised individuals, and/or enhanced social learning mediated by
61 following other individuals and small group sizes. Although the structure of shoals
62 was stable over time, we found no direct relationship between shoal social structure
63 and patterns of foraging behaviour.

64

65 **Keywords:** guppy, information, innovation, *Poecilia reticulata*, shoaling tendency,
66 social learning

67

68 Wild animal groups commonly display non-random patterns of social structure.
69 Within a species, individuals are known to associate on the basis of kinship (Ward &
70 Hart 2003, Silk et al. 2006), body size (Ward & Krause 2001), parasite load (Krause
71 & Godin 1994), disease status (Behringer et al. 2006) and colour (McRobert &
72 Bradner 1998), resulting in groups that are assorted by phenotypic characteristics.
73 These association patterns are thought to confer anti-predator benefits, such as a
74 reduction in risk through predator confusion; and foraging benefits, such as reduced
75 competition for resources (Krause & Ruxton 2002). A further level of social
76 organisation can arise when individuals preferentially associate with, or avoid,
77 conspecifics based on previous interactions (Griffiths 2003).

78

79 Preferences for associating with familiars have been reported in a number of
80 animal groups (e.g. mammals: Porter et al. 2001, birds: Senar et al. 1990, reptiles:
81 Bull et al. 2000, insects: Clarke et al. 1995), but have been particularly well studied in
82 shoaling fishes. These studies have revealed that associations based on familiarity
83 occur both in the laboratory (e.g. Barber & Ruxton 2000, Barber & Wright 2001) and
84 the field (Griffiths & Magurran 1997a, reviewed in Griffiths 2003). A number of
85 benefits to associating with familiars have been demonstrated, including enhanced
86 predator escape responses (Chivers et al. 1995), reduced levels of aggression (fishes:
87 Utne-Palm & Hart 2000; birds: Temeles 1994), increased foraging success (reviewed
88 in Krause & Ruxton 2002, Griffiths 2003, Ward & Hart 2003) and an elevated
89 performance in learning tasks (Swaney et al. 2001, Galef & Giraldeau 2001).

90

91 Previous work has demonstrated that animal groups contain pairs or small
92 groups of individuals that are linked by stable interactions (Croft et al. 2004, 2006,

93 Gero et al. 2005). However, the majority of work investigating the benefits of
94 familiarity has focused on groups of fish that are artificially familiarised in the
95 laboratory (by holding fish together in small groups for a period of two weeks or
96 more), and it is unclear whether wild (i.e. naturally assorted) shoals would gain the
97 same benefits. Wild shoals of fathead minnows (*Pimephales promelas*) show more
98 cohesive anti-predator behaviour than unfamiliar, laboratory-assembled shoals
99 (Chivers et al. 1995), but other putative benefits of familiarity have not yet been
100 studied in natural groups. Here, we investigate whether natural shoals of guppies
101 (*Poecilia reticulata*) benefit from enhanced foraging success, when compared to
102 artificial (laboratory-assembled) shoals. We used female guppies, as they display
103 greater within-shoal fidelity than males (Griffiths and Magurran 1998), are more
104 likely than males to exploit novel foods (Laland & Reader 1999a), and learn new
105 foraging tasks more rapidly than males (Laland and Reader 1999b). We present the
106 shoals with a novel foraging task, consisting of a novel foodstuff hidden within a
107 feeder, and investigate the success of shoal members in completing the task.

108

109 Previous work with fishes has shown that foraging success and performance in
110 a novel learning task are influenced by social structure, specifically group size. For
111 example, individuals in larger groups are generally more successful at locating food
112 patches e.g. Pitcher et al. 1982), and learning to escape from a moving net (Brown &
113 Warburton 1999) than individuals in smaller groups, but individuals in smaller groups
114 can locate food more quickly when the food is hidden (the conformity effect; Day et
115 al. 2001). The influence of familiarity on learning has been well studied: In fish,
116 individuals learn more successfully from familiar demonstrators than from unfamiliar
117 conspecifics (where familiar groups are created by holding individuals together in the

118 laboratory over a period of time; Swaney et al. 2001, Ward & Hart 2005), and in
119 birds, young learn how to handle a new food source more effectively from familiar
120 adults than from unfamiliar ones (Cadieu & Cadieu 2004).

121

122 One method which is becoming increasingly useful for understanding
123 associations and structure in animal populations is social network analysis (e.g. Croft
124 et al. 2004, Lusseau & Newmann 2004, Wolf 2005). Previous work on guppies using
125 this approach has demonstrated that individuals have preferred associations (i.e.
126 associations are non-random), even within small shoals of fish (Croft et al. 2004,
127 2006). We use a social networks approach to investigate the influence of social
128 structure on the performance of guppies in a novel foraging task. To our knowledge,
129 this is the first time these techniques have been used in this way. Firstly, we
130 investigate differences in social structure between natural and newly-created artificial
131 shoals, and success in the foraging task. Secondly, we investigate whether social
132 association patterns are linked to patterns of foraging and information transfer within
133 groups. We predict that the social structure of natural shoals will reflect the non-
134 random associations occurring within them (Croft et al. 2006), and thus will differ
135 from association patterns in artificial shoals, where individuals will be unfamiliar, and
136 preferred associations will not have been established. We also predict that individuals
137 in natural shoals will forage more successfully (Swaney et al 2001, Ward & Hart
138 2005), and that within shoals, individuals will be more likely to foraging with and
139 obtain social information from those shoal members with whom they have close
140 associations.

141

142

METHODS

143

144 Study Site and Holding Conditions

145 Fish were captured from the Arima River in the Northern Mountain Range of Trinidad
146 (within 500m of Verdant Vale Village, 10°41'N, 61°17'W) during May 2005,
147 between 09.00 – 16.00 hours, using a 2m beach seine. In our investigation we used
148 natural and artificial shoals of fish, each containing 8 adult females. Shoals of 8 were
149 chosen as being representative of natural shoal sizes (2-20 individuals; Croft et al.
150 2003a). Natural shoals (N=10) consisted of groups captured together in the wild, and
151 artificial shoals (N=10) were groups assembled in the laboratory from over 300 fish
152 (see below).

153

154 Natural shoals consisting of at least 10 individuals were captured from the
155 river in their entirety, any males were released back into the river and 8 females of a
156 similar body size (mean \pm SD size of females in natural shoals = 27.99 \pm 2.97mm)
157 were selected from each shoal. The remaining fish were returned to the river. A shoal
158 of guppies was defined as individuals that occurred within 4 body lengths of each
159 other (Pitcher & Parrish 1993). The 8 fish were kept together, isolated from other
160 shoals, and returned to the laboratory, where each shoal was placed in a large artificial
161 pool (diameter = 120cm, water depth = 5cm, water temperature = 26° C), and allowed
162 to acclimatise for 24 hours.

163

164 The 10 artificial shoals were created by collecting over 300 females using 36
165 seine hauls from a 500m stretch of river. The fish were returned to the laboratory and
166 placed in an artificial pool (as above) for 24 hours to allow complete mixing. From
167 this population 80 individuals of similar body size (mean \pm SD size of females in

168 artificial shoals = $28.09 \pm 4.07\text{mm}$) were selected and assigned haphazardly to 10
169 shoals. Each shoal was then placed in a visually isolated pool for 24 hours, as above.
170 Body size did not differ significantly between fish in natural and artificial shoals
171 (independent samples t-test: $t_{1,158} = -0.178$, $p = 0.859$), and there was no significant
172 difference in within-shoal standard deviation between natural and artificial shoals
173 ($t_{1,18} = -1.437$, $p = 0.168$). Unused fish were placed in two large outdoor pools, and all
174 test shoals were maintained on a diet of commercially available flake food, given
175 twice per day.

176

177 Female guppies do not have any natural markings that can be used for
178 identification purposes and thus individuals from all shoals were anaesthetised using
179 tricaine methanesulfonate (MS222), and given individual identity marks using a visible
180 implant elastomer injected in the dorsal epidermis (a standard procedure for marking
181 fish: see Croft et al. 2003b). All fish recovered quickly from the anaesthetic, normal
182 swimming behaviour was quickly resumed, and no mortality was observed as a result
183 of the marking process. Previous work has demonstrated that the procedure does not
184 affect shoaling decisions in guppies (Croft et al. 2004). After marking, shoals were
185 allowed to acclimatise for 12 – 16 hours before experimental procedures began. The
186 experimental protocol for each shoal consisted of 1) quantifying the social structure
187 and shoaling associations (see below), 2) introducing a novel foraging task to the pool
188 and observing the success of fish in completing the task, and 3) re-quantifying the
189 social structure. For each shoal, the three elements of the experimental protocol were
190 carried out sequentially, separated by periods of 10 minutes.

191

192 Quantifying Social Structure

193 We quantified patterns of association by visually observing and recording the
194 membership of sub-groups within the shoal once per minute over a 30 minute period
195 (Croft et al. 2004; Thomas et al. in press). Previous work has shown this to be a
196 sufficient time period to quantify the non-random social network structure of guppy
197 shoals (see Croft et al. 2004 online supplementary material). We defined an
198 association between two fish as occurring when the fish were positioned within four
199 body lengths of each other, a distance that falls within the range of inter-individual
200 distances most commonly observed in shoaling fishes in nature (Pitcher & Parrish
201 1993). All fish in a sub-group were within 4 body lengths of at least one other
202 member of the group (thus, if fish A and C were 6 body lengths apart, but fish B was
203 positioned between them, then all were considered members of a single sub-group).
204 One observer sat motionless, close to the edge of the pool, and a second person was
205 positioned further back from the pool to record the observations relayed to them by
206 the observer.

207

208 Novel Foraging Task

209 Ten minutes after quantifying association patterns, we introduced a novel
210 foraging task to the experimental arena. The task consisted of a white, opaque, plastic
211 cylinder (the ‘feeder’, height = 85mm, diameter at base = 75mm, diameter at top =
212 68mm) with a 20x20mm entrance hole located in the lower wall. The feeder was
213 placed with its centre 30cm from the edge of the pool closest to the observer, with the
214 entrance hole facing the observer. At the beginning of the trial, a pinch of freeze-dried
215 bloodworm (*Chironomus* spp.) was placed in the feeder, where it floated on the
216 surface of the water, but was constrained within the feeder. Any odour cues from the
217 bloodworm are likely to be well contained within the feeder (Laland, K.N.,

218 unpublished data). Bloodworm represents a high-protein food source, readily
219 consumed by the fish, and similar food items are likely to make up part of their
220 natural diet (Magurran 2005). As the bloodworm floated on the water surface, fish
221 feeding at the surface inside the feeder were not visible to fish outside the feeder.
222

223 Following the introduction of the feeder, we recorded the time taken and the
224 identity of the first fish to approach the feeder within four body lengths. After this
225 initial approach observations were made over a 30 minute period. The delay before
226 commencing the observation period ensured that the fish were settled following the
227 introduction of the feeder into the pool, and that they had identified the presence of
228 this novel object. Each time a fish entered the feeder, or fed on the bloodworm at the
229 surface, we recorded the time since the start of the observation period and the identity
230 of the fish.

231

232 After 30 minutes, we removed the feeder and any remaining bloodworm from
233 the pool using a fine-mesh dip net, and after a 10 minute settling period, we re-
234 quantified social structure and association patterns using the same procedure as above.
235 This allowed us to check whether social structure was stable over the time period of
236 the experiment. Previous work has demonstrated that in the wild guppies can move
237 between shoals very rapidly, changing shoals up to once per minute (Croft et al.
238 2003a), and that associations quantified using this method are based on active
239 preferences (Croft et al. 2004). The 30-minute time interval between the two measures
240 of (pre- and post-foraging task) social stability is therefore sufficient to allow ample
241 opportunity for individuals to move among groups. At the end of the experiment, fish

242 were removed from the experimental arena and placed in large artificial outdoor
243 pools, isolated from the river system.

244

245 Data Analysis

246 *Group Sizes and Social Stability*

247 From our observations of association patterns prior to the foraging task (see
248 ‘Quantifying social structure’, above) we calculated the number and size of sub-
249 groups occurring at each time interval (i.e. every minute for 30 minutes, yielding 30
250 observations of group size for each shoal). From these data, the mean group size was
251 calculated for every time interval and we calculated the median value for each shoal
252 independently. We compared the median group sizes of natural and artificial shoals
253 using a Mann-Whitney U test. For each shoal, we also calculated the mean
254 percentage of individuals that were present in groups of sizes 1 to 8, over the 30
255 observations, to give frequency distributions of group sizes for natural and artificial
256 shoals.

257

258 To test whether shoal associations are stable over time (i.e. before and after the
259 foraging task), we created association matrices for each shoal, describing association
260 patterns before and after the foraging trial. We compared the two association matrices
261 (before and after the foraging task) for each shoal using Mantel Tests for matrix
262 correlations. Where appropriate, p-values were combined using Fisher’s Omnibus
263 Test to examine patterns across shoals. Throughout, ‘shoal’ refers to all 8 individuals
264 in a pool, and ‘group’ is used when the shoal divides into sub-units.

265

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

277

278 *Patterns of Foraging*

279 If individuals learn socially from one another, we predict that they are likely to
280 follow one another into the feeder. To investigate whether individuals solved the task
281 by following another individual, or entering the feeder alone, we identified events
282 where an individual first entered the feeder shortly after another individual. We used
283 three definitions of following: 5, 10 and 20 seconds, and all following events were
284 included. Thus, an individual that entered the feeder 4 seconds behind another would
285 be included in all three analyses, while an individual entering 14 seconds behind
286 another would only be included in the 20 second analysis. A definition of following
287 within 5 seconds represents a situation where individuals enter closely behind another
288 individual (within about 4 body lengths), and therefore could be considered members
289 of the same shoal (Pitcher and Parrish 1993). A definition of following within 20
290 seconds, on the other hand, allows for the possibility that individuals can observe

291 another entering the feeder from some distance away, then approach and enter the
292 feeder themselves. In the most successful shoal, the total number of feeder entries
293 over the 30 minutes was 59. This means that on average, one fish fed every 30.5
294 seconds, a greater time interval than our longest following definition of 20 seconds.
295 Within a shoal type (natural or artificial) we corrected p-values using Benjamini and
296 Hochberg's (1995) method for false discovery rate (FDR) control. Adjusted p-values
297 are presented.

298

299 If individuals do follow one another into the feeder, rather than foraging
300 independently, we would predict that entries to the feeder to be more closely clustered
301 in time than would be expected by chance (i.e. the null hypothesis would be that
302 foraging events are independent of one another). To investigate whether this is the
303 case, we performed a randomisation test. We used only foraging events occurring
304 within the interquartile range of foraging times (i.e. the 'middle half' of the each trial)
305 to control for differences in response towards the feeder after it was placed in the
306 pool, and any effect of satiation or food depletion on foraging towards the end of the
307 trial. For each shoal, we calculated the total number of observed feeder entries and the
308 number of occasions on which the difference between one entry time and the
309 preceding one (the entry lag) was less than 5, 10 or 20 seconds (possible following
310 events). We then generated a random set of feeder entry times (within the time
311 available in the interquartile range), containing the observed number of feeder entries,
312 and calculated the number of times the entry lags were less than 5, 10 or 20 seconds.
313 This was repeated 999 times. We calculated the total number of randomisations where
314 the predicted number of following events was greater than or equal to the number
315 observed in the shoal, to give a conservative probability that entries were more

316 clustered in time in the observed shoal than expected by chance (one-tailed test). This
317 was repeated for all 10 natural shoals, and the 6 artificial shoals where entry events
318 were observed.

319

320 We used a further randomisation technique to investigate whether individuals
321 that first entered the feeder by following a leader ('lead-follow pairs') were
322 significantly more highly associated with that individual than would be expected if
323 they learnt the task by following another individual at random. To control for
324 differences between shoals in overall levels of association, we calculated the total of
325 the association strengths of all lead-follow pairs for each shoal. We defined lead-
326 follow pairs as two fish that entered the feeder within 20 seconds of each other,
327 assuming that individuals followed the immediately preceding fish (i.e. if three
328 individuals enter closely in time, in the order A, B and then C, we assume that B
329 follows A, and C follows B). The 20 second rule only was used due to low numbers
330 of following events for other rules in some shoals. For each shoal, we then randomly
331 selected the same number of pairs as were observed in lead-follow events, and
332 summed their association strengths. This randomisation was repeated 999 times for
333 each shoal. We then calculated how many of the randomly generated pairs had a
334 higher sum of association indices than the observed pairs, generating a probability (p-
335 value) that the observed pairs were significantly more associated than random pairs
336 (one-tailed test).

337

338

RESULTS

339

340 Differences in Social Structure and Foraging Success Between Natural and Artificial
341 Shoals?

342 Grouping behaviour differed between natural and artificial shoals. The median group
343 size was significantly larger in artificial shoals than in natural shoals (Mann-Whitney
344 U: $z=-3.659$, $N_{natural}=N_{artificial}=10$, $P<0.001$), and small groups were commonly
345 observed in shoals of naturally co-occurring fish, while larger groups were most
346 commonly found in artificial shoals (figure 1).

347

348 Natural shoals had a significantly smaller mean shoal association strength
349 (AS) than artificial shoals (Mann Whitney U: $z=-3.628$, $N_{natural}=N_{artificial}=10$, $P<0.001$;
350 figure 2a). Associations in natural shoals were also more variable than in artificial
351 shoals: the coefficient of variation in AS was higher in natural than in artificial shoals
352 (Mann Whitney U: $z=-3.175$, $N_{natural}=N_{artificial}=10$, $P=0.001$; figure 2b). Both natural
353 and artificial shoals thus showed variation in AS between pairs of individuals within a
354 shoal, giving us the opportunity to investigate patterns of learning in relation to
355 patterns of social structure.

356

357 After the feeder had been placed in the pool, fish from natural shoals
358 approached it significantly more rapidly than fish from artificial shoals (Mann
359 Whitney U: $z=-2.117$, $N_{natural}=N_{artificial}=10$, $P=0.035$; figure 3a), and more fish from
360 natural than artificial shoals entered and fed from the feeder (entering the feeder:
361 Mann Whitney U: $z=-2.701$, $N_{natural}=N_{artificial}=10$, $P=0.007$; not shown, feeding: Mann
362 Whitney U: $z=-3.752$, $N_{natural}=N_{artificial}=10$, $P<0.001$; figure 3b). In all 10 of the
363 natural shoals at least three fish fed, successfully completing the task. In one shoal, all

364 fish fed. In comparison, we observed feeding in only 5 of the artificial shoals, where a
365 maximum of three individuals fed.

366

367 Can Patterns of Association Predict Patterns of Foraging?

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

375

376 *Do individuals follow others?*

377 We found strong evidence that entries to the feeder were more closely
378 clustered in time than would be expected by chance in both natural and artificial
379 shoals, regardless of the definition of following used (Natural shoals: 5 seconds:
380 $F_{20} = 83.989$, $p < 0.001$. 10 seconds: $F_{20} = 84.011$, $p < 0.001$. 20 seconds : $F_{20} = 54.200$,
381 $p < 0.001$. Artificial shoals: 5 seconds: $F_{12} = 27.522$, $p = 0.006$. 10 seconds: $F_{12} = 44.190$,
382 $p < 0.001$. 20 seconds: $F_{12} = 46.207$, $p < 0.001$). Fish in both natural and artificial shoals
383 are therefore more likely to enter the feeder together than might be expected if each
384 individual was foraging independently, suggesting that the guppies were foraging
385 socially.

386

387 In natural shoals, the majority of fish first entered the feeder alone (using a
388 rule that individuals only followed if they entered the feeder within 5 seconds of

389 another fish), rather than following closely behind another fish (Wilcoxon signed
390 ranks test: $z=-2.501$, $N=10$, $P=0.036$ figure 4), but this was not the case in artificial
391 shoals ($z=-2.014$, $N=10$, $P=0.123$, figure 4). Using a 10 or 20 second rule, however,
392 there was no difference in the number of individuals who first entered the feeder alone
393 and the number that first entered the feeder by following another individual
394 (Wilcoxon signed ranks test: 10 seconds: natural shoals: $z=-1.869$, $N=10$, $P=0.093$;
395 artificial shoals: $z=-1.841$, $N=10$, $P=0.099$; 20 seconds: natural shoals: $z=-1.279$,
396 $N=10$, $P=0.201$; artificial shoals: $z=-1.236$, $N=10$, $P=0.216$, figure 4). Using all rules,
397 there were elevated numbers of individuals that solved the task by following in the
398 natural compared to the artificial shoals (5 seconds: Mann Whitney U: $z=-2.282$,
399 $N_{natural}=N_{artificial}=10$, $P=0.039$, 10 seconds: Mann Whitney U: $z=-2.868$,
400 $N_{natural}=N_{artificial}=10$, $P=0.008$, 20 seconds: Mann Whitney U: $z=-3.032$,
401 $N_{natural}=N_{artificial}=10$, $P=0.008$). As a proportion of the total number of individuals that
402 successfully solved the task, there was a non-significant trend towards a higher
403 proportion of individuals following in natural shoals. (20 seconds: Mann Whitney U:
404 $z=-1.810$, $N_{natural}=10$ $N_{artificial}=6$, $P=0.073$).

405

406 *Do individuals follow close associates when first entering the feeder?*

407 We confined our analysis within shoal following patterns to natural shoals for
408 two reasons. Firstly, in natural shoals, individuals may be predicted to follow familiar
409 associates, and secondly, because successful foraging (and thus the opportunity to
410 learn by following) occurred in only half of the artificial shoals. We found no
411 evidence for higher associations in observed lead-follow pairs (using the 20 second
412 rule, see methods for definition) than would be expected if individuals followed others

413 at random (Table 1b; Fisher's omnibus test to combine P -values across shoals:
414 $F_{20}=17.205$, $P=0.639$).

415

416 *Do individuals forage with close associates?*

417 Previous work has suggested that individual guppies that associate in one
418 context may also associate in another (Croft et al. 2006). We investigated whether
419 social associations before the foraging trial were significant predictors of associations
420 during the 30 minute foraging period. We again defined a pair of fish as being
421 associated during foraging when they entered the feeder within 20 seconds of one
422 another. If individuals forage with close associates more frequently than with distant
423 associates, we would predict a positive correlation between the social associations and
424 foraging associations. We used Mantel tests for matrix correlations, and found no
425 evidence to suggest that associations during foraging could be predicted by the social
426 structure before the task (Table 1c, p -values combined using Fisher's omnibus test:
427 $F_{20}=27.93$, $P=0.111$).

428

429 **DISCUSSION**

430

431 Foraging Success, Boldness, Familiarity and Social Conformity

432 This study demonstrates for the first time that naturally occurring fish have a foraging
433 advantage over randomly composed shoals. In natural shoals, more individuals
434 successfully fed from the feeder than in artificial shoals, thus benefiting from
435 enhanced foraging success. Whilst a number of factors may have influenced the
436 success of natural shoals, our results suggest three plausible explanations: (1) a *risk*
437 *perception hypothesis* – differences in the perception of danger, resulting in greater

438 risk-prone or bold behaviour in the natural shoals and more risk-averse or shy
439 behaviour in the artificial shoals; (2) a *social learning hypothesis* – elevated levels of
440 following and reduced effects of conformity in natural compared to artificial shoals;
441 and (3) a *time trade-off hypothesis* – differences in the prioritisation of foraging and
442 establishing social ties, resulting in reduced foraging motivation in artificial compared
443 to natural shoals.

444

445 Several researchers have suggested that the perception of danger (resulting in
446 risk-averse or shy behaviour) may reduce foraging motivation (Warburton 2003),
447 information transmission, and learning (Dall et al. 1999) among animals. In our study,
448 fish in natural shoals approached the feeder more rapidly after it was placed in the
449 experimental pool, and showed a lower overall shoaling tendency (illustrated by the
450 predominance of smaller groups and lower association strength) than fish in artificial
451 shoals. A short latency to approach a novel object and low shoaling tendency are often
452 used as indicators of boldness when assessing behavioural syndromes in fish (e.g.
453 Budaev 1997, Ward et al. 2004, Brown et al. 2007). The ability (Sneddon 2003) and
454 opportunity (Dugatkin & Alfieri 2003) for fish to learn a novel task has previously
455 been shown to be enhanced by increased boldness: Bold fish tend to be more
456 successful, learning more rapidly compared with shy fish. Although we cannot
457 distinguish between behavioural types (e.g. differences in boldness or innovativeness,
458 Sih et al. 2004) or differences in anxiety, motivational state or curiosity, our findings
459 are consistent with the idea that associating with natural group-mates generates a
460 reduced perception of danger.

461

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

486

487 A second potential explanation for the relative success of natural shoals is that
488 they exhibited higher levels of social learning of the route to the food source. This
489 hypothesis is supported by the observation that entries to the feeder were clustered in
490 time, and that levels of following in natural shoals were somewhat elevated in
491 comparison to artificial shoals. However, clustering was evident in both natural and
492 artificial shoals, and the proportions of individuals first entering the feeder by
493 following were similar. One factor known to influence the level of social learning is
494 the ‘conformity effect’ (positive frequency-dependent social learning) mediated by
495 shoaling patterns (Day et al. 2001; Brown & Laland 2001). We found that in natural
496 shoals, groups within the shoal were smaller than those in artificial shoals. Day et al.
497 (2001) found that although individuals in larger groups are on average generally more
498 successful at locating food than individuals in smaller groups, individuals in smaller
499 groups can find a resource more quickly when the resource is hidden. Day et al.
500 (2001) attributed this to a greater reluctance on the part of individuals to leave larger
501 than smaller groups. In our study, the feeder was opaque, thus, in order for a fish to
502 enter and feed it needed to break visual contact with the rest of the shoal. Therefore,
503 individuals in artificial shoals may have been more reluctant to leave their larger
504 groups and enter the feeder than individuals in natural shoals. Alternatively, the more
505 a shoal subdivides into smaller groups, the greater the chance that any single
506 individual will find a hidden resource. This high level of subdivision may be due to
507 lower levels of risk aversion linked to the familiar social environment.

508

509 A further hypothesis to explain the relative success of natural shoals is related
510 to the prioritisation of different activities in the different shoal types. Individuals in
511 artificial shoals may prioritise learning about each other (i.e. the process of

512 familiarisation) over immediate foraging, given the benefits associated with
513 familiarity (Griffiths 2003, Ward & Hart 2003). Larger group sizes, higher association
514 strengths and lower variation in associations in artificial shoals compared to natural
515 shoals support the idea that individuals are switching associations rapidly as part of
516 this process.

517

518 Information Transmission Within Shoals

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

532

533 There may be several explanations for our findings. Firstly, individuals may
534 choose their social partners differently from the way they choose their foraging
535 partners. Individuals may, for example, benefit by foraging with those that they know
536 to be poor foragers (Metcalf & Thompson 1995), rather than with those that are

537 preferred associates in other contexts (e.g. predator inspection, Croft et al. 2006).
538 Secondly, our method of establishing the social and foraging ties may have been
539 inadequate, although it has been previously found to be sufficient to quantify the non-
540 random structure of such groups (Croft et al. 2004 online supplementary material).
541 Thirdly, our power to detect an effect may be reduced by the presence of random
542 interactions creating ‘noise’ around the non-random preferred interactions.

543

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

558

559 Finally, we cannot rule out the possibility that the task used in this experiment
560 was easily learned asocially by individual fish, and consequently did not require social
561 information for its solution. The movement of odour cues may have facilitated this,

562 although they are likely to have been well contained (Laland, K. N. unpublished data),
563 particularly without water movement to disperse them (Vogel 1994). Experiments
564 using similar tasks, where individuals learn the route to a foraging resource, have
565 provided evidence for social learning (Reader et al. 2003), and we found evidence that
566 individuals entered the feeder in small groups, suggesting foraging was a social
567 activity. Studies where inexperienced individuals are unlikely to learn the task
568 themselves provide the most compelling evidence for social learning (Lefebvre &
569 Palameta 1988), thus individuals within a shoal could be trained in a more complex
570 task (e.g. Reader & Laland 2000, Stanley et al. in press), and the links between social
571 structure and foraging patterns investigated.

572

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

579

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

587 between social structure and patterns of information transfer, and we hope our study
588 encourages this.

589

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595 The experiments presented here comply with the laws of the country in which they
596 were carried out.

597

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825
826

827 **Table 1:** Results of the Mantel tests for matrix comparisons and within-shoal foraging
828 events, investigating a) correlations between social structure before and after the
829 foraging trial, b) whether individuals first enter the feeder by following a close
830 associate and c) correlations between social network structure and associations during
831 the foraging trial, for the 10 natural shoals only. *P*-values for significant positive
832 correlations are highlighted in bold, significant negative correlations are marked with
833 an asterisk. Combined *P* values are the result of Fisher's Omnibus tests (see text for
834 details).

835

836

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

837

838 **Figure legends**

839

840 **Figure 1:** Percentage frequency distributions of guppy groups in natural (open circles)
841 and artificial (filled circles) shoals. Values are the median percentage frequency of
842 individuals in groups of each size across all replicate trials. Error bars represent
843 interquartile range. Solid lines are used as a visual aid only, linking values for each
844 shoal type.

845

846 **Figure 2:** Comparing median values for network measures (association strength; AS)
847 between natural and artificial shoals. a) shoal AS ($z=-3.628$, $N_{natural}=N_{artificial}=10$,
848 $P<0.001$) and b) coefficient of variation in AS ($z=-3.175$, $N_{natural}=N_{artificial}=10$,
849 $P=0.001$). Error bars indicate the inter-quartile range.

850

851 **Figure 3:** Results of the foraging trial comparing natural and artificial shoals. a)
852 median time to approach the feeder ($z=-2.117$, $N_{natural}=N_{artificial}=10$, $P=0.035$) and b)
853 the median number of fish feeding in each shoal ($z=-3.752$, $N_{natural}=N_{artificial}=10$,
854 $P<0.001$). Error bars indicate the inter-quartile range.

855

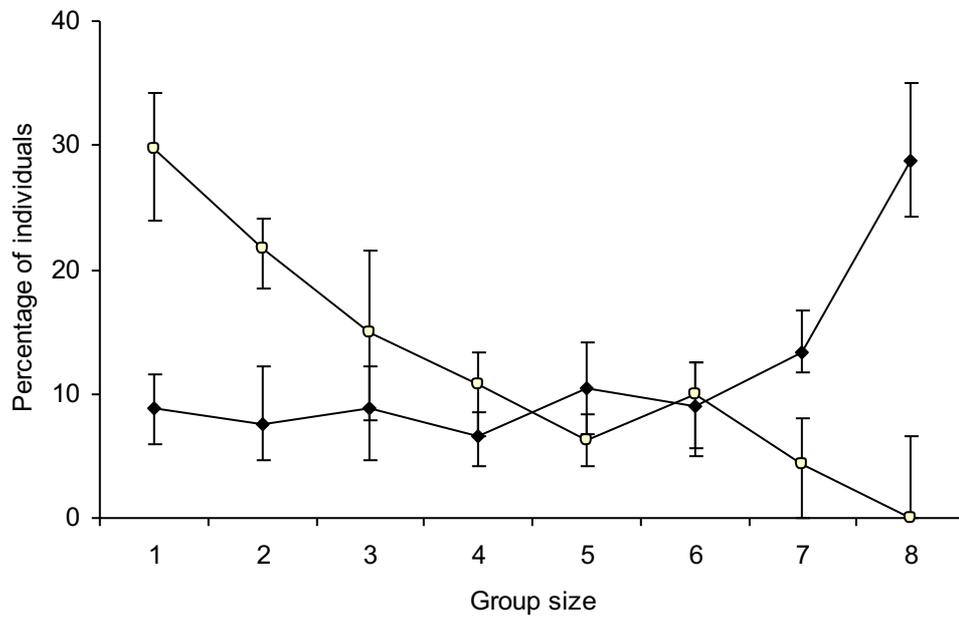
856 **Figure 4:** Median number of fish in a shoal that first entered the feeder alone (open
857 bars) as opposed to following a demonstrator (closed bars), for both a 5 second and 20
858 second following rule, in natural (5 secs: $z=-2.501$, $N=10$, $P=0.036$; 20 secs: $z=-1.279$,
859 $N=10$, $P=0.201$) and artificial (5 secs: $z=-2.041$, $N=10$, $P=0.123$; 20 secs: $z=-1.236$,
860 $N=10$, $P=0.216$) shoals. Error bars indicate the inter-quartile range.

861

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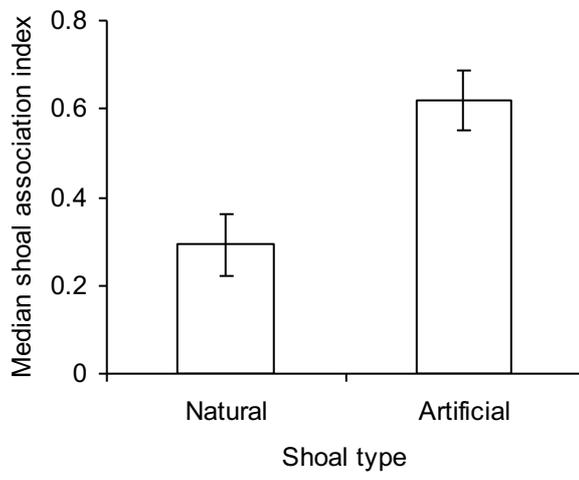
864 **Figure 1:**



865

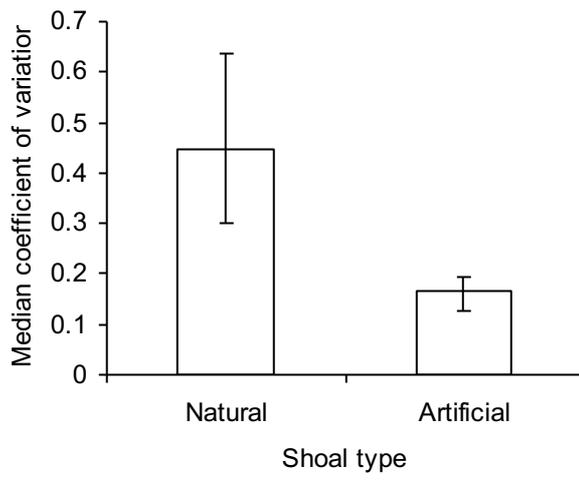
866 Figure 2

867 a)



868

869 b)

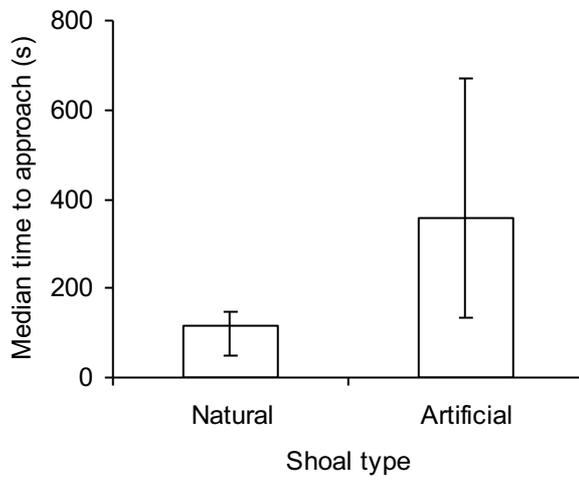


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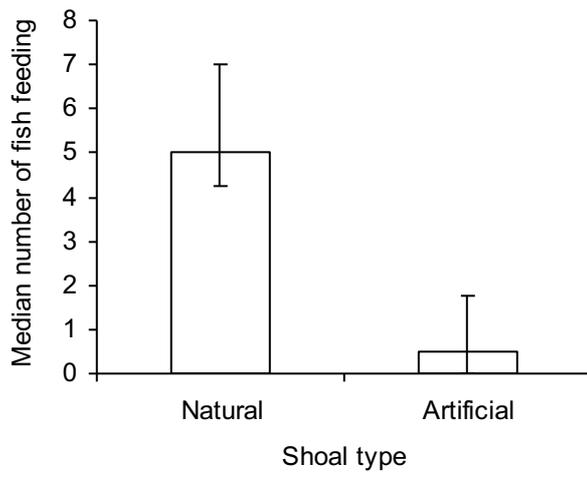
872 **Figure 3**

873 **a)**



874

875 **b)**

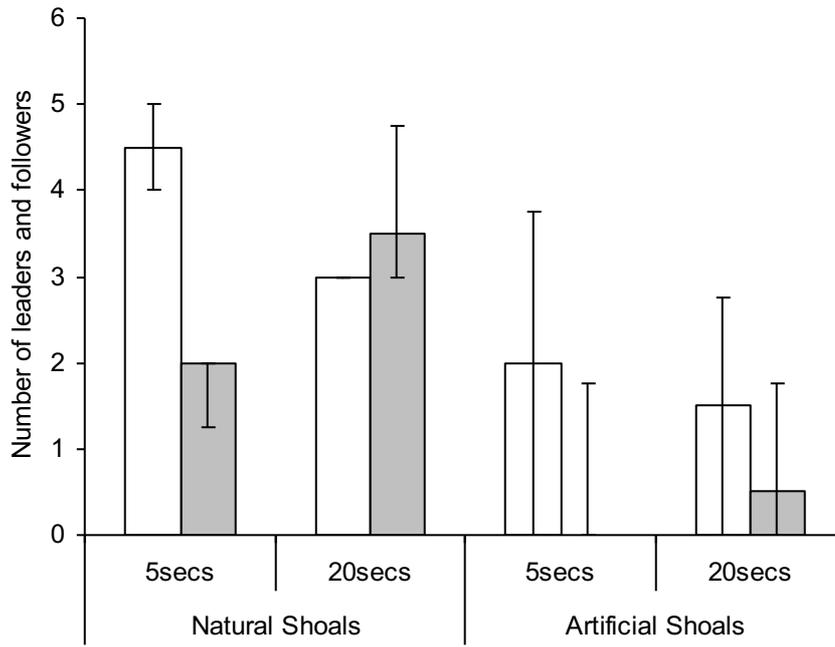


876

877

878

879 **Figure 4**



880

881

882