1 **Behavioural Trait Assortment in a Social Network: Patterns and Implications**

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24 **Abstract**

25 The social fine structure of a population plays a central role in ecological and

26 evolutionary processes. Whilst many studies have investigated how morphological traits

27 such as size affect social structure of populations, comparatively little is known about the

28 influence of behaviours such as boldness and shyness. Using information on social

29 interactions in a wild population of Trinidadian guppies (*Poecilia reticulata*) we construct

30 a social network. For each individual in the network we quantify its behavioural

31 phenotype using two measures of boldness, predator inspection tendency, a repeatable

32 and reliably measured behaviour well studied in the context of co-operation, and shoaling

33 tendency. We observe striking heterogeneity in contact patterns, with strong ties being

34 positively assorted, and weak ties negatively assorted by our measured behavioural traits.

35 Moreover, shy fish had more network connections than bold fish and these were on

36 average stronger. In other words, social fine-structure is strongly influenced by

37 behavioural trait. We assert that such structure will have implications for the outcome of

38 selection on behavioural traits and we speculate that the observed positive assortment

39 may act as an amplifier of selection contributing to the maintenance of co-operation

40 during predator inspection.

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Introduction

Social interactions rarely occur at random and individuals are often interconnected in a complex heterogeneous social network in which individuals differ in the number and strength of interactions they have (Croft et al. 2008). The structure of a social network will influence an individual's access to resources and information (Krause *et al.* 2007; Wey *et al.* 2008), which will in turn set the stage for many key behaviours including finding and choosing a sexual partner, developing and maintaining cooperative relationships, foraging and avoiding predators (Wilson 1975; Krause et al. 2007). Moreover, many important ecological processes are likely to be influenced by social network structure (Krause et al. 2007; Wey et al. 2008). Even so, comparatively little is known about factors that influence social network structure or the implications of social network structure for evolution.

There are many factors contributing to non-random social associations among individuals. For example, group-level assortment by phenotypic attributes such as species, body size and sex is well-documented in many taxa and has been attributed to a number of adaptive benefits including reduced predation risk and increased foraging efficiency (Krause and Ruxton 2002). These traits, often morphological, are known to affect social fine structure as it is revealed in social networks of wild populations (Croft *et al.* 2005). By comparison, the behavioural phenotype of individuals is largely neglected in this context (but see Pike *et al.* 2008 for a laboratory-based exception). It has long been recognized that animals exhibit consistent patterns of individual behaviour (Huntingford 1976; Magurran 1993; Wilson 1998; Gosling 2001), referred to as

66   personalities, temperaments or behavioural types (Sih et al. 2004; Reale et al. 2007).

67   Perhaps the best studied example is variation along the bold-shy axis. Bolder individuals

68   can generally be characterized as exhibiting more risk-prone behaviours across a range of

69   contexts including approaching novel objects, consuming novel food items, inspecting

70   predators, and spending more time in open habitats (see Reale et al. 2007 for a review).

71   Behavioural phenotypes often influence sociality (Roberts et al. 2008) so they should be

72   expected to influence who interacts with whom within a social network. Pike et al. (2008)

73   found that shy three-spined sticklebacks (*Gasterosteus aculeatus*) associated

74   preferentially with a small number of other group members whereas bold individuals had

75   fewer overall interactions than shy fish, and distributed their interactions more evenly

76   across all group members. The interaction between such behavioural traits and social

77   network structure in wild animal populations remains unknown.

78

79   The structure of social networks is likely to have important implications for the

80   strength and direction of selection on behavioural traits. Many behavioural traits are

81   subject to frequency dependent selection, in which the fitness of an individual will

82   depend in part on its social environment (i.e. an individual's interactions with others and

83   their accompanying behavioural types). For example, in models of conflict, the success of

84   a hawk (aggressive) or dove (yielding) strategy will be dependent on the frequency of

85   hawks and doves in an individual's local interaction network (Maynard Smith 1982).

86   Non-random interactions between individuals based on behavioural traits can

87   dramatically influence selection and in some cases may act as an amplifier of selection on

88   those traits (Ohtsuki *et al.* 2006). Thus quantifying the relationship between social

89   structure and behavioural traits may help us understand how selection acts on these traits.

90

91   In the present study we investigate whether there is evidence of social structuring by

92   behavioural phenotype in a wild population of guppies (*Poecilia reticulata*). Field

93   observations of social associations over a 10-day period were used to build a social

94   network and network analysis was used to characterise the social fine structure of our

95   population. A network is simply a graph consisting of nodes connected by edges (lines).

96   In the current investigation nodes represent individual animals and the edges the

97   relationships between them are based on social associations. We represent the intensity of

98   such interactions by giving each edge a weight proportional to the frequency of observed

99   association. Compared to more traditional approaches that focus on dyadic interactions

100   between animals in isolation, the network approach allows us to put such interactions into

101   the wider social context of the population (Krause et al. 2009). For every fish in the

102   population we quantify its predator inspection and shoaling tendency via standard

103   laboratory tests and use this to assign it a behavioural score (BS). Predator inspection is

104   indeed a consistent behavioural trait that can be reliably measured and differs between

105   individuals (Budaev 1997). It is also a behaviour that has been studied in depth in the

106   context of cooperation (Milinski 1987; Dugatkin 1988; Croft et al. 2006a). Individuals

107   leave the relative safety of a group to approach and inspect a predator, gaining

108   information on the predator's state and on the probability of attack (Pitcher et al. 1986).

109   This information is transmitted to non inspecting individuals, providing fitness benefits to

110   all group members (Magurran and Higham 1988; Godin and Davis 1995). Inspectors pay

111   a personal cost of increased risk of predation (Dugatkin 1992; Milinski et al. 1997),

112   which they can reduce by inspecting in cooperative partnerships (Milinski 1987;

113   Dugatkin 1988; Croft et al. 2006a). Theoretical work suggests that the benefits to

114   inspectors will be maximised when there is social assortment based on predator

115   inspection behaviour (Wilson and Dugatkin 1997). We look for evidence of such

116   assortment by behavioural strategy in our social network.

117

118   **Materials and Methods:**

119   *Study Population:*

120   Adult guppies were captured from a 35m section of the Arima River ($10^{o}41'$N,

121   $61^{o}17'$W) in the Northern Mountain Range of Trinidad in May 2006. Guppies here are

122   under high risk of predation due to the presence of major pisciverous predators, including

123   the pike cichlid, *Crenicichla sp*. The fish were caught in two interconnected pools

124   between which they could move freely. During fish sampling entire shoals (defined as

125   two or more fish observed within four body lengths) were captured from each of the

126   pools using a 2-m seine (Croft *et al.* 2004). After capture, shoals were housed

127   individually in sealable 2 L plastic storage bags. All adult guppies were brought to the

128   laboratory to be screened for behavioural traits. Fish were housed in two aquaria, one for

129   fish captured from each pool (l x h x w = 76 x 46 x 46cm, water depth = 35cm) that had

130   natural substrate collected from the river. Guppies were anaesthetized (MS-222 Sigma

131   Chemical) and given individual identity marks by injecting different colours of visible

132   implant elastomer (VIE) in two of six positions on the dorsal area (Croft et al. 2003a).

133   The identification mark does not have an effect on shoal choice behaviour (Croft *et al.*

134   2004). The sex and total length of each fish were recorded at the time of marking.

135

136   ***Behavioural Screening:***

137   After marking, the fish were left to acclimatise in the holding tanks for a period of

138   24 to 48 h, before behavioural screening. When an individual inspects a predator it is

139   trading off a tendency to seek refuge in a social group and a willingness to undertake

140   risky behaviour. Shy fish might also be expected to seek refuge in a shoal more than bold

141   fish, so to examine the robustness of behavioural differences between individuals we also

142   tested an individual's preference to be with conspecifics. Behavioural screening was

143   carried out in a test tank (90cm x 30cm x 30cm; water depth 15cm) made up of three

144   compartments ("release", "shoaling" and "predator inspection" respectively) each 30cm x

145   30cm x 30cm, that could be isolated using two opaque barriers. Observations were made

146   directly by an observer who was located in front of the tank and manipulated the opaque

147   barriers using a remote pulley mechanism. At the start of each trial both barriers were in

148   the down position isolating the three compartments. Initially the test fish was placed

149   alone in the release compartment (at one end of the tank). After a 10-minute period the

150   opaque barrier separating the release compartment and the shoaling compartment (the

151   central compartment) was raised using a remote pulley mechanism allowing the test fish

152   access to the shoaling compartment. The shoaling compartment contained a stimulus

153   shoal made up of two large (>25mm) and two small (<20mm) female guppies. The

154   stimulus shoal was contained within a cylindrical container (diameter=10cm) in the

155   centre of the compartment that allowed the transmission of visual, but not olfactory, cues.

156   The stimulus fish were most likely unfamiliar to the focal fish as they were caught from

157   another section of the Arima River that was more than 500m from the site of the test fish

158   capture. The amount of time that focal fish spent associating with the stimulus shoal

159   (defined as being with 5cm) was recorded over a 10-minute period. Then the second

160   partition was raised allowing the fish access to the predator compartment. The predator

161   compartment contained a model fish predator (a fishing lure) located in the rear corner

162   and faced towards the shoaling compartment. The number of approaches within a

163   standardised length of 15cm of the predator was recorded over a 10-minute period. Each

164   fish was screened for shoaling and predator inspection behaviour twice on consecutive

165   days. When not undergoing testing the fish were housed in their original holding tank

166   (see above).

167

168   ***Building the Social Network:***

169   After screening, all individuals (N=72) were simultaneously released into the

170   centre of their original pool in the Arima River. This occurred approximately 144 h after

171   capture. Re-sampling of the population began 24 h after release and was undertaken once

172   per day between 10:00 and 14:00 h for 9 consecutive days. Entire shoals were captured

173   from the pools using a 2-m seine as in the initial capture of the study population. The

174   depth of water at the location of capture was recorded for each shoal. Shoals were kept in

175   individual sealable 2 L plastic storage bags, and released back to their capture location

176   after the composition of all shoals had been recorded. Individuals were recaptured on

177   average ($\pm$SD) 4.7$\pm$2.5 times.

178

179   For each sampling day (day 0 to 9) fish were defined as associating if they were

180   observed in the same shoal. These associations were then accumulated over the 10

181   sampling days. From this data we calculated the strength of association between each pair

182   of animals using an association index. As we have no reason to believe there was a

183   sampling bias in seeing animals together or apart, we used the simple-ratio index (SRI)

184   (Cairns and Schwager 1987).

185

186     $$SRI = \frac{X}{X + Y_{ab} + Y_a + Y_b}.$$

187

188   Where X is the number of times a pair of animals (a and b) were observed in the same

189   group, Y_a is the number of times a was observed in a group but not b, Y_b is the number of

190   times b was observed in a group but not a and Y_{ab} is the number of times bother animals

191   were observed in different groups. The SRI gives indices that are scaled between 0 and 1

192   with a value of 1 indicated that the pair was always observed together and a value of 0 if

193   the pair never associated.

194

195   Guppies have a dynamic fission fusion social system in which there can be a rapid

196   change of shoal membership. Shoals sampled at one point in time may therefore contain

197   some pairs of animals that are frequently found together, and others that are rarely

198   together. The edges of the network are weighted by the strength of association (SRI)

199   between pairs of animals, so by constructing a series of networks filtered to include only

200   the stronger or the weaker associations we are able to explore the interplay between

201 social fine structure and behavioural trait at different levels of social association. Eight

202 networks were considered: four (S1-S4) were used to analyse increasingly strong social

203 ties; these were filtered to include only pairs of animals with $SRI \geq 0.1, 0.2, 0.3$ and 0.4

204 respectively. To study the structure of weak ties, the same thresholds were used, but as a

205 maximum, to produce networks W1-W4. So in W2, for example, pairs are only joined if

206 their SRI is > 0 and ≤ 0.2. For each network we calculated the mean degree (defined as

207 the average number of associations individuals have in the network) as a measure of

208 social differentiation. To quantify assortment by behavioural score in our filtered

209 networks, we correlated an individual's behavioural score with the average behavioural

210 score of its network neighbours (Newman 2003). The distribution of group sizes and

211 recapture frequencies are known to have an effect on network structure (James et al.

212 2009), so all measured network values were compared to the results of a Monte Carlo test

213 in which these variables were preserved (Croft et al. 2008). Furthermore, whilst all fish

214 within a pool on a given day have the opportunity to interact socially it is unrealistic to

215 assume that individuals in different pools have the same opportunity. For this reason we

216 further constrained the randomisation test to randomise shoal structure for fish captured

217 within a pool on a given day. A similar test was used to look for shoal-level assortment.

218 In this case the test statistic is the coefficient of variation (CV) in phenotype within each

219 shoal, averaged over all shoals.

220

221 **Results**

222 *Quantifying Behavioural Traits:*

223   Both of behavioural measures showed significant repeatability between the two testing

224   days (Spearman rank correlation, inspection, n=72 r=0.24, P=0.05 and shoaling N=72,

225   r=0.23, P=0.05). To provide a single measure for each behaviour the average of the two

226   values were calculated. We found substantial variation among individuals in the number

227   of predator inspection events during the trials (mean±(SD)=4.19±3.07) and in the time

228   they spent shoaling (mean (±SD)=351.5±92.3 sec). No significant differences were

229   observed between the sexes in either inspection tendency or shoaling tendency (ANOVA;

230   inspection: $F_{1,71}$=1.26, P=0.26; shoaling: $F_{1,71}$=0.01, P=0.91) and no relationship was

231   observed with either measure and body length, a morphological variable known to

232   explain many aspects of shoal composition in this species (Croft *et al.* 2005) (Spearman

233   rank correlation, inspection, n=72, r=-0.080, P=0.50; shoaling: n=72, r=-0.013, P=0.91).

234

235   There was a significant negative correlation between the time an individual spent

236   shoaling and its propensity to inspect a predator (Spearman rank correlation n=72, r=-

237   0.502, P<0.0001). To provide a behavioural profile for each individual we combined the

238   two scores using principal component analysis to produce its 'behavioural score' (BS) in

239   which the bolder fish (i.e. individuals with high inspection and low shoaling) have larger

240   values. The first principal component explained 76 % of the variance with both shoaling

241   tendency and inspection tendency loading on the component with a value of 0.872. No

242   significant relationship was observed between BS and average water depth (Spearman

243   rank correlation n=72, r=-0.19, P=0.115)

244

245   *Quantifying Social Network Structure:*

246 The average ($\pm$SD) SRI index between network dyads was 0.177$\pm$0.083. Nine

247 animals were seen only once, and were removed from the analysis, to avoid bias in the

248 edge weights. Network S1 is shown in Fig. 1; it includes all observed associations and

249 interconnects all 63 fish. Its mean degree is relatively high (11.1), with each individual

250 connected to nearly one fifth of the population. Fig. 2 shows that the mean degree

251 decreases rapidly as a function of association filter threshold. Thus individuals have many

252 casual associations but fewer stronger and potentially socially significant associations.

253 Also shown are the values of mean degree we should expect under a null model of shoal

254 membership. The mean degree of S1 is lower than expected; S2 and S3 higher (Fig. 2).

255 S4 contains too few edges to maintain test power. The results for S2 and S3 imply that

256 shoals are somehow assorted. We tested the shoals observed on the first day of capture

257 only (to avoid pseudo-replication) and found strong assortment by body length in shoals

258 (n=18, CV=8.64, P<0.0001 - see methods). This is a well known result for this species

259 (Croft *et al.* 2005). More interestingly, we found no evidence of assortment of shoal

260 membership by our behavioural score (n=18, CV=31.2, P=0.337).

261

262 Despite the lack of group-level assortment, we found significant positive BS

263 assortment in networks S1-S3, with the observed correlation coefficients exceeding those

264 from the model and increasing with filtering threshold (Fig. 3a). S4 again contains too

265 few edges to maintain test power. In addition we found significant negative BS

266 assortment in the W1 network (in which only edges with SRI $\leq$ 0.1 are included, Fig. 3b).

267 We also looked for correlations in our S networks by predator inspection alone (as

268 opposed to a combined inpection and shoaling behavioural score BS), since co-operative

269   predator inspection behaviour in guppies is known to occur between individuals that form

270   strong social ties (Croft et al. 2006a). The results of this analysis are consistent with the

271   analysis of the BS, in that there was a non-significant tendency for the observed

272   assortment to be greater than the expected assortment across all filtering thresholds (see

273   Fig 3c), this was only significant however for networks S2 and S3 (see Fig 3c).

274

275   We found a non-significant negative correlation between an individual's BS and

276   network degree (the number of social ties they have), with bolder individuals having a

277   tendency to form fewer network ties (Spearman rank correlation: n=63, r=-0.24, P=0.058,

278   see Figure 4a). Removal of one outlying point from the data (Fig. 4a) resulted in a

279   significant negative correlation (n=62, r=-0.29, P=0.020). We also found a significant

280   negative correlation between the average association strength an individual has with its

281   network neighbours and an individual's BS with bolder individuals having on average

282   weaker network ties (Spearman rank correlation: n=62, r=-0.35, P<0.0001; Fig. 4b).

283

284   **Discussion**

285

286   Our results provide the first insight into how social networks are structured by

287   behavioural traits in a wild population, showing evidence for non-random mixing of

288   individuals in a social network based on their behavioural traits. We have to keep in mind

289   that these results are from one social network, making it difficult to generalise about the

290   observed patterns. Replication is a common problem for ecological studies on this scale

291   but the patterns we observe are very clear. In particular, we found that the social network

292   was positively assorted by behavioural score (BS) across all ties in the network and

293   positively assorted by predator inspection tendency across strong network ties. An

294   individual's BS predicted the number and strength of interactions they had, with high-BS

295   individuals forming fewer associations that were on average weaker - a finding that

296   supports previous laboratory work (Pike et al. 2008).

297

298   There are a number of mechanisms that could contribute to the observed

299   behavioural structuring of the social network by BS. Firstly, individuals with a high BS

300   are predicted to spend less time shoaling, which we predict will lead to them having

301   fewer and weaker social interactions. This prediction is supported by our field

302   observation which strongly suggests that our measured behaviour in the laboratory

303   reflects the behaviour of individuals under natural conditions. Secondly, it is possible that

304   the observed positive behavioural assortment could be the by-product of morphological

305   assortment if behavioural traits are correlated with morphological traits (Külling and

306   Milinski 1992). The most obvious morphological candidates for this are body size and

307   sex, but no relationship was observed between size and BS and there was not a significant

308   difference in BS between the sexes, suggesting that behavioural assortment is not driven

309   as a by-product of morphological assortment in the current investigation. Thirdly, the

310   phenotypic distribution of individuals in the habitat may limit the opportunities for social

311   interactions to occur. A study on the pumpkinseed sunfish (*Lepomis gibbosus*)

312   documented that individuals of different behavioural types utilise different habitats

313   (Wilson et al. 1993). In guppies water depth is an important variable influencing the

314   phenotypic distribution of fish within the habitat, both as a function of body size and of

315 sex (Croft et al. 2003b; Croft et al. 2006b), and it has been demonstrated that a greater

316 water depth is associated with increased predation risk (Croft et al. 2006b; Darden and

317 Croft 2008). However, in our study population we did not observe a significant

318 relationship between the average water depth in which an individual was observed and its

319 behavioural score so it appears unlikely that habitat segregation based on behavioural

320 type is a significant factor in the behavioural structuring of the social network. Finally, it

321 is possible that positive assortment in the network could be driven through passive

322 mechanisms due to individual variation in social tendencies, leading to repeated

323 interactions between individuals of a similar behavioural type that are independent of

324 active partner preferences. Whilst it is easy to see how this mechanism could lead to

325 positive behavioural assortment, it is not clear how such a mechanism could lead to

326 negative behavioural assortment as is observed amongst weak ties in the social network.

327 This latter result is indeed intriguing and leads us to hypothesize that active partner

328 choice and partner updating may have a significant role to play in generating the patterns

329 of negative assortment. Further work exploring the mechanisms underpinning these

330 negatively assorted weak interactions and their functional benefits provides an exciting

331 avenue for future research. More generally, further work is needed to elucidate the

332 mechanisms underpinning the patterns of behavioural assortment. Using individual based

333 models to explore the influence of behavioural type on social network structure and vice

334 versa, could be a fruitful avenue for future research.

335

336   In addition to the potential passive mechanisms outlined above there may be

337 benefits that drive positive assortment by BS that lead to individuals actively assorting by

15

338 behavioural type. For example, if individuals of different behavioural types differ in

339 activity levels, then individuals may assort to synchronise behaviour and minimise energy

340 expenditure. Such a mechanism has been proposed to explain phenotypic assortment

341 based on sex in ungulates where the sexes differ in activity patterns such as foraging and

342 resting (Conradt 1998; Ruckstuhl 1999). Further work exploring the extent to which

343 individuals of different behavioural types assort to synchronise behaviour (such as

344 activity) could be very rewarding. Behavioural assortment may also provide anti-predator

345 benefits (Szulkin et al. 2006). It is well documented that the anti-predator benefits of

346 group living increase with phenotypic assortment of social groups and that odd

347 individuals in a group suffer an increased risk of predation due to the 'oddity effect'

348 (Ohguchi 1978; Landeau and Terborgh 1986; Theodorakis 1989). Whilst the oddity effect

349 has generally been considered in the context of morphological traits such as body size

350 and coloration (Landeau and Terborgh 1986; Theodorakis 1989), it is possible that

351 behavioural assortment increases the anti-predator benefits of grouping by decreasing

352 phenotypic oddity (Szulkin et al. 2006).

353

354   Whilst our work does not directly test the evolutionary implications of the social

355 network structure, our finding that the guppy social network was positively assorted by

356 predator inspection behaviour is interesting in the context of selection on this behavioural

357 trait (Wilson and Dugatkin 1997). Our previous work has demonstrated that pairs of

358 individuals that form stable social associations are more likely to engage in co-operative

359 predator inspection behaviour together (Croft et al. 2006a) and the results presented here

360 demonstrate that they have similar predator inspection tendencies. It has been suggested

361   that behavioural assortment by co-operative behaviour may be important in maintaining

362   co-operation (Wilson and Dugatkin 1997; Ohtsuki et al. 2006; Santos et al. 2006).

363   However, evidence of such assortment remains elusive in wild populations. Whilst we

364   can not directly infer levels of co-operation between individuals in the current

365   investigation if we speculate that individuals that have similar inspection tendencies are

366   more likely to engage in co-operative predator inspection behaviour together, then the

367   observed positive assortment of the social network may contribute to the maintenance of

368   co-operation in the population (Wilson and Dugatkin 1997; Ohtsuki et al. 2006; Santos et

369   al. 2006). It has been suggested that in dynamic social systems very simple behavioural

370   strategies such as 'walk away when encountering non-co-operation' (Aktipis 2004) may

371   lead to repeated interactions between co-operators and promote co-operation (Santos et

372   al. 2006). In fact, previous laboratory work with guppies (Dugatkin & Alfieri 1991) has

373   shown that individuals monitor the inspection behaviour of others and prefer to associate

374   with individuals with a high inspection tendency. Work on both sticklebacks and guppies

375   in the laboratory suggests that individuals form stronger social associations with whom

376   they co-operate (Milinski et al. 1990; Croft et al. 2006a), suggesting that the patterns

377   observed in the current study could be based on active choice. We also see that animals

378   have fewer ties the stronger the ties are. This is not surprising, but is consistent with

379   arguments that partner updating decreases the number of ties individuals have, which

380   may be important in maintaining co-operation (Santos et al. 2006). The possibility that

381   simple partner updating could at least aid the maintenance of co-operation via assortative

382   interactions, without the need for advanced cognitive abilities, is certainly intriguing and

383   we believe it offers an exciting avenue for future research. Furthermore, the work

384   presented here highlights the need for in-situ studies of association patterns, as previous

385   attempts to explore assortative interactions and partner switching in guppies under

386   artificial laboratory conditions have produced inconclusive results (Dugatkin and Wilson

387   2000; Thomas et al. 2008).

388

389   Our work indicates that behavioural traits influence, or perhaps are influenced by,

390   the social fine-structure of the population and that this structure may influence the

391   strength and direction of selection on those traits. Designers of future empirical studies

392   trying to unravel selection pressures on behavioural traits or to resolve the mechanisms

393   underpinning population social structure should therefore seriously consider recording

394   social contact patterns. A network analysis allows us to examine structural properties that

395   are maintained over time, or indeed those that are not, and to probe structure at any level

396   between the individual and the population. The power of the approach is clearly

397   illustrated by the fact that assortment by the behavioural trait is only evident in the

398   network; though shoals of guppies were significantly assorted by body size (a pattern that

399   is well documented in other studies (Krause et al. 2000)), they were not assorted by

400   behavioural score. A shoal-level analysis could not have captured this aspect of social

401   structure (Croft et al. 2003b).

402

403   In conclusion, we report the first evidence of social structure shaped by

404   behavioural phenotypes in a wild population. Our findings are consistent with

405   observations of human social network formation in which the personality score of

406   individuals influences the formation of network ties (Roberts et al. 2008). Our work

407 illustrates the potential of adopting a network approach for understanding how selection

408 acts on behavioural traits that are subject to frequency-dependent selection in natural

409 populations. This is an exciting and developing area of research that we believe could

410 have broad application. More work is needed to look at the mechanisms underpinning the

411 structure of social networks and the evolutionary consequences of network structure.

412

413 **Acknowledgments**

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420 **References**

421 Aktipis CA (2004) Know when to walk away: contingent movement and the evolution of

422   cooperation. Journal of Theoretical Biology 231:249-260

423 Budaev SV (1997) "Personality" in the guppy (*Poecilia reticulata*): A correlational study

424   of exploratory behavior and social tendency. Journal of Comparative Psychology

425   111:399-411

426 Cairns SJ, Schwager SJ (1987) A comparison of association indexes. Animal Behaviour

427   35:1454-1469

428   Conradt L (1998) Could asynchrony in activity between the sexes cause intersexual social

429   segregation in ruminants? Proceedings of the Royal Society of London Series B-

430   Biological Sciences 265:1359-1363

431   Croft DP, Albanese B, Arrowsmith BJ, Botham M, Webster M, Krause J (2003a) Sex

432   biased movement in the guppy (*Poecilia reticulata*). Oecologia 137:62-68

433   Croft DP, Arrowsmith BJ, Bielby J, Skinner K, White E, Couzin ID, Magurran AE,

434   Ramnarine I, Krause J (2003b) Mechanisms underlying shoal composition in the

435   Trinidadian guppy (*Poecilia reticulata*). Oikos 100:429-438

436   Croft DP, James R, Krause J (2008) Exploring animal social networks. Princeton

437   University Press, Princeton, NJ

438   Croft DP, James R, Thomas POR, Hathaway C, Mawdsley D, Laland KN, Krause J

439   (2006a) Social structure and co-operative interactions in a wild population of

440   guppies (*Poecilia reticulata*). Behavioral Ecology and Sociobiology 59:644-650

441   Croft DP, James R, Ward AJW, Botham MS, Mawdsley D, Krause J (2005) Assortative

442   interactions and social networks in fish. Oecologia 143:211-219

443   Croft DP, Krause J, James R (2004) Social networks in the guppy (*Poecilia reticulata*).

444   Proceedings of the Royal Society of London Series B-Biological Sciences

445   271:S516-S519

446   Croft DP, Morrell LJ, Wade AS, Piyapong C, Ioannou CC, Dyer JRG, Chapman BB, Yan

447   W, Krause J (2006b) Predation risk as a driving force for sexual segregation: a

448   cross-population comparison. The American Naturalist 167:867-878

449   Darden SK, Croft DP (2008) Male harassment drives females to alter habitat use and

450   leads to segregation of the sexes. Biology Letters 4:449-451

451 Dugatkin LA (1988) Do guppies play tit for tat during predator inspection visits?

452   Behavioural Ecology and Sociobiology 23:395-399

453 Dugatkin LA (1992) Tendency to inspect predators predicts mortality risk in the guppy

454   (*Poecilia reticulata*). Behavioral Ecology 3:124-127

455 Dugatkin LA, Wilson DS (2000) Assortative interactions and the evolution of

456   cooperation during predator inspection in guppies (*Poecilia reticulata*).

457   Evolutionary Ecology Research 2:761-767

458 Godin JGJ, Davis SA (1995) Who dares, benefits: predator approach behaviour in the

459   guppy (*Poecilia reticualta*) deters predator pursuit. Proceedings of the Royal

460   Society of London Series B-Biological Sciences 259:193-200

461 Gosling SD (2001) From mice to men: What can we learn about personality from animal

462   research? Psychological Bulletin 127:45-86

463 Huntingford F (1976) The relationship between anti-predator behaviour and aggression

464   among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*.

465   Animal Behaviour 24:245-260

466 James R, Croft DP, Krause J (2009) Potential banana skins in animal social network

467   analysis. Behavioral Ecology and Sociobiology 63:989-997

468 Krause J, Butlin RK, Peuhkuri N, Pritchard VL (2000) The social organization of fish

469   shoals: a test of the predictive power of laboratory experiments for the field.

470   Biological Reviews 75:477-501

471 Krause J, Croft DP, James R (2007) Social network theory in the behavioural sciences:

472   potential applications. Behavioral Ecology and Sociobiology 62:15-27

473   Krause J, Lusseau D, James R (2009) Animal social networks: an introduction.

474   Behavioral Ecology and Sociobiology 63:967-973

475   Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, Oxford

476   Külling D, Milinski M (1992) Size-dependent predation risk and partner quality in

477   predator inspection of sticklebacks. Animal Behaviour 44:949-955

478   Landeau L, Terborgh J (1986) Oddity and the confusion effect in predation. Animal

479   Behaviour 34:1372-1380

480   Magurran AE (1993) Individual differences and alternative behaviours. In: Pitcher TJ

481   (ed) Behaviour of Teleost Fishes, 2nd edn. Chapman & Hall

482   Magurran AE, Higham A (1988) Information transfer across fish shoals under predator

483   threat. Ethology 78:153-158

484   Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press,

485   Cambridge

486   Milinski M (1987) Tit-for-Tat in sticklebacks and the evolution of cooperation. Nature

487   325:433-435

488   Milinski M, Luthi JH, Eggler R, Parker GA (1997) Cooperation under predation risk:

489   Experiments on costs and benefits. Proceedings of the Royal Society of London

490   Series B-Biological Sciences 264:831-837

491   Milinski M, Pfluger D, Külling D, Kettler R (1990) Do sticklebacks cooperate repeatedly

492   in reciprocal pairs? Behavioral Ecology and Sociobiology 27:17-21

493   Newman MEJ (2003) Mixing patterns in networks. Physical Review E 67:art. no.-026126

494   Ohguchi O (1978) Experiments on the selection against colour oddity of water fleas by

495   three-spined stickelbacks. Zeitschrift für Tierpsychologie 47:254-67

496   Ohtsuki H, Hauert C, Lieberman E, Nowak MA (2006) A simple rule for the evolution of

497   cooperation on graphs and social networks. Nature 441:502-505

498   Pike TW, Samanta M, Lindström J, Royle NJ (2008) Behavioural phenotype affects

499   interactions in a social network. Proceedings of the Royal Society of London

500   Series B-Biological Sciences 275:2515-20

501   Pitcher TJ, Green DA, Magurran AE (1986) Dicing with death - predator inspection

502   behaviour in minnow shoals. Journal of Fish Biology 28:439-448

503   Reale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal

504   temperament within ecology and evolution. Biological Reviews 82:291-318

505   Roberts SGB, Wilson R, Fedurek P, Dunbar RIM (2008) Individual differences and

506   personal social network size and structure. Personality and Individual Differences

507   44:954-964

508   Ruckstuhl KE (1999) To synchronise or not to synchronise: a dilemma for young bighorn

509   males? Behaviour 136:805-818

510   Santos FC, Pacheco JM, Lenaerts T (2006) Cooperation prevails when individuals adjust

511   their social ties. PLoS Computational Biology 2:1284-1291

512   Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary

513   overview. Trends in Ecology & Evolution 19:372-378

514   Szulkin M, Dawidowicz P, Dodson SI (2006) Behavioural uniformity as a response to

515   cues of predation risk. Animal Behaviour 71:1013-1019

516   Theodorakis CW (1989) Size segregation and the effects of oddity on predation risk in

517   minnow schools. Animal Behaviour 38:496-502

518   Thomas POR, Croft DP, Morrell LJ, Davis A, Faria JJ, Dyer JRG, Piyapong C,

519   Ramnarine I, Ruxton GD, Krause J (2008) Does defection during predator

520   inspection affect social structure in wild shoals of guppies? Animal Behaviour

521   75:43-53

522   Wey T, Blumstein DT, Shen W, Jordan F (2008) Social network analysis of animal

523   behaviour: a promising tool for the study of sociality. Animal Behaviour 75:333-

524   344

525   Wilson DS (1998) Adaptive individual differences within single populations.

526   Philosophical Transactions of the Royal Society of London Series B-Biological

527   Sciences 353:199-205

528   Wilson DS, Coleman K, Clark AB, Biederman L (1993) Shy bold continuum in

529   pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological

530   trait. Journal of Comparative Psychology 107:250-260

531   Wilson DS, Dugatkin LA (1997) Group selection and assortative interactions. American

532   Naturalist 149:336-351

533   Wilson EO (1975) Sociobiology: The new synthesis. Harvard University Press,

534   Cambridge, MA

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Figures

540 **Figure 1)** Network S1, in which all edges with SRI greater than or equal to 0.1 are

541 included. The size of the node indicates the strength of individual behavioural score,

542 within larger nodes having a higher inspection tenancy. Sex of individuals is represented

543 by node colour.

544

545 **Figure 2)** Mean degree of networks S1-S4. Filled circles depict the observed values and

546 the unfilled circles the median value for 10000 randomisations. 95% two-tailed

547 confidence intervals are shown as the dashed line around the expected random value

548 ($P<0.01=**$).

549

550 **Figure 3)** Assortment by behavioural phenotype in the edge-filtered guppy social

551 networks a) Shows the analysis based on individuals behavioural scores (BS) in which

552 only edges with SRI greater than or equal to the threshold are included (S networks S1-

553 S4). b) Shows the analysis based on individuals behavioural scores (BS) in which only

554 edges with SRI less than or equal to the threshold are included (W networks W1-W4). c)

555 Shows the analysis based solely on predator inspection scores in which only edges with

556 SRI greater than or equal to the threshold are included (S networks S1-S4). Filled circles

557 depict the observed values of the Spearman rank correlation coefficient and the unfilled

558 circles the median value for 10000 randomisations. 95% two-tailed confidence intervals

559 are shown as the dashed line around the expected random value. P values are displayed

560 on the figures.

561

562 **Figure 4a)** The relationship between an individual's behavioural score and its number of

563 network neighbours (degree). b) The relationship between an individual's behavioural

564 score and the average strength of its social associations.
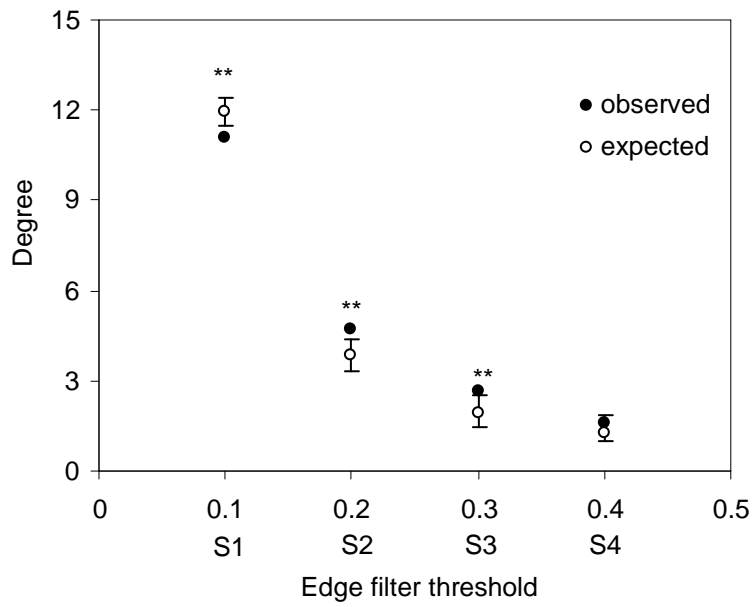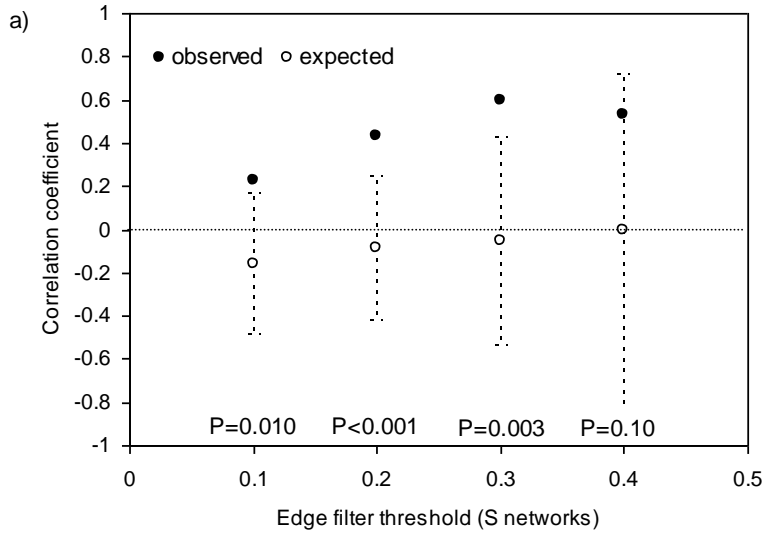
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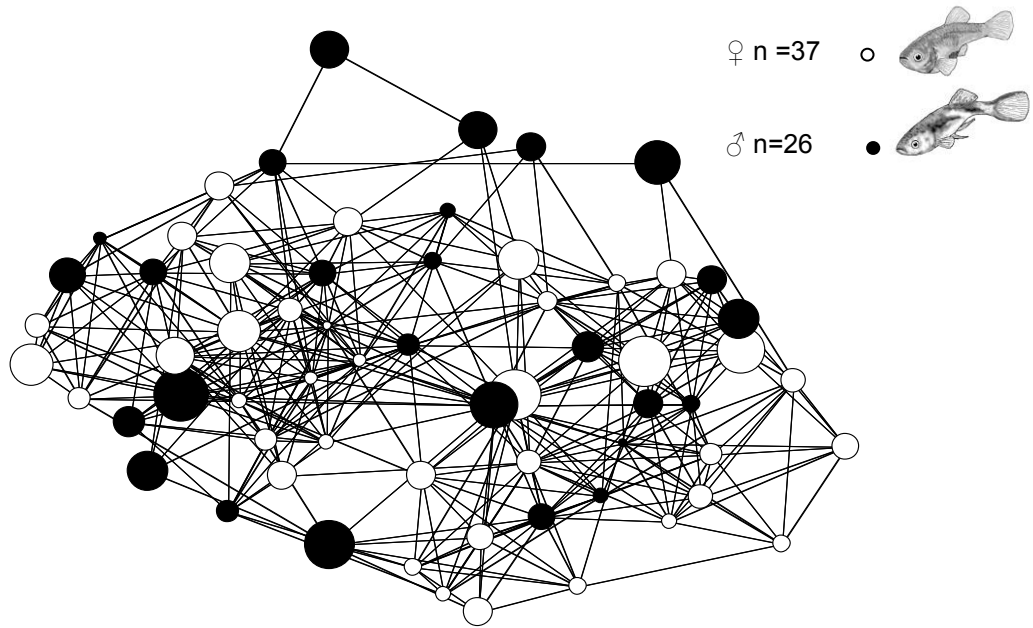
572   Figure 2

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580   Figure 3
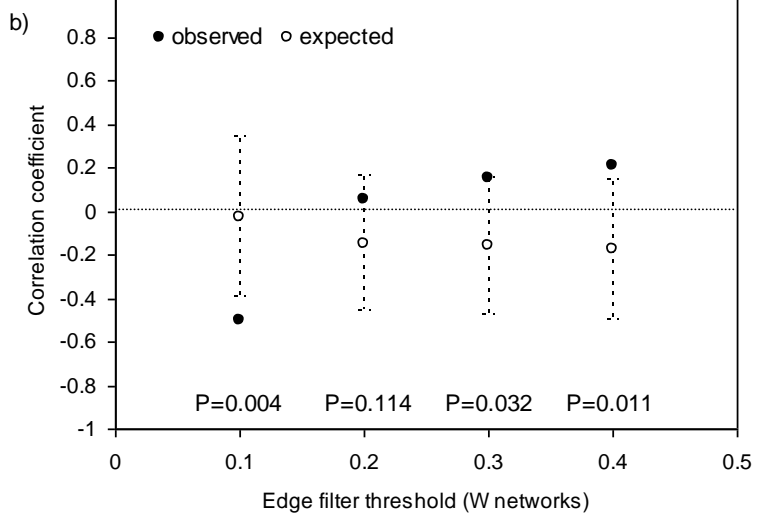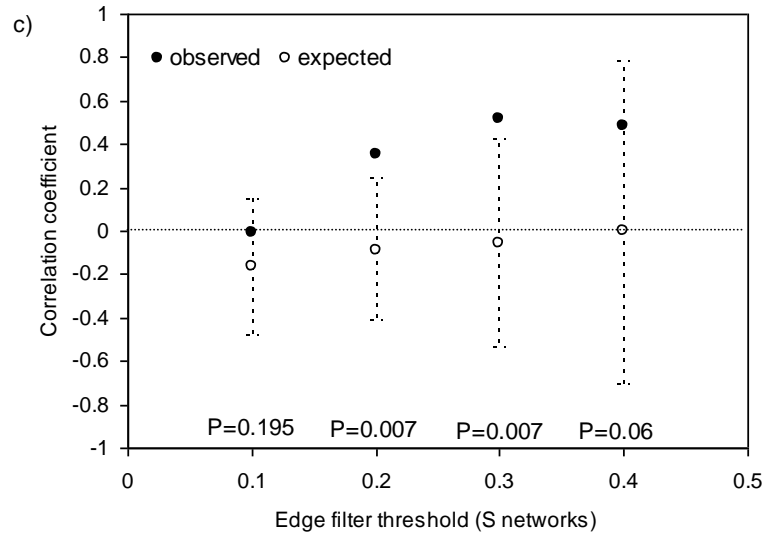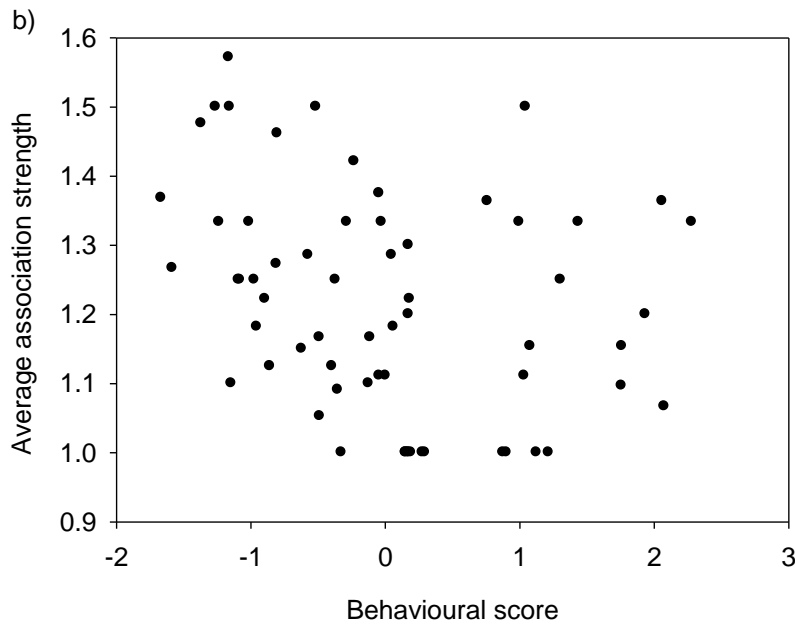
581   a)

P=0.010   P<0.001   P=0.003   P=0.10

Edge filter threshold (S networks)

589   b)

P=0.004   P=0.114   P=0.032   P=0.011

Edge filter threshold (W networks)

c)

P=0.195   P=0.007   P=0.007   P=0.06

Edge filter threshold (S networks)

603   Figure 4

a)

b)

604