Shark personalities? Repeatability of social network traits in a widely distributed predatory fish

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Summary

Interest in animal personalities has generated a burgeoning literature on repeatability in individual traits such as boldness or exploration through time or across different contexts. Yet repeatability can be influenced by the interactive social strategies of individuals, for example, consistent inter-individual variation in aggression is well documented. Previous work has largely focused on the social aspects of repeatability in animal behaviour by testing individuals in dyadic pairings. Under natural conditions individuals interact in a heterogeneous polyadic network. However, the extent to which there is repeatability of social traits at this higher-order network level remains unknown. Here we provide the first empirical evidence of consistent and repeatable animal social networks. Using a model species of shark, a taxonomic group in which repeatability in behaviour has yet to be described, we repeatedly quantified the social networks of 10 independent shark groups across different habitats, testing repeatability in individual network position under changing environments. To understand better the mechanisms behind repeatable social behaviour we also explored the coupling between individual preferences for specific group sizes and social network position. We quantify repeatability in sharks by demonstrating that despite changes in aggregation measured at the group level, the social network position of individuals is consistent across treatments. Group size preferences were found to influence the social network position of individuals in small groups but less so for larger groups suggesting network structure and thus repeatability was driven by social preference over aggregation tendency.

Key words: *aggregation behaviour; elasmobranch; personality; plasticity; repeatability; social traits*

Introduction

Individual behavioural consistency, a component of personality, has been shown to be remarkably widespread in the animal kingdom, on average accounting for >30% of phenotypic variance within populations (Bell et al. 2009). Previous work has shown that consistent individual variation in behaviour (i.e. repeatability) is also heritable in some wild populations (e.g. Dingemanse et al. 2002; van Oers et al. 2004). To date, the focus of empirical research into behavioural consistency has been largely dominated by the role of repeatability across individual-based behavioural axes such as boldness-shyness, exploration-avoidance, aggression and activity profiles with considerably less attention on sociality (Réale et al. 2007; Conrad et al. 2011). Social stability, however, can provide cohesion within a population. Studies examining the consequences of instability in social structure, for example, have demonstrated increased fragmentation and escalation of conflict in destabilised primate social groups (Flack et al. 2006; Beisner et al. 2011). Under such circumstances, repeatability in social network position is expected to be selected. However, we might also predict between-individual variation in these positions due to an ecological trade-off that results in similar fitness returns for individuals occupying different levels of social connectivity (Formica et al. 2012). Despite growing research on individual personality types (see Dall et al. 2004; Sih et al. 2004 for reviews), the extent to which individuals maintain consistent social strategies within a population and the potential mechanisms driving this consistency are rarely explored.

When considering gregarious animals, the broad ecological implications of individual behavioural consistency are undoubtedly moderated by changes in the social context of an individual's immediate environment (Webster and Ward 2010). Boldness in individual three-spined sticklebacks (*Gasterosteus aculeatus*) and in guppies (*Poecilia reticulata*) for instance, is known to be an important determinant of position within a social network (Pike et

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71 al. 2008; Croft et al. 2009). Furthermore, animals demonstrating different but consistent

72 exploratory traits might also mediate and maintain the overall structure of a social network

73 with highly exploratory individuals tending to associate broadly and thus connect poorly

74 connected conspecifics (e.g. Tanner and Jackson 2012; Aplin et al. 2013). Consequently, both

75 the direct (e.g. dyadic partnerships) and the indirect (e.g. association via intermediaries)

76 social interactions of an individual are likely to influence the ecology and evolution of

77 personality (Krause et al. 2010) and as such, social network traits, such as strength,

78 connectivity and social 'reach', offer a valuable tool with which to characterise individual

79 repeatability of behavioural traits (Wilson et al. 2013).

80   Previous research clearly demonstrates that differences in an individual's social

81 experience and connectivity not only influences group outcomes but might also carry over

82 into different future ecological contexts (Krause et al. 2009; Sih et al. 2009). For example,

83 when exploring the population dynamics of common lizards (*Lacerta vivipara*, Lichtenstein

84 1823), Cote and Clobert (2007) found that the social tolerance of individuals from different

85 population densities were strongly linked to dispersal and settlement patterns. An extension

86 of this research revealed that 'social' lizards, that are highly connected, displayed different

87 fitness outcomes under different densities, to 'asocial' lizards that are poorly connected (Cote

88 et al. 2008). In both of these studies however, sociability was not directly tested but rather

89 inferred by assessing individual tolerance of conspecific odours. Using a social networks

90 approach, specific components of social behaviour that relate to the intensity, frequency and

91 directionality of social interactions can be quantified directly and tested explicitly for

92 repeatability (Wilson et al. 2013). In doing so, the mechanisms that drive consistent, social

93 behaviour in animals can be explored.

94   Here we use a model species of oviparous elasmobranch *Scyliorhinus canicula*, Linnaeus

95 1758 (small spotted catshark) to quantify inter-individual variation in social network traits

and to examine the mechanisms that may underpin such differences. *S. canicula* are of an intermediate size for an elasmobranch and are highly amenable to being bred, maintained and handled successfully in captivity. This benthic elasmobranch is found in abundance in UK and Irish coastal waters and has been extensively studied in both wild (Sims et al. 2001, 2006; Jacoby et al. 2012a; Wearmouth et al. 2012) and captive conditions (Kimber et al. 2009; Jacoby et al. 2010). Neonate *S. canicula* hatch from egg cases that are laid on macroalgae, rocky substrata and other structurally complex marine features and like all elasmobranchs, the pups fend for themselves from the outset. During early life, juvenile benthic sharks, a likely prey item for many larger predators, must optimise behavioural strategies that will increase their chances of survival (Sims et al. 1993) and indeed in captivity at least, juvenile *S. canicula* form non-random, mixed-sexed social groups driven by individual familiarity (Jacoby et al. 2012b). Social grouping, which in the wild, may occur cryptically in both juveniles and adults (Sims et al. 1993; Wearmouth et al. 2012), together with skin camouflage, are two probable tactics individuals may adopt to enhance their survival. The extent to which sharks demonstrate repeatable behaviours under different contexts however, is not known, perhaps due to the difficulties of conducting manipulation experiments in this predatory vertebrate taxon. In the wild, conditions at hatching are likely to be rather variable between individuals due to differences in the nature of the surroundings in which eggs are deposited and the numbers of conspecifics sharing these surroundings. As such we would expect to see considerable between-individual variation in social behaviour. In this study, we examined both group level social network structure and individual social network position of replicated, juvenile shark aggregates in response to changes to the structural complexity of their environment. Specifically, we addressed the following questions: (1) Do aggregations change under different habitat types? (2) Do individuals show repeatability in social network position across these different environments? (3) How do

121 individual preferences for group size influence this, and (4) to what extent does repeatability

122 and plasticity contribute to juvenile social behaviour?

123

124 Materials and Methods

125 Experimental sharks

126 Juvenile (< 1 yr) *S. canicula* were reared in the Marine Biological Association (MBA)

127 Laboratory, Plymouth, UK, from eggs laid by wild females caught locally at Whitsand Bay,

128 Cornwall, UK (50° 20.44′ N, 4° 16.38′ W). Experiments were conducted between August and

129 September 2011 on juveniles which were approximately $8 - 10$ months old ($n = 100$) with a

130 mean total length ($L_T \pm$ SD) of 179.7 ± 27.4 mm and a mean weight of 17.98 ± 7.6 g. Size-

131 matched individuals were selected from large holding aquaria (858 l capacity, 1.65 x 0.80 x

132 0.65 m) before being tagged for individual identification using visible implant elastomer tags

133 (VIE; Northwest Marine Technology, WA, USA). Tagging procedures were authorised by

134 the MBA animal ethics committee and licensed by the UK Home Office under the Animals

135 (Scientific Procedures) Act 1986. Once tagged, 10 replicated groups (10 individuals per

136 replicate) were distributed across five smaller holding aquaria (149 l capacity, 1.22 x 0.61 x

137 0.20 m, temperature: $17.0\,^{\circ}$C, 20 individuals per aquaria) where they were allowed to recover

138 for > 10 days. As familiarity amongst conspecifics has been shown to drive non-random

139 social preferences amongst juvenile catsharks (Jacoby et al. 2012b), this recovery period also

140 provided an opportunity for individuals to familiarise with one another. Pilot studies revealed

141 that individual sex did not appear to influence association between immature juveniles

142 (D.M.P.J Unpublished data) and thus sex was chosen randomly from a stock sex ratio of

143 ~1:1. All sharks were fed approximately 2.5% wet body mass per individual per feed (Sims

144 and Davies 1994) on alternate days following data collection. Food comprised a combination

145   of white fish (mixed species), squid (*Alloteuthis subulata*) and queen scallop (*Aequipecten*

146   *opercularis*) mixed with liposome enrichment and a commercial pellet. The aquaria were

147   subject to a consistent and balanced photoperiod (12 h light/12 h dark).

148

Quantifying social behaviour

150   Each experimental replicate, consisting of 10 individuals, was transferred from the holding

151   aquaria to the large experimental arenas (858 l capacity, 1.65 x 0.80 x 0.65 m) where they

152   were allowed to acclimatise for 24 h prior to data collection. Social associations were

153   measured during daylight hours during which time activity rates in juvenile *S. canicula* are

154   relatively low (Sims et al. 1993) and individuals often aggregate socially in resting groups

155   (see Jacoby et al. 2012b). Interestingly, we found little evidence that social behaviour in

156   juveniles persists beyond group resting behaviour into active, parallel or follow swimming

157   behaviour. Indeed periods of solitary activity outside of social refuging behaviour, even

158   amongst schooling elasmobranchs, is not uncommon (e.g. Klimley and Nelson 1984). Social

159   networks were constructed over two days from scan samples of associations taken at two

160   hourly intervals between 08:00 and 18:00 h (6 samples per day). The two hourly sampling

161   frequency captured long-term, persistent associations whilst still allowing time for

162   reorganisation, and thus independent samples, between observations (see Electronic

163   Supplementary Material for raw data in which shifts in group membership can be seen to

164   occur frequently between consecutive samples). Following data collection all individuals

165   were returned to their specific holding aquaria.

166   During each sampling period, individuals were deemed in association whenever two

167   associative zones converged (i.e. a body-length radius from an individual's first dorsal fin

168   overlapped another individuals' centre point/dorsal fin). All individuals within this prescribed

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169 distance of one another were considered to be associating (Franks et al. 2010). Group

170 membership of individuals was recorded for each sample and the accumulation of these

171 associations (12 samples) provided our weighted social network data (see Supporting

172 Information for data). Using the Simple Ratio Index, SRI (Cairns and Schwager 1987), all

173 dyadic pairings (two associating individuals) were assigned a weighted value between 0 and

174 1 representing the strength of association between these individuals. An SRI closer to 0

175 indicated that individuals were never seen associating, whereas a SRI of 1 suggested

176 individuals were never observed apart. Given the size of tank relative to these small sharks, it

177 was possible that during a sample all individuals might rest alone. A matrix of association

178 from the SRI was constructed for each of the 10 replicates under each habitat treatment.

179 Individual node-based metrics, derived from matrices of association, were calculated in order

180 to (1) determine the role each individual played in overall network structure and (2) calculate

181 and compare individual repeatability in social network position across context and relative to

182 conspecific behaviour. Individual network metrics included *strength*, a direct measure of

183 individual social behaviour based on the sum of an individual's association indices with all

184 other individuals in the group; *reach*, an indirect measure of connectedness that gauges the

185 proportion of individuals that are connected to the node of interest via one, two, three links

186 etc, and *clustering coefficient*, also an indirect measure, which is an indication of the role an

187 individual plays in interconnecting groups and communities based on neighbour connectivity.

188 Unweighted network metrics were considered, however it was felt that an unweighted

189 network containing 10 nodes would not have yielded sufficient variation to test for

190 consistency. To help differentiate the underlying mechanism influencing social behaviour

191 (i.e. preferences for conspecifics or simply shared preferences for locations or group sizes)

192 and to test for plastic responses in aggregation to changes in habitat complexity the following

193 data were recorded for each scan sample: Number of individuals active/resting, the number of

194 individuals grouping/solitary, the size of the groups and the identity of those individuals

195 within them (i.e. social preferences).

196 **Habitat treatments**

197 To test for the repeatability of social traits a repeated measures design was used in which

198 each replicate 'population' were subject to three habitat treatments which differed in their

199 level of structural complexity. We used differing levels of complexity as this was expected to

200 change patterns of grouping behaviour (Pollen et al. 2007; Orpwood et al. 2008).

201   1) T1: Gravel – each experimental aquaria was given a natural, medium gravel

202   substrate (size range diameter: 8-16 mm) spread evenly throughout the area. This

203   was defined as a *simple* habitat.

204   2) T2: Stones – each experimental aquaria contained three discrete clusters of large,

205   equal sized stones (~18 x 9 x 10 cm) always in the same location and orientation.

206   (NB. Stone 'structures' were sufficiently large for several groups of individuals to

207   form independently of one another at each cluster). This was defined as a *complex*

208   habitat.

209   3) T3: Mixed – each experimental aquaria contained both of the above habitat types.

210   This was defined as a combination of *simple* and *complex* habitats.

211 Little is known about the type of habitat favoured by juvenile *S. canicula* in the wild,

212 however, based on knowledge of the structures upon which egg cases are deposited, these

213 treatments were designed to reproduce some of the habitats which are likely to be

214 experienced by young sharks of this species. The subsequent ordering of these treatments was

215 randomised for each replicate to control for any potential order effects.

Statistical analysis of social repeatability and environmental plasticity

There are inherent difficulties associated with analysing complex, social animal systems. A continued obstacle to interpreting their social networks is how to decouple those individuals that share requirements for the same resources or habitat and those that demonstrate 'true' social preferences for specific group mates (see Krause and Ruxton 2002; Croft et al. 2008; Jacoby et al. 2012c for discussion). One way in which to address these issues is to expose groups of individuals to multiple environments and control for group size preferences during the analytical randomisation of the network data. By quantifying metrics for aggregation such as group sizes and number of groups alongside social network metrics such as social strength or measures of centrality we can address whether gregarious animals faced with changes to their immediate environment are likely to respond as a group or as individuals. Furthermore we can test whether these individuals show repeatability in social network traits across different ecological environments in order to understand more deeply the complex interplay between behavioural consistency and plasticity at different ecological scales and contexts (Dingemanse et al. 2010).

To test for changing patterns of aggregation in response to structural changes in the environment, a multivariate, repeated measures general linear model (GLM) was performed on mean group level data. The dependent variables of mean group size, mean group number and mean proportion of active individuals were entered into the model, with an independent variable of treatment. Repeated, within-subject contrasts, applying the Bonferroni correction for pairwise comparisons, were used to gauge the relative effects of treatment on behaviour. Biological effect size estimates (η^2) within the GLM were also calculated to determine how much of the observed variance was explained by the independent variable.

To determine repeatability in social behaviour across different habitat types our approach was twofold; first, correlation analyses were performed on mean network metrics to explore

241   replicate level correlations in social connectivity between habitats. Second, behavioural

242   consistency was determined at the individual level by examining individual ranked

243   consistency in relative social network position across treatments, using the metric *strength* as

244   a direct measure of individual sociality. Non-orthogonal network data is problematic to

245   analyse statistically (Croft et al. 2011) and in an attempt to overcome this, a randomisation

246   procedure was devised (Wilson et al. 2013). Individuals within a replicate were assigned a

247   rank based on their relative network strength which were then analysed for concordance

248   across treatments using Kendall's coefficient of concordance (*W*). For each replicate of three

249   observed networks (n = 10), *W* was calculated and compared to values of *W* from a frequency

250   distribution of values generated by 20,000 randomised permutations of the observed data. For

251   each permutation individual ranks within each of the three treatments were permuted,

252   calculating *W* on each occasion. This rank permutation procedure, an method equivalent to a

253   node randomisation was conducted in Poptools (Hood 2010) and provided a conservative null

254   distribution against which we could determine significance values for social consistency with

255   regard to network strength, whilst controlling for non-independence between the data.

256   Independent replicated *P*-values were combined using Stouffer's method in R (R

257   Development Core Team; www.r-project.org) to give an overall value of significance

258   (Piegorsch and Bailer 2005).

259   In an attempt to decipher the relationship between social behaviour (preferences for

260   certain conspecifics) and individual preferences for specific group sizes (e.g. above/below a

261   given threshold), mean group size preferences were calculated for each individual across

262   treatments and regressed against network strength. Group size preferences were calculated as

263   a mean for each individual by averaging the size (i.e. number of individuals) of all grouping

264   events (≥ 2 inds.) in which an individual was present during sampling. Unstandardised

265   residuals from this regression were then tested for repeatability using the permutation test

266 outlined above to determine whether individual network strength was repeatable after

267 controlling for group size preference. The effect sizes were compared between controlled and

268 uncontrolled permutation tests. Effect size estimates η^2 and W are discussed in light of the

269 influence of plasticity and repeatability on juvenile shark social behaviour. Unless otherwise

270 stated, all statistical analyses were conducted in PASW Statistics 18 (IBM Corp., Somers,

271 NY, USA) and network analyses in SOCPROG 2.4 (Whitehead 2009).

272

Results

Aggregation under different habitat types

275 With the assumptions of sphericity and normality met for all three treatments ($p > 0.05$), the

276 multivariate, repeated measures GLM revealed that there was a significant main effect of

277 habitat type on aggregation behaviour ($F_{(6,32)} = 3.239$, $p = 0.013$) with an effect size estimate

278 of $\eta^2 = 0.158$. Further exploration showed that there were significant effects of habitat on the

279 number of groups forming ($F_{(2,18)} = 10.939$, $p < 0.001$) but not on the group size ($F_{(2,18)} =$

280 1.089, $p = 0.358$) or proportion of active individuals ($F_{(2,18)} = 1.150$, $p = 0.339$, Fig. 1).

281 Interestingly, average group size in each replicate, which was not necessarily expected to

282 covary with group number as all individuals were able to rest alone, remained virtually

283 constant across the three treatments. Analysis of contrasts revealed a significant increase in

284 mean group number between the *Simple* and *Complex* habitat treatments ($p = 0.005$, Fig. 1)

285 and also a significant decrease between the *Complex* and the *Mixed* (simple/complex

286 combination) randomised treatments ($p = 0.023$, Fig. 1). The result suggests that three

287 dimensionally complex structures appeared to encourage aggregation tendencies in these

288 juvenile sharks whilst the uniform gravel substrate appeared to have a dispersive influence.

289

Social repeatability in network position

Averaging network metrics at the replicate level, social network traits were found to be repeatable across habitat types (Fig. 2), with strength and clustering coefficient providing the strongest evidence for social consistency (Table 1). At the individual level, significant concordance was found in strength of individual social network position across the three different habitat types (mean $W = 0.462$ $\chi^2_{99} = 137.72$, $p = 0.0061$; Stouffer's test for independent treatments: $n = 10$, $P < 0.001$). Of the three metrics, strength was chosen as it is the most direct measure of individual sociality. Relatively high variation in W (range: 0.279 – 0.731, Table 2) was likely due to the small number of individual sharks in each experimental replicate ($n = 10$) resulting in considerable fluctuation in the random mean values for concordance (W_R) within the null model (Table 2). This consistent variation in social connectedness, under differing randomised environments, is indicative of personality traits among these young shark pups.

303

Influence of individual preference for group sizes

To what extent were these social personalities driven by individual preference for specific group sizes? The permutation test on the regression residuals revealed that after controlling for individual group size preferences, network strength was no longer repeatable (mean $W = 0.3915$, $\chi^2_{99} = 116.28$, $p = 0.1132$; Stouffer's test for independent treatments: $n = 10$, $p = 0.0835$) suggesting group size preference as a likely mechanism for driving social connectivity. Given that the biological effect size (W) only fell by 0.07 and statistically this became only marginally non significant, we felt that this result warranted closer inspection. A plot of the unstandardised residuals against group size (Fig. 3) suggested that the variance of the residuals from the model is low (i.e. small deviation from the mean (0) and thus strong

314 support for the model) when group sizes are small, but that variance increases with group size

315 (i.e. greater departure of the residuals from the mean). This indicates that the model

316 predicting social strength from group size preference becomes more inaccurate as individuals

317 have more potential social partners suggesting group size preferences drive social consistency

318 but only within small groups (Fig. 3).

319

320 **How do plasticity and repeatability effect juvenile social behaviour?**

321 The effect size estimate of average plasticity across replicates, that is the effect size of the

322 GLM ($\eta^2 = 0.158$) was low, while the effect size for repeatable social behaviour across

323 habitats ($W = 0.464$) was high. More clearly, these experiments demonstrate that changes in

324 structural complexity of the juvenile shark's habitat drives significant changes in the level of

325 aggregation observed between individuals but that amongst those that do aggregate, there are

326 consistent social relationships that form between specific sharks.

327

328 **Discussion**

329 Consistency or repeatability of individual-based behavioural axes such as boldness or

330 exploration are well reported in the literature (Sih et al. 2004; Conrad et al. 2011) and have

331 also been explored in relation to social network structure (Pike et al. 2008; Croft et al. 2009;

332 Krause et al. 2010). Whether individuals show repeatability in social network traits across-

333 context, however, has received little attention. Indeed teasing apart the behavioural

334 mechanisms underpinning individual social preferences and repeatable, consistent behaviour

335 remains a significant challenge in the ecology of marine species, although technology is

336 assisting steps towards this endeavour in terrestrial systems (e.g. Aplin et al. 2013). Here we

337   provide an empirical illustration of consistent and repeatable animal social networks using a

338   controlled and replicated approach. Individual social network traits of juvenile sharks that are

339   known to demonstrate non-random social grouping (Jacoby et al. 2012b), were found to be

340   consistent across changing environments. Despite some plasticity in tendency of these sharks

341   to aggregate under the different conditions, at the individual level the overriding influence on

342   social behaviour was to maintain a similar level of social strength and connectivity as

343   revealed through comparison of the effect sizes from the two sets of analyses. We show that

344   individual preferences for aggregating within specific group sizes prove to be a strong

345   mechanistic driver of this result but that perhaps social preferences play more of a role in

346   larger groups (i.e. above the average group size) where more options for conspecific social

347   interaction become available. To our knowledge, this is the first quantitative evidence of

348   repeatability in polyadic social network traits, an idea put forward initially by Wilson et al.

349   (2013). Furthermore, we also provide the first evidence of repeatability of behaviour in the

350   taxonomic class Chondrichthyes (sharks, rays, skates and chimeras), confirming that stable

351   social relationships in catsharks appear important in early, as well as adult life stages. These

352   results suggest the potential for personality traits in Chondrichthyians. We remain cautious,

353   however, of interpreting the results in the context of personality as individuals were not

354   explicitly assayed for any other aspects of behaviour, meaning the mechanisms behind these

355   potential personalities remain unclear (Dingemanse et al. 2010).

356   An animal's physical environment can play a significant role in influencing social

357   contact within a population (Tyler and Rose 1994). In addition, the social network position of

358   an individual is also, in part, derived by the interactive strategies of conspecifics that, in turn,

359   influence individual experience and future social behaviour (Krause et al. 2010). In the

360   presence of large, three-dimensionally complex structures, juvenile sharks in our study

361   showed an overall increase in the number of groups forming on average than in simplified

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habitat types. Throughout the experimentation, the skin colouration of *S. canicula* was observed to adopt a lighter or darker shade dependent upon the colour of the aquarium background (DMPJ pers. obs.). When presented with a gravel substrate, individuals appeared to reduce aggregation, seemingly able to background match with this substrate more effectively than the pale aquarium base, suggesting a degree of flexibility in how these animals respond to perceived risk. It has been shown through experimentation using teleost fishes that the ecological environment experienced by individuals influences the social interactions of gregarious species through the direct (Croft et al. 2006; Orpwood et al. 2008) and indirect effects of predation (Croft et al. 2003). The behaviour of juvenile, benthic elasmobranchs in the wild is largely unknown and while perceived risk of predation was not explicitly tested in this experiment, aggregation is likely one of several antipredator behavioural responses adopted by small sharks (Guttridge et al. 2012; Jacoby et al. 2012c).

Individual preferences for specific group sizes can fluctuate through time and under different ecological contexts depending upon a myriad of phenotypic, physiological and behavioural influences from colouration relative to background or conspecifics through to parasite load or foraging strategy (see Krause and Ruxton 2002 for review). Tendency to aggregate thus clearly regulates the frequency and availability of potential social interactions that might perhaps preferentially be influenced by familiarity or kinship (Barber and Wright 2001; Wiszniewski et al. 2010). Indeed these social preferences too are likely to be context dependent (Kurvers et al. 2013). Individual behavioural consistency therefore must trade off against fluctuations in social and ecological environment and indeed in the current study evidence of different aggregation behaviour (i.e. changes in the mean number of groups forming) between the treatments was observed despite consistency in relative social network traits of the individual sharks themselves. One way in which to differentiate between the environmental and social drivers of behavioural consistency would have been to re-assort

387   individuals between groups and retest them for repeatability. This would have allowed us to

388   determine more strategically whether it was individual social behaviour or the group that

389   constrains individual flexibility. While this was beyond the scope of the current experiment,

390   it would be a valuable future extension to this work.

391   When we consider the mechanism driving consistency in these experiments, the evidence

392   for social preferences remains compelling; highly consistent network metrics across

393   treatments, taken as an average for the group, support the small reduction in W when

394   consistency was tested for after controlling for group size preference at the individual level (a

395   marginally non significant result). Residual analysis suggested that perhaps group size

396   preference and social preference influence network traits implicitly at different group-level or

397   population-level densities, however this would need to be tested directly using a different

398   approach. For now, the results of the present study indicate a system whereby juvenile *S.*

399   *canicula*, a model elasmobranch species in physiological, behavioural and ecological

400   research, demonstrate consistent individual variation in social behaviour, across context,

401   based on individual preferences for aggregation. Typical of a heterogeneous social network

402   for example, some individuals appeared more solitary, recording low social network metrics

403   relative to conspecifics and using the gravel substrate as an opportunity to become

404   individually inconspicuous whilst out in the open. By contrast, other individuals appeared

405   more gregarious, recording stronger social connections and were thus more conspicuous,

406   using the stone structures to hide in and around as a group. Ecologically, this reflects the

407   notion that some individuals, where sociality perhaps correlates with other behavioural traits

408   such as boldness/shyness, harbour a disproportionate percentage of links within a social

409   network and therefore play a key role in interconnecting others (Krause et al. 2010). Further

410   research would be required to disentangle more fully some of these behavioural correlates

411   that would determine the role of personality traits in marine predators.

17

412   Using manipulation experiments to induce changes in the physical environment of young

413   sharks provided the opportunity to quantify replicated network structures. In doing so we

414   were able to explore the repeatability of individual social network position. We demonstrate

415   plasticity in aggregation tendency at the group level which we discuss in light of the different

416   behaviour of individuals of high and low social connectivity. In addition we show

417   consistency in individual network traits of sharks under changing environments and assess

418   the influence of group size preferences on this result in an attempt to understand the

419   mechanisms behind repeatable social behaviour in these animals. In beginning to understand

420   the social preferences and behaviour of these often elusive predators, this study paints a more

421   complex picture of social personalities than perhaps originally thought.

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428

429   **Ethical Standards**

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431   Animal maintenance, husbandry and tagging procedures were authorised by the MBA animal

432   ethics committee and were carried out by licensed individuals in accordance with the UK

433   Home Office Animals (Scientific Procedures) Act 1986.

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Figures

Fig. 1 Interaction graph (± SE) of the number of active individuals (solid line), the group size (dashed line) and the number of groups (dotted line) during the three habitat manipulation experiments. Only the dotted lines show significant differences between treatments at the $p <$ 0.05 level

Fig. 2 Group level correlations in mean social network metrics, *strength* (filled circles), *Reach* (open circles) and *Clustering coefficient* (filled triangles) between three randomised habitat treatments (T1, T2 and T3). See Table 1 for accompanying statistics

Fig. 3 Unstandardised residuals from regressing individual preference for group size and social network strength plotted in relation to group size (filled circles = T1, unfilled triangles = T2 and unfilled circles = T3). Dotted line represents mean group size (2.94) across treatments with the zero line representing no deviation from the regression model. Variance increases with greater group sizes suggesting a decoupling of group size preference and social strength with increasing options for social interactions

571 **Tables**

572 Table 1 Group level correlations between social network metrics across three habitat

573 treatments. See Fig. 2 for graphical representation

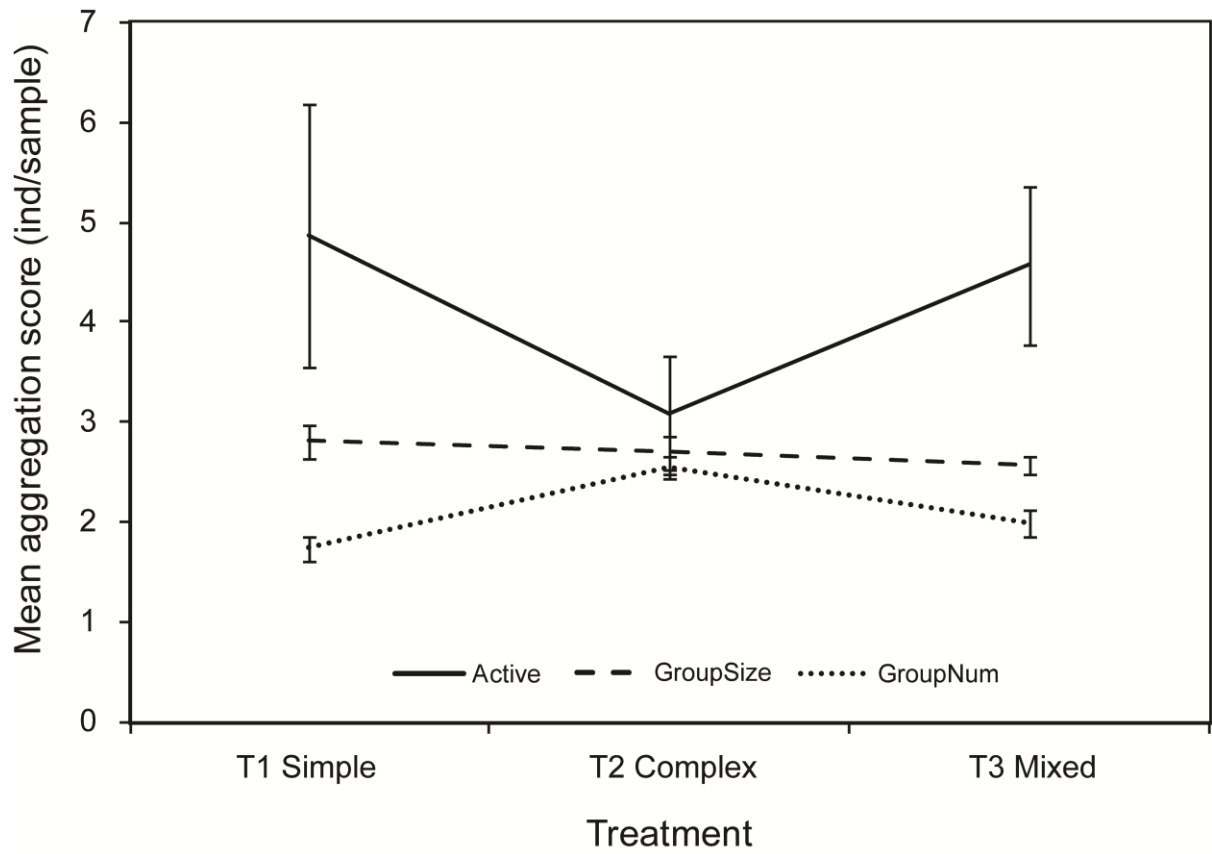| Network metric	Treatment correlation	*n*	*r*	*p*
Strength	1/2	10	0.455	0.093
(Spearman)	1/3	10	0.612	**0.030**
	2/3	10	0.576	**0.041**
Reach	1/2	10	0.406	0.122
(Spearman)	1/3	10	0.624	**0.027**
	2/3	10	0.527	0.059
Clustering Coefficient	1/2	10	0.576	**0.041**
(Pearson)	1/3	10	0.678	**0.016**
	2/3	10	0.347	0.163

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576   Table 2 Observed ($_O$) and randomised ($_R$) concordance (W) of social network position based

577   on strength of individual social affiliation across three independent habitat treatments

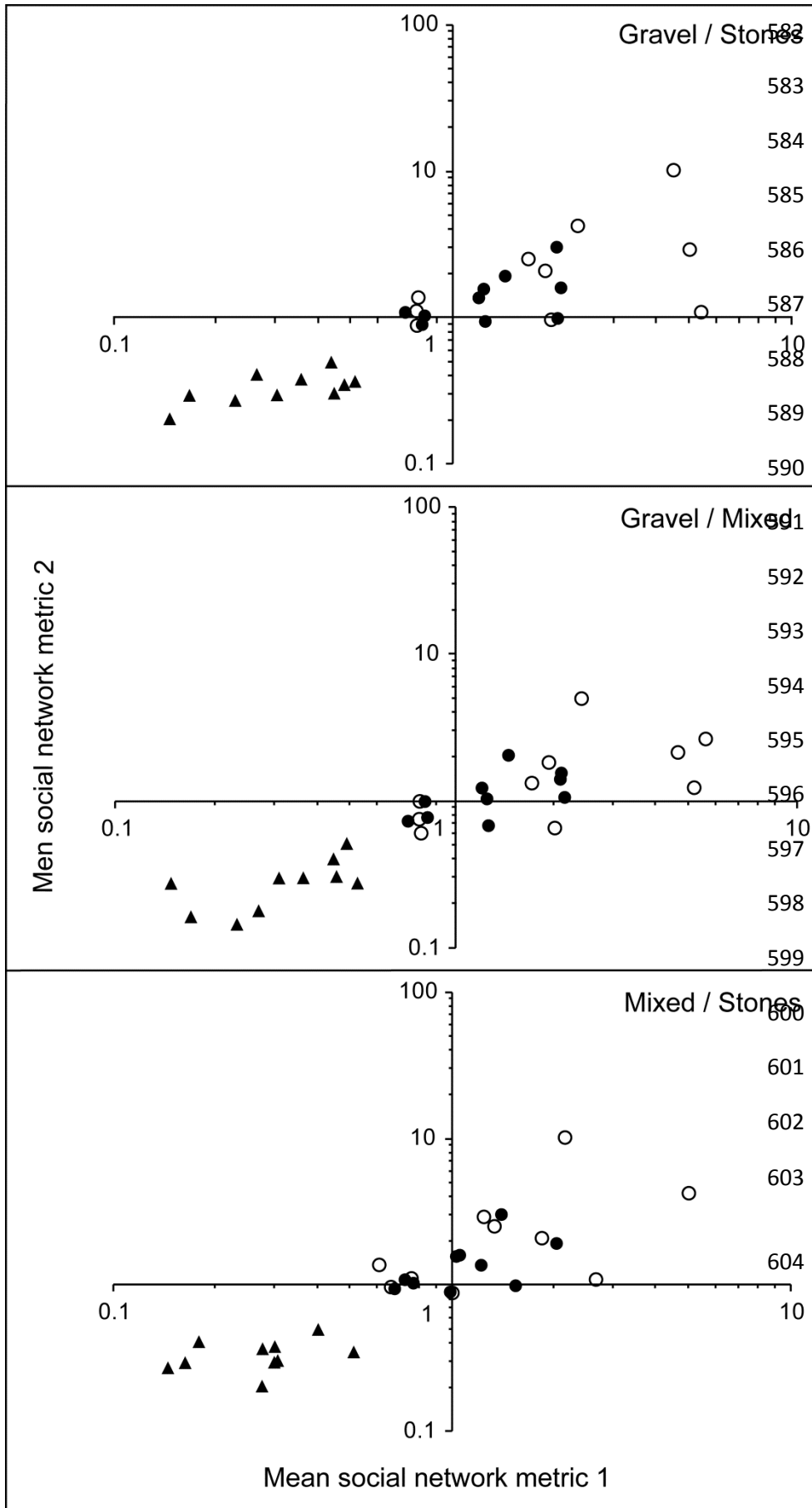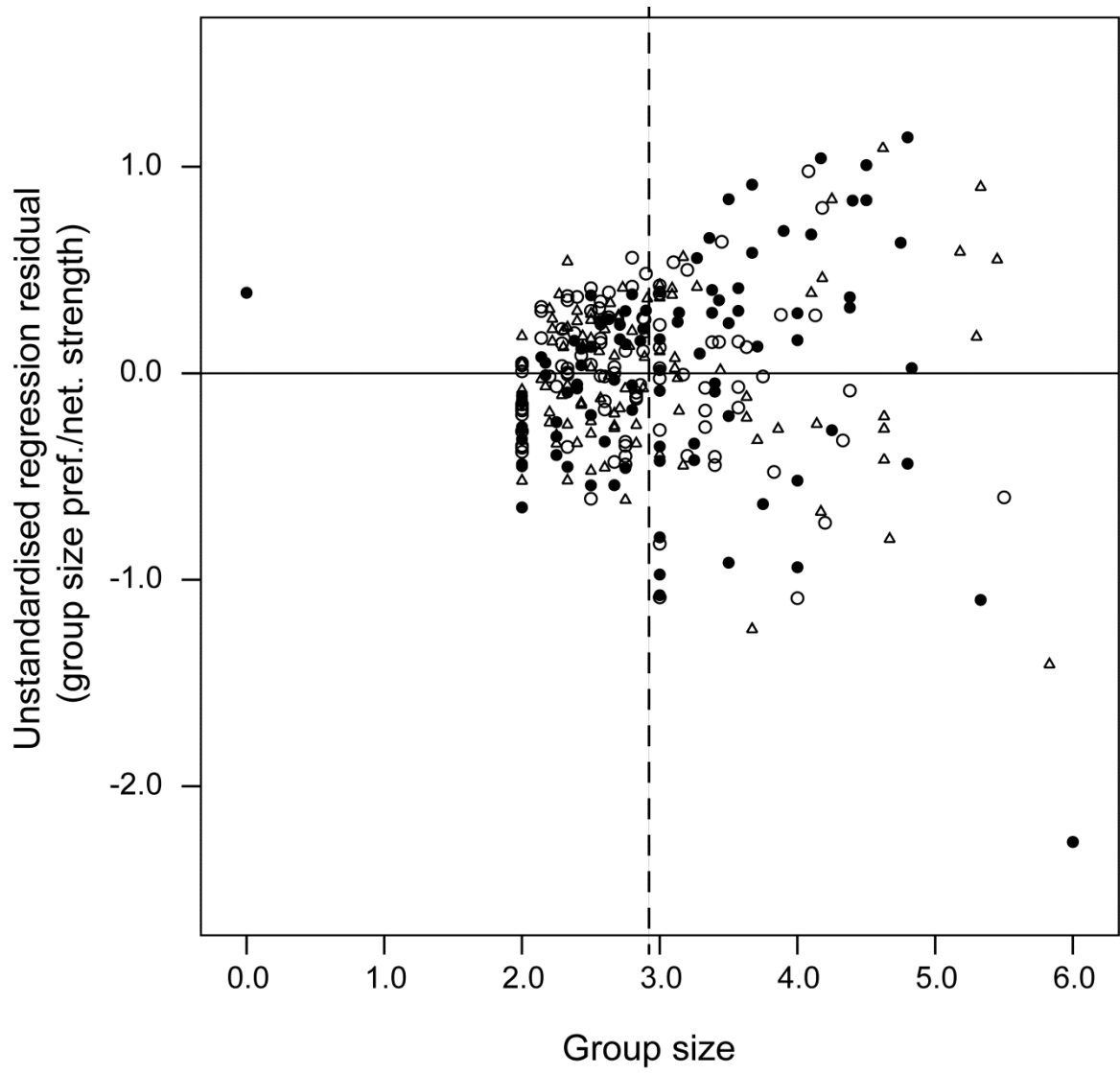| Replicate | Treatment order | Ranked social network concordance | | |
		W_O	W_R	p
1	1,2,3	0.372	0.251	0.1058
2	1,3,2	0.279	0.160	0.1033
3	2,3,1	0.512	0.416	0.0566
4	2,1,3	0.731	0.356	0.0011
5	3,1,2	0.472	0.512	0.1082
6	3,2,1	0.453	0.420	0.1062
7	1,2,3	0.562	0.261	0.0106
8	1,3,2	0.426	0.277	0.1053
9	2,3,1	0.391	0.394	0.1066
10	2,1,3	0.419	0.136	0.1075
			Stouffer's combined P	**< 0.001**

578

579   Figure 1.

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Figure 2.

605   Figure 3.

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