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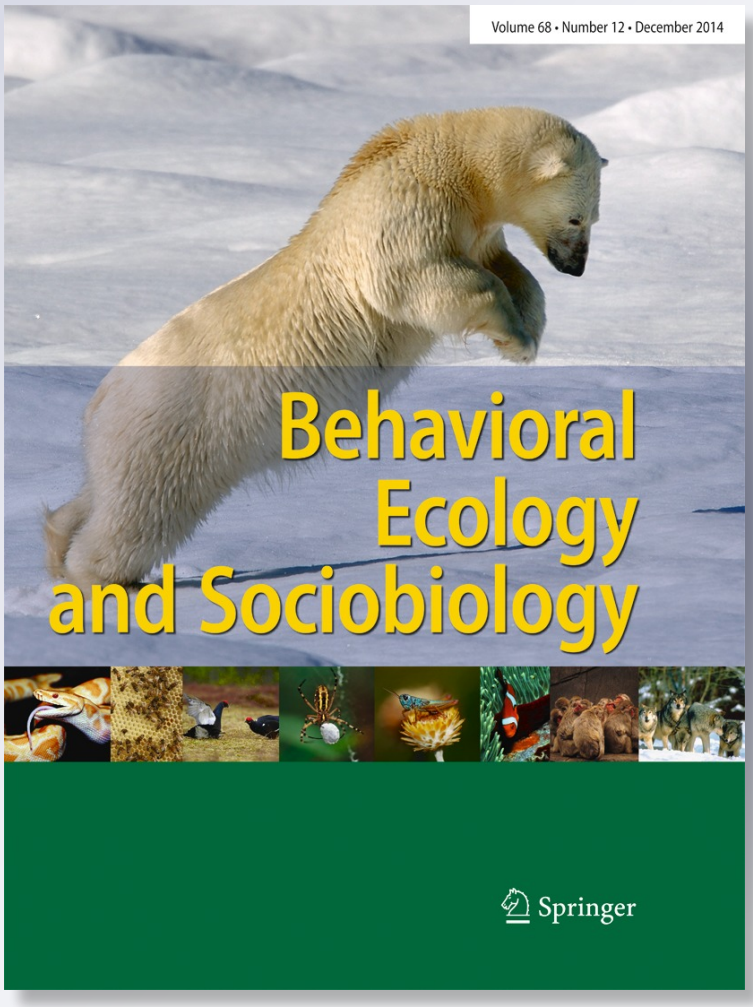


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ORIGINAL PAPER

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

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**Abstract** 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 ten 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.

**Keywords** Aggregation behaviour · Elasmobranch · Personality · Plasticity · Repeatability · Social traits

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## 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

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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 al. 2008; Croft et al. 2009). Furthermore, animals demonstrating different but consistent exploratory traits might also mediate and maintain the overall structure of a social network with highly exploratory individuals tending to associate broadly and thus connect poorly connected conspecifics (e.g. Tanner and Jackson 2012; Aplin et al. 2013). Consequently, both the direct (e.g. dyadic partnerships) and the indirect (e.g. association via intermediaries) social interactions of an individual are likely to influence the ecology and evolution of personality (Krause et al. 2010), and as such, social network traits, such as strength, connectivity and social 'reach', offer a valuable tool with which to characterise individual repeatability of behavioural traits (Wilson et al. 2013).

Previous research clearly demonstrates that differences in an individual's social experience and connectivity not only influences group outcomes but might also carry over into different future ecological contexts (Krause et al. 2009; Sih et al. 2009). For example, when exploring the population dynamics of common lizards (*Lacerta vivipara*, Lichtenstein 1823), Cote and Clobert (2007) found that the social tolerance of individuals from different population densities were strongly linked to dispersal and settlement patterns. An extension of this research revealed that 'social' lizards, that are highly connected, displayed different fitness outcomes under different densities, to 'asocial' lizards that are poorly connected (Cote et al. 2008). In both of these studies however, sociability was not directly tested but rather inferred by assessing individual tolerance of conspecific odours. Using a social network approach, specific components of social behaviour that relate to the intensity, frequency and directionality of social interactions can be quantified directly and tested explicitly for repeatability (Wilson et al. 2013). In doing so, the mechanisms that drive consistent, social behaviour in animals can be explored.

Here, we use a model species of oviparous elasmobranch *Scyliorhinus canicula*, Linnaeus 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 individual preferences for group size influence this? and (4) to what extent does repeatability and plasticity contribute to juvenile social behaviour?

## Materials and methods

### Experimental sharks

Juvenile (<1 year) *S. canicula* were reared in the Marine Biological Association (MBA) Laboratory, Plymouth, UK,

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from eggs laid by wild females caught locally at Whitsand Bay, Cornwall, UK (50° 20.44′ N, 4° 16.38′ W). Experiments were conducted between August and September 2011 on juveniles which were approximately 8–10 months old ($n$= 100) with a mean total length ($L_T$±SD) of 179.7±27.4 mm and a mean weight of 17.98±7.6 g. Size-matched individuals were selected from large holding aquaria (858 l capacity, 1.65×0.80×0.65 m) before being tagged for individual identification using visible implant elastomer tags (VIE; Northwest Marine Technology, WA, USA). Tagging procedures were authorised by the MBA animal ethics committee and licensed by the UK Home Office under the Animals (Scientific Procedures) Act 1986. Once tagged, 10 replicated groups (10 individuals per replicate) were distributed across five smaller holding aquaria (149 l capacity, 1.22×0.61× 0.20 m, temperature: 17.0 °C, 20 individuals per aquaria) where they were allowed to recover for >10 days. As familiarity amongst conspecifics has been shown to drive non-random social preferences amongst juvenile catsharks (Jacoby et al. 2012b); this recovery period also provided an opportunity for individuals to familiarise with one another. Pilot studies revealed that individual sex did not appear to influence association between immature juveniles (D.M.P.J unpublished data), and thus, sex was chosen randomly from a stock sex ratio of ~1:1. All sharks were fed approximately 2.5 % wet body mass per individual per feed (Sims and Davies 1994) on alternate days following data collection. Food comprised a combination of white fish (mixed species), squid (*Alloteuthis subulata*) and queen scallop (*Aequipecten opercularis*) mixed with liposome enrichment and a commercial pellet. The aquaria were subject to a consistent and balanced photoperiod (12 h light/12 h dark).

## Quantifying social behaviour

Each experimental replicate, consisting of ten individuals, was transferred from the holding aquaria to the large experimental arenas (858 l capacity, 1.65×0.80×0.65 m) where they were allowed to acclimatise for 24 h prior to data collection. Social associations were measured during daylight hours during which time activity rates in juvenile *S. canicula* are relatively low (Sims et al. 1993) and individuals often aggregate socially in resting groups (see Jacoby et al. 2012b). Interestingly, we found little evidence that social behaviour in juveniles persists beyond group resting behaviour into active, parallel or follow swimming behaviour. Indeed, periods of solitary activity outside of social refuging behaviour, even amongst schooling elasmobranchs, is not uncommon (e.g. Klimley and Nelson 1984). Social networks were constructed over two days from scan samples of associations taken at two hourly intervals between 08:00 and 18:00 h (six samples per day). The two hourly sampling frequency captured long-term, persistent associations whilst still allowing time for reorganisation and thus independent samples, between observations (see Electronic Supplementary Material for raw data in which shifts in group membership can be seen to occur frequently between consecutive samples). Following data collection, all individuals were returned to their specific holding aquaria.

During each sampling period, individuals were deemed in association whenever two associative zones converged (i.e. a body-length radius from an individual's first dorsal fin overlapped another individuals' centre point/dorsal fin). All individuals within this prescribed distance of one another were considered to be associating (Franks et al. 2010). Group membership of individuals was recorded for each sample, and the accumulation of these associations (12 samples) provided our weighted social network data (see Supporting Information for data). Using the simple ratio index (SRI) (Cairns and Schwager 1987), all dyadic pairings (two associating individuals) were assigned a weighted value between 0 and 1 representing the strength of association between these individuals. An SRI closer to 0 indicated that individuals were never seen associating, whereas a SRI of 1 suggested that individuals were never observed apart. Given the size of tank relative to these small sharks, it was possible that during a sample, all individuals might rest alone. A matrix of association from the SRI was constructed for each of the ten replicates under each habitat treatment. Individual node-based metrics, derived from matrices of association, were calculated in order to (1) determine the role each individual played in overall network structure and (2) calculate and compare individual repeatability in social network position across context and relative to conspecific behaviour. Individual network metrics included *strength*, a direct measure of individual social behaviour based on the sum of an individual's association indices with all other individuals in the group; *reach*, an indirect measure of connectedness that gauges the proportion of individuals that are connected to the node of interest via one, two, three links etc. and *clustering coefficient*, also an indirect measure, which is an indication of the role an individual plays in interconnecting groups and communities based on neighbour connectivity. Unweighted network metrics were considered; however, it was felt that an unweighted network containing ten nodes would not have yielded sufficient variation to test for consistency. To help differentiate the underlying mechanism influencing social behaviour (i.e. preferences for conspecifics or simply shared preferences for locations or group sizes) and to test for plastic responses in aggregation to changes in habitat complexity, the following data were recorded for each scan sample: number of individuals active/resting, the number of individuals grouping/

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solitary, the size of the groups and the identity of those individuals within them (i.e. social preferences).

### Habitat treatments

To test for the repeatability of social traits, a repeated measure design was used in which each replicate 'population' was subject to three habitat treatments which differed in their level of structural complexity. We used differing levels of complexity as this was expected to change patterns of grouping behaviour (Pollen et al. 2007; Orpwood et al. 2008).

1. T1: Gravel—each experimental aquaria was given a natural, medium gravel substrate (size range diameter: 8–16 m) spread evenly throughout the area. This was defined as a *simple* habitat.
2. T2: Stones—each experimental aquaria contained three discrete clusters of large, equal-sized stones (~18×9×10 cm) always in the same location and orientation. (NB. Stone 'structures' were sufficiently large for several groups of individuals to form independently of one another at each cluster). This was defined as a *complex* habitat.
3. T3: Mixed—each experimental aquaria contained both of the above habitat types. This was defined as a combination of *simple* and *complex* habitats.

Little is known about the type of habitat favoured by juvenile *S. canicula* in the wild; however, based on knowledge of the structures upon which egg cases are deposited, these treatments were designed to reproduce some of the habitats which are likely to be experienced by young sharks of this species. The subsequent ordering of these treatments was 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 ($\eta^2$) 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 replicate level correlations in social connectivity between habitats. Second, behavioural consistency was determined at the individual level by examining individual ranked consistency in relative social network position across treatments, using the metric strength as a direct measure of individual sociality. Non-orthogonal network data is problematic to analyse statistically (Croft et al. 2011), and in an attempt to overcome this, a randomisation procedure was devised (Wilson et al. 2013). Individuals within a replicate were assigned a rank based on their relative network strength which were then analysed for concordance across treatments using Kendall's coefficient of concordance ($W$). For each replicate of three observed networks ($n$=10), $W$ was calculated and compared to values of $W$ from a frequency distribution of values generated by 20,000 randomised permutations of the observed data. For each permutation, individual ranks within each of the three treatments were permuted, calculating $W$ on each occasion. This rank permutation procedure, a method equivalent to a node randomisation, was conducted in Poptools (Hood 2010) and provided a conservative null distribution against which we could determine significance values for social consistency with regard to network strength, whilst controlling for non-independence between the data. Independent replicated $p$ values were combined using Stouffer's method in R (R Development Core Team; www.r-project.org) to give an overall value of significance (Piegorsch and Bailer 2005).

In an attempt to decipher the relationship between social behaviour (preferences for certain conspecifics) and individual preferences for specific group sizes (e.g. above/below a given threshold), mean group size preferences were calculated

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for each individual across treatments and regressed against network strength. Group size preferences were calculated as a mean for each individual by averaging the size (i.e. number of individuals) of all grouping events (≥2 inds.) in which an individual was present during sampling. Unstandardised residuals from this regression were then tested for repeatability using the permutation test outlined above to determine whether individual network strength was repeatable after controlling for group size preference. The effect sizes were compared between controlled and uncontrolled permutation tests. Effect size estimates $\eta^2$ and $W$ are discussed in light of the influence of plasticity and repeatability on juvenile shark social behaviour. Unless otherwise stated, all statistical analyses were conducted in PASW Statistics 18 (IBM Corp., Somers, NY, USA) and network analyses in SOCPROG 2.4 (Whitehead 2009).

## Results

### Aggregation under different habitat types

With the assumptions of sphericity and normality met for all three treatments ($p>0.05$), the multivariate, repeated measure GLM revealed that there was a significant main effect of habitat type on aggregation behaviour ($F_{(6,32)}=3.239$, $p=0.013$) with an effect size estimate of $\eta^2=0.158$. Further exploration showed that there were significant effects of habitat on the number of groups forming ($F_{(2,18)}=10.939$, $p<0.001$) but not on the group size ($F_{(2,18)}=1.089$, $p=0.358$) or proportion of active individuals ($F_{(2,18)}=1.150$, $p=0.339$, Fig. 1). Interestingly, average group size in each replicate, which was not necessarily expected to covary with group number as all individuals were able to rest alone, remained virtually constant across the three treatments. Analysis of contrasts revealed a significant increase in mean group number between the simple and complex habitat treatments ($p=0.005$, Fig. 1) and also a significant decrease between the complex and the mixed (simple/complex combination) randomised treatments ($p=0.023$, Fig. 1). The result suggests that three dimensionally complex structures appeared to encourage aggregation tendencies in these juvenile sharks whilst the uniform gravel substrate appeared to have a dispersive influence.

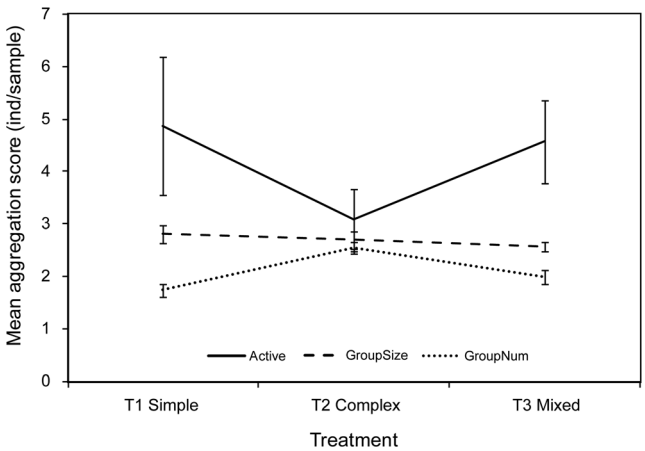


**Fig. 1** Interaction graph (±SE) of the number of active individuals (*solid line*), the group size (*dashed line*) and the number of groups (*dotted line*) during the three habitat manipulation experiments. Only the *dotted lines* show significant differences between treatments at the $p<0.05$ level

### 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.

### 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 support for the model) when group sizes are small, but that variance increases with group size (i.e. greater departure of the residuals from the mean). This indicates that the model predicting social strength from group size preference becomes more inaccurate as individuals have more potential social partners suggesting group size

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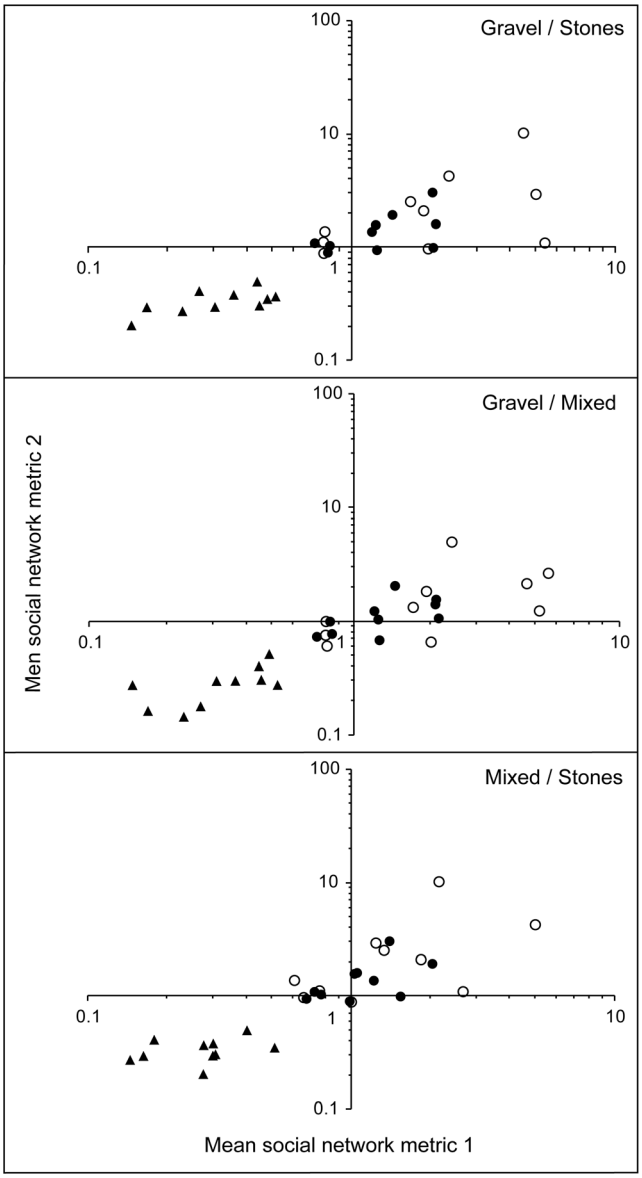


**Fig. 2** Group level correlations in mean social network metrics, *strength* (*filled circles*), *reach* (*open circles*) and *clustering coefficient* (*filled triangles*) between three-randomised habitat treatments (T1, T2 and T3). See Table 1 for accompanying statistics

preferences drive social consistency but only within small groups (Fig. 3).

How do plasticity and repeatability effect juvenile social behaviour?

The effect size estimate of average plasticity across replicates, that is the effect size of the GLM ($\eta^2$=0.158), was low, while the effect size for repeatable social behaviour across habitats ($W$=0.464) was high. More clearly, these experiments demonstrate that changes in structural complexity of the juvenile shark's habitat drive significant changes in the level of aggregation observed between individuals, but that amongst those that do aggregate, there are consistent social relationships that form between specific sharks.

**Table 1** Group-level correlations between social network metrics across three habitat 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 |

Correlations that were significant at the <0.05 level are highlighted in bold

## Discussion

Consistency or repeatability of individual-based behavioural axes such as boldness or exploration are well reported in the literature (Sih et al. 2004; Conrad et al. 2011) and have also been explored in relation to social network structure (Pike et al. 2008; Croft et al. 2009; Krause et al. 2010). Whether individuals show repeatability in social network traits across context, however, has received little attention. Indeed, teasing apart the behavioural mechanisms underpinning individual social preferences and repeatable, consistent behaviour remains a significant challenge in the ecology of marine species, although technology is assisting steps towards this endeavour

**Table 2** Observed ($_O$) and randomised ($_R$) concordance ($W$) of social network position based on strength of individual social affiliation across three independent habitat treatments

| Replicate | Treatment order | Ranked social network concordance | | $p$ |
|---|---|---|---|---|
| | | $W_O$ | $W_R$ | |
| 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 |

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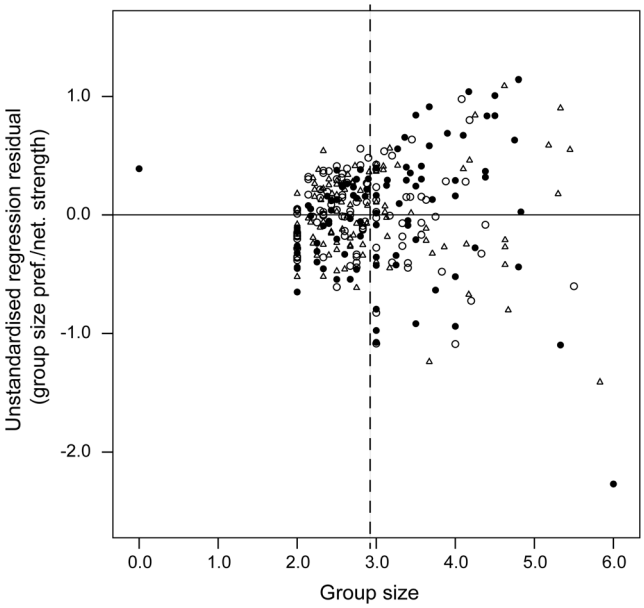


**Fig. 3** Unstandardised residuals from regressing individual preference for group size and social network strength plotted in relation to group size (*filled circles* T1, *unfilled triangles* T2 and *unfilled circles* T3). *Dotted line* represents mean group size (2.94) across treatments with the *zero 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

in terrestrial systems (e.g. Aplin et al. 2013). Here, we provide an empirical illustration of consistent and repeatable animal social networks using a controlled and replicated approach. Individual social network traits of juvenile sharks that are known to demonstrate non-random social grouping (Jacoby et al. 2012b) were found to be consistent across changing environments. Despite some plasticity in tendency of these sharks to aggregate under the different conditions, at the individual level, the overriding influence on social behaviour was to maintain a similar level of social strength and connectivity as revealed through comparison of the effect sizes from the two sets of analyses. We show that individual preferences for aggregating within specific group sizes prove to be a strong mechanistic driver of this result but that perhaps social preferences play more of a role in larger groups (i.e. above the average group size) where more options for conspecific social interaction become available. To our knowledge, this is the first quantitative evidence of repeatability in polyadic social network traits, an idea put forward initially by Wilson et al. (2013). Furthermore, we also provide the first evidence of repeatability of behaviour in the taxonomic class Chondrichthyes (sharks, rays, skates and chimeras), confirming that stable social relationships in catsharks appear important in early, as well as adult life stages. These results suggest the potential for personality traits in Chondrichthyians. We remain cautious, however, of interpreting the results in the context of personality as individuals were not explicitly assayed for any other aspects of behaviour, meaning the mechanisms behind these potential personalities remain unclear (Dingemanse et al. 2010).

An animals physical environment can play a significant role in influencing social contact within a population (Tyler and Rose 1994). In addition, the social network position of an individual is also, in part, derived by the interactive strategies of conspecifics that, in turn, influence individual experience and future social behaviour (Krause et al. 2010). In the presence of large, three-dimensionally complex structures, juvenile sharks in our study showed an overall increase in the number of groups forming on average than in simplified 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 (D.M.P.J. personal observation). 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 reassort individuals between groups and retest them for repeatability. This would have allowed us to determine more strategically whether it was individual social behaviour or the group that constrains individual

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flexibility. While this was beyond the scope of the current experiment, it would be a valuable future extension to this work.

When we consider the mechanism driving consistency in these experiments, the evidence for social preferences remains compelling; highly consistent network metrics across treatments, taken as an average for the group, support the small reduction in *W* when consistency was tested for after controlling for group size preference at the individual level (a marginally non-significant result). Residual analysis suggested that perhaps, group size preference and social preference influence network traits implicitly at different group-level or population-level densities; however, this would need to be tested directly using a different approach. For now, the results of the present study indicate a system whereby juvenile *S. canicula*, a model elasmobranch species in physiological, behavioural and ecological research, demonstrate consistent individual variation in social behaviour, across context, based on individual preferences for aggregation. Typical of a heterogeneous social network for example, some individuals appeared more solitary, recording low social network metrics relative to conspecifics and using the gravel substrate as an opportunity to become individually inconspicuous whilst out in the open. By contrast, other individuals appeared more gregarious, recording stronger social connections and were thus more conspicuous, using the stone structures to hide in and around as a group. Ecologically, this reflects the notion that some individuals, where sociality perhaps correlates with other behavioural traits such as boldness/shyness, harbour a disproportionate percentage of links within a social network and therefore play a key role in interconnecting others (Krause et al. 2010). Further research would be required to disentangle more fully some of these behavioural correlates that would determine the role of personality traits in marine predators.

Using manipulation experiments to induce changes in the physical environment of young sharks provided the opportunity to quantify replicated network structures. In doing so, we were able to explore the repeatability of individual social network position. We demonstrate plasticity in aggregation tendency at the group level which we discuss in light of the different behaviour of individuals of high and low social connectivity. In addition, we show consistency in individual network traits of sharks under changing environments and assess the influence of group size preferences on this result in an attempt to understand the mechanisms behind repeatable social behaviour in these animals. In beginning to understand the social preferences and behaviour of these often elusive predators, this study paints a more complex picture of social personalities than perhaps originally thought.

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