Behavioural Trait Assortment in a Social Network: Patterns and Implications

Darren P. Croft *1,2**, Jens Krause *3*, Safi K. Darden*1,2*, Indar W. Ramnarine *4*, Jolyon J. Faria *3* & Richard James *5*.

1 School of Biological Sciences, College of Natural Sciences. Bangor University, Bangor ***2*** Centre for Research in Animal Behaviour, School of Psychology, University of Exeter, Exeter ***3*** Institute of Integrative and Comparative Biology, University of Leeds, Leeds ***4*** Department of Life Sciences. The University of the West Indies St. Augustine, Trinidad & Tobago. ***5*** Department of Physics, University of Bath, Bath.

*To whom correspondence should be addressed. E-mail: darren_croft@hotmail.com, Tel: 0044 (0) 1392 264626, Fax: 0044 (0) 1392 264623

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Abstract

The social fine structure of a population plays a central role in ecological and evolutionary processes. Whilst many studies have investigated how morphological traits such as size affect social structure of populations, comparatively little is known about the influence of behaviours such as boldness and shyness. Using information on social interactions in a wild population of Trinidadian guppies (*Poecilia reticulata*) we construct a social network. For each individual in the network we quantify its behavioural phenotype using two measures of boldness, predator inspection tendency, a repeatable and reliably measured behaviour well studied in the context of co-operation, and shoaling tendency. We observe striking heterogeneity in contact patterns, with strong ties being positively assorted, and weak ties negatively assorted by our measured behavioural traits. Moreover, shy fish had more network connections than bold fish and these were on average stronger. In other words, social fine-structure is strongly influenced by behavioural trait. We assert that such structure will have implications for the outcome of selection on behavioural traits and we speculate that the observed positive assortment may act as an amplifier of selection contributing to the maintenance of co-operation during predator inspection.

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 personalities, temperaments or behavioural types (Sih et al. 2004; Reale et al. 2007). Perhaps the best studied example is variation along the bold-shy axis. Bolder individuals can generally be characterized as exhibiting more risk-prone behaviours across a range of contexts including approaching novel objects, consuming novel food items, inspecting predators, and spending more time in open habitats (see Reale et al. 2007 for a review). Behavioural phenotypes often influence sociality (Roberts et al. 2008) so they should be expected to influence who interacts with whom within a social network. Pike et al. (2008) found that shy three-spined sticklebacks (*Gasterosteus aculeatus*) associated preferentially with a small number of other group members whereas bold individuals had fewer overall interactions than shy fish, and distributed their interactions more evenly across all group members. The interaction between such behavioural traits and social network structure in wild animal populations remains unknown.

The structure of social networks is likely to have important implications for the strength and direction of selection on behavioural traits. Many behavioural traits are subject to frequency dependent selection, in which the fitness of an individual will depend in part on its social environment (i.e. an individual's interactions with others and their accompanying behavioural types). For example, in models of conflict, the success of a hawk (aggressive) or dove (yielding) strategy will be dependent on the frequency of hawks and doves in an individual's local interaction network (Maynard Smith 1982). Non-random interactions between individuals based on behavioural traits can dramatically influence selection and in some cases may act as an amplifier of selection on those traits (Ohtsuki *et al.* 2006). Thus quantifying the relationship between social structure and behavioural traits may help us understand how selection acts on these traits.

In the present study we investigate whether there is evidence of social structuring by behavioural phenotype in a wild population of guppies (*Poecilia reticulata*). Field observations of social associations over a 10-day period were used to build a social network and network analysis was used to characterise the social fine structure of our population. A network is simply a graph consisting of nodes connected by edges (lines). In the current investigation nodes represent individual animals and the edges the relationships between them are based on social associations. We represent the intensity of such interactions by giving each edge a weight proportional to the frequency of observed association. Compared to more traditional approaches that focus on dyadic interactions between animals in isolation, the network approach allows us to put such interactions into the wider social context of the population (Krause et al. 2009). For every fish in the population we quantify its predator inspection and shoaling tendency via standard laboratory tests and use this to assign it a behavioural score (BS). Predator inspection is indeed a consistent behavioural trait that can be reliably measured and differs between individuals (Budaev 1997). It is also a behaviour that has been studied in depth in the context of cooperation (Milinski 1987; Dugatkin 1988; Croft et al. 2006a). Individuals leave the relative safety of a group to approach and inspect a predator, gaining information on the predator’s state and on the probability of attack (Pitcher et al. 1986). This information is transmitted to non inspecting individuals, providing fitness benefits to all group members (Magurran and Higham 1988; Godin and Davis 1995). Inspectors pay a personal cost of increased risk of predation (Dugatkin 1992; Milinski et al. 1997), which they can reduce by inspecting in cooperative partnerships (Milinski 1987; Dugatkin 1988; Croft et al. 2006a). Theoretical work suggests that the benefits to inspectors will be maximised when there is social assortment based on predator inspection behaviour (Wilson and Dugatkin 1997). We look for evidence of such assortment by behavioural strategy in our social network.

Materials and Methods:

Study Population:

Adult guppies were captured from a 35m section of the Arima River (10^{o}41´N, 61^{o}17´W) in the Northern Mountain Range of Trinidad in May 2006. Guppies here are under high risk of predation due to the presence of major pisciverous predators, including the pike cichlid, *Crenicichla sp*. The fish were caught in two interconnected pools between which they could move freely. During fish sampling entire shoals (defined as two or more fish observed within four body lengths) were captured from each of the pools using a 2-m seine (Croft *et al.* 2004). After capture, shoals were housed individually in sealable 2 L plastic storage bags. All adult guppies were brought to the laboratory to be screened for behavioural traits. Fish were housed in two aquaria, one for fish captured from each pool (l x h x w = 76 x 46 x 46cm, water depth = 35cm) that had natural substrate collected from the river. Guppies were anaesthetized (MS-222 Sigma Chemical) and given individual identity marks by injecting different colours of visible implant elastomer (VIE) in two of six positions on the dorsal area (Croft et al. 2003a).

The identification mark does not have an effect on shoal choice behaviour (Croft *et al.* 2004). The sex and total length of each fish were recorded at the time of marking.

Behavioural Screening:

After marking, the fish were left to acclimatise in the holding tanks for a period of 24 to 48 h, before behavioural screening. When an individual inspects a predator it is trading off a tendency to seek refuge in a social group and a willingness to undertake risky behaviour. Shy fish might also be expected to seek refuge in a shoal more than bold fish, so to examine the robustness of behavioural differences between individuals we also tested an individual's preference to be with conspecifics. Behavioural screening was carried out in a test tank (90cm x 30cm x 30cm; water depth 15cm) made up of three compartments ("release", "shoaling" and "predator inspection" respectively) each 30cm x 30cm x 30cm, that could be isolated using two opaque barriers. Observations were made directly by an observer who was located in front of the tank and manipulated the opaque barriers using a remote pulley mechanism. At the start of each trial both barriers were in the down position isolating the three compartments. Initially the test fish was placed alone in the release compartment (at one end of the tank). After a 10-minute period the opaque barrier separating the release compartment and the shoaling compartment (the central compartment) was raised using a remote pulley mechanism allowing the test fish access to the shoaling compartment. The shoaling compartment contained a stimulus shoal made up of two large (>25mm) and two small (<20mm) female guppies. The stimulus shoal was contained within a cylindrical container (diameter=10cm) in the centre of the compartment that allowed the transmission of visual, but not olfactory, cues.

The stimulus fish were most likely unfamiliar to the focal fish as they were caught from another section of the Arima River that was more than 500m from the site of the test fish capture. The amount of time that focal fish spent associating with the stimulus shoal (defined as being with 5cm) was recorded over a 10-minute period. Then the second partition was raised allowing the fish access to the predator compartment. The predator compartment contained a model fish predator (a fishing lure) located in the rear corner and faced towards the shoaling compartment. The number of approaches within a standardised length of 15cm of the predator was recorded over a 10-minute period. Each fish was screened for shoaling and predator inspection behaviour twice on consecutive days. When not undergoing testing the fish were housed in their original holding tank (see above).

Building the Social Network:

After screening, all individuals (N=72) were simultaneously released into the centre of their original pool in the Arima River. This occurred approximately 144 h after capture. Re-sampling of the population began 24 h after release and was undertaken once per day between 10:00 and 14:00 h for 9 consecutive days. Entire shoals were captured from the pools using a 2-m seine as in the initial capture of the study population. The depth of water at the location of capture was recorded for each shoal. Shoals were kept in individual sealable 2 L plastic storage bags, and released back to their capture location after the composition of all shoals had been recorded. Individuals were recaptured on average (±SD) 4.7±2.5 times.

For each sampling day (day 0 to 9) fish were defined as associating if they were observed in the same shoal. These associations were then accumulated over the 10 sampling days. From this data we calculated the strength of association between each pair of animals using an association index. As we have no reason to believe there was a sampling bias in seeing animals together or apart, we used the simple-ratio index (SRI) (Cairns and Schwager 1987).

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

Where X is the number of times a pair of animals (a and b) were observed in the same group, Y_a is the number of times a was observed in a group but not b, Y_b is the number of times b was observed in a group but not a and Y_{ab} is the number of times bother animals were observed in different groups. The *SRI* gives indices that are scaled between 0 and 1 with a value of 1 indicated that the pair was always observed together and a value of 0 if the pair never associated.

Guppies have a dynamic fission fusion social system in which there can be a rapid change of shoal membership. Shoals sampled at one point in time may therefore contain some pairs of animals that are frequently found together, and others that are rarely together. The edges of the network are weighted by the strength of association (*SRI*) between pairs of animals, so by constructing a series of networks filtered to include only the stronger or the weaker associations we are able to explore the interplay between social fine structure and behavioural trait at different levels of social association. Eight networks were considered: four (S1-S4) were used to analyse increasingly strong social ties; these were filtered to include only pairs of animals with $SRI \geq 0.1$, 0.2, 0.3 and 0.4 respectively. To study the structure of weak ties, the same thresholds were used, but as a maximum, to produce networks W1-W4. So in W2, for example, pairs are only joined if their SRI is > 0 and ≤ 0.2. For each network we calculated the mean degree (defined as the average number of associations individuals have in the network) as a measure of social differentiation. To quantify assortment by behavioural score in our filtered networks, we correlated an individual's behavioural score with the average behavioural score of its network neighbours (Newman 2003). The distribution of group sizes and recapture frequencies are known to have an effect on network structure (James et al. 2009), so all measured network values were compared to the results of a Monte Carlo test in which these variables were preserved (Croft et al. 2008). Furthermore, whilst all fish within a pool on a given day have the opportunity to interact socially it is unrealistic to assume that individuals in different pools have the same opportunity. For this reason we further constrained the randomisation test to randomise shoal structure for fish captured within a pool on a given day. A similar test was used to look for shoal-level assortment. In this case the test statistic is the coefficient of variation (CV) in phenotype within each shoal, averaged over all shoals.

Results

Quantifying Behavioural Traits:

Both of behavioural measures showed significant repeatability between the two testing days (Spearman rank correlation, inspection, n=72 r=0.24, P=0.05 and shoaling N=72, r=0.23, P=0.05). To provide a single measure for each behaviour the average of the two values were calculated. We found substantial variation among individuals in the number of predator inspection events during the trials (mean±(SD)=4.19±3.07) and in the time they spent shoaling (mean (±SD)=351.5±92.3 sec). No significant differences were observed between the sexes in either inspection tendency or shoaling tendency (ANOVA; inspection: $F_{1,71}$=1.26, P=0.26; shoaling: $F_{1,71}$=0.01, P=0.91) and no relationship was observed with either measure and body length, a morphological variable known to explain many aspects of shoal composition in this species (Croft *et al.* 2005) (Spearman rank correlation, inspection, n=72, r=-0.080, P=0.50; shoaling: n=72, r=-0.013, P=0.91).

There was a significant negative correlation between the time an individual spent shoaling and its propensity to inspect a predator (Spearman rank correlation n=72, r=-0.502, P<0.0001). To provide a behavioural profile for each individual we combined the two scores using principal component analysis to produce its 'behavioural score' (BS) in which the bolder fish (i.e. individuals with high inspection and low shoaling) have larger values. The first principal component explained 76 % of the variance with both shoaling tendency and inspection tendency loading on the component with a value of 0.872. No significant relationship was observed between BS and average water depth (Spearman rank correlation n=72, r=-0.19, P=0.115)

Quantifying Social Network Structure:

The average (±SD) SRI index between network dyads was 0.177±0.083. Nine animals were seen only once, and were removed from the analysis, to avoid bias in the edge weights. Network S1 is shown in Fig. 1; it includes all observed associations and interconnects all 63 fish. Its mean degree is relatively high (11.1), with each individual connected to nearly one fifth of the population. Fig. 2 shows that the mean degree decreases rapidly as a function of association filter threshold. Thus individuals have many casual associations but fewer stronger and potentially socially significant associations. Also shown are the values of mean degree we should expect under a null model of shoal membership. The mean degree of S1 is lower than expected; S2 and S3 higher (Fig. 2). S4 contains too few edges to maintain test power. The results for S2 and S3 imply that shoals are somehow assorted. We tested the shoals observed on the first day of capture only (to avoid pseudo-replication) and found strong assortment by body length in shoals (n=18, CV=8.64, P<0.0001 - see methods). This is a well known result for this species (Croft *et al.* 2005). More interestingly, we found no evidence of assortment of shoal membership by our behavioural score (n=18, CV=31.2, P=0.337).

Despite the lack of group-level assortment, we found significant positive BS assortment in networks S1-S3, with the observed correlation coefficients exceeding those from the model and increasing with filtering threshold (Fig. 3a). S4 again contains too few edges to maintain test power. In addition we found significant negative BS assortment in the W1 network (in which only edges with SRI $\leq$ 0.1 are included, Fig. 3b). We also looked for correlations in our S networks by predator inspection alone (as opposed to a combined inpection and shoaling behavioural score BS), since co-operative predator inspection behaviour in guppies is known to occur between individuals that form strong social ties (Croft et al. 2006a). The results of this analysis are consistent with the analysis of the BS, in that there was a non-significant tendency for the observed assortment to be greater than the expected assortment across all filtering thresholds (see Fig 3c), this was only significant however for networks S2 and S3 (see Fig 3c).

We found a non-significant negative correlation between an individual's BS and network degree (the number of social ties they have), with bolder individuals having a tendency to form fewer network ties (Spearman rank correlation: n=63, r=-0.24, P=0.058, see Figure 4a). Removal of one outlying point from the data (Fig. 4a) resulted in a significant negative correlation (n=62, r=-0.29, P=0.020). We also found a significant negative correlation between the average association strength an individual has with its network neighbours and an individual's BS with bolder individuals having on average weaker network ties (Spearman rank correlation: n=62, r=-0.35, P<0.0001; Fig. 4b).

Discussion

Our results provide the first insight into how social networks are structured by behavioural traits in a wild population, showing evidence for non-random mixing of individuals in a social network based on their behavioural traits. We have to keep in mind that these results are from one social network, making it difficult to generalise about the observed patterns. Replication is a common problem for ecological studies on this scale but the patterns we observe are very clear. In particular, we found that the social network was positively assorted by behavioural score (BS) across all ties in the network and positively assorted by predator inspection tendency across strong network ties. An individual’s BS predicted the number and strength of interactions they had, with high-BS individuals forming fewer associations that were on average weaker - a finding that supports previous laboratory work (Pike et al. 2008).

There are a number of mechanisms that could contribute to the observed behavioural structuring of the social network by BS. Firstly, individuals with a high BS are predicted to spend less time shoaling, which we predict will lead to them having fewer and weaker social interactions. This prediction is supported by our field observation which strongly suggests that our measured behaviour in the laboratory reflects the behaviour of individuals under natural conditions. Secondly, it is possible that the observed positive behavioural assortment could be the by-product of morphological assortment if behavioural traits are correlated with morphological traits (Külling and Milinski 1992). The most obvious morphological candidates for this are body size and sex, but no relationship was observed between size and BS and there was not a significant difference in BS between the sexes, suggesting that behavioural assortment is not driven as a by-product of morphological assortment in the current investigation. Thirdly, the phenotypic distribution of individuals in the habitat may limit the opportunities for social interactions to occur. A study on the pumpkinseed sunfish (*Lepomis gibbosus*) documented that individuals of different behavioural types utilise different habitats (Wilson et al. 1993). In guppies water depth is an important variable influencing the phenotypic distribution of fish within the habitat, both as a function of body size and of sex (Croft et al. 2003b; Croft et al. 2006b), and it has been demonstrated that a greater water depth is associated with increased predation risk (Croft et al. 2006b; Darden and Croft 2008). However, in our study population we did not observe a significant relationship between the average water depth in which an individual was observed and its behavioural score so it appears unlikely that habitat segregation based on behavioural type is a significant factor in the behavioural structuring of the social network. Finally, it is possible that positive assortment in the network could be driven through passive mechanisms due to individual variation in social tendencies, leading to repeated interactions between individuals of a similar behavioural type that are independent of active partner preferences. Whilst it is easy to see how this mechanism could lead to positive behavioural assortment, it is not clear how such a mechanism could lead to negative behavioural assortment as is observed amongst weak ties in the social network. This latter result is indeed intriguing and leads us to hypothesize that active partner choice and partner updating may have a significant role to play in generating the patterns of negative assortment. Further work exploring the mechanisms underpinning these negatively assorted weak interactions and their functional benefits provides an exciting avenue for future research. More generally, further work is needed to elucidate the mechanisms underpinning the patterns of behavioural assortment. Using individual based models to explore the influence of behavioural type on social network structure and vice versa, could be a fruitful avenue for future research.

In addition to the potential passive mechanisms outlined above there may be benefits that drive positive assortment by BS that lead to individuals actively assorting by behavioural type. For example, if individuals of different behavioural types differ in activity levels, then individuals may assort to synchronise behaviour and minimise energy expenditure. Such a mechanism has been proposed to explain phenotypic assortment based on sex in ungulates where the sexes differ in activity patterns such as foraging and resting (Conradt 1998; Ruckstuhl 1999). Further work exploring the extent to which individuals of different behavioural types assort to synchronise behaviour (such as activity) could be very rewarding. Behavioural assortment may also provide anti-predator benefits (Szulkin et al. 2006). It is well documented that the anti-predator benefits of group living increase with phenotypic assortment of social groups and that odd individuals in a group suffer an increased risk of predation due to the ‘oddity effect’ (Ohguchi 1978; Landeau and Terborgh 1986; Theodorakis 1989). Whilst the oddity effect has generally been considered in the context of morphological traits such as body size and coloration (Landeau and Terborgh 1986; Theodorakis 1989), it is possible that behavioural assortment increases the anti-predator benefits of grouping by decreasing phenotypic oddity (Szulkin et al. 2006).

Whilst our work does not directly test the evolutionary implications of the social network structure, our finding that the guppy social network was positively assorted by predator inspection behaviour is interesting in the context of selection on this behavioural trait (Wilson and Dugatkin 1997). Our previous work has demonstrated that pairs of individuals that form stable social associations are more likely to engage in co-operative predator inspection behaviour together (Croft et al. 2006a) and the results presented here demonstrate that they have similar predator inspection tendencies. It has been suggested that behavioural assortment by co-operative behaviour may be important in maintaining co-operation (Wilson and Dugatkin 1997; Ohtsuki et al. 2006; Santos et al. 2006). However, evidence of such assortment remains elusive in wild populations. Whilst we can not directly infer levels of co-operation between individuals in the current investigation if we speculate that individuals that have similar inspection tendencies are more likely to engage in co-operative predator inspection behaviour together, then the observed positive assortment of the social network may contribute to the maintenance of co-operation in the population (Wilson and Dugatkin 1997; Ohtsuki et al. 2006; Santos et al. 2006). It has been suggested that in dynamic social systems very simple behavioural strategies such as ‘walk away when encountering non-co-operation’ (Aktipis 2004) may lead to repeated interactions between co-operators and promote co-operation (Santos et al. 2006). In fact, previous laboratory work with guppies (Dugatkin & Alfieri 1991) has shown that individuals monitor the inspection behaviour of others and prefer to associate with individuals with a high inspection tendency. Work on both sticklebacks and guppies in the laboratory suggests that individuals form stronger social associations with whom they co-operate (Milinski et al. 1990; Croft et al. 2006a), suggesting that the patterns observed in the current study could be based on active choice. We also see that animals have fewer ties the stronger the ties are. This is not surprising, but is consistent with arguments that partner updating decreases the number of ties individuals have, which may be important in maintaining co-operation (Santos et al. 2006). The possibility that simple partner updating could at least aid the maintenance of co-operation via assortative interactions, without the need for advanced cognitive abilities, is certainly intriguing and we believe it offers an exciting avenue for future research. Furthermore, the work presented here highlights the need for in-situ studies of association patterns, as previous attempts to explore assortative interactions and partner switching in guppies under artificial laboratory conditions have produced inconclusive results (Dugatkin and Wilson 2000; Thomas et al. 2008).

Our work indicates that behavioural traits influence, or perhaps are influenced by, the social fine-structure of the population and that this structure may influence the strength and direction of selection on those traits. Designers of future empirical studies trying to unravel selection pressures on behavioural traits or to resolve the mechanisms underpinning population social structure should therefore seriously consider recording social contact patterns. A network analysis allows us to examine structural properties that are maintained over time, or indeed those that are not, and to probe structure at any level between the individual and the population. The power of the approach is clearly illustrated by the fact that assortment by the behavioural trait is only evident in the network; though shoals of guppies were significantly assorted by body size (a pattern that is well documented in other studies (Krause et al. 2000)), they were not assorted by behavioural score. A shoal-level analysis could not have captured this aspect of social structure (Croft et al. 2003b).

In conclusion, we report the first evidence of social structure shaped by behavioural phenotypes in a wild population. Our findings are consistent with observations of human social network formation in which the personality score of individuals influences the formation of network ties (Roberts et al. 2008). Our work illustrates the potential of adopting a network approach for understanding how selection acts on behavioural traits that are subject to frequency-dependent selection in natural populations. This is an exciting and developing area of research that we believe could have broad application. More work is needed to look at the mechanisms underpinning the structure of social networks and the evolutionary consequences of network structure.

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Figures

Figure 1) Network S1, in which all edges with SRI greater than or equal to 0.1 are included. The size of the node indicates the strength of individual behavioural score, within larger nodes having a higher inspection tenancy. Sex of individuals is represented by node colour.

Figure 2) Mean degree of networks S1-S4. Filled circles depict the observed values and the unfilled circles the median value for 10000 randomisations. 95% two-tailed confidence intervals are shown as the dashed line around the expected random value ($P<0.01$=**).

Figure 3) Assortment by behavioural phenotype in the edge-filtered guppy social networks a) Shows the analysis based on individuals behavioural scores (BS) in which only edges with SRI greater than or equal to the threshold are included (S networks S1-S4). b) Shows the analysis based on individuals behavioural scores (BS) in which only edges with SRI less than or equal to the threshold are included (W networks W1-W4). c) Shows the analysis based solely on predator inspection scores in which only edges with SRI greater than or equal to the threshold are included (S networks S1-S4). Filled circles depict the observed values of the Spearman rank correlation coefficient and the unfilled circles the median value for 10000 randomisations. 95% two-tailed confidence intervals are shown as the dashed line around the expected random value. P values are displayed on the figures.

Figure 4a) The relationship between an individual’s behavioural score and its number of network neighbours (degree). b) The relationship between an individual’s behavioural score and the average strength of its social associations.

Figure 1

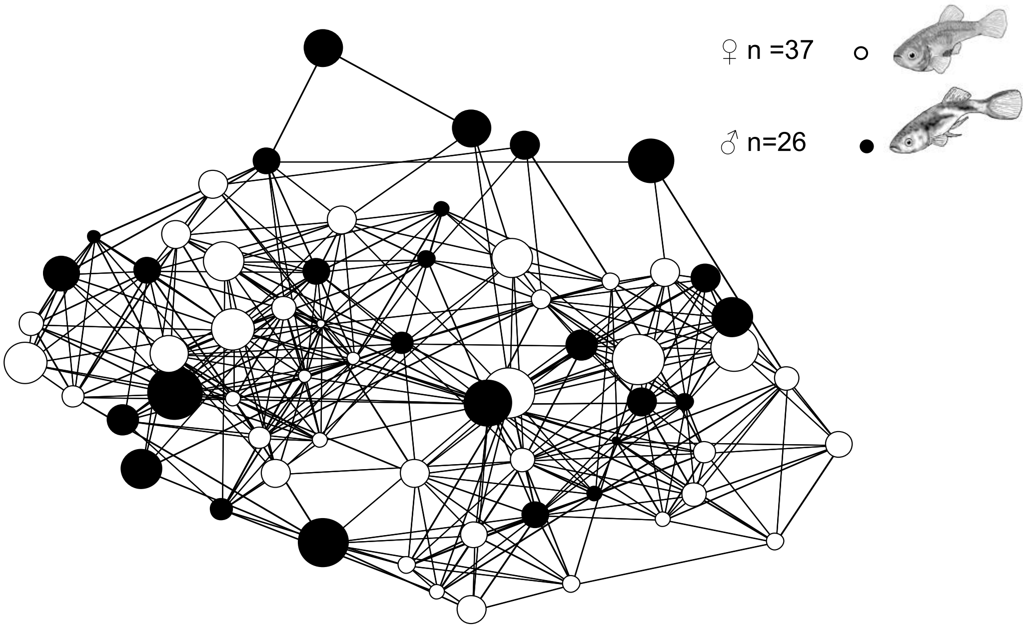


Figure 2

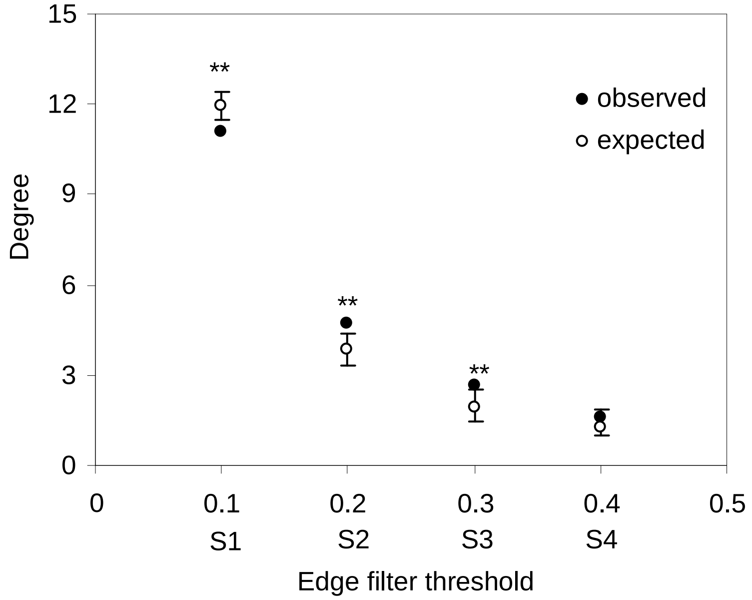

15
12
9
6
3
0
Degree
**
**
**
● observed
○ expected
0
0.1
0.2
0.3
0.4
0.5
S1
S2
S3
S4
Edge filter threshold

Figure 3

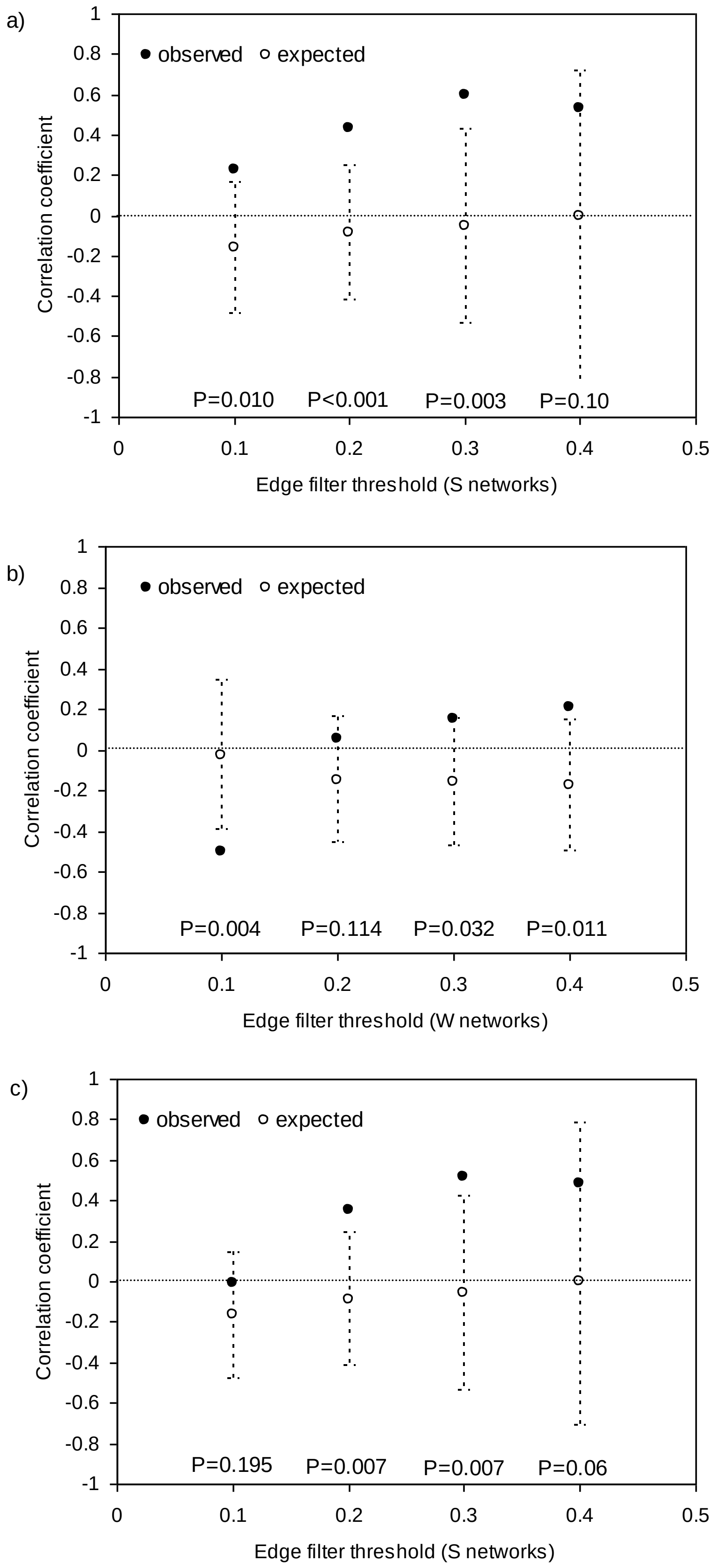
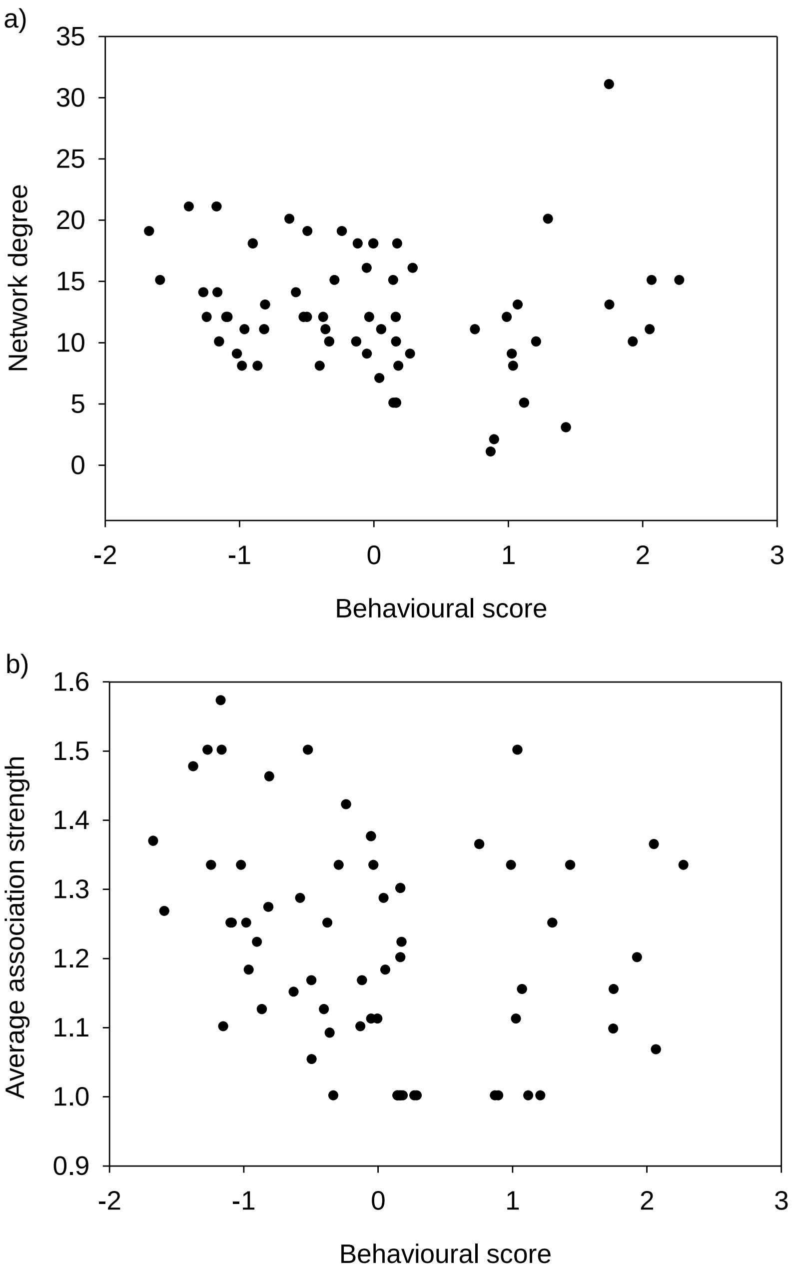

a)
● observed ○ expected
Correlation coefficient
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
P=0.010
P<0.001
P=0.003
P=0.10
0
0.1
0.2
0.3
0.4
0.5
Edge filter threshold (S networks)
b)
● observed ○ expected
Correlation coefficient
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
P=0.004
P=0.114
P=0.032
P=0.011
0
0.1
0.2
0.3
0.4
0.5
Edge filter threshold (W networks)
c)
● observed ○ expected
Correlation coefficient
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
P=0.195
P=0.007
P=0.007
P=0.06
0
0.1
0.2
0.3
0.4
0.5
Edge filter threshold (S networks)

Figure 4


a)
35
30
25
20
15
10
5
0
Network degree
-2
-1
0
1
2
3
Behavioural score
b)
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
Average association strength
-2
-1
0
1
2
3
Behavioural score