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Assortative interactions and social networks in fish

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Abstract The mechanisms underpinning the structure of social networks in multiple fish populations were investigated. To our knowledge this is the first study to provide replication of social networks and therefore probably the first that allows general conclusions to be drawn. The social networks were all found to have a non-random structure and exhibited ‘social cliquishness’. A number of factors were observed to contribute to this structuring. Firstly, social network structure was influenced by body length and shoaling tendency, with individuals interacting more frequently with conspecifics of similar body length and shoaling tendency. Secondly, individuals with many social contacts were found to interact with each other more often than with other conspecifics, a phenomenon known as a ‘positive degree correlation’. Finally, repeated interactions between pairs of individuals occurred within the networks more often than expected by random interactions. The observed network structures will have ecological and evolutionary implications. For example, the occurrence of positive degree correlations suggests the possibility that pathogens and information (that are socially transmitted) could spread very fast within the populations. Furthermore, the occurrence of repeated interactions between pairs of individuals fulfils an important pre-requisite for the evolution of reciprocal altruism.

Keywords Guppies · Sticklebacks · Group living · Social organisation

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Introduction

Understanding the social organisation of animal societies has been of interest to biologists for some time. Previous investigations have generally considered the nature of dyadic interactions between individuals (see Whitehead and Dufault 1999 for a review). However, social interactions rarely occur in isolation; so, to truly understand sociality, we need to consider the structure of the social network within which dyadic interactions occur. For example, co-operation, information and disease transmission cannot be fully understood in social species without considering the social network structure over which such processes occur (Abramson and Kuperman 2001; Latora and Marchiori 2001; Moore and Newman 2000; Watts and Strogatz 1998). Very few investigations have quantified social network structure for animal populations (Croft et al. 2004a; Lusseau 2003) and virtually nothing is known about factors influencing social network structure.

Social interactions between animals are often characterised by non-random partner selection (see Whitehead and Dufault 1999 for a review of the literature), and may be influenced by a number of phenotypic, behavioural and ecological factors. For example, in fishes, shoals frequently assort by phenotype characteristics including; body-length, species, colour and parasite load (see Krause et al. 2000 for a review). Such assortative interactions may confer important adaptive benefits, including reduced predation risk through predator confusion (Theodorakis 1989). Phenotypic assortment by size may also have implications for foraging efficiency (Krause 1994; Ranta et al. 1994). There may also be adaptive benefits of associating with familiar individuals, including reducing the risk of predation (Chivers et al. 1995), and increasing food intake through reduced competition (Utne-Palm and Hart 2000). Accordingly, active preference for familiars has been documented in a number of fish species (see Griffiths 2003; Ward and Hart 2003 for reviews), though little is known about how

inter-individual interactions on a local scale link with larger scale population structure.

Social network theory can help bridge the gap between social interactions at the local and global level and provides a framework for the study of sociality. Social networks can be constructed from information on inter-individual interactions (see Newman 2003 for a review), with individual animals (nodes) inter-connected by their social ties (edges) (Fig. 1). From such a network, standard measures can be calculated including path length (L), clustering coefficient (C) and mean degree of connectedness (k) (Albert and Barabási 2002; Newman 2003), characterising network structure. L is calculated as the mean number of connections in the shortest path between two individuals in the network (see Newman 2003). L describes a global property of the network, and may be used to give a simple indicator of how quickly social information and socially transmissible diseases will spread in an animal population (e.g. in a population of a given size, disease can be expected to spread more quickly for lower values of L). C is a measure of the cliquishness of the network, calculated as the mean fraction of all possible connections that occur in the local neighbourhood (see Newman 2003). C describes an

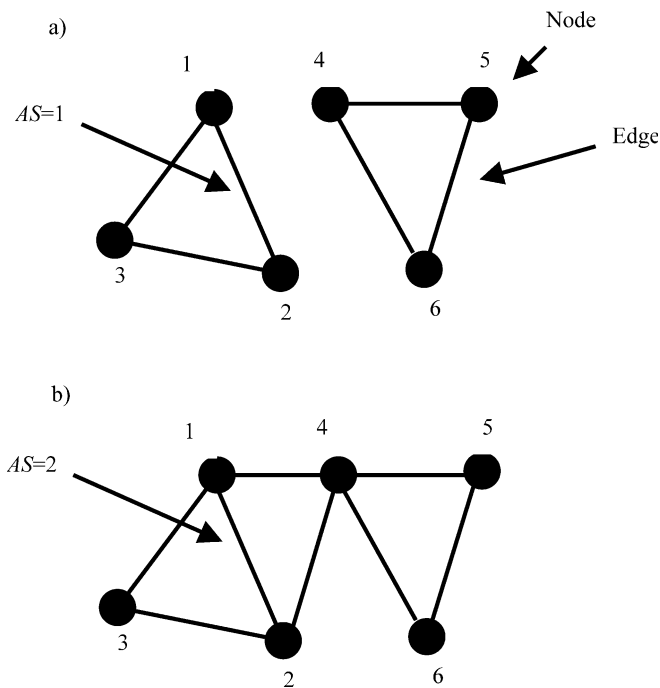


Fig. 1 Building a network from mark-recapture data in a group-living animal species. Animals are represented as dots (nodes) and interconnected by a line (edge) if they were found together in the same group. In a population of 6 marked and released individuals, two groups are caught on day 1 and one group on day 2. Superimposing the data from day 2 onto day 1 interconnects the whole population. As pairs of individuals are recaptured in the same group their AS increases. For example, individuals 1 and 2 were captured in the same group on both days 1 and 2, giving them an AS of two on day 2. The values of the associated network descriptors are displayed. Day 1: 2 groups, (1 2 3) (4 5 6), $L=1$, $C=1$, $k=2$. Day 2: 2 Groups, (1 2 4), $L=1.6$, $C=0.778$, $k=2.667$

average local property of the network, and is of particular interest because it measures the extent to which two of one's network neighbours are themselves neighbours; in social animals this local structure may be due to active associations (e.g. phenotype assortment or associations between familiar individuals). The degree of an individual (from which k is derived) is simply the number of direct social connections (edges) that an individual has (Fig. 1). The mean degree for the network (k) is then calculated as the average of the individual degrees. Together values of L , C and k can be used to describe the structural properties of the network (see Watts and Strogatz 1998).

Recent work on both fish (guppies, *Poecilia reticulata*) (Croft et al. 2004a) and dolphins (*Tursiops truncatus*) (Lusseau 2003), suggests that wild animal populations are characterised by non-random social network structure. In particular, networks appear to have relatively short path lengths (small L values) whilst being highly structured (large C values) (Croft et al. 2004a). Very little is known about the factors underlying this structuring. For example, the extent to which assortative interactions based on phenotype (e.g. size and sex) influence network structure in animal populations remains largely unexplored. Individuals in social networks may also assort by their social tendencies; it is well documented that social networks in humans are generally characterised by a positive degree correlation (Newman 2003), whereby individuals with a high degree are connected to others with a high degree, and vice-versa (see Fig. 2). However it is largely unknown to what extent animals assort by degree. The nature of the degree correlation within a population will have potentially important implications for the transmission of information and disease. For example, a pathogen can be expected to spread very quickly between all individuals with high degree in a population with positive

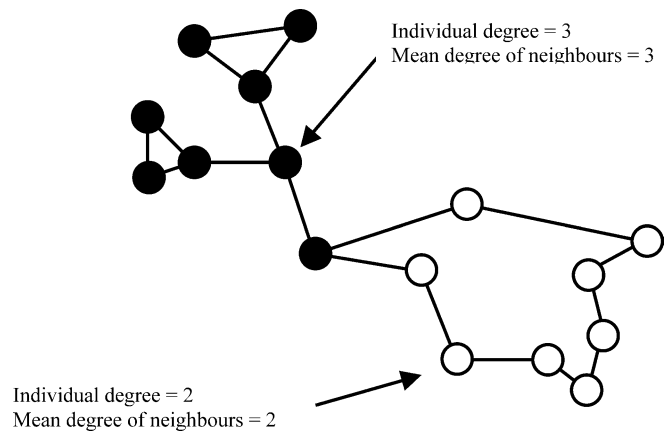


Fig. 2 A toy network that exhibits a positive degree correlation, whereby individuals directly interact with others with a similar degree (filled circle degree=3 (i.e. individuals are connected to three other individuals), open circle degree=2, k (mean degree)=2.5)

degree correlation, leading to an extremely virulent epidemic.

A major constraint with previous investigations into the structure of social networks in wild animal populations (e.g. Croft et al. 2004a; Lusseau 2003) is that they lack replication, making it difficult, if not impossible, to draw any general conclusions. In the current investigation, we present data on the network structure of multiple populations of the guppy and one population of three-spined stickleback (*Gasterosteus aculeatus*), giving insight into the generality of social network structure in fish populations.

To probe the role of assortative mixing in influencing network structure, we investigate assortative interactions both as a function of body length and individual degree in the fish networks. Given the adaptive benefits of phenotypic assortment (see above), we predict that individuals will directly associate in the network with others of a similar body length. We investigate assortative mixing by degree by plotting the degree correlation (in which the degree of each individual is correlated with the mean degree of its immediate network neighbours (Pastor-Saorras et al. 2001)) (see Fig. 2). However, as the mechanisms underlying assortative mixing by degree are not truly understood (Newman 2003), no directional prediction can be made in this regard for these populations.

Finally, we investigate how the composition of the network changes with increasing ‘‘association-strength’’ (AS, defined below) between pairs of animals, both as a function of body length and sex. Male guppies are known to move between pools (populations) more than females (Croft et al. 2003b), and this movement is thought to be adaptive allowing males to search for mating opportunities with novel females that are more receptive to their mating attempts (Farr 1977; Hughes et al. 1999). Thus, we predict that if we construct networks in which edges exist only if their AS exceeds some chosen threshold, the fish involved in these networks will become female-biased as the threshold is raised. Furthermore, we investigate the tendency for individuals to form persistent pair-wise interactions, predicting that social interactions between individuals will be stable, thus facilitating the development of familiarity (and its associated benefits, see above).

To test these predictions, we conducted a number of mark release and recapture investigations, individually tagging fish and recording their shoal companions on a daily basis. From this information we were able to construct social networks for the populations that allow us to extract information on the social organisation of the populations.

Materials and methods

Study species

Both guppies and sticklebacks are particularly suitable as models for the application of network theory to

describe social structure for several reasons. Firstly, both are classic models in evolutionary and behavioural biology (Magurran et al. 1995; Milinski 1987; Ranta and Lindström 1990; Ward et al. 2002) and as a result much is known about their behaviour and ecology (see Bell and Foster 1994; Houde 1997). Furthermore, both species can be given individual identification marks, exhibit limited spatial movement and are easily recaptured (Croft et al. 2003a; Ward et al. 2002), allowing us to monitor social interactions over extended time periods.

Population sampling

Guppies

All adult guppies were captured from four pools (Table 1) in the Arima river (within 500 m of Verdant Vale Village, 10°41'N, 61°17'W) in the Northern Mountain Range of Trinidad during May 2002 (pools 1 and 2) and 2003 (pools 3 and 4). Adult fish were captured by making three passes in each pool using a 2-m beach seine (mesh size = 2 mm). In a previous investigation Croft et al. (2003a) demonstrated that this sampling technique was highly effective, with population estimates using MICROFISH 3.0, (Van Deventer and Platts 1983; 1985) not differing from the total catch in five pools after three sampling passes. After capture, each population was kept in a separate holding pool (diameter = 160 cm, water depth = 15 cm) for marking purposes. Guppies were given individual identity marks by injecting different colours of visible implant fluorescent elastomer (VIE) in two of six positions on the dorsal area (for details of marking technique see Croft et al. 2003a). In a control experiment guppies marked with VIE exhibited 1.25% (one fish) tag loss and low mortality (6.25%, five fish) over an 8-day period (see Croft et al. 2003a). Furthermore, the presence of the identification mark did not have a significant effect on shoal choice behaviour (Croft et al. 2004a).

All fish from a pool were simultaneously released into the centre of their original pool 24 h after capture. Resampling began 24 h after release and was undertaken once per day between 1000 and 1400 hours for a period of 7 days. However, for population 1 it was not possible to carry out the resampling procedure on one of the days (day 5) because the river was flooded. During

Table 1 Pool dimensions for each of the four populations of guppies. Also presented are the number of males and females captured per pool

Population	Length (m)	Width (m) (max)	Depth (m) (max)	♀	♂
Guppy pool 1	10	5.3	0.31	72	75
Guppy pool 2	14.6	6	0.48	77	46
Guppy pool 3	14	6.6	0.54	81	29
Guppy pool 4	23	6.9	0.56	77	66

each resampling event entire shoals were captured from the pools using a 2-m beach seine (see Croft et al. 2003b for details). Shoals were only released back into the pool after the composition of all shoals had been recorded.

Sticklebacks

Nine shoals of three-spine sticklebacks were captured during September 2001, using a two-person beach seine (see Ward et al. 2002 for details), from a 90-m straight stretch of the main inflow channel to Morice Lake (near Sackville, New Brunswick, Canada, 45°55'N, 64°21'W) (see Ward et al. 2002 for further details of the study site). Shoals were visually identified prior to capture and only shoals where both observers were satisfied that the entire shoal had been captured were used in the investigation. All fish in the nine shoals ($N=101$) were individually marked in the field using the method described by Ward et al. (2002), whereby fish were tagged with unique tags using a small section of Tygon laboratory tubing placed on the anterior dorsal spine. Fish were released at the point of capture immediately after all fish in the shoal had been tagged. In a control experiment, sticklebacks marked with the above method exhibited 0% tag loss and no mortality over a 5-day period (Ward et al. 2002). The presence of the tubing tag did not have a significant effect on shoal choice behaviour, with untagged test fish exhibiting no preference when presented with a choice between a tagged and an untagged stimulus fish (Wilcoxon test, $N=12$, $z = -0.39$, $P=0.695$).

Shoals were recaptured over a 5-day period between 0900 and 1600 hours, within a 15-m long stretch of the main inflow channel, where shoals frequently encounter each other (Ward et al. 2002), creating the potential for considerable exchange of individuals between shoals. The identities of all tagged fish captured in a shoal were recorded, and shoals were released back into the experimental area only after the composition of all shoals had been recorded.

Building social networks

The social networks we considered were constructed from the membership of the recaptured shoals (where a shoal is defined as two or more fish within four body lengths (see Croft et al. 2003b)), and accumulated over the 7 days of the experiment (Fig. 1). A direct network edge was taken to exist between a given pair of fish if those fish were ever caught together in the same shoal (see Croft et al. 2004a). The AS of each pair (edge) was defined as the number of days on which that pair were caught together in a shoal (Fig. 1).

Characterising social network structure

Most conventional measures of network structure (Albert and Barabási 2002) have been developed for the

analysis of unweighted networks, in which the AS of all existing pair-wise connections between fish is given unit strength, irrespective of how many times that pair was found together. In the interests of consistency, we constructed unweighted networks for each of our five populations. From these networks we calculated standard network measures, including path length (L) clustering coefficient (C) and mean degree of connectedness (k) (see above). We compared the observed network values of L and C to the values calculated for a network containing the same number of social connections, but with the connections placed randomly between agents (see Watts and Strogatz 1998), highlighting the extent to which the observed network deviated from that expected by random interactions between individuals.

Assortative interactions in social networks

We investigated the extent of assortative mixing in the networks both as a function of degree and body length. We measured the degree correlation in our fish population by correlating the degree of each individual with the mean degree of its network neighbours (Pastor-Saorras et al. 2001) (see Fig. 2). Similarly, we investigated the role of body length in structuring social interactions in the network by correlating the mean body length of the network neighbours of an individual with the body length of that individual.

The standard network measures described above are based on unweighted ties between individuals and thus do not allow us to analyse features of the network as a function of association-strength. Initially, we investigated if the composition of the network changes as a function of AS. For example, it may be that associations at a higher strength are largely the result of individuals of a certain size or sex interacting together. To investigate this, we calculated the median body length of individuals and sex composition of the network (percentage males) at $AS \geq 1$, ≥ 2 and ≥ 3 .

Repeated pair-wise interactions

To calculate the persistence of pair-wise interactions, we denote all pairs with $AS \geq 3$ as “persistent” ($AS=7$ is the maximum value when defining persistent pairs in the current investigation). To test for the repeated co-occurrence of pairs of fish, we compared the observed number of persistent pairs ($AS \geq 3$) in each population to the expected value from a null model of shoal membership. To generate these expected values, marked fish were reallocated at random to the observed recaptured daily shoal sizes (see Ward et al. 2002), and the weighted social network for each “random catch” constructed and analysed. This operation was repeated 1,000 times to provide expected frequency distributions of our test statistic. P -values were obtained by

comparing the expected values for pair-wise interactions with three or more ties with the observed ones (see Crowley 1992).

Results

Characterising social network structure

Substantial proportions of fish were recaptured at least once in each population (between 60% and 90% Table 2). Unweighted networks were constructed for each population. As an example, the social network for guppy population 1 consists of a giant connected component (GCC) containing $N=134$ of 136 fish recaptured, plus one isolated network (consisting of two fish). The GCC network is sparse, containing 1,465 different connections (E) out of a possible 8,911 (E_{\max}), yet highly structured, a trend that is consistent across all five populations (Table 2).

From the GCCs, standard network measures were calculated for each population (Table 2). For example, in guppy population 1, $L=2.04$ (i.e. on average any two fish out of $N=134$ can be connected via 2.04 others), $C=0.64$ indicating high cliquishness, and k (the average number of conspecifics a fish is directly connected to, see Fig 1) is 21.9. Values of L and C are consistent across populations and between species with $L \geq 2$ and $C \geq 0.5$ (Table 2).

Table 2 Standard network values for each population. N_{total} is the number of individuals marked and released. $\%_{\text{recap}}$ is the proportion of individuals recaptured one or more times. N is the total number of fish connected in the GCC. E_{\max} is the maximum number of possible connections in the network ($E_{\max}=1/2 N(N-1)$) and E is the observed number of different connections in the network. L is mean path length, C is the clustering coefficient and k is the mean degree (mean number of total connections per

Population	N_{total}	$\%_{\text{recap}}$	N	E_{\max}	E	k	L	L_{rand}	C	C_{rand}	NP	P
Guppy 1	147	92	134	8,911	1,465	21.9	2.04	1.59	0.64	0.16	5	0.62
Guppy 2	123	82	99	4,851	726	14.7	2.34	1.71	0.77	0.15	29	<0.001
Guppy 3	110	96	97	4,656	837	17.3	2.00	1.61	0.57	0.18	9	0.11
Guppy 4	143	93	133	8,778	1,511	22.7	2.01	1.60	0.60	0.17	9	0.07
Sticklebacks	110	67	94	4,371	1,325	28.2	2.05	1.36	0.87	0.3	6	0.02

Table 3 The recapture profile of each population, showing the frequency at which individuals were captured. Also shown are the results of Spearman correlations of the degree of each individual with the mean degree of its network neighbours (see Fig. 2), their

Population	Number of times recaptured							N	Mean degree	Recapture frequency	Mean shoal size
	1	2	3	4	5	6	7				
Guppy 1	32	26	28	29	11	8		134	$r_s=0.66 P<0.001$	$r_s=0.48 P<0.001$	$r_s=0.74 P<0.001$
Guppy 2	43	32	5	4	7	7	1	99	$r_s=0.70 P<0.001$	$r_s=0.84 P<0.001$	$r_s=0.67 P<0.001$
Guppy 3	14	19	22	16	13	9	4	97	$r_s=0.28 P<0.005$	$r_s=0.79 P<0.001$	$r_s=0.50 P<0.001$
Guppy 4	20	34	24	36	15	3	1	133	$r_s=0.50 P<0.001$	$r_s=0.80 P<0.001$	$r_s=0.62 P<0.001$
Sticklebacks	40	30	16	8				94	$r_s=0.66 P<0.001$	$r_s=0.43 P<0.001$	$r_s=0.76 P<0.001$

Also shown in Table 2 are the values of L and C that would be expected of networks with the same N , k and number of pair-wise connections, but with E connections entirely randomised between fish. In each population the observed values of L are close to random whilst the observed values of C are substantially larger than random.

Assortative interactions in social networks

The degree correlation was positive for all five populations (Table 3). Note, however, that k was also positively correlated with the recapture frequency of fish and their shoaling tendency (Table 3). A positive correlation was also observed between the body length of an individual and the mean body length of its network neighbours in all four guppy populations (Fig. 3). However, it should be noted that body length data was unavailable for some individuals (population 1: $N=6$, population 2: $N=3$, population 4: $N=3$). This trend was not analysed for the population of sticklebacks due to a large proportion of body length data missing ($N=25$).

Association strength did not have a significant effect on the body length composition of the network in any population (see Table 4). Furthermore, overall AS did not have a significant effect on the sex composition of the network across the guppy populations (Friedman Test $df=2$, $\chi^2=2$, $P=0.37$, see Table 4).

individual). Also presented are the expected values of L (L_{rand}) and C (C_{rand}) assuming random interactions between individuals in the network (see Watts and Strogatz 1998 for details). NP is the observed number of pairs caught 3 or more times per populations. Also presented is the probability (P) that the observed number of pairs caught 3 or more times was greater than the expected value, based on a null model built on random shoal membership

respective recapture frequency (no. of times a fish was re-caught over the 7 days) and the shoaling tendency (mean shoal size a fish was found in over the sampling period)

Table 4 The median (\pm inter-quartile range) body length of individuals and the sex composition (percentage males) of the network at different association strengths. Also shown are the results of Kruskal Wallis tests comparing median body length of the network as a function of AS in the networks

Population	AS \leq 1		AS \geq 2		AS \geq 3		Kruskal-Wallis test
	Body length (mm)	Males (%)	Body length (mm)	Males (%)	Body length (mm)	Males (%)	
Guppy 1	24 (-22, +29) N=128	48.43	23.5 (-25, +30) N=64	45.31	27 (-21.7, +32) N=8	25	$\chi^2 = 0.38, df=2, P=0.83$
Guppy 2	24 (-22, +30) N=99	33.33	24 (-22, +28.2) N=36	36	23.5 (-22, +25.75) N=12	41	$\chi^2 = 0.23, df=2, P=0.9$
Guppy 3	23 (-21, +26) N=97	28	23 (-21, +26) N=61	21	26 (-22, +31) N=15	13.33	$\chi^2 = 5.16, df=2, P=0.08$
Guppy 4	23 (-21, +27) N=133	45.9	24 (-21.5, +30.5) N=84	39.3	27 (-23, +34) N=17	23.5	$\chi^2 = 4.6, df=2, P=0.10$
Sticklebacks	41 (-36, +45) N=69	—	42.5 (-38, +45) N=40	—	43 (-41, +44.25) N=7	—	$\chi^2 = 0.2, df=2, P=0.91$

Repeated pair-wise interactions

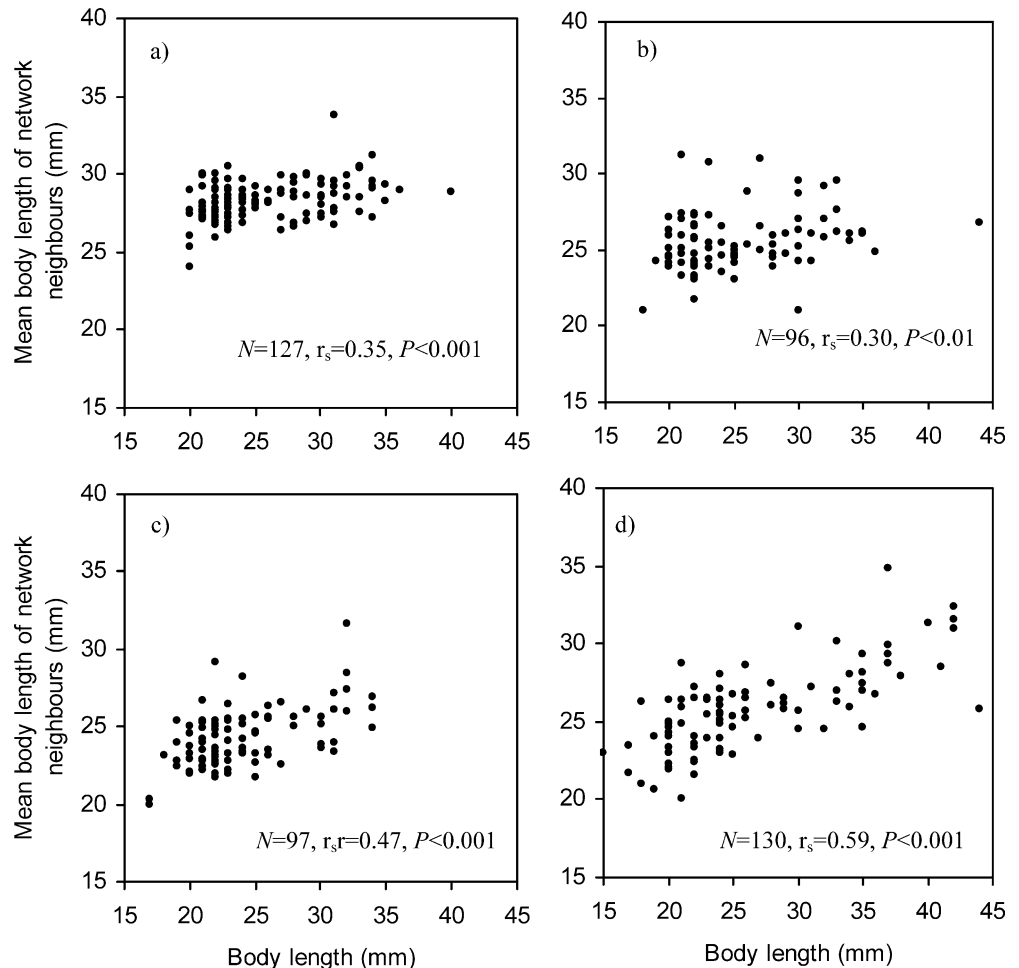
Persistent pairs were observed much more frequently than expected (using the null model of random recapture outlined above) in one of the guppy populations (population 2) and in the stickleback population (Table 2). An overall analysis that combined the data for persistent pairs for all four guppy populations revealed that there is a general trend for persistent pairs to occur more frequently than expected (Fisher's omnibus test $N=4$, $df=8$, $\chi^2=20.5$, $P<0.01$).

Discussion

Substantial proportions of marked fish were recaptured in each population (both in guppies and sticklebacks), the vast majority of which were socially interconnected. However, despite the frequency of fish being captured three or more times, only a small proportion of the total possible pair-wise connections between individuals existed, indicating that the networks were highly structured. The observed values of L and C in all populations are consistent with the "small world" phenomenon, in that the network is highly structured (the observed values of C much larger than the random), but with an average path length close to that expected in a random network. The small world phenomenon ("six degrees of separation" Milgram 1967) has been found in a diverse array of systems including biological, technical, and social networks (Watts and Strogatz 1998). The small world characteristics described here will contribute to the rapid transmission of social information through the populations (Latora and Marchiori 2001). However, the increased rate of information transmission may come at the cost of an increased rate of disease transmission (Watts and Strogatz 1998). Although the composition of the network did not change with a change in AS, we found significant pair-wise interactions in the networks, a finding that fulfils a pre-requisite for the evolution of reciprocity (see Dugatkin 1997).

A number of factors may have contributed to the observed non-random structure in the unweighted networks. Firstly, we observed a positive degree correlation in all populations (whereby individuals are connected to others with a similar degree, see Fig. 2), which may result from individuals with a strong shoaling tendency being associated with others that shoal strongly. Positive degree correlations have been reported from human social networks, such as co-authorships on scientific papers and email address books (Newman 2003). In contrast metabolic networks, food webs and neural networks tend to exhibit a negative degree correlation (Newman 2003). The mechanisms underlying these patterns are not yet fully understood and provide an interesting field for further investigations. The observed positive degree correlation will have implications for the transmission of information and disease in the

Fig. 3 The mean body length of the network neighbours of an individual plotted against the body length of that individual (**a** guppy 1, **b** guppy 2, **c** guppy 3 and **d** guppy 4). Also shown are the results of Spearman rank correlations



populations affecting, for example, the speed with which a pathogen could spread.

Secondly, assortative interactions based on body length were observed in the networks, with individuals being more likely to interact with others of a similar body length. The body length assortment of fish shoals is well documented across a range of species (see Krause et al. 2000). However, this is the first investigation to illustrate how assortative interactions based on body length influence interactions in a social network. Such assortment may confer important adaptive benefits (see above). Body length assortment in the network may result from both passive and active mechanisms. For example, active choice for shoal mates of a similar body length has been demonstrated in many fish species (see Krause et al. 2000) including guppies (Croft et al. 2003b; Lachlan et al. 1998). However, the phenotypic assortment of social groups will also be dependent on the distribution of individuals in the habitat (Croft et al. 2003c). There is evidence that guppies have habitat preferences that correlate with both body length and sex, with larger individuals, in particular large females, occupying deeper water (Croft et al. 2003b; Croft et al. 2004b), thus providing a potential passive mechanism for generating assortative interactions based on body

length. Understanding the relationship between the spatial network (i.e. the distribution of individuals in the habitat) and the social network is an exciting area for future research.

Within the weighted networks no significant effect of association strength was found on network structure either as a function of body length or sex, despite the tendency for male guppies to show higher movement rates than females (Croft et al. 2003a). Repeated interactions (at $AS \geq 3$) in the weighted networks were observed to be significantly different from that expected by random associations in both guppies and sticklebacks. In both species shoals encounter each other frequently (Croft et al. 2003b; Ward et al. 2002), and break down at dusk and reform at dawn (Croft et al. 2003b). Thus the repeated co-occurrence of pairs exists despite the opportunity for extensive mixing of individuals between shoals. The occurrence of stable pairs is thought to be an important pre-requisite for the evolution of co-operative behaviour (Milinski 1987; Milinski et al. 1990), which has been investigated in both species in the form of predator inspection (Dugatkin 1988; Milinski 1987). However, the role of active choice (or avoidance) in generating persistent pair-wise interactions in the field remains unknown (evidence from laboratory

experiments suggests that pair-wise persistence could be based on active choice (Croft et al. 2004a)). Future investigations should explicitly test for active partner preference between persistent pairs that occur in the field. For example, by using a binary choice test, whereby a test fish is giving a choice between its observed partner and a phenotypically similar partner from the same location with which it rarely or never associates.

The potential for individual recognition may be constrained by the total population size. For example, Griffiths and Magurran (1997) demonstrated that guppies appear to remember approximately 30 other individuals. Although in the current investigation population size exceeded 30 individuals in each case, guppies directly interacted with a limited number of others in the network, between 15 and 22 (Table 2). Thus it is possible that all guppies that are directly connected in the networks are familiar with each other. However, further work is required to establish if this number remains stable over longer time periods.

The application of network theory to the social networks of animal populations is an exciting area for future research. Here, we show how network theory may be used to investigate assortative interactions in animal populations, an understanding of which will have implications for a variety of important issues. For example, an understanding of the topology of social networks in wild populations may allow us to make predictions regarding patterns of co-operative behaviour (Abramson and Kuperman 2001), and the social transmission of information (Latora and Marchiori 2001) and disease (Watts and Strogatz 1998) through populations.

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