

# Social networks in the guppy (*Poecilia reticulata*)

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Recd 10.03.04; Accptd 09.04.04; Published online 11.06.04

**Social network theory is used to elicit details of the social structure of a population of free-ranging guppies, *Poecilia reticulata*. They were found to have a complex and highly structured social network, which exhibited characteristics consistent with the ‘small world’ phenomenon. Stable partner associations between individuals were observed, a finding that fulfils the basic prerequisite for the evolution of reciprocal altruism. The findings are discussed in relation to the ecology and evolution of the wild population, highlighting the potential application of network theory to social associations in animals.**

**Keywords:** information transmission; reciprocal altruism; group living; social organization; shoaling

## 1. INTRODUCTION

Network theory, used to describe the local and global properties of many interconnected agents, is highly interdisciplinary, attracting the attention of, among others, mathematicians, sociologists and physicists (Newman 2003b). However, there have been very few attempts to use network theory to investigate social associations between animals (see Lusseau (2003) for an exception), despite its potential to deliver quantification of inter-individual associations within and between groups, spanning the population as a whole. A network approach may help to further our understanding of the social organization of animal populations, particularly those that are characterized by high rates of inter-group exchange and unstable group structure.

A network is simply a graph consisting of nodes connected by edges (see figure 1). The edges can represent any interaction (or association) between two nodes. In this study, each node represents a free-ranging guppy (*Poecilia reticulata*) and each edge a social association between two guppies. Our network was built by monitoring daily (for 7 days) the shoal membership of a population of individually marked fishes. We present conventional quantitative measures on this network, which reveal both local and global network properties of the guppy population. Furthermore, we tested whether frequent pairwise associations between guppies occurred more often than expected from a randomized daily catch. Guppy shoals are usually small (2–20 fishes) and encounter each other approximately every 14 s. They also disperse overnight, resulting in the breakdown of shoal composition and a reassembly every

morning (Croft *et al.* 2003b). Thus any non-random social structure found in a network constructed cumulatively over multiple days would exist despite the potential for complete and rapid mixing of all individuals.

Persistent pairwise associations are of particular interest because repeated associations are thought to be important in the development of familiarity, which can confer a number of important advantages such as reduced food competition and increased predator evasion (see Griffiths 2003). Furthermore, repeated associations between pairs are the basic requirement for the evolution of reciprocal altruism (Milinski 1987). In a separate part of the study we tested whether the observed pairwise associations may be based on active choice.

## 2. MARK-RECAPTURE METHODS

All adult guppies ( $n = 123$ ; 46 males and 77 females) were captured from a pool (length of 14.6 m; maximum width of 6 m; maximum depth of 48 cm) in the Arima River (Verdant Vale Village, Northern Mountain Range, Trinidad). They were kept together in one holding tank and given individual identity marks by injecting different colours of visible implant fluorescent elastomer (VIE) in two out of six dorsal positions (for details of the 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%) over an 8-day period.

To control for the potential effect of the identification mark on shoal-choice behaviour we gave individual test fish a choice between two size-matched ( $\pm 1.5$  mm) stimulus shoals (see electronic Appendix A for details of the experimental design). One shoal contained four marked fish and the other four sham-injected fish. No significant preference for marked or sham-injected fish was observed ( $t$ -tests,  $n = 15$ ,  $p > 0.05$ ).

As a further control, we captured 21 shoals of adult guppies from the Arima River and recorded the sex and body length of each fish. The body length variation within shoals in this sample ( $n = 21$ ) was not greater than that expected by random assortment, either for the combined male and female data (randomization test: 1000 simulations, Fisher’s omnibus test  $f_{42} = 37.33$ ,  $p > 0.05$ ), or for either sex analysed independently (males: randomization test: 1000 simulations, Fisher’s omnibus test  $f_{42} = 5.67$ ,  $p > 0.05$ ; females: randomization test: 1000 simulations, Fisher’s omnibus test  $f_{42} = 5.32$ ,  $p > 0.05$ ).

In the mark–recapture experiment, all fish were released simultaneously into the centre of the original pool 24 h after capture. Resampling began 1 day after release and was undertaken once per day ( $\pm 2$  h of midday) for 7 days. Each day entire shoals were captured from the pool using a beach seine (see Croft *et al.* 2003b). Shoals were returned to the pool only after the composition of all shoals had been recorded. For release, all shoals were combined into one bucket and released together in the centre of the pool thus randomizing shoal composition once a day.

After 7 days a total of 101 (35 males and 66 females) out of 123 marked fish had been recaptured at least once, consistent with the expected emigration rate of *ca.* 20% in guppies (Croft *et al.* 2003a). All fish that were found together in a shoal (defined as two or more fish within four body lengths; see Croft *et al.* 2003b) were deemed to have a direct network connection. This assumption is based on the fact that guppy shoals are sufficiently small (Croft *et al.* 2003b) to allow all individuals in a shoal to interact directly, and the evidence of Griffiths & Magurran (1998) who showed that wild female guppies were ‘familiar’ with their shoal companions.

## 3. STANDARD NETWORK ANALYSIS

The network of connections after 7 days (counting each co-occurrence of a pair only once) for the population is shown in figure 1a. It consists of a ‘giant connected component’ (GCC) containing nearly all ( $n = 99$  out of 101) captured fish, plus two isolated males. The GCC is sparse, in that only 726 out of a possible 4851 edges ( $= 1/2n(n-1)$ ) exist, yet it is highly structured. Figure 2a illustrates how the final network built up over time. On day 1, 12 shoals were caught, so the social network contains 12

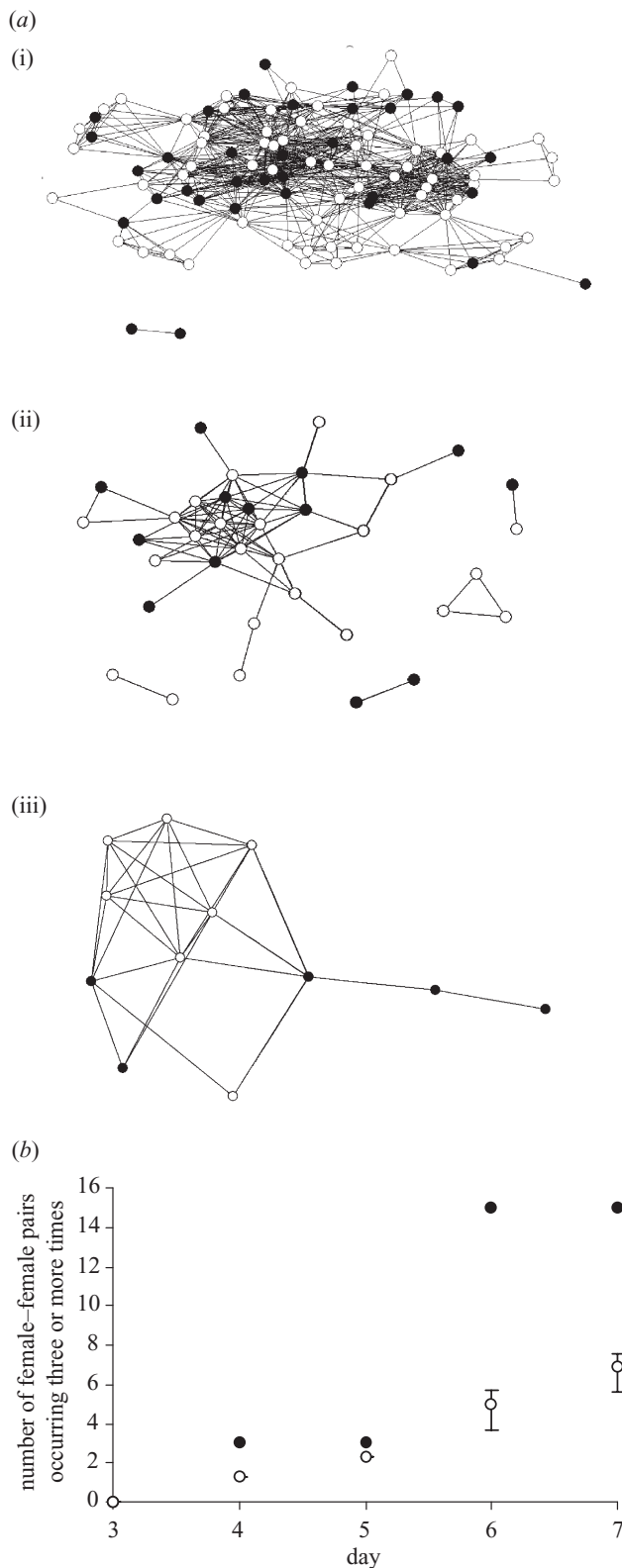


Figure 1. (a)(i) The social network after 7 days of resampling (males, filled circles; females, open circles) drawn using the UCINET program (Borgatti *et al.* 2002), using spring embedding based on distance. Sub-networks are shown for different association strengths in which connections are displayed between two fish only if they were caught in the same shoal: (ii) at least twice; and (iii) at least three times. (b) The temporal build-up of the number of female–female persistent pairs. Observed values, filled circles; medians ( $\pm$  inter-quartile ranges) of the number of female–female persistent pairs in 1000 simulations (open circles, see § 4).

completely connected and isolated sub-networks. By day 2, a GCC already exists, spanning most of the 101 fish.

Figure 2*b* shows ‘standard’ network measures (Newman 2003*b*) of the GCC for each day, namely the mean degree ( $k$ ), the average cluster coefficient ( $C$ ) and the average path length ( $L$ ). The ‘degree’ of an individual node (fish) is the number of edges joined to it. The average degree for all nodes is  $k$ . Knowledge of the degree of an individual can, for instance, be important in predicting the probability that a learning innovation will spread through a population. If the innovator is highly connected, the probability that the innovation will spread in the network will be greater than if the individual has a low degree. The geodesic between any two nodes is the smallest number of edges by which one node can be reached from the other.  $L$  is the average geodesic (measured in network edges), the average being taken over all possible pairs of nodes.  $L$  is a global network measure, and is of particular interest because it can illustrate the speed at which disease and information will spread through an animal population. For example, in a population of a given size, a short mean path length ( $L$ ) indicates that individuals in the network are closely interconnected, resulting in rapid transmission. Finally, the average clustering coefficient ( $C$ ) is a local measure of cliquishness. If a chosen node has  $m$  nearest neighbours, that neighbourhood contains a maximum  $1/2m(m-1)$  edges. The fraction of these edges that actually exists in the network defines the cliquishness of our node, and  $C$  is found by averaging over all nodes. The cluster coefficient is of particular interest because high values ( $C$  must lie between 0 and 1) illustrate a deviation from a randomly wired network, which in social animals may be owing to association preferences (e.g. phenotype assortment or associations between familiar individuals). Knowledge of  $C$  may also contribute to our understanding of population susceptibility to epidemics. For example, Newman (2003*a*) found that high levels of clustering decrease the spread of epidemics because the infection will be largely contained among a few individuals that are highly interconnected with each other, as opposed to spreading globally to all reaches of the network.

As figure 2*b* illustrates, after 3–4 days  $L$ ,  $C$  and  $k$  remain relatively stable. The final network GCC on day 7 has  $L = 2.34$ ,  $C = 0.77$  and  $k = 14.7$ . Also shown in figure 2*b* are the values of  $L$  and  $C$  that would be expected of a network with the same  $n$ ,  $k$  and number of pairwise connections, but with connections placed randomly between fish (see Watts & Strogatz (1998) for details).

#### 4. ANALYSIS OF WEIGHTED NETWORKS

Standard network theory is primarily based on unweighted associations between individuals and thus does not allow the analysis of the biological feature of most interest, which is the occurrence of stable pairs of fish in wild populations. To measure the persistence of pairwise associations, we used an ‘association strength’ (AS), which indicates the number of days (out of seven) that a pair of fish was caught together in a shoal. Figure 1*a* shows the sub-networks formed by considering  $AS \geq 2$  and  $AS \geq 3$ . We denote all pairs with  $AS \geq 3$  as ‘persistent’.

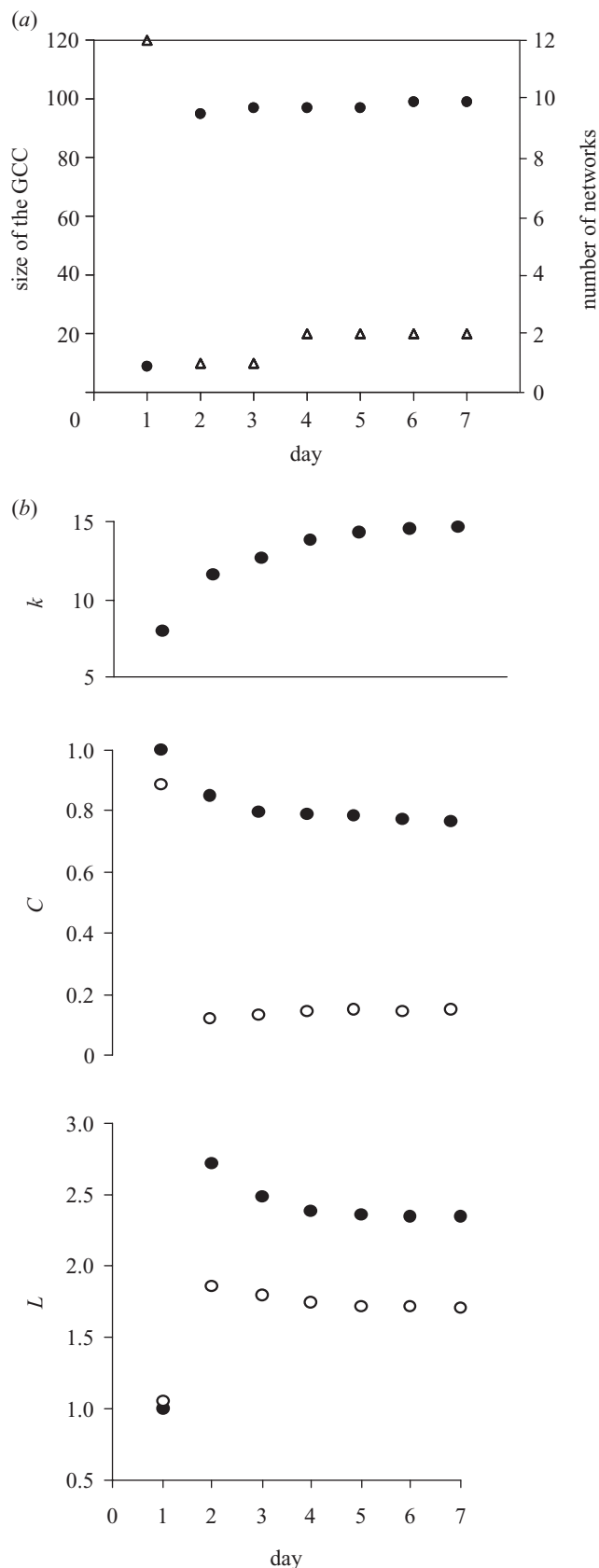


Figure 2. The development of social networks with time. (a) The number of networks in the population (open triangles) and the size of the GCC (filled circles). (b) The mean degree ( $k$ ), average clustering coefficient ( $C$ ) and average path length ( $L$ ) of the GCC. See § 3 for details. Filled circles, observed values of  $L$  and  $C$ ; open circles, values for an equivalent randomly wired network.

To test the significance of the observed number of persistent ( $AS \geq 3$ ) pairs we compared it with the expected number assuming random associations between individuals. In our model, marked fish were re-allocated at random to the observed recaptured daily shoal sizes (thus controlling for shoal size). This operation was repeated 1000 times to provide the expected frequency distributions of our test statistic. The  $p$ -values were obtained by comparing the expected values for persistent pairs with the observed ones.

From day 6 persistent pairs were observed much more frequently than expected (randomization test at days 6 and 7: 1000 simulations,  $p < 0.01$ ; figure 1b). Further analysis reveals that only female–female associations were significantly persistent (day 7: female–female,  $p = 0.01$ ; male–male,  $p = 0.37$ ; female–male,  $p = 0.24$ ).

## 5. DISCUSSION

We found the final guppy network GCC to be highly structured, with a mean degree  $k = 14.7$ , indicating that individuals are directly connected to *ca.* 15% of the network. Furthermore, the social network constructed for this population of wild guppies is consistent with our having a ‘small world’ network (Watts & Strogatz 1998), whereby the observed path length ( $L$ ) is almost as short as that expected in a random network, whereas the observed cluster coefficient ( $C$ ) is much larger than that of the corresponding random network (figure 2b). The occurrence of a small world is of particular interest because the short path length in a highly structured network is associated with a rapid transmission of information and disease through a population (Watts & Strogatz 1998). Also, it should be noted that the measured values of  $L$  and  $C$  are not simply drifting towards those of a completely interconnected network of  $n$  agents (figure 2b), as might be expected from the cumulative construction of pairwise associations over several days. This is partly owing to emigration of fish during the experiment, but may also reflect a stable network structure, which may be influenced by factors such as habitat use, site fidelity and the active choice of social partners in the daily reassembly of shoals. These issues warrant further study.

Although persistent pairwise associations were infrequent in the wild population, they were significant between females. Our findings are unlikely to be entirely explained simply by size sorting, as the size composition of adult guppy shoals was not different from random. Furthermore, the findings of our laboratory investigation, where we controlled for active preference/avoidance of individuals based on phenotype (size and sex; see electronic Appendix A) suggests that persistent pairs are likely to be based on an active preference, at least in females. Repeated pairwise associations are thought to be an important prerequisite for the evolution of cooperative behaviour, which has been investigated in the guppy in the form of tit-for-tat predator inspection (see Dugatkin 1997). The presence of persistent female–female pairs suggests that there is the potential for the development of cooperation between females in the wild population.

In conclusion, we document the social network structure for one population, and thus do not illustrate the general network patterns in guppies or indeed fishes in general.

However, we do illustrate the use of this exciting new technique for the analyses of social associations in wild animals.

### Acknowledgements

D.P.C. was supported by a Frank Parkinson scholarship, University of Leeds. The authors are very grateful to the three referees whose constructive comments greatly improved this manuscript.

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