Social networks in elasmobranchs and teleost fishes

A D M Wilson[1], D P Croft[2] & J Krause[1,3]

[1]Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, 12587 Berlin, Germany; [2]Centre for Research in Animal Behaviour, College of Life and Environmental Sciences, University of Exeter, Exeter, EX4 4QG, UK; [3]Department for Crop and Animal Sciences, Humboldt-University of Berlin, Philippstrasse 13, 10115 Berlin, Germany

Abstract

Over the last decade, there has been an exponential increase in studies using social network analysis to describe the structure of animal societies. In this synthesis, we examine the contribution of social network analysis towards developing our understanding of the social organization of elasmobranchs and teleost fishes. We review and discuss the current state of knowledge of the mechanisms and functions underpinning social network structure in fishes with particular emphasis on cooperation, familiarity, site fidelity, population structure and the welfare of captive populations. We also discuss important methodological issues (e.g. how to identify and mark fish) and highlight new developments in this area of research and their implications for the study of fish behaviour. Finally, we outline promising future research areas for the application of social network analysis to teleost fishes and elasmobranchs.

Correspondence:
A D M Wilson
Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, 12587 Berlin, Germany
Tel.: 49 (0)30 64181 719
Fax: 49 (0)30 64181 750
E-mail: alexander.wilson@ymail.com

Introduction

Over the last three decades, there has been an increasing recognition that understanding the social fine structure of animal populations (who interacts with whom) is fundamental for understanding ecological and evolutionary processes in natural populations (Krause *et al.* 2007, 2009a; Wey *et al.* 2008; Sih *et al.* 2009). For example, at

the individual level, animal interactions have important consequences for predator avoidance, access to resources and mates, as well as exposure to information and disease (Croft *et al.* 2008; Krause *et al.* 2010). At the population level, individual interactions have consequences for population genetic structure, sexual selection, the transmission of information and disease as well as the evolution and maintenance of social phenomena (i.e. cooperation) (Newman 2003; Ohtsuki *et al.* 2006; McDonald *et al.* 2013).

Teleost fish have proven important models for studies of the structure and function of animal societies (Krause and Ruxton 2002). For example, previous work looking at the composition of social groups (shoals or schools) has demonstrated that group living can provide a number of benefits including increased antipredator vigilance, risk dilution (i.e. the 'Selfish Herd' effect, Hamilton 1971) and predator confusion as well as increased foraging and locomotory efficiency (see Krause and Ruxton 2002). Traditionally, studies of social behaviour in teleost fishes have focused at the level of the group, for example, examining patterns of shoal assortment by body size, sex, species, etc. (Krause and Ruxton 2002). While such an approach has given important insights into the evolution of sociality, it does not capture the structure of social interactions/relationships within groups. Indeed, even in non-group living species, individuals will necessarily have to interact with conspecifics for limited time periods to mate and for other transitory requirements or benefits.

Studying group behaviour and the implicit interaction dynamics between individuals can be difficult, particularly when trying to assess the importance of particular individuals for group-level properties. However, the advent of social network analysis, or the study of the relationships between a set of actors, provided a novel range of statistical tools for describing the attributes and social fine structure of animal groups and populations in ways that were previously not possible (Croft *et al.* 2008). For example, sociograms with depictions of individuals that are socially connected have been around in biology for a long time and have been frequently used by primatologists since the 1960s (see Brent *et al.* 2011 for a discussion). That said, the statistics-based modern approach of social networks in animal behaviour started primarily with studies on teleosts and cetaceans (Ward *et al.* 2002; Lusseau 2003; Croft *et al.* 2004). This

might seem surprising given that the network approach was first developed for use on human relationships (and should therefore have easily transferred to non-human primates) and fish do not seem an obvious candidate for social network studies. However, methodological advances in statistical physics put an emphasis on quantitative analysis techniques and replication which are much easier to obtain for small organisms such as guppies (*Poecilia reticulata*, Poeciliidae) or sticklebacks (e.g. *Gasterosteus aculeatus*, Gasterosteidae) that can be readily manipulated experimentally (Croft *et al.* 2004, 2008). Furthermore, in teleost fishes, there was already a rich literature on assortative behaviour by factors such as body size, sex and species (see Krause *et al.* 2000 for a review) and it was only a small step to extend this approach to looking at associations between individuals in the context of social networks (Ward *et al.* 2002). Increasingly, the nature of group living in elasmobranchs has also become a subject of research attention and investigations into the underlying mechanisms of social interactions using network analysis has become progressively more common and recognized as important (Jacoby *et al.* 2012a).

In this synthesis, we give an overview of what is known about the social networks of teleost fishes and elasmobranchs and what contribution this approach has made to our understanding of their social organization (Table 1). While it is difficult to suggest any one test or methodological approach for a particular network question (as this will vary greatly with experimental goals, taxa, etc.), we include a section on methodological issues (e.g. how to identify and mark fish) to provide newcomers with sound basis in potential necessary techniques regarding marking and tracking individuals as well as data collection and analysis. Further, we discuss the biological relevance of the network approach with regard to several important areas of ecological research and highlight how promising developments in these topics might have implications for the study of fish behaviour.

Methodological issues

Marking and data collection techniques

The network approach requires that individuals be uniquely recognizable which can generally be achieved by marking them in some manner.

Table 1 Overview of the species of teleosts and elasmobranchs and subject areas which have been investigated using the network approach.

Species	Topic	References
Teleost Fishes		
Guppy *Poecilia reticulata* (Poeciliidae)	Social structure, cooperation, personality, sexual behaviour, environmental factors, fission–fusion, parasite transmission	Croft *et al.* (2004, 2005, 2006, 2009a,b, 2012), Couzin *et al.* (2006), Darden *et al.* (2009), Edenbrow *et al.* (2011), Kelley *et al.* (2011), Morrell *et al.* (2008), Thomas *et al.* (2008)
Threespine stickleback *Gasterosteus aculeatus* (Gasterosteidae)	Personality, partner preferences, information transfer	Ward *et al.* (2002), Pike *et al.* (2008), Atton *et al.* (2012), Webster *et al.* (2013)
Zebrafish *Danio rerio* (Cyprinidae)	Social role	Vital and Martins (2011)
Salmon *Salmo salar* (Salmonidae)	Welfare, aggression	Jones *et al.* (2010, 2011, 2012)
Sunbleak *Leucaspius delineatus* (Cyprinidae)	Invasive species	Beyer *et al.* (2010)
Cichlid *Neolamprologus pucher* (Cichlidae)	Aggression	Schürch *et al.* (2010)
Elasmobranchs		
Lemon shark *Negaprion brevirostris* (Carcharhinidae)	Partner preferences, leadership	Guttridge *et al.* (2010, 2011)
Eagle ray *Aetobatus narinari* (Myliobatidae)	Partner preferences	Krause *et al.* (2009b)
Catshark *Syliorhinus canicula* (Scyliorhinidae)	Social structure	Jacoby *et al.* (2010, 2012b)
Blacktip reef shark *Carcharhinus melanopterus* (Carcharhinidae)	Social structure	Mourier *et al.* (2012)

Exceptions are animals with natural variation in patterns which allow individual identification (e.g. whale sharks, *Rhincodon typus*, Rhincodontidae: Arzoumanian *et al.* 2005; eagle rays, *Aetobatus narinari*, Myliobatidae: Krause *et al.* 2009b). Different types of marking techniques exist depending on whether the fish are studied in the laboratory or in the field, the size of the animals and whether observations are made directly by a human observer or remotely by a machine. Remote sensing involves a surgical procedure to implant an electronic device such as a PIT tag (passive integrated transponder), an active transmitter for telemetry purposes or a proximity logger. PIT tags require the fish to swim over an antenna which reads and records the code identifier together with a time stamp (Klefoth *et al.* 2012). The arrival sequence of individuals at the location where the antenna is positioned can provide information from which association patterns of individuals can be reconstructed (Psorakis *et al.* 2012). However, receivers often have problems with the registration of the simultaneous arrival of two or more individuals (Klefoth *et al.* 2012). Hydroacoustic telemetry can be used to obtain the three-dimensional location of fish in entire lakes or other restricted areas, but the spatial resolution of these systems can be a limiting factor in defining associations (Cooke in press). Finally, proximity loggers can record the identity of encounters with other loggers (carried by fish) but without information on where the encounter took place. The signal strength and frequency are usually a function of the distance between the loggers (Guttridge *et al.* 2010).

For direct observations in the laboratory and field, various wire tags and subcutaneous dyes can be used (Beukers *et al.* 1995). A popular method is the use of visible implant elastomer (VIE, Northwest Marine Technology), which comes in different colours, can be injected subcutaneously and is externally visible over periods of weeks or even months (Croft *et al.* 2004; Wilson and Godin 2009). Additionally, Webster and Laland (2009) developed a tagging method for sticklebacks whereby PVC discs are mounted on the dorsal spines (Fig. 1b). All marking or tagging procedures should be accompanied by controls which establish whether and to which degree the behaviour of the fish is affected.

Depending on the objectives of a given study, there are both direct and indirect forms of network data collection that involve either the active pres-

Figure 1 Photographs of two suitable marking techniques (visible elastomer implants (a) on a bluegill sunfish (*Lepomis macrochirus*, Centrarchidae) and PVC discs (b) on a threespine stickleback (*Gasterosteus aculeatus*, Gasterosteidae) that can be used to identify and track individuals during network studies in fishes. Corner figures for each technique provide greater enlargements of individual tags).

ence of an observer or various technologies in lieu of such observers. For example, observers might identify, record and track marked individuals in a fish shoal and their various interactions with other group members (e.g. egocentric networks, Croft *et al.* 2008). Alternatively, a social network can be inferred based on repeated sampling events of (i) dyadic association between two individuals within a certain distance of each other (Pike *et al.* 2008) or directed interactions between two individuals (Jones *et al.* 2010, 2011, 2012) and (ii) a fish shoal or shoals over some set period of study (Croft *et al.* 2004, 2009a; Guttridge *et al.* 2012). Shoal sampling incorporates a 'gambit of the group' approach which assumes that individuals that are found in the same group are connected in some ecologically relevant manner (Croft *et al.* 2004). Care should be taken with this approach to insure that only individuals shoaling together are sampled as some collection techniques (i.e. beach seining) may result in extraneous individuals (e.g. hiding in refuge, foraging on similar food source) being collected accidentally that were not part of the initial group of interacting individuals.

In contrast, indirect forms of data collection tend to rely on various tracking technologies to establish individual-level identification and interactions as well as the larger global network. For example, recent technological developments make it possible to study the interaction patterns of fish species which cannot be easily observed directly because they live in deeper water and range over large distances. Proximity loggers, for example, can be mounted on individuals and will pick up the identity of other such devices within certain distances (Guttridge *et al.* 2010). If a sufficient proportion of individuals in a population were to carry loggers, it becomes possible to obtain information on encounters in unprecedented quantity and detail. Another option that is particularly suitable for lakes, ponds or otherwise enclosed systems is the use of hydroacoustic telemetry (Cooke in press). The advantage of this type of approach is that the three-dimensional position of many individuals can be obtained simultaneously and further, that the proximity of individuals can be estimated based on frequent logging measurements of spatial positions. Therefore, both the location of the individuals is known as well as their proximity to conspecifics. In contrast, the proximity loggers do not provide information on where encounters took place. A potential weakness of proximity
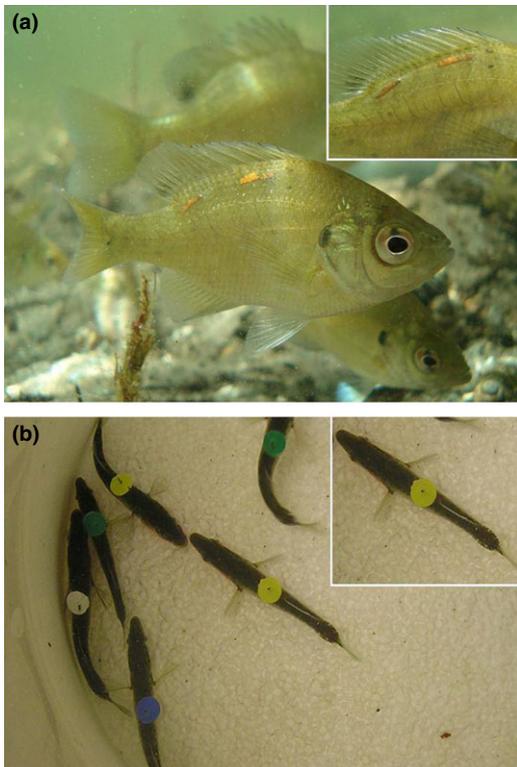
loggers is that spatial proximity does not automatically mean that an interaction in fact occurred (Krause *et al.* 2011). Further information about the duration of proximity, the location of an encounter and additional sensors (which can pick up heart or respiration rates) should be used (where possible) to decide whether an encounter resulted in an interaction. While this technology is still in its infancy in terms of usage in fishes, sensors that record physiological changes in response to stress or other stimulation could be very useful for understanding the importance of various interactions (i.e. mating, aggression) if properly calibrated to differentiate between incoming data.

At the other end of the spectrum, new options have emerged in the laboratory for tracking the behaviour of individual fish in tanks (Herbert-Read *et al.* 2011; Katz *et al.* 2011). This approach makes it possible to obtain information on social networks in an automated (or at least semi-automated) way. Improved computer vision and tracking software facilitate the accumulation of huge data sets which give accurate information on individual locations in time which can be used for constructing activity profiles of fish, characterize personalities and infer social interactions (e.g. Herbert-Read *et al.* 2013).

Data analysis techniques

The advent of network analysis introduced a novel range of statistical tools to the study of animal social behaviour. These tools allow the characterization of social fine structure at different levels of social complexity (i.e. individuals, groups, communities and populations) and provided new insights into social phenomena (e.g. dominance, cooperation). Network metrics can be divided into two categories of descriptors, that of node-based (or individual-based) measures and that of network-based measures. Node-based metrics quantify various attributes of particular individuals in a network. Some of the more common metrics used in network studies include node degree, betweenness and clustering coefficient (but see Newman 2003; Croft *et al.* 2008 for additional examples and descriptions). An individual's *degree* refers to the number of immediate neighbours an individual has in a network. Similarly, node *betweenness* measures the extent to which a focal individual lies in shortest paths between pairs of other individuals (Croft *et al.* 2008). Both of these measures are

considered to characterize aspects of network 'centrality' by estimating the social importance of an individual based on its number and frequency of interactions with other group members (with higher values being given to individuals with more interactions). An individual's *clustering coefficient*, on the other hand, is a measure cliquishness derived from local network structure (e.g. assortment by familiarity or phenotypic attributes) and determines the extent to which the neighbours of a given focal individual are themselves neighbours (Croft *et al.* 2008).

In contrast, network-based descriptors tend to convey information about relationships between nodes or reflect particular attributes of the network itself. For example, the impacts of different mean *path lengths* (or relative distance between a pair of nodes) in 'small-world' networks and their implications for the rapid transmission of information and disease in highly clustered networks (Watts and Strogatz 1998). Similarly, scale-free networks (or networks with power-law degree distributions) also generate interesting possibilities as they tend to exhibit different disease and information-carrying properties than typical random networks and are more robust to the removal of nodes or edges. However, while the properties of small-worlds and scale-free networks are compelling, their value and ecological significance in natural systems remains unclear (see Croft *et al.* 2008).

A frequent challenge in network studies is also determining whether the interactions between nodes should be treated as weighted or unweighted and directed or undirected. In a weighted network, the edges (or relationships between nodes) are given values based on the particular strength or value of a tie (with higher values having a greater 'weight', or influence in a network). In an unweighted network, all edges are considered equally. Directedness on the other hand refers to whether or not a tie is mutual or directional. For example, in a directed network, one individual may act upon another (e.g. an aggressive interaction) whereas in an undirected network, ties are assumed to be mutual (e.g. cooperation) (Croft *et al.* 2008). Most network studies tend to use weighted networks to use information both on the number of social partners an individual had as well as the strength of those interactions.

Numerous analytical techniques have been described previously (see Croft *et al.* 2008) that

allow the quantification of such network attributes manually or using various available statistical software packages (e.g. UCINET, SOCPROG). However, recent technological advances in collecting network data such as those mentioned in the previous section (i.e. biologging), generate huge amounts of data which can be difficult to interpret and typically require some form of automated processing to identify patterns in the recorded behavioural data. While these data can be analysed using traditional social network analysis techniques, potential issues might arise regarding how to deal with missing data points (e.g. missing individuals or device malfunction) and the potential disregard for rare or unusual behaviours (Krause *et al.* 2011). This is especially the case in free-ranging animals where only a certain proportion or subset of a population can be fitted with tracking devices due to logistical constraints. As such, identifying new analytical techniques for dealing with such issues is an important area of research need and represents a problem that is increasingly receiving attention (Marschall 2007; Croft *et al.* 2011b; Cross *et al.* 2012).

Biological relevance of network approach

Population structure

Social network analysis provides an excellent tool for studying social behaviour at different organizational levels (i.e. individual, dyad, group, community, population, metapopulation and species). Prior to social network analysis, it was known that fish can have preferences for particular partners possessing certain attributes, for example many species of teleost fish show a preference for associating with others of the same body size (e.g. Croft *et al.* 2009a), however, this information had not been put in the context of social units larger than that of the group (Metcalfe and Thomson 1995; Krause *et al.* 2000). It seemed unlikely, if not outright impossible, that in wild populations where hundreds or potentially thousands of other fish are encountered every day (Croft *et al.* 2003) that particular individuals would show a tendency to associate over periods of days and weeks. Novel marking procedures and tracking techniques in combination with the network approach (see Methodological issues) greatly enhanced our understanding of the social substructure of fish populations. Network analysis allowed the identifi-

cation of population substructures, so-called communities, in which individuals are more closely connected than with others in the population (Fig. 2). It is known that community structure in humans has important implications for processes such as disease and information transmission (Granovetter 1973; Newman 2010). However, in fish populations, this notion remains untested.

At the level of the population, work on guppies and sticklebacks has shown that although there is a great deal of social mixing (i.e. the social networks are much interconnected), there is homophily in the networks with similar individuals more likely to associate with each other. For example, Croft and colleagues found that in both guppy and stickleback populations social networks were significantly assorted by body size (Croft *et al.* 2004). Further work across a range of species has demonstrated that individuals form stable social associations with others and that they repeatedly co-occur with particular partners more often than we would expect by chance (e.g. Ward *et al.* 2002; Croft *et al.* 2005). Social segregation of the population by phenotypic traits such as size and sex will significantly contribute to such patterns of social stability. Indeed demonstrating that two fish co-occur more often than would be expected compared to a simulation of random association does not provide evidence that the fish have an active preference for one another (see Data analysis techniques, Methodological issues). However, as we will outline in the following section, work on familiarity and individual recognition has demonstrated that, at least for some fish species, individual recognition and partner preferences based on social familiarity are important mechanisms driving social network structure in some fish populations.

An important factor that is likely to drive population social structure is the behavioural traits of individuals. It is now widely recognized that across taxonomic groups individuals show consistent differences in behavioural traits, both across time and situations. This behavioural variation incorporates a range of behavioural axes including boldness, exploration, activity and aggression among others and is thought to be indicative of animal personality (Sih *et al.* 2004; Réale *et al.* 2007). Indeed, teleost fish have been important model systems for the study of animal personality (Ward *et al.* 2004b; Wilson and Godin 2009). At the level of the individual, an individual's personality may affect its position in a social network (Krause *et al.* 2010;
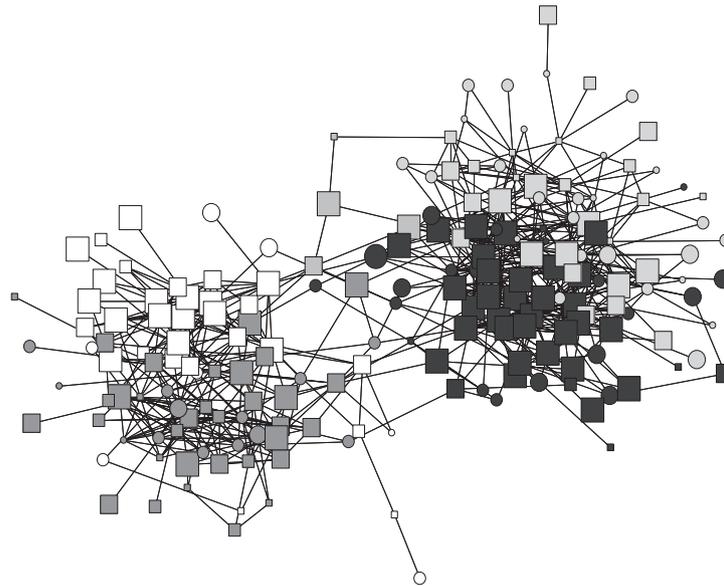
Figure 2 A social network of a guppy (*Poecilia reticulata*, Poeciliidae) population in Trinidad (redrawn from Croft *et al.* 2008). All guppies from two interconnected pools were marked and released. Over the next two weeks, approximately 20 shoals were captured daily and fish that belonged to the same shoal were connected in the network. Over time, a completely connected network developed that comprises 197 fish. Each circle represents an individual male fish and each square an individual female. The size of the symbol is indicative of the body length of the fish. Individuals interconnected by lines were found at least twice together. Five distinct communities (indicated by different grey shades) were identified in the guppy network.

Wilson *et al.* 2013). At the level of the population, the social mix of individuals in a population may have consequences for the emergent population social network. An assessment of the personality traits of guppies revealed that individuals of similar attributes were more likely to be connected in the wild (Croft *et al.* 2009b). In a study where two behaviour types, shoaling and predator inspection, were measured, a strong negative correlation was found between them. Fish were found to be strongly assorted by a composite variable of the two behaviours which might be indicative of the willingness of individuals to cooperate (Croft *et al.* 2009b). Furthermore, highly connected (i.e. more social connections) individuals were often found to be connected to other highly connected ones which could have important consequences for transmission processes in populations (Croft *et al.* 2005). Pike *et al.* (2008) reported in sticklebacks that bold and shy fish differed in their connectivity with bold individuals having fewer interactions which are more evenly distributed, whereas shy ones had more interactions with stronger preferences for particular individuals. This variation in behaviour types can have ecological and evolutionary consequences in the context of behaviourally mediated

trophic cascades (Ioannou *et al.* 2008; Wolf and Weissing 2012).

Familiarity and site fidelity

Social network studies require that researchers can identify individual fish, but they do not necessarily require that the fish can individually recognize each other. Social recognition mechanisms can operate at different levels and individual recognition is just one of them. In fact, surprisingly few critical tests have been carried out on individual recognition in fish given how important this ability is for the study of reciprocal altruism (Griffiths and Ward 2011). In contrast, numerous tests have been carried out on familiarity and identifying the ability of fish to recognize others which share the same habitat and therefore smell familiar (cue-familiarity; Ward *et al.* 2004a). Most of the work which has been carried out on social networks in fish was carried out on individuals from the same local area or pool that were familiar with each other (e.g. Croft *et al.* 2004). However, this means that work on fish has largely missed out on a topic of particular interest in the social network literature, namely how different communities are inter-

connected via weak ties (i.e. social associations) by a few individuals which have links into more than one community (Granovetter 1973). Exceptions are the work on adjacent guppy pools where some individuals crossed between pools and on eagle rays and blacktip reef sharks (*Carcharhinus melanopterus*, Carcharhinidae) roaming around islands (Croft *et al.* 2006; Krause *et al.* 2009b; Mourier *et al.* 2012). The study on eagle rays highlighted the need to assess and control for spatial preferences (site fidelity) of individuals when testing for association patterns (Krause *et al.* 2009b).

Using small species of teleost fish as a model system to study animal sociality has the advantage that it is possible to manipulate population structure under replicated conditions. One example of this is a study by Darden *et al.* (2009) which investigated the effect of sexual coercion by males on patterns of social network structure in female guppies and the development of social familiarity. In their study, Darden and colleagues found that the presence of harassing males disrupted the stability of female–female associations (Fig. 3). Moreover, this social disruption prevented females from developing social familiarity. Similar results have been reported by Jacoby *et al.* (2010) in a study on female catsharks (*Scyliorhinus canicula*, Scyliorhinidae). These studies clearly demonstrate that the social mix in a population can have a profound effect on the emergent social network structure and the development of social familiarity.

Cooperation

Unravelling the mechanisms that underpin the evolution of cooperation is a long standing challenge in the biological sciences (Dugatkin 1997a). Why should one individual pay a cost so another can receive a benefit? The key to unlocking the paradox of cooperation is an understanding of the patterns of social mixing in animal societies and the pathways that can lead to assortment among co-operators (Fletcher and Doebeli 2009). Work on threespine sticklebacks and guppies in the late 1980s and 1990s pushed the boundaries of our understanding of the evolution of reciprocal altruism suggesting that some fish species have the ability to individually recognize conspecifics, to remember the outcome of social interactions and to use this information to determine their social interactions (Dugatkin 1997b). Most of the early work on these species was carried out in the labo-
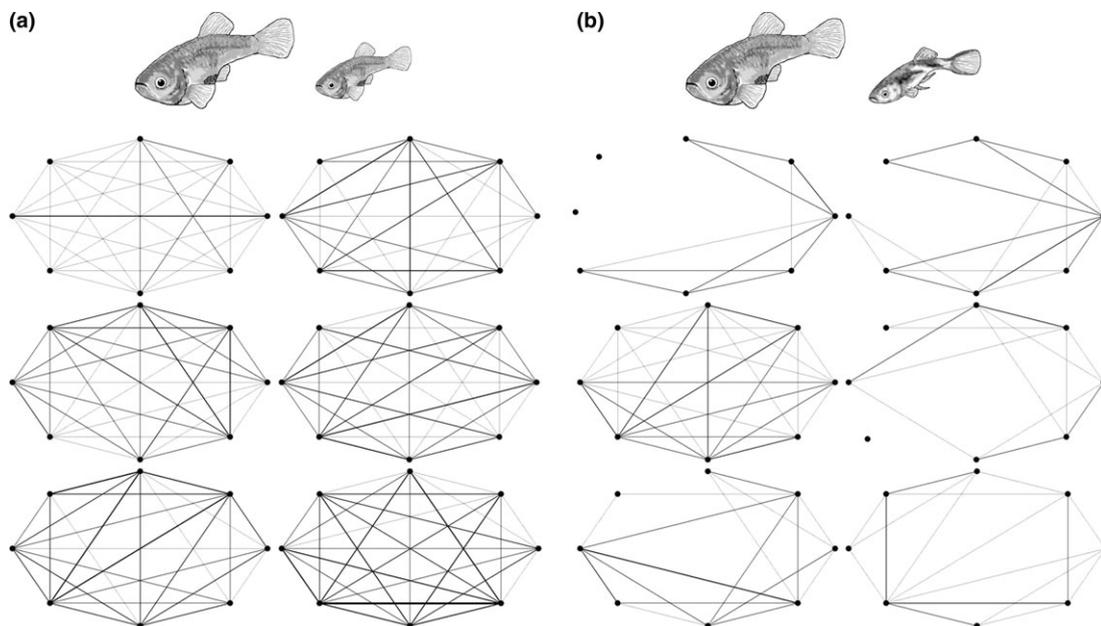

Figure 3 Example of how the presence of sexually harassing males can influence association patterns among female guppies (*Poecilia reticulata*, Poeciliidae) in a population (redrawn from Darden *et al.* 2009). Graphs of focal female social network ties when they are experimentally housed with (a) other females and (b) harassing males. Females are represented as nodes and social associations between them edges [lines]. The strength of the association is indicated by edge weight.

ratory and it was not immediately clear whether the patterns of cooperation that were observed in captivity were also present in and relevant for wild populations of fishes. The expectation (based on laboratory work) was that fish in the wild would have preferred social partners with whom they spend large amounts of time and most importantly, during those periods when cooperative behaviours are required (e.g. during predator inspection). On the other hand, fission–fusion models were predicting a regular exchange of individuals between groups (Couzin *et al.* 2002; Couzin and Krause 2003) and empirical evidence showed that fish were not faithful to a particular shoal (Hoare *et al.* 2000) but had frequent encounters with other shoals and switched between them (Croft *et al.* 2003).

A number of studies combining both laboratory and field work on guppies indicated that female but not male fish spent more time with preferred partners than with other individuals (Croft *et al.* 2004, 2006). Preference tests showed that fish recognize each other (Croft *et al.* 2006; Ward *et al.* 2009) and prefer those individuals with whom they are often seen associating with in the wild (Croft *et al.* 2006). It was observed that strong associations between pairs of fish were a good predictor of which individuals cooperated during predator inspection (of a potentially dangerous pike cichlid, *Crenicichla frenata*, Cichlidae) (Croft *et al.* 2006) and that female guppies formed cooperation networks of individuals that frequently cooperated with each other and avoided defectors (individuals which do not cooperate during risky predator inspection; Croft *et al.* 2009b). Moreover, recent work suggests that kinship has little or no role to play in structuring the social network of a wild population of adult guppies, and thus, cooperation in this context is unlikely to be underpinned by indirect genetic benefits (Russell *et al.* 2004; Croft *et al.* 2011a,b; Piyapong *et al.* 2011). Such advances were made possible through direct observations of interactions between marked individuals (i.e. VIE implant tags) and when considered together with advances in network statistics might offer important new insights into the evolution of cooperation in fishes.

Welfare

A number of studies have used the network approach to measure intra-specific aggression in salmonids (e.g. *Salmo salar*, Salmonidae) in differ-

ent animal welfare contexts such as feed restriction (Jones *et al.* 2010), stocking densities (Jones *et al.* 2011) and unpredictable feed delivery (Jones *et al.* 2012; Table 1). The focus of these studies was on the causes and consequences of fin damage in salmonid aquaculture. The authors used individual marking tags (Floy Tags, Polyepaltichtylene streamer tags) in combination with social network tools to quantify associations (defined by spatial distance) and aggressive behaviour calculating in- and out-degree (i.e. actions received and initiated by a focal individual) for individual fish to reflect the directedness of aggressive behaviours. The latter approach allowed them to identify initiators and receivers, and this information was related to fin damage and growth. Under feed restriction, salmon networks were observed to show a higher density and greater cluster coefficients (i.e. degree neighbours of some focal individual are themselves neighbours) compared to control networks (Jones *et al.* 2010). Feed restriction, unpredictable feed delivery and high densities all resulted in individuals differentiating into receivers and initiators of aggression which is reflected in their in- and out-degrees in the aggression network. Initiators showed higher growth rates and less fin damage (Jones *et al.* 2010). An interesting aspect of this work is the use of directed interactions to quantify aggression which is relatively rare in animal social network studies in general.

Perspectives

The use of network analysis has been largely restricted to small freshwater species and it remains to be seen to which extent the results obtained for these species (regarding assortative tendencies and population structure) can be extended to larger species which inhabit deeper water and in particular, marine species which can range over larger distances. The little information we have so far on sharks and rays (Krause *et al.* 2009b; Guttridge *et al.* 2010, 2011; Mourier *et al.* 2012) suggests that network analysis has a useful role to be played here as well but also identifies differences in space use between individuals as an important additional consideration. For example, social network data collected on interactions from larger spatial areas can become confounded by the site fidelity of individuals. In such cases, social network analysis may suggest that individuals form

communities and have individual preferences when the more parsimonious explanation might be that individuals simply differed in their space use. One explanation does not necessarily always preclude the other of course. For example, social interactions can result in differential space use through dominance and avoidance responses. However, we should use caution when invoking such explanations in the absence of direct evidence. Sometimes it might be the case that spatial separation of individuals is such that social interactions never take place and it would be wrong to then imply that the interaction frequencies are driven by social factors rather than spatial ones. Mourier *et al.* (2012) show evidence for community formation in blacktip reef sharks but also report differences in space use. As such, it is unclear whether social factors in fact contribute to community formation in this case. In a similar study on eagle rays, social structure support for community organization was initially strong. However, it was found that once space use was accounted for, no evidence for social factors structuring the network could be detected (Krause *et al.* 2009b). The studies of marine social networks of large marine species show that both direct observation of associations between individuals and indirect methods for data collection such as proximity loggers (see Methodological issues section for details) were used (Krause *et al.* 2009b; Guttridge *et al.* 2010, 2011; Mourier *et al.* 2012). Often social 'hotspots' where many interactions take place within a relatively restricted and easy to observe area have proved useful (Guttridge *et al.* 2011, 2012).

In recent years, studies on teleost fishes and elasmobranchs have increased in number and taxonomic diversity (Table 1). However, the opportunities for doing ground-breaking work on social networks using fish are still underutilized. Many species of teleosts (e.g. poeciliids, sticklebacks, damselfish, cichlids) are very appealing for experimental use because they are often relatively easy to maintain and breed in the laboratory, to study in the field and they are available in almost unlimited numbers allowing for replication and also population comparisons. Many interesting questions and predictions regarding sexual selection and sperm competition (McDonald *et al.* 2013), cooperation (Ohtsuki *et al.* 2006; Santos *et al.* 2006), parasite transmission and social learning (Krause *et al.* 2009a) could benefit from using the network

approach. Furthermore, when using network analysis behavioural studies can be combined with ecological work to investigate how populations respond to environmental perturbations or invasive species (Beyer *et al.* 2010).

Among the poeciliids, only the guppy has been investigated using social network analysis, whereas many other species should be amenable to this approach as well. Transparent skin makes poeciliids highly suitable for marking with fluorescent elastomer which allows easy recognition in both the field and laboratory. Mollies, an important study organism in evolutionary biology (Schlupp *et al.* 1994; Schartl *et al.* 1995) might in particular be a prime candidate for such work.

Another taxonomic group where social network analysis might provide an excellent way forward are the damselfishes which are a species-rich fish family found on coral reefs worldwide. Given that they form medium-size groups that spend large proportions of their life within just a few square metres of a small number of coral heads, they should form an ideal system for studying social networks (Booth 1995). Unlike the fission–fusion systems of many other teleost species, the same individuals spend several years together and form social hierarchies where the recent work by Shizuka and McDonald (2012) could provide a blueprint for the study of their social dynamics. Although there are many more promising candidates for the network approach, the last taxonomic group among the teleosts which we want to highlight in this context are the cichlids. The complexity of their social organization, their relatively small size and ease with which they can be kept and bred in the laboratory highlight their potential for social network studies (Schürch *et al.* 2010).

One area where a social networks approach has provided a great deal of insight into human populations is disease transmission (Newman 2003). Teleost fish have been used as model systems to study disease; however, this work has yet to make full use of a network approach to quantify how the patterns of social interactions in a population relate to transmission dynamics. Across a range of species certain individuals may play a disproportionate role in disease transmission and are often termed 'super spreaders' (Newman 2003). A key component of the ability of super spreaders to transmit disease is likely to be their patterns of social contact and their social network position. Teleost fish and their external parasites offer a

potentially tractable model system to look at the relationship between disease transmission and social network structure. For example, Croft *et al.* (2011a,b) studied the effect of the introduction of an individual infected with gyrodactylid ectoparasites on the social network structure of small groups of fish. The results suggest that individuals modify their patterns of social interactions in such a way that will reduce not just their own exposure to disease but also the transmission of disease across the group (which is most likely a by-product of individuals minimizing their own exposure). A challenge for future work in this area is to develop real time tracking of disease transmission (e.g. Lacharme-Lora *et al.* 2009) in social networks which will allow researchers to link the structure of social networks to real world transmission dynamics.

So far, little research has been carried out investigating whether particular individuals occupy specific positions in social networks and play an important role for disease or information transmission in populations. Work by Vital and Martins (2011) indicated the removal of highly connected individuals has an effect on group performance in learning tasks and that there is population variation in this regard. It is also known that in goatfish, individuals adopt specific roles of chasing and blocking (Strubin *et al.* 2011), but this has not be investigated in the wider context of social networks. A recent methodological study by Wilson *et al.* (2013) provides a test to examine whether individuals consistently occupy certain network positions. This approach might help identify the existence of 'key' individuals or behavioural types in fish populations.

Acknowledgements

References

Arzoumanian, Z., Holmberg, J. and Norman, B. (2005) An astronomical pattern-matching algorithm for computer-aided identification of whale sharks *Rhincodon typus. Journal of Applied Ecology* **42**, 999–1011.

Atton, N., Hoppitt, W., Webster, M.M., Galef, B.G. and Laland, K.N. (2012) Information flow through three-spine stickleback networks without social transmission. *Proceedings of the Royal Society B: Biological Sciences* **279**, 4272–4278.

Beukers, J.S., Jones, G.P. and Buckley, R.M. (1995) Use of implant microtags for studies on populations of small reef fish. *Marine Ecology-Progress Series* **125**, 61–66.

Beyer, K., Gozlan, R.E. and Copp, G.H. (2010) Social network properties within a fish assemblage invaded by non-native sunbleak *Leucaspius delineatus. Ecological Modelling* **221**, 2118–2122.

Booth, D.J. (1995) Juvenile groups in a coral-reef damselfish: density-dependent effects of individual fitness and population demography. *Ecology* **76**, 91–106.

Brent, L.J.N., Lehmann, J. and Ramos-Fernández, G. (2011) Social network analysis in the study of nonhuman primates: a historical perspective. *American Journal of Primatology* **73**, 720–730.

Cooke, S.J. (in press) Biotelemetry and biologging. In: *Fisheries Techniques* (eds A.V. Zale, D.L. Parrish and T.M. Sutton). American Fisheries Society, Bethesda.

Couzin, I.D. and Krause, J. (2003) Self-organization and collective behavior in vertebrates. In: *Advances in the Study of Behavior*, Vol 32. (eds P.J.B. Slater, J.S. Rosenblatt, C.T. Snowdon and T.J. Roper). Elsevier Academic Press Inc, San Diego, CA, pp. 1–75.

Couzin, I.D., Krause, J., James, R., Ruxton, G.D. and Franks, N.R. (2002) Collective memory and spatial sorting in animal groups. *Journal of Theoretical Biology* **218**, 1–11.

Couzin, I.D., James, R., Mawdsley, D., Croft, D.P. and Krause, J. (2006) Social organization and information transfer in schooling fishes. In: *Fish Cognition and Behaviour.* (eds C. Brown, K.N. Laland and J. Krause). Blackwell Publishing, Oxford, pp. 166–185.

Croft, D.P., Arrowsmith, B.J., Bielby, J. *et al.* (2003) Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata. Oikos* **100**, 429–438.

Croft, D.P., Krause, J. and James, R. (2004) Social networks in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society B: Biological Sciences* **271**, S516–S519.

Croft, D.P., James, R., Ward, A.J.W., Botham, M.S., Mawdsley, D. and Krause, J. (2005) Assortative interactions and social networks in fish. *Oecologia* **143**, 211–219.

Croft, D.P., James, R., Thomas, P.O.R. *et al.* (2006) Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology* **59**, 644–650.

Croft, D.P., James, R. and Krause, J. (2008) *Exploring Animal Social Networks*, Vol. Princeton University Press, Princeton.

Croft, D.P., Darden, S.K. and Ruxton, G.D. (2009a) Predation risk as a driving force for phenotypic assortment: a cross-population comparison. *Proceedings of the Royal Society B: Biological Sciences* **276**, 1899–1904.

Croft, D.P., Krause, J., Darden, S.K., Ramnarine, I.W., Faria, J.J. and James, R. (2009b) Behavioural trait assortment in a social network: patterns and implications. *Behavioral Ecology and Sociobiology* **63**, 1495–1503.

Croft, D.P., Edenbrow, M., Darden, S.K., Ramnarine, I.W., van Oosterhout, C. and Cable, J. (2011a) Effect of gyrodactylid ectoparasites on host behaviour and social network structure in guppies *Poecilia reticulata*. *Behavioral Ecology and Sociobiology* **65**, 2219–2227.

Croft, D.P., Madden, J.R., Franks, D.W. and James, R. (2011b) Hypothesis testing in animal social networks. *Trends in Ecology and Evolution* **26**, 502–507.

Croft, D., Hamilton, P.B., Darden, S.K. *et al.* (2012) The role of relatedness in structuring the social network of a wild guppy population. *Oecologia* **170**, 955–963.

Cross, P., Creech, T., Ebinger, M., Heisey, D., Irvine, K. and Creel, S. (2012) Wildlife contact analysis: emerging methods, questions, and challenges. *Behavioral Ecology and Sociobiology* **66**, 1437–1447.

Darden, S.K., James, R., Ramnarine, I.W. and Croft, D.P. (2009) Social implications of the battle of the sexes: sexual harassment disrupts female sociality and social recognition. *Proceedings of the Royal Society B: Biological Sciences* **276**, 2651–2656.

Dugatkin, L.A. (1997a) *Cooperation Among Animals: A Modern Perspective*, (Monographs in Ecology and Evolution). Oxford University Press, Oxford.

Dugatkin, L.A. (1997b) *Cooperation Among Animals: An Evolutionary Perspective*. Oxford University Press, Oxford.

Edenbrow, M., Darden, S.K., Ramnarine, I.W., Evans, J.P., James, R. and Croft, D.P. (2011) Environmental effects on social interaction networks and male reproductive behaviour in guppies, Poecilia reticulata. *Animal Behaviour* **81**, 551–558.

Fletcher, J.A. and Doebeli, M. (2009) A simple and general explanation for the evolution of altruism. *Proceedings of the Royal Society B: Biological Sciences* **276**, 13–19.

Granovetter, M.S. (1973) The strength of weak ties. *American Journal of Sociology* **78**, 1360–1380.

Griffiths, S.W. and Ward, A.J.W. (2011) Learned recognition in fishes. In: *Fish Cognition and Behaviour*. (eds C. Brown, K.N. Laland and J. Krause). Blackwell Publishing, Oxford, pp. 139–165.

Guttridge, T.L., Gruber, S.H., Krause, J. and Sims, D.W. (2010) Novel acoustic technology for studying free-ranging shark social behaviour by recording individuals' interactions. *PLoS One* **5**, e9324.

Guttridge, T.L., Gruber, S.H., DiBattista, J.D. *et al.* (2011) Assortative interactions and leadership in a free-ranging population of juvenile lemon shark *Neg-aprion brevirostris*. *Marine Ecology-Progress Series* **423**, 235–245.

Guttridge, T.L., Gruber, S.H., Franks, B.R. *et al.* (2012) Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Marine Ecology Progress Series* **445**, 279–291.

Hamilton, W.D. (1971) Geometry for the selfish herd. *Journal of Theoretical Biology* **31**, 295–311.

Herbert-Read, J.E., Perna, A., Mann, R.P., Schaerf, T.M., Sumpter, D.J.T. and Ward, A.J.W. (2011) Inferring the rules of interaction of shoaling fish. *Proceedings of the National Academy of Sciences* **108**, 18726–18731.

Herbert-Read, J.E., Krause, S., Morrell, L.J., Schaerf, T.M., Krause, J. and Ward, A.J.W. (2013) The role of individuality in collective group movement. *Proceedings of the Royal Society B: Biological Sciences* **280**, doi:10.1098/rspb.2012.2564.

Hoare, D.J., Ruxton, G.D., Godin, J.G.J. and Krause, J. (2000) The social organization of free-ranging fish shoals. *Oikos* **89**, 546–554.

Ioannou, C.C., Payne, M. and Krause, J. (2008) Ecological consequences of the bold-shy continuum: the effect of predator boldness on prey risk. *Oecologia* **157**, 177–182.

Jacoby, D.M.P., Busawon, D.S. and Sims, D.W. (2010) Sex and social networking: the influence of male presence on social structure of female shark groups. *Behavioral Ecology* **21**, 808–818.

Jacoby, D.M.P., Croft, D.P. and Sims, D.W. (2012a) Social behaviour in sharks and rays: analysis, patterns and implications for conservation. *Fish and Fisheries* **13**, 399–417.

Jacoby, D.M.P., Sims, D.W. and Croft, D.P. (2012b) The effect of familiarity on aggregation and social behaviour in juvenile small spotted catsharks *Scyliorhinus canicula*. *Journal of Fish Biology* **81**, 1596–1610.

Jones, H.A.C., Hansen, L.A., Noble, C., Damsgard, B., Broom, D.M. and Pearce, G.P. (2010) Social network analysis of behavioural interactions influencing fin damage development in Atlantic salmon (*Salmo salar*) during feed-restriction. *Applied Animal Behaviour Science* **127**, 139–151.

Jones, H.A.C., Noble, C., Damsgard, B. and Pearce, G.P. (2011) Social network analysis of the behavioural interactions that influence the development of fin damage in Atlantic salmon parr (*Salmo salar*) held at different stocking densities. *Applied Animal Behaviour Science* **133**, 117–126.

Jones, H.A.C., Noble, C., Damsgard, B. and Pearce, G.P. (2012) Investigating the influence of predictable and unpredictable feed delivery schedules upon the behaviour and welfare of Atlantic salmon parr (*Salmo salar*) using social network analysis and fin damage. *Applied Animal Behaviour Science* **138**, 132–140.

Katz, Y., Tunstrom, K., Ioannou, C.C., Huepe, C. and Couzin, I.D. (2011) Inferring the structure and dynam-

ics of interactions in schooling fish. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 18720–18725.

Kelley, J.L., Morrell, L.J., Inskip, C., Krause, J. and Croft, D.P. (2011) Predation risk shapes social networks in fission-fusion populations. *PLoS One* **6**, e24280.

Klefoth, T., Skov, C., Krause, J. and Arlinghaus, R. (2012) The role of ecological context and predation risk-stimuli in revealing the true picture about the genetic basis of boldness evolution in fish. *Behavioral Ecology and Sociobiology* **66**, 547–559.

Krause, J. and Ruxton, G.D. (2002) *Living in Groups*, Vol. Oxford University Press, Oxford.

Krause, J., Butlin, R.K., Peuhkuri, N. and Pritchard, V.L. (2000) The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field. *Biological Reviews* **75**, 477–501.

Krause, J., Croft, D.P. and James, R. (2007) Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology* **62**, 15–27.

Krause, J., Lusseau, D. and James, R. (2009a) Animal social networks: an introduction. *Behavioral Ecology and Sociobiology* **63**, 967–973.

Krause, S., Mattner, L., James, R. *et al.* (2009b) Social network analysis and valid Markov chain Monte Carlo tests of null models. *Behavioral Ecology and Sociobiology* **63**, 1089–1096.

Krause, J., James, R. and Croft, D.P. (2010) Personality in the context of social networks. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**, 4099–4106.

Krause, J., Wilson, A.D.M. and Croft, D.P. (2011) New technology facilitates the study of social networks. *Trends in Ecology & Evolution* **26**, 5–6.

Lacharme-Lora, L., Perkins, S.E., Humphrey, T.J., Hudson, P.J. and Salisbury, V. (2009) Use of bioluminescent bacterial biosensors to investigate the role of free-living helminths as reservoirs and vectors of *Salmonella*. *Environmental Microbiology Reports* **1**, 198–207.

Lusseau, D. (2003) The emergent properties of a dolphin social network. *Proceedings of the Royal Society B: Biological Sciences* **270**, S186–S188.

Marschall, N. (2007) *Methodological Pitfalls in Social Network Analysis: Why Current Methods Produce Questionable Results*, Vol. VDM Verlag, Saarbrücken.

McDonald, G.C., James, R., Krause, J. *et al.* (2013) Sexual networks: measuring sexual selection in structured, polyandrous populations. *Philosophical Transactions of the Royal Society B-Biological Sciences* **368**, doi:10.1098/rstb.2012.0356.

Metcalfe, N.B. and Thomson, B.C. (1995) Fish recognize and prefer to shoal with poor competitors. *Proceedings of the Royal Society B: Biological Sciences* **259**, 207–210.

Morrell, L.J., Croft, D.P., Dyer, J.R.G. *et al.* (2008) Association patterns and foraging behaviour in natural and artificial guppy shoals. *Animal Behaviour* **76**, 855–864.

Mourier, J., Vercelloni, J. and Planes, S. (2012) Evidence of social communities in a spatially structured network of a free-ranging shark species. *Animal Behaviour* **83**, 389–401.

Newman, M.E.J. (2003) The structure and function of complex networks. *Siam Rev* **45**, 167–256.

Newman, M.E.J. (2010) *Networks: An Introduction*, Vol. Oxford University Press, Oxford.

Ohtsuki, H., Hauert, C., Lieberman, E. and Nowak, M.A. (2006) A simple rule for the evolution of cooperation on graphs and social networks. *Nature* **441**, 502–505.

Pike, T.W., Samanta, M., Lindstrom, J. and Royle, N.J. (2008) Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society B: Biological Sciences* **275**, 2515–2520.

Piyapong, C., Butlin, R.K., Faria, J.J., Wang, J. and Krause, J. (2011) Kin assortment in juvenile shoals in wild guppy populations. *Heredity* **106**, 747–756.

Psorakis, I., Roberts, S.J., Rezek, I. and Sheldon, B.C. (2012) Inferring social network structure in ecological systems from spatio-temporal data streams. *Journal of the Royal Society Interface* **9**, 3055–3066.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T. and Dingemanse, N.J. (2007) Integrating animal temperament within ecology and evolution. *Biological Reviews* **82**, 291–318.

Russell, S.T., Kelley, J.L., Graves, J.A. and Magurran, A.E. (2004) Kin structure and shoal composition dynamics in the guppy, *Poecilia reticulata*. *Oikos* **106**, 520–526.

Santos, F.C., Pacheco, J.M. and Lenaerts, T. (2006) Evolutionary dynamics of social dilemmas in structured heterogeneous populations. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 3490–3494.

Schartl, M., Wilde, B., Schlupp, I. and Parzefall, J. (1995) Evolutionary origin of a parthenoform, the amazon molly *Poecilia formosa*, on the basis of a molecular genealogy. *Evolution* **49**, 827–835.

Schlupp, I., Marler, C. and Ryan, M.J. (1994) Benefit to male sailfin mollies of mating with heterospecific females. *Science* **263**, 373–374.

Schürch, R., Rothenberger, S. and Heg, D. (2010) The building-up of social relationships: behavioural types, social networks and cooperative breeding in a cichlid. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**, 4089–4098.

Shizuka, D. and McDonald, D.B. (2012) A social network perspective on measurements of dominance hierarchies. *Animal Behaviour* **83**, 925–934.

Sih, A., Bell, A. and Johnson, J.C. (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19**, 372–378.

Sih, A., Hanser, S.F. and McHugh, K.A. (2009) Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology* **63**, 975–988.

Strubin, C., Steinegger, M. and Bshary, R. (2011) On group living and collaborative hunting in the yellow saddle goatfish (*Parupeneus cyclostomus*). *Ethology* **117**, 961–969.

Thomas, P.O.R., Croft, D.P., Morrell, L.J. *et al.* (2008) Does defection during predator inspection affect social structure in wild shoals of guppies? *Animal Behaviour* **75**, 43–53.

Vital, C. and Martins, E.P. (2011) Strain differences in zebrafish (*Danio rerio*) social roles and their impact on group task performance. *Journal of Comparative Psychology* **125**, 278–285.

Ward, A.J.W., Botham, M.S., Hoare, D.J. *et al.* (2002) Association patterns and shoal fidelity in the three-spined stickleback. *Proceedings of the Royal Society B: Biological Sciences* **269**, 2451–2455.

Ward, A.J.W., Hart, P.J.B. and Krause, J. (2004a) The effects of habitat- and diet-based cues on association preferences in three-spined sticklebacks. *Behavioral Ecology* **15**, 925–929.

Ward, A.J.W., Thomas, P., Hart, P.J.B. and Krause, J. (2004b) Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology* **55**, 561–568.

Ward, A.J.W., Webster, M.M., Magurran, A.E., Currie, S. and Krause, J. (2009) Species and population differences in social recognition between fishes: a role for ecology? *Behavioral Ecology* **20**, 511–516.

Watts, D.J. and Strogatz, S.H. (1998) Collective dynamics of 'small-world' networks. *Nature* **393**, 440–442.

Webster, M.M. and Laland, K.N. (2009) Evaluation of a non-invasive tagging system for laboratory studies using three-spined sticklebacks *Gasterosteus aculeatus*. *Journal of Fish Biology* **75**, 1868–1873.

Webster, M., Atton, N., Hoppit, W. and Laland, K.N. (2013) Environmental complexity influences association network structure and network-based diffusion of foraging information in fish shoals. *American Naturalist* **181**, 1–10.

Wey, T., Blumstein, D.T., Shen, W. and Jordan, F. (2008) Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour* **75**, 333–344.

Wilson, A.D.M. and Godin, J.G.J. (2009) Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behavioral Ecology* **20**, 231–237.

Wilson, A.M., Krause, S., Dingemanse, N. and Krause, J. (2013) Network position: a key component in the characterization of social personality types. *Behavioral Ecology and Sociobiology* **67**, 163–173.

Wolf, M. and Weissing, F.J. (2012) Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution* **27**, 452–461.