

# Social network theory in the behavioural sciences: potential applications

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**Abstract** Social network theory has made major contributions to our understanding of human social organisation but has found relatively little application in the field of animal behaviour. In this review, we identify several broad research areas where the networks approach could greatly enhance our understanding of social patterns and processes in animals. The network theory provides a quantitative framework that can be used to characterise social structure both at the level of the individual and the population. These novel quantitative variables may provide a new tool in addressing key questions in behavioural ecology particularly in relation to the evolution of social organisation and the impact of social structure on evolutionary processes. For example, network measures could be used to compare social networks of different species or populations making full use of the comparative approach. However, the networks approach can in principle go beyond identifying structural patterns and also can help with the understanding of processes within animal populations such as disease transmission and information transfer. Finally, understanding the pattern of interactions in the network (i.e. who is

connected to whom) can also shed some light on the evolution of behavioural strategies.

**Keywords** Social networks · Social organisation · Mate choice · Disease transmission · Information transfer · Cooperation

## Introduction

One of the long-standing challenges in biology is to bridge the gap between individual behaviour and population biology (Sutherland 1996). Population structure is a result of local interactions between individuals and their environment, and we need a framework to integrate over the different scales of individual behaviour, group-level phenomena and population-level patterns. In all cases where animal (and human) populations have been investigated, there has been evidence for social interaction patterns to strongly deviate from randomness (i.e. individuals have a greater affinity to interact with some than with others) and for individual variation in social contact patterns (e.g. some individuals have many while others have few contacts; Krause and Ruxton 2002). The existence of social assortativity and individual variation (in contact patterns) has important consequences for population level processes such as the transmission of information in an animal population, the spread of diseases within and between populations and the evolution of behavioural strategies. For instance, the speed with which a disease will spread in a population can be very much dependent on which individuals get infected first. Are they highly and globally interconnected in the population and therefore carry a high risk of infecting many others over a short time span, or are they poorly connected meaning that no large outbreak will

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occur or only a localised one? We may also want to look at the structure of the population as a whole and ask if individuals with many social connections are connected to others with many connections (i.e. positive assortativity) in which case the disease might be expected to spread very fast. Therefore, in brief, we could ask what the implications of social structure are for the evolution of mate choice, learning strategies and disease transmission and how social structure allows animals to adapt to changing environments. To address these questions, we need to understand more about the social fine structure of the animal population in question, and the social networks approach is an ideal tool for doing so.

Wilson (1975) identified the social networks approach as one of the main techniques for studying sociality in animals in his pioneering book “Sociobiology—the new synthesis.” The networks approach provides details for a better understanding of the fitness implications of social structure at the level of the individual and the population. The social fine structure of a population as revealed by a social network might explain to us why an individual might be more susceptible to an infectious disease as a result of its particular network position and why the population as a whole might be vulnerable to the rapid transmission of a disease (as we will show below). However, Wilson’s (1975) book was published more than 30 years ago. Therefore, why has the idea of using a networks approach in animal behaviour not become mainstream already? Wilson was a visionary in recognising the potential of network theory for the study of animal behaviour long before computational power was sufficient to make full use of it. Furthermore, many of the conceptual advances necessary to apply this technique to animal behaviour (such as meaningful network descriptors) have only been developed in recent years. In this review, we aim to highlight areas where we feel that a networks approach could be used as a valuable tool to address longstanding questions in behavioural ecology.

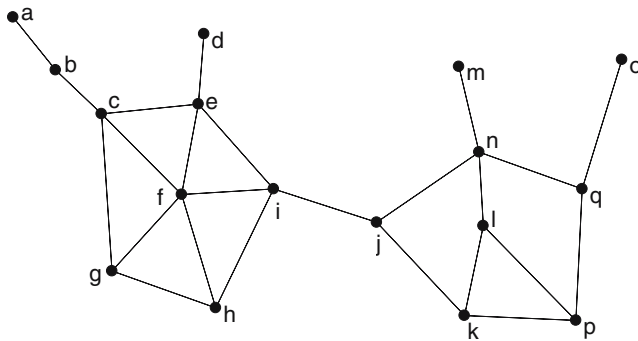
### What is a social network?

The network approach originated in the mathematical graph theory and has a long and distinguished history in the social sciences and psychology where it has been used to investigate human social organisation (see Scott 2000 for a review) with its main strengths being the potential to address population-level or cross-population-level problems by building up complex social structures from individual-level interactions. Furthermore, network statistics can be used to derive novel quantitative measures that characterise social structure at the level of the individual, and these measures can then be used alongside other standard statistical variables (i.e. measures of relatedness or repro-

ductive success). However, the appeal of the networks approach goes well beyond sociology and psychology and has widespread technological applications as well. Anything from transport networks (Sen et al. 2003) to communication systems such as the internet (Tadic 2001) can be considered as a system of interacting components. In biology, the network approach has been used in various areas, as biologists have realised that to better understand complex systems, we need to study interactions between components of the system not in isolation but as part of a network of interactions. Such an approach has made important contributions across biological disciplines and across different levels of biological organisation. For example, work on gene and protein interaction networks has provided unique insight into the functional organisation of the cell (Barabasi and Oltvai 2004), work on neural networks has demonstrated how cells are interconnected to control complex processes (Laughlin and Sejnowski 2003) and considering trophic interactions between organisms as a food web has provided insight into how stable communities are to perturbation or the invasion of a new species (Dunne et al. 2002). Surprisingly, in the discipline of animal behaviour, this approach has received relatively little attention despite its enormous potential.

A network consists of nodes and edges (Fig. 1). When applied to animal groups or populations, nodes usually represent individual animals and the edges the relationships between them (Croft et al. 2007). This statement highlights one important distinction from conventional statistics, namely that we deal with relational data (i.e. data that represent how individuals relate to each other) in networks rather than with attribute data (i.e. data that assign attributes such as body size or colour to individuals), although attribute data often play a crucial role as explanatory variables for the observed structural patterns. Social networks can capture some of the complexity of social organisation that eludes other methods. Relationships in networks can represent any type of social behaviour such as cooperative, hostile, predatory, competitive and aggressive interactions to name but a few possible associations. Furthermore, we can investigate the intensity, frequency and directedness (i.e. who initiated an aggressive interaction or provided support) of such interactions. Compared to more traditional approaches that focus on dyadic interactions between animals in isolation, the network approach allows us to put such interactions into the wider social context of the population.

Networks tell us who is connected to whom in the population and by what relationship. An individual’s network position (i.e. its social environment) may also have important fitness consequences. As Maynard Smith 1982 pointed out, the frequency of behavioural strategies in the population can affect the evolution of individual



**Fig. 1** Example of a social network where nodes (black circles) symbolise individuals and edges (lines) social connections between them. This fictitious network comprises 17 individuals (labelled a–p). See Table 1 for individual-based measures

behaviour. However, to better understand under which conditions behavioural strategies can evolve, we need to go beyond the frequencies of each strategy and obtain information on how the individuals are inter-connected. For example, in models of conflict, the success of a hawk (aggressive) or dove (yielding) strategy will be dependent on the frequency of hawks and doves in an individual’s local interaction network. Skyrms and Permante (2000) gave several examples of how social structure can arise from pair-wise interactions in a dynamic model in which agents receive positive and negative feedback from their interactions. At the level of the population, this means that the way in which individuals are inter-connected in a population, i.e. the network structure, can strongly influence the outcome of

evolutionary processes (a topic we will return to in the section on cooperation).

In Fig. 1, we have provided a simple example to demonstrate some of the potential uses of the network approach. For the purposes of this illustration, we have created a fictitious animal population of which we present a network of social contacts. Network theory provides us with a range of statistical descriptors that we can use to characterise the network as a whole as well as the properties of individuals in the network. Table 1 provides some examples of such descriptors. We can calculate for each individual in the network its degree (number of immediate neighbours), cluster coefficient (the degree to which an individual’s immediate neighbours are connected), path length (number of connections on the shortest path between two individuals) and node betweenness (the number of shortest paths between pairs of individuals that pass through a particular individual; see Croft et al. 2007 for a detailed discussion of the terms and their calculation). We can also calculate these statistics for the network as a whole, which gives an idea of the global properties of the network system. Many of these network statistics can be calculated using UCINET (Borgatti et al. 2002; see also Croft et al. 2007 for a detailed discussion of the meaning of the different descriptors), which is readily available from the internet.

Any changes that occur in this network such as the experimental removal or addition of individuals can potentially have a profound effect on the network and can be measured using the above descriptive statistics. For example, the removal of a single individual (in this case, j)

**Table 1** Some individual-based measures for Fig. 1

Node/individual	Degree	Path length (to/from a node)	Clustering coefficient	Betweenness
a	1	4.75 (3)	–	0
b	2	3.875 (2.125)	0	15 (7)
c	4	3.0625 (1.5)	0.333	29 (13)
d	1	3.5625 (2.5)	–	0
e	4	2.625 (1.625)	0.333	28.5 (8.5)
f	5	2.5625 (1.5)	0.5	21.5 (5.5)
g	3	3.25 (1.875)	0.667	1.5 (1.5)
h	3	2.875 (2.125)	0.667	4.5 (0.5)
i	4 (3)	2.3125 (2)	0.333 (0.667)	65 (1)
j	3 (absent)	2.375 (absent)	0 (absent)	64 (absent)
k	3	2.9375 (2)	0.333 (1)	15
l	3	3.4375 (1.667)	0.333	2 (3)
m	1	3.6875 (2.333)	–	0 (0)
n	4 (3)	2.75 (1.5)	0	41 (6)
o	1	4.3125 (2.333)	–	0
p	3	3.4375 (1.667)	0.333	3 (3)
q	3	3.375 (1.5)	0	16 (6)
Mean values	2.82 (2.625)	3.25 (1.953)	0.295 (0.403)	18.0 (3.438)

In brackets are the values that change after the removal of individual/node j. See text for a definition of the measures. In the case of the path length, we have calculated the distances to and from a particular node.

from the network can have a number of drastic effects on network structure. First of all, at the global level, the network now subdivides into two sub-networks, and there is a drastic reduction in the average path length. This subdivision into sub-networks and the reduced path length may have important consequences for the transmission of socially learnt information in this population, for disease transmission and other processes, which we will explore in this review. At the individual level, we can also observe some strong effects. For example, individuals  $i$  and  $n$ , which were initially very central to the network, have a much reduced betweenness after removal of  $j$ . We could experimentally test now whether in real life the removal of one or more individuals does indeed produce the effect on social systems that the network analysis predicts. In our example (Fig. 1), we selected an individual for removal that occupies a crucial position in the network, which is not always the case. Therefore, it is important to keep in mind that the removal of single individuals (or even small groups) does not necessarily produce any strong effect on network measures particularly if the network is very large. In fact, many network structures are very robust against removal of individuals (which is considered a strength in technological networks and also found in some colonies of social insects; Krause and Ruxton 2002).

In the following, we want to highlight a number of areas where we believe the network approach could make important contributions to the study of animal behaviour and social organisation. For this purpose, we have adopted a bottom-up approach by first discussing how the behaviour of individuals can be described, analysed and predicted in novel ways using the network approach. In the second section, we will look at processes (such as information transfer, disease transmission etc.) that can take place on networks that connect individuals forming a group or population. The third section is devoted to the topic of network comparisons. In this section, we explore how the same network of individuals can be compared between different contexts (i.e. social structure during control situation and during predation threat) and how networks of entire populations that are exposed to different ecological conditions can be compared. In this context, the network approach provides novel measures at the population level that allow us to obtain an understanding of how social structures are influenced by ecological conditions. The final section of this review is concerned with an overview of different taxonomic groups where the network approach has been applied and identifies avenues for future work.

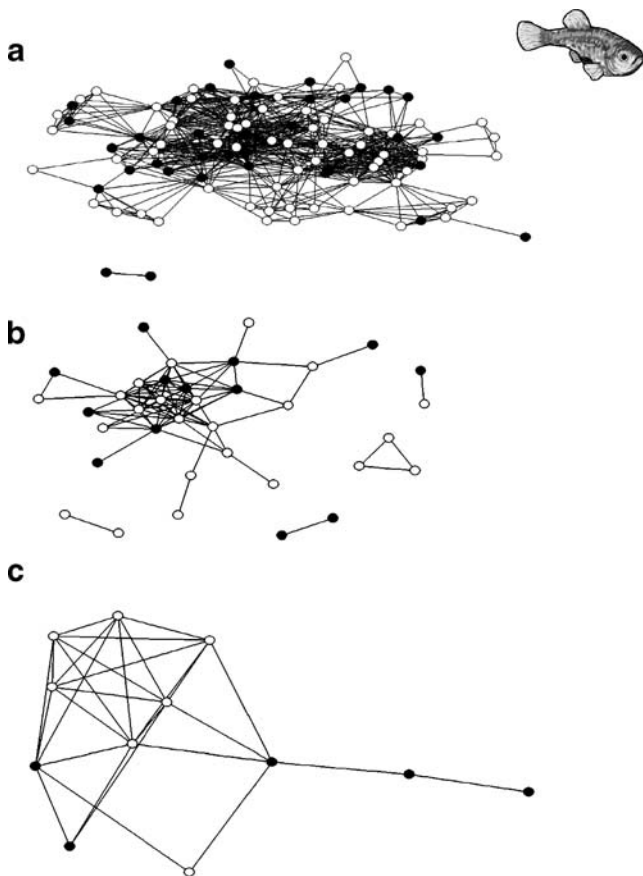
### Behavioural strategies of individuals

Game-theoretical work by Maynard Smith (1982) and others demonstrated that the evolution of behavioural strategies

can be frequency dependent if certain conditions are satisfied. This work was fundamental for our understanding of animal behaviour because it could explain how different behavioural strategies could co-exist over evolutionary time. To understand at what frequency two competing strategies obtain the same fitness, we need to know the details of the pay-off matrix regarding the interactions between the two strategies. The traditional game-theoretical approach, however, is non-spatial, and all individuals are equally likely to interact with one another. If we look at real animal populations, it becomes clear very quickly that the latter is not normally the case and that certain individuals are more likely to interact with certain other ones for a variety of reasons (e.g. neighbouring territories). This is where networks come in because they help us understand who interacts with whom and how often and what the total number of connections is that an individual has in a network. This type of information can be very useful for the study of cooperation (Croft et al. 2006; Ohtsuki et al. 2006). Ohtsuki et al. (2006) showed that the evolution of cooperation is strongly dependent on the structure of the social network and is favoured if the benefit of the altruistic act  $b$ , divided by the cost  $c$ , is larger than the average number of neighbours,  $k$ , in the network (i.e.  $b/c > k$ ). In an unstructured environment where all individuals are equally likely to interact with each other, defectors will have an advantage over co-operators. Understanding the network structure in relation to the behavioural strategies of individuals can thus provide new insights into the evolution of co-operation.

Croft et al. (2006) examined the network structure of free-ranging guppy (*Poecilia reticulata*) populations and found non-randomness in the form of strong repeated interactions between pairs of females (Fig. 2). No persistent pairs were found between males or between a male and a female. When faced with a predator, these fish perform inspection behaviour, which means that the predator is approached by small groups of fish. Pairs of females that were frequently observed together in the social network (before predator exposure) were also frequently found together during predator inspection, which suggests that the social network was a good predictor of the inspection network. In subsequent tests, pairs of fish were isolated and exposed to predators, and their inspection behaviour was analysed. Pairs of fish that had frequently co-occurred together in the social network were found to perform the inspection behaviour more co-operatively (frequently switching the more dangerous lead position) than pairs of fish that were usually not found together.

Taking the work by Ohtsuki et al. (2006) and Croft et al. (2006) a step further, one could try to investigate what the network structure of wild populations is in terms of



**Fig. 2** Social networks of Trinidadian guppies with males in *black* and females in *white* (Croft et al. 2006). The original network (**a**) in which all interactions are displayed was filtered so that (**b**) only those interactions are shown that occurred twice or more or (**c**) thrice or more. The latter (**c**) was a good indicator of cooperative interactions between pairs of individuals during predator inspection behaviour

defectors and co-operators and the implications of this structure for the evolution of co-operative strategies in the population.

Sexual networks and questions regarding who mates how often and with whom have been addressed in the sexually transmitted diseases literature cited below. However, the network theory also provides us with several novel quantitative characteristics that can be tested as potential predictors of male mating success. Measures of network ‘centrality’ (Scott 2000) such as degree or betweenness of an individual (see Fig. 1) may have a bearing on social status or position in the hierarchy and thereby influence mating opportunities. However, we have to keep in mind that some of these quantitative measures are very sensitive to error. For example, high betweenness in an individual can change dramatically if only one or two observations are missing or were wrongly recorded from a network making this a risky parameter to operate with (Fig. 1). Imagine for instance that the connection between individuals  $i$  and  $j$  was overlooked in Fig. 1 because of an observational error. This

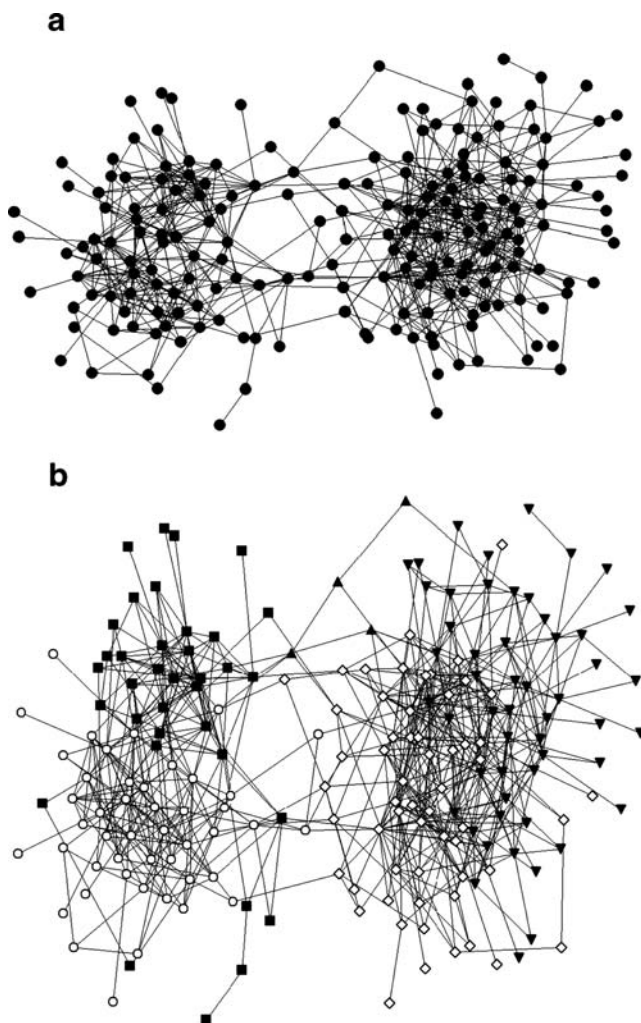
would result in two separate sub-networks and give individuals  $i$  and  $j$  much lower values of betweenness. In contrast, degree is a cumulative measure, and unless we have a case of mistaken identity in our network, this parameter is less likely to be affected by sampling errors. The degree of individuals could therefore provide a promising alternative when trying to link network position with social status or mating success.

## Identifying the role of individuals

### Population substructure

The search for substructures or so-called communities within networks is based on a few simple conceptual ideas (although the calculation of network communities is not trivial; Croft et al. 2007; Wolf et al. 2007). Communities in animal social networks are defined as ‘groups’ of individuals that are more connected amongst themselves than with other individuals in the network in direct analogy to human social communities.

Why is the search for communities in networks important? We stated above that information flow or disease transmission in networks might be influenced by network structure, and communities are an important part of this structure. Figure 3 shows a network of the Trinidadian guppy, *Poecilia reticulata*, that was found to subdivide into five communities (Croft et al. 2006). One of the first predictions that one could make is that information flow or disease transmission might predominantly occur within communities before it spreads between them. Given that communities are based on the interconnectedness of individuals, this seems a plausible assumption. In this context, one could study for instance how the absence or presence of community structures in networks influences transmission processes in the network. Other aspects of interest are the individuals inter-connecting communities (Lusseau and Newman 2004). If there was a disease outbreak in a human population, presumably the first individuals one would want to vaccinate would be the ones inter-connecting communities so that the spread of the disease could be contained within the community where it first arose. Clearly, the individuals that inter-connect communities occupy a key position in this context. One could further investigate why these particular individuals inter-connect communities and what makes them different from others in the network (Lusseau and Newman 2004). This would raise questions such as whether they occupy these inter-connecting positions only temporarily or over long time periods (potentially all their lives), and this could be linked up with the study of behavioural syndromes (Sih et



**Fig. 3** **a** Social network of Trinidadian guppies taken from two interconnected pools in the Arima River. Individuals interconnected by lines were found at least twice together. **b** Five communities were detected in this system using simulated annealing (see Croft et al. 2007 for details of the method). The nodes are shaped according to which of the five communities they were found to be in (filled squares, filled inverted triangles, filled triangles, empty diamonds and empty circles)

al. 2004). Network position could also be linked to social status and hierarchies, and one could test whether individuals that inter-connect groups are of particularly high or low rank in their group.

Above we discussed how network structure might determine mating success and thereby the flow of genetic material in populations. However, we could also investigate the reverse, namely how the genetic structure of a population affects the social structure. We might expect that at least in some animal populations, the degree of relatedness could be a good predictor of close social interactions—something that could be investigated by testing whether communities within networks are assorted by the degree of relatedness.

## Population level processes

### Disease transmission

A number of studies have used networks to investigate how social contact patterns might influence disease transmission in both animal and human populations (Watts and Strogatz 1998; Potterat et al. 2002; Cross et al. 2004; Corner et al. 2003). In humans, disease transmission, unlike some of the other research areas that we discuss in this review, is probably the field in which the use of networks is already fairly well established (see for instance the literature on socially transmitted sexual diseases in humans such as human immunodeficiency virus infection; see Klodahl 1985; Rothenberg et al. 2000; Potterat et al. 2002). However, very few studies have been conducted on animals so far using the network approach despite its obvious potential. Traditional epidemiological models do not take into account the differences between individuals (e.g. differences in the number of social connections; see Fig. 1) regarding their potential to transmit diseases through a population, and this is precisely where the network approach can make a contribution with its detailed information on individual interaction patterns.

The structure of social networks is important in that it is likely to help predict the speed with which the disease will be transmitted through the population and the pathway of the transmission chain. In some cases, the network theory can also be used to identify super-transmitters, i.e. individuals that have an unusually large number of connections in the network that can result in very fast spreading of a disease. In the case of a disease outbreak, targeted vaccination of super-transmitters could be an effective way of disrupting transmission despite the fact that only a relatively small proportion of the population was vaccinated.

There is great potential in integrating information on network conditions with disease transmission dynamics in animal populations. Cross et al. (2004) used behavioural data on association patterns of African buffaloes (*Syncerus caffer*) to study the potential spread of bovine tuberculosis. Their model is based on a fission–fusion system in which individuals can switch between herds, and the probability of getting infected is a function of the time spent in a herd with infected conspecifics. They found that the dynamics of the association patterns play an important role for disease transmission particularly if the disease requires only a relatively short association period for transmission. Using a slightly different approach, Corner et al. (2003) investigated the spread of bovine tuberculosis via brushtail possums (*Trichosurus vulpecula*) in New Zealand using a networks approach. We are not aware of a similar work for badger-transmitted bovine tuberculosis, but the potential for

modelling between-species interactions using the network approach is obvious.

Recent examples in which the network approach had potential for making an important contribution to disease control are the foot-and-mouth outbreak in Britain and the severe acute respiratory syndrome (SARS) epidemic (Bowen and Laroe 2006). The way in which domestic animals are kept and moved around creates contact patterns that can be highly conducive to the spread of diseases (Webb 2005). Therefore, knowledge of the network structure of a population can be of vital importance for making predictions about the disease dynamics as well as for taking preventive measures in terms of vaccinations of individuals (a point we discussed earlier in the section on network communities).

The implications of network structure for disease transmission dynamics is one issue; the probability of a particular individual to get infected is another. From a network's perspective an individual's chance of getting infected is primarily a function of how many connections it has in a network, what proportion of its network 'neighbours' are infected, the frequency and intensity of contact with those neighbours and the potential directedness of those connections (i.e. in some cases, transmission may be dependent on who initiates the contact or takes which role in the interaction). The study of Cross et al. 2004 highlights the importance of combining behavioural observations of social contact patterns with epidemiological expertise. For instance, it remains a challenge to find suitable criteria for establishing when contact can result in disease transmission between individuals. This concerns the type of interaction that is required, its duration and frequency to name but a few factors.

#### Information transfer

Similar arguments to the ones used above apply to the transmission of information via social learning in animal populations. However, even if we use the same population, the interactions that are relevant for the transmission of information can (but do not have to) be very different from those that result in the transmission of disease. An additional complexity of information transmission over networks is that social interactions (such as winning and losing in contests) are often witnessed by other members of the group or population. This can result in important information being acquired by the observer and in a change of future interactions (see McGregor 2005 for communication networks).

Network models have been used to describe the process by which ideas, opinions, information and innovations spread through human societies. Such models provide a means to estimate at what rate the diffusion will occur. Emphasis has been placed on identifying the key individ-

uals in a community that may influence information diffusion (Valente 1995; Rogers 1995).

The traditional starting point for studying information transmission in animal populations is to assume random interactions between the individuals in the system. However, all populations that have been studied so far clearly show strongly non-random elements in their interaction structure (Table 2) with individuals often forming preferential associations with others resulting in social assortativity (Krause et al. 2000; Krause and Ruxton 2002). Individuals also show marked differences in their ability to learn from others and in their effectiveness to transmit such information within a population (Brown et al. 2006).

With the help of the network theory, we can therefore try to predict the pathway that socially learnt information takes through a group or population (Valente 1995). We can also make predictions about the speed of such processes. Furthermore, we can investigate to what degree the transmission of information through a population is influenced by the attributes of individuals (e.g. age, experience etc.) and their network position (e.g. central or peripheral to the network; Fig. 4) provided of course that the two (attributes and network position) are not correlated in the first place. We may predict that information is most likely to reach individuals via strong links (network connections that are based on interactions that occur frequently and have a long duration). The frequency and duration of strong links should ensure that the probability of information transfer is maximised between its participants. Sociological research has shown, however, that this is only partially true in human communities. Often, individuals that are strongly linked also share similar experiences (because they live in the same area, have similar work patterns etc.) and are therefore not likely to provide very novel pieces of information for each other. In contrast, weak links with individuals outside one's normal social environment were much more likely to provide such information (Granovetter 1974).

#### Comparing networks

An area of great interest in behavioural ecology is the issue of how ecological conditions shaped the behaviour of individuals and thereby the social organisation of populations/species (Harvey and Pagel 1991). Usually, closely related species (or different populations of the same species) are compared to investigate how differences in ecological conditions could have led to the evolution of differences in behaviour and morphology. Pioneering studies by Crook (1964) on weaver birds and Jarman (1974) on African ungulates have demonstrated the power of this approach. For instance, Brashares et al. (2000) in a

**Table 2** Empirical studies of animal social networks by taxonomic groups

Species	Authors	Research area
<b>Fish</b>		
Guppies ( <i>Poecilia reticulata</i> )	Croft et al. (2004 <sup>a</sup> , 2005 <sup>a</sup> , 2006 <sup>a</sup> )	Patterns of social interaction in a wild population Replicated networks Cooperation
Threespine stickleback ( <i>Gasterosteus aculeatus</i> )	Croft et al. (2005 <sup>a</sup> )	Patterns of social interactions in wild populations
<b>Cetaceans</b>		
Dolphins ( <i>Tursiops truncatus</i> )	Lusseau (2003 <sup>a</sup> ), Lusseau et al. (2005 <sup>a</sup> ) Lusseau and Newman (2004 <sup>a</sup> )	Patterns of social interactions in wild populations Which individuals are important in tying a network together
<b>Insects</b>		
Social insects	Fewell (2003 <sup>a</sup> )	Modulation of foraging behaviour
<b>Primates</b>		
Rhesus monkeys ( <i>Macaca mulatta</i> )	Chepko-Sade et al. (1989) Corr (2001)	Social structure Changes in social networks over the lifespan of an individual
Ring-tailed lemurs ( <i>Lemur catta</i> )	Berman et al. (1997)	Infant social networks
Northern muriquis ( <i>Brachyteles arachnoids hypoxanthus</i> )	Deputte and Quris (1997)	Infant gender and socialisation process
Emperor tamarind ( <i>Sanguinus imperator</i> )	Nakamichi and Koyama (2000)	Intra-troop affiliative relationships of females
Nicaraguan mantled howler monkeys ( <i>Alouatta palliata</i> )	Strier et al. (2002)	Male–male relationships
Western lowland gorillas ( <i>Gorilla gorilla gorilla</i> )	Know and Sade (1991)	Agonistic networks
Western gorillas ( <i>G. g. gorilla</i> )	Bezanson et al. (2002)	Social structure
Macaques	Stoinski et al. (2003)	Proximity patterns of female western lowland gorillas
Spider monkeys ( <i>Ateles geoffroyi</i> )	Bradley et al. (2004)	Extra-group, kin-biased behaviours
Pigtailed macaques ( <i>Macaca nemestrina</i> )	De Waal 1996)	Macaque social culture: Development and perpetuation of affiliative networks Food sharing
Primates (comparative study)	Pastor-Nieto (2001)	Policing stabilizes construction of social niches in primates
Humans ( <i>Homo sapiens</i> )	Flack et al. (2006 <sup>a</sup> )	Network size and neocortex size Disease transmission Disease transmission Community structure
<b>Ungulates</b>		
African buffalo ( <i>Syncerus caffer</i> )	Kudo and Dunbar (2001)	Modelling disease transmission, social structure
Grevy's zebra, onager	Potterat et al. (2002) Klovdahl (1985) Newman (2003)	Comparison of social structure
<b>Elephantidae</b>		
African elephants ( <i>Loxodonta africana</i> )	Wittemyer et al. (2005)	Multiple-tier social structure
<b>Marsupials</b>		
Brush-tail possums ( <i>Trichosurus vulpecula</i> )	Corner et al. (2003 <sup>a</sup> )	Social-network analysis of disease transmission among captive possums
<b>Domestic animals</b>		
Sheep	Webb (2005)	Contact structure for disease modelling
Pigs (Large white landrace)	Durrell et al. (2004)	Preferential associations

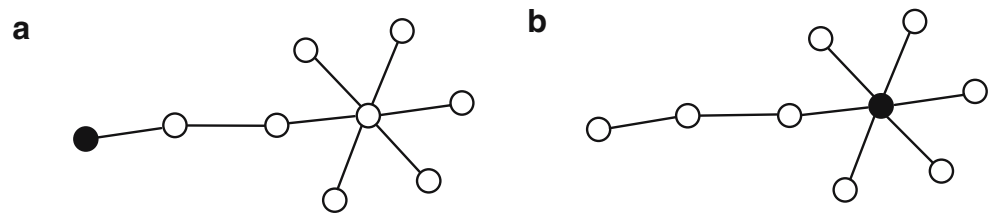
<sup>a</sup> Indicates that the network approach is central to the paper

re-analysis of Jarman's data set of 75 species of African ungulates showed that species that live in open habitats formed larger groups than those that live in bush- or woodland. Furthermore, species with more selective diets were found to live in smaller groups than ones that were less selective in their diet.

Therefore, what can social networks do for us in this context? The strength of the social network approach is that it gives us a wealth of new statistical descriptors that characterise the social fine structure of an entire population ranging from measures that focus on individual connectedness in the network, community structures that



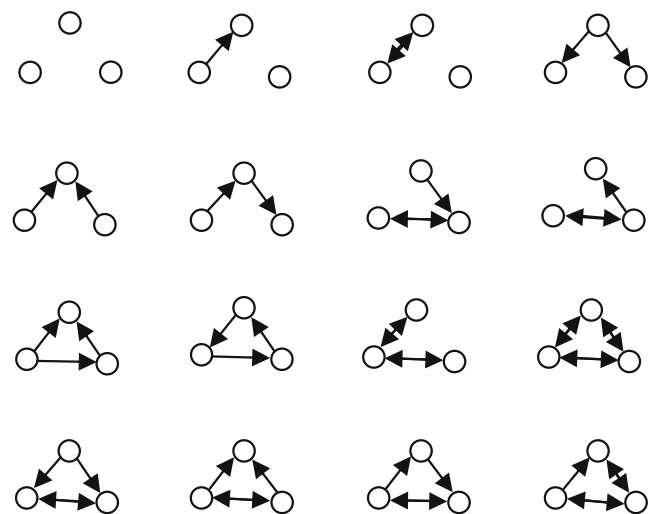
**Fig. 4** Different network positions of individuals and their potential influence on information transmission through a population. In **a**, a peripheral individual becomes the source of information and in **b**, a central individual



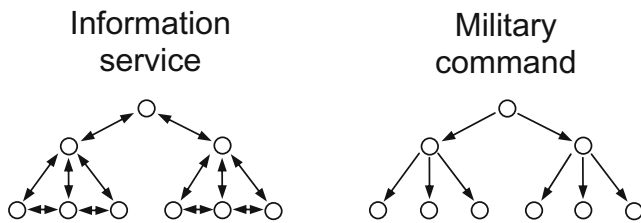
form the building blocks of a network and global descriptors of the entire network (see Croft et al. 2007, chapter 4, for details). If we stick with our example of the African ungulates a moment longer, we could use the network theory to go beyond simple measures of group size and try to identify how the individuals in the population are connected to each other and relate the position of individuals in the network to their attributes. For instance, we could look at whether females take up more central network positions than males and/or we could test whether females are more likely to interconnect the network than males—a measure that is known as betweenness in network lingo (see Fig. 1). Alternatively or additionally, we could look at whether individuals tend to form strong repeated ties with others or many weak (unrepeated) ties. These kinds of descriptors of social networks could form the basis of comparisons between species. Basically, all of the individual- and population-level measures that we introduced in the sections above lend themselves to this approach. Thus, it should be possible to investigate the implications of ecological conditions for various network patterns and processes. For instance, we should be able to determine whether populations that live in different habitats differ in their network structure and whether these differences have implications for processes such as information transfer or disease transmission throughout the networks. An interesting paper in this context is the one by Sundaresan et al. (2007) who have used the networks approach to compare populations of Grevy's zebra (*Equus grevyi*) and onager (*Equus hemionus*) (Asian wild ass).

An alternative method of comparing networks was introduced by Faust and Skvoretz (2002) who characterised each network largely in terms of a census of structural elements often referred to as 'motifs.' Motifs describe the interactions between a small number of nodes (individuals), which are usually restricted to dyadic or triadic interactions (Fig. 5). Faust and Skvoretz (2002) used the motif census as the basis for a comparison of a number of human and non-human social networks. However, Faust (2006) has pointed out that only networks of similar density (with a similar proportion of actual connections out of the total possible ones) should be compared because density will influence the motif census.

We can also look at a specific group or population and their social structure in different contexts (e.g. presence or absence of a predator; differences in resource distribution) to understand how context-dependent social structures are (Fig. 6). This could be a very powerful approach when thinking about human social networks. For example, Wilson (1975) argues that we might expect a human communication network to show highly inter-connected components to maximise information flow. In contrast, a military chain of command would be strictly hierarchical with information flow occurring only in one direction. Such a comparative approach has been applied to animal populations. Wittemyer et al. (2005) studied the social network of an elephant population over a 4-year period and reported that certain aspects of the social structure (such as family units) were relatively unaffected by seasonal variation, whereas higher-order social units were strongly affected by ecological variables such as resource competition. One example of how the link might be made between network structure and processes on network is given by Cross et al. (2004) who investigated the spread of bovine tuberculosis in African buffaloes. A comparison between two years suggested changes in the social network structure (which appears to have been driven by changes in environmental conditions) may have facilitated the faster spread of bovine tuberculosis in the population.



**Fig. 5** Network motifs are local structural configurations in networks such as dyads and triads. Here is an example of a directed network with some possible configurations (modified from Faust and Skvoretz 2002)



**Fig. 6** Differences in network structure between different contexts in fictitious human networks: information services network and military command. The number of individuals is the same, but the way in which they are linked differs (modified from Wilson 1975)

Future work examining how network structure is influenced by different ecological conditions and the implications of this structure for population level process such as information and disease transmission is eagerly anticipated.

## Outlook and future directions

### Interpretation and further tests

The social network theory is clearly not independent of spatial structure, but it can go beyond it. Individuals that are often close in space may not necessarily interact much, and conversely, individuals that are rarely close in space may have a strong link (through mating or disease transmission). It is precisely this supra-spatial element that makes network theory such a useful tool for the study of animal groups and populations.

One way of finding out whether individuals that are connected in our network just happen to have a similar routine or speed of locomotion or whether their association is based on social preference is to carry out choice or preference tests in which the individuals have to pick each other out from others that are matched for size, sex and other characteristics. Croft et al. (2006) for instance showed that guppies that frequently co-occurred in the wild also preferentially shoal with each other when size- and sex-matched control individuals are introduced to the same tank. Similar choice experiments have been carried out using sheep (Michelena et al. 2005). An alternative to using choice experiments is the use of playback experiments, which may allow us to make inference about social recognition (i.e. identification of individuals or familiars) in our study species (Janik et al. 2006).

### Experimental manipulations of networks

In the above section, we discussed the use of networks to identify social connections of particular importance, which can then be tested in preference tests or by using playback

experiments. Another way of testing network predictions is to use manipulation experiments. We can address questions like the ones raised in the section on network communities. To which degree would disease transmission or information transfer follow community structures? Which types of interactions do we need to record to make such predictions? What is the role of individuals in inter-connecting different communities?

Individuals can be removed from networks, trained (to learn new behaviours) or infected with a disease and re-introduced (provided we have adequate controls for such procedures). In the form of a replicated experimental design, such approaches are urgently needed to address some of the above questions. For instance, Croft et al. (2006) recorded the social network of guppies before, during and after predator inspection to find out whether inspection events changed social structure. Furthermore, they simulated defection events to investigate whether this would result in ‘avoidance’ of defectors and weaken the social ties between pairs of fish that had previously cooperated in the network (Thomas et al. 2007).

Another example of a manipulation experiment is the elegant work by Flack et al. (2006) who studied the social organisation of pigtailed macaques (*Macaca nemestrina*). Flack et al. (2006) employed the network approach to characterise the social organisation of a group of monkeys making full use of several novel statistical descriptors that allow a detailed assessment of the social relationships between individuals. A removal experiment demonstrated that the presence of several high-ranking individuals was essential to retain group cohesion and that the social network fractured into several sub-units in their absence because of increased levels of conflict between individuals. The network tools provide sensitive measures of both individual- and group-level characteristics, which would be hard to measure and analyse without taking a network approach.

Such removal experiments can be conducted on real animal groups, but they can also be carried out on virtual populations on the computer to make predictions about how the removal of a single individual or groups of individuals could potentially affect network structure in terms of the degree, path length, betweenness and assortativity. Again, the strength of the network approach here is that it provides a whole new range of descriptive statistics that we can use to describe social systems.

Finally, we can investigate whether there are connections between the position that individuals occupy in their group or population (as characterised by novel network statistics such as betweenness) and more traditional measures of individual mating success or social status (position in a hierarchy). Thus, the network approach allows us to probe deeper into the social structure of animal

groups and populations than before and to link this information to fitness-relevant variables, which could substantially increase our understanding of the social dynamics of animals.

### Empirical network studies

In Table 2, we have given an overview of some of the empirical work on animal social networks. This is by no means a complete list. We selected some of the more prominent studies for different taxonomic groups to provide a general overview. A complete list would be impossible because there are many studies which are at the borderline in the sense that they use the term social network but do not apply any of the network methodology. Other studies present sociograms but no statistical analysis of them. In the end, it remains a little subjective which studies to include and which not to. We added an “a” to those studies where the social network approach plays a central role in connection with detailed statistical tests.

From the table, it becomes obvious that most of the network studies to date have been carried out on non-human primates (given the restriction on space, we have only named a few studies on humans, but there is of course a vast number of papers in the psychology and sociology literature and indeed even an entire journal specifically for this sort of work; for further details specifically on human networks, see Scott 2000). This should not surprise us given that the social network theory was developed to investigate human relationships, and therefore this approach relatively easily transfers to other primates. At the same time, it is clear that many criteria that we expect from scientific research (such as standardisation, replication, manipulation etc.) are more easily reached with some of the other taxonomic groups because the animals are smaller, more numerous and more easily manipulated. Particularly, the social insects stand out as a system that should be highly promising for the network approach. The evolution of division of labour and the frequent interactions between workers belonging to different casts cries out for an approach in which system performance can be developed from social sub-units and ultimately dyadic social interactions. Fewell (2003) developed a process-oriented network to study division of labour in honey bees (Table 2). However, this could be extended using individually marked colony members.

Domestic animals (such as cows, pigs and sheep) are another group with high potential for the network approach. The fact that these animals can be easily marked individually and observed continuously (often using automated systems) should provide us with a wealth of information on their social relationships that

could help addressing some of the important and urgent welfare issues.

Finally, relatively little use has been made of the network approach in the context of inter-specific interactions (apart from the rich literature on food webs [i.e. who eats whom]) in ecosystems (Dunne et al. 2002; Sole and Montoya 2001). The case of disease transmission where pathogens cross from animal hosts into humans (e.g. recent SARS outbreak) or from one animal species into another (e.g. badgers and bovine tuberculosis) should be highly promising systems for network studies. Another area of inter-specific interactions that lends itself to the network approach is pollination where insect–plant interactions are at the heart of the matter.

In general, we know relatively little about how animals are integrated into existing social structures or about how new social structures form or how long it takes for social systems to reach an equilibrium (and indeed if they do). What are the effects of removing or adding individuals on social structure, and what are the consequences of changes in social structure for processes on networks (such as disease transmission and information transfer)? Social networks could be a way into this sort of questioning. There are many research areas where this kind of approach could make a contribution such as release programmes of animals into the wild or holding conditions of domestic animals or captive animals in zoos where the effects of environmental enrichment could be measured by using a social networks approach.

In summary, there is an enormous potential benefit in adopting a networks approach to a very wide range of behavioural studies of animals in many diverse taxonomic groups. Although we have not discussed them in detail here, there are one or two methodological hurdles that we will need to jump before the analysis of relational data sets, in the form of networks, becomes as routine and robust as it is for attribute data (Croft et al. 2007). Nonetheless, we believe that these issues are surmountable and that the ends will clearly justify the means.

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