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REVIEW

Animal social networks: an introduction

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Abstract Network analysis has a long history in the mathematical and social sciences and the aim of this introduction is to provide a brief overview of the potential that it holds for the study of animal behaviour. One of the most attractive features of the network paradigm is that it provides a single conceptual framework with which we can study the social organisation of animals at all levels (individual, dyad, group, population) and for all types of interaction (aggressive, cooperative, sexual etc.). Graphical tools allow a visual inspection of networks which often helps inspire ideas for testable hypotheses. Network analysis itself provides a multitude of novel statistical tools that can be used to characterise social patterns in animal populations. Among the important insights that networks have facilitated is that indirect social connections matter. Interactions between individuals generate a social environment at the population level which in turn selects for behavioural strategies at the individual level. A social network is often a perfect means by which to represent heterogeneous relationships in a population. Probing the biological drivers for these heterogeneities, often as a function of time, forms the basis of many of the current uses of network analysis in the behavioural sciences. This special issue on social networks brings together a diverse group of practitioners whose study systems range from social insects over reptiles to birds, cetaceans, ungulates and primates in order to illustrate the wide-ranging applications of network analysis.

Keywords Social networks · Animal interactions · Social organisation

Introduction

At the mention of social networks, many may think "So what, hasn't this method been around for decades?" and they are right. The origins of the network concept are in mathematical graph theory that can be traced back for centuries (Euler 1736 in Biggs et al. 1986) and its use in social network analysis was instigated by sociologists and psychologists in the first half of the 20th century (Scott 2000). However, what's new is the fact that the subject has undergone a dramatic and rapid transformation in recent years. Increasing globalisation has seemingly interconnected everything, our communication networks (e.g. internet, mobile phone) and transport systems span the globe, economic integration of nations and communities becomes ever closer and more complex with a growing number of multinational organisations and environmental problems transcending national boundaries. The fact that our world is becoming more and more interconnected has led to an exponential interest in understanding networks because they are an effective way of studying this process

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of increasing social inter-connectedness (see Newman 2003 for a review). As a result of this strong interest, there have been major conceptual advances in several areas, including statistical physics that have pushed the boundaries of our understanding of networked systems. Software programs have been developed that make the use of network analyses more user-friendly, opening these methods up for the mainstream. So far, however, the fields of animal behaviour and behavioural ecology have benefited relatively little from the new possibilities that these recent analytical advances offer us and the purpose of this special edition is to address this issue.

So what's so special about network analyses then? Network analysis provides tools which allow us to test for the first time some of the long-standing conceptual frameworks of social organisation and structure (e.g. Wilson 1975; Hinde 1976). Most conventional analyses might permit exploration of social structure at the level of the individual, dyad, group or population. Network analyses allow us to span these scales, and scales in between, making it possible for us to build up larger social units from pair-wise interactions. Though such analyses have long been possible for some types of relational data (such as associations among group-living animals), the strength of the network approach is that so many types of interaction (sexual, aggressive, cooperative; who eats whom and so on) can be treated within the same conceptual framework, and using the same visual and analytic tools. Perhaps "Animal Interaction Networks" would be a more suitable title for this field, given the generality of the potential applications.

This generality means we can look at how individual behaviour influences what happens at the population level and we can likewise study the fitness implications of the latter for the individual (Fig. 1). This kind of feedback loop is fundamental for an understanding of the role of self-organisation in social systems (Camazine et al. 2001; Couzin and Krause 2003). A great advantage of a networks approach is that we do not need to decide a priori on the level of social organisation that must be key to understanding our animal system. We always deal simply with nodes (animals) and edges (interactions between them) and search the patterns they reveal, through statistical tools, models or both.

Finally, the network approach also allows the contemplation of a much neglected aspect: specifically that the social (network) structure of the population can have important repercussions for the fitness of individuals (Fig. 2). This argument is familiar to most of us from game theoretic models. The frequency at which different behavioural strategies are used in a population can have important fitness consequences for individuals in the population (Maynard Smith 1982). Early game theoretic models assumed that all individuals mix freely with each other. In most animal and human populations, however, not everybody interacts with everybody else and we see a highly structured social organisation that reflects differences between individuals in the number of social interactions, the degree to which some individuals are central or peripheral to the population network and the tendency to interconnect different communities that form substructures within networks (Krause and Ruxton 2002; Krause et al. 2007; Croft et al. 2008). More recent "evolutionary graph theory" models (for example Ohtsuki et al. 2006; Santos et al. 2008) use networks to quantify social heterogeneity, and account for it, in models of, for example, the evolution and maintenance of cooperation. While the nature of the "social networks" invoked in evolutionary game theory may be rather different from the social networks observed and analysed by empiricists, the parallel is an interesting one.

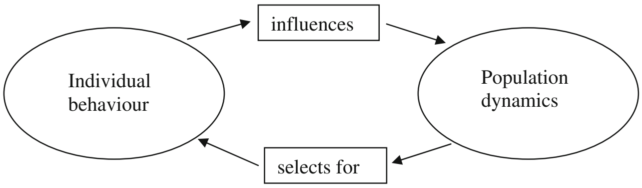

Fig. 1 Schematic relationship between individual behaviour and population dynamics (after Kokko unpublished)

A similar point can be made about conventional epidemiological models and the modelling of socially transmitted information. The initial assumption of random interactions between individuals turns out to be too simplistic and does not fit the finding that most social systems have a more or less heterogeneous structure that should not be neglected when studying the processes that take place on these systems.

An example

A network can be described as consisting of nodes (individuals) and edges (interactions between them) (Fig. 3). Part of the appeal of the network approach is its

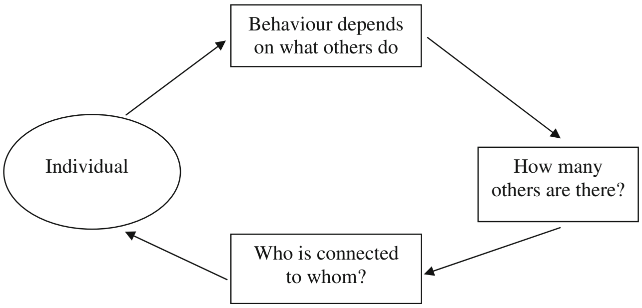

Fig. 2 Schematic representation of the importance of the frequency of behavioural strategies and the social fine-structure for the evolution of behaviour

simplicity and generality because almost any system that comprises multiple components (whether biological or technological) can be described in the form of a network.

In Fig. 3, we have constructed a simple example to illustrate some of the features that network theory offers. We can calculate a whole new range of descriptive statistics that can be used to characterise structural components of the networks and the position of chosen individuals in relation to others. For example, 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. 2008 for details). These statistics (which are just a small proportion of those already available from the social sciences literature) can be averaged over all individuals in the network to give an idea of the local and global properties of the network (Table 1).

Of course, the measures we use to characterise network structure are most useful if they reflect structures of biological interest. An individual's degree, for example, might be related to the likelihood that the individual can spread disease or information in a network, with highly connected individuals more likely to trigger an epidemic or a rumour. Path length and cluster coefficient might tell us something about the likelihood that a pathogen will remain a local outbreak or become global in a population. Betweenness may indicate how important individuals are in interconnecting different sections of the network. In the context of social learning, individuals with high betweenness that can reach into different communities may be more likely to be responsible for the global spread of information. Many of these network statistics and others can be calculated using the social sciences package UCINET (Borgatti et al. 2002; see also Croft et al. 2008) which is readily available from the internet. Other measures, such as reach and, in particular, measures of "centrality" are now being developed and used by behavioural scientists, as readers of the papers in this volume will see for themselves. Lusseau et al. (2008) commented on which measures may be particularly appropriate for animal behaviour data.

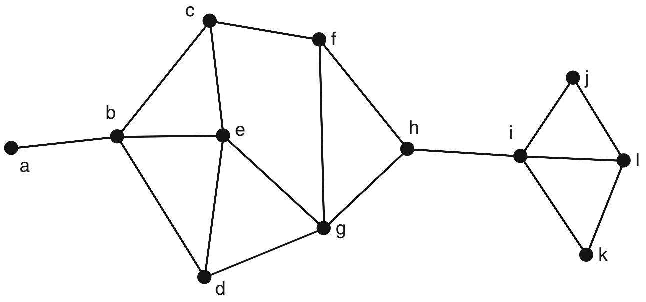

Fig. 3 Example of a social network where nodes (*black circles*) symbolise individuals and edges (*lines*) social connections between them. This fictitious network comprises 12 individuals (labelled *a*–*l*). See Table 1 for individual-based measures

Table 1 Some individual-based measures for the network in Fig. 3

Node/ individual	Node degree	Path length (to/from a node)	Clustering coefficient	Node betweenness
a	1	3.64	0	0
b	4	2.73	0.333	10.5
c	3	2.36	0.333	5.8
d	3	2.36	0.667	4.3
e	4	2.27	0.5	5.3
f	3	2.09	0.333	8.8
g	4	2	0.333	18.2
h	3	2	0.333	28
i	4	2.36	0.333	24.5
j	2	3.18	1	0
k	2	3.18	1	0
l	3	3.09	0.667	0.5
Mean values	3	2.61	0.486	8.83

See text for a definition of the network measures. In the case of the path length, we have calculated the mean distance of nodes to and from a particular node

Some of the uses of network theory

Our hope is that the papers in this edition will provide a whole range of examples of and ideas for the use of networks in the behavioural sciences that will inspire readers to become active themselves in this exciting and rapidly developing research area.

In many ways, the developments in the use of network analysis in the behavioural sciences have tracked similar developments in the social sciences. We have the advantage, though, in that "discovering" networks several decades later than social scientists we have ready access to their ideas and methods, plus those that continue to emerge in other fields. We also have cheap computing power to implement sometimes rather involved statistical tests and analyses.

It is probably fair to say that the majority of applications of network analysis in the behavioural sciences to date have been of a descriptive nature; a network is constructed and analysed for the patterns it contains. Most of us have employed what Whitehead and Dufault (1999) called the "gambit of the group", in which individuals are assumed to be associating if they are seen in the same group; these associations are accumulated over a number of observations, to produce an association matrix, which is itself a representation of a social network. Thus, all the tools developed for the analysis of association data (Whitehead 2008) may be regarded as tools available for network analysis of data compiled via the gambit of the group, even if they are not always explicitly reported as such.

This approach, whether explicitly using networks or not, can help us identify patterns of social organisation (including how they change with time) that can lay the foundation for understanding key components of social structure, and for making comparisons of different populations, contexts or species. This approach has plenty of mileage left in it. Early network examples include the work of Lusseau (2003) on dolphins and Croft et al. (2004) on guppies, *Poecilia reticulata*. In this volume, there are many excellent examples of the use and analysis of group-derived data. Most of the examples are for mammals; this reflects, as much as anything, that there are a good number of long-term studies of mammals that contain information ripe for network studies.

One such example in the volume is the analysis of the association patterns in a long-term study of a group of spider monkeys (*Ateles geoffroyi*) (Ramos-Fernández et al. 2009). The authors used lagged association rates (Whitehead 2008), a classic "association data" measure, to look at the temporal stability (over years) of relationships among females plus the more obviously network-derived measures of node strength and eigenvector centrality to differentiate individual social roles. They found that adult females as a class are at the core of the social structure, but that within that class there is little evidence for anything other than random associations.

In a similar vein, Henzi et al. (2009) used a two-pronged approach to unravel details of the temporal variation in relationships among female chacma baboons (*Papio hamadryas ursinus*). The authors measured lagged association rates and fed these into eight alternate models of social structure. In addition, they constructed weighted association networks and used individual node measures to quantify social roles. Each approach led to the conclusion that there is seasonal variation in the extent to which female baboons maintain differentiated relationships, results which challenge established views about primate societies.

Also in this volume, Fischhoff et al. (2009) looked at associations among adult male plains zebra (*Equus burchelli*) over a 4-year period. They are interested in the question of whether the reproductive status of the males (bachelor or stallion) has an effect on social groupings and bond formation. In order to test this, the authors developed a permutation test that compares bachelors and stallions while controlling for temporal patterns in grouping and sampling. They were able to conclude that bachelors form stronger, more persistent bonds than stallions.

This last example highlights that relational data, such as a network, need particular care at the analysis stage, since we can rarely assume independence of our data points. Though there are plenty of methods already available (Whitehead 2008; Croft et al 2008), new questions still often require at least a tweak on old methods, or sometimes a completely new approach. There is still plenty of room for developments in network methodology, many of which appear in the various contributions to this volume. James et al. (2009) warn us of some of the potential pitfalls of applying some of the existing methods, analyses and interpretations without quite enough thought. Krause et al. (2009) point out that, even for those of us that have appreciated the need for careful statistical analysis, it is still surprisingly easy to build a null model of social associations that is itself not without bias. On a slightly different front, Franks et al. (2009) present a method to generate user-controlled ensembles of random networks that they hope will form the foundation of a framework to develop a quantitative network sampling methodology.

The toy network in Fig. 3 also illustrates other structural features which may be explored via network analysis, and which may be of great biological importance. Nodes *a*–*h* and *i*–*l* form clusters of nodes (communities in network parlance) more densely connected among themselves than to others. Many methods for detecting such communities have been developed both in the networks and the animal association literature (see Croft et al. 2008), and these too have been used in the animal sciences to find layers of social structure in the largely unexplored scale between the group and the population. For example, association matrix methods were used by Vonhof et al. (2004) and Wittemyer et al. (2005) to find multiple levels of social structure in bats, *Thyroptera tricolor*, and elephants, *Loxodonta africana*, respectively, while Wolf et al. (2007) used an explicitly network-based approach to find unexpected layers of social structure in a colony of sea lions, *Zalophus wollebaeki*.

In this volume, Lusseau and Conradt (2009) made use of a community analysis as part of their study of bottlenose dolphins (*Tursiops* sp.). Social animals can benefit from group living by combining diverse information to make consensus decisions (Conradt and Roper 2005). This area has seldom been explored in the context of social networks. Lusseau and Conradt (2009) looked for evidence of "unshared consensus decisions" among bottlenose dolphins. They brought together behavioural observations associated with a collective switch in patch searching with network analysis of which animals form clusters or communities, and which are likely to be best informed, plus a model of consensus decision making to deduce that well-informed individuals can induce a collective decision by the group in this species.

One of the features of this last example is its use of a quantitative model to try to tease out what is happening in the data. There are many examples of the use of *null* models in network analysis, and rightly so, as these are often necessary to show that a relational data set contains something of biological interest. Examples of models trying to do more are rather rarer. One nice example is the work of Ramos-Fernández et al. (2006) which used an individual-based model of foraging in an environment where feeding patches vary in size. This simple model produces richly structured networks even when there is nothing but simple aggregation bringing animals together. There is plenty of room in the future for more models of network formation and dynamics.

It has long been realised that we can use our understanding of social patterns to look at the implication for processes such as information transfer or disease transmission (Corner et al. 2003; Cross et al. 2004). In this volume, Godfrey et al. (2009) made a more direct attempt to map disease pathways between individual gidgee skinks (*Egernia stokesii*). Their interactions are again associative, via shared use of rock crevices. However, the real interest of the authors is in parasite transmission, which they addressed by constructing a "transmission network", in which two lizards are connected if they used the same crevice within an estimated transmission time for parasite infection. This novel approach allowed the authors to begin to analyse the interplay between parasite load and social position in this species.

Of course, the network paradigm will become much more generally appealing if it can be used for making predictions, and there are a couple of convincing studies where this has been achieved. Flack et al. (2006) predicted the effect of social policing on the structure of interactions among a group of primates, and McDonald (2007) showed that the network connectivity of young male long-tailed manakins (*Chiroxiphia linearis*) predicted their future breeding success. In this volume, McDonald (2009) followed up on this earlier study by asking whether it is kinship that shapes the "young-boy" network of the earlier work. The answer, as the author points out, is a rather intriguing "no".

Another example of network prediction, albeit on a much shorter timescale, appears in the contribution to this volume by Eagle and Pentland (2009). These authors looked at the underlying structure in daily patterns of human behaviour, using models. The structure was represented through what the authors call "eigenbehaviors", a set of characteristic vectors within the multimodal data set detailing the daily routines of individuals and groups.

In parallel with the development of network methods to look at the structure and development of vertebrate societies, those working with invertebrates have taken a slightly different path (Fig. 4). When studying vertebrates, we are more or less forced to observe associations or interactions which, when amalgamated, yield patterns that hopefully make biological sense. Having found these patterns, we naturally ask what effect they will have on, among other things, process. Assuming that the patterns we find are representative, we ask what effect they will have on the transmission of information or disease through a population, for example. By contrast, network studies of invertebrates, of which there are now several (Fewell 2003; Naug 2008, 2009), tend to proceed the other way round. In most cases, it is (an instance of) the process, such as the passage of food through a colony, that is observed directly. The patterns exhibited by the process tend to come second. It is also worth noting that the networks are not group derived, but none of these differences prevents the use of network analysis as the tool of choice.

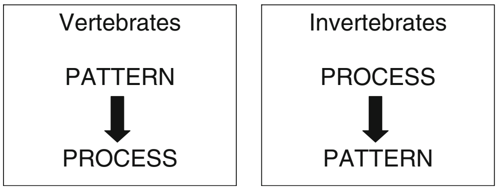

Fig. 4 Schematic representation of the current emphasis in network analyses applied to vertebrate and invertebrate social systems

There is one example of this type of research in this volume. Naug (2009) presented networks of mouth-to-mouth contacts in nine colonies of the social wasp *Ropalidia marginata*. He found that most colony members have a similar number of contacts, but there are relatively few contacts between behavioural classes. He then manipulated the colonies to test the resilience of the interaction networks to removal of individuals. Manipulation and replication of this kind is rare in network studies but a particularly promising area for further research.

The examples used in this volume do not begin to exhaust all the possible uses of network analysis in the behavioural sciences. For example, we have not touched upon the possible contributions of network analyses to the comparative method, though this is a potentially rich vein. Examples so far in this area include the work by Croft et al. (2006) on guppies and the comparison of two closely related ungulate species by Sundaresan et al. (2007). Much of the innovation in network analysis and its application have so far come from other disciplines such as sociology and statistical physics (Wasserman and Faust 1994; Newman 2003; see Croft et al. 2008 for a review). In addition to novel statistical descriptors for networks, there are many new ideas, methods and testable hypotheses to be found particularly in the sociology literature. For instance, Granovetter's (1973) idea of the importance of weak links (for information transmission) has yet to be tested in animal systems.

Of course, we behavioural scientists are not without our own ideas and methods. Readers are referred to books by Whitehead (2008) and Croft et al. (2008), plus a number of recent reviews, including those by Krause et al. (2007) and Wey et al. (2008). This volume includes a view of the future possible uses of network theory for behavioural ecologists (Sih et al. 2009) which, we hope, will whet the appetite of any readers wondering whether network analysis might be of use to them.

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