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Friends of friends: are indirect connections in social networks important to animal behaviour?

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Friend of a friend relationships, or the indirect connections between people, influence our health, well-being, financial success and reproductive output. As with humans, social behaviours in other animals often occur within a broad interconnected network of social ties. Yet studies of animal social behaviour tend to focus on associations between pairs of individuals. With the increase in popularity of social network analysis, researchers have started to look beyond the dyad to examine the role of indirect connections in animal societies. Here, I provide an overview of the new knowledge that has been uncovered by these studies. I focus on research that has addressed both the causes of social behaviours, i.e. the cognitive and genetic basis of indirect connections, as well as their consequences, i.e. the impact of indirect connections on social cohesion, information transfer, cultural practices and fitness. From these studies, it is apparent that indirect connections play an important role in animal behaviour, although future research is needed to clarify their contribution.

Sociality is a strategy most animals use to cope with their environments, allowing them to survive and reproduce in conditions that may not be conducive to survival and reproduction (Dunbar, 1988). To further our understanding of this essential facet of life, studies of animal behaviour have set out to determine the evolutionary forces that shape social behaviours and the proximate mechanisms that underlie their production (Mayr, 1961; Tinbergen, 1963). To date, studies have tended to focus on associations between pairs of animals: who interacts with whom and in what manner (Krause, James, & Croft, 2010). However, social behaviour almost always occurs within a polyadic network of social ties (Madden, Drewe, Pearce, & Clutton-Brock, 2011) (Fig. 1a, b). Animals are not only connected to the individuals with whom they interact directly (direct connections), but are also tied indirectly to the partners of their social partners (indirect connections) (Croft, James, & Krause, 2008; Krause, James, & Lusseau, 2009; Sih, Hanser, & McHugh, 2009; Wey & Blumstein, 2010) (Fig. 1c). Indirect connections can extend up to multiple degrees of separation (the partners of your partners' partners' partners' partners) and can ultimately result in everyone in a population being connected to everyone else (Fig. 1d). In human parlance, we refer to these connections as friends of a friend (or enemies of an enemy) and these relationships have been shown to affect peoples' health, well-being and financial success, including how happy a person feels (Fowler & Christakis, 2008), how much they weigh (Christakis & Fowler, 2007), as well as their ability to find a job (Pellizzari, 2010). Friend of a friend relationships in people have also been shown to be heritable (Fowler, Dawes, & Christakis, 2009) and to influence fertility (Balbo & Barban, 2014). In humans at least, understanding the causes and consequences of sociality seems to in part depend on understanding indirect connections. We must therefore ask, are indirect connections important to other animals? And what information, if any, do researchers studying animal behaviour gain by extending their view beyond dyadic associations?

Here, I aim to demonstrate that there is mounting evidence that indirect connections are important to our understanding of animal behaviour. Social network analysis is the leading technique used to detect and quantify indirect connections. The rise in popularity of social network analysis in animal behaviour research (Brent, Lehmann, & Ramos-Fernández, 2011; Croft et al., 2008; Wey, Blumstein, Shen, & Jordan, 2008) has meant that the number of

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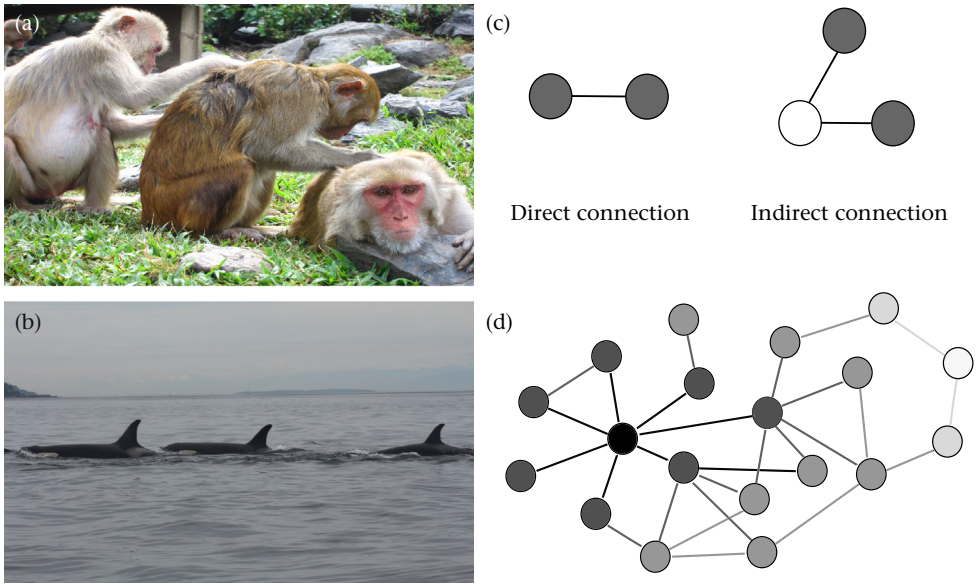

Figure 1. Direct and indirect connections in animal social networks. Social interactions occur in a polyadic network of social ties in gregarious species such as (a) rhesus macaques, *Macaca mulatta*, and (b) killer whales, *Orcinus orca*. Indirect connections can emerge from a number of different types of association, including (a) grooming and (b) nearest-neighbour proximity. In both (a) and (b), the individual on the far left is indirectly connected to the individual on the far right via their mutual direct connections to the individual in the middle. Direct and indirect connections can be represented graphically in social networks, whereby nodes are connected via lines representing associations. Here, grey nodes represent individuals that are connected to each other directly or indirectly (c). Together, direct and indirect connections can result in every actor being connected to every other actor in a population. In the cartoon network (d), the black node is connected to all other nodes, with node darkness decreasing as social distance to the black node increases. Photos: L. J. N. Brent.

studies that have examined indirect connections has grown rapidly in recent years. I provide an overview of many of these studies, which I have organized into six broad sections intended to represent some of the major lines of research in which indirect connections have made, or have the potential to make, the greatest impact. These lines of research explore (1) the genetic basis of indirect connections, (2) the fitness consequences of indirect connections, (3) the association between indirect connections and social cohesion, (4) the impact of indirect connections on the transmission of information, (5) the maintenance of cooperation through indirect connections and (6) the cognitive basis of indirect connections. In each section, I attempt to highlight studies that have uncovered new and important information that would not have been revealed had the focus been solely at the level of dyadic associations. I conclude by summarizing of some of the major outstanding questions in the hopes of directing future research. I begin, however, by reviewing the different ways individuals can be indirectly connected and how those differences can be measured using social network analysis.

MEASURING INDIRECT CONNECTIONS USING SOCIAL NETWORK ANALYSIS

Social network analysis is a powerful analytical tool that allows researchers to investigate the complex webs of interconnections that exist between individual members of populations. One of the principal advantages of social network analysis is that it provides an array of measures of individual sociality, often referred to as network position or centrality, which represent the extent to which an individual is connected to others (Borgatti, Mehra, Brass, & Labianca, 2009; Wasserman & Faust, 1994). This includes both direct and indirect connections and thus allows researchers to explore both types of association simultaneously.

In social network analysis there are two main direct measures of centrality, called degree and strength, respectively. These measures are equivalent to those traditionally used in animal behaviour research, whereby centrality is quantified using either an individual's number of partners (degree) and/or the amount of time they spend associating with others (strength) (Brent, Lehmann, et al., 2011; Wey et al., 2008). In addition, there are a number of social network-based measures that reflect indirect connections between individuals by taking into account both an actor's centrality, as well as her contribution to the centrality of the others (Madden et al., 2011). In Table 1, I describe in detail the indirect measures of centrality most commonly used in animal behaviour research, which include reach, clustering coefficient, betweenness, eigenvector centrality, closeness and information centrality. Reach, for example, represents the number of degrees of separation (k) between individuals (Milgram, 1967). Individuals with high reach are connected to a large number of others who are k degrees of separation away (Fig. 2). Reach is important because it can detect behavioural contagion (Flack, Girvan, de Waal, & Krakauer, 2006): individual A can direct aggression towards individual B, which can induce B to direct aggression towards C. Thus individual A directly impacts upon the social life of individual C, despite the fact they do not interact directly. Clustering coefficient, on the other hand, reflects the extent to which an individual's local social network is interconnected, i.e. whether or not an individual's social partners are partners with each other (Newman, 2003), and can be important for fission–fusion dynamics and collective foraging (Fig. 2). For example, individual A can only forage next to individuals B and C if B and C also have a relationship of mutual tolerance. Betweenness is another measure that captures the interconnectedness of subgroups. However, unlike clustering coefficient, individuals with high betweenness tend to interact with individuals who do not interact with one another (Freeman, 1977). By connecting disparate parts of the network, betweenness can be important for maintaining group cohesion, as well as influence the transfer of information, disease and resources between group members (Freeman, 1977). Measures of centrality can be based on associations that are directionless (there is no giver or receiver) and that are coded in a binary fashion (yes = an association occurred, no = no association

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