Animal Behaviour 141 (2018) 29–44

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Estimating the robustness and uncertainty of animal social networks using different observational methods

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ARTICLE INFO

Article history:
Received 23 June 2017
Initial acceptance 18 August 2017
Final acceptance 19 March 2018

MS. number: A17-00503R

Keywords:
animal social network
focal sampling
observational sampling method
proximity network
scan sampling
social organization

Social network analysis is quickly becoming an established framework to study the structure of animal social systems. To explore the social network of a population, observers must capture data on the interactions or associations between individuals. Sampling decisions significantly impact the outcome of data collection, notably the amount of data available from which to construct social networks. However, little is known about how different sampling methods, and more generally the extent of sampling effort, impact the robustness of social network analyses. Here, we generate proximity networks from data obtained via nearly continuous GPS tracking of members of a wild baboon troop (*Papio anubis*). These data allow us to produce networks based on complete observations of interindividual distances between group members. We then mimic several widely used focal animal sampling and group scanning methods by subsampling the complete data set to simulate observational data comparable to that produced by human observers. We explore how sampling effort, sampling methods, network definitions and levels and types of sampling error affect the correlation between the estimated and complete networks. Our results suggest that for some scenarios, even low levels of sampling effort (5–10 samples/individual) can provide the same information as high sampling effort (>64 samples/individual). However, we find that insufficient data collected across all potentially interacting individuals, certain network definitions (how edge weights and distance thresholds are calculated) and misidentifications of individuals in the network can generate spurious network structure with little or no correlation to the underlying or 'real' social structure. Our results suggest that data collection methods should be designed to maximize the number of potential interactions (edges) recorded for each observation. We discuss the relative trade-offs between maximizing the amount of data collected across as many individuals as possible and the potential for erroneous observations.

To understand the complexity of group structure and how individual behaviours impact group-level dynamics, we need to consider all relationships linking group members. Social network analysis provides a powerful framework to analyse the variety and variability of interindividual connections within groups, including the strength and extent of relationships between group members (Wey, Blumstein, Shen, & Jordan, 2008). This analytical social network approach has provided insight into cooperation (Croft et al., 2006; Ohtsuki, Hauert, Lieberman, & Nowak, 2006), mating success (Ryder, McDonald, Blake, Parker, & Loiselle, 2008; Schlicht, Valcu, & Kempenaers, 2015; Scott, 1991), information transfer (Allen, Weinrich, Hoppitt, & Rendell, 2013; Aplin et al., 2015; Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Brown, 1986; Couzin, James, Mawdsley, Croft, & Krause, 2007; Farine, Aplin, Sheldon, & Hoppitt, 2015; Valente, 1995), disease transmission (Adelman, Moyers, Farine, & Hawley, 2015; Cross et al., 2004; Duboscq, Romano, Sueur, & MacIntosh, 2016; VanderWaal, Atwill, Isbell, & McCowan, 2014; Watts & Strogatz, 1998) and the selective consequences of the social environment (Brent et al., 2013; Farine & Sheldon, 2015; Formica et al., 2011; Fowler & Christakis, 2008; Oh & Badyaev, 2010; Wey, Burger, Ebensperger, & Hayes, 2013).

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https://doi.org/10.1016/j.anbehav.2018.04.012

However, although existing studies use a wide variety of approaches to capture social relationships, how different data collection methods impact the results in social networks studies is rarely investigated.

At its simplest, a social network represents a set of individual entities, represented as ‘nodes’, and the connections between them, represented as ‘edges’ (Wasserman & Faust, 1994). The aim of social network analysis is to quantify the extent or strength of relationships between individuals and explore the group- or population-level structure that emerges. Relationships can be defined based on particular interactions, such as grooming or dominance, or from associations defined by spatial proximity (see Carter, Lee, & Marshall, 2015; Castles et al., 2014; Farine, 2015, for a discussion on the relationship between these measures). Edges typically represent the rate or probability that two individuals interact or associate in time (Farine, 2015; Whitehead, 2008), with stronger relationships having larger edge values. The set of connections that the edges form can then be captured, or described, using different social network metrics. Metrics can be calculated at the individual level (e.g. degree, how many connections each individual has or how well connected it is relative to others), or at the level of the entire network (e.g. edge density, the proportion of all possible edges that are present in the network). Individual-level and network-level metrics are influenced both by the biology of the study organism and also the definitions used to record observations. For example, using a large distance threshold to capture spatial associations will result in more associations per observation and, thus, a higher individual average degree and higher network density. Essential factors to consider when designing social network studies include the definition of an association or interaction, the method used to calculate network edge weights, the potential for and impact of observation errors and the resolution at which the data can be collected.

An important feature of animal social networks is that the number of connections (edges) between individuals often greatly exceeds the number of individuals in the study system or group. Furthermore, because network metrics are constructed from many edges, the quality of a network is only as good as its most uncertain edge. Thus, large quantities of data across all edges are required to build an accurate and meaningful social network because data must be collected on all pairs of individuals that could potentially interact. Without sufficient sampling, the resulting network model may have little basis in reality (James, Croft, & Krause, 2009). Missing connections between individuals can have significant implications on social network structure, even when the missing relationships are weak (see Figure 2 in Farine & Whitehead, 2015). In fact, weak edges form a critical aspect of social structure that has long been used to justify the importance of studying social networks in human and animal systems (Granovetter, 1973). Simulation studies have shown that the number of observations of each pair of individuals in the study is the most important factor determining how well a network represents the underlying patterns of interactions. Franks, Ruxton, and James (2010) suggested that to construct a robust representation of a real social network, a minimum of 20 potential observations (i.e. both individuals are observed associating or not associating) for each pair of individuals is necessary (see also Farine & Strandburg-Peshkin, 2015). Other analyses show that a minimum of 15 independent observations where two individuals could have interacted is essential to obtain 95% confidence in the strength of their relationship (Whitehead, 2008). Thus, for large networks containing many individuals and many edges, this could amount to thousands of necessary observations. The results of these simulation studies hold equally true for networks constructed from associations or from interactions. Furthermore, the importance of accurately quantifying each edge in the network can far exceed the need to sample every individual in a population, which can seem counterintuitive. Silk, Jackson, Croft, Colhoun, and Bearhop (2015) found that as few as 30% of individuals are needed to form an accurate representation of those individuals' relative positions in the social network, suggesting that priority should be given to collecting more samples per dyad (edges) rather than more individuals (nodes). Additionally, some observational methods collect data on more pairwise associations per unit time than others. At present, empiricists lack guidance as to the relative trade-offs between sampling strategies for defining social networks.

The behavioural data that are central to social network analysis can be collected in a variety of ways, with the sampling regime, level of sampling effort and the definition of interactions (edges) often differing from study to study (see Supplementary material 1, Table S1). Focal sampling and scan sampling are the two main approaches to collect observational data on animal behaviour (Altmann, 1974). Focal sampling centres on the actions of a single individual over a set period of time, while with group scan sampling, observers take a ‘snapshot’ where they record the behaviours of all visible members of the group at designated points in time. Studies of animal social networks also vary substantially in their sampling effort, in terms of the number of individuals sampled, the length of each sample, the number of repeated samples and the overall duration of the study (see Table S1). For example, based on our review of the literature, studies of primate social networks range from 18 3-minute focal follows per individual over 2 weeks (brown capuchins, *Cebus apella*, and common squirrel monkeys, *Saimiri sciureus*: Dufour, Sueur, Whiten, & Buchanan-Smith, 2011) to almost 10 h focal follows over a period of 9 years (chimpanzees, *Pan troglodytes*: Lehmann & Boesch, 2009). Sampling effort for scan sampling also varies widely across different animal species studied, from 20 total group scans over a period of 10 days where all individuals were visible in a study of Kuhl's pipistrelle bats, *Pipistrellus kuhlii* (Ancillotto, Serangeli, & Russo, 2012) to over 73 790 group scans over 27 years in humpback whales, *Megaptera novaeangliae* (Allen et al., 2013). Studies also vary in how they define relationships or associations. In the case of spatial proximity networks, many studies use a threshold, where all individuals within a certain radius of the focal individual are noted (Crofoot, Rubenstein, Maiya, & Berger-Wolf, 2011; Fraser, Schino, & Aureli, 2008; Furuichi, 1983; Matthews, 2009; Nakamichi & Koyama, 1997; Szykman et al., 2001). Other studies note the identity and distance of the focal individual's nearest neighbour (Henzi, Lusseau, Weingrill, van Schaik, & Barrett, 2009; King, Sueur, Huchard, & Cowlishaw, 2011; Silk, Altmann, & Alberts, 2006), or use a combination of nearest neighbour and threshold methods, recording the nearest neighbour up to a certain distance (Clark, 2011; Suzuki & Sugiura, 2011; Watts, 1992). A further alternative is the chain rule, or ambit (see Rimbach et al., 2015; Viscido & Shrestha, 2015). Here, individuals within a certain proximity of each other are connected, and the total set of individuals that can be linked together without any breaks are considered to be connected to one another (Ramos-Fernández, Boyer, Aureli, & Vick, 2009; Wolf, Mawdsley, Trillmich, & James, 2007).

The definition of edge weights (i.e. the strength of individuals' relationships) provides yet another layer of variation in research on animal social networks. While most studies calculate a rate over time (e.g. the proportion of observations of animal A in which it groomed animal B), some studies (e.g. Castles et al., 2014; Fraser et al., 2008) instead estimate the proportion of interactions directed towards each social partner (e.g. the proportion of animal A's grooming events directed towards animal B). While the latter may be useful when investigating the relative investment made by an individual towards all its potential interaction partners, Farine (2015) argues that this approach is not appropriate for estimating