Animal Behaviour 96 (2014) 59–67

Contents lists available at ScienceDirect

Animal Behaviour

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

Commentary

Social networks created with different techniques are not comparable

Madelaine Castles [a,1], Robert Heinsohn [a], Harry H. Marshall [b,c,1,2], Alexander E. G. Lee [b,c,2], Guy Cowlishaw [b], Alecia J. Carter [a,b,d,*]

[a] The Fenner School of Environment and Society, The Australian National University, Acton, Canberra, ACT, Australia
[b] The Institute of Zoology, Zoological Society of London, Regent's Park, London, U.K.
[c] Division of Ecology and Evolution, Department of Life Sciences, Imperial College London, Silwood Park, Berkshire, U.K.
[d] Large Animal Research Group, Department of Zoology, University of Cambridge, Cambridge, U.K.

ARTICLE INFO

Article history:
Received 17 February 2014
Initial acceptance 20 March 2014
Final acceptance 18 July 2014
Published online 21 August 2014
MS. number: 14-00139R

Keywords:
association
baboon
interaction
Papio ursinus
social connection
social network analysis

The recent application of social network analysis to animal populations has provided a tool to quantify group dynamics and individual social positions, which may enhance our understanding of the costs and benefits of sociality and the evolution of behavioural strategies within societies. Despite this, uncertainties remain about whether comparisons can be drawn between studies in which different sampling techniques have been used. We compared social networks constructed from two interaction and three proximity techniques that are frequently used in the literature, at both the ego network and global network levels, using data collected annually for two troops of chacma baboons, *Papio ursinus*, over 3 years. We obtained very different results at both the global and individual levels, demonstrating the clear distinction between networks built using different interaction and proximity techniques. While interaction techniques may be comparable at the whole global level, proximity techniques were not, and we found the opposite at the ego network level: proximity techniques could be compared whereas interaction techniques could not. As there was a clear distinction between the networks created, caution should be taken when using proximity as a proxy for social interactions (and vice versa) in social network studies. Further, our results showed high variation between troops and study seasons, reemphasizing the importance of incorporating temporal change in the analysis of social networks. Researchers should consider the effects of sampling technique on the networks produced when comparing networks created from different techniques.

Sociality has played an important role in the ecology and evolution of many species and vice versa (Croft, James, & Krause, 2008; Krause & Ruxton, 2002; Silk, 2007). The patterns of interactions and the relationships that individuals form can have important fitness consequences by affecting, for example, longevity (Silk et al., 2010), reproductive success (Cameron, Setsaas, & Linklater, 2009) and offspring survival (Silk et al., 2009). These patterns of interaction also underpin the overall structure of society which can determine the transmission of disease (Hamede, Bashford, McCallum, & Jones, 2009) and the flow of information (Voelkl & Noë, 2008). By understanding individual behaviour, patterns of association and population-level structure, biologists can unlock the function, evolution and implications of social living (Croft et al., 2008).

Despite the importance and fitness implications of an individual's social network position, little attention has been given to how the connections between individuals that make a social network are defined (but see Lehmann & Ross, 2011). Ideally, all interactions between individuals would be recorded; however, this is extremely difficult to achieve in wild populations (Croft et al., 2008). Instead, an array of techniques has been developed to sample social interactions in populations (Altmann, 1974; Whitehead & Dufault, 1999). These techniques can be grouped into two overarching categories. First, 'interaction methods' comprise techniques based on observed physical contact or behavioural interactions between individuals (e.g. grooming in chacma baboons, *Papio ursinus*: Henzi, Lycett, & Weingrill, 1997). Second, 'proximity' or 'association methods' are used when interactions cannot be observed, such as with aquatic animals (e.g. dolphins, *Tursiops* spp.: Lusseau, 2003) or 'undemonstrative' species (e.g. kangaroos,

---

[*] Correspondence: A. J. Carter, Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.
E-mail address: ac854@cam.ac.uk (A. J. Carter).

[1] Present address: Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Cornwall, U.K.

[2] These authors contributed equally.

http://dx.doi.org/10.1016/j.anbehav.2014.07.023

Macropus giganteus: Carter, Macdonald, Thomson, & Goldizen, 2009). Under this category, a connection is assumed through spatial proximity or shared resource use. Although these two broad techniques may suit the study species or purpose of the research in question, they may present a different perspective of the network. For example, there may be many reasons for individuals to associate that do not relate to a positive social relationship (Pinter-Wollman et al., 2014). These include periods of shared resource use (e.g. shade) or for exploitation of information (Barton & Whiten, 1993), and each aspect may affect individuals' social environment in different ways. Consequently, comparing populations or species for which different techniques have been utilized is unlikely to be justified without an investigation of different sampling effects in the same population.

Few studies have attempted social network comparisons within species using different data collection techniques. This is a potential oversight, as comparisons could lead to better understanding of the aspects of social life determining an individual's fitness and hence the evolutionary forces shaping social behaviour (Davies, Krebs, & West, 2012). Better understanding of how different techniques affect the resulting network will make comparisons more robust and powerful. To our knowledge, only three studies have directly compared networks constructed using different data collection techniques. Lehmann and Ross (2011) used multiple behavioural interactions to determine networks in a troop of olive baboons, *Papio anubis*. The behaviour used to create a network strongly affected its shape and the position of individuals within the network, leaving the authors to conclude that the use of multiple types of social interactions was necessary to gain the most accurate understanding of the network. Further, Madden, Drewe, Pearce, and Clutton-Brock (2011) studied behavioural connections in meerkats, *Suricata suricatta*, and came to a similar conclusion. However, both of these studies compared only networks based on interactions. A study by Hobson, Avery, and Wright (2013) utilized interaction and association techniques in a captive setting to examine how networks form over time and found a clear difference between the two techniques. However, no studies have yet explicitly compared weighted networks that have been constructed using both proximity and interaction techniques in a wild population. This is an important comparison as, in a large proportion of wild species and systems, proximity data are often used as a substitute where interactions cannot be directly observed.

We aimed to make a thorough comparison of the two broad categories of techniques used to gauge sociality in animal populations, namely proximity and interactions between individuals. We calculated ego- and global-level network metrics to compare these techniques when applied to proximity and interaction data from chacma baboons, collected over 3 years. Chacma baboons are an ideal study system as the social environment of baboons is well studied (Henzi, Lusseau, Weingrill, Schaik, & Barrett, 2009; King, Clark, & Cowlishaw, 2011; King, Douglas, Huchard, Isaac, & Cowlishaw, 2008; Silk et al., 2010), social relationships are highly differentiated (Silk, Alberts, & Altmann, 2006) and have significant consequences for individual fitness (Silk, Alberts, & Altmann, 2003; Silk et al., 2009). Importantly for this study, chacma baboons allow for the simultaneous collection of both proximity and interaction data, facilitating direct comparison between these two widely used sampling techniques. As the overall (global) network structure and individuals' positions (local network) within it determine the characteristics of a population (Croft et al., 2008), we aimed to address two specific questions regarding these network levels. (1) Do different proximity and interaction techniques for defining a connection create structurally similar networks at the global level? (2) Do individuals exhibit similar local positions in both types of network?

METHODS

Field Site and Study Species

We studied wild baboons in Tsaobis Nature Park, a semiarid environment on the edge of the Namib Desert in the Erongo region, Namibia (22°22′S 15°44′E; for detailed information on the landscape and climate see Cowlishaw, 1997). We collected data on two habituated troops of baboons, ‘L’ and ‘J’, over 3 years (2010–2012; Table 1). In all years only adult and subadult individuals were recorded. Baboons younger than 4 years (infants and young juveniles) were not included, as infant baboons and other primates maintain a social environment similar to that of their mothers' which extends into their early juvenile years (for example, rhesus macaques, *Macaca mulatta*, Berman, 1982). Numbers of adults and subadults in the group ranged from 22–23 and 27–31 individuals in L and J troops, respectively. Females made up 74–77% of the adult population in L troop and 52–63% of J troop. Females were not chosen as focal subjects while they were in oestrus owing to documented changes in the behaviour and social connections of chacma baboons and other closely related species at these times (Kawai, 1979; Nyakudya, Fuller, Meyer, Maloney, & Mitchell, 2012). They were, however, recorded when they were involved in an interaction or connection with other individuals under observation.

Observers followed the troops from dawn until dusk collecting data on social connections using both continuous focal and scan sampling methods (Altmann, 1974). Data were collected from May to September 2010, June to August 2011 and May to October 2012 (Table 1) using Hewlett-Packard iPAQ 112 and 114 Personal Digital Assistants (Bracknell, Berkshire, U.K.) and Motorola MC35 and ES400 (Libertyville, IL, U.S.A.) with the sequence-based data entry program CyberTracker3 (http://cybertracker.org) and a customized spreadsheet in SpreadCE version 2.03 (Bye Design Ltd 1999), respectively. All adult and subadult baboons were individually identifiable.

Individual baboons were observed for 15–30 min periods using continuous focal sampling. Focal observations that lasted under 15 min were discarded. Individuals were sampled in a semirandom manner, balancing cumulative focal time recorded for each individual to ensure even sampling over four time periods in each day (0600–0900, 0900–1200, 1200–1500 and 1500–1800 hours). We avoided sampling the same individual within 6 h of a previous observation to maximize the independence of observations. Over the 3 years, we recorded 718 h of focal observation data for L-troop individuals and 942 h for J-troop individuals. If any individual was not present with its troop for the entire data collection season within a year, that individual was removed from the analyses for that field season. In the majority of cases, such losses of individuals were due to adult male emigration (2010: $N = 3$; 2011: $N = 1$);

Table 1
The sample sizes for each of the five sampling methods and two troops over the 3 years of data collection

Year	Troop	*N*	Chain rule scans	Distance rule scans	Nearest neighbour	Affiliative interactions	Grooming interactions
2010	L troop	23	370	394	272 h 16 min	318	7 h 43 min
	J troop	30	433	458	346 h 37 min	454	5 h 27 min
2011	L troop	23	174	247	122 h 43 min	135	4 h 31 min
	J troop	27	233	283	142 h 37 min	212	3 h 48 min
2012	L troop	22	346	412	210 h 46 min	335	11 h 20 min
	J troop	31	467	583	274 h 57 min	291	9 h 47 min

Presented are the number of individuals (*N*) and the counts of chain rule scans, distance rule scans and affiliative interactions. The nearest neighbour and grooming interactions are presented as a total time. Note that the nearest-neighbour time represents the total focal time.