Animal Behaviour 85 (2013) 1397–1405

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

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

Structural balance in the social networks of a wild mammal

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ARTICLE INFO

Article history:
Received 6 December 2012
Initial acceptance 2 January 2013
Final acceptance 6 March 2013
Available online 21 April 2013
MS. number: A12-00922R2

Keywords:
network motif
Procavia capensis
rock hyrax
social network
social structure
structural balance theory

The social structure of a population is based on individual social associations, which can be described using network patterns (motifs). Our understanding of the forces stabilizing specific social structures in animals is limited. Structural balance theory was proposed for exploring social alliances and suggested that some network motifs are more stable than others in a society. The theory models the presence of specific triads in the network and their effect on the global population structure, based on the differential stability of specific triad configurations. While structural balance was shown in human social networks, the theory has never been tested in animal societies. Here we use empirical data from an animal social network to determine whether or not structural balance is present in a population of wild rock hyraxes, *Procavia capensis*. We confirm its presence and show the ability of structural balance to predict social changes resulting from local instability. We present evidence that new individuals entering the population introduce social instability, which counters the tendency of social relationships to seek balanced structures. Our findings imply that structural balance has a role in the evolution of animal social structure.

Long-term social alliances have been studied extensively in various taxa, although the focus has been mainly on primates and cetaceans (e.g. Silk 2007; Randić et al. 2012). It has been argued that cognition is important in the maintenance of long-term relationships (Emery et al. 2007; Holekamp et al. 2007). Social integration has been shown to affect reproductive success (e.g. Silk 2007; Cameron et al. 2009) and longevity (Barocas et al. 2011). Nevertheless, our knowledge about the structure and function of social bonds in many species is lacking (Silk 2007). We have limited understanding of the reasons why certain animals aggregate in groups of various sizes, and of various internal social structures and levels of stability. These structures are the result of behavioural choices of individuals that construct them, and therefore individual preferences are expected to affect changes in social networks through time. To understand these mechanisms, there is a need to examine how local social structures emerge and change, and how individual actions contribute to local and global changes in the social network. The recent application of network theory to animal sociality has refuelled an interest in animal social structure (McDonald 2007; Croft et al. 2008; Wey et al. 2008; Krause et al. 2009). Analyses of social networks have produced remarkable insights, such as identifying key individuals in a social structure (Lusseau & Newman 2004), describing the cohesion of social groups (Lusseau 2003) and deciphering the interaction between sociality and disease transmission (Hamede et al. 2009). However, little is known about how social preferences at the individual level affect the global social landscape and its temporal dynamics (Lusseau et al. 2006).

The analysis of small network motifs as building blocks of complex networks has recently gained recognition (Milo et al. 2002; Mangan & Alon 2003). An early use of network motifs can be found in the theory of structural balance, one of the most influential theories describing social structure in humans (Heider 1946; Cartwright & Harary 1956). This theory describes the relationships between individuals in terms of triads, with each triad containing three individuals and three signed ties (ties having positive or negative values) between them (Fig. 1). Triads are considered balanced if all three nodes are 'friends' of each other (+++), or if two of them are 'friends' while both are 'enemies' of the third node (+−−). The other two options (++−,−−−) are considered unbalanced, since the inherent tension in these triads may drive them into more balanced configurations. In a ++− triad, the theory predicts a shift towards +++ or +−−, which are considered balanced. For a −−− triad, the theory posits that

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0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2013.03.032

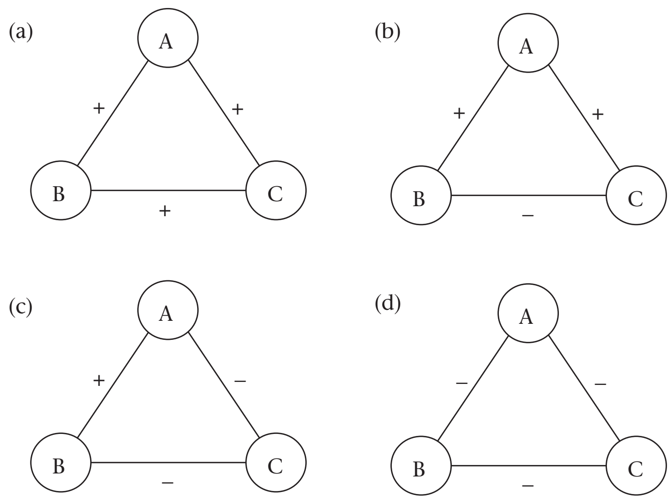

Figure 1. Four types of triads are possible if each tie between two individuals stands for a positive (+) or a negative (−) association. Triads (a) and (c) are considered balanced, while triad (b) is unbalanced. Triad (d) is considered balanced under weak structural balance and unbalanced under strong structural balance.

eventually, an alliance is expected to form between two of the three enemies. A −−− triad, in which all nodes are 'enemies', is none the less considered balanced under 'clustering' (Davis 1967), later termed 'weak structural balance' (Leskovec et al. 2010). Weak, or generalized, structural balance is empirically more common than strong (regular) structural balance in human social networks (Leskovec et al. 2010; van de Rijt 2011), although recently, strong structural balance was demonstrated in a large human online network (Szell et al. 2010). The potential power of structural balance theory is in its ability to predict social changes, based on a given triad configuration. In contrast, by examining social structure only at the dyad level, one cannot make any predictions other than the trivial prediction that the dyad edge would remain in the same state. A dyad current state cannot predict any future state without other specific knowledge, for example we may know that 'friends' in a specific group may not be 'friends' in the future.

Why should balanced triads be preferred from an evolutionary point of view? A member of an unbalanced ++− triad is found in a constant contradiction; if an individual in such a triad cooperates with another member of the triad, it ultimately harms its interests (e.g. cooperation) regarding the third member. For example, let us consider individual B in Fig. 1b. If he cooperates with A, he indirectly helps A's other ally, namely C, however C is his competitor. This contradiction is solved only in balanced triads. For example, in a +−− triad (Fig. 1c), if B helps A there is no conflict of interests, as both A and B are competitors of C. Thus, the basic rules of cooperation are those that favour certain triad types over others. In turn, this leads to specific favourable social structures, in which individuals are members of groups, and the members of one group compete with those of another.

Analysis of network triads should take into account lower-order network properties such as dyads, since these have been shown to explain some of the variance in triad types (Faust 2008). For example, a network in which the number of positive associations is high is expected to have a high proportion of +++ triads. In addition, the degree distribution (the distribution of the number of positive and negative ties each individual has) of the network should also be taken into account, since triads may be a consequence of differences in sociality between individuals.

The main prediction of strong structural balance is that for a social network to remain balanced, all individuals should compose a single group, or alternatively two groups in which every pair of individuals in the same group are 'friends', while no friendships occur between the two groups (Cartwright & Harary 1956; Marvel et al. 2011). Strong structural balance allows up to two groups only because under this configuration the unbalanced −−− triads cannot be formed. Under 'weak structural balance', where all-negative (−−−) triads are considered balanced, the prediction is of several groups following the same rule (Kułakowski et al. 2005; Fig. 2). Any positive ties between members of different groups are expected to disturb the structural balance through the formation of ++− triads, which are considered unbalanced (Cartwright & Harary 1956).

We analysed social bonds in a free-living rock hyrax, *Procavia capensis*, population, using 8 years of accumulated behavioural data collected in Ein Gedi, Israel. The group-living rock hyrax is a plural breeder, and the cohesive social units are mainly composed of females. Reproductive skew is low among females, with most female group members able to annually reproduce (Koren 2000; Koren & Geffen 2009). Male hyraxes disperse as juveniles, between the ages of 16 and 30 months, and are mostly solitary (Hoeck 1982). Rock hyraxes are an ideal system to test theories of social changes and temporal stability of network motifs because their social associations are relatively stable within years but undergo changes between years (Barocas et al. 2011).

We used observational data of social associations of the rock hyrax to answer the following questions. (1) Does structural balance apply to wild populations of the rock hyrax? (2) Do local social ties change over time according to structural balance predictions (i.e. towards more balanced social configurations)? (3) Does sex ratio affect the destiny of unbalanced social configurations? Since male hyraxes tend to be more aggressive than females, we predicted that unbalanced triads including only females will tend to change to +++, while triads including one or more males will tend to change to −−− or +−− triads. (4) Do new individuals contribute to instability more than expected by chance?

METHODS

Ethical Note

The rock hyrax is a wild animal protected under Israeli law. Research permits are issued by a governmental agency, The Nature

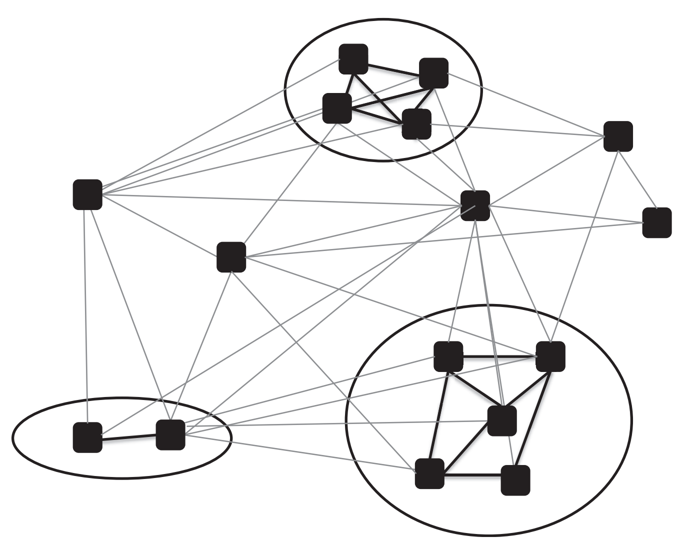

Figure 2. An illustration of the prediction of the Cartwright & Harary (1956) theorem for weak structural balance. A population should theoretically form separate groups where any two members within a group have a positive (+) tie between them, while any two individuals from different groups have a negative (−) tie between them. Note that a group may have only a single individual in it. Black bold lines represent positive edges while grey lines represent negative edges.