Structural balance in the social networks of a wild mammal

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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.
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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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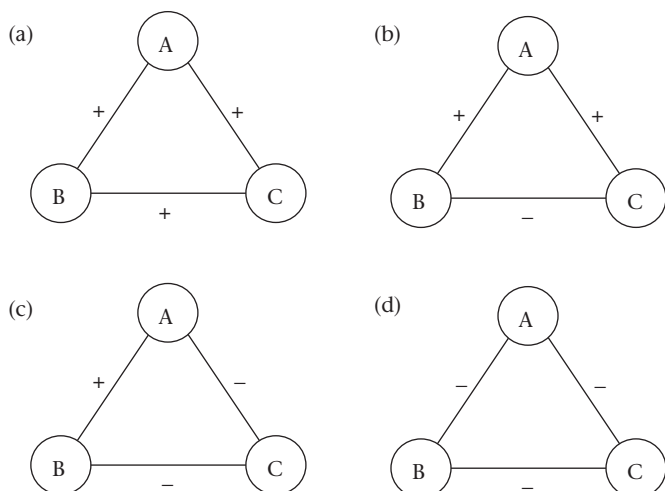 *E-mail address:* amiyaal@gmail.com (A. Ilany).

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
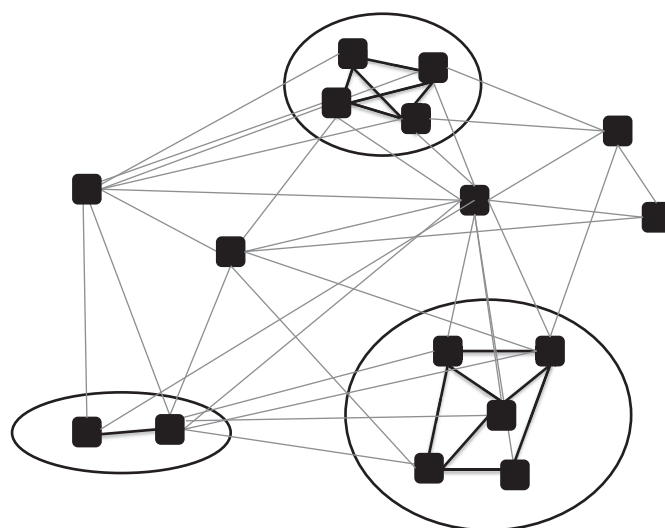

Figure 2. An illustration of the prediction of the Cartwright & Harary (1956) theorem for weak structural balance. A population should theoretically form separate groups where any two members within a group have a positive (+) tie between them, while any two individuals from different groups have a negative (−) 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.

and Parks Authority (NPA), which is responsible for all research done on wildlife in Israel. Permits for capturing, marking and handling hyraxes in Ein Gedi were issued and reviewed annually by the NPA (permit numbers: 2000/8871, 2001/8871, 2002/14674, 2003/14674, 2004/17687, 2005/17687, 2007/27210, 2008/31138, 2009/32871). Animals were observed from a distance of more than 50 m, unless they came closer to the observers, to minimize interference in their activities. Trapping and marking procedures are detailed in the next section.

Study Site and Population

We have been conducting a long-term study on rock hyrax behaviour at the Ein Gedi Nature Reserve (31°28′N, 35°24′E) since 1999. Our study sites are located in two deep gorges, David and Arugot, which constitute part of the reserve situated west of the Dead Sea, Israel. During each field season, which varied in length from 3 to 6 months, rock hyraxes were trapped and observed daily. We used Tomahawk live box traps, which were placed in secure shady spots, and baited with cabbage and kohlrabi. Since rock hyraxes are diurnal, traps were opened for 3 h in the morning to minimize stress to animals. Trapped animals were anaesthetized with ketamine-hydrochloride (0.1 mg/kg), fitted subcutaneously with microchips (Datamars SA, Bedano, Switzerland), as well as with either an eartag or a light collar (weighing < 5 g) with tags attached for individual identification. Captured hyraxes were sexed, weighed and measured. Animals were allowed 90–150 min of recovery after anaesthesia and were kept in shaded locations to protect them from overheating. To prevent the risk of choking after anaesthesia and because hyraxes were rarely observed drinking, no food or water was supplied during recovery. Recaptures were not anaesthetized and were released immediately after weighing. An average of 35.3 individuals were observed in each population/year (Table 1).

Behavioural Observations and Network Analysis

Hyrax activity was observed 5 days per week during the field season using 10 × 42 binoculars and a telescope with 50–100X magnification (C5 spotting scope, Celestron, Torrance, CA, U.S.A.). Observations were conducted in the morning from first light until noon, when hyraxes in Ein Gedi retreat to their shelters. Each day, a focal group was randomly chosen and followed (Altmann 1974). We recorded social interactions within a group, and interactions with nongroup members in a given area. Hyraxes spend most of their time foraging and resting (e.g. Sale 1970; Ilany et al. 2013), making it easy to follow multiple individuals simultaneously. However, we could not measure the exact duration of all pairwise social interactions due to limited visibility (e.g. uneven terrain, rocks, trees and bushes). We used a resolution of 1 day to define whether two individuals were seen interacting socially, regardless of the duration of the interaction. Every year a mean ± SE of 95 ± 0.5% of the hyraxes in our study populations were marked, facilitating minimal bias in recording the social structure of each population. The few social interactions that included unmarked individuals were excluded from the analysis. We defined positive interactions as any that included physical contact (i.e. huddle or hole up together in a sleeping burrow), or those that showed coordinated activity (move together in close proximity and sit by one another, but not in an agonistic context such as a chase). More than 95% of the positive interactions were coordinated movements. In contrast, antagonistic behaviours included displacement, exposing large incisors, growling, grinding molars, snapping, chasing and biting other hyrax (Estes 1991; Koren et al. 2008).

While the social structure of the Ein Gedi population is relatively stable during the field seasons, there are many changes between

years due to dispersal, births and changes in social affiliations inside the population. Consequently, for each year (i.e. field season) and population (David, Arugot) we constructed a network as follows: if two individuals were observed in at least one positive interaction during the year, the value of the association between them was set to +1; otherwise, it was set to 0. Thus, the constructed network depicts for each two hyraxes whether they were overall 'friends' or not (i.e. 'nonfriends'). It is important to note that 'nonfriends' are distinct from strangers. We define 'nonfriends' as two individuals that live in the same area, and therefore have high chances of interacting, yet were not observed in any positive interaction. In contrast, strangers would be individuals that live in different areas and have little or no chance to meet. To corroborate the classification of associations described previously, we used the binomial expansion to calculate the probability of obtaining the number of observed affiliated associations out of all observations for each individual pair. Pairs of individuals that had a significantly higher number of affiliated associations than expected by chance were assigned as '+1', whereas all other pairs were assigned as '0'. This statistical approach was congruent in 94.4% of cases with the classification used above. While both methods provided similar results, we chose to use our own classification since it is less influenced by small sample size, facilitating the definition of pairs that were observed in positive interactions only a few times as 'friends', based on our argument that these positive interactions are not random, but rather reflect a positive affiliation. The mean ± SD number of positive interactions for dyads that were defined as 'friends' was 4.3 ± 4.6 ($N = 1885$ interactions). Our data show that positive interactions are 10 times more common than negative ones (total of 5072 positive interactions versus 485 negative interactions). In contrast to positive interactions, there were only a few cases of repeated negative interactions, making it impossible to define 'enemies' with confidence. If two individuals were not observed together during a specific year, we assumed that they actively avoided meeting, as hyraxes in each study population roam in a small area (about 0.5 km^2) and their home ranges overlap. All members of each population share the same resources and commonly visit central locations (e.g. foraging in the same trees) where random meetings could occur. Further support for our decision comes from the fact that 92.4% of the negative interactions ($N = 485$) were observed in pairs that were defined as 'nonfriends'. In addition, for all dyads defined as 'friends', the number of positive interactions was greater than the number of negative interactions.

To validate our results, we repeated the main analyses with a subset of the data including only individuals that were observed at least five times per year. Pups (less than 1 year old) were omitted from the analysis. The networks were constructed using SOCPROG 2.4 (Whitehead 2009) and UCINET 6.258 (Borgatti et al. 2002). All ensuing network analysis was done in Matlab (version 2009b; MathWorks Inc., Natick, MA, U.S.A.).

After constructing a signed network for each population and year where data were available (2000–2004, 2007–2009 for Arugot population; 2007–2009 for David population), we tested whether each of the four defined triad types (+++, ++−, +−−, −−−) was present more or less than expected by chance. We compared the observed networks to two different null models, both retaining the number of nodes. (1) A model retaining the degree distribution in the random networks, so that each individual retained the number of positive and negative ties. (2) A model retaining only the number of positive and negative edges in the random networks. Random networks were generated using the software PNet (Wang et al. 2006). We then counted the number of each triad type in the random networks and compared it to the real network using a randomization test (Szell et al. 2010). To compensate for multiple tests, we applied a sequential Bonferroni

correction (Rice 1989). We were aware that networks of successive years in the same site were not fully independent. However, the mean ± SD sequential change of network membership between years was 23 ± 11%, which implies that, within 3–4 years, new individuals replace most members of a given network.

To further substantiate our findings, we used exponential-family random graph models (ERGM; Wasserman & Pattison 1996; Robins et al. 2007). The aim of ERGM is to predict the joint probability that a set of edges exists on nodes in a network and describe the local selection forces that shape the global structure of the network (Handcock et al. 2008). The models tested the prevalence of +++ and ++− in the networks. We conducted the ERGM analysis using the statnet package in R (Handcock et al. 2003).

Exponential random models express the probability of observing a network (x) on a fixed set of nodes (N) as a function of specific network configurations or motifs. These network configurations are denoted as parameters (θ) in the model. The expression is $\Pr(X = x) = (1/\kappa) \exp\left(\sum_{ij} \theta_{ij} z_{ij}(x)\right)$, where θ_{ij} represents parameters i and j, $z_{ij}(X)$ represents counts of configurations corresponding to model parameters i and j in the observed network (x), and κ is a normalizing constant (Snijders et al. 2006). Node attributes such as age and sex, or dyadic attributes such as relatedness, enter the model as covariate parameters (y) so that the probability X is conditional on covariates y (Robins et al. 2001). We used the Markov chain Monte Carlo maximum likelihood estimation procedure, utilizing the Robbins–Monro algorithm (Snijders 2002) for fitting ERGMs to the networks. This method creates networks from an initial guess of parameter estimates and updates these estimates iteratively to find parameters that replicate the observed network.

Model degeneracy (Robins et al. 2007), a common problem in fitting ERGMs in which the algorithms converge to an empty or full network, did not allow us to use the simple triad census, which counts each triad type, as a term in the models. As an alternative, we chose two other terms, namely gwesp and gwnsp, to test for the prevalence of +++ and ++− triads in our networks. In the ERGM models, gwesp and gwnsp are geometrically weighted terms, which were found to be effective at overcoming the degeneracy problems (Hunter et al. 2008). In general, the gwesp term models the number of edges that serve as the common base for a number of distinct triangles (+++ triads). In a similar fashion, the gwnsp term models the number of couples of vertices in the network that are not connected, but would close a triangle if they were connected (++− triads). Last, the ERGM approach does not allow testing the prevalence of all four triad types; thus, we only examined the +++ and ++− triad types.

For each network, we fitted a model including the gwesp and gwnsp terms, while controlling for the degree distribution. Thus, we tested whether the corresponding triad types were significant factors in the network structure. Goodness of fit was verified by simulating networks according to the model and comparing network properties that were not part of the model to the same properties in the observed network. The properties we compared were the edgewise-shared partner distribution, the geodesic distance distribution, the triad census distribution and the degree distribution. The selected model was the one that was not degenerate and also showed perfect goodness of fit (Simpson et al. 2011).

To determine the changes in triad types between years, we compared triads that included the same individuals. Data were available for eight between-year transitions. For each specific triad, we tracked its type the following year if all three individuals were still in the population. We used permutation tests to determine whether unbalanced triads changed to balanced triads more than vice versa.

In addition, for each unbalanced triad (++−) we checked the type of triad it had changed to the following year, as a function of the number of males in the triad. We could only determine the outcome of a triad the following year if all three individuals had survived and stayed in our study site. Permutation tests were used to test whether the number of males in a triad influenced the type of transition from unbalanced to balanced triads.

RESULTS

When controlling for the degree distribution, in the 11 networks tested (eight from the Arugot population and three from the David population), the balanced +++ triads were more common than expected by chance in 10 networks (randomization tests: $P < 0.001$ in all networks), while the unbalanced ++− triads were less common than expected by chance in 10 out of 11 networks (randomization tests: $P < 0.001$ in all networks). The balanced +−− triads also were more common than expected by chance in 10 of the networks, and the −−− triads were less common than expected by chance in eight of the networks (Table 1). Overall, these results support the presence of strong structural balance, in which −−− triads are considered unbalanced.

When controlling for the number of positive and negative edges in the network, in all 11 networks tested the balanced +++ triads were more common than expected by chance (randomization tests: $P < 0.001$ in all networks), while the unbalanced ++− triads were less common than expected by chance (randomization tests: $P < 0.001$ in all networks). In seven of the networks the balanced +−− triads were more common than expected by chance, while in the other four networks the result was not significant. The −−− triads were more common than expected by chance in five networks, less common than expected by chance in one network, and the result was not significant in the remaining five networks (Table 1). To validate our results, we repeated the above analyses with a data set including only individuals that were observed at least five times in a year. The results of both analyses that excluded the rarely seen individuals (described in the Supplementary Material) showed qualitatively similar trends as the analyses using all individuals and overall supported the weak structural balance, in which only ++− triads are considered unbalanced.

ERGM models supported these results, as in all networks the best model showed a significant positive coefficient for +++ triads and a significant negative coefficient for ++− triads (Table 1). To summarize this part, all models supported the presence of structural balance, but they contradicted each other in regards to the prevalence of −−− triads. Figure 3 shows the 11 networks in which there were mostly two main groups and a few singleton hyrax occurrences. Positive relationships were mostly found inside the groups, while negative relationships occurred between the groups.

When testing the shift in each of the specific triad types between successive years, a significant frequency of balanced triads according to weak structural balance (+++, +−−, −−−) remained balanced in all eight year-by-year transitions, while a significant frequency of unbalanced triads (++−) changed to balanced triad types in seven out of eight transitions (Table 2). However, when considering −−− triads as unbalanced, this result was not significant. Furthermore, while 68% of −−− triads remained as such in the following year, only 9% of ++− triads remained at this configuration (Fig. 4). Therefore, the next tests regarding unbalanced triads were performed only on the ++− triads, which are considered unbalanced by both strong and weak structural balance theories and were found to be unfavourable by rock hyraxes, as shown by their preference to change out of them to other triad types the following year. Similar results were obtained by using only individuals that were observed at least five times in a year (Fig. S1).

Unbalanced triads (++−) that included only females were more likely to change to +++ triads the following year than were triads

Table 1
Number of rock hyrax triads of each type (N_{triad}), its fraction in comparison to null model expectations and the corresponding P values

Network	N_{hyrax}	Triad	N_{triad}	f_{obs}	f_{model1}	P	f_{model2}	P	$ERGM_{cof}$	P
Arugot 2000	39	+++	3291	0.36	0.14	<0.001[sw]	0.18	<0.001[sw]	0.102	<0.001[sw]
		++−	503	0.06	0.35	<0.001[sw]	0.42	<0.001[sw]	−0.205	<0.001[sw]
		+−−	4698	0.51	0.34	<0.001[sw]	0.32	<0.001[sw]		
		−−−	647	0.07	0.17	<0.001[s]	0.08	<0.001[s]		
Arugot 2001	30	+++	140	0.03	0.06	<0.001	0.01	<0.001[sw]	0.232	<0.001[sw]
		++−	187	0.05	0.25	<0.001[sw]	0.09	<0.001[sw]	−0.331	<0.001[sw]
		+−−	1586	0.39	0.33	<0.001[sw]	0.38	0.085		
		−−−	2147	0.53	0.36	<0.001[w]	0.52	0.148		
Arugot 2002	29	+++	282	0.08	0.03	<0.001[sw]	0.03	<0.001[sw]	0.205	<0.001[sw]
		++−	296	0.08	0.17	<0.001[sw]	0.18	<0.001[sw]	−0.278	0.002[sw]
		+−−	1802	0.49	0.40	<0.001[sw]	0.44	<0.001[sw]		
		−−−	1274	0.35	0.40	<0.001[s]	0.35	0.455		
Arugot 2003	29	+++	592	0.16	0.06	<0.001[sw]	0.06	<0.001[sw]	0.351	<0.001[sw]
		++−	423	0.12	0.25	<0.001[sw]	0.29	<0.001[sw]	−0.539	0.026[sw]
		+−−	1752	0.48	0.39	<0.001[sw]	0.43	<0.001[sw]		
		−−−	887	0.24	0.30	<0.001[s]	0.22	<0.001[w]		
Arugot 2004	37	+++	396	0.05	0.01	<0.001[sw]	0.01	<0.001[sw]	0.289	<0.001[sw]
		++−	463	0.06	0.13	<0.001[sw]	0.13	<0.001[sw]	−0.064	0.012[sw]
		+−−	3521	0.45	0.39	<0.001[sw]	0.42	<0.001[sw]		
		−−−	3390	0.44	0.47	<0.001[s]	0.44	0.498		
Arugot 2007	43	+++	1031	0.08	0.02	<0.001[sw]	0.01	<0.001[sw]	0.221	<0.001[sw]
		++−	325	0.03	0.13	<0.001[sw]	0.14	<0.001[sw]	−0.414	0.001[sw]
		+−−	5318	0.43	0.37	<0.001[sw]	0.42	0.005[sw]		
		−−−	5667	0.46	0.48	0.001[s]	0.43	<0.001[w]		
Arugot 2008	44	+++	1096	0.08	0.02	<0.001[sw]	0.02	<0.001[sw]	0.29	<0.001[sw]
		++−	470	0.04	0.14	<0.001[sw]	0.15	<0.001[sw]	−0.161	<0.001[sw]
		+−−	6104	0.46	0.38	<0.001[sw]	0.43	<0.001[sw]		
		−−−	5574	0.42	0.46	<0.001[s]	0.41	<0.001[w]		
Arugot 2009	47	+++	744	0.05	0.01	<0.001[sw]	0.01	<0.001[sw]	0.304	<0.001[sw]
		++−	491	0.03	0.09	<0.001[sw]	0.09	<0.001[sw]	−0.133	0.028[sw]
		+−−	5966	0.37	0.33	<0.001[sw]	0.37	0.105		
		−−−	9014	0.56	0.57	0.004[s]	0.53	<0.001[w]		
David 2007	27	+++	35	0.01	0.002	<0.001[sw]	0.001	<0.001[sw]	0.225	<0.001[sw]
		++−	53	0.02	0.04	<0.001[sw]	0.03	<0.001[sw]	−0.465	<0.001[sw]
		+−−	764	0.26	0.25	0.005[sw]	0.27	0.400		
		−−−	2073	0.71	0.71	0.206	0.70	0.237		
David 2008	29	+++	165	0.05	0.01	<0.001[sw]	0.01	<0.001[sw]	0.165	<0.001[sw]
		++−	190	0.05	0.10	<0.001[sw]	0.10	<0.001[sw]	−0.306	<0.001[sw]
		+−−	1393	0.38	0.37	0.023[sw]	0.39	0.120		
		−−−	1906	0.52	0.52	0.337	0.50	0.004[w]		
David 2009	34	+++	311	0.05	0.01	<0.001[sw]	0.01	<0.001[sw]	0.346	<0.001[sw]
		++−	60	0.01	0.09	<0.001[sw]	0.09	<0.001[sw]	−0.238	0.002[sw]
		+−−	2339	0.39	0.33	<0.001[sw]	0.37	<0.001[sw]		
		−−−	3274	0.55	0.57	0.002[s]	0.54	0.060		

f_{obs}: frequency of the triad type in the observed networks; f_{model1}: frequency in model 1, controlling for degree distribution; f_{model2}: frequency in model 2, controlling only for the number of positive and negative edges; $ERGM_{cof}$: coefficient of the gwesp (+++) and gwnsp (++−) terms according to the best model fitted. Support for strong structural balance is indicated by 's', as supported by model 1. Support for weak structural balance is indicated by 'w', as supported by model 2. All statistically significant results remained significant after applying the sequential Bonferroni correction.

that had one or more males (paired test by permutations: $t_6 = 3.6$, $P = 0.012$; Fig. 5). Conversely, ++ triads that had one or more males were more likely to change to +−− or to −−− triads than were triads that included only females, although the change to +−− was not statistically significant (++−change to +−−: $t_6 = 2.2$, $P = 0.069$; ++− change to −−−: $t_6 = 8.5$, $P = 0.0002$; Fig. 5). Triad sex ratio did not affect the probability that the triad would stay in the ++− state the following year ($t_6 = 1.5$, $P = 0.190$; Fig. 5).

Despite the high rate of unbalanced triads changing to balanced types, networks retained a level of instability. We examined whether hyraxes new to the network formed unbalanced triads, and found that, in all networks, the proportion of new hyraxes (i.e. those that were not present in the network the previous year) in unbalanced (++−) triads was larger than their proportion in all triads, although this tendency was not significant (paired test by permutations: $t_7 = 2.2$, $P = 0.064$).

DISCUSSION

This study is the first to show that structural balance theory is relevant to nonhuman animals. We found that, in rock hyrax social

networks, balanced triads are more common, while unbalanced triad are less common, than expected by chance. We also show that triads tend to change over time according to structural balance predictions and that triad sex ratio affects triad change.

The results from our first model, controlling for the degree distribution, largely supported the presence of strong structural balance, in which −−− triads are regarded as unbalanced, although for individuals observed more than five times per year, weak structural balance was supported (see Supplementary Material). In contrast, the second model, controlling only for the number of positive and negative edges, supported the existence of 'weak structural balance' (Davis 1967) in five out of 11 networks we tested, while 'strong structural balance' (where −−− triads are considered unbalanced) was demonstrated for only a single network (i.e. Arugot 2000). The unusually high number of positive male−male associations in the Arugot 2000 network, which were likely due to late dispersal during that year, may have decreased the number of −−− triads. Nevertheless, solitary males, which have negative relationships with all other individuals, were present in all networks. This presence of singletons does not support the pre- diction of strong structural balance, which allows for only one or
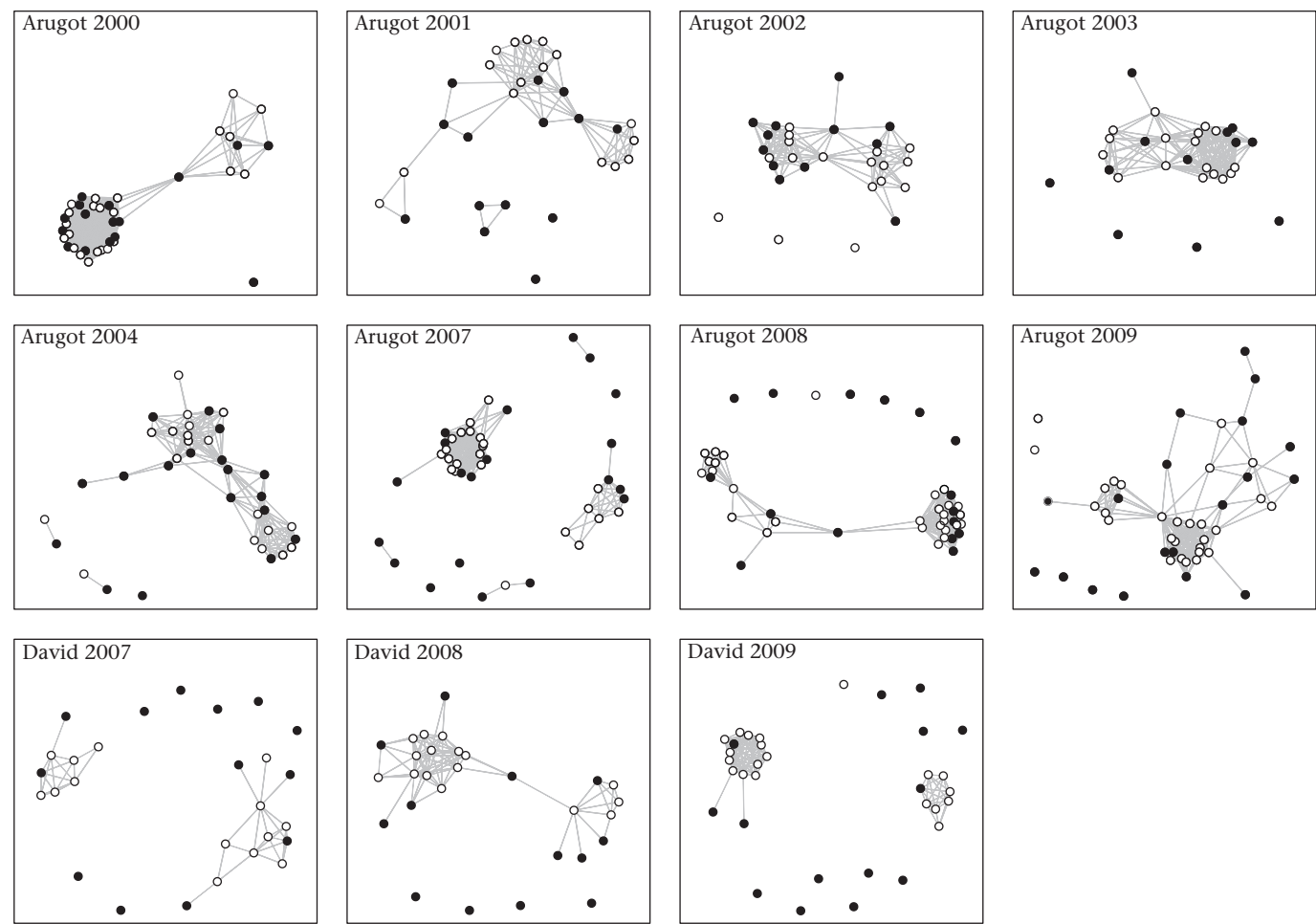
Figure 3. Hyrax social networks. Black and white circles represent males and females, respectively. Only positive associations, indicated by grey lines, are shown. Negative associations occurred in all other dyads (not shown). The structure of these social networks generally conformed to the Cartwright & Harary (1956) theorem. Changes between years were mostly due to individual movements and not a result of group merging or splitting.

two groups to form in a population, and supports the presence of weak structural balance. Indeed, if strong structural balance were the rule, populations of wild animals would be predicted to consist of up to two groups only, which is far from reality. Structural balance has been demonstrated in several studies on human social structure (Doreian & Mrvar 1996; Doreian et al. 1996; Szell et al.

2010), as well as in studies on international relations between countries (Healy & Stein 1973). In nonhuman animals, Lusseau et al. (2006) mentioned the triadic closure model as a possible cause for network degree homophily (i.e. individuals with similar degree tend to connect with each other) in bottlenose dolphins, *Tursiops truncatus*, but they did not directly test for the existence of structural balance.

Table 2
Unbalanced $(++-)$ rock hyrax triads changed to balanced triads in the following year more often than expected by chance, while balanced triads remained balanced more often than expected by chance

Network	N_{++-}	f_{++-}	P_{++-}	N_{balanced}	f_{balanced}	P_{balanced}
Arugot 2000	72	0.44	0	2228	0.56	1
Arugot 2001	55	0.18	0.0290	761	0.82	1
Arugot 2002	64	0.29	0.0003	752	0.71	1
Arugot 2003	123	0.25	0	1417	0.75	1
Arugot 2007	209	0.20	0.0250	5775	0.80	1
Arugot 2008	271	0.16	0	10389	0.84	1
David 2007	25	0.04	0.0003*	1305	0.96	1
David 2008	135	0.17	0	1636	0.83	1

We followed each triad in which all three members survived to the following year, and recorded the triad type it changed to. N_{++-}: number of $++-$ triads in each network; f_{++-}: expected frequency of $++-$ triads when retaining the number of positive and negative edges; P_{++-}: probability of the observed frequency in the following year; N_{balanced}, f_{balanced} and P_{balanced} describe the same for the balanced triads $(+++, +--, ---)$. The asterisk depicts an opposite result (i.e. in the following year there were more $++-$ triads than expected by the null model).
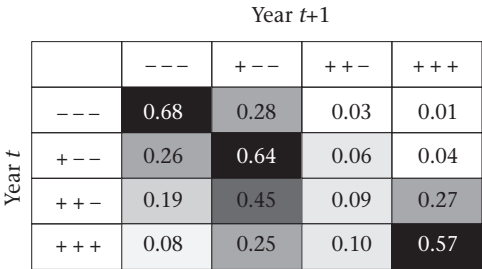

Figure 4. A heat map summarizing triad changes in rock hyraxes between consecutive years. Each row shows the outcome of the triads originally belonging to one triad type. Results are the fractions of triad changes from one year to the next in eight cases, representing 25 217 triads and 279 individuals. Darker backgrounds indicate higher values. While the unbalanced $++-$ triads mostly changed to other triad types, other triad configurations mostly remained unchanged, supporting the presence of weak structural balance.
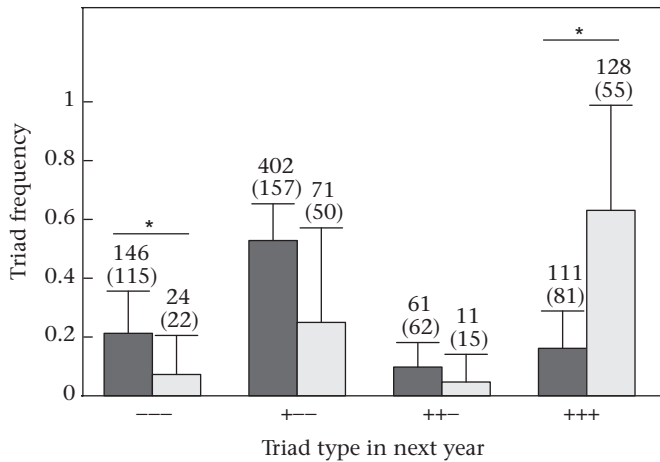
Figure 5. The fraction of unbalanced $(++-)$ rock hyrax triads that changed to other triad types the following year for triads including males (dark bars), and for triads with females only (light bars). The number of triads and the number of individuals (in parentheses) involved in those triads are denoted above the bars. Data are summarized over all yearly changes. An asterisk denotes $P \leq 0.05$.

Evidently, structural balance is dependent on local interactions between individuals. For example, a dispersing hyrax female that is positively interacting with a group female may still be chased away by another group member. Such situations may limit the creation of positive associations between a group member and an outsider. Alternatively, the dispersing female may be accepted into the group, thus changing some unbalanced $++-$ to balanced $+++$ triads. Furthermore, juveniles growing up in a group may have two balanced options in terms of triad configurations. The first is to stay in the group, thus remaining friends of all or most of its members. The second option is to leave the group, thus becoming a nonfriend of the group members, while optionally forming positive associations with another group. In our field site, female hyraxes usually remain in their natal group, while males leave it when reaching adulthood, remaining solitary while trying to join other groups (Barocas et al. 2011). In other species, the mechanism could be different, but the outcome is expected to conform to structural balance. Therefore, while structural balance may not define the social structure of species, it may help to stabilize specific structures and may play a selective role in the evolution of social structures. Furthermore, it may facilitate 'network reciprocity', in which individuals form groups and cooperate with their group members (Nowak 2006). We expect structural balance to be common in species in which the social structure is relatively stable. In other species, where groups are not stable and changes are frequent, structural balance may not be common (Lott & Minta 1983). For example, the social network of onagers, *Equus hemionus khur*, suggests that this species may not demonstrate structural balance (Figure 3b in Sundaresan et al. 2007).

When considering structural changes across successive years, hyraxes showed a preference to change only $++-$ triads to other triad types, suggesting they only recognize this triad type as unbalanced. This finding supports the existence of weak structural balance over a strong one, in which $---$ triads are also considered unbalanced. These findings further support the role of structural balance as a stabilizing force in social structure. In accordance with structural balance predictions (Cartwright & Harary 1956), hyraxes seem to actively change unbalanced configurations, by forming new positive associations or deleting old ones in a way that leads to more balanced structures. The outcome of these is the social structure of the whole population (Fig. 3). Thus, structural balance may enhance the stability of groups via its selective force on triads.

The division of a social network into subgroups, as predicted by structural balance, is a condition for the maintenance of general reciprocity (van Doorn & Taborsky 2012), and thus structural balance may serve as a mechanism behind the evolution of cooperation. Moreover, we show the predictive power of structural balance: while assuming that dyadic interactions alone cannot lead to predictions of social changes, our longitudinal analysis of triads shows that changes in consecutive years can be mostly predicted.

We found that unbalanced triads changed to balanced triads in 91% of the cases, but that nevertheless some level of imbalance remained in the networks. When exploring temporal changes in the networks (Fig. 3), we did not detect major merging or splitting of groups, but rather changes caused by the movement of individuals. When attempting to determine the sources of imbalance, we predicted that they would be due to new individuals in the population, which in the hyrax system are either dispersing males joining the population (Hoeck et al. 1982; Koren et al. 2006) or juveniles that were born to group residents. Indeed, new individuals in the network (i.e. that had not been present in the previous year) were present in unbalanced triads slightly more than in all other triads. This tendency ($P = 0.06$) approached statistical significance, suggesting that some imbalance may be maintained in the population due to new individuals that tend to form unbalanced social structures. While structural balance is driving these to settle into balanced configurations, again new individuals join, and those may bring in new instability. The level of balance in a population may then depend on the interplay between imbalance, presumably introduced mainly by incoming individuals, and the stabilizing forces of structural balance. Nevertheless, some imbalance may come from individuals within the network. In primates, stable social configurations may induce stress to subordinate individuals (Sapolsky 2005). This could serve as a mechanism by which stress may lead subordinates to make social changes, maintaining a level of instability in the system. While the adaptive value of structural balance may lie in its maintenance of social stability, where social roles are clear (Senar et al. 1990), some individuals may suffer from disadvantageous roles and may thus challenge them, and introduce social instability.

Our study has shown that the sex ratio of unbalanced triads can predict their future triad type. Considering the rock hyrax' social system, it is logical that $++-$ triads containing only females changed mostly to balanced $+++$ triads, following the triadic closure model (Lusseau et al. 2006). Females may require a degree of cooperation in rearing their young, which could be achieved by group formation. In contrast, unbalanced triads including at least one male changed mostly to $---$ triads. As males are usually more aggressive than females, it is not surprising that triads with more males have more negative ties. Nevertheless, this finding encourages further research into the factors affecting local social changes.

While most studies in humans have defined relationships as 'friends' or 'enemies' (e.g. Szell et al. 2010), we have used a less strict definition of 'friends' and 'nonfriends', which reflects the fact that some of the pairs defined as 'nonfriends' were not observed in any interaction. Therefore, the '−' sign of these pairs may be regarded as 'not +'. Nevertheless, our results support the basic predictions of structural balance, in which $++-$ triads are considered unbalanced. The number of these triads was small, and existing $++-$ triads changed to balanced triads. This behaviour suggests that hyraxes identify 'nonfriends' as opponents, and that they avoid interactions with them. We suggest that network motif analysis (Milo et al. 2002) holds promise in elucidating the complex social structure of animal societies. Specifically, structural balance theory, extended into multiple systems, may emerge as an important tool for understanding the evolution of complex natural social systems.

Acknowledgments

Supplementary Material

Supplementary material for this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2013.03.032.

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