Quantifying Social Complexity

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Social complexity has been invoked as a driving force shaping communicative and cognitive abilities, and brain evolution more generally. Despite progress in the conceptual understanding of societal structures, there is still a dearth of quantitative measures to capture social complexity. Here we offer a method to quantify social complexity in terms of the diversity of differentiated relationships. We illustrate our approach using data collected from Barbary macaques (*Macaca sylvanus*) at 'La Forêt des Singes' in Rocamadour, France, as well as simulated data sets for a proof-of-concept. Based on affiliative and agonistic behavioural categories, we calculated four indices that characterize social relationships (diversity of behavioural patterns, dyadic composite sociality index, relative interaction frequency, and tenor). Using cluster analyses, we identified four different relationship types: rarely interacting agonistic dyads, rarely interacting affiliative dyads, moderately frequently interacting ambivalent dyads and frequently interacting affiliative dyads. We then calculated for each individual a derived diversity score that integrates information about the number and diversity of relationships each subject maintained. At the individual level, one may be interested to identify predictors of this individual diversity score, such as age, rank, or sex. At the group level, variation in the relative shares of affiliative and agonistic interactions affects the distribution of individual diversity scores to a greater extent than the interaction frequency, while the omission of ambivalent relationships (i.e. a discontinuous variation in the share of affiliative or agonistic relationships) leads to greater variation in diversity scores. The number of realized relationships had only a moderate effect. Overall, this method appears to be suited to capture social complexity in terms of the diversity of relationships at the individual and group level. We suggest that this method is applicable across different species and facilitates quantitative tests of putative drivers in brain evolution.

Keywords

Barbary macaques, Cluster analysis, Diversity Indices, Macaque, Primate, Social brain hypothesis, Social complexity, Social relationships

Ever since Jolly (1966) and Humphrey (1976) proposed that group-living played a crucial role in driving brain evolution, researchers have aimed to operationalize different aspects of social life to test predictions from this “social brain hypothesis” (Dunbar, 1998; Dunbar & Shultz, 2007a). In particular, it has been proposed that social complexity is the key driver in the evolution of primate brains and cognition (Bergman & Beehner, 2015; Platt, Seyfarth, & Cheney, 2016; Seyfarth & Cheney, 2015; but see DeCasien, Williams, & Higham, 2017).

In some of the earlier studies (Dunbar, 1998; Humphrey, 1976; Jolly, 1966), group size was used as a proxy for social complexity, although it was conceded that this is only a crude measure for social complexity (Dunbar, 1998). Byrne and Whiten (1988) noted that primate social complexity is characterized by behaviours involving cooperation, manipulation and deception, and Freeberg, Dunbar and Ord (2012) pointed out that in complex social systems, individuals frequently interact in many different contexts with many different individuals, and often repeatedly with the same individuals over time (Seyfarth & Cheney, 2015). Bergman and Beehner (Bergman & Beehner, 2015), finally, proposed that social complexity could best be understood in terms of the number of differentiated relationships individuals maintain.

While all of these concepts cover important aspects of social complexity, there is no agreement how to quantify the notion of social complexity at the individual and the group level, despite the existence of numerous indices that describe specific aspects of a social relationship between two individuals (Blumstein & Armitage, 1997; Cords & Aureli, 1993; Fraser, Schino, & Aureli, 2008; Silk, Alberts, & Altmann, 2003). For example, Sapolsky, Alberts and Altmann (1997) created a social connectedness index, based on eight behaviours including affiliative and agonistic categories. Subsequent studies by Silk and colleagues (Silk et al., 2010, 2003; Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012; Silk, Alberts, & Altmann, 2006; Silk, Altmann, & Alberts, 2006) quantified social bonds in terms of their (i) strength by the composite sociality index (CSI; including grooming and proximity data as measure for social integration), (ii) quality by a grooming equality index (indicating the difference of grooming given and received) and (iii) stability by investigating the consistency of relationships to three top partners based on the CSI and the subsequent calculation of a partner stability index (PSI). Using a different approach, Fraser et al. (2008) used nine different behaviours (affiliative, but also submissive and aggressive behaviour) to derive three principal components termed value, compatibility, and security of a given relationship (but see Silk, Cheney, & Seyfarth, 2013). All of these indices are used to describe a given relationship between two individuals, but they have not been integrated in a way that would allow capturing social complexity in a quantitative and comparative fashion.

The aim of this paper is to introduce a method to describe social complexity in a quantitative way. At the individual level, social complexity has been defined as the number of differentiated (in the sense of different types of) relationships individuals maintain (Bergman & Beehner, 2015); at the group level, this notion of social complexity would affect the distribution (average and skew) of individual levels of social complexity. This conception requires quantifying the different types of relationships that exist within a group, the assessment of individual social complexity and ultimately the assessment of the distribution of different types of relationships across individuals at the group level. We are borrowing from concepts describing ecological diversity to derive measures of diversity at the social level. The ultimate aim is to derive variables that can be used to facilitate comparisons between groups (or species).

To illustrate our approach, we are first using behavioural data recorded from Barbary macaques living in the enclosure “La Forêt des Singes”. Second, as a proof-of-concept, we created different simulated data sets in which we varied the type and frequency of interaction, as well as group size, to explore how this variation affects our suggested measure of social complexity at the group level. To arrive at this measure, we first derived a set of indices that describe the diversity of different behavioural patterns that make up a relationship, as well as the frequency and tenor of the relationship, as proposed by Silk et al. (2013). We then used cluster analysis to identify different types of relationships. In a next step, we calculate the diversity of relationship types individuals maintain (Individual Relationship Diversity Index or "IRDI"). This is largely in line with Bergman and Beehner's conception of social complexity. We suggest that the distribution of the IRDI at the group level provides a measure of complexity that can be applied in broader comparative studies, such as testing core predictions from the "social brain hypothesis".

MATERIAL AND METHODS

We used behavioural data collected from Barbary macaques at the monkey park "La Fôret des Singes" in Rocamadour, France during two periods, i.e. the birth season (April to June 2009, hereafter 'Season 1') and mating season (September to October 2009, hereafter 'Season 2'). In total, there were 100 days and 598.5 h of observation of 19 female focal animals differing in age, rank and matrilinear descent. These females encompassed the majority of all adult (N=24) females in the group. In total, the group consisted of 56 subjects, including 23 males aged 5 years and older, and 9 juveniles and infants, in addition to the 24 females aged 5 years and older mentioned above. Observations followed the focal animal sampling rule with continuous recording of defined behaviours for 30 minutes (Martin & Bateson, 2007). Behavioural data were recorded using a portable minicomputer (Tungsten E2, PalmOne, Inc. 2005, Milpitas, CA, U.S.A.) running custom forms created with the Pendragon software (Version 5.0, Pendragon Software Cooperation, U.S.A.). The data were originally collected for different purposes, but deemed suitable for this study.

Determining interaction patterns

For simplicity, we reduced the behavioural contexts in which interactions were recorded to three aggressive categories (threats, chases, attacks; ethogram in Hesler & Fischer, 2007) and two affiliative categories – i.e., body contacts and grooming interactions. We did not consider ambiguous behaviours such as a bared teeth display that is shown in submissive and affiliative interactions (Hesler & Fischer, 2007). Further, we excluded submission, as it is often a response to aggressive behaviour, yielding redundant information. We further excluded behaviours of triadic interactions –

i.e., infant handling, or other behaviours, which involved a third animal, to keep the analysis simple. In summary, we determined counts of threat (abbreviated as *t* in following equations), chase (*c*), attack (*a*), body contact (*bc*) and grooming (*g)* interactions for 416 dyads (out of a possible total number of 1275) in spring and 421 dyads in fall.

Choice of indices

First, we calculated the Behavioural Diversity Index (BDI) to describe the diversity of different behavioural interactions (see Silk et al., 2013; Equation 1).

$$(\mathbf{1})\ \frac{1}{\left(p_t^2 + p_c^2 + p_a^2 + p_{bc}^2 + p_g^2\right)}$$

We derived this score from the Simpson diversity index, which is frequently used in ecology to operationalize ecosystem diversity based on species number and evenness of species distribution (Begon, Townsend, & Harper, 2006; Simpson, 1949). Here we treated the different behaviour categories as "species". This Behavioural Diversity Index (BDI), therefore, takes into account the number of different behaviours and the evenness of their distribution; both of these factors contribute to the diversity of a relationship. Since only proportions are included, the index describes the diversity only and not absolute or relative frequency of specific behaviours (Magurran, 2003).

Second, we employed the Dyadic Composite Sociality Index (DCSI) as a measure for the strength of affiliative relationships (Silk et al., 2003, 2013; Silk, Alberts, et al., 2006), which focuses on the frequency dimension of affiliative relationships (Equation 2).

$$(\mathbf{2})\ \frac{\left({R_{bc}}/{\bar{R}_{bc}} + {R_g}/{\bar{R}_g}\right)}{2}$$

We calculated the index by dividing the rates R (i.e. the number of interactions per hour of observation time) of body contacts (bc) and grooming (g) from one dyad with the mean rates of all dyads and by dividing this term by n, the number of behaviours involved. Therefore, it shows the divergence of dyad X from the mean of all dyads. Also, using rates ensures correction for different observation times of individual focal animals.

Third, we determined the Interaction Frequency Index (IFI) (Equation 3), which is a modification of the DCSI.

$$(\mathbf{3})\ \frac{\left({R_t}/{\bar{R}_t} + {R_c}/{\bar{R}_c} + {R_a}/{\bar{R}_a} + {R_{bc}}/{\bar{R}_{bc}} + {R_g}/{\bar{R}_g}\right)}{5}$$

It is calculated in an identical fashion as the DCSI, but included agonistic as well as affiliative behaviours. It thereby gives an impression of the overall interaction frequency of a dyad, regardless of whether the relationship is agonistic, affiliative or ambivalent. Note that in the IFI, variation in rare behaviours (e.g., physical attacks) drive variation in this index markedly.

Fourth, we used the index Tenor as a measure of the identically-named dimension proposed by Silk et al. (2013) to give an impression whether a relationship is relatively more affiliative or agonistic. We calculated Tenor by dividing the rate of all affiliative behaviours by the rate of affiliative and aggressive behaviours. It ranges between zero and one; zero being a purely agonistic relationship and 1 being a purely affiliative one (Equation 4).

$$(\mathbf{4})\ \frac{R_{affiliative}}{R_{overall}}$$

Determining different relationship types – Cluster analysis

For all analyses, we only selected dyads that appeared in both seasons. Our final sample thus included 257 dyads. We used a two-step cluster analysis (IBM SPSS Statistics 22) to investigate whether relationships can be classified into distinct types. For these analyses, we used data of Season 1. We used two different approaches, one based on the original behavioural data, and a second one based on the four indices. The reasoning was that the indices might prove to be more powerful in distinguishing different types of relationships than the mere behavioural patterns, as they already aggregate information. We entered behavioural measures and the derived indices as continuous variables. The Schwarz's Bayesian Criterion was used to identify the best cluster solution, and the Log-likelihood ratio was taken as a distance measure. Furthermore, the quality of each cluster analysis was assessed using the silhouette value, which ranges between -1 and 1, one representing a clear cluster separation (Rousseeuw, 1987). Cluster solutions with a Silhouette value above 0.5 were considered as valuable (Rousseeuw, 1987). The selection criterion how many times a dyad must be observed to enter the cluster analysis has an important influence on the outcome. Therefore, we compared the effect of three different selection criteria (at least three, five and seven interactions).

Stability of relationship types – Discriminant analysis

We used discriminant analysis (IBM SPSS Statistics 22) to corroborate the results of the cluster analysis for the Barbary macaque data. Specifically, we investigated whether the relationship types found in season 1 could also be found in season 2. For this, we first conducted a cluster analysis for season 1 with dyads interacting at least three times. Then, we calculated the discriminant functions, using cluster membership (relationship type) as grouping variable and the values of the four indices as independent variables. We then applied the classification procedure of the discriminant function analysis, in which cases are assigned to the different groups based on their features. Cases from season 1 (that had been used to create the functions in the first place) were treated as 'selected cases', and cases from season 2 as 'unselected' cases, which were then assigned to the groups (or clusters) based on their features. High classification results for the unselected cases indicate a high concordance between the two cluster solutions. In order to inspect the separation of the clusters, we plotted the first two discriminant functions and inspected the correlation of the indices with the discriminant functions.

Individual level relationship diversity

Next, we calculated the Individual Relationship Diversity Index (IRDI; equation 5). This index was calculated in identical fashion to the BDI and captured the diversity of a focal animal's relationship types as established by the cluster analysis (abbreviated Cl in equation 5).

$$(\mathbf{5})\,\frac{1}{(p_{Cl1}^2+p_{Cl2}^2+p_{Cl3}^2+p_{Cl4}^2)}$$

In order to investigate the effects of individual attributes such as age and rank on individual relationship diversity measures for the Barbary macaque data, we conducted a multiple regression with the predictors age and rank, and IRDI and the number of partners as dependent variables. We ensured that residuals follow a distribution via quantile-quantile plots using R function qqplot. Moreover, we checked for homogeneity of the residuals via residuals vs. fitted values scatterplots. We fitted the model in R (Version 3.2.0, R Development Core Team, 2015) using the function lm.

Group level relationship diversity

From an ecological or evolutionary perspective, comparisons at the group, population or species level are of particular interest. We first inspected the distribution of relationship diversity indices across all individuals in the Barbary macaque group. To facilitate comparisons, we normalized the data by dividing the actual diversity index of each individual by the maximum number of possible relationship types (i.e., number of clusters).

Data sets for proof-of-concept simulation study

We systematically varied the likelihood of the occurrence of either affiliative or agonistic interactions between a set number of subjects within a supposed group, which allowed us to assess the effects of two key components while keeping the number of different parameter combinations at a manageable level. We created two scenarios, in which the number of realized relationships, and the type and frequency of interactions were systematically varied. For the different types of relationships, we established three categories along the valence axis, resulting in predominantly agonistic (80% agonistic and 20% affiliative interactions), ambivalent (50% agonistic and 50% affiliative interactions), and predominantly affiliative relationships (80% affiliative and 20% agonistic interactions). Affiliative behavioural categories are grooming and body-contact (each realized from a Bernoulli distribution with equal probabilities of 0.5 for both possible outcomes, i.e. grooming and body contact); agonistic behavioural categories were threat, chase, and attack (each realized from a multinomial distribution with a probability of 0.7 for threat, 0.2 for chase, 0.1 for attack). Within the predominantly affiliative category, we varied the interaction frequency dimension, resulting in weak (N=50 interactions per dyad), medium (N=75 interactions per dyad), and strong affiliative relationships, also termed 'strong bonds' (N=100 interactions per dyad). All agonistic and ambivalent relationships were classified as weak, with 50 interactions each.

The first scenario consisted of N = 36 individuals, resulting in 630 potentially observable dyads, and no differentiation between different sexes. We created two subsets, one in which all potential relationships were realized, and one in which only 70% were realized. Within these two conditions, we assembled the following sub-scenarios: (1A) 1/6 strong affiliative relationships, no medium affiliative relationships, and equal probabilities for weak affiliative, ambivalent, and agonistic relationships ((1-1/6)/3); (1B) no strong affiliative relationships, 1/6 medium affiliative relationships, and equal probabilities for weak affiliative, ambivalent, and agonistic relationships ((1-1/6)/3); (1C) 1/6 strong affiliative relationships, and equal probabilities for medium affiliative relationships, weak affiliative and agonistic relationships; (1D) 1/6 strong affiliative relationships, and equal probabilities for medium and weak affiliative relationships, as well as weak ambivalent and weak agonistic relationships ((1-1/6)/4). In summary, the first sub-scenario lacked medium affiliative bonds, the second lacked strong affiliative relationships, the third lacked weak ambivalent relationships, and the fourth contained all possible combinations. Thus, the first three sub-scenarios contained 4 different combinations each, while the last contained 5 different combinations.

The second main scenario encompassed N = 90 individuals, resulting in N = 4005 potentially observable dyads. Within this set, 60 individuals were designated as 'female' and 30 as 'male'. Two-thirds of the relationships were realized (N = 2670 dyads, out of which 1177 were 'female-female' dyads). We stipulated that only females could develop strong affiliative relationships with 100 interactions per dyad. The other relationships were all categorized as weak, with N = 50 interactions each. We now varied the share of female-female dyads that had strong affiliative relationships: (2A) 1/8 (N = 147 dyads); (2B) 1/12 (N = 98 dyads); (2C) 1/16 (N = 47 dyads). The remaining relationships were distributed equally among the three types of weak relationships.

By realizing the different interactions with a given probability, this created a certain statistical variability within relationship classes (see below). We then calculated the four indices based on the different types of relationships we assembled for the different scenarios following the descriptions for the Barbary macaque data set, and used these as input for the cluster analysis. Finally, we examined the distribution of relationship diversity indices for the different scenarios. The simulation study was run in the R environment (R Development Core Team, 2015). The script can be found here: https://github.com/holgersr/Quantifying_Social_Complexity_Simulation_R_code.

Ethical note

The behavioural observations were conducted on fully habituated Barbary macaques residing in the monkey park "La Forêt des Singes" at Rocamadour. The data collection conformed to ASAB/ABS's guidelines for ethical research with animals.

RESULTS

Cluster analysis based on behaviour categories

The cluster analysis based on the five behaviours attack, chase, threat, grooming and body contact for all dyads that interacted at least three times resulted in two clusters, one with 84.4% of dyads that interacted infrequently and the second with 15.6% of dyads that interacted frequently (Table 1). The cluster solution had a Silhouette value of 0.6, indicating a good solution.

Cluster analysis based on indices

In the second analysis, we used the four indices (BDI, DCSI, IFI, Tenor) as input variables for the cluster analysis. As noted above, these indices might prove to be more powerful in distinguishing different types of relationships than the mere behavioural patterns. In a first step, we investigated the effect of different numbers of interaction per dyad (at least three, five and seven) as selection criterion for the dyads to be entered in the cluster analysis (Table 2, Fig. 1, Tables A1 and A2).

Figure 1 shows the different cluster solutions dependent on the number of minimum interactions. The cluster solution with ≥ 3 interactions yielded four clusters that differed mainly in terms of the frequency of interaction and dyadic tenor. Cluster 1 was characterized by a few dyads which showed very high values of frequency and diversity indices, and slightly affiliative tenor (referred to as 'frequent affiliative'). Cluster 2 comprised one third of all relationships; these were characterized by ambivalent tenor and slightly higher diversity and frequency ('ambivalent'). Cluster 3 comprised dyads that interacted rarely but in an affiliative fashion ('rare affiliative'). Cluster 4, finally, contained dyads with rare agonistic interactions ('rare agonistic'; Fig. 1, Table 2).

When ≥ 5 or ≥ 7 interactions were used, only two categories distinguished by the frequency and type of interactions remained (Tables A1 and A2), similar to the cluster analysis including behavioural data (Table 1). Note that the cluster solution with ≥ 3 interactions had a Silhouette value of 0.6 indicating a better quality of cluster separation than the solutions based on ≥ 5 or ≥ 7 interactions (both 0.5). We conducted the following analysis with the solution based on ≥ 3 interactions, because the higher cut-off values systematically excluded weak relationships.

Stability of relationship types

To assess the validity of the cluster solution, we conducted a discriminant analysis in which we used the cluster memberships of season 1 as grouping variable and the indices as independent variables (see Method). 89.4% of all cases of season 2 were correctly assigned to the respective cluster, indicating that the relationship characteristics for both seasons are relatively stable.

The discriminant function analysis resulted in three discriminant functions, where the first function (F1) explained 54.62% of the variance and correlated highly with tenor. The second function (F2) explained 28.01% of the variance and correlated with frequency, while the third function explained 17.36% of the variance and correlated with behavioural diversity. Figure 2 shows the plot of the discriminant function scores for the four clusters and both seasons. Dyads that belonged to cluster 1 were characterized by a affiliative tenor and high interaction frequencies. Dyads that belonged to the other clusters could mainly be distinguished by their tenor (Fig. 2).

Individual relationship diversity index

In order to investigate whether specific attributes predicted the diversity of relationships individuals maintained, we conducted a multiple regression analysis with age and rank as predictors, and the relationship diversity index (IRDI) and the total number of dyads (number of partners) as response variables. Individuals had on average 2.84 different relationship types (range 1 to 4) with on average 6.42 partners (range 1 to 14). Subjects had between zero and two frequent affiliative relationships (on average 0.53) with only eight animals having relationships that exceeded the mean. Subjects had between zero and six ambivalent and rare affiliative relationships with the average being 1.79 and 2.32, respectively. Moreover, on average individuals had 1.79 rare agonistic relationships with a range of zero to eight.

We did not observe a marked influence of age and rank on individual relationship diversity ($F_{2,16}$=2.764, P=0.093), although the question whether older animals have less diverse relationships warrants further investigation in light of the observed trend (Table 3). The full model for the effect of the number of dyads per individual (i.e. number of partners) supported the view that age and rank predict the number of partners ($F_{2,16}$=6.534, P=0.008). More specifically, we found strong evidence that older subjects had fewer partners. We also found some weak evidence that higher ranking subjects had a higher number of partners (Table 3).

Comparisons at the group level

We examined the distribution of the IRDI in the whole group consisting of 19 focal animals (Fig. 3). The 19 scores are distributed normally (as assessed by qqplots and Shapiro-Wilk tests W = 0.983, P = 0.97), albeit slightly right-skewed. On average animals had a normalised relationship diversity score of 0.58.

Simulation study

For both the full data set and the reduced data set in the first scenario, the cluster analysis yielded 4 clusters (i.e., 'relationship types') in each combination, except for the scenario that lacked ambivalent relationship types, where the best solution contained only two clusters (predominantly agonistic and predominantly affiliative interactions, irrespective of relationships strength). For the large group, we identified four clusters for set A with 1/8th strong bonds, 6 clusters for set B with 1/12th strong bonds, and 4 clusters for set C with 1/16th strong bonds.

Figure 4 shows the distribution of the indices for the first scenario. The distribution of DCSI and Tenor in A and B are highly similar, while they differ in C and D. Thus, it appears that the four indices vary (partly) independently and are thus all informative for the analysis. The distribution of individual relationship diversity indices (IRDI) differed between the different scenarios (Fig. 5). Variation in the relative shares of affiliative and agonistic interactions affected the distribution of individual diversity scores to a greater extent than the interaction frequency, while the omission of ambivalent relationships led to greater variation in diversity scores. The number of realized relationships had only a moderate effect, resulting in a slight increase in average IRDI values with the higher number of realized relationships.

In the second scenario, we assessed the effects of variation in the proportion of strong affiliative relationships (Fig. 6). An increase of a presumed social selectivity (i.e. a smaller number of strong affiliative relationships) led to a more pronounced peak in IRDI and a decreased spread of the distribution.

DISCUSSION

We used cluster analysis to identify different types of relationships in female Barbary macaque social behaviour and identified four main types of relationships, namely frequently interacting affiliative dyads, moderately frequently interacting ambivalent dyads, rarely interacting affiliative dyads and rarely interacting agonistic dyads, respectively. The discriminant analysis indicated that the relationship types for the dyads were stable across seasons, tentatively supporting the validity of clusters. This high similarity is notable in light of the remarkably different characteristics of the birth vs. the mating season (Small, 1990).

In the next step, we calculated an individual diversity index that captures the diversity of relationships an individual maintains, and assessed the variation across different types of 'societies' via the simulation study. This study revealed in which way the composition of specific types of relationships affected the individual relationship diversity, and consequently the distribution of the corresponding index (IRDI) at the group level (see Fig. 7 for a summary of the procedure). We found that the distribution is sensitive to the occurrence of ambivalent relationships, which greatly increased the variability. Interestingly, the share of realized relationships was less important. Finally, an increase in selectivity for ‘strongly bonded partners’ decreased the variation in IRDI as well. Notably, the IRDI is robust against the number of behaviour patterns initially chosen in the analyses. Even interactions with no clear affiliative or agonistic character may be included, although it is evident that the assessment of tenor hinges on the classification of some interactions as either affiliative or agonistic.

We suggest that the assessment of the IRDI rather complements than replaces other ways of characterizing societal structures such as cliquishness, network modularity and community structure for instance are identified via Social Network Analyses (SNA) (e.g., Beisner, Jin, Fushing, & Mccowan, 2015; Pasquaretta et al., 2014; Sueur, Jacobs, Amblard, Petit, & King, 2011). SNA, however, provides no straightforward way to incorporate different types of interactions. Previous studies have attempted to do so but ultimately relied on separate analyses of grooming, agonistic and proximity networks, and their interrelations (Barrett, Henzi, & Lusseau, 2012; Lehmann & Ross, 2011). The assessment of the distribution of the IRDI, in contrast, allows encapsulation of both the variation in relative frequencies of interactions as well as the proportion of different types of interactions – resulting in different relationship types – into a comprehensive metric. Although we confined our analysis to some select scenarios, the observed variation in the distribution of the IRDI followed a predictable pattern.

Some methodological caveats need to be considered, however. As is commonly the case with cluster analyses, both sampling issues and cut-off values may have strong effects on the outcome. When we compared different cluster solutions based on dyads with differing minimum numbers interactions for the Barbary macaque data set, the solution with dyads that interacted at least three times showed the most conclusive solution, comprising four clusters. Silk and colleagues discussed the sampling problem in the context of assessing the symmetry in behaviour, such as the grooming equality index (Silk, Altmann, et al., 2006; Silk et al., 2013). Silk et al. (2013) advocated the use of high cut-off values to ensure that dyadic skew is not simply a chance finding. However, a trade-off of high cut-off values is that an important aspect within the structure of social groups would be lost, namely the fact that some dyads may only rarely or in fact never interact. Thus, in addition to inspecting the possible relationship types, the number of realized relationships within a social group also provides important information for assessing the complexity of a group.

Interestingly, in the initial analysis of the Barbary macaque data, the cluster solution based on indices proved to be more informative than the one based on behaviour patterns, suggesting the indices capture important aspects of relationships that do not become immediately available when the behaviour patterns alone are used. A further advantage of using indices is that they avoid problems that may stem from comparisons with different levels of granularity in the recording of behaviour patterns. As stated above, the use of indices takes care of the problem that either different species require the use of different and/or additional types of behaviour. Nevertheless, the simulation study provided evidence that the chosen indices capture different aspects of the animals' relationships, and it thus seems warranted to include all four in the cluster analysis. Finally, there are issues with the use of diversity indices (Schleuter, Daufresne, Massol, & Argillier, 2010; Silk et al., 2013), and one may favour one index over another, or apply corrections.

Individual relationship diversity

We found no strong support for the idea that age or rank are associated with variation in individual relationship diversity, although an inspection of the data tentatively suggested that older animals have lower diversity scores than younger ones. Mirroring previous findings (partly based on the same data set; Almeling, Hammerschmidt, Sennhenn-Reulen, Freund, & Fischer, 2016), we found good support for the notion that older animals have fewer social partners. Moreover, there was weak support that higher ranking subjects also had a higher number of social partners. Future studies might be able to use the diversity of an individual's relationships as a predictor of reproductive success, longevity or infant survival, in a similar fashion as personality characteristics (Seyfarth, Silk, & Cheney, 2012, 2014) or measures derived from social network analysis have been used (Cheney, Silk, & Seyfarth, 2016). While there is now ample evidence that baboons with close social bonds have greater longevity and higher offspring survival (Silk et al., 2010, 2003), it remains unclear whether and in which way other types of relationships may be affecting reproductive success in a positive or negative way. For instance, a large number of rare affiliative relationships may provide a 'fall back' option when strong bond partners disappear (Engh et al., 2006). Another productive research avenue could be to test in which way personality traits such as cognitive ability, boldness, perseverance or frustration tolerance (Nettle & Penke, 2010) map onto individual relationship diversity measures. Caution is needed here to avoid circular reasoning, however, such as mapping aggressive tendencies to the occurrence of agonistic relationships.

Relationship diversity at the group level

Ultimately, we aim for measures that can be used in large scale comparative analyses, in which either brain measures (Dunbar & Shultz, 2007a, 2007b), cognitive skills (Rowe & Healy, 2014), or vocal complexity (Fischer, Wadewitz, & Hammerschmidt, 2016; Freeberg et al., 2012) are related to social complexity (but see Healy & Rowe, 2007). In this context, it is important to note that complexity and diversity are strictly speaking not the same thing: while (ecological) diversity describes the number and abundance of different types, an information-based notion of complexity describes complex systems as such that are neither completely ordered, nor completely disordered, but rather stand in between these two extremes (Crutchfield, 2011; Tononi, Edelman, & Sporns, 1998). How one would quantitatively relate different distributions of diversity indices to measures of complexity requires further investigation (see Fischer et al., 2016). Yet, for the time being, a highly right skewed distribution would indicate that most individuals in the group would have a low degree of differentiation of their relationships, while a normal distribution would point to a higher diversity of relationships, and hence a higher complexity in the colloquial sense of the term. A left skewed distribution would indicate that most animals have a high number of different relationships. It is to be expected that the higher the individual diversity score, the more difficult it is to predict which type of relationship a specific individual may develop with – for instance – a new group member. Hence, one may postulate that the cognitive affordances for acquiring and representing the social relationships of others within a group rises with increasing average diversity. It is important to note, however, that the diversity per se is blind to the tenor of the relationship. For instance, one could also imagine a society with either weak ambivalent or strong agonistic relationships. Thus, a full picture only emerges when further information is considered. Finally, it is important to note that the derived values for the Barbary macaques were calculated for females only. For a full comparison across species, both sexes and all age categories need to be examined (or else, the comparison needs to be restricted to females only).

Conclusion

The identification of relationship types based on cluster analyses, and the calculation of diversity scores at the behavioural and individual level, as well as implementation onto the group level appears to be suited to capture specific aspects of animal societies that have not yet been integrated in simple scores or social network indices. They may therefore provide important additional information about the quality of a society as a whole and lend itself for comparative analyses and quantitative tests of hypotheses regarding the evolution of the social brain.

Acknowledgements

We are grateful to Ellen Merz as well as Gilbert and Guillaume de Turckheim for permission to conduct this study at 'La Forêt des Singes' in Rocamadour, the team on site for their continuing support, Andreas Ploss for the data collection, and Rebecca Jürgens for help with the bibliography. The constructive criticism of two anonymous reviewers is gratefully acknowledged.

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Figure Legends

Figure 1. Cluster solutions for the different numbers of minimum interactions. Shown are the proportions of each cluster in three cluster solutions with different sets of dyads, characterized by three different cut-off values of interaction (IA) numbers for the observational study. Indicated as well are the approximated reductions of clusters from the first (left) cluster solution to the middle and right one. While the cluster solution with at least 3 interactions showed four clusters, characterized mostly by the frequency of interaction and tenor, the other two showed two clusters separated by frequency. Abbreviations: Freq. affil.: frequent affiliative.

Figure 2. Distribution of clusters**.** The 122 dyads observed in (a) season 1 and (b) season 2 in the observational study were subdivided into four clusters illustrated by symbols of different shape and colours. Cluster 1 (blue diamonds) consists of frequently interacting affiliative dyads, Cluster 2 (green circles) consists of moderately frequently interacting dyads with ambivalent tenor, Cluster 3 (beige squares) consists of rarely interacting affiliative dyads and Cluster 4 (purple inverted triangles) of rarely interacting agonistic dyads. Centroids of every cluster are represented by a square. F1: discriminant function 1, correlating with Tenor, F2: discriminant function 2, correlating with IFI and DCSI.

Figure 3. Histogram of the normalised Individual Relationship Diversity Index for the 19 Barbary macaque females in the observational study.

Figure 4. Boxplots for the indices in the simulation study (median of respective index values as thick solid horizontal line, 1st quartile (*Q1*) and 3rd quartile (*Q3*) as upper and lower box boundaries; upper whisker as min(max(x), *Q3* + 1.5 * *IQR*) and lower whisker as max(min(x), *Q1* – 1.5 * *IQR;* Observations outside the whiskers are shown as single observations; BDI: Behavioural Diversity Index; IFI: Interaction Frequency Index; DCSI: Dyadic Composite Sociality Index; Tenor) in the four

different variants in scenario 1. (a): no medium affiliation; (b): no high affiliation; (c): no ambivalent relationships; (d): full variation (see inserts in Fig. 5). The distributions are given for the subset with 70% realized relationships.

Figure 5. Distribution of the Individual Relationship Diversity Index (IRDI) in the first scenario of the simulation study. (a)-(d): all realized relationships, (e)-(h): 70% realized relationships. (a) and (e): no medium affiliation; (b) and (f): no strong affiliation: (c) and (g): no ambivalent relationships; (d) and (h): full variation. Inserts depict the types of relationships created simulation study, with their different combinations of valence (from left to right: largely agonistic, ambivalent, largely affiliative) and interaction frequency (IF) in the chosen scenarios.

Figure 6. Distribution of the Individual Relationship Diversity Index (IRDI) in the second scenario of the simulation study. The ‘selectivity’, i.e. the share of strong bonds (largely affiliative with a high interaction frequency) decreases from A to C.

Figure 7. Summary of steps in the calculation of relationship diversity scores. Each dyadic relationship is based on sequences of interactions (circles: affiliative, triangles: agonistic, with different colour shades representing different categories within the affiliative or agonistic domain). These patterns are aggregated over time and a number of indices are derived. Cluster analysis is then used to identify different relationship types. In the next step, the individual relationship diversity is assessed, based on the number and diversity of different relationship types (Individuals I1, I2, I3 representing 3 different individuals). For between group comparisons, the distribution of the individual diversity scores can be used.

Table 1. Results of the cluster analysis based on behaviour categories in the observational study.

	Cluster 1 Rare amb.	Cluster 2 Freq. affil.	Importance for Cluster separation
N	103 (84.4%)	19 (15.6%)	
attacks	0.00	0.58	1
body contact	3.58	22.37	0.51
grooming	1.32	6.32	0.42
chases	1.09	2.95	0.23
threats	1.96	5.32	0.20

Cluster size (number and proportion of dyads), importance of behaviour categories for cluster separation, and mean number of interactions which dyads in the respective clusters had for each behaviour category (122 dyads). Abbreviations: Freq. = frequent; affil: affiliative; amb: ambivalent.

Table 2. Results of the cluster analysis based on behavioural indices in the observational study.

	Cluster 1 Freq. affil.	Cluster 2 Ambivalent	Cluster 3 Rare affil.	Cluster 4 Rare agon.	Importance for Cluster separation
Proportion	10 (8.2%)	34 (27.9%)	44 (36.1%)	34 (27.9%)	
Tenor	0.77	0.51	0.89	0.13	1
IFI	7.46	2.52	0.95	0.89	0.85
DCSI	12.22	2.23	1.95	0.15	0.67
BDI	1.92	2.92	1.60	1.70	0.66

Cluster size (number and proportion of dyads), importance of the indices for cluster separation and mean of the index values of all dyads in the respective clusters (122 dyads). Abbreviations: IFI: Interaction Frequency Index; DCSI: Dyadic Composite Sociality Index; BDI: Behavioural Diversity Index; Freq.: frequent; affil.: affiliative; agon.: agonistic.

Table 3. Influence of age and rank on relationship diversity and the number of dyads per individual.

Diversity Index	Estimate	*SD*	*t*	*P*
Intercept	2.328	0.134	17.437	<0.001
Age	-0.286	0.139	-2.059	0.056
Rank	-0.108	0.139	-0.779	0.448
Number of partners				
Intercept	6.421	0.643	9.980	<0.001
Age	-2.195	0.670	-3.275	0.005
Rank	1.376	0.670	2.032	0.057

Predictor variables were z-transformed.

Appendix Tables

Table A1. Cluster analysis results of 68 dyads that interacted at least five times (observational study).

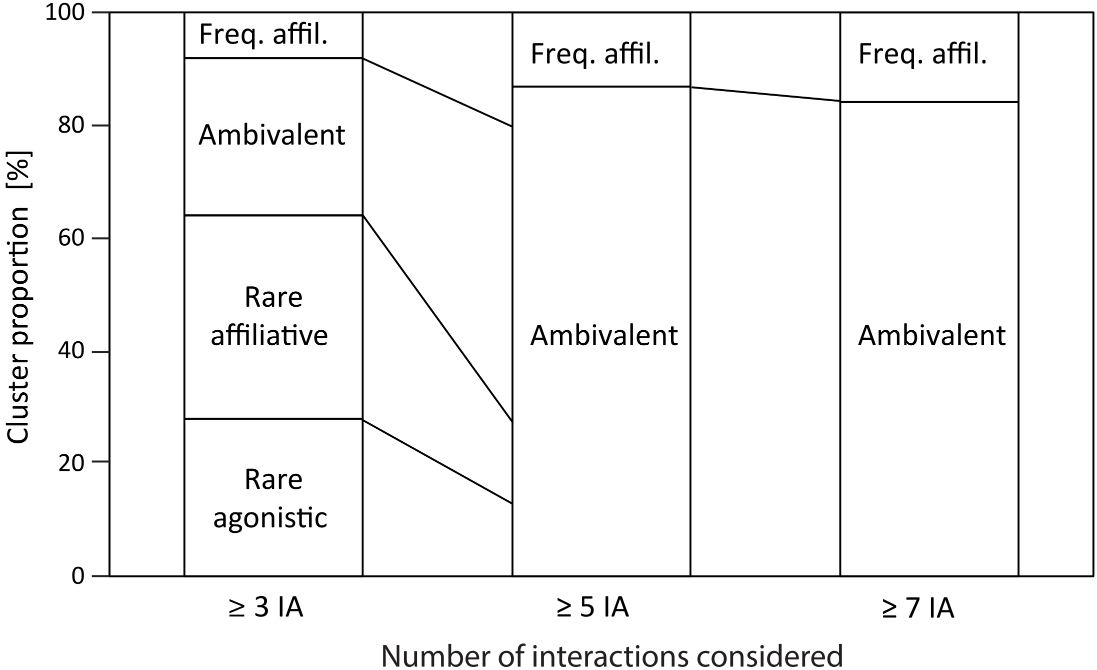
Dyads with	rare IA	Freq. affil. IA	Importance for Cluster separation
Proportion	86.8% (59)	13.2% (9)	
IFI	1.77	7.92	1
DCSI	2.02	12.67	0.74
Tenor	0.59	0.75	0.04
BDI	2.28	2.01	0.03

Cluster analysis was conducted with index values Tenor, Interaction Frequency Index (IFI), Dyadic Composite Sociality Index (DCSI) and Behavioural Diversity Index (BDI) for every dyad. The resulting cluster solution had a Silhouette value of 0.5. Also shown is the importance of each index for cluster separation. The values in each column represent the mean of the clusters index. Each cluster is further described by the percentage of dyads included and the absolute number in parentheses. Abbreviations: Freq. = frequent; affil: affiliative; IA: interaction.

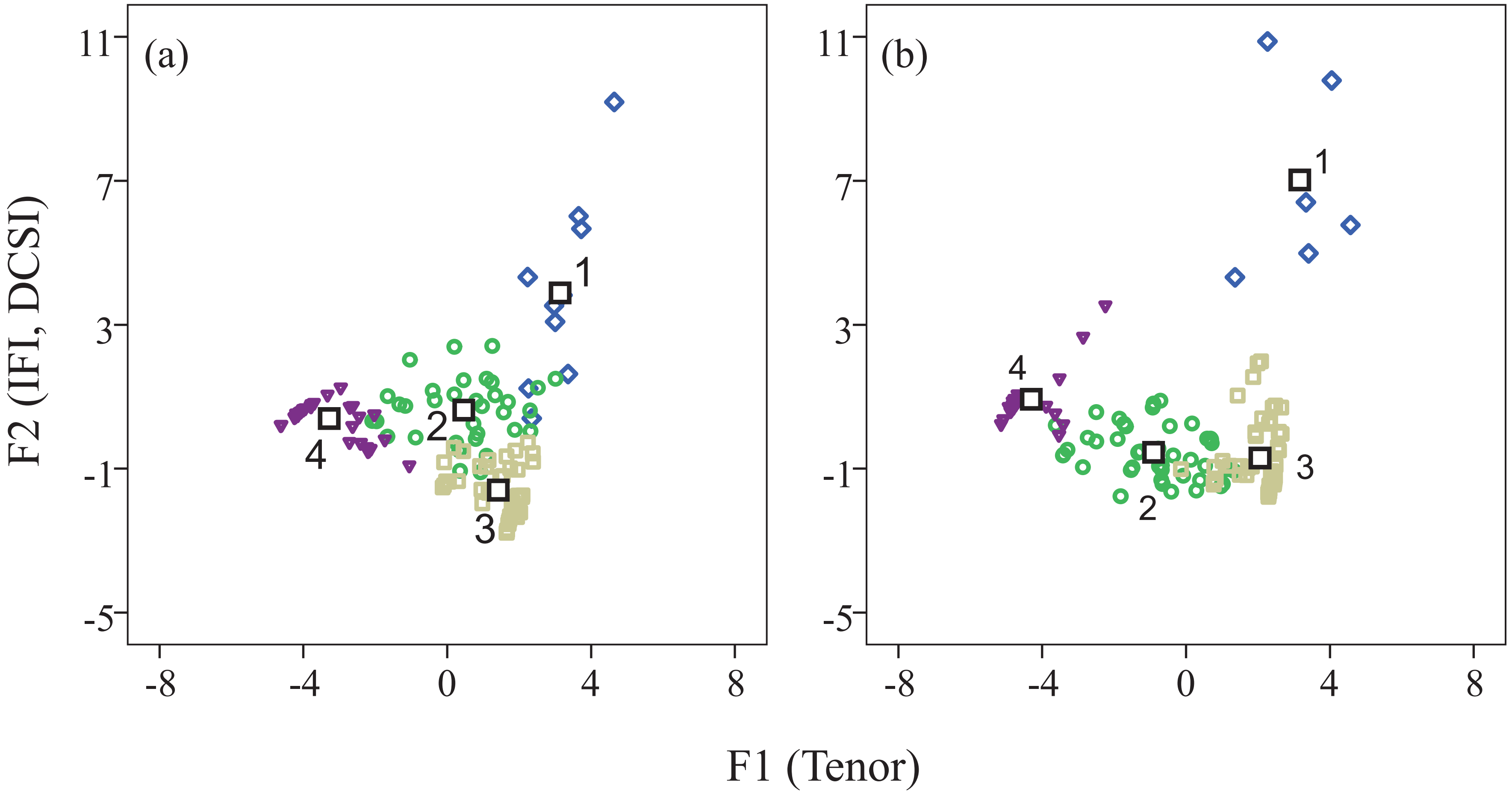
Table A2. Cluster analysis results of 44 dyads that interacted at least seven times (observational study).

Dyads with	rare IA	Freq. affil. IA	Importance for Cluster separation
Proportion	84.1% (37)	15.9% (7)	
DCSI	2.42	15.07	1
IFI	2.36	7.87	0.67
Tenor	0.57	0.83	0.11
BDI	2.37	2.11	0.04

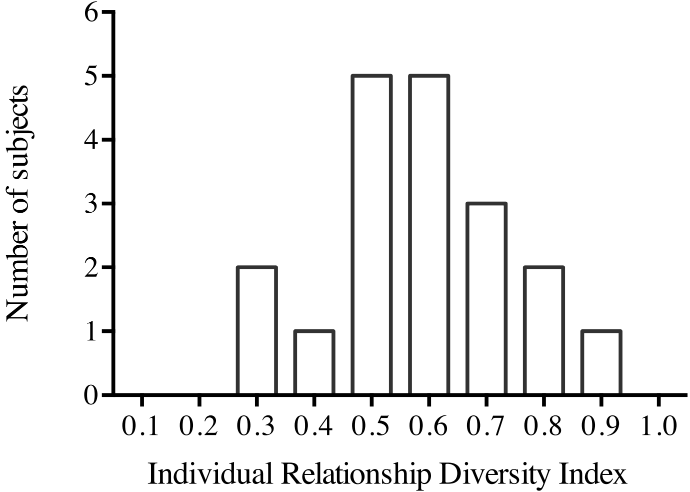
Cluster analysis was conducted with index values Tenor, Interaction Frequency Index (IFI), Dyadic Composite Sociality Index (DCSI) and Behavioural Diversity Index (BDI) for every dyad. The resulting cluster solution had a Silhouette value of 0.5. Also shown is the importance of each index for cluster separation. The values in each column represent the mean of the clusters index. Each cluster is further described by the percentage of dyads included and the absolute number in parentheses. Abbreviations: Freq. = frequent; affil: affiliative; IA: interaction.



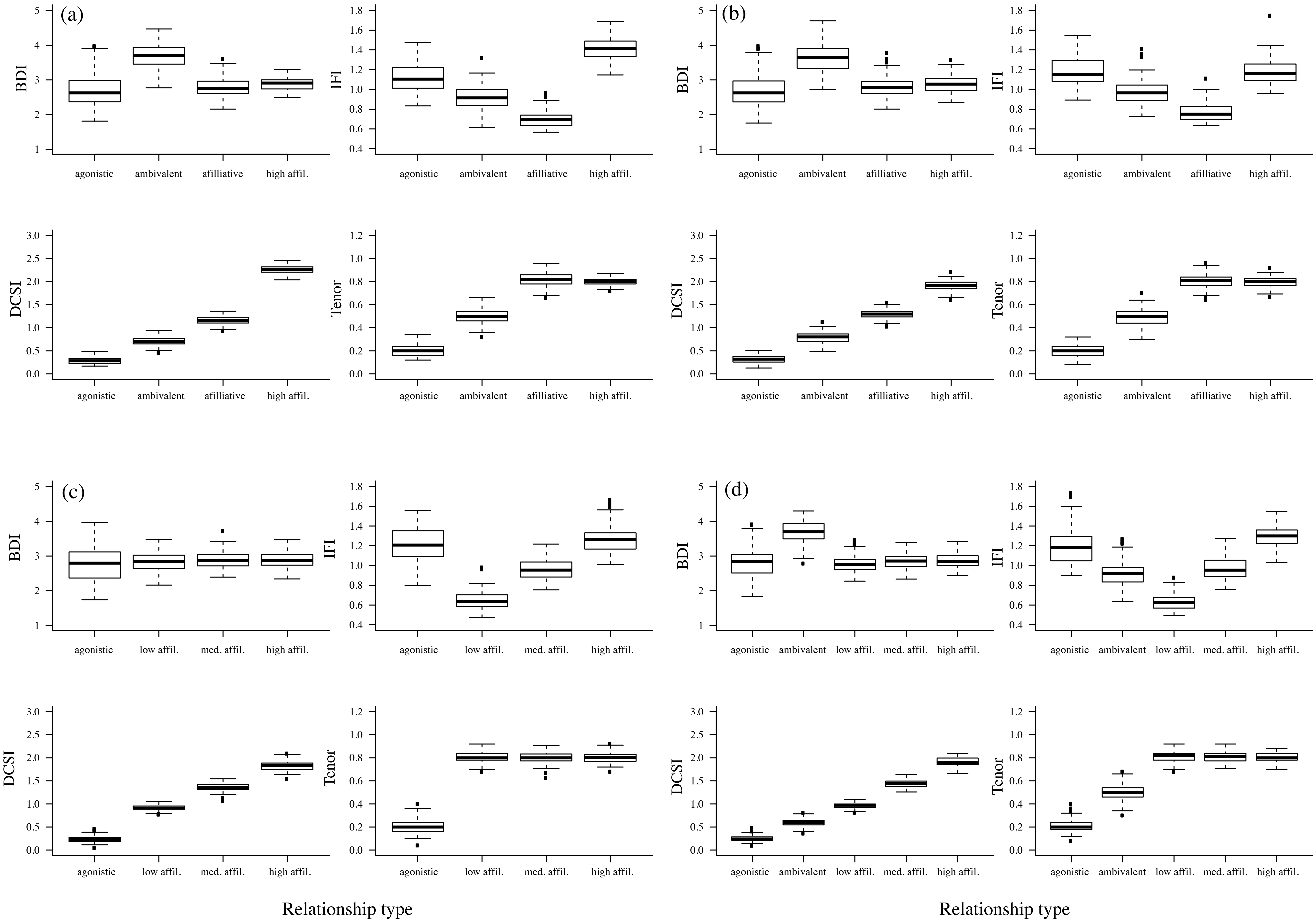
100
80
60
40
20
0
Cluster proportion [%]
Freq. affil.
Ambivalent
Rare affiliative
Rare agonistic
Freq. affil.
Ambivalent
Freq. affil.
Ambivalent
≥ 3 IA
≥ 5 IA
≥ 7 IA
Number of interactions considered

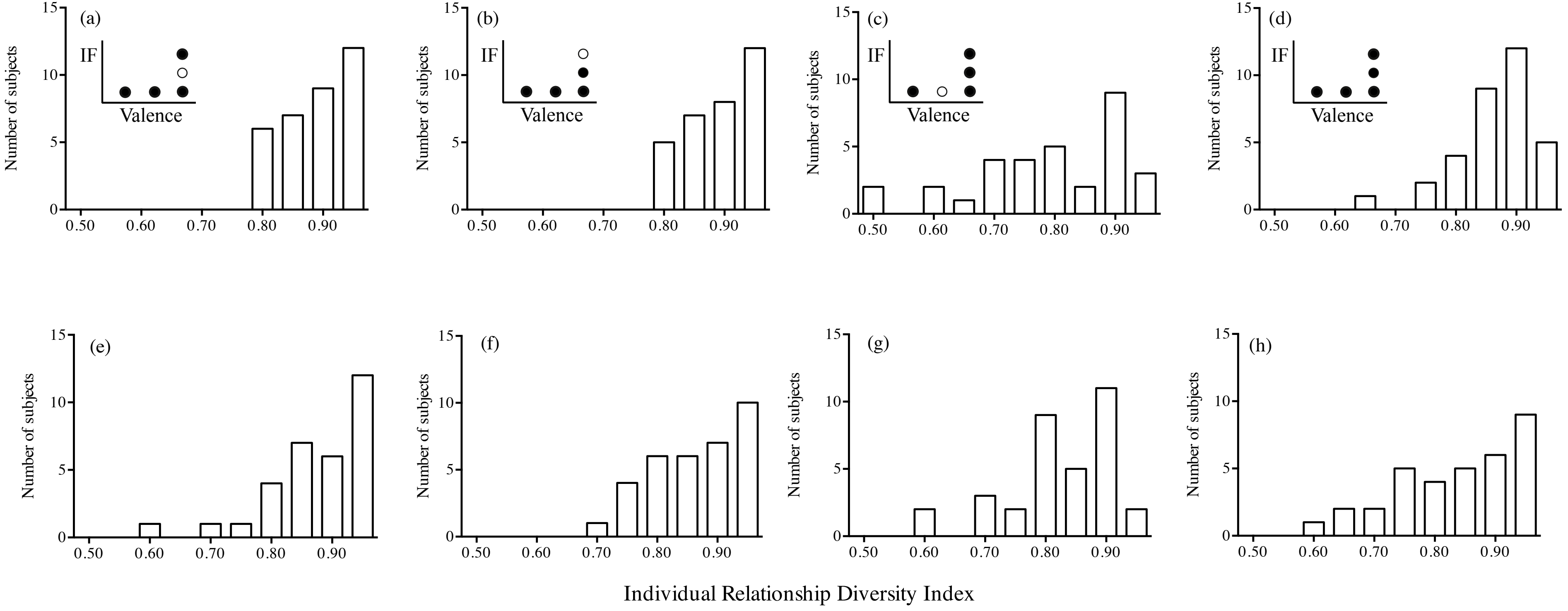


(a)
(b)
11
7
3
-1
-5
-8
-4
0
4
8
1
2
3
4
F2 (IFI, DCSI)
F1 (Tenor)

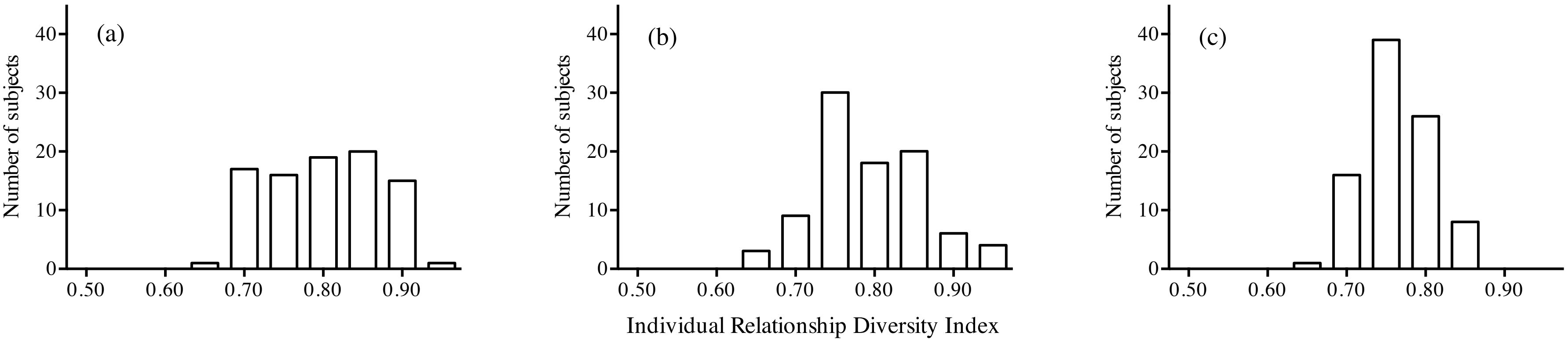


Number of subjects
0
1
2
3
4
5
6
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Individual Relationship Diversity Index

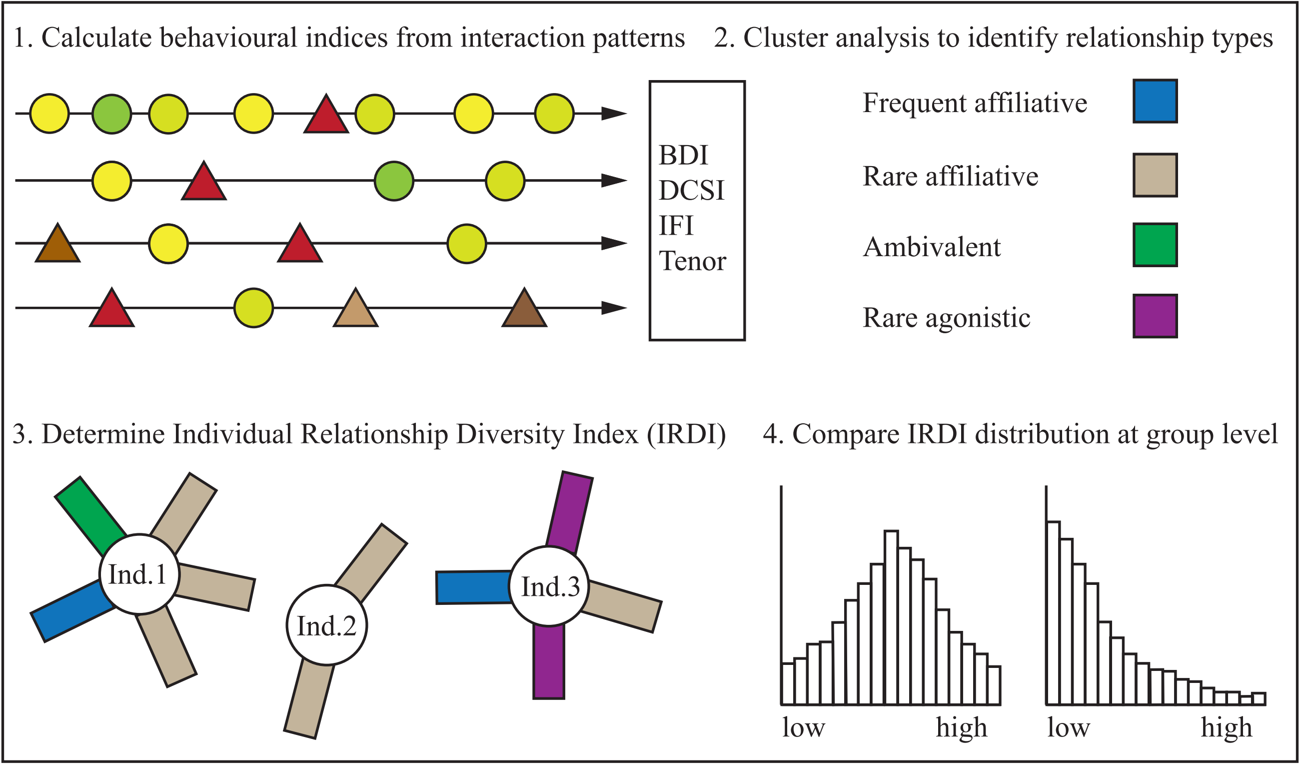

(a)
(b)
(c)
(d)
BDI
IFI
DCSI
Tenor
agonistic
ambivalent
afilliative
high affil.
low affil.
med. affil.
Relationship type
Relationship type



(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
IF
Valence
Number of subjects
0
5
10
15
0.50
0.60
0.70
0.80
0.90
Individual Relationship Diversity Index



(a)
(b)
(c)
Number of subjects
0
10
20
30
40
0.50
0.60
0.70
0.80
0.90
Individual Relationship Diversity Index


1. Calculate behavioural indices from interaction patterns
BDI
DCSI
IFI
Tenor
2. Cluster analysis to identify relationship types
Frequent affiliative
Rare affiliative
Ambivalent
Rare agonistic
3. Determine Individual Relationship Diversity Index (IRDI)
Ind.1
Ind.2
Ind.3
4. Compare IRDI distribution at group level
low
high
low
high