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(Article begins on next page)

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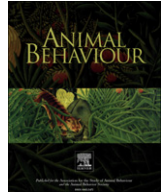
A comparative network analysis of social style in macaques

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ARTICLE INFO

In group-living species, individuals gain significant advantages from establishing an extensive network of social relationships. This results in complex organizations that are difficult to quantify in a comprehensive manner. In this respect, network analyses are an ideal means to pinpoint the overall properties of social structures, and the place of each individual within these structures. We used network measurements to investigate cross-species variations in the social style of macaques, and studied 12 groups from four species. Two species (*Macaca mulatta*, *Macaca fuscata*) were characterized by a relatively weak social tolerance, a steep gradient of dominance and a strong preference for kin. The other two species (*Macaca nigra*, *Macaca tonkeana*) were known to display higher levels of tolerance, relaxed dominance and low kinship bias. We used a centrality index based on eigenvector centrality to show that in a comparison of intolerant and tolerant species, top-ranking individuals were more central than other group members in the former species than the latter. We also found that networks had higher modularity in intolerant species, indicating that kin-related partners interacted more frequently in subgroups of these species than in those of tolerant species. Consistently, the matrix of body contacts was more strongly correlated with the kinship matrix in intolerant species. This study demonstrates the efficiency of network methodology in detecting fine and overall contrasts in social structures, and also reveals novel dimensions in the social style of macaques.

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Living in groups generates selection pressures that favour those animals more capable of gaining access to resources by competing and cooperating with other groupmates. When the benefits of cooperation exceed the costs it imposes, the creation of an extensive network of social relationships is advantageous for individuals (Krause & Ruxton 2002). Social relationships involve a succession of social interactions between partners that know each other (Hinde 1976). At the dyadic level, individuals can reliably predict the behaviour of the other. At the group level, affiliative relationships underpin various patterns of social life such as coalitions, collective movements or information transmission (Chepko-Sade & Sade 1979; Silk et al. 2004; Sueur & Petit 2008; Voelkl & Noë 2008). Coalitions allow individuals to win in social competition or to gain support in collective decisions by recruiting mates and kin (Chapais 1995); moreover, some key individuals can favour the spread of information or disease by their central position in social networks (Sueur et al. 2011).

Societies are by nature complex phenomena; they differ from one species or population to another in various dimensions that are difficult to compare in a homologous way. In this context, social network analyses provide a set of analytical tools that can be applied to various societies, thus allowing them to be examined and compared within the same conceptual framework (Newman 2010). The recent development of the network approach has helped us make significant progress in our understanding of social organizations in taxa as diverse as bottlenose dolphins, *Tursiops truncatus*, African elephants, *Loxondota africana*, bats and primates (Kerth & König 1999; Lusseau & Newman 2004; Wittemyer et al. 2005; Flack et al. 2006; Kasper & Voelkl 2009).

Social networks are well developed in many nonhuman primates, especially because they live in stable groups with overlapping generations, favouring the occurrence of clusters within groups (Campbell et al. 2010). The occurrence of coalitions between individuals and subgroups adds further complexity to their social organization (Chapais 1995). This is particularly true for macaques, which form multimale, multifemale groups of several dozen individuals (Thierry et al. 2004). Females spend their entire lifetime in their natal group, while males emigrate when reaching adulthood. As

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a consequence, social groups are structured in matrilines composed of maternal relatives who maintain preferential bonds and support each other during conflicts, with matrilines maintaining stable dominance relationships between them (Chapais 1988).

The genus *Macaca* is a good model to test to what extent network analyses can detect finely tuned contrasts between societies. Whereas all macaque species show the same basic patterns of social organization, they display broad interspecific variation in their social style, and any evolutionary explanation must account for the covariation of behavioural traits from one species to another resulting from linkages between traits (Waal & Luttrell 1989; Thierry et al. 2004; Thierry 2007). In species with strict dominance relationships, the risk of being bitten in a conflict is relatively high and the best tactic for targets of aggression is either to submit or to flee rather than to retaliate, which impairs the occurrence of affiliative interactions between previous opponents. Conversely, when the intensity of the aggression is lower, as in more relaxed species, targets may counterattack, forcing their adversaries to become more cautious. In this case, affiliative interactions can arise more easily between opponents. Aggression intensity, dominance asymmetry and affiliation rates after conflicts can therefore be considered to belong to the same system of interrelated traits (Petit et al. 1997; Thierry 2007). The occurrence of coalitions most probably creates a positive feedback loop between levels of dominance asymmetry and nepotism. When most coalitions involve relatives, the dominance status of individuals depends primarily on the power of the kin subgroup to which they belong. This increases rank differences between nonrelatives and promotes coalitions between kin, generating social networks based on strong hierarchies. In contrast, a less-pronounced kin bias results in more coalitions involving nonrelatives, and dominance relationships are more balanced, with close bonds arising even between unrelated group members (Thierry 2007).

Macaques can be ordered along a continuum from species characterized by rather strong social intolerance, steep gradient of dominance and strong preference for kin, to others displaying higher levels of tolerance, relaxed dominance and low kinship bias. Social styles can be classified as 'despotic' and 'egalitarian' (Waal & Luttrell 1989; Matsumura 1999; Hemelrijk 2000), and macaque styles have been more accurately ranked on a 4-grade scale from less to more tolerant species (Thierry et al. 2000; Thierry 2007). This scale is mainly based on patterns of agonistic and affiliative interactions. In the more tolerant macaques, conflicts involve more protests and counterattacks, and are more frequently followed by reconciliation between previous opponents. Submissive displays are absent or less formalized in tolerant macaques than in intolerant ones. Moreover, whereas dominance and kinship relations have an overwhelming effect on patterns such as interindividual distance or support in conflicts in intolerant macaques, their influence is significantly lower in tolerant macaques.

Despite early attempts to apply social network metrics to the study of primate social organization (Sade 1972, 1989; Sade et al. 1988), previous studies of social styles were limited to the level of social interactions and relationships. Here, we aimed to study these social styles at the level of social structures, that is, the networks of social relationships as defined by Hinde (1976). We used social network analyses to reveal novel dimensions in the social styles of macaques. We compared four species taken from the extremities of the 4-grade scale, that is, rhesus macaques, *Macaca mulatta*, and Japanese macaques, *Macaca fuscata*, taken from one extreme of the scale (grade 1: less tolerant relationships), and crested macaques, *Macaca nigra*, and Tonkean macaques, *Macaca tonkeana*, from the other (grade 4: more tolerant relationships). We investigated affiliative networks based on interindividual body contacts in different groups, using both group and individual measures. Since species from grade 1 display stronger social intolerance and nepotism than species

from grade 4, we predicted that the former would display a lower network density (i.e. the number of observed relationships divided by the number of possible relationships), higher community division (i.e. the strength of subgrouping/clustering of individuals). If species from grade 1 show a lower network density and a higher community division, compared to species from grade 4, they should also display a higher average trajectory (i.e. length of the shortest path between two nodes) and a higher diameter (i.e. the longest path length in the network), but a lower transitivity (i.e. density of transitive triples in a network). Following previous indications that top-ranking individuals are the most frequently groomed individuals in more intolerant species (Schino 2001; Nakamichi & Shizawa 2003; Silk et al. 2003), we further predicted that the centrality of top-ranking individuals (i.e. the degree of association between conspecifics) would be higher in intolerant species than in tolerant ones. Until now, the dominance gradient had mainly been measured by the percentage of counterattacks in conflicts, or the directional consistency of the dominance order. Here, we used a new index, the centrality index, which is based solely on the distribution of affiliative contacts according to dominance rank. This centrality index, defined as the difference in centrality between the top-ranking individual and other group members, should be higher in intolerant species than in tolerant ones. Lastly, we tested the possible effects of sociodemographic factors such as group size and sex ratio on the properties of social networks.

METHODS

Subjects

The study was carried out on 12 different groups of macaques taken from four species (*M. mulatta*, *M. fuscata*, *M. nigra*, *M. tonkeana*). Only one group (No. 7 and 9, Table 1) was sampled twice, once in 1988 and once again 9 years later, when its demographic composition was different. Animals were housed at research centres and zoological parks. Table 1 provides information about location and sociodemographic parameters for each group. Each group lived in captivity (an enclosure measuring approximately 100 m^2) or in semicaptivity (in a 0.3 ha park with trees, bushes and grassy areas). They had an inside shelter where commercial pellets and water were provided ad libitum. Fruits and vegetables were distributed once per week, outside the observation sessions. Only adults and subadults, that is, individuals 3–5 years old, were included in analyses. We defined 'group size' as the total number of adults and subadults per group, 'sex ratio' as the number of males divided by the number of females and 'kin ratio' as the mean number of maternal relatives divided by the number of nonrelatives by individual. The latter ranged from 0 to 1, with 0 meaning that an individual had no relative, and 1 that all group members were related. Two individuals were considered as related when they belonged to the same matriline. We assessed dominance relationships in each group using supplantations and unidirectional conflicts spontaneously occurring in groups plus those recorded during drinking competition tests around a single source of orange fruit juice (see Thierry et al. 1994). We then ranked individuals in a matrix of interactions, and used Matman software to check for linearity in the dominance hierarchy (de Vries et al. 1993; Sueur et al. 2011).

Affiliative Relationships

We used instantaneous scan sampling (Altmann 1974) to measure affiliative relationships from the number of body contacts between individuals (social grooming or contact sitting). Scans were discarded when all individuals were not simultaneously visible. Measures were based on the absolute number of body contacts. Groups were

Table 1
Information about species, location and sociodemographic parameters of groups

No.	Species	Location	Grade	Group size	Sex ratio (males: females)	Source	Year of study
1	*M. mulatta*	Centre de Primatologie, Strasbourg, France	1	10	0.67	C. Desportes & B. Thierry, unpublished data	1989
2	*M. mulatta*	Madingley, University of Cambridge, Great Britain	1	7	0.40	C. Desportes & B. Thierry, unpublished data	1990
3	*M. mulatta*	Madingley, University of Cambridge, Great Britain	1	9	0.36	C. Desportes & B. Thierry, unpublished data	1990
4	*M. fuscata*	Parc Zoologique de Paris, Vincennes, France	1	22	0.57	Petit et al. 1997	1991−1992
5	*M. mulatta*	Centre de Primatologie, Strasbourg, France	1	15	0.15	Sueur 2010; Sueur et al. 2010	2006
6	*M. fuscata*	Primate Research Institute, Takahama, Japan	1	25	0.56	A. Jacobs & K. Watanabe, unpublished data ; Jaman & Huffman 2008	2008
7	*M. tonkeana*	Centre de Primatologie, Strasbourg, France	4	14	0.4	Petit & Thierry 1994; C. Desportes & B. Thierry, unpublished data	1988
8	*M. nigra*	Jersey Wildlife Preservation Trust, Channel Islands, Great Britain	4	16	0.60	Petit et al. 1997	1992
9	*M. tonkeana*	Centre de Primatologie, Strasbourg, France	4	25	1.00	C. de Saint-Rat & B. Thierry, unpublished data	1997
10	*M. tonkeana*	Centre de Primatologie, Strasbourg, France	4	7	0.40	Sueur 2010; Sueur et al. 2009, 2010	2005
11	*M. tonkeana*	Zoo de l'Orangerie, Strasbourg, France	4	16	1.25	De Marco et al. 2010	2006
12	*M. tonkeana*	Parco Faunistico di Piano dell'Abatino, Poggio San Lorenzo, Italy	4	7	1.33	De Marco et al. 2010	2007

observed for 5−7 months, and 4−5 h per day according to groups. This observation period was sufficient to identify social networks; there were no significant differences in observation time between groups from intolerant and tolerant species (median$_{\text{Intolerant}}$ = 6 [interquartiles: 5, 7], median$_{\text{Tolerant}}$ = 7 [5, 7]; Mann−Whitney test: $U = 15$, $N_{\text{Intolerant}} = N_{\text{Tolerant}} = 6$, $P = 0.699$). More information about scored data can be found in the articles cited in Table 1. We established a matrix of contacts for each group. We divided the number of contacts $M(i,j)$ for each pair ij on row j by the sum of contacts $\sum_i^N (M(i,j))$ on row j. The matrix was then symmetrized ($M(i,j) = M(j,i)$) to perform social network analyses. This automatic symmetrization by SocProg 2.4 helps avoid possible errors made by the observers regarding a directed behaviour such as social grooming, and enables us to incorporate it correctly into the matrix. Analyses were run on these weighted networks: the edge (relationship) value between two nodes (individuals) ranged from 0 to 1 according to the strength of associations between two individuals (Wasserman & Faust 1994; Whitehead 2009; Sueur et al. 2010).

Social Network Analyses

We first analysed whether networks in each group were random (Erdos−Renyi random graph: the distribution of degree or eigenvector coefficients follows a linear law) or scale free (the distribution follows a power law). We ranked individuals from the one with the highest eigenvector to the one with the lowest, and tested the distribution of eigenvector coefficients using a curve estimation test. Networks seemed to be more random than scale free, so we used the linear constant a (from $y = ax + b$) as a measure of the variance of eigenvector coefficients within a group. Indeed, the higher this constant a, the more the eigenvector coefficient is different between individuals.

We used the matrix of body contacts, calculated group indices (network density and modularity of community division) and individual indices (eigenvector centrality coefficient and centrality index) for each group.

Network measures were defined as follows.

Density: the number of observed edges divided by the number of possible edges ($N^2 - N$ with N being the number of individuals per group).

Transitivity: the density of transitive triples in a network. Three vertices u, v, w are transitive if u is connected to vertex v, vertex v is connected to vertex w and vertex u is connected to vertex w. The density of transitive triples is the number of triples that are transitive divided by the number of paths of length 2, that is, the

number of triples that have the potential to be transitive (Borgatti et al. 2002).

Average trajectory (or average distance): the length of the shortest path between two nodes. The length of a path is the number of edges it contains. The average trajectory is the average of all trajectories (shortest paths) in a network.

Diameter: the longest path length in the network.

Modularity: the difference between the proportion of the total association of individuals within clusters (i.e. subgroups) and the expected proportion, given the summed associations of the different individuals (Newman 2004; Whitehead 2008). The coefficient ranged from 0 to 1: the higher the modularity, the higher the division between different subgroups will be (Whitehead 2008, 2009). Here, higher modularity means a high number of contacts within a subgroup, but few contacts between subgroups. Conversely, low modularity means a homogeneous distribution of contacts between all group members. These subgroups may correspond to matrilines, to individuals of the same sex, or to individuals having the same nutrient requirements. As we aimed to assess differences in nepotism between grades, we only compared these patterns using the Modularity method with matrilines.

Individual eigenvector centrality coefficient (Newman 2004; Bonacich 2007): the connection degree of an individual within its group. It is calculated using the number and strengths of connections, while also taking into account the identities of those partners to which it is connected (see Whitehead 2008 for more information about the calculation of this index). According to Kasper & Voelkl (2009) this coefficient is more telling than other centrality coefficients for groups of nonhuman primates.

Mean eigenvector coefficient per group: average of all individual eigenvector centrality coefficients within a group.

Centrality index per group: the difference between the eigenvector centrality coefficient of the top-ranking individual, and the mean eigenvector centrality coefficient of other group members. It ranges between −1 and +1. It is close to 0 for egalitarian networks, where all individuals would have equal relationships, and +1 for unequal networks, where individuals would have social relationships only with the top-ranking individual.

For each group, we also used the Spearman rank correlation to measure the coefficient between individual hierarchical rank and eigenvector centrality coefficient, and the Dietz's R correlation coefficient between kinship and body contact matrices. We called the first measure the dominance−centrality coefficient, and the second measure the kin−contact coefficient.

We performed social network analyses using Socprog 2.4 (Whitehead 2009) and Ucinet 6.0 (Borgatti et al. 2002). Four social networks are represented in Fig. 1.

Statistical Analyses

We used Wilcoxon signed-ranks tests between the regression coefficients of the power distribution and the linear distribution of the eigenvector coefficients to assess whether the networks were random or scale free. We used Mann–Whitney U tests to check possible contrasts between groups from tolerant and intolerant species in both sociodemographic parameters and social network measures. We tested the influence of sociodemographic parameters (group size, sex ratio and kin ratio) on network measures, using the Spearman rank correlation coefficient test. It was not necessary to correct values by phylogenetic distances since in each grade being studied, both species (rhesus/Japanese macaques on one side,

crested/Tonkean macaques on the other side) were close in evolutionary terms (Fooden 1976; Hoelzer & Melnick 1996). The significance level was set at 0.05. We used the exact significance method for small sample sizes (Mundry & Fischer 1998). Sequential Bonferroni correction was used (step-down sequential: Holm 1979; García 2004) for multiple variables analyses. We indicate the new α after this correction. All tests were two tailed. We carried out the analyses using SPSS 10.0 (SPSS Inc., Chicago, IL, U.S.A.). Values are presented as medians (m_I = median for intolerant species; m_T = median for tolerant species) and interquartiles.
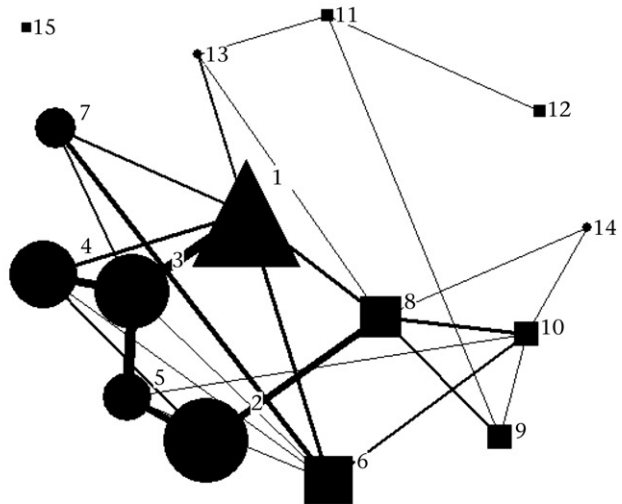
RESULTS

Influence of Sociodemographic Factors

Transitivity, average trajectory and diameter are not commonly used with unweighted networks; they are directly dependent on
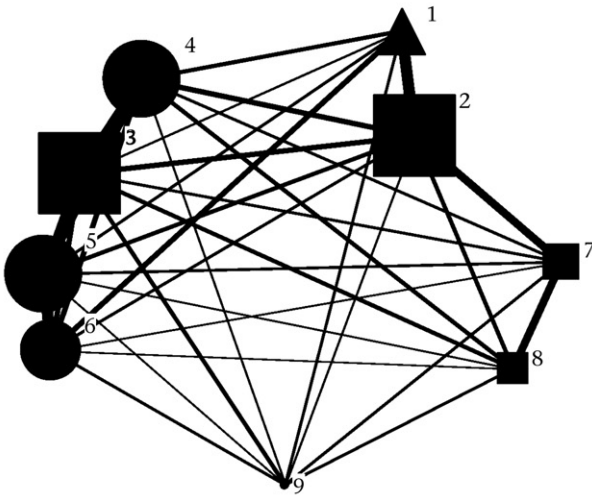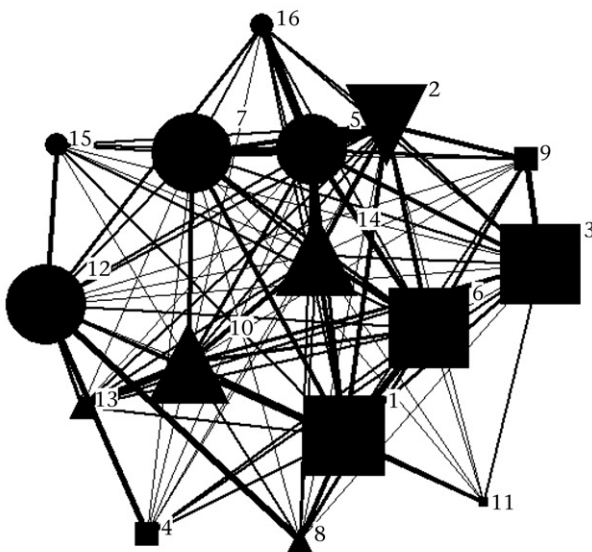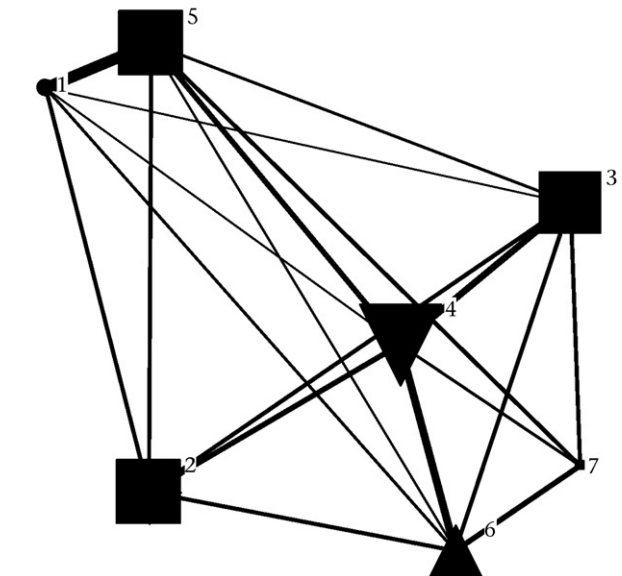

Figure 1. Examples of social network graphs in four groups. We built the networks via Netdraw in UCINET 6.0 (Borgatti et al. 2002). Nodes represent individuals. Numbers indicate the hierarchical rank of each individual. Distances between individuals represent their relationships in term of numbers of body contacts, which were calculated via multidimensional scaling (Sueur et al. 2011). Similar shapes characterized individuals belonging to the same matriline. The size of a node is directly related to the individual eigenvector centrality coefficient: the higher the centrality coefficient is, the more important the individual is for the joining of other group members.

the network density. Two of these three variables were significantly correlated with the network density (transitivity: $r_S = 0.99$, $N = 12$, $P < 0.00001$, $\alpha = 0.05$; average trajectory: $r_S = -0.99$, $N = 12$, $P < 0.00001$, $\alpha = 0.025$; diameter: $r_S = -0.66$, $N = 12$, $P = 0.02$, $\alpha = 0.016$), but the variance of the diameter was too weak to test the difference between grades. We therefore limited our assessment to whether the density differed between groups of tolerant and intolerant macaques. Results are displayed in Table 2 for the four variables.

Even if the distribution of eigenvector coefficients followed both a power law and a linear one for all networks, it appears that networks were more random than scale free; a linear function explained the distribution of eigenvector coefficients better than a power function ($Z = -2.20$, $N = 12$, $P = 0.028$; Table 3).

We found no significant differences in group size ($m_I = 15$ [7.0, 18.3], $m_T = 12.5$ [8.5, 22.8]; $U = 17.5$, $P = 0.937$, $\alpha = 0.016$), sex ratio ($m_I = 0.48$ [0.31, 0.59], $m_T = 0.80$ [0.4, 1.27]; $U = 8$, $P = 0.132$, $\alpha = 0.05$) and kin ratio ($m_I = 0.60$ [0.47, 0.68], $m_T = 0.65$ [0.09, 1.34]; $U = 12.0$, $P = 0.917$, $\alpha = 0.025$) between groups from both intolerant and tolerant species (Mann−Whitney tests: $N_I = N_T = 6$).

Group size was significantly correlated with the mean eigenvector coefficient (Spearman correlation: $r_S = -0.90$, $N = 12$, $P < 0.0001$, $\alpha = 0.05$), but not with centrality index, network density, modularity, dominance−centrality coefficient and kin−contact coefficient ($-0.46 \leq r_S \leq 0.17$, $N = 12$, $P \geq 0.131$, $\alpha = 0.01$). More precisely, the relation between group size and the mean eigenvector coefficient appeared to follow a power law (curve estimation test: $R^2 = 0.87$, $F_{1,10} = 56.7$, $P < 0.0001$, $y = 1.02x^{-0.53}$; Fig. 2), meaning that the larger the group size, the lower the centrality per individual was. Kin ratio was correlated with the mean eigenvector coefficient ($r_S = -0.78$, $N = 12$, $P = 0.008$, $\alpha = 0.025$), but not with any other variable ($-0.50 \leq r_S \leq 0.22$, $N = 12$, $P \geq 0.140$, $\alpha = 0.008$). Sex ratio was not correlated with any variable ($-0.52 \leq r_S \leq -0.64$, $N = 12$, $P \geq 0.031$, $\alpha = 0.016$).

Influence of Social Style

A Mann−Whitney test ($N_I = N_T = 6$) showed that network density was not significantly different in groups from intolerant and tolerant species ($m_I = 0.67$ [0.47, 0.85], $m_T = 0.90$ [0.81, 0.98]; $U = 5$, $P = 0.036$, $\alpha = 0.0125$; Fig. 3, Table 1). Modularity was higher in groups from intolerant species ($m_I = 0.33 \pm 0.08$, $m_T = 0.21 \pm 0.03$; $U = 1$, $P = 0.004$, $\alpha = 0.05$; Fig. 3).

The linear constant of the distribution of eigenvector coefficients was not significantly different between groups from intolerant and tolerant species ($m_I = -0.017$ [−0.028, −0.007], $m_T = -0.012$ [−0.021, −0.008]; $U = 14$, $P = 0.589$, $\alpha = 0.008$; Table 3). We found no significant difference in the mean eigenvector centralities between groups from intolerant and tolerant species ($m_I = 0.25$ [0.19, 0.34], $m_T = 0.26$ [0.22, 0.33]; $U = 16$, $P = 0.818$, $\alpha = 0.0055$;

Table 2
Density, transitivity, average trajectory and diameter of groups

Group (no.)	Density	Transitivity (%)	Average trajectory	Diameter
1	0.71	50.0	1.29	2
2	0.63	41.8	1.36	2
3	0.94	85.5	1.06	2
4	0.54	35.9	1.46	2
5	0.27	17.1	2.01	4
6	0.82	64.0	1.18	2
7	0.98	98.4	1.02	2
8	0.82	63.2	1.18	2
9	0.77	52.9	1.23	2
10	0.82	64.2	1.18	2
11	0.98	94.1	1.02	2
12	1	100	1.00	1

Table 3
Regression coefficients and constants of the power and linear distribution of eigenvector coefficients for each group

Group (no.)	R^2 power function	R^2 linear function	Power exponent	Linear constant a
1	0.92	0.94	−0.212	−0.016
2	0.71	0.87	−0.157	−0.025
3	0.69	0.93	−0.190	−0.018
4	0.94	0.79	−0.322	−0.0085
5	0.71	0.92	−1.600	−0.038
6	0.44	0.75	−0.183	−0.0045
7	0.77	0.95	−0.372	−0.023
8	0.87	0.96	−0.255	−0.011
9	0.91	0.93	−0.161	−0.004
10	0.82	0.91	−0.269	−0.021
11	0.95	0.90	−0.245	−0.009
12	0.88	0.92	−0.179	−0.014

Fig. 3), but the centrality index was higher in the former ($m_I = 0.07$ [0.04, 0.15], $m_T = -0.03$ [−0.08, 0.02]; $U = 3$, $P = 0.015$, $\alpha = 0.016$; Fig. 3), which shows that top-ranking males were more central in relation to other group members in groups from intolerant species compared with those of tolerant species.

No significant difference in dominance−centrality coefficients appeared between groups from intolerant and tolerant species ($m_I = 0.21$ [0.13, 0.77], $m_T = 0.29$ [−0.10, 0.50]; $U = 15$, $P = 0.631$, $\alpha = 0.007$; Fig. 4). This could be caused by the high variance in the dominance−centrality coefficient observed within grades (see Fig. 5 for the highest and lowest correlations found in groups from intolerant and tolerant species). We obtained similar results, that is, no significant difference in the dominance−centrality coefficient between the two kinds of groups, from the separate analysis of dominance in males and females ($m_I = -0.10$ [−0.53, 0.13], $m_T = -0.22$ [−0.24, −0.07]; $U = 0.40$, $P = 0.811$, $\alpha = 0.006$) or in each matriline ($m_I = -0.20$ [−0.62, −0.01], $m_T = -0.15$ [−0.62, 0.20]; $U = 0.81$, $P = 0.500$, $\alpha = 0.001$). However, the kin−contact coefficient was significantly higher in groups from intolerant species than in those from tolerant species ($m_I = 0.70$ [0.65, 0.83], $m_T = 0.21$ [0.12, 0.61]; $U = 2$, $P = 0.012$, $\alpha = 0.025$; Fig. 4), which means that individuals had more numerous or stronger relationships with their
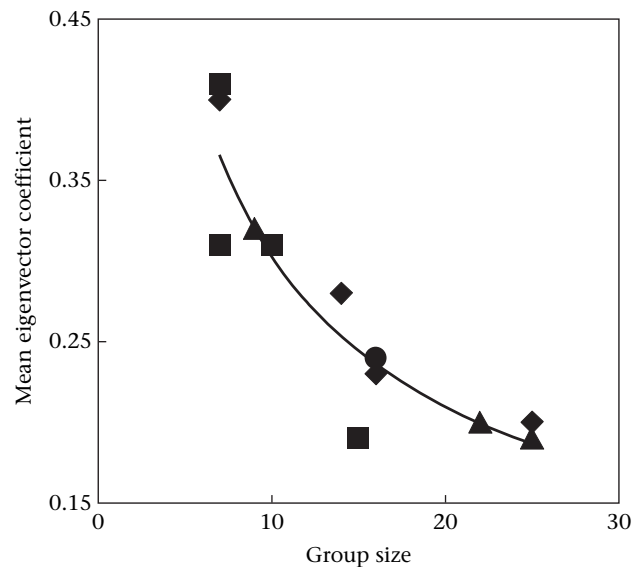
Figure 2. Mean eigenvector centrality coefficient per group as a function of group size. The line represents the theoretical relationship between variables. Squares represent groups of rhesus macaques, triangles Japanese macaques, lozenges Tonkean macaques and the circle the group of crested macaques.
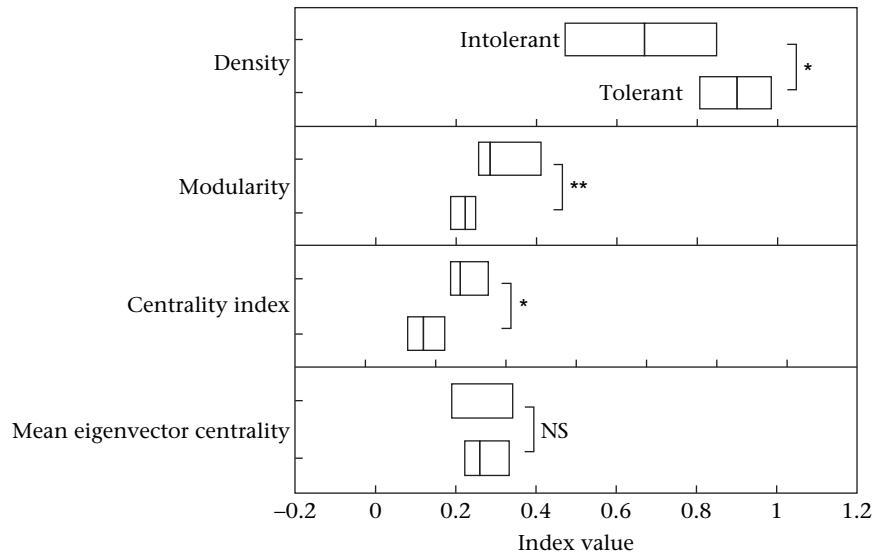
Figure 3. Comparison of network density, modularity, centrality index and eigenvector centrality coefficient between groups from intolerant (upper bars) and tolerant species (lower bars). Box plots show the median and interquartiles. *$P < 0.05$; **$P < 0.01$.
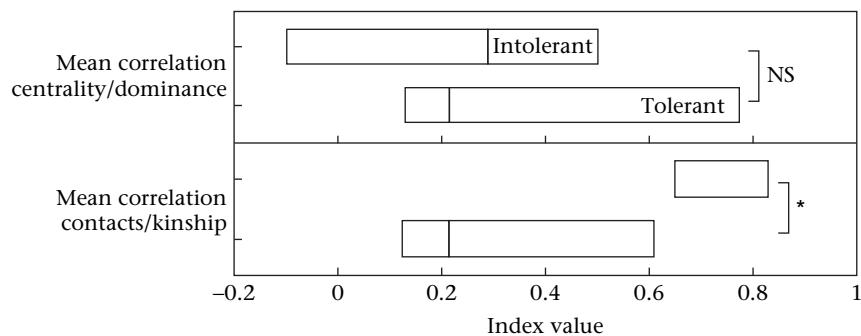
relatives in groups from intolerant species than in groups from tolerant ones.

DISCUSSION

The use of social network analyses confirmed and extended the conclusions drawn from previous comparative studies (Thierry et al. 2004, 2008). It shows that the indices provided by such methods can successfully reveal new aspects of social styles of macaques. The differences found between grades were consistent with previous studies despite significant variations in network measures. Similar variability was reported in a comparative analysis including 70 social groups of nonhuman primates (Kasper & Voelkl 2009). That study indicated that network measures do not differ systematically between distant taxonomic groups, whereas they can vary significantly between groups of closely related species. Such variability is probably partly caused by disparities in sociodemographic parameters. We did indeed find that the mean eigenvector centrality coefficient of groups was linked to their size, in accordance with theoretical (Bonacich 1998) and empirical (Kasper & Voelkl 2009) studies in primates. Given the different availability of potential partners, the centrality of individuals appears to decrease when group size increases (Kudo & Dunbar 2001; Lehmann & Dunbar 2009). The kin–contact coefficient was correlated with the proportion of females in groups, which is consistent with the fact that female kinship bonds in macaques are stronger than those of males.

This coefficient also shows that subgrouping patterns were more influenced by kinship in groups containing few males. The correlation between the kin ratio and the mean eigenvector coefficient indicates that the more individuals were related in a group, the more central certain individuals were. Individuals are indeed more connected to each other in highly kin-related groups, with particular links to individuals linking matrilines, which are often the most dominant or the oldest ones (Schino 2001; Nakamichi & Shizawa 2003; Silk et al. 2003, 2009; King et al. 2008).

Dominance rank has a stronger influence on the patterning of affiliative interactions in species characterized by a steep dominance gradient than in those with a more relaxed style of dominance (Waal & Luttrell 1989; Thierry et al. 2004). In general, lower-ranking individuals are seen to groom and exchange body contacts more often with higher-ranking individuals, especially with the top-ranking male (Schino 2001; Nakamichi & Shizawa 2003; Silk et al. 2003). However, neither the dominance–centrality coefficient nor the distribution of eigenvector coefficients supported the finding that top-ranking individuals were more central in tolerant than in intolerant macaques. Conversely, the high centrality index measured in groups from intolerant species indicates that top-ranking males from these species had more numerous and stronger social relationships than other group members. This result reveals an aspect of social style that was unknown until now. It is understandable that the status of the top-ranking male covaries with other social traits. The higher centrality index of top-ranking males in intolerant

Figure 4. Comparison between groups from intolerant (upper bars) and tolerant species (lower bars) for mean correlation coefficient between eigenvector centrality coefficients and hierarchical ranks, and mean correlation coefficient between matrices of kinship and body contacts. Box plots show the median and interquartiles. *$P < 0.05$.
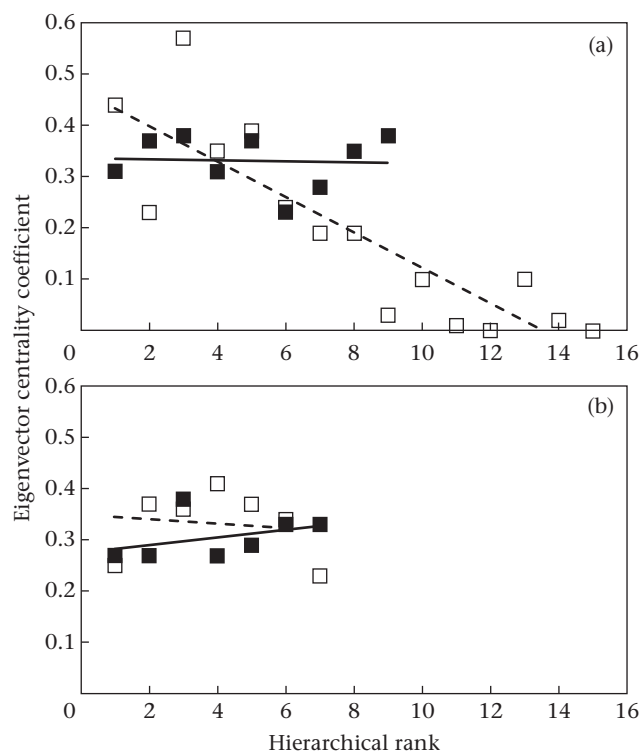
Figure 5. Relation between hierarchical rank and eigenvector centrality coefficient of individuals for the group with the highest correlation (white squares, dashed line) and the group with the lowest correlation (black squares, solid line) in (a) intolerant and (b) tolerant species. Groups of intolerant species are *M. mulatta*, and groups of tolerant species are *M. tonkeana*.

macaques might result from (1) this male seeking body contact with many subordinates to establish his dominance, or (2) subordinate individuals seeking contact with the top-ranking male to benefit from his tolerance and protection from others, and gain better access to food resources (Schino 2001; Majolo et al. 2008).

The measurement of modularity and kin–contact coefficients extends existing results on kin bias. On the one hand, the modularity coefficient reflects the clustering of individuals into subgroups; it showed that groups from intolerant species split more frequently into subgroups of definite composition than groups from tolerant ones. On the other hand, the kin–contact coefficient shows that subgrouping patterns were more strongly shaped by kinship bonds in intolerant than in tolerant species, given that individuals belonging to the same matrilines interacted more often in the former. These results confirm that intolerant species are more nepotistic than tolerant ones; individuals interacted with kin more often in rhesus and Japanese macaques than in Tonkean and crested macaques. They also highlight the fact that patterns previously drawn from the study of social relationships can be revealed by network analyses at the social structure level.

To summarize, our results show that social groups from intolerant species were more clustered compared with groups from tolerant species. In the former, top-ranking individuals had higher centrality than other group members. This was not seen to be the case in top-ranking individuals from tolerant species. Previous studies (Lusseau 2003; Flack et al. 2006; Croft et al. 2008; Whitehead 2008) indicated that patterns of network density, modularity and centrality are indices of group stability. We could ask whether our results mean that groups from intolerant species are less stable than those from tolerant ones. However, further investigations will be necessary to address this issue.

Macaque species differ in the degree of social tolerance of individuals and their ability to manage conflicts of interests through conciliatory behaviours. Such species-specific patterns at the level of social interactions and relationships produce interspecific variations at the level of social structures. By providing methods to investigate sets of relationships quantitatively, social network analyses give us the possibility to recognize the overall properties of a social structure, and the place of each individual within this structure (Croft et al. 2008; Whitehead 2008; Sueur et al. 2011). This study demonstrates that the social styles of macaque species, or at least in those situated at the extremities of the 4-grade scale (despotic/grade 1 versus egalitarian/grade 4: Thierry et al. 1994, 2004, Matsumura 1999), can be successfully compared using network analyses. Several different measures have enabled researchers to grasp different aspects of social styles. As Kasper & Voelkl (2009) wrote, network analyses offer an operational continuum of quantitative measures to qualify social styles in macaques. It would be valuable to test whether the macaque species placed intermediately on the 4-grade tolerance scale (i.e. from grades 2 and 3) do indeed range between the extreme grades studied here. As previously noted, a significant variability was found in each grade. Future research should broaden these analyses to a larger number of groups and species to balance intraspecific versus interspecific variation (see Berman & Thierry 2010).

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