

## RESEARCH ARTICLE

# Baboon (*Papio anubis*) Social Complexity—A Network Approach

JULIA LEHMANN\* AND CAROLINE ROSS

Department of Life Sciences, Roehampton University, London, United Kingdom

Although many studies have analyzed the causes and consequences of social relationships, few studies have explicitly assessed how measures of social relationships are affected by the choice of behaviors used to quantify them. The use of many behaviors to measure social relationships in primates has long been advocated, but it was analytically difficult to implement this framework into primatological work. However, recent advances in social network analysis (SNA) now allow the comparison of multiple networks created from different behaviors. Here we use our database of baboon social behavior (*Papio anubis*, Gashaka Gumti National Park, Nigeria) to investigate (i) to what extent social networks created from different behaviors overlap, (ii) to what extent individuals occupy similar social positions in these networks and (iii) how sex affects social network position in this population of baboons. We used data on grooming, aggression, displacement, mounting and presenting, which were collected over a 15-month period. We calculated network parameters separately for each behavior. Networks based on displacement, mounting and presenting were very similar to each other, whereas grooming and aggression networks differed both from each other and from mounting, displacement and presenting networks. Overall, individual network positions were strongly affected by sex. Individuals central in one network tended to be central in most other networks as well, whereas other measures such as clustering coefficient were found to vary depending on the behavior analyzed. Thus, our results suggest that a baboon's social environment is best described by a multiplex network based on affiliative, aggressive and sexual behavior. Modern SNA provides a number of useful tools that will help us to better understand animals' social environment. We also discuss potential caveats related to their use. *Am. J. Primatol.* 73:775–789, 2011. © 2011 Wiley-Liss, Inc.

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## INTRODUCTION

In socially complex species, such as primates, animals interact using a range of affiliative and aggressive social behaviors that may link individuals in various ways. Animals may also exchange information allowing them to gain knowledge about one another without physical interaction, e.g. by attending to calls. All of these experiences together make up an individual's social environment, which has important consequences for an individual's fitness [Cameron et al., 2009; Silk et al., 2003, 2009, 2010].

Early frameworks for the study of primate sociality [Hinde, 1976; Kummer, 1968] emphasized the importance of using multiple measures of social behavior to fully understand an animal's social relationships and a species' social structure. However, in reality, the analysis and integration of such multiplex measures have often been difficult. Primatologists have used a variety of different measures to quantify aspects of social bonding, such as grooming patterns, coalition formation and reconciliation, to name a few (see also Cords [1997]). In an attempt to capture an aspect of the multiplex nature of social relationships, many have

used composite indices of sociality, combining several (often correlated) behavioral measures into one dimension, which is subsequently used for statistical analysis [Cords & Aureli, 1993]. For example, Silk et al. [2003] used a composite "sociality index" to assess the effects of social bonding on infant survival, combining data on grooming behavior and proximity, whereas Fraser et al. [2008] used nine different behaviors to derive three principle components of relationship quality in chimpanzees. To quantify social position of individuals primatologists have also traditionally used dominance rank, usually calculated from frequencies of winning and losing during displacements and aggressive interactions [Drews, 1993].

\*Correspondence to: Julia Lehmann, Department of Life Sciences, Roehampton University, London, SW15 4JD, United Kingdom. E-mail: j.lehmann@roehampton.ac.uk

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Although sociality indices have been used successfully in the past, researchers have to make a number of critical decisions when calculating them, such as what behaviors to include in their measure of social bonds and how to combine different measures into one single variable [Fraser et al., 2008]. Thus, there is a risk that the resulting measure does not actually capture all the components that are important for the study individual. In addition, information about individuals' social positions within a group can be difficult to obtain, e.g. when dominance relationships are not linear, are unstable, or cannot be determined for all individuals of a group, as in many New World monkeys [Strier, 1997], *Presbytis thomasi* [Sterck et al., 1997], *Alouatta palliata* [Jones, 1980] and *Erythrocebus patas* [Isbell & Pruettz, 1998]. Social roles and positions, however, can have far reaching consequences for individuals, as they can affect individual stress level [Sachser et al., 1998; Wittig et al., 2008], coping strategies during stressful situations, infant survival and reproductive success for males [Schuelke et al., 2010] and females [Cameron et al., 2009; Silk et al., 2003, 2009, 2010].

To obtain a complete picture of an individual's social environment, and thus understand the fitness consequences of sociality, it is important to quantify correctly an individual's social position and its embeddedness in its social world. As indicated by Hinde's [1976] and Kummer's [1968] frameworks, the social environment is composed of all social experiences, but sociality indices are often constructed from only one or a few very similar behaviors, so that such indices may not always be an accurate description of an individual's social world. In reality an individual's social experience will be combined of all interactions in which it is involved. An individual that receives frequent grooming and frequent aggression may live in a very different social world than one that receives frequent grooming and very little aggression. Furthermore, species may differ in the number dimensions needed to describe their social environment. It has been hypothesized that in socially highly complex primates many behavioral dimensions may be needed to capture accurately an individual's social position, whereas in less socially complex species a few dimensions may be sufficient [Lehmann et al., 2010]. Thus, in socially complex species an analysis of only one part of the social environment (e.g. patterns of affiliation) while ignoring other components (e.g. aggression) could create a very biased picture [Sapolsky & Ray, 1989]. Consequently, more data on a wide range of different behavioral measures are needed to assess the extent to which these measures provide different information about individual social bonds and positions.

Recently, social network analysis (SNA) has become a popular tool for studies of animal behavior

[Krause et al., 2007]. A social network can be defined as a set of social units (individuals) and the links (interaction) between them [Wasserman & Faust, 1994]. These networks can then be described statistically and compared across multiple behavioral dimensions, thereby providing an alternative approach to advance our understanding of animal social relationships. In addition, SNA also provides us with quantifiable measures of the position an individual has in its social group indicative of social roles beyond hierarchies or number of interaction partners [Brent et al., 2011; Sueur et al., 2011]. We can, for example, quantify how central an individual is in its network (see *Methods* for definition of centrality) and determine which individual properties (such as sex or age) can be used to predict its position. Individual roles and positions can also be compared across networks based on different behaviors. Recent SNA studies have revealed the importance of different behavioral dimensions to measure how individuals are embedded in their social world [Lea et al., 2010; Madden et al., 2009; Wey & Blumstein, 2010]. Both Wey and Blumstein [2010] and Lea et al. [2010] found that affiliative and agonistic networks describe different dimensions of marmot sociality; surprisingly, seemingly costly agonistic relationships were found to be beneficial and heritable, whereas affiliative relationships appeared to be less important for individual reproductive success [Lea et al., 2010] and network cohesion as measured by affiliative relationships was mainly due to yearlings' affiliative behaviour [Wey & Blumstein, 2010]. Thus, individuals' social positions, at least in marmots, varied across behaviors and development, indicating that it is indeed important to measure all aspects of sociality.

Here we use network analysis to investigate whether different measures of social interactions create similar networks and if individuals have similar positions in each of these networks. In other words, are social relationships measured by different behaviors similar? We chose olive baboons (*Papio anubis*) as our model species for several reasons. First, previous studies indicate that baboons (*Papio*) have highly differentiated social relationships with behavioral interaction patterns differing substantially between dyads [Silk et al., 2006a,b] and that these relationships can have significant consequences for individual longevity [Silk et al., 2010] and fitness in general [Silk et al., 2003, 2009]. Second, although most baboon populations show easily identifiable social hierarchies for males and females, in some populations stable dominance hierarchies cannot be detected easily (as in our study population in at least some years), so that many of the traditional approaches used to assess the effects of social position on baboon fitness cannot be used. Third, we are interested in the determinants of individual network positions. One of the most

obvious factors potentially affecting network position is sex. Baboon males and females differ in many behaviors such as dispersal patterns [Altmann et al., 1981; Barton et al., 1996; Pusey & Packer, 1987; Rasmussen, 1981], interactions with infants [Altmann, 1980], frequency and nature of interactions with members of the same sex [Aldrich-Blake et al., 1971; Boese, 1975; Colmenares, 1991; Hall, 1962; Saayman, 1971], rank acquisition [Hausfater, 1975; Hausfater et al., 1982] and activity budgets [Davidge, 1978]. Although baboon sociality is well studied (reviewed in Swedell [2011]), the extent to which sex determines social positions beyond rank in primate networks has not been addressed quantitatively before. Thus, we aimed to address the following specific questions:

1. How similar are baboon networks across a range of behaviors?
2. Do individual's positions in their social network remain similar across networks based on different behaviors or do individual baboons occupy very different social roles, depending on the behavior analyzed?
3. Do males and females have sex-specific positions in their networks?

Finally, as using network analysis is still relatively new in the study of primate behavior we also aim to highlight the potential benefits and some pitfalls for researchers using social network tools.

## METHODS

### Study Group

This habituated troop of forest-living baboons in Gashaka Gumti National Park, Nigeria has been studied since January 2000 [Higham et al., 2009; Ross et al., 2011; Warren et al., 2011]. Since April 2002, field assistants and researchers have followed the Kwano troop for 20 days a month, usually at least 6 hr/day. The group's home range is within a mosaic of Southern Guinea savannah woodland, lowland forest, riverine gallery forest and grassland that is maintained by burning during the dry season [Sommer et al., 2004; Warren, 2003; Warren et al., 2011]. Data for this study were collected from February 2007 to May 2008. Troop size varied from 29 to 34 individuals, which is relatively small for baboons [Ross et al., 2011]. Age/sex classes were defined following Warren [2003] with 10 adult females (who have reached reproductive age, approximately 5–11+ yrs), 1 subadult female (who has started cycling but not yet reproduced, aged 4–5 yrs), 5–6 adult males (large with fully developed secondary sexual characteristics, aged 8–12 yrs+), 2–3 natal subadult males (with well-developed secondary sexual characteristics who have not yet started mating, aged 6–7 yrs) and 10–15 juveniles

(weaned, with males smaller and less well-developed than subadults, without mantle and shoulder hair) and infants (dependent individuals). Only adults and subadults were included in the analysis.

### Data Collection

Field assistants and research students collected data on social interactions using both continuous focal sampling on 14 of the 20 adults and ad libitum sampling [Altmann, 1974]. They usually observed the animals between 6 am and 1 pm, with occasional afternoon observations. Observers chose focal animals in a pseudo-random manner, attempting to provide equal coverage of all animals at different times of day, although due to the demands of other concurrent projects this was not always possible. Individual focal samples lasted on average for 1 hr, after which focal subjects were changed. On average we observed baboons for 13.4 days/month (range: 6–20 days) and for  $51.3 \pm \text{SD } 5.9$  hr per subject over the entire study period.

We included the following social interactions in the analyses (all recorded as events): allogrooming (the animal grooms or is groomed by another individual); aggression (threat, bite, chase or other physical aggression received from or given to another individual); displacement (the individual displaces or is displaced by another individual); present (all occasions of presenting hindquarters to another or receiving a presentation) and mount (individual mounts or is mounted by another individual, including copulation).

This group of baboons exhibits relatively high levels of sub-grouping [Warren, 2003], and they range in a forest habitat where visibility is limited. Consequently, not all members of the group were always visible to each other (and to the observer) and were thus not always available as social partners [Warren, 2003; Warren et al., 2011]. To control for the availability of social partners, we analyzed the frequency of social behaviors in relation to subgroup composition. We determined subgroup composition from scan data, which were taken every 15 mins during a focal follow, recording all animals visible to the observer (and thus presumably to the baboons). From these scans we calculated dyadic association times. On average, we found that dyads were observed together for  $19 \pm \text{SD } 13$  hr in the 15-month study period ( $N = 181$  dyads). We then divided social interaction frequencies by these association times, which gave us a value for interaction frequency per hour association time. We used this corrected value in all subsequent analyses.

By calculating interaction frequencies per association hour, we aimed to reduce potential biases in the data arising from uneven focal observation efforts and ad libitum data collection. We assumed that remaining biases were relatively constant across

networks and hence unlikely to affect the results significantly. There was no indication that some of the behaviors recorded (such as “silent” behaviors like grooming, presenting and displacement) were consistently more or less likely to be observed in ad libitum sampling (another potential bias); if that were the case, it could potentially affect the network position comparison. A comparison of ad libitum and focal grooming data in chimpanzees has shown that both data sets yielded extremely similar results [Slater, 2008]. In addition, some of the metrics we used in this analysis were based on binary matrices (recording only presence/absence of a behavior), which we believe further reduces the potential for biases.

We did not normalize or standardize values further nor did we use a cut-off value to determine relationships as we were not primarily interested in association strength and friendship patterns but rather in interaction networks resulting from these behaviors. Thus, we considered even very infrequent behaviors as meaningful interactions.

### Research Ethics

All research protocols followed were assessed and approved by Roehampton University’s Research Degrees Board, which included ethical approval, and adhered to all legal requirements of both Nigeria and the UK. The research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Nonhuman Primates.

### Network Parameters

We created matrices of dyadic interaction frequencies for all five behaviors. Because all of our behaviors were directional (e.g. we distinguished between receiving grooming and giving grooming), all matrices were asymmetric. We aimed at using basic network descriptors (Table I) that would allow for nonsymmetric, directed networks and excluded

those that force networks to be symmetric, as the directionality of our behavioral measures has clear biological relevance. When possible we used the valued data set (i.e. the one that indicated the frequency of the behavior) but for some network variables, binary networks (indicating only the presence/absence of a link, and not its strength) were required (Table I). In such cases we transformed valued matrices into binary matrices by defining all values larger than 0 as 1 and all values equal to zero as 0, i.e. all individuals that were observed to interact at least once during the 15 months were defined as having a relationship.

To compare overall network structures (Aim 1), we calculated some of the most basic and commonly used network descriptors [Croft et al., 2008; Kasper & Voelkl, 2009; Madden et al., 2009]: density based on binary (presence/absence) data (indicating the proportion of all possible links present in the network, where density of 0 indicates no connections between individuals); mean density of the valued (interaction frequency) data (indicating overall average interaction frequencies); clustering coefficient of valued data (indicating how closely connected neighborhoods are, i.e. the extent to which the network consists of individual clusters); and average shortest path length (indicating how closely individuals in general are connected within the network, where distance of 1 indicates that all individuals interact directly with each other).

To assess individual positions within networks (Aim 2), we concentrated on individual network measures that (i) quantify individual network centrality (= position), (ii) are commonly used, (iii) are likely to be relevant for primates and (iv) allow us to include directionality of behavior. We used the network statistics (see also Kasper and Voelkl [2009]) Degree, Closeness and Betweenness, all of which capture different aspects of an individuals’ centrality, i.e. its position relative to other individuals in the network. Degree is a measure of how well an

**TABLE I. Network Variables Used to Describe Individual Positions Within Network**

Network variables	Description	Data type
Degree (mean) (two measures)	Proportion of possible connections that are actually present; indicates also centrality, i.e. well connected individuals are more central in their network; calculated separately for IN and OUT going connections	Binary data
Degree (mean) (two measures)	Average individual link strength, i.e. the mean of an individual’s interaction frequencies; calculated separately for IN and OUT going links	Valued data
Closeness (two measures)	Measure of centrality, based on calculating the distance from ego to all other group members and then standardizing it to overall network closeness; a low value indicates that the individual is not closely connected to others; separate measures were calculated for IN and OUT	Binary data
Betweenness	Another measure of centrality; measures the proportion of dyads that are connected through ego (only shortest connections count)	Valued data
Clustering	An indication of how clustered an individuals’ neighborhood is; calculates the proportion of existing to all possible links of ego’s interaction partners	Binary data

individual is connected to others. We calculated this as binary (presence/absence) measure, indicating the number of social interaction partners of individual baboons and as a valued measure (interaction frequency), indicating average interaction strength. Closeness measures how closely linked the individual is to all other group members. Betweenness indicates how often an individual is situated on the shortest path connecting two other individuals [Wasserman & Faust, 1994]. We also calculated a measure of “cliquishness,” the Clustering Coefficient, which indicates how well an individual’s direct neighborhood is connected. Strong clustering could indicate the existence of stable individual subgroups, in which most interactions take place, whereas weak clustering indicates that the group is cohesive.

We used these five measures (Degree (binary and valued), Closeness, Betweenness and Clustering Coefficient) to determine how well the position of an individual in one network corresponded to its position in another network. Because of the directionality of the behaviors used to build networks, we had to calculate some of the network measures separately for actors and receivers. This resulted in a total of eight measures per network, namely individual In (receiver) and Out (actor) Degree for valued (using interaction rates) and binary (presence/absence of a link) networks (providing four measures), individual In and Out Closeness (two measures), Betweenness (one measure) and Clustering coefficient (one measure; Table I).

## Statistics

We calculated Density, Degree, Closeness and individual Cluster Coefficients in UCInet [Borgatti et al., 2002] and overall Clustering Coefficient and Betweenness in tnet [Opsahl, 2007–2010], as the latter provides procedures to calculate these metrics for valued networks. For statistical analyses we used UCInet, and PASW 17.00 [© SPSS, Inc., Chicago, IL]. Because dyadic data are not independent from each other (strictly speaking data on social behavior within a social group are never independent), we used permutation tests for all analyses unless indicated otherwise. In such tests the distribution against which the data set is tested is derived from random permutations and the probability of obtaining a value as small or large as the observed is given ( $P$ -value). These permutation tests do not usually produce a test statistic. All tests used were two-tailed. We compared overall network densities to a fully connected network of a density of 1 using the bootstrap method provided by UCInet, where a random distribution is created by sampling repeatedly from the same network after randomly redistributing the links within the network. To investigate how similar overall networks and how comparable individual social relationships are across networks based on different behavioral measures

(Aim 1) we compared networks across behaviors using a bootstrap equivalent of the paired sample  $t$ -test provided by UCInet. We used 5,000 permutations to create the sampling distribution.

We compared individual network positions (Aim 2) between networks based on different behaviors using Pearson or Spearman rank correlation analysis, depending on whether data were normally distributed (tested with the Kolmogorov–Smirnov (KS) test). To improve comparability we used Spearman rank correlation for all five behaviors if the network measure of at least one behavior deviated from normality. Following this rule, we used Spearman rank correlations for Closeness and Betweenness (KS-test:  $P < 0.05$  for at least one network measure) and Pearson correlation for Degree and Clustering Coefficient (KS-test: all  $P > 0.05$ ). As each network measure was used in four different analyses (e.g. aggression Degree could be correlated with displacement, grooming, mounting and presenting Degree) we used a Bonferroni correction, so that the new significance level was set to  $P = 0.05/4 = 0.0125$ .

To analyze sex differences in individual network positions (Aim 3) we used a permutation  $t$ -test (5,000 permutations) provided by UCInet on node-level network parameters. As the number of parameters derived for each behavior was 8, a Bonferroni correction gave a new significance level of  $P < 0.00625$ .

## RESULTS

### How Similar are Baboon Networks Across Different Behaviors?

#### Overall networks

Most networks (with the exception of aggression) showed a clear distinction between the sexes, with females usually located in the center, whereas males were located around the edges (Fig. 1). All five networks showed very similar densities with between 30% (mounting) and 44% (grooming) of all possible links present (Table II). Only grooming and displacement networks differed significantly in density from each other (valued data, permutation paired-samples  $t$ -test with 5,000 permutations: bootstrap  $t = -1.8$ ,  $N = 380$ ,  $P < 0.05$ ), indicating that on average grooming interactions were more frequent than displacements. None of the other networks differed significantly from each other in density (permutation paired-samples  $t$ -test: all  $P > 0.1$ ).

The presenting network was highly clustered (Table II), indicating that high frequencies of presenting tended to occur in relatively tight clusters of individuals. Grooming, aggression and mounting networks were considerably less clustered with very similar values, suggesting a more even spread of these interactions among all troop members. Average distance, i.e. the average length of the shortest connection between any two individuals in

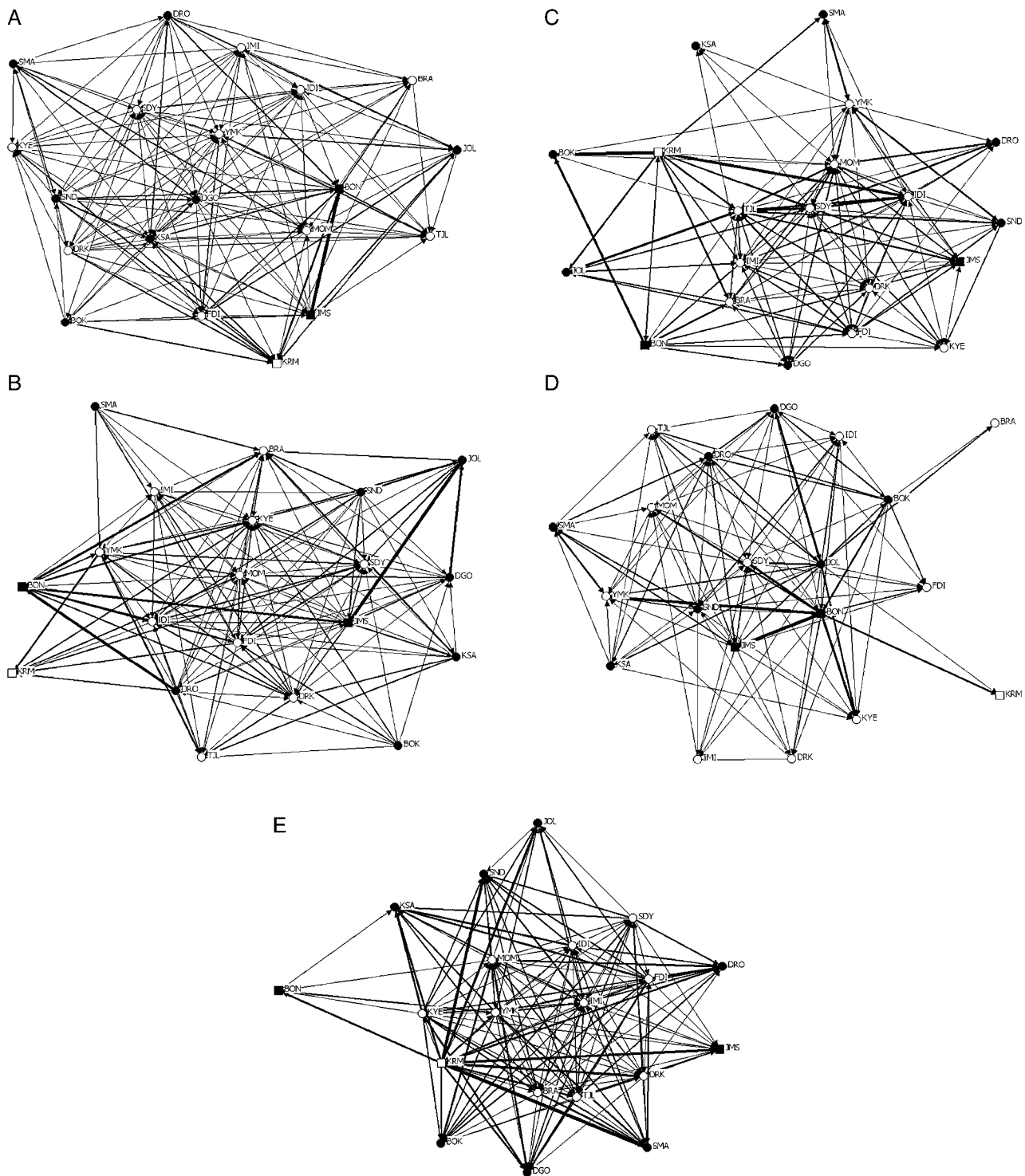


Fig. 1. Baboon social networks, based on (A) aggressive, (B) displacement, (C) grooming (D) mounting and (E) presenting behavior. Nodes represent individual baboons, with circles showing adults and squares indicating subadult individuals, white demarcates females, whereas black indicates males. Lines indicate that the behavior was observed between a particular dyad (arrow heads indicate directions) and line strength indicates relative frequency of the interactions (corrected for association times). Line strength is scaled within each behavior with thickest lines indicating frequent interactions five times higher than thinnest lines. All figures are based on the "spring embedding" procedure, which places individuals in such a way that those with the smallest distance to one another are closest to each other in the graph.

the network, was relatively low (the minimum average distance in a network is 1 if all dyads directly interact with each other) and similar across networks. The highest average distance was found in the aggression and the grooming networks, as some dyads were not observed to groom or show aggressive behavior (Table II, Fig. 1), whereas the lowest average distance was found in the presenting network, as most individuals presented to each other at least once.

In summary, grooming and aggression networks were largely similar to each other in their structure, displacement and mounting networks were also similar to each other, whereas the presenting network differed from the other four networks. In other words, baboons distribute aggression and grooming as well as displacement and mounting in a very similar fashion across group members while presenting differs, as it occurs more frequently and is overall highly clustered.

#### Individual social relationships

Each of the five networks deviated significantly (Bootstrap test: all  $z$ -values between  $-6.14$  and  $-27.25$ ,  $N = 380$ , all  $P < 0.001$ ) from a theoretical fully connected network (density = 1), indicating that individual baboons had highly differentiated social relationships (i.e. they did not distribute their interactions evenly across all group members), even though we did not employ a cut-off value to our dataset.

We then tested to what extent networks correlated with each other, i.e. to what extent the probability of a link between two individuals in one binary (presence/absence) network can predict the probability of a link in another binary network (as hypothesized if there is little difference between social networks) and to what extent the strength of a link in one network predicts link strength in the other network (using valued networks). Using valued networks, we found no significant correlation between grooming and displacement networks, or between grooming and mounting networks (Table III). Aggression networks were not significantly correlated with either grooming or mounting networks although in both cases there was a weak tendency toward significance ( $0.1 > P > 0.05$ ; Table III). All other networks were significantly correlated, but  $r$ -values were low (Table III). Most notably, the presenting network was correlated with all other networks—negatively with aggression, displacement and mounting and positively with grooming. Interestingly, dyads that presented frequently to each other were less likely to show frequent aggression, displacement or mounting, as indicated by the significantly negative correlation of the valued networks. Results for binary networks were very similar to those for valued networks, with the exception that aggression and mounting networks were found to be significantly correlated ( $r = 0.679$ ,  $P < 0.001$ ).

Because of the uneven spread of observation time and association frequencies we also correlated behavior networks with association time and found

**TABLE II. Overall Network Characteristics for the Four Behaviors Analyzed**

	Density (binary)	Mean density (valued data)	Clustering coefficient (valued data)	Average path length (binary)
Aggression	0.4158	0.0669	0.61	<b>1.662</b>
Displacement	0.3579	<i>0.0487</i>	0.72	1.397
Groom	<b>0.4447</b>	0.0897	<i>0.60</i>	1.608
Mount	<i>0.3051</i>	0.0676	0.64	1.44
Presenting	0.4316	<b>0.1046</b>	<b>0.92</b>	1.288

Values are proportions ranging between 0 and 1; Density (binary) indicates the proportion of all possible links present in the network; Mean density indicates average interaction frequency across the entire network; Clustering coefficient indicates how clustered the network overall is, i.e. to what extent the interaction partners of one individual also interact strongly among themselves. Average path length indicates how closely/directly individuals are linked in their network (a mean distance of 1 would indicate all individuals interact directly with each other, higher values indicate that some individuals are only indirectly connected). Values in bold indicate the highest value across networks, whereas values in italics indicate the lowest value across behaviors.

**TABLE III. Results of Network Correlations Across Networks Based on Different Behaviors**

$N = 380$	Aggression	Displacement	Groom	Mount	Presenting
Aggression	—	<b>0.18 (0.01)*</b>	−0.07 (0.06)	0.08 (0.07)*	− <b>0.16 (&lt;0.001)*</b>
Displacement		—	−0.02 (0.38)	<b>0.27 (0.001)*</b>	− <b>0.21 (&lt;0.001)*</b>
Groom			—	−0.06 (0.21)	<b>0.12 (0.048)*</b>
Mount				—	− <b>0.19 (&lt;0.001)*</b>

The table represents correlation coefficients and  $P$ -values (in parentheses) for valued (frequency of behavior) networks based on Bootstrap Pearson correlation with 5,000 permutations. Significant results of binary networks are indicated by asterisk. Values in bold emphasize significances.

that aggression, grooming and mounting were significantly positively correlated with association frequencies (Bootstrap Pearson correlation: all  $N = 380$ ,  $r_{agg} = 0.13$ ,  $P_{agg} < 0.01$ ;  $r_{groom} = 0.16$ ,  $P_{groom} < 0.05$ ;  $r_{mount} = 0.23$ ,  $P_{mount} < 0.01$ ), despite our correction for association patterns which led us to calculate interaction frequencies per association hour, see *Methods*). Thus, to ensure that the correlations in Table III were not simply caused by association frequencies we re-ran analyses for valued data using multiple regression analysis, which enabled us to account for the effects of association time. All significances (as indicated in Table III) remained the same after controlling for association frequencies. However, the above-mentioned tendencies for aggression and grooming and aggression and mounting to correlate disappeared (i.e.  $P > 0.1$ ).

### Do Individual Network Positions Remain Constant Across Networks?

The results of the correlation analyses of the eight network variables (individual In and Out Degree for valued and binary networks, individual Closeness (In/Out), Betweenness and Clustering coefficient, Table IV) indicated that measures of individual centrality tended to be correlated across different

networks. For example, the number of partners each individual had (Out-Degree) was highly correlated across all five networks (Table IV; 8 out of 10 possible correlations were significant). Similarly, Out-Degree (valued) and Out-Closeness as well as In-Degree (binary) and In-Closeness showed strong correlations between behaviors. This indicates that individuals that were central in one behavioral network were predictably central (or peripheral in case of negative correlations) in the other behavioral network. In contrast, Betweenness and individual Clustering Coefficient were not strongly correlated across different behaviors; in other words, baboons that showed high Betweenness or a high Clustering Coefficient in one behavioral network were not found to have a similar network position in most of the other behaviors. This indicates that relatively direct measures, such as number of social partners or social interaction frequencies, correlate across different behaviors, whereas more “indirect” measures of individual roles and positions are highly behavior-specific.

Of the behavioral networks analyzed here, grooming appeared to be the most “specific” network structurally, in the sense that there was relatively little correlation between individual positions in the grooming network and those in other networks (less than 1/3 of all possible correlations were actually

TABLE IV. Correlation Coefficients of Individuals’ Roles Within Their Network Across Behaviors

		Aggression	Displacement	Grooming	Mount	Presenting
Out/In Degree (Binary) (# of partners)	Aggression		0.856**	ns	0.636**	-0.63**
	Displacement	0.795**		ns	0.681**	-0.615**
	Grooming	ns	0.622**		-0.647**	0.804**
	Mount	ns	0.577**	0.67**		-0.88**
	Presenting	-0.617**	ns	ns	ns	
Out/In Degree (Valued)	Aggression		0.868**	ns	0.585**	-0.551*
	Displacement	ns		ns	0.665**	-0.554*
	Grooming	ns	ns		ns	0.745**
	Mount	ns	ns	ns		ns
	Presenting	ns	-0.76**	ns	ns	
Out/In Closeness	Aggression		0.789**	ns	0.651**	-0.606**
	Displacement	0.814**		-0.608**	0.853**	-0.752**
	Grooming	ns	ns		-0.596**	0.725**
	Mount	0.655**	0.759**	0.596**		-0.770**
	Presenting	-0.760**	-0.826**	ns	-0.787**	
Betweenness (no directionality)	Aggression					
	Displacement	ns				
	Grooming	ns	ns			
	Mount	ns	0.587**	ns		
	Presenting	ns	ns	ns	ns	
Clustering (no directionality)	Aggression					
	Displacement	ns				
	Grooming	ns	ns			
	Mount	ns	ns	ns		
	Presenting	ns	ns	0.685**	-0.666**	

Values above the diagonal of each matrix are correlation coefficients for actors (Out-Degree and Out-Closeness), whereas values below the diagonals are correlation coefficients for receivers (In-Degree and In-Closeness). If no differentiation between actors and receivers was made (Betweenness and Clustering) values are represented in the lower half. Cell with gray shading indicate those for which no data exist, i.e. the diagonal and variables without directionality; ns = not significant. \*\*indicates  $P$ -values with  $P < 0.001$ ; \*indicates  $P$ -values between 0.010 and 0.0125. Owing to multiple testing only  $P$ -values with  $P < 0.0125$  were considered significant.



significant, Table IV). Thus, the roles individuals had in their grooming network were not closely reflected in any of the other behavioral networks. By contrast, the positions individuals had in the displacement and mounting networks were highly correlated with those they had in other networks (nearly 2/3 of all possible correlations were significant, Table IV).

### Do Males and Females have Sex-Specific Positions in their Networks?

For some behaviors males and females appeared to play different roles in their networks (Fig. 1), with females often at the centre of the network, whereas males were at the periphery. We used a permutation *T*-test ( $N = 20$  for all measures) to analyze if sexes differed significantly in their network positions across the five behaviors (Fig. 2). There were relatively few

sex differences in the aggression and the grooming networks (3 out of 8 variables), whereas positions were found to be highly sex-specific in the mounting, displacement, and presenting networks (5, 6 and 6 out of 8 variables, respectively) (Fig. 2). The presenting and mounting networks were reciprocal to each other, with females showing significantly more presenting behavior (as indicated by Out-Degree measures) and receiving more mounting (In-Degree) and males showing more mounting behavior (Out-Degree) and receiving more presenting (In-Degree). Similarly, males displaced more individuals more frequently, whereas females were more often displaced and by more individuals (In- and Out-Degree). These sex differences in behavior translated into sex-specific positions in their respective networks, as Closeness and Clustering Coefficient also differed significantly between the sexes in several of these

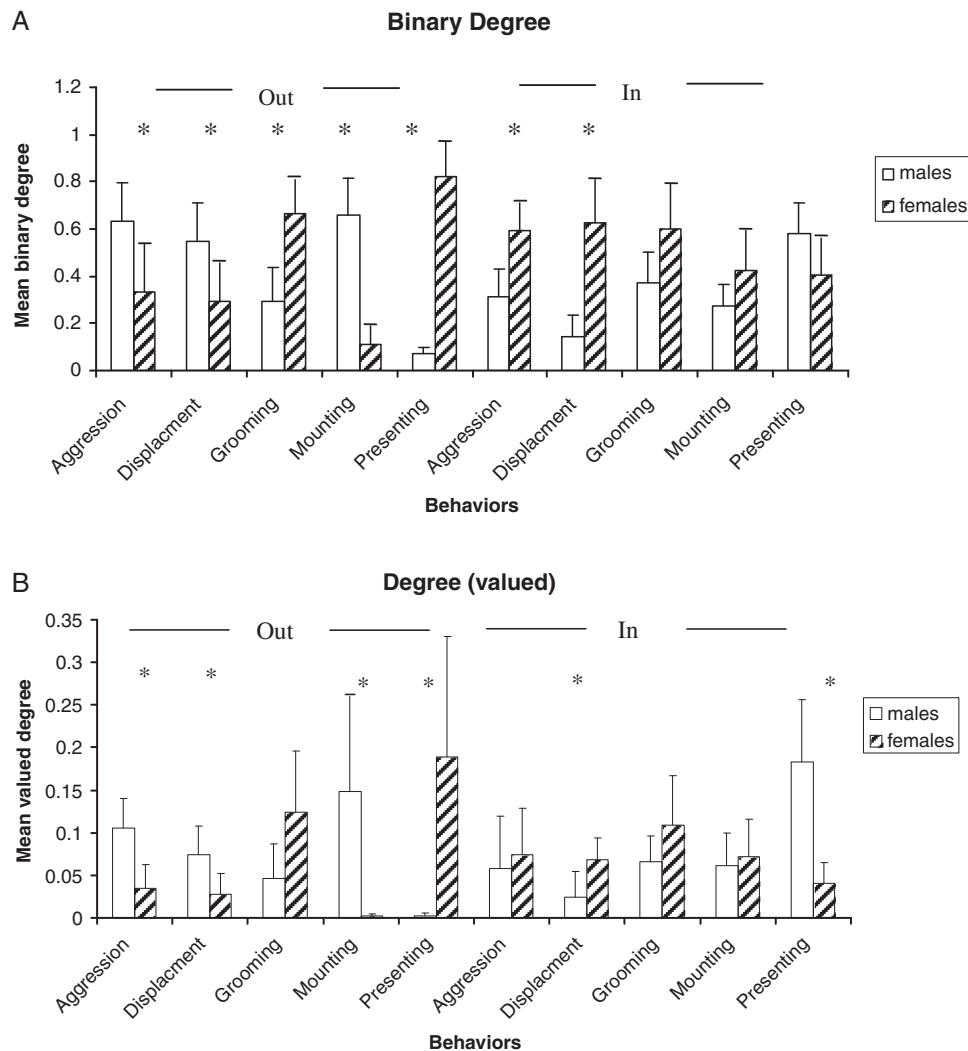


Fig. 2. Sex differences in individual network position across different behaviors. Bars represent mean (+SD) of individual network measures for males and females; significant differences are indicated by asterisk ( $P < 0.00625$ ). “In” and “Out” indicate separate measures for receiving (= In) a behavior or acting (= Out) measures. Because there were no significant sex differences for Betweenness it is not depicted here.

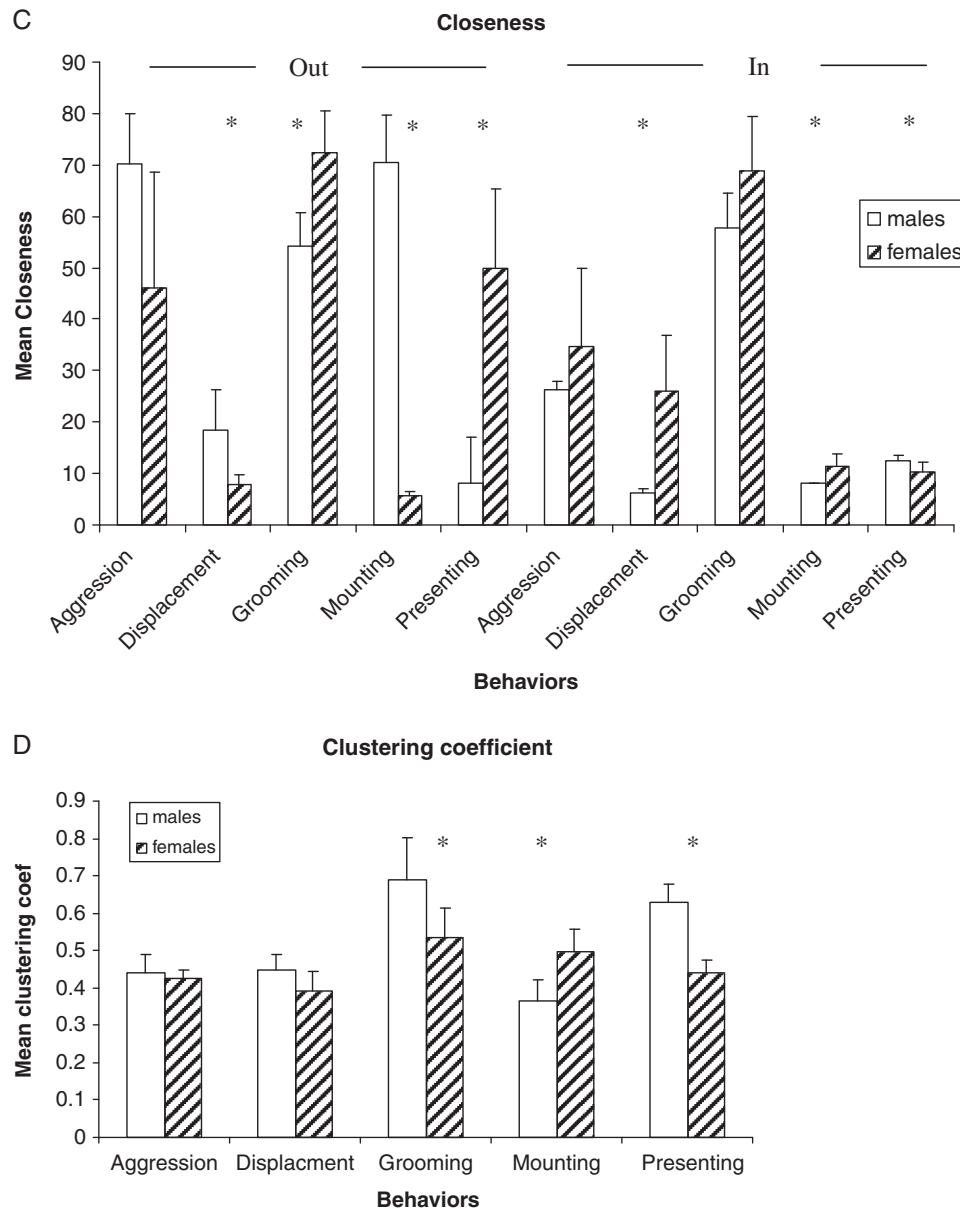


Fig. 2. Continued.

networks (Fig. 2). Although we found a clear sex difference in displacement behavior, the effect was less strong for aggression. As with displacement, males were generally found to be more aggressive than females (Out-Degree) but this did not translate into clear sex-specific roles as measured by Betweenness, Closeness and Clustering coefficient. Similarly, sex differences in grooming networks were not very pronounced. Females had significantly more grooming partners than males (binary Out-Degree) but no sex difference was found regarding grooming frequencies. Males, however, had grooming networks that were generally more clustered than female networks. This analysis illustrates not only

fundamental sex differences in baboon behavior but also shows how such sex differences can in some cases lead to sex-specific roles in the respective networks.

## DISCUSSION

Although a few other studies of baboon social networks exist [Henzi et al., 2009; King et al., 2011], this is, to our knowledge, the first comparison of baboon networks based on a variety of social behaviors. All five networks indicated that baboons maintained highly differentiated social relationships and that individual network positions were strongly determined by sex, i.e. females tended to be more

central than males in the grooming and presenting network but more peripheral in the aggression, displacement and mounting network. Below we address each of our original aims.

### How Similar are Baboon Networks and Social Relationships Across a Wide Range of Behaviors?

Our analysis suggests that some, but not all, of the five social networks correlate. Most notably, grooming, a behavior often used in studies relating to sociality and social bonds [e.g. Seyfarth, 1977; Silk et al., 1999], showed little correlation with other behaviors, and is thus not necessarily representative of an individual's social network in general (Cords [1997] discusses potential reasons for this). To understand a baboon's entire social environment, several social behaviors should be analyzed together, namely affiliative, agonistic and sexual behaviors. More specifically, although social bonds defined by mounting, presenting and displacement behavior appeared to be very similar in our study population, they differed from those obtained from grooming and aggression networks, indicating that it is important to investigate a variety of social behaviors to capture the full complexity of baboon social relationships. The value of considering multiple aspects of individual's social relationships when investigating the evolutionary benefits of sociality has also recently been highlighted for other species, where networks based on different behaviors show little or no relationship [Lea et al., 2010; Madden et al., 2009; Wey & Blumstein, 2010].

### Individual Positions in Social Networks

Although some network measures were highly correlated across networks, baboons did not have the same roles in all the networks analyzed. Individuals tended to maintain their number of social partners and relationship strength patterns (Degree) as well as their Closeness status (measure of how closely linked ego is to all others) across different behaviors. However, Centrality as measured by Betweenness (extent to which ego lies between two others) and Clustering Coefficients (measure of how cliquish ego's neighborhood is) varied across networks based on different behaviors.

The extent to which individuals are integrated into their social world can have far reaching consequences: for baboons [Silk, 2007; Silk et al., 2003, 2009, 2010] and feral horses [Cameron et al., 2009] strong affiliative social bonds in females are correlated with enhanced longevity and infant survival. In humans, numerous studies have shown that social network positions correlate with individual longevity [Giles et al., 2005] and susceptibility to disease [Friedman et al., 1997; Seeman, 1996]. Furthermore, a large body of data now shows that social environments of group living animals are multifaceted and

interlinked. For example, Crockford et al. [2008] show that social stressors strongly affect baboon stress levels and that coping strategies depend on their social networks. Most studies, however, concentrate on socio-positive behaviors, whereas very little is known so far about the effect of socio-negative behaviors on individual fitness and stress levels (but see Sapolsky [2005]). We found that individual roles and network positions based on grooming behavior were not representative of network positions derived from other behaviors. Thus, positive effects of grooming relationships could be offset by negative consequences of aggressive interactions (and vice versa), so that an individual that is central in its grooming and peripheral in its aggression network may do much better than an individual that is central in both networks. Indeed, Lea et al.'s [2010] recent study on marmot social networks shows that agonistic relationships can be crucial for an understanding of the connection between sociality and fitness.

The analyses presented here emphasize that individuals' network positions vary, depending on the behavior analyzed. As few similar comparative studies have been done, we know little about how social networks differ between behaviors, species, populations or study periods. There is at least good indication that primate grooming networks can be plastic, depending on competitive regime, food availability and/or group composition [Engh et al., 2006; Henzi et al., 2009; Lehmann and Boesch, 2009]. On the other hand, limited evidence also suggests that at least some network parameters may remain stable over considerable periods [Drewe et al., 2009; Lehmann and Ross, 2009], but more data are needed to fully understand the extent of network plasticity across species.

### Sex-Specific Network Positions

A relationship between gender and grooming and/or aggressive behavior has been demonstrated in many species (e.g. *Papio* spp. [Smuts, 1985]; *Pan troglodytes* [Lehmann & Boesch, 2008]; *Pan paniscus* [Hohmann & Fruth, 2002]; *Ateles geoffroyi yucatanensis* [Slater et al., 2008]; *Macaca assamensis* [Cooper & Bernstein, 2000, 2002]). In baboons, males are generally more aggressive than females [Hall, 1962; Seyfarth, 1976; Smuts, 1987] and are more likely to be wounded [Smuts, 1987]. In line with such findings, the males in our study population were significantly more aggressive and also showed more mounting and displacement behavior (which differs from Seyfarth [1976] who reported that males are slightly less likely than females to be involved in displacement activity). Female baboons have been reported to spend a greater proportion of time in total social activity (grooming, fighting and play combined) than males [Davidge, 1978], but were equally likely to be

groomers or groomees in any given grooming bout [Hall, 1962]. Similarly, we did not find a significant sex difference in grooming frequency (Fig. 2B). In addition, our grooming networks reflect previously reported sex-specific partner preferences [Hall, 1962; Saayman, 1971]: adult males frequently groomed females but not other males, whereas females groomed adults of both sexes (Fig. 1C). We also found that females had higher presenting frequencies compared with males.

Our data further demonstrate that these behavioral sex differences translate into sex-specific network positions and individual roles; males tended to be more central in the aggression, displacement and mounting networks, whereas females were more central in the grooming and the presenting networks. This is perhaps not surprising, given that most of these behaviors have a clear sex-specific directionality, i.e. it is usually females who present to males and males that mount and displace females. However, mounting as well as presenting was also frequently observed within same-sex dyads (Fig. 1), thus strong sex differences in network centrality do not necessarily follow from this general directionality in behavior. Furthermore, even though we found no significant sex difference in grooming frequency, females were significantly more central in the grooming network, suggesting that small nonsignificant differences in behavior can nevertheless translate into sex-specific social positions. In addition, sex differences in network positions were much more common for actors (i.e. Out-Degrees and Out-Closeness) than for receivers (i.e. In-Degrees and In-Closeness), indicating that, although baboons interact with others in a sex-specific manner, both sexes were relatively similar in terms of receiving grooming or aggression. Although many of the gender-specific network positions found in this study are in line with previous findings of baboon sociality that suggest that females have a central role in affiliative interactions [DeVore & Hall, 1965; Smuts, 1985], the use of SNA allows additional fine-scaled interpretations about individual network positions even in the absence of significant differences in frequency of behavior (as in the case of grooming).

#### *Further implications: social complexity in baboons*

Dunbar [1998] suggested that species-specific brain size variation in primates is linked to social complexity. However, little consensus exists about what social complexity is and how it can be measured. The degree of network fragmentation (i.e. the extent to which a network is fragmented into different subgroups) and overlap (i.e. the degree to which networks based on different behaviors are identical) may provide quantifiable measures for social complexity [Lehmann et al., 2010; Lehmann & Dunbar, 2009]. Our data suggest that olive baboons

at Gashaka-Gumti National Park show an intermediate to high level of social complexity, as all network densities were around 0.4, which is at the low end of densities reported for primate networks [Kasper & Voelkl, 2009; 0.75 = median density for 70 primate groups across 30 species, range 0.49–0.93]. The low densities in our baboon networks indicate that more than half (~60%) of all possible connections in the network were actually absent and thus these dyads were only indirectly connected (via other individuals). However, several of the networks were highly correlated, indicating that there was a relatively high amount of overlap between some networks and that individuals can hold similar positions across several networks. Finally, none of the networks showed strong fragmentation (Fig. 1), suggesting that consistent subgroups/cliques were not present (Fig. 1; statistics not shown, but see discussion below), even though this troop of baboons showed a high level of subgrouping behavior [Warren, 2003]. Without comparative data from other species, however, it is difficult to conclude how typical such values are for primates. A recent comparative study of primate grooming networks [Kasper & Voelkl, 2009] indicated that networks vary between primate species, but more data for a wider range of species and behaviors are needed to test the hypothesis that these network metrics can be used to quantify social complexity. Indeed, we do not even know to what extent network metrics reflect species-specific social structure. Madden et al. [2009] showed that affiliative as well as agonistic networks (intra-group networks) can vary greatly between groups of meerkats and that these networks are strongly affected by demographic and ecological variables, suggesting that little or no species-specific characteristics exist. By contrast, networks based on social interactions between groups of meerkats (inter-group encounters) were found to be remarkably stable over time [Drewe et al., 2009]. Primate social networks may be highly flexible and quickly adapt to changes in local conditions [Crockford et al., 2008; Engh et al., 2006; Henzi et al., 2009; Lehmann & Boesch, 2009] but to date there are no real comparative data on the effects of these changes on overall network structure and fragmentation.

#### *Limitation of network analysis*

SNA allows us to capture aspects of animal sociality which were previously neglected, such as the quantification of how individuals are embedded in their overall social world [Brent et al., 2011; Croft et al., 2008; Sueur et al., 2011]. Here we have shown how network analysis can be used to compare social roles and network position across behaviors, revealing that measures of social bonds in baboons can be markedly different depending on the behavior analyzed.

However, a number of limitations should be considered when network analysis is used. First, many network metrics require binary data (and often even symmetric matrices), which means that much information on individual link strength gets lost. A researcher using binary data has to judge which levels of interactions are meaningful for the animals—which may be difficult. In this analysis we decided to use all observed interactions, but this decision may have introduced biases (as would have a cut-off value) and results may differ when other criteria are used. The networks presented in Figure 1 (including all observed relationships, no cut-off value employed) were all fully connected, without evidence for subgroups/cliques (analysis not shown). However, the use of a cut-off value, as suggested by some [James et al., 2009; Lehmann et al., 2010] would change the picture. In this study group, many individuals demonstrated strong links with one or two other individuals and much weaker links with many other group members; thus, the application of a 10% cut-off value produced networks that are much less well connected and that consist of more subgroups (unpub. data), giving evidence for strong fragmentation in the network. Grooming and presenting networks are then highly fragmented, with individuals belonging on average to 36% of the subgroups; aggression provided the least fragmented network with members being on average involved in 85% of subgroups (data not shown).

This example illustrates that decisions researchers have to make while employing network analysis may strongly affect the results—and these decisions need to be made without knowing what exactly is relevant for the individual baboon. Rare but important events may be overlooked if a cutoff is employed. For example, if A interacts aggressively with B every day we may assume that this is of biological importance—but what about those rare aggressive events with individuals C, D, E, F and G, all of which account for less than 10% of the overall time spent in aggressive interactions? Are these a mere nuisance or are these important events, because they indicate something interesting, e.g. that the hierarchy may be challenged? The good news is that algorithms for valued (weighted) networks are becoming increasingly more available [Kasper & Voelkl, 2009; Newman, 2004], albeit with the complication that there is usually more than one way to calculate network metrics.

A second limitation is that it is not always clear how network metrics (which were developed for human studies) can be interpreted in a meaningful way in nonhuman animals. In this study we limited our analysis to variables which we believe are meaningful to a baboon, but such judgments may not be straightforward. For example, does it matter to a baboon to how many other individuals it is indirectly connected via a grooming chain (and not through direct interactions) in a grooming network?

For the transmission of diseases or parasites this is hugely important, but how important is it in other contexts?

Despite these limitations, we believe that SNA can further our understanding of primate sociality [see also Brent et al., 2011; Sueur et al. 2011], especially when carefully employed. A particular interesting application is to see how individuals are embedded into their overall social world over time when analyses include multiple social behaviors [Sueur et al., 2011]. Our study provides a first overview of baboon social networks as based on a number of different behaviors, but more in-depth analyses investigating, for example, the structure, causes and consequences of such multiplex networks are needed to fully understand individual roles in their social environment [see also Sueur et al., 2011]. In addition, to test if social complexity indeed relates to the ability to maintain separate networks across different behaviors and to deal with indirect relationships, as suggested in Lehmann et al. [2010], more data on a variety of species are needed.

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