

RESEARCH ARTICLE

Grooming Network Cohesion and the Role of Individuals in a Captive Chimpanzee Group

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Social network analysis offers new tools to study the social structure of primate groups. We used social network analysis to investigate the cohesiveness of a grooming network in a captive chimpanzee group ($N = 17$) and the role that individuals may play in it. Using data from a year-long observation, we constructed an *unweighted* social network of preferred grooming interactions by retaining only those dyads that groomed above the group mean. This choice of criterion was validated by the finding that the properties of the *unweighted* network correlated with the properties of a *weighted* network (i.e. a network representing the frequency of grooming interactions) constructed from the same data. To investigate group cohesion, we tested the resilience of the *unweighted* grooming network to the removal of central individuals (i.e. individuals with high betweenness centrality). The network fragmented more after the removal of individuals with high betweenness centrality than after the removal of random individuals. Central individuals played a pivotal role in maintaining the network's cohesiveness, and we suggest that this may be a typical property of affiliative networks like grooming networks. We found that the grooming network correlated with kinship and age, and that individuals with higher social status occupied more central positions in the network. Overall, the grooming network showed a heterogeneous structure, yet did not exhibit scale-free properties similar to many other primate networks. We discuss our results in light of recent findings on animal social networks and chimpanzee grooming. Am. J. Primatol. 73:758–767, 2011. © 2010 Wiley-Liss, Inc.

Key words: social network; grooming; primates; betweenness; resiliency

INTRODUCTION

Studying the structure and emerging properties of social groups is of great importance for a better understanding of the complex interactions in human as well as in animal groups. Social network analysis was initially developed to study networks of human interactions, but has been increasingly applied to the study of animal behavior [Croft et al., 2008; Wey et al., 2008]. Social network analysis has provided new insight into the social organization of species like guppies (*Poecilia reticulata*) [Croft et al., 2004] or spider monkeys (*Ateles geoffroyi*) [Ramos-Fernández et al., 2009] and has revealed differences in the social organization of closely related species [Grevy's zebras (*Equus Grevyi*) & Onagers (*Equus hemionus khur*): Sundaesan et al., 2007; Tonkean macaques (*Macaca tonkeana*) & Rhesus macaques (*Macaca mulatta*): Sueur & Petit, 2008; Sueur et al., 2010]. Moreover, it has shown that group structures can vary in a single species depending on the type of social interaction and the group studied [Meerkats (*Suricata suricatta*): Madden et al., 2009]. Finally,

social network analysis has proven to be a useful tool in investigating animal well-being and husbandry [Rhesus macaques (*Macaca mulatta*): McCowan et al., 2008].

Lately, researchers have begun to use social network analysis to investigate the cohesion of networks and the different roles that individuals may play in it. Studying network cohesion is theoretically important because it can provide insight into network properties across different species and even across different biological systems. Many complex biological networks, for example protein

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interactions, have been found to consist of a few highly connected nodes [Barabási, 2009]. These so-called scale-free networks are tolerant to errors (i.e. the random removal of nodes from the network), yet, they are very susceptible to the removal of central, well-connected nodes [Albert et al., 2000]. In contrast, random networks have more homogeneously connected nodes and are susceptible to the removal of central as well as random nodes [Albert et al., 2000; Erdős & Rényi, 1960]. Although some animal social networks show scale-free properties [bottlenose dolphins *Tursiops truncatus*: Lusseau, 2003; Columbian ground squirrels *Spermophilus columbianus*: Manno, 2008], recent studies analyzing social networks of different primate groups did not find any evidence for scale-free properties [Flack et al., 2006; Kasper & Voelkl, 2009; McCowan et al., 2008; Ramos-Fernández et al., 2009].

The study of network cohesion does not only allow determining general network properties, but it also allows gaining new insight in animals' social organization. For example, Flack et al. [2005, 2006] demonstrated that levels of aggression and conflict among group members increased significantly, when three high-status males were experimentally removed from a group of captive pigtail macaques (*Macaca nemestrina*). When they then simulated the removal of these individuals from empirically derived networks, such as grooming, play, and proximity networks, the diversity of the networks decreased and they showed signs of fragmentation [Flack et al., 2006]. Specifically, individuals in grooming and play networks had on average fewer interactions partners (i.e. a lower degree), whereas individuals in proximity networks were connected more closely with direct neighbors (i.e. the mean clustering coefficient increased)—indicating that the network became more cliquish. Similarly, when individuals that connect a lot of other individuals (i.e. individuals with high betweenness centrality) were theoretically removed from an amicable network in wild Columbian ground squirrels (*Spermophilus columbianus*), the network fragmented into smaller clusters containing only a few individuals [Manno, 2008]. Yet, the network was resilient to the removal of random individuals. Individuals with high betweenness centrality thus played a prominent role in maintaining the cohesiveness of the amicable squirrel network. In contrast, an association network in bottlenose dolphins (*Tursiops truncatus*) stayed cohesive after the theoretical removal of individuals with high betweenness and individuals with most associates, respectively—even though the length of information paths between individuals was shortened [Lusseau, 2003; Lusseau & Newman, 2004]. These reported differences in network cohesion after the removal of central individuals may be either due to differences in social group structure or due to the different types of social interactions studied. For example, the

dolphin network was based on association (i.e. how often individuals were seen together), whereas the squirrel network (and some of the macaque networks) were based on affiliative interactions such as grooming and play. This suggests that the cohesion of affiliative networks may depend on certain central individuals, but further studies on animal social network cohesion are needed to support this claim. Thus, we wanted to investigate network cohesion and the role of individuals in the grooming network of a captive chimpanzee group. Such analyses help to shed light on the properties of affiliative networks and the role that certain individuals may play in these networks. In addition, they help to predict the effects of removal (or death) of certain group members on a group and can thus be a useful tool for the management of captive groups.

This article focuses on the analysis of grooming interactions because of their crucial social function. Grooming does not only play a role in maintaining animals' hygiene by removing parasites or cleaning wounds, but it is also important for relieving stress and social tension and for strengthening social bonds between individuals [see Spruijt et al., 1992, for an overview]. In addition, it may serve as an interchange "currency" for either itself or for other services such as tolerance or agonistic support [Henzi & Barrett, 1999]. Nonhuman primates, in particular, frequently engage in grooming activities and can spend up to about 20% of their daily time grooming [Dunbar, 1991]. Grooming has been studied extensively in captive and wild chimpanzees. In the wild, male chimpanzees devote more time to grooming than females and direct grooming toward higher ranking individuals or individuals close in rank, whereas female chimpanzees preferably groom close kin [Goodall, 1986; Watts, 2000b]. However, studies in the wild and in captivity found that both male and female chimpanzees reciprocated grooming independent of partner rank or rank distance [Hemelrijk & Ek, 1991; Watts, 2000a] and to do so on a long-term basis [Gomes et al., 2009]. In addition, chimpanzees interchange grooming for agonistic support [Hemelrijk & Ek, 1991; Koyama et al., 2006; Watts, 2002] and possibly for food [de Waal, 1997]. Recently, grooming has also been related to different dominance "styles" in wild male chimpanzees [Foster et al., 2009].

In order to investigate the cohesion of a chimpanzee grooming network and the role that individuals may play in it, we used data from a 1-year observation (466 hr) of a captive group with 17 individuals at Wolfgang Köhler Primate Research Center (Germany). In general, grooming interactions are directed from one partner to another and dyads often groom at different frequencies. However, in order to analyze the cohesion of the grooming network, it was necessary to construct a network that represented the mere presence of an interaction (i.e. an *unweighted* network). Previous studies have

usually calculated a half-weight index for each dyad (i.e. how often a dyad was seen together corrected by how often each member of the dyad was seen alone) and then retained only those dyads that associated more often than expected from random association [e.g. Lusseau, 2003; Manno, 2008]. Yet, this approach was not suitable for an association measure, such as grooming, where too many meaningful interactions might be removed from the network if too conservative a criterion is used. We thus created an *unweighted* grooming network where we retained only connections between dyads that groomed above group mean and defined these interactions as preferred grooming interactions. As this approach has no precedence in the literature, we validated our criterion by comparing the *unweighted* grooming network to a *weighted* grooming network (i.e. a network representing the frequency of interactions) that we constructed from the same grooming data. By testing whether the properties of the two networks correlated, we could thus investigate whether the *unweighted* network adequately reflected the structure of the group's grooming interactions. Finally, to study the cohesion of the *unweighted* grooming network, we simulated the removal of individuals with high betweenness centrality and of random individuals using the techniques described by Lusseau [2003].

METHODS

Data Collection

We observed 17 West African chimpanzees (*Pan troglodytes verus*, 6 males, 11 females, see Table I for details). Apes were housed in the Wolfgang Köhler

Primate Research Center, Leipzig, Germany, with access to sleeping rooms, semi-natural indoor, and outdoor enclosures (total of 4,500sqm). They were fed a variety of fruits and vegetables, occasionally supplemented by meat, eggs, and yoghurt and had access to water ad lib. Enclosures were equipped with environmental enrichment. Additional enrichment materials were provided for each subject every afternoon. Subjects were neither food nor water deprived. All research reported in this manuscript adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates as well as to all German laws regarding animal holding and testing (German "Tierschutzgesetz").

The group was observed from January 2007 to December 2007 for a total of 466 hr. Observation sessions usually lasted for 2 hr and took place between 10 am and 6 pm. We typically conducted four sessions per week, which were equally distributed over the day. All subjects were observed simultaneously and the frequency of grooming events was coded using a live coding procedure. A single grooming event was defined as "subject A (initiator) continuously grooms B (recipient) for at least 10 sec." In each session, we only coded the first grooming event between each possible initiator-recipient combination.

Data Analysis

In order to construct a *weighted* grooming network, we summed for each dyad the grooming events in both initiator-recipient directions (i.e. summing events where A groomed B and B groomed A). Summing of grooming events for dyads was warranted by the fact that grooming was reciprocal in the group (Dietz'R matrix correlation: $R_s = 0.47$,

TABLE I. Individuals in the Chimpanzee Group and Their Grooming Network Indices

Name	Age	Sex	Rank	Unweighted network				Weighted network	
				Clustering coefficient	Degree	Betweenness centrality	Eigenvector centrality	Betweenness centrality	Eigenvector centrality
Corrie	Mature	F	9	0.51	10	15.12	0.37	0.40	0.41
Dorien	Mature	F	5	0.93	6	0.50	0.29	0.15	0.23
Fraukje	Mature	F	8	0.44	9	30.82	0.33	0.40	0.30
Frodo	Adolescent	M	2	0.56	10	15.80	0.39	0.40	0.31
Kara	Infant	F	16	–	1	0	0.05	0	0.10
Kofi	Infant	M	17	–	1	0	0.04	0.15	0.09
Lobo	Infant	M	15	1.00	2	0	0.10	0.15	0.11
Lome	Juvenile	M	13	1.00	2	0	0.10	0.40	0.17
Natascha	Mature	F	4	0.68	8	7.50	0.34	0.40	0.32
Patrick	Adolescent	M	6	0.83	4	0.50	0.19	0.40	0.21
Pia	Juvenile	F	12	–	1	0	0.05	0.40	0.12
Riet	Mature	F	3	0.50	5	10.80	0.17	0.40	0.24
Robert	Mature	M	1	0.49	10	19.98	0.37	0.40	0.37
Sandra	Adolescent	F	10	0.50	4	4.85	0.13	0	0.17
Svela	Adolescent	F	11	0.80	6	0.75	0.27	0.40	0.19
Tai	Juvenile	F	14	1.00	2	0	0.04	0.40	0.12
Ulla	Mature	F	7	0.57	7	17.38	0.28	0.15	0.32

$P < 0.001$). We then calculated the mean number of grooming events in the group and defined dyads that groomed above group mean as preferred interaction partners. We constructed an *unweighted* network using these preferred interactions as connections between individuals. Grooming interactions that occurred less often than the group mean were not considered for this *unweighted* network. We visualized the networks—the *weighted* and the *unweighted* one—using Netdraw in Ucinet 6.0 [Borgatti et al., 2002]. We also constructed matrices of kinship, sex, and age (using Goodall [1986] to classify individuals as infant, juvenile, adolescent, or adult). In the kinship matrix, the relationship between two individuals was coded as 1 if they were related and as 0 if they were unrelated. In the sex matrix, dyads of individuals with the same sex were coded as 1 and dyads of different sex were coded as 0. Finally, the age matrix represented the age difference between the individuals in each dyad.

Network cohesion and individual roles

For each individual in both networks (the *weighted* one and the *unweighted* one), we calculated the degree, the global clustering coefficient, the betweenness centrality, and the eigenvector centrality using Ucinet 6.0 [Borgatti et al., 2002]. We also correlated individuals' betweenness and eigenvector centralities in both networks to their dominance rank using a Spearman rank correlation test. Dominance ranks were assessed based on the strength and direction of agonistic interactions (threatening, contact aggression, and chasing) between individuals in the same observation period using MatMan [de Vries, 1993b]. We used agonistic interactions to assess dominance ranks, because other behaviors such as pant-grunting were limited to certain members of the group (i.e. females pant-grunting to males). Agonistic interactions, however, took place among all members of the group. We found a linear dominance hierarchy ($h' = 0.43$, $P = 0.001$). We correlated eigenvector and betweenness centralities of the *unweighted* network with the ones of the *weighted* network to assess whether individuals played similar roles in the two networks.

Next, we simulated the removal of individuals from the *unweighted* network using the techniques described by Lusseau [2003] and Flack et al. [2006]. We simulated the removal of individuals with high betweenness centrality (targeted removal) and the removal of random individuals (random removal). We used UCINET 6.0 [Borgatti et al., 2002] to simulate targeted and random removals. Both types of removals were repeated for ten times. We focused on three parameters to study the impact of targeted and random removals using the following measures [see also Albert et al., 2000; Manno, 2008]:

- (1) changes in the number of edges in the largest cluster of the network, i.e. the largest cluster of individuals in the network that are still connected,
- (2) changes in the mean number of edges in the isolated clusters, i.e. clusters other than the largest one, and
- (3) changes in the network's diameter.

Effects of removals were analyzed using Wilcoxon tests and curve estimation tests. Analyses were carried out in SPSS 10.0 ($\alpha = 0.05$).

General network properties

We used the modularity method to identify subgroups in the *weighted* and the *unweighted* grooming networks [Newman, 2004]. Subgroups in the *unweighted* network were compared with subgroups in the *weighted* network using a Spearman rank correlation test. We also investigated whether the *weighted* and the *unweighted* grooming network correlated with kinship, sex, and age using Dietz'R matrix correlation tests as implemented in Socprog2.3 [Whitehead, 1997, 2009]. For each correlation test, we performed 10,000 permutations (permuting the rows and columns of one of the two matrices and calculating statistical values for each permutation), which provides more accurate and stable P -values than other methods [de Vries, 1993a; Hemelrijk, 1990]. In addition, we calculated the diameter, the mean (global) clustering coefficient, and the mean degree of the *unweighted* network. We compared the degree distribution of the *unweighted* grooming network with a Poisson distribution using χ^2 goodness-of-fit tests. Finally, we used curve estimation tests to compare the cumulative distribution of degree and betweenness centrality to a linear function (representing the property of a random network, where the distribution of degrees and betweenness are linear) and to a power-law function (representing a scale-free network, where the distribution of degrees and betweenness follow a power-law). We also compared the cumulative distribution of degree in the *weighted* network with a linear and a power function. In order to study the properties of the *unweighted* chimpanzee grooming network in greater depth, we simulated a random network and a scale-free network having the same number of nodes (individuals) and the same number of interactions as the observed grooming network. These theoretical networks were obtained using models developed under Netlogo 3.15 and were then compared with the observed one using a curve estimation test. Finally, we created ten random networks containing the same number of nodes (i.e. individuals) and edges (i.e. connections) as the *unweighted* grooming network [Lusseau, 2003; Manno, 2008]. We calculated the diameter, the mean (global) clustering coefficient, and the average degree of the random networks. In addition, we compared

the degree distribution of the random networks with a Poisson distribution using χ^2 goodness-of-fit tests.

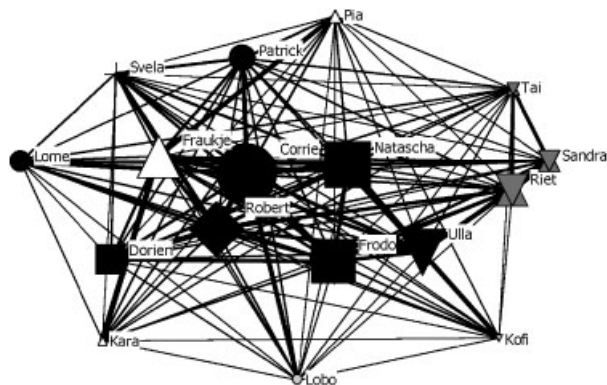


Fig. 1. The *weighted* social network of grooming interactions. The social network was drawn using Netdraw in Ucinet 6.0 [Borgatti et al., 2002]. Nodes represent individuals and the size of nodes represents the individual's betweenness centrality. Distances between individuals represent associations and were calculated using the Multidimensional Scaling method [Whitehead, 2009]. Width of lines represents the strength of the association. Similar shapes characterize individuals belonging to the same matriline. Similar colors represent individuals belonging to the same subgroup [division by modularity, Whitehead, 2009].

RESULTS

We scored 8,212 grooming interactions in the group during the observation period. On average, dyads groomed $30.19 \pm \text{SD } 31.98$ times (range: 0–132). One hundred and thirty-one dyads (of 136 possible dyads) had at least one grooming interaction. Figure 1 shows the *weighted* network of grooming interactions. Forty-four dyads groomed above group mean (i.e. more than 30 times) and thus corresponded to preferred interaction partners, which are displayed in the *unweighted* grooming network (Fig. 2A).

Network Cohesion and Individual Roles

In the *unweighted* network, betweenness centrality differed between individuals and the five individuals with the highest betweenness were Fraukje, Robert, Ulla, Frodo, and Corrie (see Table I). Individuals with a high betweenness centrality also had a high eigenvector centrality (Spearman rank correlation: $r = 0.85$, $N = 17$, $P < 0.001$). Dominance rank correlated significantly with betweenness centrality (Spearman rank correlation: $r = -0.77$, $P < 0.001$, $N = 17$) and with eigenvector centrality (Spearman rank correlation: $r = -0.82$, $P < 0.001$,

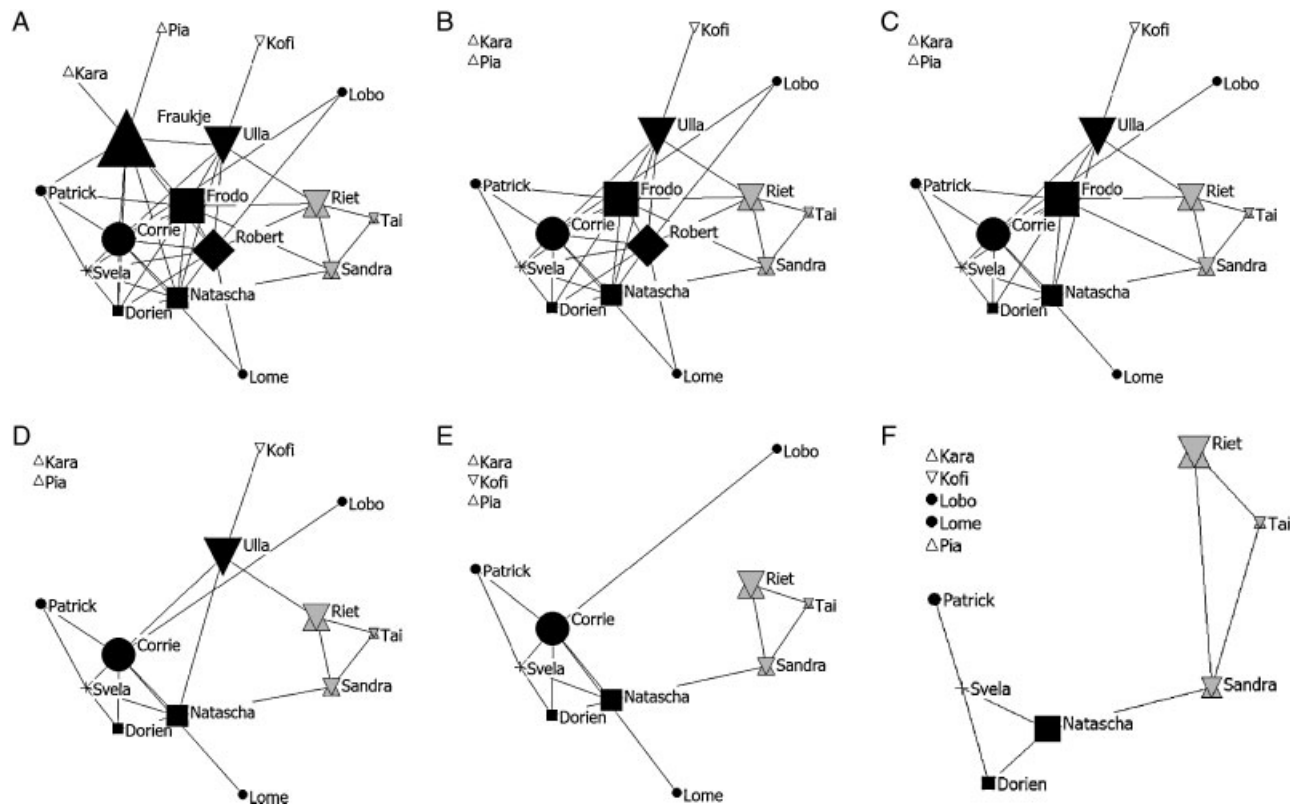


Fig. 2. Changes in the *unweighted* grooming network during removal of the five individuals with the highest betweenness centrality. (A) Shows the intact social network, (B–F) Shows the social network during subsequent removal of the five individuals with the highest betweenness centrality. The social networks were drawn using Netdraw in Ucinet 6.0 [Borgatti et al., 2002]. Nodes represent individuals and the size of nodes represents the individual's betweenness centrality. Distances between individuals represent associations and were calculated using the Multidimensional Scaling method [Whitehead, 2009]. Similar shapes characterize individuals belonging to the same matriline. Similar colors represent individuals belonging to the same subgroup [division by modularity, Whitehead, 2009].

$N = 17$), indicating that the individuals with a higher position in the dominance hierarchy also had a higher betweenness and eigenvector centrality. In the *weighted* network, the five individuals with the highest eigenvector centrality were Corrie, Robert, Natasha, Ulla, and Frodo (see Table I). Eigenvector centralities correlated significantly with dominance rank (Spearman rank correlation: $r = -0.90$, $P < 0.001$, $N = 17$), but there was no correlation between rank and the betweenness centralities of individuals (Spearman rank correlation: $r = -0.16$, $P = 0.659$, $N = 17$). However, eigenvector centralities in the *weighted* network correlated with eigenvector centralities in the *unweighted* network (Spearman rank correlation: $r = 0.91$, $P < 0.001$, $N = 17$).

We removed individuals with high betweenness centrality (targeted removal) from the *unweighted* network (see Fig. 2A–F). We found that the network diameter did not change significantly (Wilcoxon signed-ranks test: $Z = -1.732$, $P = 0.250$, $N = 8$; Fig. 3A) and, additionally, that there was no significant linear relation between the diameter and the number of removed individuals (linear curve estimation test: $R^2 = 0.13$, $F_{1,7} = 1.077$, $P = 0.334$). However, when individuals were removed randomly from the network (random removal), the network diameter decreased significantly (Wilcoxon signed-ranks test: $Z = -2.527$, $P = 0.008$, $N = 8$) and it did so with a significant linear trend (linear curve estimation test: $R^2 = 0.96$, $F_{1,7} = 184.13$, $P < 0.001$).

Focusing on changes of the largest cluster in the grooming network (Fig. 3B), we found that the size of the largest cluster decreased significantly after targeted removal (Wilcoxon signed-ranks test: $Z = -2.521$, $P = 0.008$, $N = 8$) and there was a linear relation between the size of the cluster and the number of removed individuals (linear curve estimation test: $R^2 = 0.92$, $F_{1,7} = 71.82$, $P < 0.001$). Similarly, the size of the largest cluster decreases significantly after random removal (Wilcoxon signed-ranks test: $Z = -2.521$, $P = 0.008$, $N = 8$), and it did so in a linear way (linear curve estimation test: $R^2 = 0.96$, $F_{1,7} = 138.45$, $P < 0.001$). Nevertheless, it decreased significantly more after targeted removal than after random removal (Kolmogorov–Smirnov test: $Z = 1.750$, $P = 0.002$, $N = 8$).

When investigating changes in the mean size of the isolated clusters (i.e. the mean number of individuals in clusters other than the largest one), we found that the mean size increased significantly after targeted removal (Wilcoxon signed-ranks test: $Z = -2.714$, $P = 0.008$, $N = 8$) and that it did so following a power-law (power curve estimation test: $R^2 = 0.96$, $F_{1,7} = 211.500$, $P < 0.001$; linear curve estimation test: $R^2 = 0.35$, $F_{1,7} = 3.851$, $P = 0.090$). We also found a significant change in the mean size of the isolated cluster after random removal (Wilcoxon signed-ranks test: $Z = -1.2530$, $P = 0.008$, $N = 8$). This change could be fitted by a power-law function

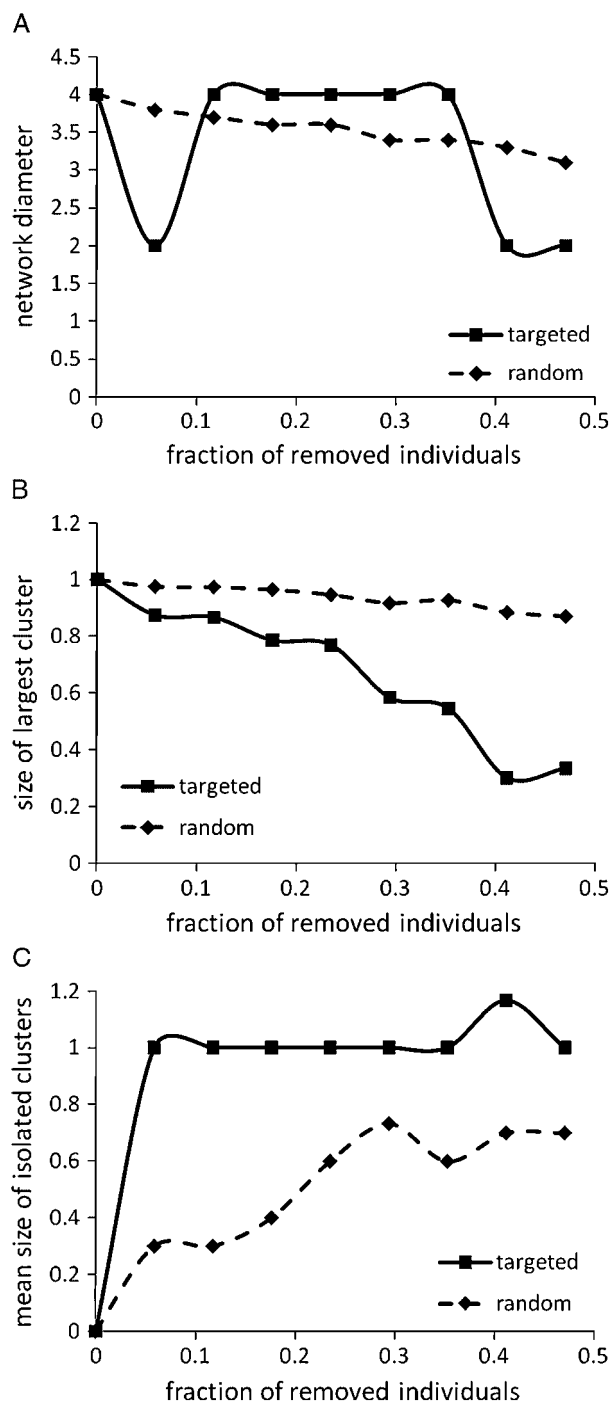


Fig. 3. Changes in network diameter (A), in the size of the largest cluster in the network (B), and in the mean size of the isolated clusters (i.e. the mean number of individuals in clusters other than the largest one) (C) as a function of the fraction of individuals removed from the *unweighted* network.

as well as a linear function (power curve estimation test: $R^2 = 0.99$, $F_{1,7} = 941.11$, $P < 0.001$; linear curve estimation test: $R^2 = 0.82$, $F_{1,7} = 33.923$, $P < 0.001$; Fig. 3C). However, the mean size of the isolated clusters increased significantly more after targeted

removal than after random removal (Kolmogorov-Smirnoff test: $Z = 2.000$, $P < 0.001$, $N = 8$).

General Network Properties

We identified three subgroups in the *unweighted* grooming network (modularity of the arrangement = 0.717) with the largest subgroup consisting of ten individuals and the smaller subgroups of three individuals each (see Fig. 2A). We found that the network correlated with kinship and age class (Dietz'R matrix correlation: kinship: $r = 0.28$, $P = 0.022$; age class: $r = 0.34$, $P < 0.001$), but not with sex (Dietz'R matrix correlation: $r = 0.01$, $P = 0.487$). Subgroups in the *unweighted* network correlated with subgroups in the *weighted* networks (Spearman rank correlation: $r = 0.85$, $P < 0.001$, $N = 17$). Moreover, the *weighted* grooming network correlated with kinship and age (Dietz'R matrix correlation: kinship: $r = 0.41$, $P < 0.001$; age class: $r = 0.42$, $P < 0.001$), but not with sex (Dietz'R matrix correlation: $r = -0.002$, $P = 0.589$).

The average degree of the *unweighted* grooming network was 5.18 ± 3.38 . The *unweighted* grooming network had a lower diameter than the random networks but the difference was nonsignificant (grooming: 4.00, random: 4.5 ± 0.5 ; Wilcoxon signed-ranks tests: $Z = -2.236$, $P = 0.061$, $N = 10$). However, the *unweighted* grooming network had a significantly higher mean (global) clustering coefficient than the random networks (grooming: 0.70 ± 0.21 ; random: 0.30 ± 0.21 ; Wilcoxon signed-ranks test: $Z = -2.807$, $P = 0.002$, $N = 10$). Although the degree distribution in the *unweighted* grooming network differed significantly from a Poisson distribution (goodness-of-fit tests: $\chi^2 = 35.25$, $P = 0.004$), the degree distribution in the random networks did not (goodness-of-fit tests: $\chi^2 < 9.273$, $P > 0.785$). This indicates that the degree distribution in the *unweighted* grooming network was heterogeneous, whereas the degree distribution in the random network was homogenous.

Finally, the cumulative distribution of the degree in the *unweighted* grooming network could be fitted by both, a linear and a power function (linear curve estimation test: $R^2 = 0.97$, $F_{1,11} = 342.71$, $P < 0.001$; power curve estimation test: $R^2 = 0.99$, $F_{1,11} = 6,754.43$, $P < 0.001$; Fig. 4A). Similarly, the cumulative distribution of the betweenness centrality could be fitted by a linear and a power function (linear curve estimation test: $R^2 = 0.91$, $F_{1,6} = 92.34$, $P < 0.001$; power curve estimation tests: $R^2 = 0.91$, $F_{1,6} = 101.29$, $P < 0.001$; Fig. 4B). In the *weighted* network, the cumulative distribution of the degree could be fitted by both, a linear and a power function (linear curve estimation test: $R^2 = 0.97$, $F_{1,15} = 531.59$, $P < 0.001$; power curve estimation test: $R^2 = 0.81$, $F_{1,15} = 65.206$, $P < 0.001$). In order to assess the properties of the *unweighted* network in more depth, we constructed theoretical networks—random ones

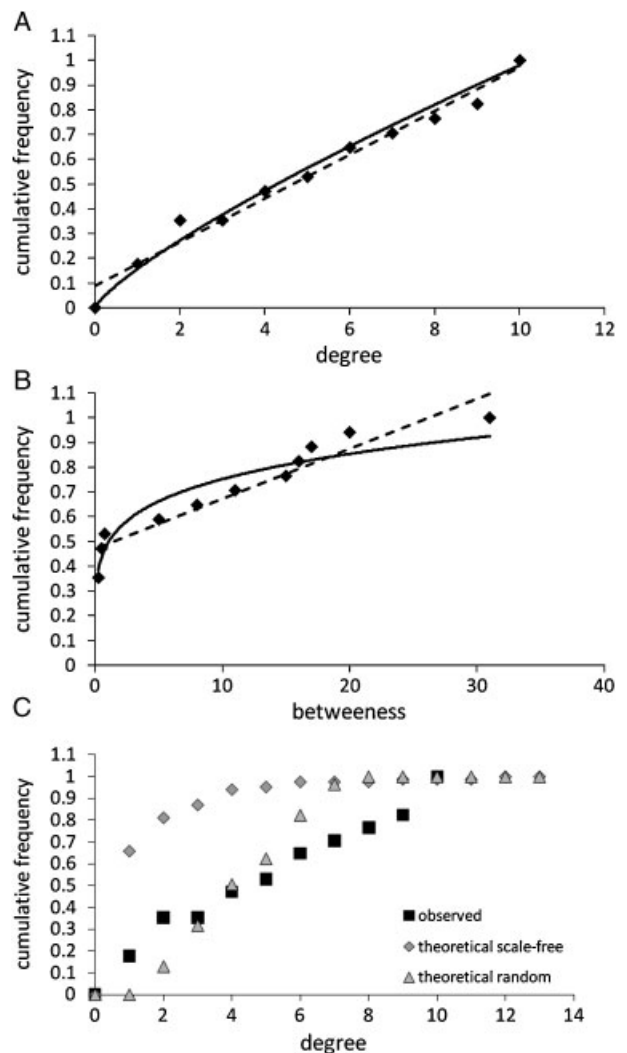


Fig. 4. The cumulative distribution of the nodes' degree (A) and the cumulative distribution of betweenness centrality coefficients (B) in the *unweighted* grooming network. Dashed lines indicate linear curve fits, solid lines power-law fits to the distributions. (C) Shows the cumulative distribution of the nodes' degree in a theoretical scale-free network, a theoretical random network, and the actual observed distribution in the *unweighted* grooming network.

and scale-free ones—based on the *unweighted* network (see Fig. 4C). The *unweighted* network was more similar to a random network (linear curve estimation test: $R^2 = 0.96$, $F_{1,12} = 271.781$, $P < 0.001$) than to a scale-free network (linear curve estimation test: $R^2 = 0.45$, $F_{1,12} = 9.801$, $P = 0.009$).

DISCUSSION

In order to investigate the cohesion of a chimpanzee grooming network, we simulated the removal of individuals with high betweenness centrality from the *unweighted* grooming network (targeted removal). The betweenness centrality of individuals in the network varied considerably and

five individuals (Fraukje, Robert, Ulla, Frodo, Corrie) possessed the highest betweenness centrality coefficients. After the targeted removal of individuals with high betweenness centrality, the size of the largest cluster of individuals in the network decreased more than after random removal. Similarly, the mean size of the isolated clusters (i.e. clusters that have no connections to the largest cluster) increased more after targeted removal than after random removal. In fact, the mean size of the isolated clusters already increased dramatically after the removal of the first key individual. These findings indicate that individuals with high betweenness centrality played an important role in maintaining the cohesion of the grooming network. Previously, affiliative networks in captive pigtail macaques (*Macaca nemestrina*) and wild Columbian ground squirrels (*Spermophilus columbianus*) fragmented after the removal of central individuals [Flack et al., 2006; Manno, 2008]. Thus, across different species and social systems the cohesion of affiliative networks seems to depend crucially on the presence of central individuals—a property that has not yet been found in association networks [e.g. bottlenose dolphins *Tursiops truncatus*, Lusseau, 2003]. Given the important social function of affiliative interactions like grooming, actual removal of central individuals through death or human interference (e.g. management of captive animals) may result in increased stress and social tension, and thus considerably affect animal well-being.

Interestingly, the diameter of the *unweighted* network remained fairly stable even when the seven individuals with the highest betweenness centrality were removed. The length of the information-path between individuals was thus not affected by the removal of central individuals [see Lusseau, 2003, for contrary findings]. This indicates that not only the speed of information transmission in the group (e.g. social learning) but also the spread of diseases would remain unchanged even in the absence of central individuals. However, when more individuals were removed, the network diameter decreased, shortening the length of the information-path between individuals. This may have been a result of the low number of individuals and connections remaining in the network. The network diameter decreased significantly, however, after removal of random individuals—probably due to the random removal of peripheral individuals with few connections.

When further investigating the role of individuals in the *unweighted* network, we found that eigenvector and betweenness centralities correlated with each other and also both strongly correlated with rank, meaning that individuals with higher social status had more grooming partners (or more well-connected grooming partners) than individuals with lower status. Similarly, eigenvector centralities in the *weighted* grooming network correlated with

dominance rank. In addition, they correlated with eigenvector centralities in the *unweighted* network, suggesting the close correspondence between individual roles in the two networks. Betweenness centrality in the *weighted* network did not correlate with dominance rank. Yet, this coefficient is generally more informative regarding *unweighted* networks than *weighted* networks, as it does not take the strength of interactions into account. Overall, most high-status individuals were also central individuals in both networks and two (not mutually exclusive) explanations could account for these findings: on the one hand, higher ranking individuals are more attractive grooming partners [Schino, 2001; Watts, 2000b], on the other hand, these individuals could be using grooming tactically to maintain dominance [Foster et al., 2009].

The *weighted* and the *unweighted* grooming network both correlated with age and kinship. The correlation with kinship probably reflects the group's sex-bias toward (mature) females, which were previously shown to preferentially groom close kin [Goodall, 1986]. Similarly, the weak correlation with age most likely echoes a more general tendency for an increase in grooming frequency and partners with age [Merrick, 1977]. Furthermore, we identified three subgroups in the *unweighted* network (that also correlated with the subgroups in the *weighted* network)—though the largest subgroup consisted of more than half the group members. One of the remaining subgroups comprised the alpha female (Riet) and her two daughters thus indicating their preference to groom kin. The other subgroup comprised a juvenile and two infants being only preferably groomed by their respective mothers, which most likely mirrors the tendency for younger group members to have a very limited number of preferred grooming partners.

We found that the *unweighted* grooming network had a higher mean (global) clustering coefficient, and a lower (though nonsignificantly lower) diameter than corresponding random networks. Moreover, the degree distribution in the grooming network indicated that the network possessed a heterogeneous structure. However, curve estimation tests on the degree distribution revealed that the grooming network resembled more a random network [Erdős & Rényi, 1960] than a scale-free network [Albert et al., 2000]. These findings indicate that some individuals in the network had more interaction partners than others, but that differences between individuals were not very pronounced. Generally, individuals' degree distribution did not show properties typically found in scale-free networks (i.e. a few highly connected individuals). Even though it might sometimes be difficult to unambiguously determine the presence or absence of scale-free properties in small animal networks [James et al., 2009], we demonstrated that random and scale-free

networks could both be theoretically obtained using the same sample size ($N = 17$) as the study group. Although some animal social networks show scale-free properties [bottlenose dolphins *Tursiops truncatus*: Lusseau, 2003; Columbian ground squirrels *Spermophilus columbianus*: Manno, 2008], social networks in different primate groups do not seem to possess scale-free properties [Flack et al., 2006; Kasper & Voelkl, 2009; McCowan et al., 2008; Ramos-Fernández et al., 2009]. Therefore, it is conceivable that primate networks in general do not show scale-free properties, but more systematic analyses of primate groups of different sizes are needed to justify this claim.

Our analysis of the grooming network's cohesion depended crucially on the transformation of the *weighted* grooming network into an *unweighted* one. This transformation was essential for two reasons. First, techniques for analyzing network cohesion have only been developed for *unweighted* networks and cannot be applied to *weighted* networks such as grooming networks where almost all individuals interact with each other. Second, in order to analyze network cohesion, we removed individuals with high betweenness centrality, which is only a meaningful coefficient with respect to *unweighted* networks, as it does not reflect the strength of an interaction. Whenever a *weighted* network is transformed into an *unweighted* one using a certain criterion (in our case grooming above the group mean), it becomes necessary to verify correspondence between the two networks to avoid the construction of an *unweighted* network that is unwarranted by the data. In this study, we found that all properties of the *weighted* and the *unweighted* network apart from individuals' betweenness centralities correlated significantly. This indicates good correspondence between the two networks and validates our choice of criterion. Overall, this demonstrates that criteria for preferred/avoided associations that are unprecedented in the literature can be used to gain a better understanding of the properties of animal social networks.

Finally, it needs to be pointed out that the grooming network in our study described a captive group in which all group members were usually present during observation times. In the wild, however, chimpanzees live in fission–fusion groups, where group composition often varies [Mitani et al., 2002]. Nevertheless, some general characteristics of the grooming interactions in our captive group matched what had been previously found in wild populations (e.g. female's grooming of close kin, correlation between grooming centrality and social status, etc.). Yet, further analyses of grooming network cohesion in wild populations are needed to investigate whether the importance of central individuals for network cohesion is specific to certain groups or environments or whether it represents

a more general property of chimpanzee grooming networks.

To conclude, we found that individuals with high social status were central to the chimpanzee grooming network and played a pivotal role in maintaining its cohesiveness. The importance of central individuals for network cohesion may be a characteristic property of affiliative animal network. Similar to other primate networks, the grooming network did not show scale-free properties.

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