

Social grooming network in captive chimpanzees: does the wild or captive origin of group members affect sociality?

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Abstract

Many chimpanzees throughout the world are housed in captivity, and there is an increasing effort to recreate social groups by mixing individuals with captive origins with those with wild origins. Captive origins may entail restricted rearing conditions during early infant life, including, for example, no maternal rearing and a limited social life. Early rearing conditions have been linked with differences in tool-use behavior between captive- and wild-born chimpanzees. If physical cognition can be impaired by non-natural rearing, what might be the consequences for social capacities? This study describes the results of network analysis based on grooming interactions in chimpanzees with wild and captive origins living in the Kumamoto Sanctuary in Kumamoto, Japan. Grooming is a complex social activity occupying up to 25 % of chimpanzees' waking hours and plays a role in the emergence and maintenance of social relationships. We assessed whether the social centralities and roles of chimpanzees might be affected by their origin (captive vs wild). We found that captive- and wild-origin chimpanzees did not differ in their grooming behavior, but that theoretical removal of individuals from

the network had differing impacts depending on the origin of the individual. Contrary to findings that non-natural early rearing has long-term effects on physical cognition, living in social groups seems to compensate for the negative effects of non-natural early rearing. Social network analysis (SNA) and, in particular, theoretical removal analysis, were able to highlight differences between individuals that would have been impossible to show using classical methods. The social environment of captive animals is important to their well-being, and we are only beginning to understand how SNA might help to enhance animal welfare.

Keywords

Pan troglodytes, Social network analysis, Grooming, Early rearing differences, Behavioral development, Well-being

Introduction

Due to their phylogenetic similarity to humans, chimpanzees (*Pan troglodytes*) have attracted attention from both zoos and researchers, and hundreds of individuals have been brought into captivity from their African habitats (Goodall and Peterson 1993). As a social species, chimpanzees live in groups of several members (Inskipp 2005). Chimpanzee societies, which are known for their complexity, are demanding in terms of social cognition. They display fission–fusion dynamics (Aureli et al. 2008), wherein the community splits into smaller subgroups during one or even several days (Nishida 1968). Despite this, community cohesion and social bonds among members are maintained. The social network of the community is thus complex (Shimada and Sueur 2014), with some individuals playing central roles in the collective social life (Kanngiesser et al. 2011).

In captivity, group members may arrive from other places where they were also captive; they may be born into captivity, or they may have come from the wild. The early rearing of captive infant chimpanzees is not always performed by the mother, whereas the infant stays very close to its mother for the first 2 or 3 years in the wild (Bard 1995). It is thought that normal behavioral development depends, in part, on the early circumstances of the infant. Severe sensory and social isolation during these formative years results in behavioral consequences, reducing the individuals' ability to live in social groups, copulate, and raise infants of their own (Bloomsmith et al. 2006). Nursery-reared chimpanzees show more frequent abnormal behaviors than their maternally reared counterparts (Ross 2003; Bloomsmith and Haberstroh 1995), have reduced sexual and maternal abilities (Brent et al. 1996), and are less likely to reproduce as adults (King and Mellen 1994). The physical cognition of nursery-reared

chimpanzees is also impaired: they have reduced problem-solving skills (Brent et al. 1995), and seem to show less adaptive behavior than their wild-born counterparts (Morimura and Mori 2010). In addition, this impairment may extend to social aspects of their behavior, as behaviors such as tool use are usually learned through social learning during infancy both in the wild and in captivity (Biro et al. 2003; Hirata and Celli 2003; Matsuzawa et al. 2006), and the aggressiveness of offspring is also influenced by the aggressiveness of their mothers (Thierry et al. 2004).

The position of an individual in the social network (i.e., centrality) largely determines an individual's behavior with respect to other members (Sueur et al. 2011a, b). The maintenance of social relationships in a social network through grooming behavior is a time-consuming task and, if the physical cognition of nursery-reared chimpanzees is impaired, social cognition, particularly the ability to develop and maintain relationships, may also be impaired. Social network analysis (SNA) tools are also valuable in primate behavioral management: in rhesus macaques (*Macaca mulatta*), social network measures were shown to be good predictors of aggressiveness (McCowan et al. 2008). In chimpanzees, SNA allowed the assessment of social preferences in a captive group, validating the use of a large modern facility where individuals are not forced to interact (Clark 2011). Using SNA, another study showed that, following the successful integration of two adult groups, chimpanzees choose with whom they wished to associate and interact via a very gradual process of building strong affiliative relationships with unfamiliar individuals (Schel et al. 2013). Social network analysis showed that central individuals (showing a high betweenness coefficient) in groups of dolphins (*Tursiops truncatus*) link different sub-populations, acting as “brokers” and allowing the transmission of information among the entire population (Lusseau et al. 2006). In other studies, the simulated removal of central individuals from a network in captivity according to decreasing centrality resulted in greater network fragmentation and loss of group stability than did the removal of random targets (chimpanzees: Kanngiesser et al. 2011; mandrills: Bret et al. 2013).

In this study, we assessed whether the grooming behavior and social centrality of 15 chimpanzees differed according to their origin: captive-born vs wild-born. We measured and compared several centrality indices between wild- and captive-origin members, also considering the hierarchical rank and age of individuals. We expected social network centralities to be linked to individual attributes such as age or dominance rank, as shown in Kanngiesser et al. (2011). On the other hand, we expected to observe differences among individuals according to their origin, with wild-origin chimpanzees showing greater social ability with their congeners and displaying higher centrality. We anticipated homophily according to origin, with clustering between wild-origin and captive-origin individuals. Indeed, Massen and Koski (2013) showed that chimpanzee relationships are based on similarities in individual characteristics such as personality.

We also use theoretical methods to remove individuals from the social network and assess the impact of removing either captive- or wild-born members on group stability and cohesiveness. We hypothesized that group stability would also be better maintained by wild-origin individuals.

Methods

Subjects and environment

The observed chimpanzees were housed in the Kumamoto Sanctuary (KS), Japan, in an all-male captive group of 15 individuals, seven of whom were of wild origin and eight of whom were of captive origin (see Morimura et al. 2011 for more information on the facility and its history). The captive-born chimpanzees were not all reared maternally. Four of them were rejected by their mothers within 4 months of birth and subsequently hand-reared. One individual was separated from its mother at the age of 7 months following the breeding policy of the owner institute at that time and then hand-reared. All of these hand-reared individuals were put together with other hand-reared individuals of similar age into peer groups by 1 year of age, but two of them (Mi and Ka, see Table 1) were isolated and kept alone in a cage before 3 years of age, while three (Ni, Ke, and To) grew up in peer groups with 1–5 members until adulthood. The remaining three individuals (Mk, Mt, and Sat) were mother-reared for at least the first 2 years, but they were housed as mother–infant pairs, and did not have contact with other conspecifics. During our study, the chimpanzees had access to three outdoor enclosures from 9:00 a.m. to 5:00 p.m., and their group compositions differed each day. That is, the total of 15 individuals was divided into two or three parties, based on the divisions between enclosures. Parties consisted either of three groups of five individuals or one group of five individuals and another of 10. The social group we studied had been stable for 2 years (no arrival or departure of individuals). Details of the KS chimpanzees are summarized in Table 1. Our study was solely observational, and involved no handling or invasive experiments. The chimpanzees were already habituated to human presence in proximity to their enclosure.

Behavioral data

Data were collected from 9:00 a.m. to 4:30 p.m. over 25 days in May–June 2012. We used behavior-dependent sampling (Altmann 1974) during 20 min sessions, for a total of 54.5 h of observations. All grooming events were recorded during a session,

including groomer and groomee identity and duration of grooming (Fig. 1). Grooming behavior is a useful way to measure the strength of social relationships in primates, particularly in chimpanzees (Fedurek and Dunbar 2009). This behavior is a complex social activity occupying up to 25 % of chimpanzees' waking hours (grooming time is often limited in wild groups because of other activities; Majolo et al. 2008). It is also useful, as it allows studying the reciprocity of interactions: the direction of grooming is easier to measure than is that of physical approaches or contacts, and the time a pair spends grooming is easily measurable using instantaneous sampling. We also used ad libitum recorded pant-grunt data (10 months, records from caretakers and M.L.) to establish the dominance hierarchy (Landau's linearity index, $N = 408$, $h' = 0.24$, $p = 0.003$; De Vries 1998). Hierarchical rank was correlated with age ($N = 15$, $r = 0.59$, $p = 0.021$).

Social network measures

We derived a simple ratio index (Cairns and Schwager 1987) from the behavioral observations as follows:

$$\text{Index} = \frac{X_{ab}}{X_{ab} + Y_{ab} + Y_a + Y_b}$$

where X_{ab} is the proportion of time individuals a and b were observed grooming together, Y_{ab} is the proportion of time individuals a and b were observed together but not grooming, and Y_a (or Y_b) is the proportion of time individual a (or individual b) was observed alone. We obtained a weighted matrix of interactions and measured from this network the degree (the number of relationships each group member has with others), eigenvector (a measure of the influence of an individual, depending on the strengths of its relationships but also on the influence of the other group members with whom he is connected), and reach (a measure of the proportion of group members one individual can reach, depending on the number of necessary path steps) of each individual using Ucinet (Borgatti et al. 2002). We also measured the clustering coefficient, assessing how the members with whom an individual is connecting are themselves linked. Global SNA measures were also calculated: density (the proportion of observed relationships compared with all possible ones) and the diameter of the network (longest and shortest path from one individual to another in the network).

Simulated removal of individuals

After preliminary analyses, we transformed this weighted matrix into a binary unweighted matrix (0–1) by establishing a threshold, ignoring all values under this threshold (0), and assigning all remaining values the same weight (1), as in Kanngiesser et al. (2011). The chosen threshold was that leading to maximum network modularity (established with SOCPROG 2.5; Whitehead 2009). We set two other thresholds (average and average + one-third standard deviation; Gilby and Wrangham 2008; Fedurek et al. 2013), but we obtained similar results as with the maximum modularity threshold. Thus, we present only the results with the maximum modularity threshold, as this method is more objective.

Using Ucinet software (Borgatti et al. 2002), we simulated the removal of individuals from the binary network. We followed the same protocol as that described in Lusseau (2003) and Flack et al. (2006), and Kanngiesser et al. (2011). We removed up to seven of the 15 individuals (50 %), from highest to lowest betweenness (the betweenness of a node quantifies how many pairs can be formed using this node as a bridge between two other nodes). In one simulation, we removed only wild-origin members, and only captive-origin members were removed in another. At each step of removal (i.e., each individual removed), we measured the diameter and density of the network, the size (the number of group members) of the largest cluster (the cluster gathering the most members), and the number of isolated clusters.

Statistical analysis

First, using Mann–Whitney tests, we tested whether the percentages of total grooming (received and given), received grooming, and given grooming differed between captive-born and wild-born individuals.

Next, we used Spearman rank correlation tests to assess the influence of hierarchical rank, age, and number of years separated from the mother or since capture on centrality measures of the weighted network. We used Mann–Whitney tests to assess the influence of origin—captive vs wild—on centrality measures, still on the weighted network. We also measured the effect of origin on changes in global measures during theoretical removals on the unweighted network using Kolmogorov–Smirnov tests. We used Monte Carlo resampling procedures (Berry and Mielke 2000) for the Spearman rank correlation tests, and we used exact tests (Good 2005) for the Mann–Whitney and Kolmogorov–Smirnov tests. All statistical tests were performed with R 2.8.1 (R Development Core Team, Hothorn and Everitt 2014]) with $\alpha = 0.05$.

Influence of origin on grooming

The percentage of total grooming did not differ between captive-born and wild-born individuals ($\text{median}_{\text{captive}} = 4.82 \pm 9.95$; $\text{median}_{\text{wild}} = 5.32 \pm 10.02$; $W = 50,898$; $p = 0.301$). Wild-born individuals neither gave ($\text{median}_{\text{captive}} = 3.54 \pm 5.84$; $\text{median}_{\text{wild}} = 2.93 \pm 5.33$; $W = 12,249$; $p = 0.221$) nor received ($\text{median}_{\text{captive}} = 3.52 \pm 6.29$; $\text{median}_{\text{wild}} = 2.88 \pm 4.78$; $W = 11,574$; $p = 0.727$) more grooming than captive-born ones.

Influence of individual attributes on centrality

We first tested the amount of grooming performed by individuals of each origin. The weighted network had a density of 0.614 and a diameter of 2 (Fig. 2a). Hierarchical cluster analysis shows three subgroups of five, three, and two individuals and four individuals not belonging to any subgroup (Fig. 3). In this way, there is no group division according to origin. The maximum modularity was 0.43, and the cophenetic correlation coefficient was 0.89. Modularity and cophenetic correlation coefficients greater than about 0.3 and 0.8, respectively, are taken to indicate a useful division of the population (Newman 2004, 2006).

Hierarchical cluster analysis based on the maximum modularity of the focal chimpanzee group. Individuals are named on the *right*. Individuals with similar colors belong to the same subgroup, except for those denoted in *black*, which were solitary

Centrality measures for each individual are indicated in Table 1. There was no correlation (Spearman correlation test) between the hierarchical rank and the degree ($r = -0.37$, $p = 0.169$), the eigenvector ($r = -0.06$, $p = 0.820$), the reach ($r = -0.06$, $p = 0.830$), or the clustering coefficient ($r = -0.02$, $p = 0.939$). Similarly, we found no correlation between the age of individuals and the degree ($r = -0.08$, $p = 0.780$), the eigenvector ($r = -0.08$, $p = 0.772$), the reach ($r = -0.08$, $p = 0.780$), or the clustering coefficient ($r = -0.1$, $p = 0.725$).

Centrality measures did not differ between wild- and captive-origin members regardless of the measure tested ($p \geq 0.676$, $U \geq 24$, $-0.293 \leq z \leq -0.464$, Table 2). The origin of the members had no effect on their integration into the network. For individuals of captive origin, only the eigenvector coefficient was correlated with the number of years separated from the mother ($r = 0.72$, $p = 0.04$ vs $r \leq 0.58$, $p \geq 0.132$ for all other coefficients). This was driven primarily by one individual being separated very late from his mother compared with other group members. Age at capture for wild-origin individuals was not correlated with any centrality coefficients ($r \leq 0.39$, $p \geq 0.383$).

Simulated removals of individuals

The binary network had a density of 0.238 and a diameter of 3 (Fig. 2b). After removals, changes in the binary network diameter showed no differences between wild-origin and captive-origin removals (K–S, $z = 0.650$, $p = 0.627$).

The fraction of members in the largest cluster changed significantly during the removals (Fig. 4) for both wild- (Wilcoxon signed-rank test, $p = 0.013$, $T = 36$) and captive-origin (Wilcoxon signed-rank test, $p = 0.0078$, $T = 36$) removals. However, changes differed according to the number of removals (K–S, $z = -2.21$, $p = 0.03$), and there was greater variation for wild-origin removals (45 %) than for captive-origin removals (25 %).

Changes in the number of isolated clusters differed according to the origin of individuals removed (K–S, $z = 1.5$, $p = 0.022$; Fig. 4). There was a significant change in the number of isolated clusters when removing wild-origin members (Wilcoxon signed-rank test, $p = 0.014$, $T = 36$), whereas the number of isolated clusters during captive-origin removal was stable with no observable changes.

Changes in density differed according to the origin of individuals removed (K–S, $z = 1.5$, $p = 0.022$, Fig. 5). The density changed significantly during wild-origin removals (Wilcoxon signed-rank test, $p = 0.00078$, $T = 36$), but was stable during the removal of captive-origin individuals.

Discussion

The maintenance of captive groups of primates entails considerable involvement in group management (McCowan et al. 2008; Clark 2011; Dufour et al. 2011). Individuals with deprived early-rearing conditions may have trouble behaving appropriately in their social groups. Social network analysis is a way of evaluating the integration of individuals into the group network based on their centrality and the group's stability. Here, we wanted to assess whether an individual's origin (i.e., wild vs captive) affected her/his social integration.

Short observation times, a limitation in most studies, were useful here, as we studied a complex and dynamic social network. Even if the social network of a chimpanzee group can be considered stable over some period of time, changes might still occur. In a captive managed group, individuals may be added regularly, resulting in position changes in the social network. The most recent addition to the group we studied arrived in 2010, and thus the group had been stable for 2 years. However, this does not

necessarily mean that the social network had been stable for 2 years. Few studies have focused on the temporal dynamics of social networks, and we had no clear idea of the time needed for a social network to stabilize. Therefore, short-term observations minimized confounding variation due to social network evolution, which might have otherwise obscured variation due to the wild or captive origin of members. Moreover, a new chimpanzee was planned to be added to the group at the end of the observation period, making it impossible to gather data during this period.

Based on four different network centralities (degree, eigenvector, reach, and clustering coefficients), chimpanzees did not differ in their network centralities, regardless of origin. Likewise, they did not differ in time spent grooming or being groomed. As centrality measures indicate the power (eigenvector), integration (degree and reach), or cohesion (clustering) of network members, wild- and captive-origin members share similar power repartitioning and integration in this grooming network. They are similarly connected to others in terms of the quantity of ties (measured by the degree), the separation from or cohesion with other members (measured by the reach and clustering coefficients), and the connectivity with others (measured by the eigenvector). If there were differences based on wild or captive origin, or differences due to the arrival of a new individual in the social group, they were no longer visible in the state of network evolution we observed. Indeed, during our study, group composition had been stable for 2 years, a time that is apparently sufficient for the social integration of group members. To this end, Schel et al. (2013) concluded that 1 year is needed for aggression between newly integrated groups of chimpanzees to subside, although association data still indicated the persistence of two distinct subgroups. Such negative results might also be due to group composition. The group we studied was composed of approximately half captive-born and half wild-born individuals. As a consequence, any single group member, whatever his origin, had a high probability of interacting with individuals of both origins, which might impact social centralities. However, we hypothesized that captive-born individuals would not be less attractive to other group members but would instead be less prone to interacting with their congeners. According to this hypothesis, we should nonetheless have observed some differences in centrality according to origin, whatever the number of individuals per condition. These centralities could also be strongly affected by other factors, reducing the effect of origin; however, we found no influence of hierarchical rank or age on the centrality measures. Several studies of chimpanzees showed a link between hierarchy and social centrality (Kanngiesser et al. 2011; Rushmore et al. 2014), with high-ranking individuals having the highest centrality values. However, high social network variability seems to exist between chimpanzee groups due to group composition or the personalities of key individuals (Van Leeuwen et al. 2013; Cronin et al. 2014). Thus, we cannot say whether the lack of correlation in our study group was due to captive conditions, group composition, or variation in the social network. Schel et al. (2013) also suggested that some individuals were important

in facilitating the integration of other members. This may have been the case in our group, with one or more individuals behaving in a way that mitigated the origin effect.

We tested the theoretical removal of individuals on four measures. Of these, only the diameter remained unchanged when removing members of captive vs wild origin. For the other measures, removing individuals of wild origin yielded greater changes in the network than did removing captive-origin individuals. These removals were based on the betweenness coefficients of individuals. The betweenness coefficient is a measure of an individual's function in group cohesion, linking different subgroups. Lusseau and Newman (2004) defined these specific individuals in dolphins as “brokers who act as links between sub-communities and who appear to be crucial to the social cohesion of the population as a whole.” Although we did not find any differences with respect to the four centrality measures described above, it appeared that removing wild-origin individuals with higher betweenness had a greater impact than did removing those of captive origin. The evolution of the fraction of members in the largest cluster and of the number of isolated clusters differed between the wild- and captive-origin removals. Density was much more strongly impacted when removing wild-origin than captive-origin chimpanzees. The fraction of members in the largest cluster, the number of isolated clusters, and the density covaried, with a peak at four wild-origin individuals removed (30 %). Similar results were obtained using the same methodology in ground squirrels (Manno 2008) and in chimpanzees (Kanngiesser et al. 2011): after increasing or remaining stable, density decreased when additional individuals were removed because of their low centralities. Thus, more links are broken by removing wild-origin individuals than by removing captive-origin ones. Overall, it seems that, on an individual level, the centrality of wild-born individuals did not differ significantly from that of captive-born ones but that, at the group level, the former had a greater impact on network stability.

Our results show that differences may emerge between individuals being early reared in the wild or in captive settings. However, the differences we observed were weaker than we expected and did not seem to impact the integration of individuals into their groups. Wild-origin individuals seem, however, to be more important for group cohesion. We hypothesized that social cognition would be affected by captive-born conditions. However, in contrast to the long-term effects on physical cognition (Brent et al. 1995; Morimura and Mori 2010), our results showed that living in social groups might compensate for the negative effects of non-natural rearing and that non-natural rearing did not obviously impair social cognition, notwithstanding the effect during theoretical removal. One might suggest that the space was too restricted in our study to observe the social preferences of chimpanzees (Clark 2011). However, Fig. 2a highlights variation in the strength of social relationships. Further studies should be undertaken as new individuals are introduced into the group (Schel et al. 2013) to observe how social

relationships are established and reorganized according to group member attributes. Nevertheless, it is noteworthy that SNA, and theoretical removal analysis in particular, was able to highlight differences between individuals that would have been impossible to show with classical methods. The social environment of captive animals is important for their well-being (McCowan et al. 2008; Asher et al. 2009; Koene and Ipema 2014), and we are only beginning to understand how SNA might enhance animal welfare. A better understanding of these topics could help in selecting individuals before forming new groups of captive animals or identify socially deprived animals who might benefit from social or physical cognitive enrichment (Sueur and Pelé 2015).

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Table 1 Characteristics and centrality measures of each group member studied

Individual	Age	Rank	Origin	Number of years^a	Degree	Eigenvector	Reach	Clustering
Ge	33	6	w	1	5	0	8.18	0.03
Go	30	9	w	1	5	0.17	293.77	0.11
Ka	21	2	c	0.3	13	0.2	368.64	0.09
Ke	22	8	c	0.01	8	0.25	509.7	0.08
Le	42	12	w	6	9	0.51	708.3	0.12
Mk	20	3	c	4.3	8	0.12	224.88	0.07
Mt	20	1	c	8.5	10	0.54	757.54	0.09
Mi	22	4	c	0.2	10	0.11	209.28	0.06
Na	31	11	w	2	6	0.07	133.92	0.03
Ni	24	13	c	0.6	9	0.23	437.46	0.09
No	31	7	w	2	13	0.07	133.76	0.06
Sat	17	5	c	2.2	9	0.12	222.37	0.1
Sh	30	10	w	1	12	0.44	699.63	0.06
Ta	34	15	w	2	9	0.15	274.6	0.09
To	21	14	c	0.01	4	0.01	14.69	0.04

Table 2 Average of centrality measures for captive- and wild-origin chimpanzees (±standard deviation)

Origin	Degree	Eigenvector	Reach	Clustering
Captive	8.87 ± 2.53	0.19 ± 0.16	343 ± 227	0.08 ± 0.02
Wild	8.43 ± 3.25	0.20 ± 0.20	321 ± 278	0.08 ± 0.04

Fig. 1 Male chimpanzees engaging in social grooming at Kumamoto Sanctuary



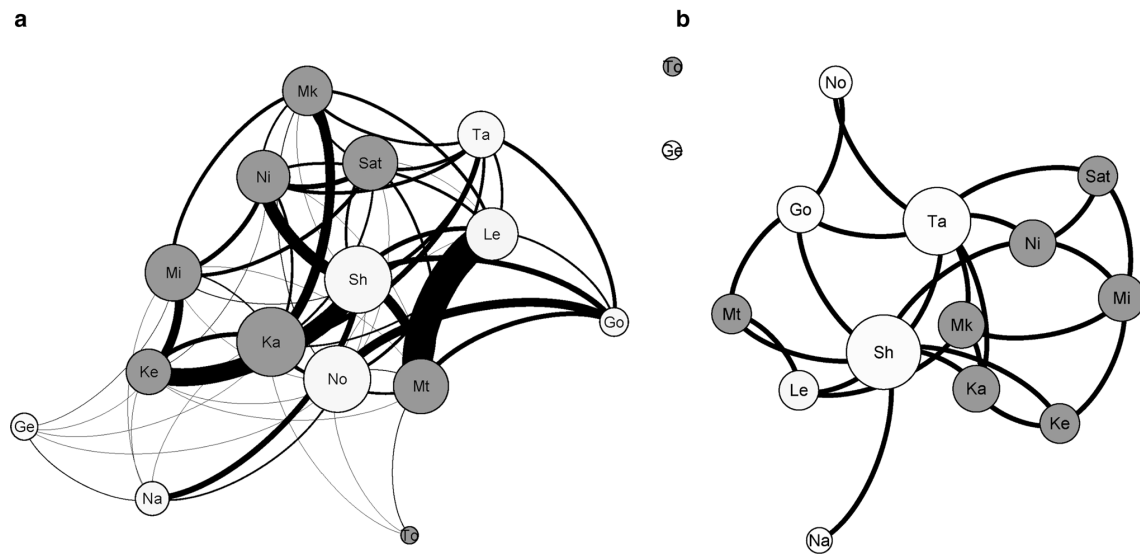


Fig. 2 a Weighted social networks and, b binary (unweighted) social networks of grooming interactions in the groups studied. Nodes represent group members, with larger size indicating higher degrees. White indicates wild origin, whereas gray indicates captive origin. The procedure used to binarize the network is described in the methods section. Graphs were drawn using Gephi 0.8.2 (Bastian et al. 2009)

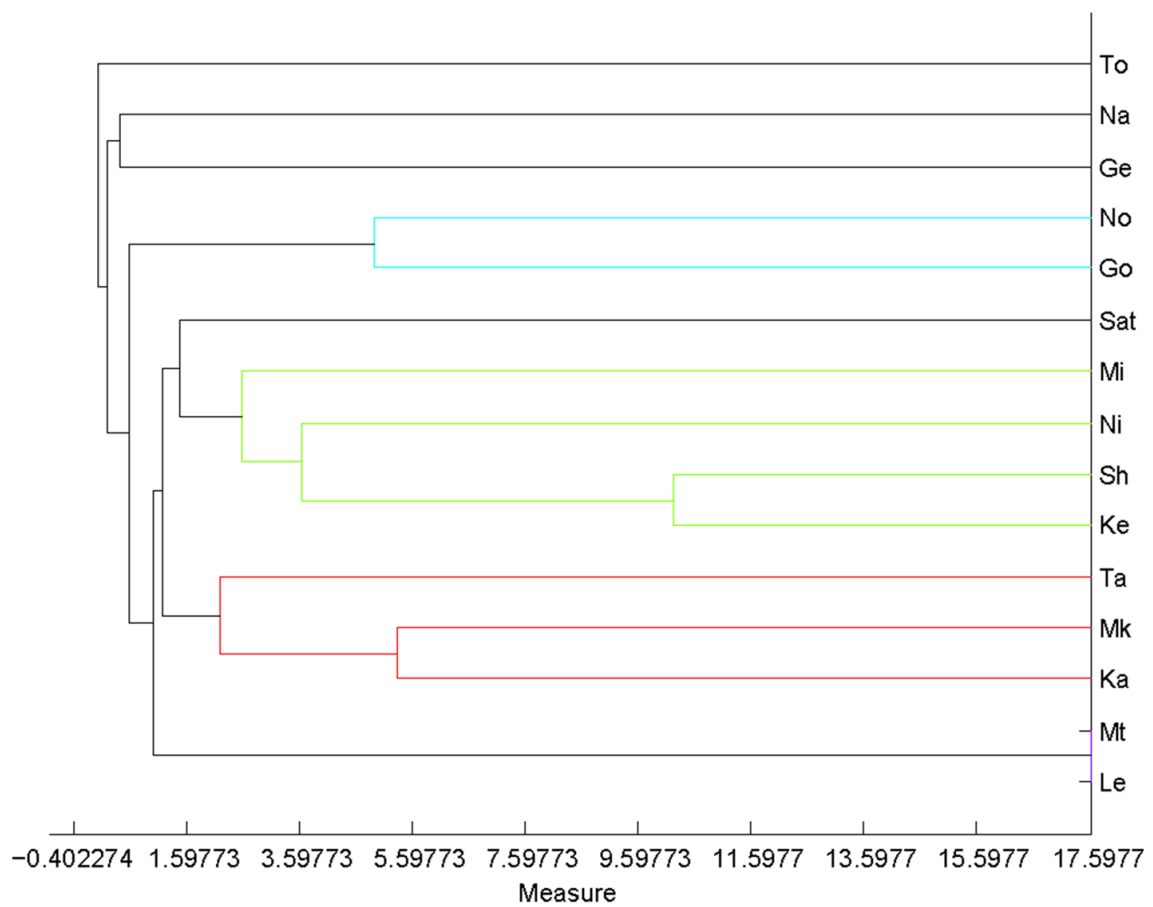


Fig. 3 Hierarchical cluster analysis based on the maximum modularity of the focal chimpanzee group. Individuals are named on the right. Individuals with similar colors belong to the same subgroup, except for those denoted in black, which were solitary

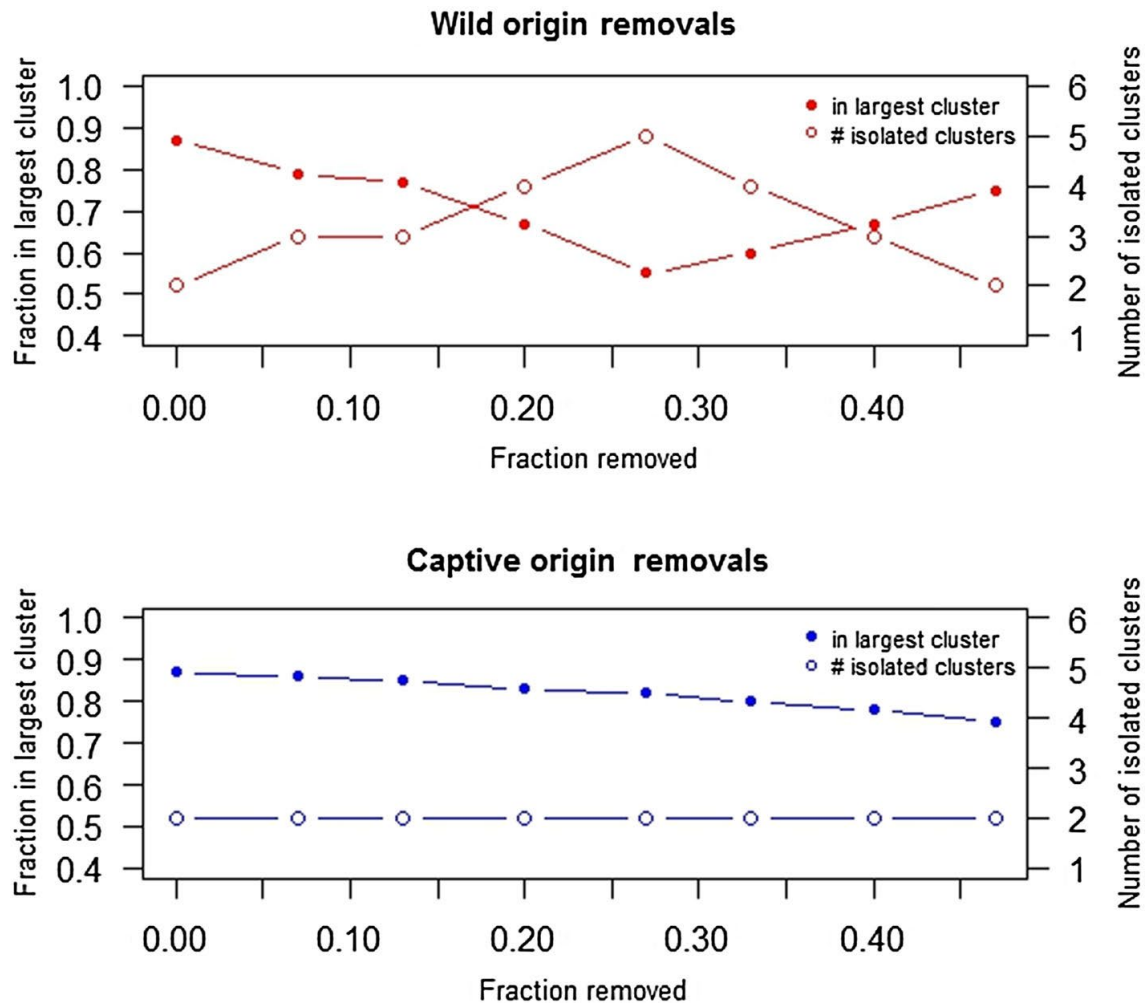


Fig. 4 Evolution of the size of the largest cluster and the number of isolated clusters during the theoretical removals of wild-origin (*top*) and captive-origin (*bottom*) members

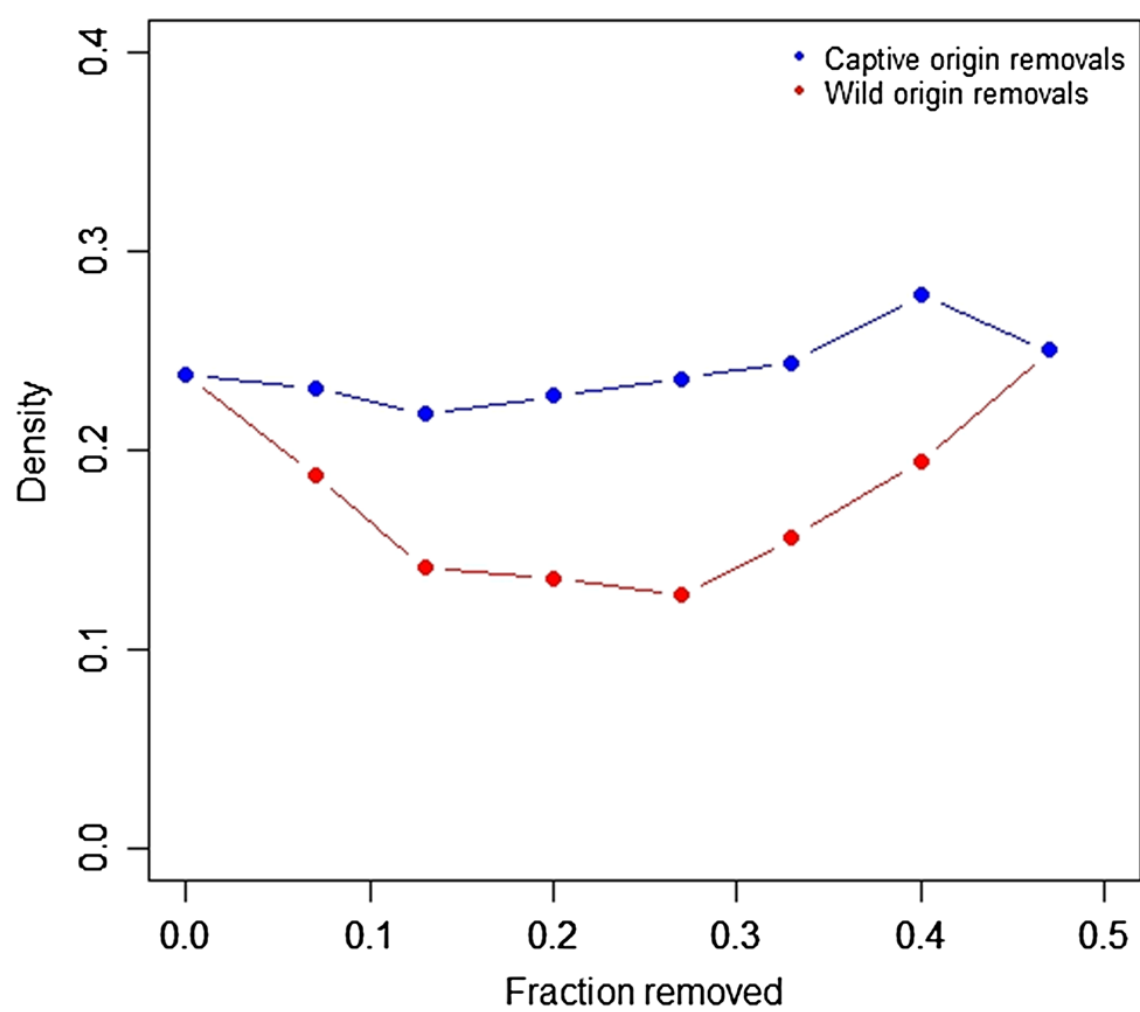


Fig. 5 Evolution of network density during theoretical removals