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Demographic Factors Are Associated with Intergroup Variation in the Grooming Networks of Female Colobus (*Colobus vellerosus*)

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Abstract Intergroup variation in social networks can have important implications for inferring the evolution of primate social relationships, but the underpinnings of this variation remain poorly understood. To further our understanding of this topic, we investigated whether intergroup variation in colobus grooming networks was associated with group size, the proportion of female kin and infants, and stability in female group composition. Between 2008 and 2009, we collected behavioral data via focal sampling of 61 females in 8 groups at Boabeng-Fiema, Ghana, which we used to calculate grooming network metrics. We collected demographic data during the same time period to determine group sizes and group compositions, while we used longitudinal data (2000–2009) to estimate stability in group composition. We determined kinship via partial pedigrees and genetic data from 17 short tandem repeat loci. Females in larger groups had more grooming partners but did not form weaker networks than females in smaller groups. This finding suggests that time constraints linked to large group sizes do not limit sociality in this population, which is similar to findings in other folivorous black-and-white colobus but contrasts with those in many frugivorous primates. Groups with a larger proportion of infants spent more time grooming, similar to some other mammals. Group stability correlated positively with centralization, i.e., inequity, for incoming ties. Networks were not affected by kin compositions of groups, in contrast to those in some female resident-nepotistic cercopithecines. We suggest that the relative importance of demographic factors in shaping social networks may vary between populations depending on diet and social structure.

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Introduction

Strong and enduring affiliative relationships between group members are an occasional outcome of gregariousness (Olson and Blumstein 2009; Whitehead and Kahn 1992; Wrangham 1980), and these relationships can have important fitness consequences (Cameron *et al.* 2009; Durant *et al.* 2004; Koenig 1994; Lambin and Yoccoz 1998; Moses and Millar 1994; Ruan and Wu 2008; Silk *et al.* 2003, 2009, 2010). Despite potential fitness benefits, individuals do not always form strong bonds with all group members; i.e., they form differentiated social relationships (Hinde 1976). Such differentiated social relationships occur in many mammalian taxa, including primates (Seyfarth and Cheney 2012).

Major advancements in our understanding of the evolution of primate social relationships come from cross-species or cross-population comparisons (Di Fiore and Rendall 1994; Rendall and Di Fiore 1995, 2007; Sterck *et al.* 1997; van Schaik 1989; Wrangham 1980). However, these studies are often limited to data from one or a few groups per population or species, and the validity of their conclusions rests on the assumption that variation in social structure is higher between than within populations. Although it is now well known that social relationships can vary within and between groups in the same population (Bergstrom and Fedigan 2013; Berman and Kapsalis 2012; Berman *et al.* 2008; Strier 1994; Wikberg *et al.* 2013, 2014b), few studies have used social network analysis to systematically investigate intergroup variation in social networks. The few notable exceptions indicate that there can be considerable intergroup variation in social networks, which is often explained by demographic factors such as group size, the kin composition of groups, the presence of infants, and the stability in group membership (Guan *et al.* 2013b; Madden *et al.* 2009; McCowan *et al.* 2008; Wey and Blumstein 2010).

There may be a threshold for group size beyond which animals cannot devote enough time to form strong relationships with every other group member (the time constraints model: Dunbar 1991; Henzi *et al.* 1997; Lehmann *et al.* 2007). Animals need to allocate a certain amount of time to critical activities related to food and mate acquisition, and there is therefore a limit to how much time animals can devote to social activities (Dunbar 1991). Because of these constraints, larger groups will form differentiated and less well-connected social networks than smaller groups. This model accurately predicts the patterns of group-level social network metrics in some populations. For example, meerkats (*Suricata suricatta*) form sparser grooming networks in larger groups (Madden *et al.* 2009), and feral goats (*Capra aegagrus hircus*) consistently form core groups containing 12–13 individuals while the remainder of the group members are peripheral (Stanley and Dunbar 2013). If the group is too large for all other group members to interact with each other, animals may focus their grooming effort on social partners with high resource holding potential, such as male chimpanzees (*Pan troglodytes*) in an unusually large community do (Watts 2000). This could lead to larger groups forming a more centralized social network, where certain individuals receive and/or give more grooming than others, i.e., show greater power differences.

The kin composition of groups may also explain intergroup variation in social networks. White-faced capuchins (*Cebus capucinus*) and several species of macaques (*Macaca* spp.) form social networks that are shaped by an interaction effect between the group's size and kin composition. Animals show stronger kin bias in larger groups, in which there is more variation in kinship between potential social partners (Bergstrom and Fedigan 2013; Berman *et al.* 1997; Berman and Thierry 2010; Perry *et al.* 2008). Macaques also form affiliative networks of lower inequity in groups with a higher ratio of kin (Sueur *et al.* 2011) and more similar-sized matrilines (McCowan *et al*. 2008).

It has long been recognized that newborn infants affect dyadic social relationships between females (Altmann 1980; Hrdy 1976). Infants can also have a noticeable effect on group-level social network metrics. This is the case in degus (*Octodon degus*), in which females form stronger and more well-connected association networks during lactation (Wey *et al.* 2013). Studies of multiple colonies of yellow-bellied marmots (*Marmota flaviventris*) and multiple units, i.e., stable social groupings of sperm whales (*Physeter macrocephalus*) also show that young animals are important actors in the social network (Gero *et al.* 2013; Wey and Blumstein 2010). Sperm whale calves act as hubs around which social interactions are clustered, and as a result, the mothers and the calves' primary babysitters become important actors in the social network (Gero *et al.* 2013). Although this pattern is the same across units (Gero *et al.* 2013), the results from this study suggest that different proportions of infants will lead to variation in group-level social network metrics. In contrast to the expected pattern, rhesus macaques (*Macaca mulatta*) form less well-connected and more egalitarian social networks during the birth season (Brent *et al.* 2013). Brent and colleagues (2013) suggest that this pattern is due to the formation of consorts during the mating season. Some females will shift their attention from their preferred female partners to their male consorts whereas females that do not form consorts may groom a wider range of social partners to compensate for the temporary loss of their preferred partners (Brent *et al.* 2013).

Changes in group composition can also affect social networks. Groups sometimes contain key players that are important for maintaining cohesion, and the death or dispersal of these key players may lead to a weaker and more substructured social network (Flack *et al.* 2006; Lusseau and Newman 2004; Schel *et al.* 2013). For example, when such a key player was temporarily missing from a community of bottlenose dolphins (*Tursiops* spp.), the interaction ties between two adjacent communities became sparser (Lusseau and Newman 2004). Animals entering a population can also lead to social instability (Ilany *et al.* 2013) and disrupt social interactions, particularly for individuals with already weak ties (Jacoby *et al.* 2010). However, the initial effect new individuals have on the social network may eventually wear off. For example, the affiliative network increased in strength over time after two captive groups of chimpanzees (*Pan troglodytes*) were integrated (Schel *et al.* 2013). The effect of immigrants has also been demonstrated in a study of western black-crested gibbons (*Nomascus concolor jingdongensis*), in which the group with a more stable group composition formed a more well-connected grooming network (Guan *et al.* 2013b). To facilitate social integration, recent immigrants and young animals that lack an established position as a breeder often give more grooming to long-term resident animals than vice versa, and this may lead to a centralized grooming network (Guan *et al.* 2013b; Idani 1991; Wey and Blumstein 2010). Taken together, these studies indicate that several demographic factors are important in explaining the variation in social networks between groups in the same population.

Female white-thighed colobus (also known as ursine colobus, *Colobus vellerosus*) spend low proportions of time socializing (Teichroeb *et al.* 2003) and rarely engage in coalitionary aggression against other female group members (Saj *et al.* 2007; Wikberg *et al.* 2014b). However, females form coalitions against males and extragroup females (Saj *et al.* 2007; Wikberg *et al.* 2014b), and strong grooming relationships predict cooperative food defense in our study population (Wikberg 2012). In addition, grooming relationships may serve an important social function by increasing tolerance while feeding (Lehmann and Boesch 2009) and by creating a benign environment to raise young (Cameron *et al.* 2009; Silk *et al.* 2003). The white-thighed colobus is an excellent study species for examining how demographic factors affect social networks because of considerable variation in group size (Wong and Sicotte 2006), kin composition of groups (Wikberg *et al.* 2012), and stability of female group membership (Teichroeb *et al.* 2009; Wikberg *et al.* 2012). Group sizes range from 9 to 38 individuals in our study population (Wong and Sicotte 2006). Females are facultative dispersers, which leads to intergroup variation in the kin composition of groups and in the stability of the female group membership (Teichroeb *et al.* 2009; Wikberg *et al.* 2012). In comparison to other primate species, females engage in high rates of natal attraction, i.e., inspecting and touching other females' infants, and infant handling (Bădescu *et al.* 2014; Brent *et al.* 2008). The presence of infants may therefore shape female social networks.

We specifically investigated if the grooming networks were differentiated, and if demographic factors can explain intergroup variation in centralization, clustering, density, degree, relationship strength, and time spent grooming (Tables I and II). Owing to time constraints associated with large group sizes, we predicted that the grooming network's connectedness and quality would decrease while substructuring and power differences would increase with group size (Dunbar 1991; Henzi *et al.* 1997;

Table I Network parameters used in our study of the white-thighed colobus at Boabeng-Fiema (May 2008–June 2009)

Parameter	Network type	Description
Centralization	Weighted	Indicates power differences or inequity. High values mean that the networks are centered on a smaller proportion of individuals.
Clustering	Binary	Indicates substructuring. High values can indicate many well-connected subgroups within the group.
Density	Binary	Indicates connectedness. High values mean that most individuals are directly connected to each other.
Degree	Binary	Indicates connectedness. High values indicate a high number of social partners.
Grooming time	Weighted	Indicates the quality of the connections. Higher values mean that individuals devote a larger proportion of their activity budget to grooming.
Strength	Weighted	Indicates the quality of the connections. High values can indicate that individuals form very strong ties with a few group members or that individuals form intermediately strong ties with most group members.

Table II Predictions of the relationship between social network metrics and following demographic factors: female group size, the proportion of infants (infants), the proportion of female kin (kin), and the number of years with stable female group membership (stability) in the white-thighed colobus at Boabeng-Fiema (May 2008–June 2009)

Demographic factor	Connectedness (degree or density)	Quality (grooming time and strength)	Substructuring (clustering)	Power differences (centralization)
Group size	−	−	+	+
Kin	+	+	+	−
Infants	+	+[a]	+	−
Stability	+	+	−	−

[a] Indicate predictions supported by our study

Lehmann *et al.* 2007; Madden *et al.* 2009; Stanley and Dunbar 2013; Watts 2000). Females often form the strongest relationships with female kin (Kapsalis 2004), but female colobines show kin-biased grooming networks only in groups with a high number of kin (Wikberg *et al.* 2014b). Therefore, we expected the grooming networks in groups with a high proportion of kin to consist of large, strong clusters with little power differences (Sueur *et al.* 2011). Because female colobines are attracted to young infants (Bădescu *et al.* 2014; Brent *et al.* 2008) and females often groom mothers for access to their infants (Frank and Silk 2009; Fruteau *et al.* 2011; Gumert 2007; Henzi and Barrett 2002; Tiddi *et al.* 2010), we predicted that a larger proportion of females with infants would be associated with stronger and larger grooming clusters (Gero *et al.* 2013; Wey and Blumstein 2010; Wey *et al.* 2013). Although mothers and the most frequent infant handlers are likely important players in the grooming network (Gero *et al.* 2013), we expected to find centralized grooming networks only in groups with a low proportion of young infants. When all females have infants, no female will be a more important actor than another, leading to low centralization in the grooming network. Finally, we predicted that increasing stability in female group membership would be associated with more well-connected and higher quality grooming networks with lower substructuring and centralization, based on findings from previous studies (Flack *et al.* 2006; Guan *et al.* 2013b; Idani 1991; Jacoby *et al.* 2010; Lusseau and Newman 2004; Schel *et al.* 2013; Wey and Blumstein 2010).

Methods

Data Collection

Our study site, Boabeng-Fiema Monkey Sanctuary, is located in central Ghana (7°43 N and 1° 42 W). It consists of a 1.92-km^2 dry semideciduous forest (Hall and Swaine 1981) that is connected to other forest fragments via narrow riparian forest corridors. P. Sicotte and her students started observing two colobus groups at this site in 2000 (BS and WW), and we added more study groups during the following years (DA and RT: 2004; SP and OD: 2006; NP: 2007; BO: 2008) with total of eight groups when behavioral data collection for this study started. The 8 study groups contained a total of 61 adult (>5 yr) and subadult (3–5 yr) females. We continuously recorded grooming interactions during 10-min focal samples of these females (Altmann 1974) between May 2008 and June 2009.

The social network parameters used in this study are sensitive to sampling effort (Croft *et al.* 2008). Because sampling effort differed between females, we analyzed only a subset of focal follows. We randomly selected focal follows to make up 7.3–7.5 focal hours per female. These focal data were used to calculate the time spent giving grooming (the number of seconds A spent grooming B/the number of focal hours for A and B). The grooming interactions were entered into weighted, directed matrices. We also created binary matrices that contained only the presence and absence of grooming between animals. We did not filter these matrices to remove weak ties, i.e., low values of grooming, and we considered all grooming connections as biologically meaningful (*sensu* Brent *et al.* 2011).

Kinship Determination

We collected at least two fecal samples from each focal individual for DNA extraction, quantification, and genotyping at 17 short tandem repeat loci (Wikberg *et al.* 2012, 2014a, b). We used CERVUS (Kalinowski *et al.* 2007; Marshall *et al.* 1998) to assign parentage and COANCESTRY (Wang 2011) to calculate dyadic estimated relatedness (*R*) values (Wikberg *et al.* 2012, 2014b). We combined genetic data and partial pedigree information to determine kinship (Langergraber *et al.* 2009). We classified females with an *R* value >0.23 as kin, and this threshold can accurately distinguish known kin, i.e., kin according to the demographic records or the parentage assignments, from known nonkin in our study population (Wikberg *et al.* 2014a, b).

Variables

We used either the binary matrices or the weighted matrices to calculate the following variables: total proportion of time spent grooming ("grooming time" hereafter), relationship strength, mean degree, density, weighted clustering coefficient, and centralization (Table I). The grooming time is the proportion of a female's activity budget that is devoted to grooming, and we calculated the mean grooming time per group. Relationship strength (strength hereafter) is the mean time spent grooming each of the other females, and we calculated the mean of all females' relationships strength per group. It indicates the average quality of the grooming connections. Mean degree is the mean number of group members with recorded interactions (Hanneman and Riddle 2005). Density is the proportion of ties present (Hanneman and Riddle 2005). Mean degree and density indicate how connected the social network is on a group level. The weighted clustering coefficient (clustering hereafter) indicates the proportion of ties between the focal individual's neighbors, i.e., individuals that have ties to the focal, and the mean value is weighted by each actor's degree (Hanneman and Riddle 2005). Low clustering indicates that the neighbors are not well connected (Hanneman and

Riddle 2005). However, extremely high clustering might be due to all group members being connected to each other, i.e., little substructuring and differentiation, or to the focal females having few but tightly connected neighbors, i.e., high substructuring and differentiation. It is possible to determine which of the two scenarios causes high clustering by comparing clustering with density. Centralization is the difference in mean relationship strength between group members (Hanneman and Riddle 2005). A centralization value of 100 indicates a completely unequal network in which all the social interactions are focused on one group member. Lower values indicate that social interactions are distributed more evenly across group members. We calculated the centralization separately for incoming (focal is the recipient) and outgoing ties (focal is the actor) for the directional grooming network. We used UCINET 6 to calculate these social network variables (Borgatti *et al.* 2002).

We calculated four different demographic variables: female group size, kin composition of groups, proportion of females with infants, and group stability. Female group size, i.e., the number of subadult and adult females, remained constant throughout our study, and it varied from 5 to 11 between groups. Total group size (range: 18–31) correlates with female group size ($r_S=0.76$, $P<0.05$), and the results are similar if using total group size instead of female group size. We calculated the mean proportion of female kin for each group, i.e., the mean of all females' mean proportions. For each group, we calculated the proportion of females that had a young infant (0–3 mo old) at any time during the study period. We included only infants <3 mo because they have a contrasting coat color and receive higher rates of natal attraction and infant handling than older infants with a black-and-white coat (Bădescu *et al.* 2014). We determined group stability as the number of years with stable female group membership, i.e., without female emigration, death, or immigration. The value for RT group represents the minimum number of years with stable group membership because no females immigrated or emigrated since we started to study this group in 2004. We excluded BO group from the analysis pertaining to the stability in female group membership because we lacked longitudinal demographic data from this group.

Data Analysis

We tested if there was a significant difference in density between each group's network and a theoretical network with a density of 1, i.e., all actors are fully connected, using bootstrapping with 5000 simulations (Borgatti *et al.* 2002). We investigated if the social network variables (centralization, clustering, mean degree or density, grooming time, and strength) correlated with the demographic variables (female group size, kin composition, proportion of infants, and group stability). We used Kendall's rank correlations to investigate the relationship between group size and the social network variables. When investigating the correlation between female group size and connectedness, we used mean degree, i.e., the mean number of female social partners, instead of density, i.e., the number of social partners divided by the total number of available partners, because density takes group size into account. Because group size may affect network variables (James *et al.* 2009), we used partial Kendall's rank correlations controlling for female group size when investigating the relationship between the other demographic variables (kin composition, proportion of infants, and group stability) and the social network variables centralization, clustering, grooming time, and strength. To investigate the relationship between the demographic variables and density, we used simple Kendall's rank correlations because density is calculated based on the group size. We used the package ppcor (Kim 2012) in R version 3.1.0 (R Core Team 2014). We set the significance level to $P=0.05$ for all analyses. We did not correct the significance level for multiple testing because of very small sample sizes (Nakagawa 2004).

To investigate the limitations of having such a small sample size, we conducted a power analysis using the R package pwr (Champely 2012). Our sample size was sufficient to attain the recommended power at the 0.80 level (Colin 1992) to detect significant results ($P=0.05$) if the correlation was strong ($r=0.85$). In contrast, a sample size of 29 was required for statistical power to detect significant moderate correlations ($r=0.50$). Thus, we were able to determine whether demographic factors and social network metrics correlated strongly, while nonsignificant results for moderate correlations should be interpreted with caution.

Ethical Note

We gained permission from the Ghana Wildlife Division, the management committee at Boabeng-Fiema Monkey Sanctuary, and the University of Calgary's Animal Care Committee to conduct this study. The methods of this study also complied with the laws of Ghana.

Results

Most females were directly or indirectly connected to each other in the grooming network (Fig. 1). The only exception was one female in NP group that did not direct or receive grooming from any of the other females in her group. The grooming networks showed considerable variation in density (range: 0.36–0.74), strength (range: 1.53–6.83), clustering (range: 0.25–0.74), and centralization (range outgoing ties: 7.78–33.32; range incoming ties: 8.79–44.5).

In seven of eight groups, the observed density of the grooming network differed significantly from that of a fully connected theoretical network (z ranged from –2 to –7 and all $P<0.05$), indicating that grooming networks were differentiated. Females in the remaining group (RT) did not form a differentiated grooming network (z-value=–2, $P=0.09$).

The observed mean degree ranged from 1.6 to 4.7, and it was lower than the number of available grooming partners in all groups (Fig. 2). The mean degree increased with female group size (Fig. 2, Table III). Female group size did not correlate with any of the other social network variables (Table III).

The proportion of female kin did not correlate with any of the social network variables (Table III). In groups with a higher proportion of females with infants, females spent more time grooming (Fig. 3). The proportion of infants did not correlate with any of the other social network variables (Table III).

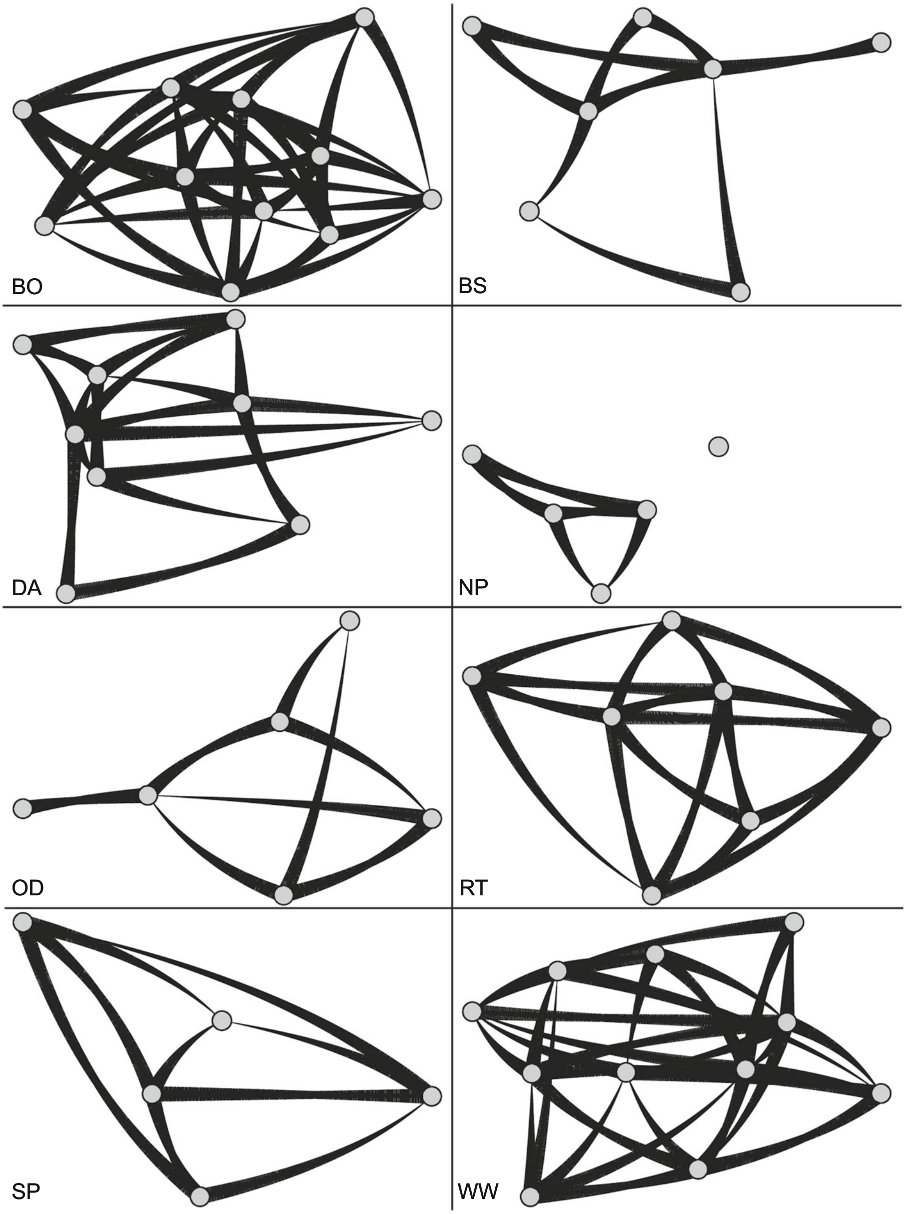
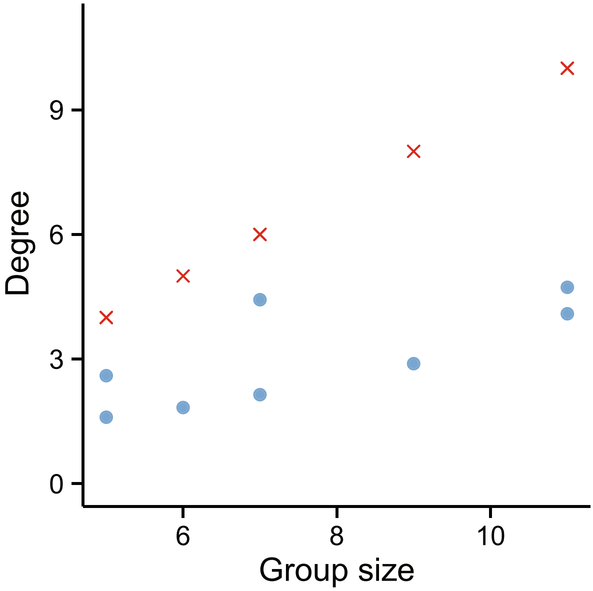


Fig. 1 Directed binary grooming networks of white-thighed colobus at Boabeng-Fiema (May 2008–June 2009). The thick end of the line represents the giver's end of the tie. Bidirectional relationships are indicated by lines with two thick ends.

Group stability was associated with higher centralization for incoming ties (Fig. 4), which indicates that some females receive more grooming than others in groups with a more stable female group composition. Centralization for outgoing ties did not correlate with group stability (Table III). Centralization for outgoing ties was highest in the

Fig. 2 Mean degree, i.e., mean number of social partners, of the grooming network in differently sized groups of white-thighed colobus at Boabeng-Fiema (May 2008–June 2009). The observed values are indicated by points and the maximum values by crosses.



groups with the most unstable group compositions, while it was similar for groups in which the composition had been stable for 1–4 yr (Fig. 4). This finding suggests that some females give more grooming than others after a recent change in the female group composition, while all females give similar amounts of grooming after the first year with a stable group composition. The period of stable group membership did not significantly correlate with any of the other social network variables (Table III).

Discussion

The majority of study groups formed differentiated grooming networks, although there was considerable intergroup variation in density, clustering, and centralization. The variation in centralization between our study groups is comparable to the variation reported in a cross-species comparison of the social networks of 40 primate species (Kasper and Voelkl 2009). Some of the intergroup variation in our study was associated with the proportion of infants and the stability in group membership.

The mean number of grooming partners was always lower than the number of available social partners, suggesting some limitation to the size of the grooming network. However, females had a higher number of grooming partners in larger groups, indicating that they do not limit their social interactions to a subset of social partners because of time constraints linked to large group sizes. This finding contrasts with the observed time constraints associated with large groups in the grooming network of other mammals (Kasper and Voelkl 2009; Lehmann *et al.* 2007; Madden *et al.* 2009; Sueur *et al.* 2011). For example, female chacma baboons (*Papio ursinus*) restrict their number of grooming partners to about seven and show noticeable time constraints in groups with eight or more females (Henzi *et al.* 1997). An unusually large chimpanzee community with 24 males also shows signs of time constraints because males distribute

Table III Simple and partial Kendall's τ-b correlation coefficients and P-values between social network metrics and the following demographic factors: female group size, the proportion of infants (infants), the proportion of female kin (kin), and the number of years with stable female group membership (stability) in the white-thighed colobus at Boabeng-Fiema (May 2008–June 2009)

Demographic factor	Social network metrics	τ	*P*
Group size	Centralization in	–0.04	0.90
N=8	Centralization out	–0.57	0.06
	Clustering	–0.04	0.90
	Mean degree	0.64	0.03
	Grooming time	0.34	0.25
	Strength	–0.26	0.38
Infants	Centralization in	0.21	0.50
N=8	Centralization out	–0.46	0.15
	Clustering	0.58	0.07
	Density	0.87	0.38
	Grooming time	0.62	0.05
	Strength	0.58	0.07
Kin	Centralization in	0.35	0.27
N=8	Centralization out	–0.22	0.49
	Clustering	0.14	0.67
	Density	0.13	0.90
	Grooming time	0.00	1.00
	Strength	0.07	0.83
Stability	Centralization in	0.75	0.03
N=7	Centralization out	–0.60	0.09
	Clustering	0.12	0.73
	Density	–0.16	0.87
	Grooming time	0.43	0.20
	Strength	0.39	0.26

their grooming less evenly and have only slightly more grooming partners than males in smaller communities (Watts 2000). The largest number of females in our study groups was 11, and it is possible that this number is below the threshold at which time constraints take effect in our study population. However, we deem this unlikely based on two lines of reasoning. First, females formed differentiated grooming networks in most groups. Second, other species of black-and-white colobus do not show an effect of time constraints either, although they reside in groups that are smaller than our study groups (Lehmann *et al.* 2007). The black-and-white colobus in Lehmann and colleagues' (2007) study appeared to form well-connected grooming networks in large groups by increasing the amount of time they spent grooming others. This was not the case in our study population because females in larger groups did not devote a larger proportion of their activity budget to grooming than females in smaller groups. Because females in our study population do not suffer from reduced mean relationship strengths in larger groups even though they do not devote more time to grooming, it is unclear how they can continue to add more grooming partners as group size increases. It may be that females make fine-scale adjustments to their distribution of grooming as group size increases, and an interesting venue for future research

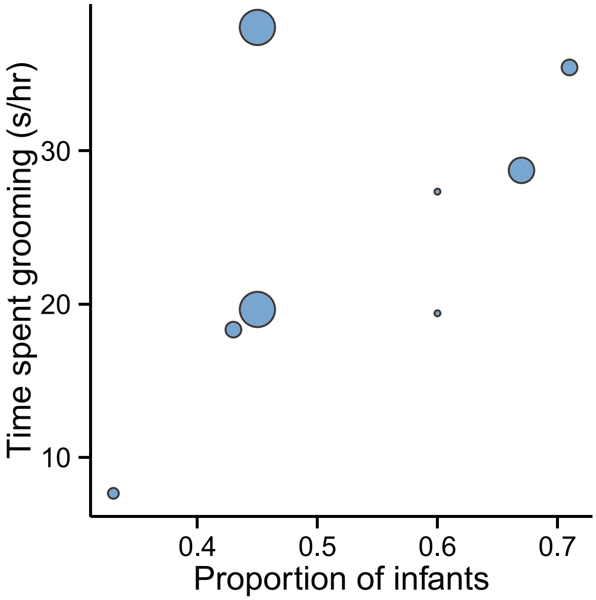


Fig. 3 Relationship between grooming time and the proportion of females with infants in groups of white-thighed colobus at Boabeng-Fiema (May 2008–June 2009). The size of the point indicates relative group size.

is to investigate intragroup grooming dynamics as group sizes change over time (Pinter-Wollman *et al.* 2014).

Our findings beg the question of why the colobus grooming networks do not conform to the pattern observed in many other mammals. We suspect that this disparity is due to a low proportion of time spent grooming that is typical for black-and-white colobus and may be linked to their folivorous diet (Fashing 2011; Oates 1977; Saj *et al.* 2007; Teichroeb *et al.* 2003; Teichroeb and Sicotte 2009). Difficult to digest, low-

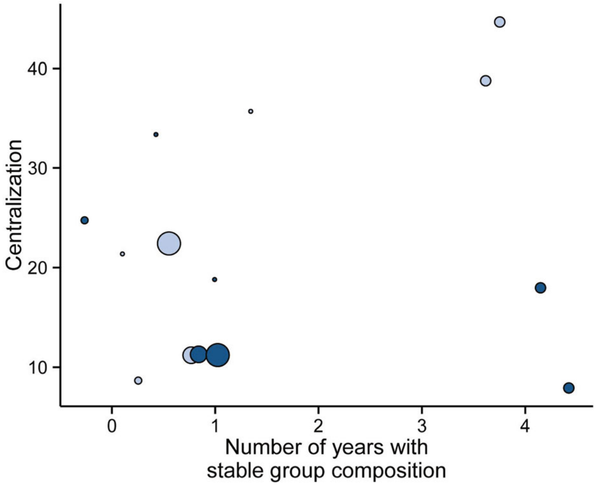


Fig. 4 Centralization for incoming (light points) and outgoing (dark points) ties in the grooming network of white-thighed colobus at Boabeng-Fiema (May 2008–June 2009), plotted against the number of years with stable female group membership. The size of the point indicates relative group size.

quality food items such as mature leaves require long retention times (Lambert 1998), and folivorous animals often adopt energy-minimizing behavior strategies (Dasilva 1992). The colobines at Boabeng-Fiema fit this pattern because they spend a high proportion of time resting and a small proportion of time socializing (Teichroeb *et al.* 2003). The time constraints linked to their diet and their digestive system may force these monkeys to restrict their grooming time and to focus their grooming effort on a small proportion of the available social partners even in groups that contain few females. Time constraints linked to their diet may lead to differentiated and relatively weak grooming networks even in small groups, whereas there is no additional effect of time constraints associated with large group sizes. This reasoning can explain why our study groups form sparser grooming networks (mean degree=0.47, range: 0.36–0.74) than many primate groups included in Kasper and Voelkl's (2009) study (mean degree=0.75, range: 0.49–0.93). Because our study species forage on mature leaves to a larger degree than most other African colobines (Fashing 2011), extreme time constraints linked to their diet may also explain why our study females cannot devote more time to grooming in larger groups, in contrast to other species of black-and-white colobus (Lehmann *et al.* 2007).

The kin composition of our study groups was not associated with differences in the grooming network, in contrast to macaques (McCowan *et al.* 2008; Sueur *et al.* 2011). It may be that kinship is less important in shaping the grooming networks of female colobines because they lack strict, nepotistic dominance hierarchies (Wikberg *et al.* 2013). Also in contrast to macaques, female colobines may disperse from their natal group, and not only kinship but also female residency status shapes female social relationships in our study population (Wikberg *et al.* 2014a, b). Groups that consist solely of long-term resident females form kin-biased grooming networks, whereas this is not the case in groups with recent female immigrants (Wikberg *et al.* 2014b). Thus, the effect of kinship on social relationships may be overridden by the effect of residency status in groups that contain recent female immigrants (Wikberg *et al.* 2014a, b). Currently, we do not have a sufficient number of study groups to investigate if the proportion of kin shapes group-level social network metrics differently in groups with and without immigrant females, but this is an interesting topic for future research.

Females devoted more time to grooming in groups with a larger proportion of females with infants, consistent with previous studies using group-level social network metrics (Gero *et al.* 2013; Wey *et al.* 2013). This finding is not surprising considering that young infants attract considerable interest from females other than their own mothers in our study population (Bădescu *et al.* 2014; Brent *et al.* 2008). It is possible that this increase in grooming time in groups with a high proportion of infants is due to females grooming mothers to gain access to their infants, which occurs in other primate species (Frank and Silk 2009; Fruteau *et al.* 2011; Gumert 2007; Henzi and Barrett 2002; Tiddi *et al.* 2010). Because infant handling occurs frequently and for extended time periods in our study species (Bădescu *et al.* 2014), female colobus may not only groom the mother, but also the current handler, to gain access to the infant. This could lead to an increase in grooming time, not only between mothers and infant handlers, but also between the infant handlers themselves. Alternatively, the increase in time spent grooming in groups with a high proportion of infants may be due to mothers increasing the time they devote to grooming. A preliminary analysis of yearly grooming interactions in our study population indicates that females with infants form more reciprocal grooming relationships with their social partners than females without infants (E. C. Wikberg *unpubl. data*). Thus, mothers may not only receive more grooming but also reciprocate the grooming, perhaps because it is important for them to form a strong social network. Mothers may associate with other females to facilitate infant socialization and to have access to babysitters while foraging, which may increase forage efficiency (Altmann 1980; Altmann and Samuels 1992; Forster and Cords 2005). Females also provide each other with coalitionary support against infanticidal males (Saj *et al.* 2007), and social bonds can ultimately increase infant survival by reducing harassment from both males and females (Cameron *et al.* 2009). Mothers may temporarily strengthen their social network during the time period when infant handling is most beneficial to them if handlers provide a valuable service such as babysitting (Bădescu *et al.* 2014; Gero *et al.* 2013). Alternatively, mothers may form long-lasting bonds to create a benign environment in which to rear their young (Cameron *et al.* 2009; Silk *et al.* 2003). Although further studies are required to investigate the ultimate fitness benefits of social bonds in our study species, the current study adds to a growing body of evidence showing that infants have a large impact on group-level social network metrics (Brent *et al.* 2013; Gero *et al.* 2013; Wey *et al.* 2013).

Females' interest in mothers and their newborn infants will likely make mothers important players in the grooming network (Gero *et al.* 2013). We expected this to lead to centralized grooming networks in groups with a low proportion of young infants, whereas no female would be a more important actor than another when most females have young infants. These predictions were not met, and the proportion of infants did not affect centralization. It may be that primates' attraction to others' newborn infants wears off as the infants age (Fruteau *et al.* 2011; Gumert 2007). In our study population, young infants with a natal coat color receive more natal attraction and infant handling than older infants with an adult coat color (Bădescu et al. 2014). As a result, a mother may not consistently occupy a central position in the grooming network over a full year in contrast to sperm whale mothers (Gero *et al.* 2013). According to preliminary findings (Brent *et al.* 2013), female colobines do not always groom mothers to gain access to their infants. This is the case when there are relatively few potential infant handlers in relation to infants in some primate populations (Frank and Silk 2009; Fruteau *et al.* 2011; Gumert 2007; Henzi and Barrett 2002; Tiddi *et al.* 2010), whereas the relative numbers do not affect the exchange of grooming for access to infants in other populations (Frank and Silk 2009; Tiddi *et al.* 2010). The number of available infant handlers and infants did not have a large impact on natal attraction or infant handling in our study species (Bădescu *et al.* 2014), but we have yet to investigate how these factors affect an exchange of grooming for access to infants. We also predicted that the strength and clustering of the grooming network would increase with the proportion of females with infants. We did not find support for these predictions, but it may be due to the limited power to detect significant, moderate correlations in such a small data set. Thus, further studies with larger sample sizes are required to investigate whether or not there is a relationship between the proportion of females with infants and the grooming network's strength and clustering.

Stability in female group composition correlated with centralization in the grooming network. Our results indicate that some females received more grooming than others in groups with stable group composition whereas some females tended to groom more than others in groups with recent changes in the group composition. This effect is not surprising considering that female residency status shapes dyadic social relationships (Guan *et al.* 2013a; Watts 1991; Wikberg *et al.* 2014a, b). In our study groups, females prefer to interact affiliatively with females of similar residency status (Wikberg *et al.* 2014b). When females of different residency status do interact, recent immigrant females groom long-term resident females more than vice versa (Wikberg *et al.* 2014b). In some populations with female dispersal, young and recent immigrants prefer to groom old, well-established females, perhaps to facilitate social integration (Guan *et al.* 2013b; Idani 1991; Wey and Blumstein 2010). In the two study groups with the most unstable group compositions, it was a natal female transitioning to adulthood that groomed the most, perhaps to reduce the risk of being evicted (Teichroeb *et al.* 2009). It is more difficult to explain why centralization for incoming ties increases with group stability. It is possible that high-ranking females become more popular grooming partners (Seyfarth 1977) once the social upheaval associated with the demographic changes has settled and females have established a stable dominance hierarchy. Indeed, alpha or beta females received the most grooming in groups with stable group compositions. This is a peculiar finding because changes in female group composition do not lead to unstable dominance hierarchies (Wikberg *et al.* 2013), and dominance rank does not affect dyadic social relationships in our study population (Wikberg *et al.* 2014b). Thus, we are currently unable to provide a sound explanation for the association between group stability and centralization for incoming grooming ties. We are hoping that future studies of the social network dynamics after changes in female group composition will shed light on this issue.

The intergroup variation in the colobines' grooming networks highlights the importance of studying several groups from the same population to gain a better understanding of its social structure (Madden *et al.* 2009). We are hoping that the findings from our and Madden and colleagues' (2009) study will encourage other researchers to collect data from multiple groups in the same study population. Because such data sets document the range of possible social network structures within a single population, they provide a baseline against which interpopulation differences in social networks should be evaluated. These data sets are therefore important additions to the empirical database required for developing and testing models of how demographic, ecological, and social factors shape the evolution of primate social relationships.

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