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Kinship and Similarity in Residency Status Structure Female Social Networks in Black-and-White Colobus Monkeys (Colobus vellerosus)

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KEY WORDS kin bias; kin selection; similarity hypothesis; partner's resource holding potential

ABSTRACT Kinship shapes female social networks in many primate populations in which females remain in their natal group to breed. In contrast, it is unclear to which extent kinship affects the social networks in populations with female dispersal. Female *Colobus vellerosus* show routine facultative dispersal (i.e., some females remain philopatric and others disperse). This dispersal pattern allowed us to evaluate if facultative dispersed females form social networks shaped by an attraction to kin, to social partners with a high resource holding potential, or to similar social partners in terms of maturational stage, dominance rank, and residency status. During 2008 and 2009, we collected behavioral data via focal and *ad libitum* sampling of 61 females residing in eight groups at Boabeng-Fiema, Ghana. We determined kinship based on partial pedigrees and genotypes at 17 short tandem repeat loci. Kinship influenced coalition and affiliation networks in three groups consisting of long-term resident females with access to a relatively high number of female kin. In contrast, similar residency status was more important than kinship in structuring the affiliation network in one of two groups that contained recent female immigrants. In populations with female dispersal, the occurrence of kin structured social networks may not only depend on the kin composition of groups but also on how long the female kin have resided together. We found no consistent support for females biasing affiliation toward partners with high resource holding potential, possibly due to low levels of contest competition and small inter-individual differences in resource holding potential. Am J Phys Anthropol 153:365–376, 2014. © 2013 Wiley Periodicals, Inc.

Kin bias in association patterns, affiliation, and cooperation characterize a wide range of primates and other animals (bats: Wilkinson, 1986; carnivores: Gompper et al., 1997; Wahaj et al., 2004; Hirsch et al., 2012; ungulates: Guilhem et al., 2000; Carter et al., 2013; birds: Griffin and West, 2003; primates reviewed in Kapsalis, 2004; elephants: Archie et al., 2006). This kin bias in social interactions is often explained within the framework of the kin selection theory, which states that animals can gain indirect fitness benefits from biasing affiliative and cooperative behaviors toward kin (Hamilton, 1964). The amount of indirect fitness benefits that the actor will accrue depends on how costly the behavior is to the actor, how beneficial the behavior is to the recipient, and the degree of relatedness between the actor and the recipient (Hamilton, 1964). Furthermore, biasing affiliative and cooperative behaviors toward kin can also lead to direct fitness benefits because kin may be the most reliable and compatible social partners (Colvin, 1983; Chapais, 2001). Due to these potential direct and indirect fitness benefits, it is not surprising that kinship has a profound effect on animal social relationships. In this article, we will use the term "kinship hypothesis" to refer to the predicted kin bias in behaviors without implications as to whether the benefits derived from this kin bias are direct, indirect, or both.

Most evidence in support of the kinship hypothesis comes from populations in which the majority of females are philopatric and have the opportunity to form long-lasting social bonds with female kin in their natal group (e.g., Kapsalis, 2004). How kinship affects social interactions in predominantly female dispersed populations is less clear (Kapsalis, 2004), although familiar animals sometimes disperse to the same group (Korstjens and Schippers, 2003; Sterck et al., 2005; Bradley et al., 2007; Teichroeb et al., 2009; Wikberg et al., 2012). Despite showing mainly female dispersal, female *Gorilla beringei beringei* (mountain gorilla) bias affiliation toward female kin whenever they reside together (Harcourt, 1979;

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Watts, 1994), whereas female *Pan paniscus* (bonobo) do not form stronger affiliative bonds with maternal kin than non-kin (Hashimoto et al., 1996). The pattern in female *Pan troglodytes* (chimpanzee) remains unclear (Langergraber et al., 2009). It is possible that kinship has a relatively small impact on the social dynamics in populations with female dispersal because female kin rarely reside together (Kapsalis, 2004) or because strong bonds with female kin leads to few fitness benefits in this context (Sterck et al., 1997).

In populations with female dispersal, it is possible that factors other than kinship influence patterns of social interactions. The similarity hypothesis proposes that animals prefer to interact affiliative with social partners that share similar needs and resource holding potentials, which make them more compatible social partners (Colvin, 1983; de Waal and Luttrell, 1986). Females should therefore prefer to interact with females that are similar not only in kinship, but also in age, dominance rank, and residency status (Seyfarth, 1977; Harcourt, 1979; Penzhorn, 1984; Watts, 1994; Kapsalis and Berman, 1996; Perry, 1996; Mitani and Amsler, 2003; Silk et al., 2006; Heitor and Vicente, 2010; Wey and Blumstein, 2010; McFarland and Majolo, 2011). Females may also bias affiliative behaviors toward group members with a high resource holding potential if doing so gives them increased access to valuable commodities such as coalitionary support or increased access to food (Seyfarth, 1977; Noe and Hammerstein, 1995; Henzi and Barrett, 1999). In species with strict dominance hierarchies such as *Cebus capucinus* (white-faced capuchin), *Macaca mulatta* (rhesus macaque), and *Crocuta crocuta* (spotted hyena), females sometimes bias affiliation toward high-ranking females that have the ability to monopolize access to food (Kapsalis and Berman, 1996; Perry, 1996; Smith et al., 2007). In *Loxodonta africana* (African elephant), young females are attracted to old, more knowledgeable matriarchs that may provide protection from predators and increased access to food (McComb et al., 2001; Gobush and Wasser, 2009). In species with occasional female dispersal such as *Marmota flaviventris* (yellow-bellied marmot), immature females bias affiliation toward long-term resident adult females that may have a higher resource holding potential because they are well-established in the group's social network (Wey and Blumstein, 2010). Similarly, recent immigrant female *P. paniscus* often form strong bonds with a well-established long-term resident female, which may facilitate social integration in their new group (Idani, 1991). Thus, what constitutes partners with high resource holding potential may vary between species, and the high resource holding potential hypothesis can explain why animals prefer to interact with high-ranking, old, and/or long-term residents in the above mentioned species.

Many studies have described patterns of social interactions in predominantly female philopatric species in which females frequently engage in social interactions and form strict dominance hierarchies (e.g., cercopithecines: reviewed in Kapsalis, 2004; *C. crocuta*: Holekamp et al., 2012). These species represent only a small percentage of group living mammals, and species from more diverse taxa with different social structures should be studied to increase our understanding of what factors shape female social networks. We focus here on a species with a different social structure, *Colobus vellerosus* (white-thighed colobus or ursine colobus). Females in our study population form individualistic dominance hierarchies of intermediate strength (Wikberg et al., 2013), show facultative dispersal (Teichroeb et al., 2009; Wikberg et al., 2012), and have varying access to female kin (Wikberg et al., 2012). These traits likely lead to a situation where dominance rank, kinship, and residency status do not always correspond with each other, in contrast to the common pattern in cercopithecines and hyenas. First, we investigate if social networks are structured by kinship. Following the kinship hypothesis, we expect kinship to have a negative impact on the aggression network and a positive effect on the proximity, grooming, and coalition networks (Hamilton, 1964; Colvin, 1983; Chapais, 2001; but see Kurland, 1977). Second, we examine if social networks are structured by female maturational stage (e.g., adult versus subadult), dominance rank, and residency status. If *C. vellerosus* conform to the similarity hypothesis, similarity in maturational stage, dominance rank, and residency status will have a negative effect on the aggression network and a positive effect on the proximity, grooming, and coalition networks (de Waal and Luttrell, 1986). If *C. vellerosus* instead are attracted to social partners with a high resource holding potential, we expect females to direct more affiliation, coalitionary support, and less aggression to female partners that are higher ranking, older (i.e., adult rather than subadult), and long-term residents (Seyfarth, 1977; Watts, 1991; Kapsalis and Berman, 1996; Perry, 1996; Henzi and Barrett, 1999; McComb et al., 2001; Gobush and Wasser, 2009; Wey and Blumstein, 2010).

METHODS

This study was conducted at Boabeng-Fiema Monkey Sanctuary (BFMS), which is a 1.92 km^2 dry semi-deciduous forest (Hall and Swaine, 1981) located in central Ghana (7°43'N and 1°42'W). At BFMS, *C. vellerosus* reside in groups consisting of 9–38 animals (Wong and Sicotte, 2006). We focused our study on eight social groups that contained 5–11 adult ($\geq$5 years) and subadult females (3–4 years) (Fig. 1), 1–8 adult ($\geq$7 years) and subadult males (3–6 years), and 2–10 juveniles and infants (<3 years).

We collected data between May 2008 and April 2009 with the exception of BO group from which we collected data between October 2008 and June 2009. We recorded social behaviors *ad libitum* and during 10-min continuous focal samples (Altmann, 1974) of 61 adult and subadult females. During the focal samples, we also took point samples (Altmann, 1974) every 2.5 min in which we recorded the state behavior of the focal animal and the identity of the individuals that were within one meter of the focal animal. We have 2159 contact hours (BO: 185; BS: 292; DA: 314; NP: 162; OD: 173; RT: 333; SP: 284; WW: 416) and 1101 focal hours with a mean of 16 hours per focal animal (BO: 10; BS: 17; DA: 17; NP: 17; OD: 17; RT: 19; SP: 18; WW: 18). Despite lower sampling effort in BO group, we recorded a similar number of interactions in BO group as in the groups with higher sampling effort (see Results).

Our team started to observe the different study groups between 2000 and 2008 (2000: BS and WW; 2004: DA, NP, OD, and RT; 2006: SP; and 2008: BO). However, individual recognition has increased from recognizing only a few to all group members in 2004 (BS and RT), 2006 (DA, NP, OD, SP, and WW) or 2008 (BO).

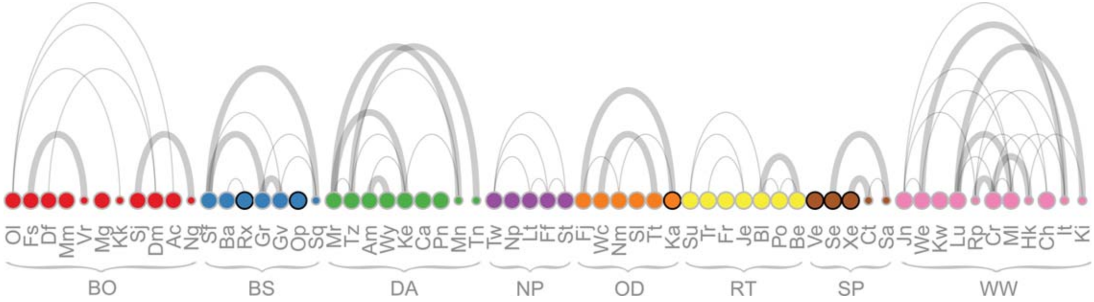

Fig. 1. Subadult and adult female group compositions. Colors and two letter codes at the bottom of the figure indicate different groups. Small circles indicate subadult females and large circles adult females. Black borders represent recent immigrant females. Females are ordered within groups according to their dominance rank with the highest ranking female on the left. Thick lines connect mother–daughter dyads and thin lines connect other kin (i.e., full-siblings, half-siblings, and grandmother-granddaughter dyads).

Demographic data were collected by ECW and members of PS's research team at least once a month when observers were present at the field site (for data collection periods see Teichroeb et al., 2011). This allowed us to determine partial pedigree information of individuals in the study groups and to detect cases of female immigration. Two females immigrated into BS group 4 years before the start of this study (Teichroeb et al., 2009) and one female immigrated into OD group in the year before this study (ECW unpublished data) (Fig. 1). These females were classified as recent immigrant females while all other females in BS and OD group were classified as long-term residents. Note that female Ka immigrated to the group where her mother resided. We suspect that Ka is one of the females that emigrated from OD in 2006 (Teichroeb et al., 2009), but the observer could no longer reliably recognize this female when she reentered the group in 2008 because she lacks distinct physical traits. It is also possible that Ka's mother is an immigrant female who transferred to OD group before 2006, which was the first year that all adult females were individually recognized. We did not use residency status as a predictor variable when analyzing the social networks in the other groups because female residency status was unknown (BO), all females had the same residency status (DA, NP, RT, and WW), or female residency status co-varied with female maturational stage (SP) (Fig. 1). The three adult females in SP group originated in different groups and established a new group because they failed to immigrate into already existing groups.

We also collected at least two fecal samples from each study animal for subsequent DNA extraction, genotyping, and analysis of 17 short tandem repeat loci to infer kinship. For details regarding the laboratory methods and protocol see Wikberg et al. (2012). We used partial pedigree information and genetic data to determine kinship (Langergraber et al., 2009; Wikberg, 2012) using the software CERVUS (Marshall et al., 1998; Kalinowski et al., 2007) and COANCESTRY (Wang, 2011) (for details see Supporting Information). The percentage of kin dyads ranged from 11% in BO group to 50% in NP group (BO: 6/55; BS: 7/21; DA: 9/36; NP: 5/10; OD: 4/15; RT: 6/21; SP: 3/10; WW: 18/55; see Fig. 1).

We classified females as adult or subadult based on their body size and the presence of elongated nipples. Maturational stage was not included as a predictor variable when analyzing the social networks in NP, OD, and RT group because these groups only contained adult females. We used submissive interactions (e.g., avoid, displace, flee, grimace, present, and snuffling vocalizations) collected *ad libitum* and during focal samples to determine the females' dominance ranks (Wikberg et al., 2013). The majority of dyads (96%) formed unidirectional submissive relationships, and we did not detect any rank changes during our study period (Wikberg et al., 2013). We used Elo-ratings to compute females' probabilistic dominance ranks (Neumann et al., 2011), and we standardized each female's rank by dividing it by the maximum rank in each group. As a result, the alpha female in each group had a rank of 1 and the subordinate females' ranks ranged between 0 and 1. We calculated the differences in standardized ranks between pairs of females by subtracting the standardized rank of the focal female from the standardized rank of the female partner.

Data analyses

We created four types of interaction matrices that we used as dependent variables in our models. We used the grooming data collected continuously during the focal samples to calculate the percentage of time spent giving grooming [e.g., (duration of grooming (s) that individual A directed to individual B)/(dyadic focal time (s) for A and B) × 100]. Because grooming is a relatively rare behavior in *C. vellerosus*, we also used the time spent in close proximity as an indicator of affiliative relationships. Proximity scores were calculated as the percentage of point samples that females were within 1 m of each other [(number of point samples that A and B were within one meter)/(number of point samples collected from animal A and B) × 100]. We excluded all point samples during which the focal was engaged in aggressive behaviors. We used the focal data and the *ad libitum* data to code for the presence and absence of giving aggression (e.g., bite, hit, lunge at, snap at, swipe at, and wrestle) and coalitionary support to other females. We constructed directed weighted matrices for grooming; undirected weighted matrices for proximity; and directed binary matrices for aggression and coalitions. Because coalitionary support was rare and only occurred more than once in two study groups, we only analyzed the coalitionary matrices for these two study groups.

We created different types of independent matrices to examine the following three hypotheses. To investigate the kinship hypothesis (Tables 1 and 2), we created a matrix in which females were categorized as non-kin,

TABLE 1. How kinship and partner similarity in maturational stage, dominance rank, and residency status affect the social networks (proximity, grooming, aggression, and coalitions)

		Model		Kinship		Maturational stage		Dominance rank		Residency status	
Behavior	Group	R^2	P^a	Coefficient	P^a	Coefficient	P^a	Coefficient	P^a	Coefficient	P^a
Proximity	BO	0.029	0.133	0.017	0.465	0.005	0.456	0.970	0.139	–	–
	BS	0.291	**0.012**	−0.698	**0.043**	1.332	0.138	1.599	0.236	1.725	**0.027**
	DA	0.156	**0.025**	1.261	**0.045**	0.190	0.460	−2.889	0.214	–	–
	NP	0.700	**0.014**	3.008	**0.019**	–	–	−3.795	0.131	–	–
	OD	0.153	0.060	−0.365	0.291	–	–	5.168	0.159	0.816	0.062
	RT	0.034	0.244	−0.164	0.350	–	–	1.048	0.240	–	–
	SP	0.236	**0.008**	−0.136	0.333	0.632	0.167	−0.299	0.171	–	–
	WW	0.115	**0.007**	0.338	**0.014**	0.062	0.386	0.555	0.243	–	–
Groom	BO	0.140	**0.004**	0.066	0.088	−0.155	**0.025**	−0.294	0.087	–	–
	BS	0.068	0.054	−0.004	0.443	0.034	0.314	−0.080	0.287	0.013	0.456
	DA	0.323	**0.003**	0.338	**0.016**	−0.187	0.240	1.595	**0.012**	–	–
	NP	0.237	0.060	0.300	**0.038**	–	–	0.389	0.304	–	–
	OD	0.115	0.064	0.059	0.150	–	–	−0.006	0.520	0.074	0.051
	RT	0.052	0.158	−0.019	0.357	–	–	−0.160	0.264	–	–
	SP	0.098	**0.032**	−0.040	0.140	−0.056	0.356	0.148	0.349	–	–
	WW	0.119	**0.006**	0.038	**0.008**	−0.008	0.333	0.117	0.067	–	–
Aggression	BO	0.062	**0.008**	0.017	0.415	−0.120	0.080	−0.406	0.082	–	–
	BS	0.202	**0.012**	−0.017	0.438	0.152	0.170	−1.300	**0.007**	−0.057	0.332
	DA	0.116	**0.004**	0.115	0.097	−0.358	**0.041**	1.250	**0.008**	–	–
	NP	0.174	**0.024**	0.120	0.168	–	–	0.839	0.065	–	–
	OD	0.073	0.057	0.180	0.121	–	–	0.779	0.207	−0.061	0.297
	RT	0.006	0.329	0.032	0.365	–	–	−0.034	0.466	–	–
	SP	0.250	**0.014**	−0.033	0.332	−0.188	0.242	−1.100	0.079	–	–
	WW	0.037	**0.036**	−0.046	0.247	0.105	0.093	−0.189	0.256	–	–
Coalition	NP	0.348	**0.049**	0.507	0.079	–	–	0.300	0.350	–	–
	WW	0.065	**0.006**	0.066	**0.024**	0.043	0.147	−0.201	0.149	–	–

[a] Significant *P*-values are indicated in bold and significant results that support the kinship hypothesis or the similarity hypothesis are boxed.

other kin (i.e., half-siblings, full-siblings, and grandparent-grandoffspring), and mother–daughter dyads. To investigate the similarity hypothesis (Table 1), we created matrices in which we coded the following: (a) the absolute difference in standardized ranks between the partner and the focal female (i.e., the difference in standardized ranks without indicating if the partner is higher or lower ranking); (b) whether or not females belonged to the same maturational stage (i.e., adult or subadult); and (c) whether or not females had the same residency status (i.e., long-term residents or recent immigrants). To investigate the resource holding potential hypothesis (Table 2), we used matrices in which we indicated the following: (a) the partner's relative dominance rank (i.e., the relative difference in standardized ranks between the partner and the focal female, which indicates if the partner is higher or lower ranking); (b) relative maturational stage (i.e., if the partner belonged to a younger, the same, or an older maturational stage); and (c) residency status (i.e., if the partner had a residency status with a shorter, the same, or a longer group tenure).

The similarity and resource holding potential hypotheses are mutually exclusive while the kinship hypothesis is not. Therefore, we created one model that investigated the effect of kinship and partner similarity (Table 1) and one model that examined the effect of kinship and partners' resource holding potential (Table 2) on the grooming network, the aggression network, and the coalition network (e.g., the interaction matrices described above). Because the proximity network was undirected, we could not investigate if the social partner with lower or higher resource holding potential was responsible for maintaining proximity. Therefore, we only evaluated the effect of kinship and partner similarity on the proximity network.

We evaluated the significance of our models using double-decker semipartialing multiple quadratic assignment procedures in UCINET (Borgatti et al., 2002). This procedure regresses a dependent matrix (proximity, grooming, aggression, and coalitions) against multiple independent matrices (kinship, maturational stage, dominance rank, and residency status). This method is particularly well suited for analyzing social networks because it can control for autocorrelation in the data (Hanneman and Riddle, 2005). We used 10,000 permutations during which rows and columns were randomly reshuffled, and R-square and regression coefficients were calculated after each permutation. These permuted values were used to create a sampling distribution, against which the observed values were compared to evaluate whether or not they were significantly different from random. We set the significance level to $P < 0.05$ for all analyses, and we did not correct the critical value for multiple testing, following Nakagawa's (2004) recommendation for analyses of small sample sizes. All figures were created using the packages arcdiagram (Sanchez, 2013) and ggplot2 (Wickham, 2009) in R version 2.13.2 (R Development Core Team, 2011).

RESULTS

Kinship and similarity hypotheses

Females were in proximity with each other in 0–14% of the point samples (mean: 3%). All dyads except one were in proximity during at least one point sample (BO:

TABLE 2. How kinship and an attraction towards partners with high resource holding potential (with respect to maturational stage, dominance rank, and residency status) shape the social networks (grooming, aggression, and coalitions).

		Model		Kinship		Maturational stage		Dominance rank		Residency status	
Behavior	Group	R^2	P^a	Coefficient	P^a	Coefficient	P^a	Coefficient	P^a	Coefficient	P^a
Groom	BO	0.162	**0.002**	0.088	0.064	−0.073	0.064	−0.220	**0.021**	–	–
	BS	0.064	**0.037**	−0.012	0.370	0.010	0.382	−0.018	0.427	−0.042	0.182
	DA	0.206	**0.012**	0.302	**0.023**	0.112	0.144	0.000	0.548	–	–
	NP	0.242	**0.030**	0.265	0.080	–	–	−0.124	0.355	–	–
	OD	0.144	0.059	0.047	0.177	–	–	−0.234	0.097	0.114	0.054
	RT	0.009	0.360	−0.015	0.393	–	–	−0.038	0.380	–	–
	SP	0.243	**0.014**	−0.007	0.500	0.010	0.505	0.237	0.258	–	–
	WW	0.110	**0.004**	0.040	**0.006**	0.024	0.103	0.006	0.441	–	–
Aggression	BO	0.143	**0.001**	0.026	0.348	0.015	0.350	−0.554	**0.001**	–	–
	BS	0.044	**0.038**	0.011	0.442	0.058	0.213	−0.303	**0.034**	−0.092	0.248
	DA	0.083	**0.007**	0.086	0.164	0.048	0.370	−0.410	0.099	–	–
	NP	0.028	0.235	0.115	0.256	–	–	−0.045	0.424	–	–
	OD	0.136	**0.033**	0.052	0.371	–	–	−0.933	**0.041**	−0.004	0.492
	RT	0.101	**0.050**	0.035	0.363	–	–	−0.460	0.080	–	–
	SP	0.088	0.094	−0.077	0.207	0.186	0.341	−0.622	0.212	–	–
	WW	0.099	**0.001**	−0.035	0.292	−0.055	0.182	−0.330	**0.011**	–	–
Coalition	NP	0.399	**0.036**	0.541	0.062	–	–	0.374	0.104	–	–
	WW	0.079	**0.002**	0.076	**0.014**	0.039	0.090	0.023	0.390	–	–

[a] Significant *P*-values are indicated in bold and significant results that support the kinship hypothesis or the resource holding potential hypothesis are boxed.

54/55, BS: 21/21, DA: 36/36, NP: 10/10, OD: 15/15, RT: 21/21, SP: 10/10, WW: 55/55). The proximity model was significant in five of eight groups, and it explained 12–70% of the observed variation (Table 1). Although the R-square in remaining groups suggests that between 3% and 15% of the observed variation was explained by the model, these results may not differ from random because the model was not significant. In NP group, all females that co-resided with female kin formed the strongest proximity relationship with a female kin (Fig. 2). Female Np, who lacked kin in her group, formed relatively strong proximity relationships with two non-kin (Fig. 2). Kinship had a significant, positive effect on the proximity network in NP group and two large groups (DA and WW whose networks are not depicted), which supports the kinship hypothesis. Two of the study groups contained long-term resident and recent immigrant adult females (BS and OD). The majority of females in BS and OD group had access to both kin and non-kin (11/13 females) and to social partners of both similar and dissimilar residency status (12/13 females). Only four of these females spent most of their time in proximity with a female kin while ten spent most of their time in proximity with a female of similar residency status (Figs. 3 and 4). As a matter of fact, kinship had a significant negative impact on the proximity network in BS group, which contrasts to the predictions derived from the kinship hypothesis. Although similarity in residency status had a larger impact than kinship on the proximity network in both groups, it was only in BS group that the effect of residency status was significant (Table 1). Thus, we only found support for an attraction to partners with similar residency status in one of the two groups. Similar maturational stage and dominance rank did not structure the proximity network in contrast to the predictions generated by the similarity hypothesis.

The percentage of time females spent grooming each available female ranged from 0% to 3% with a mean of 0.1% across the eight study groups. Females directed grooming toward 69% of the available partners (BO: 63%, BS: 67%, DA: 69%, NP: 65%, OD: 57%, RT: 88%, SP: 80%, WW: 62%). The grooming model was significant in four of the eight groups, in which it explained 10% to 32% of the observed variation (Table 1). All females in NP group who resided with female kin groomed kin the most (Fig. 2), and kinship had a large positive effect on the grooming network. Kinship also had a large positive effect on the grooming network in DA group and a small positive effect on the grooming network in WW group. Thus, the grooming networks in these three groups provided support for the kinship hypothesis. In BS and OD group, two of the three recent immigrant females (Op and Ka) only received grooming from one long-term resident female (Figs. 3 and 4). The third recent immigrant female (Rx) was well integrated in the grooming network, and she formed bidirectional grooming relationships with the majority of the long-term resident females (Fig. 3). Even though 11 of 12 females with access to social partners of both similar and dissimilar residency status groomed a female with similar residency status the most (Figs. 3 and 4), having a similar residency status did not have a significant effect on the grooming network in BS and OD group. This contrasts with the predictions of the similarity hypothesis. Similarity in dominance rank positively structured the grooming network in DA group, which supports the similarity hypothesis. Belonging to the same maturational stage had a negative impact on the grooming network in BO group, which is in the opposite direction than predicted by the similarity hypothesis. Six of eight adult females in BO group directed most of their grooming to a subadult female while all subadult females directed most of their grooming to an adult female. The majority of subadult–adult dyads with strong grooming relationships were not close kin, however, and only one mother–daughter dyad formed a relatively strong grooming relationship in BO group.

Females directed aggression toward 0–75% of the other females in their group with a mean of 22% (BO: 16%, BS: 14%, DA: 26%, NP: 15%, OD: 27%, RT: 33%,

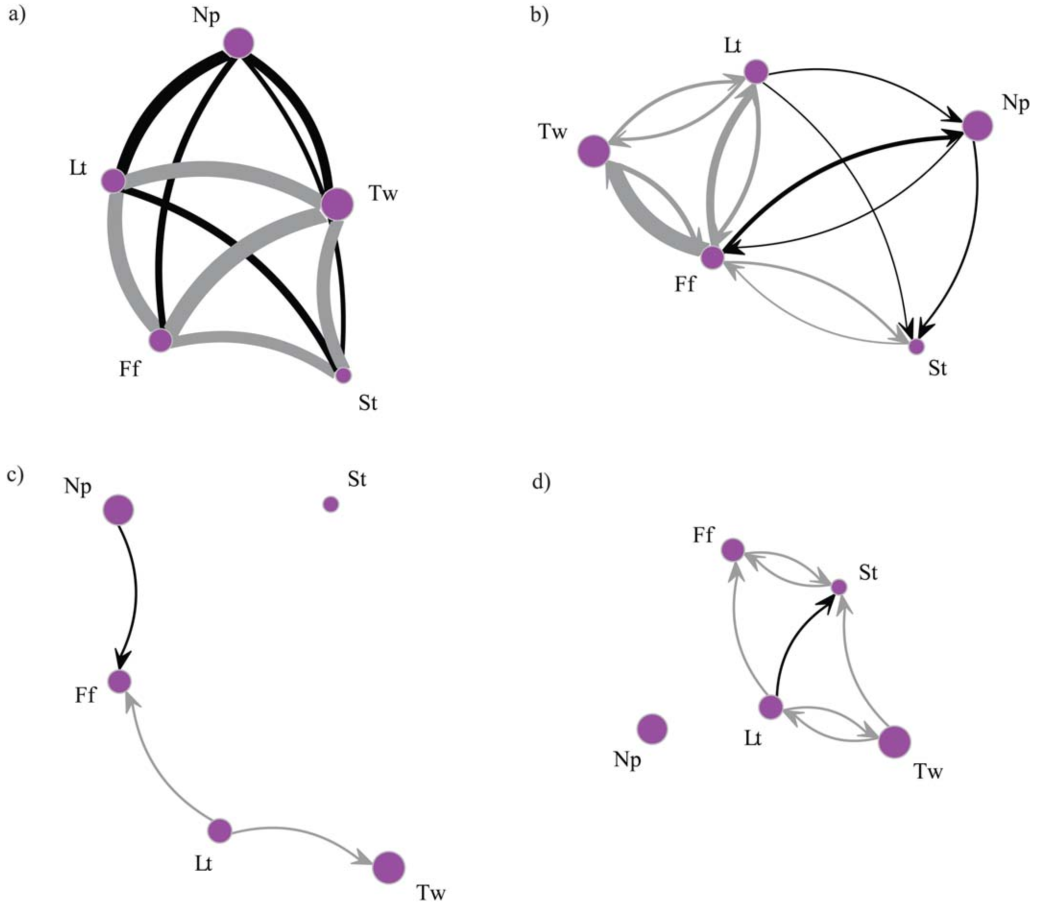

Fig. 2. NP group's undirected, weighted proximity network (a); directed, weighted grooming network (b); binary, directed aggression network (c); and binary, directed coalition network (d). Each female is represented by a circle, and larger circles indicate higher-ranking females. For ease of visualizing the ties, females are not always positioned in the same relative location. Interactions between kin and non-kin are indicated by grey and black lines, respectively. For the directed networks, the direction of the interaction is represented by arrows leading from the actor to the recipient. For weighted networks, the thickness of the lines indicates how often the interaction occurred. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

SP: 30%, WW: 19%). The aggression model explained 4% to 25% of the observed variation in the six groups with significant models (Table 1). In support of the predictions of the similarity hypothesis, we found a negative correlation between similarity in maturational stage and the aggression network in DA group. Subadult and adult females were more aggressive to each other than to females belonging to the same maturational stage. Dominance rank structured the aggression network in BS and DA group, albeit in different directions. Females with similar dominance ranks were more aggressive toward each other in DA group and less aggressive toward each other in BS group (Fig. 3). This provides ambiguous support for an attraction to partners with similar dominance ranks. The aggression networks were not structured by kinship or similarity in residency status (Figs. 2–4) in contrast to our predictions generated by the kinship hypothesis and the similarity hypothesis.

We only observed coalitionary support in 14 female–female dyads (BS: 1; NP: 7; WW: 6). Females gave coalitionary support to a mean of 5% of the available partners (BO: 0%, BS: 2%, DA: 0%, NP: 35%, OD: 0%, RT: 0%, SP: 0%, WW: 6%). The coalitions were always directed against unrelated co-resident males or extra-group males and females that were attacking resident females. Female kin received coalitionary support in 13 cases. In the remaining case, a female in NP group supported another female that was classified as non-kin in our study (Fig. 2). However, the R-value for these females ($R = 0.25$) was just below the threshold we used for defining kin ($R = 0.28$). The only female in NP group that never gave or received coalitionary support did not reside with any female kin (Fig. 2). In WW group, five of eleven females were not involved in coalitions although four of them had access to female kin. The coalition model was significant, and it explained 35% of the variation in coalitions in NP group and 7% of the variation in WW group (Table 1). Kinship predicted the coalition network in WW group but not in NP group. Thus, one of two groups provided support for the kinship hypothesis. Similarity in maturational stage and dominance rank did not structure the coalition network in contrast to the predictions of the similarity hypothesis.

Kinship and resource holding potential hypotheses

The grooming model was significant in six of eight groups, and it explained between 6% and 24% of the

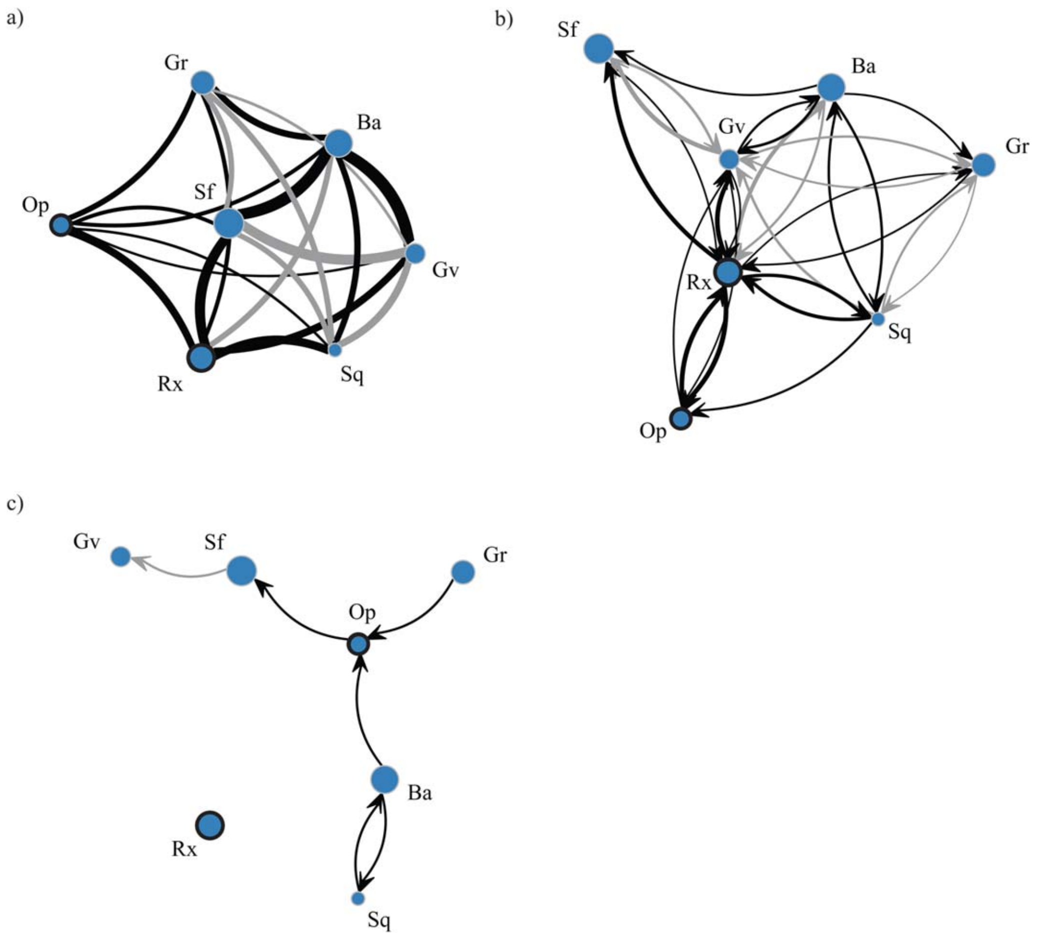

Fig. 3. BS group's undirected, weighted proximity network (a); directed, weighted grooming network (b); and binary, directed aggression network (c). Circles with black borders indicate recent immigrant females. For explanation of symbols and lines, see Fig. 2. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

variation (Table 2). In support of the kinship hypothesis, kinship had a large positive effect on the grooming network in DA group and a small positive effect on the grooming network in WW group. The partner's dominance rank structured the grooming network in BO group. However, females in BO group groomed lower ranking females more, which is in the opposite direction than predicted if females were attracted to partners with high resource holding potential. The partner's maturational stage and residency status did not structure the grooming network in contrast to the predictions generated by the resource holding potential hypothesis.

The aggression model was significant in six groups, and it explained 4–14% of the variation (Table 2). The partner's dominance rank structured the aggression network in four groups and the pattern was the same in all groups—females directed less aggression toward higher ranking partners. The aggression network was not structured by maturational stage or residency status, which differs from our predictions generated by the resource holding potential hypothesis. In contrast to the predictions from the kinship hypothesis, kinship did not affect the aggression network.

The coalition model was significant and explained 40% and 8% of the observed variation in NP and WW group, respectively (Table 2). Kinship had a significant but small positive effect on the coalition network in WW group while the effect of kinship was not significant in NP group. This provides partial support for the kinship hypothesis. The partner's maturational stage and dominance rank did not affect the coalition network in contrast to our predictions generated by the resource holding potential hypothesis.

DISCUSSION

Kinship, residency status, dominance rank, and maturational stage affected at least some types of female social networks in the eight study groups of black-and-white colobus. However, the effect of these factors varied between groups, most likely due to differences in the groups' demographic compositions. These findings suggest that females adopt different strategies for choosing their social partners depending on the type of behavior and their current social environment. The affiliation and coalition networks provided some support for the kinship hypothesis and the similarity hypothesis in terms of residency status, whereas the high resource holding potential hypothesis was not supported.

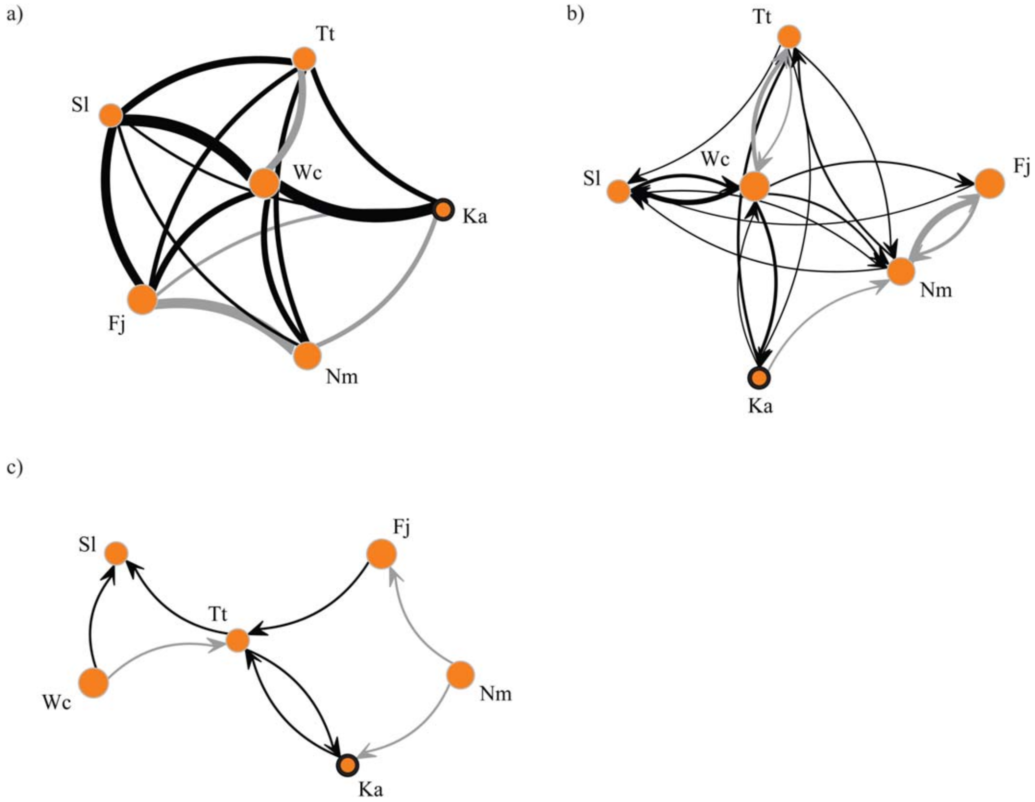

Fig. 4. OD group's undirected, weighted proximity network (a); directed, weighted grooming network (b); and binary, directed aggression network (c). For explanation of symbols and lines, see Fig. 2 and Fig. 3. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Kinship hypothesis

The importance of kinship in structuring networks differed among behaviors, which is expected by the kin selection theory if the cost-benefit ratio of behaviors differs. Behaviors that are more costly should theoretically be biased toward kin to a higher degree than less costly behaviors (Hamilton, 1964; Chapais, 2001). Certainly, the most costly behavior that we investigated was coalitionary support because it was often directed against resident or extra-group males (males are larger than females in this species: Saj and Sicotte, 2013). Coalitionary support was rare, and it only occurred relatively frequently in the two groups with the highest mean number of female kin. The support was almost always given to close kin, which is similar to the results reported in several other studies (e.g., Chapais et al., 1997; Widdig et al., 2006; Perry et al., 2008; Smith et al., 2010; but see Hirsch et al., 2012).

Kinship did not structure the aggression network in any of the groups in contrast to our expectations based on the kinship hypothesis. Despite potential indirect fitness benefits of directing aggression toward non-kin rather than kin, many studies have found the opposite pattern or no connection at all between aggression and kinship (*Macaca fuscata*: Kurland, 1977; *M. mulatta*: Bernstein et al., 1993; Widdig et al., 2002; *Passer domesticus*: Toth et al., 2009a; *Nasua nasua*: Hirsch et al., 2012; *Suricata suricatta*: Madden et al., 2012; *Procyon lotor*: Hauver et al., 2013). These findings suggest that the kin selection theory has limited power in predicting the pattern of aggression. Alternatively, the lack of kin bias in our study may be linked to female–female within-group aggression being rare, short-lasting, and never leading to visible wounds. Therefore, aggression may have a limited impact on the reproductive success of the interactants in which case kin bias should be weak or absent according to the kin selection theory. Widdig et al. (2002) similarly suggested that biasing aggression against kin may lead to relatively small or no fitness benefits in comparison to kin bias in affiliation. If this is indeed that case, it is not surprising that positive kin bias in grooming, proximity, and coalitions are more common than negative kin bias in aggression in many animal taxa (e.g., Kurland, 1977; Widdig et al., 2002; Toth et al., 2009a; Toth et al., 2009b; Hirsch et al., 2012).

Kinship shaped the proximity and grooming networks in some but not all groups. Similar variation in kin bias has previously been observed in capuchins and macaques, and this variation was linked to demographic factors (Berman et al., 2008; Perry et al., 2008; Berman and Thierry, 2010; Bergstrom and Fedigan, 2013). Female *C. capucinus* only showed kin bias in grooming during years when they had access to both close kin and non-kin in their group (Perry et al., 2008). Therefore, the authors suggested that the level of variation in kinship between a female's potential social partners will determine whether or not kinship structures social interactions. The majority of our study animals resided with several non-kin and at least one female kin (Fig. 1), but kinship only structured the social networks in groups with a relatively high mean number of female kin (Fig.

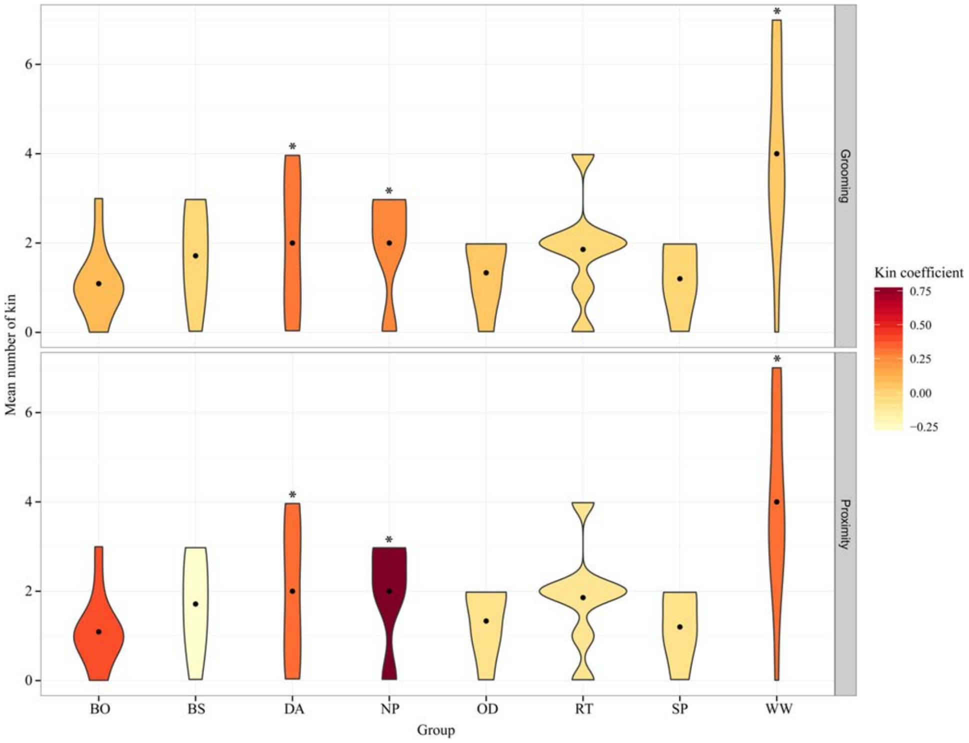

Fig. 5. The number of co-resident kin for females in each group. The mean for each group is represented by a dot. The length of the violin plot shows the range of values and the width shows the relative number of females with access to a certain number of kin. The color indicates the relative value of the kin coefficient in the proximity and grooming networks. The kin coefficient is derived from the results of the kinship-similarity model (Table 1). Significant effects of kinship are indicated with an asterisk. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

5). Curiously, females in RT group did not form kin structured social networks despite a high mean number of female kin, and this is the only study group that did not show differentiated grooming networks (Wikberg, 2012). Taken together, these studies depict temporal (Berman et al., 2008; Perry et al., 2008; Berman and Thierry, 2010) and between-group variation (our study; Bergstrom and Fedigan, 2013) in kin structured social networks that may be linked to the number of co-resident kin and non-kin. To further investigate if this variation in *C. vellerosus* is due to differential access to kin rather than random variation between groups, future studies should focus on a larger number of groups at different time periods.

Similarity hypothesis

Not only kinship but also how familiar the kin is may be important in structuring social interactions (Sackett and Fredrickson, 1987; Koenig, 1994; Erhart et al., 1997; Villavicencio et al., 2009). Indeed, familiarity is the most likely kin recognition mechanism in primates, as there is only ambiguous support for primates being able to discriminate unfamiliar kin (Rendall, 2004). This means that kin that did not mature together or that were separated for a long time may not treat each other like kin that remained in the same group (Sackett and Fredrickson, 1987). This reasoning can explain why the majority of groups consisting solely of long-term resident females showed support for the kinship hypothesis (DA, NP, WW but not RT) while the groups that contained kin with different residency status did not (BS and OD). In the two groups that contained adult females with different residency status, similarity in residency status had a greater impact on the affiliation networks than kinship. This effect was only significant for BS group's proximity network, and the lack of a significant effect in OD group may be due to the group only containing one recent immigrant female. Residency status also affected the social network in *G. b. beringei, Nasua narica* (white-nosed coati), and *P. troglodytes*, in which recent immigrant females received more aggression and less affiliation from long-term residents (Nishida, 1989; Watts, 1991; Gompper et al., 1997; Kahlenberg et al., 2008). These findings highlight the importance of considering not only the kin composition of groups but also the residency status of these kin when investigating the occurrence of kin structured social networks in populations with female dispersal.

Similarity in dominance ranks structured the aggression network in two groups. Females with similar dominance ranks were less aggressive toward each other in a group with long-term hierarchical stability (Wikberg et al., 2013). In contrast, females with similar dominance ranks were more aggressive toward each other in one group with a less stable dominance hierarchy. This group contained two young adult females that had increased in rank a year prior to the start of this study. Although females did not change dominance ranks during our study, the dominance hierarchy may have been unstable as indicated by bidirectional and non-linear (i.e., intransitive or circular) submissive relationships

(Wikberg et al., 2013). Therefore, it is possible that close-ranking females were more aggressive toward each other either to ascertain their new dominance rank or as an attempt to increase in rank. Thus, not only the dominance rank of the social partners but also the stability of the dominance hierarchy may be important in shaping the aggression network. The aggression network might conform to the predictions generated by the similarity hypothesis when the dominance hierarchy is stable while this may not be the case during periods of rank instability.

The grooming network was positively affected by similarity in dominance ranks in one group and by dissimilar maturational stage in another group. The proximity network was not structured by similarity in dominance rank or maturational stage in any of our study groups. The lack of a consistent pattern in female preferences for affiliative partners based on age and dominance rank is similar to the findings from *M. mulatta* (Kapsalis and Berman, 1996) and *S. suricatta* (meerkat) (Madden et al., 2011). The lack of a constant effect of partner similarity on the social networks suggests that partner compatibility is sometimes but not always predicted by similarity or dissimilarity in maturational stage and dominance rank. What constitutes a compatible partner is likely to vary with the type of behavior and also over time as we mentioned above in regards to periods with hierarchical instability. This variation highlights the importance of studying several groups over time to fully understand how individual characteristics structure social networks (Madden et al., 2011).

Resource holding potential hypothesis

The grooming networks were not structured by an attraction to adult females or long-term resident females in contrast to the findings from two other species with female dispersal (Idani, 1991; Wey and Blumstein, 2010). In *M. flaviventris* and *P. paniscus*, females direct more grooming toward well-established females (e.g., older, long-term residents), perhaps to facilitate social integration in the group (Idani, 1991; Wey and Blumstein, 2010). In *C. vellerosus*, dispersing females sometimes follow resident males to their group (Saj et al., 2007), and it is possible that these females form strong bonds with the resident males rather than the resident females to facilitate social integration in their new group. On the other hand, targeted female aggression occurs in this species (Teichroeb et al., 2009), and having strong bonds with other resident females may reduce the risk of being evicted. Further studies are needed to investigate how social bonds affects group membership, and if this can explain why female *C. vellerosus* do not direct grooming toward more well-established female partners in contrast to other species with female dispersal.

Dominance rank had a significant effect on the aggression network in four groups, and females directed most of their aggression to lower ranking females. However, the affiliative and cooperative social networks did not show any support for females being attracted to social partners with high dominance rank. Due to low levels of within-group contest competition in our study population (Saj and Sicotte, 2007), females may only show slight differences in resource holding potentials. A female may not gain great benefits from associating with a social partner that only has slightly higher resource holding potential than herself, and she may therefore not be particularly attracted to this social partner (Seyfarth, 1977). Our results are therefore consistent with the notion of a weak rank effect on social relationships when power differences are small (Barrett and Henzi, 2006).

CONCLUSION

Female kinship had a weaker impact on the social networks in our study species compared to several well-studied species of cercopithecines (Kapsalis, 2004). Nevertheless, kinship was the most import factor in structuring the affiliation networks in groups that contained long-term resident females with access to a relatively high number of kin. In contrast, similarity in residency status was more important than kinship in structuring the affiliation networks in groups that contained recent female immigrants. Thus, taking into account the kin composition of groups and the familiarity of these kin might help to reconcile some of the apparent differences in kin bias between populations with female dispersal (Harcourt, 1979; Watts, 1994; Hashimoto et al., 1996; Langergraber et al., 2009).

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