Kinship and intra-group social dynamics in two sympatric African colobus species

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ABSTRACT

Kinship has been described as a major factor shaping primates’ social dynamics, with individuals biasing their affiliative interactions to their related counterparts. However, it has also been demonstrated that, under certain circumstances, social bonding can be established in the absence of kin. The fact that *Colobus polykomos* (Western black-and-white colobus) and *Procolobus badius temminckii* (Temminck’s red colobus) often live in sympatry (subject to the same ecological/anthropogenic pressures) but exhibit contrasting social systems, makes them good models to test which factors shape their social systems. We investigated the influence of kinship on intra-group social dynamics of one focal group of each species present in Cantanhez National Park, Guinea-Bissau. Between October 2008 and June 2009 we used focal sampling to collect information on the individuals’ nearest neighbors and *Ad libitum* sampling to collect data on intra-group social interactions. We estimated pairwise relatedness using fecal DNA from nine *Colobus polykomos* individuals and 15 *Procolobus badius temminckii* individuals genotyped at 15 microsatellite loci. We found that, in the *Colobus polykomos* focal group, individuals showed no preference to interact or be spatially closer to related partners. Moreover, mainly unrelated females and related males composed the *Procolobus badius temminckii* focal group but grooming was most frequent among female dyads and only rarely involved male dyads. We conclude that kinship is not an important factor determining the social bonding in either study species suggesting that other factors (e.g anthropogenic, ecological) may be at play shaping these groups’ social bonding.

Key-words: colobines; non-invasive sampling; relatedness; time-budgets; social
INTRODUCTION

Since cooperating with kin increases inclusive fitness, the assumption that individuals should preferentially address their affiliative and cooperative behavior to close kin constitutes a starting point for many of the models that attempt to explain the evolution of primate social systems (e.g. Chapais 2001; Gouzoules and Gouzoules 1987; Hamilton 1964a, b; Silk 1987, 2002;). Accurately testing this hypothesis has been facilitated by the development of molecular techniques for quantifying relatedness (Lynch and Ritland 1999; Pamilo and Crozier 1982; Queller and Goodnight 1989). By allowing the assessment of paternity, kinship and population structures, molecular data can provide insights into these features of social systems (Di Fiore 2003). For example, long-term observational studies of chimpanzee (Pan troglodytes) communities have demonstrated the existence of strong affiliative and cooperative bonds among philopatric males, suggesting that related males exhibit closer affiliation than non-related females (e.g. Watts and Mitani 2001; Wrangham and Peterson 1996). However, studies that evaluated intra-community relatedness of chimpanzees showed that the affiliative and cooperative behaviors observed among males did not arise as a direct result of kin selection and that other evolutionary mechanisms may be at play (e.g. mutualism, reciprocal altruism; Gagneux et al. 1999; Vigilant et al. 2001). The same was demonstrated for Colobus vellerosus for which all groups’ social dynamics were female bonded regardless of their relatedness (Wikberg et al. 2012). Cooperation has also been demonstrated in the absence of kinship in other studies, reinforcing the notion that intra-group relatedness is not always enough to explain social dynamics (e.g. in
primates *Papio cynocephalus*: Bercovitch 1988; Noe 1990; and non-primates *Tursiops aduncus*: Connor et al. 2001 and *Chiroxiphia linearis*: McDonald and Potts 1994). For instance, an increase in intra-group competition can induce the establishment of social bonds among non-related individuals in wild primates (e.g. Barton et al. 1996; Lehmann & Boesch 2009). This clearly suggests that intra-group social dynamics can change as a result of changes in the socio-ecological context.

The increasing changes in natural habitats that result from anthropogenic-related pressures and climate change, are forcing wild animals to rapidly adapt to poorer environmental conditions (Hockings et al. 2015; Mortelliti et al. 2010). The extent to which a species is able to persist in more degraded habitats is highly dependent on its socio-ecological plasticity (Di Fiore and Rodman 2001, Frankham 2006; Hockings et al. 2015; Villard 2002). Some primate populations have shown the ability to adapt their dispersal system, group size, home range size, diet composition and/or behavioral patterns when faced with changing environments (e.g. *Colobus polykomos*: Minhós et al. 2013a; *Colobus guereza*: Onderdonk and Chapman 2000; *Cercopithecus cephus*: Tutin 1999; *Procologbus rufomitratus*: Decker 1994; *Macaca sylvanus*: Ménard et al. 2013, *Colobus galeritus*: Wieczkowski 2005; *Pan troglodytes verus*: Carvalho et al. 2013; Hockings et al. 2012; Sousa et al. 2011).

*Colobus polykomos* (Western black-and-white colobus) and *Procologbus badius temminckii* (Temminck’s red colobus) exhibit very different social systems despite being phylogenetically related and often living sympatrically (and thus subject to similar ecological/anthropogenic pressures), making them excellent models to evaluate the factors shaping their social dynamics. *Colobus polykomos* live in relatively small groups, comprising 1-3 adult males and 4-6 adult females (Dasilva 1989; Galat and
Galat and Galat-Luong 1985). As in all other Colobus species, dispersal is thought to be male-biased with episodes of female migration (e.g. *Colobus polykomos*; Minhós et al. 2013a; *Colobus satanas*; Fleury and Gautier-Hion 1999; *Colobus guereza*; Harris et al. 2009; *Colobus vellerosus*; Teichroeb et al. 2009; Wikberg et al. 2012). It has been suggested that *Colobus polykomos* females only disperse when the cost of staying in their natal group is high (e.g. inbreeding avoidance: Isbell and van Vuren 1996, Isbell 2004, Korstjens et al. 2005). Within social units, *C. polykomos* females either maintain closer relationships with one another than they do with males or exhibit loose social bonds with no preference to interact affiliatively with other females (Korstjens et al. 2002; Oates 1977; Struhsaker and Leland 1979). This provides evidence that different strategies can be adopted by females in response to different ecological and/or social constraints. Affiliative interactions among males are almost non-existent and they display a clear dominance hierarchy (Dasilva 1989).

*Procolobus badius temminckii* live in large multi-male, multi-female groups that range from 12 to 65 individuals (Galat and Galat-Luong 1985; Korstjens 2001; Struhsaker 1975; Struhsaker and Oates 1975;). As in all other red colobus, *P. b. temminckii* dispersal is female-biased, with a patrilineal society (Minhós et al. 2013a; Starin 1991, Struhsaker 2010). Social interactions among females are rare and allo-grooming is more frequent among males (Struhsaker and Leland 1979, Struhsaker 2010). In the highly fragmented Abuko Nature Reserve, The Gambia, Starin (1991, 1994) found lower rates of inter-male grooming and proximity for *P. b. temminckii* than described for other red colobus populations. Males only cooperated when either an alien male or a neighboring troop was in proximity. The differences exhibited by the population from Abuko Nature Reserve compared to other red colobus highlight the
importance of understanding the factors shaping these primates’ social dynamics.

Here we present a socio-genetic study of two sympatric social groups of the Endangered *Procolobus badius temminckii* and the Vulnerable *Colobus polykomos* (Oates et al. 2008a,b). We conducted the study in Cantanhez National Park, Guinea-Bissau, where previous population genetic analysis has shown that dispersal is mainly mediated by females in *P. b. temminckii* and by both sexes in *C. polykomos* (Minhós et al. 2013a). Our aim is to understand if kinship is the main factor shaping the social dynamics of these species. To achieve this goal we examine the relationship between intra-group relatedness and social bonding. According to the hypothesis that kinship plays a major role shaping these primates’ social systems, we expected individuals to direct their affiliative behaviors (e.g. grooming) mostly to their related counterparts and their aggression towards non-related partners. Alternatively, in the case that other factors (e.g. ecological/anthropogenic) determine intra-group social bonding, we predicted no correspondence between affiliative or aggressive behaviors and kinship (Di Fiore 2003; Hamilton 1964a;).

**METHODS**

**Study site and social groups**

Cantanhez National Park (CNP) comprises a mosaic of savannah, forest and mangrove habitat and covers an area of 1.067 km$^2$ (105 767 ha) in the southwest of Guinea-Bissau (NE limit: 11°22’58”N, 14°46’12”E; SW limit: 11°2’18”S. 15°15’58”W (WGS 84); Fig 1). The park has a high human population density (22,505
people distributed through 110 villages) with extensive agriculture (Hockings and Sousa 2013). As a consequence, the forests are severely fragmented comprising several patches of various sizes (ranging from 47.5 to 250 ha; Simão 1997). The annual temperature ranges from 28ºC to 31ºC and the annual rainfall is 2000 to 2500mm (Simão 1997).

We observed one group of *Colobus polykomos* and one group of *Procolobus badius temminckii*. Both groups’ home ranges overlapped with a village that is also a tourist site, though the primates were not provisioned. As a result, the groups were already partially habituated, allowing observations to commence at the beginning of the study. Proximity to the tourist site may provide these groups some protection from local hunters. Even though CNP is a protected area, both colobus species are hunted within the park. The hunting pressure seems more intense for *P. b. temminckii* than for *C. polykomos* (T. Minhós pers obs; Hockings and Sousa 2013). For *P. b. temminckii*, we counted a minimum of 27 animals in the group, including three adult males, 10 adult females, six juveniles and eight infants. However, it was not possible to see all group members at the same time and accurately determine the size of the group. For *C. polykomos*, we were able to individually recognize all group members. The group comprised 10 individuals: one adult male, one sub-adult male, four adult females, two juvenile males, one juvenile female and one infant. By the end of March 2009, the adult male, sub-adult male, a juvenile male and an adult female with the infant left the group and did not return so the group was reduced to half of its initial size.

*Ethical note*

We carried out all sampling with the approval and under the legal requirements of
the National Institute for Biodiversity and Protected Areas (IBAP) and the Forestry and Fauna Department (DGFC) from Guinea Bissau.

*Intra-group relatedness*

We collected fecal samples for all known individuals of the *Colobus polykomos* focal group and several *Procolobus badius temminckii* individuals for which we identified the sex and age class. We extracted fecal DNA using the QIAampDNA Stool Kit following the manufacturer’s instructions and stored at -20 °C (Qiagen, Valencia, CA). We genotyped all samples for 15 human-derived microsatellite loci. The genotyping procedures and the information on the microsatellite loci used are described in detail in Minhós et al. (2013a). In the *C. polykomos* focal group, we were able to genotype most of the original group: one adult male, one sub-adult male, three adult females, two juvenile males and one juvenile female. For the *P. b. temminckii* focal group we were able to genotype 11 adult females and four adult males. We estimated the relatedness coefficient of Queller and Goodnight (1989) for all intra-group dyads using Kingroup v2_101202 (Konovalov et al. 2004). We applied a maximum-likelihood relatedness estimator, where we only considered the significantly related dyads (p < 0.05) to be truly related. We based these estimates on the allelic frequencies from a bigger sample of the population (52 *C. polykomos* and 72 *P. b. temminckii* individuals; for detailed description see Minhós et al. 2013a) and not only from the individuals in the focal groups. The *C. polykomos* relatedness analyses correspond to the full genetic characterization of the social group. For *P. b. temminckii*, our data represents minimum estimates, since there were more adult individuals in the group from which we did not
obtain genotypes. We calculated the mean pairwise relatedness for all possible dyads of individuals and assessed the number of pairs of closely related females and pairs of closely related males in the group. We do not use our microsatellite panel to make inferences on the level of relatedness (e.g. parent-offspring, full-or half-siblings), but only to access whether a pair of individuals is related or not, regardless of their degree of relatedness.

Social interactions

We collected *Ad libitum* data between October 2008 and March 2009 on a daily basis (Altmann 1974). We observed each social group on 19 separate days, from 7:00 to 19:00. We alternated observations of the two groups on a weekly basis and recorded date, time, habitat, location, individual, activity and their partner. We attempted to record the individual identities or age-sex classes of the interactants, whenever possible. We collected data continually during the day, every time we observed a social interaction. For the *Colobus polykomos*, we only used the data prior to the disappearance of the males from the focal group. Since it was not possible to observe all group members of *Procolobus badius temminckii* simultaneously, we observed the largest subset of temporarily adjacent individuals to record the maximum number of interactions possible. We recorded the following activities: agonism (aggressive and submissive interactions involving two individuals such as threat, fight, chase, displace, flea, present), grooming, social fight (aggression involving three or more individuals), copulation, play and vocalizations. For allo-grooming we considered only one event for
each individual even if the grooming direction changed several times. For all behavioral
categories, if the interaction was interrupted for less than 3 minutes, we considered it as
the same event (Korstjens et al. 2002).

Spatial proximity

We only inferred the relationship between spatial proximity and relatedness
among pairs of individuals for the Colobus polykomos group, as we did not individually
recognize all Procolobus badius temminckii group members. We carried out focal
sampling between March and June 2009. Each focal observation was four hours long,
and three sessions were carried out per day. We recorded the identity of the nearest
neighbor (within 3m) of each focal individual every half-hour. When the individual
under the focal observation was out of sight, we paused the sample and continued after
finding the individual again. If the focal individual was out of sight for more than 30
minutes straight, we terminated the focal sampling. We only included focal samples in
the final dataset that contained more than 1h of observation. We sampled all group
members and whenever possible, resampled them following the same order. We never
sampled the same individual twice in the same day and each individual was sampled
during three periods throughout the day (7am-11am, 11am-3pm, 3pm-7pm). We carried
out 276 hours of focal observations on one adult male, one sub-adult male, four adult
females, two juvenile males and one juvenile female.

Within-species comparisons

We used generalized linear mixed effects models (GLMM) with Poisson error
distribution to test for the effects of the sex combination (i.e. male dyads, female dyads and male-female dyads) on the daily rates of intra-group agonistic and grooming interactions (Bolker et al., 2009). Here, we considered each observation day as the sampling unit in both social groups and calculated the mean rate of each social interaction (i.e. number of times a given social interaction was observed for each sex combination/total number of observations for that social interaction) across the total number of observation days. We included the observation days as random factors in the model and analyzed each variable using a separate univariate model. We carried out GLMM using the lme4 package in R 2.14.1 (Bates et al. 2011; R Development Core Team, 2012). We tested the statistical significance of the full model (with the sex combination as the fixed factor) by comparing it to a null model (excluding the sex combination variable) using a likelihood ratio test (R function “anova”) (Dobson & Barnett, 2002). We ran analyses for each species separately and only included adult and sub-adult individuals in this analysis.

As we could individually recognize all group members of the *Colobus polykomos* focal group, we were able to test whether grooming, agonistic interactions or proximity more frequently involved related or non-related individuals. For each animal we estimated the percentage of times that each social interaction happened with a related or with a non-related partner. We then calculated the mean of those percentages for the social group. Each individual had a different number of related and non-related partners within the group. Therefore, we corrected for this potential bias in partner availability by dividing the percentage of each social behavior with related and non-related partners by the total number of available related and non-related partners in the group. We tested differences using Wilcoxon signed-rank tests implemented in R v.
2.12.0 (R Development Core Team 2009). In this analysis, we used all genotyped individuals except for one juvenile male, as we had very limited data on social interactions for this individual.

**Between-species comparisons**

We used GLMMs with Poisson error distribution to test for a species effect on the daily rates of each intra-group social interaction (i.e. number of observations of a given social interaction/total number of social interactions observed), as described for the within-species comparisons. We included observation days as random factors and species as the fixed factor in the model.

As group size in *Procolobus badius temminckii* was much larger than in *Colobus polykomos*, the number of social interactions was much higher in *P. b. temminckii*. To correct for this bias, we expressed social interaction results as the proportion of each social activity relative to the total of intra-group observed social interactions for each observation day. We only included adult and sub-adult individuals in this analysis.

**RESULTS**

**Intra-group relatedness**

In the *Colobus polykomos* focal group, of all 28 possible dyads only 9 (32%) were significantly related (Table 1). Of those, there was only one dyad of related adult
females (Adult female 2 and 3) out of three possible dyads, meaning that one of the three adult females (Adult female 1) was not related to any other adult female in the group. Additionally, the adult male was significantly related to two of the adult females (Adult female 2 and 3) and the juvenile female. The sub-adult male was only related to the Adult female 1.

In the *Procolobus badius temminckii* focal group, of all 55 possible dyads of adult females only seven pairs were significantly related (12.7%). However, for the adult males, four of six possible dyads (66.7%) were significantly related.

**Social bonding**

*Within-species comparisons*

When we compared the sexes, there were species differences in agonistic and grooming events between adults (Fig 2 and 3). In *Colobus polykomos*, we found an effect of the sex combination on grooming, which occurred at a lower frequency among male dyads compared to female and mixed dyads (Table 2, $\chi^2 = 9.42, P = 0.009$). However, the sex combination did not have an effect on the observed levels of intra-group agonism, since we found no differences between the model containing the sex combination factor and the null model ($\chi^2 = 4.25, P = 0.119$). In *Procolobus badius temminckii*, we found an effect of the sex combination in both types of interactions. Agonism was lower in female dyads compared to male and mixed-sex dyads (Table 2, $\chi^2 = 7.70, P = 0.021$). The opposite pattern was true for allo-grooming, which occurred at higher levels among dyads of females and less among males or individuals of
different sexes (Table 2, $\chi^2 = 14.90, P = 0.001$).

*Colobus polykomos* individuals had more non-related than related partners in the group (mean values, Table 3). We found no kin-biases in either grooming (Table 3, Wilcoxon signed-rank test, N= 7, Z=−0.51, $P = 0.61$; corrected: $Z=−0.51, P = 0.61$) or agonistic interactions (Table 3, Wilcoxon signed-rank test, N= 7, Z=−0.84, $P = 0.40$; corrected: $Z=−0.21, P = 0.83$). Additionally, there was no difference in the time individuals were spatially closer to related vs. non-related individuals (Table 3, Wilcoxon signed-rank test, N= 7, Z=−1.15, $P = 0.25$; corrected: $Z=−0.31, P = 0.75$). We could not apply the same approach to *Procolobus badius temminckii* because we could not individually recognize the members of this group.

*Between-species comparisons*

For *Colobus polykomos*, we recorded 321 interactions (mean: 16.89 interactions/day ± SD 12.08). For *Procolobus badius temminckii*, we recorded a total of 828 interactions (mean: 43.63 interactions/day ± SD 16.68). Grooming was the most frequent social behavior displayed by both species, followed by agonistic interactions (Fig. 4, Table 4). Both groups also showed low levels of social fights and copulations (Fig 4, Table 4). Social interactions were not significantly different between the species, as demonstrated through the comparison of the model that included the factor species with the null model (Table 4, Aggression: $\chi^2 = 0.28$, d.f. = 1, $P = 0.597$; Grooming: $\chi^2 = 0.31$, d.f. = 1, $P = 0.578$; Social Fight: $\chi^2 = 0.19$, d.f. = 1, $P = 0.6575$; Copulation: $\chi^2 = 1.99$, d.f. = 1, $P = 0.158$; Play: $\chi^2 = 0.66$, d.f. = 1, $P = 0.418$; Vocalization: $\chi^2 = 0.09$, d.f. = 1, $P = 0.769$).
DISCUSSION

The combination of behavioral and genetic data in this study enabled us to exclude kinship as a determinant factor shaping the intra-group social dynamics of two sympatric African colobus monkeys.

Pairs of related and unrelated females composed the *Colobus polykomos* focal group with no kin bias in grooming, showing an absence of female-based kin-structure and social bonding. At the individual level, *C. polykomos* individuals showed no preference for directing any type of social interaction or maintaining proximity to related versus non-related partners. Such results clearly demonstrate that, at least in this particular *C. polykomos* social group, kinship is not the major factor shaping the social dynamics for either sex. A similar pattern has also been described for a *Colobus vellerosus* population from Ghana (Wikberg et al. 2012). This population was characterized by great variation in its social system, with some social groups showing female dispersal, absence of female kin-based structure and social bonding.

The *Procolobus badius temminckii* group is characterized by female-biased dispersal, a male-based kin-structure and female-based social bonding, strongly suggesting that kinship is not the main determinant for the observed social dynamics. Although there were some related adult females, their numbers in the group are too few to explain the extremely high frequency of grooming exchanged between females. Additionally, if kinship is the main factor shaping this group’s social dynamics we would expect grooming between males to be more frequent, as it is in other studied red colobus groups (Struhsaker and Leland 1979, Struhsaker 2010). A paucity of male-male
grooming was also described for red colobus males in both Abuko (*P. b. temminckii*) and Jozani, Zanzibar (*Procolobus kirkii*) but it was only in Abuko that females also groomed other females more than they groomed males (Siex 2003; Starin 1991). One explanation is that females may have transferred into the Abuko group along with other females from the same natal group (parallel dispersal, van Hooff 2000) (Starin, 1991). If so, this could mean that females in a group are closely-related and, therefore, strongly bonded. It is possible that parallel dispersal occurs in *P. b. temminckii* from CNP and such related females prefer to groom each other instead of grooming non-related females. However, we suggest that due to the low percentage of related females, parallel dispersal and kinship among females cannot fully explain the strong social bonding among these females, similar to what we found for the sympatric *Colobus polykomos* group. Factors besides kinship, such as high resource competition, may be strong enough for it to be advantageous for these females to establish strong social bonds with non-related females.

The existence of strong social bonding in the absence of relatedness has already been shown for *Colobus spp.* elsewhere (Wikberg et al. 2012, 2014). The forest of CNP is highly fragmented and colobus monkeys are the target of human hunting (Costa et al. 2013; Minhós et al. 2013b; Sá et al. 2013) The fact that these particular groups have their home range overlapping with the tourist village indirectly protects them from both humans and others predators (e.g. chimpanzees). Poaching has never been reported in these groups unlike several other groups in the surroundings (T. Minhós pers obs; Hockings and Sousa 2013). The hunting pressure combined with the increased forest loss and fragmentation elsewhere in CNP has caused increased colobus density in this area, which is likely to increase the intra-group competition for resources, as suggested
for Procolobus rufomitratus at Tana River (Decker 1994). Under such a scenario, it may be that colobus gain immediate benefits (e.g. coalitionary support in resource defense) by forming social bonds with non-related individuals, which functions as an adaptive survival strategy in response to anthropogenic changes in the habitat (Chapais 2001; Seyfarth 1977). Research has described how primate females direct affiliative behaviors to non-related group members if they provide them with coalitionary support or increase their opportunities to access limited resources (Seyfarth 1977). For example, female baboons (Papio spp.) showed higher levels of affiliation and coalitions under a scenario of high intra-group contest competition for food (Barton et al. 1996). Lehmann & Boesch (2009) also described an increase in social bonding among non-related female chimpanzees during periods of high intra-group competition.

By combining data on social interactions and patterns of intra-group relatedness we provide evidence that intense ecological and/or anthropogenic-related pressures may act as major factors shaping intra-group social dynamics in two West African colobus groups.

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