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Familiarity is more important than phenotypic similarity in shaping social relationships in a facultative female dispersed primate, *Colobus vellerosus*

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ABSTRACT

Animals often bias affiliative behaviors toward kin, but it is unclear what mechanism most species use to discriminate kin. We investigated if facultative dispersed female primates use phenotype matching and/or familiarity to discriminate female kin. We studied 38 adult female *Colobus vellerosus* at Boabeng-Fiema, Ghana. We determined dyadic co-residency status and age proximity using long-term demographic data, *R*-values from 17 short tandem repeat loci, and interaction rates using focal samples collected during one year. Approach rates were not strongly affected by how long females had resided together, which contrasts to the familiarity hypothesis. Females approached and groomed maternal kin more than other females, which supports the mother-mediated familiarity hypothesis. Females did not discriminate paternal half siblings from non-kin, and they did not prefer to interact with females of similar age. Short-term co-resident kin did not bias affiliation toward each other, indicating that female colobus cannot consistently recognize less familiar kin via phenotype matching or that biasing behaviors toward less familiar kin is not beneficial. Despite showing facultative dispersal that may reduce the accuracy of using familiarity as a kin recognition mechanism, female choice of social partners was based on familiarity, which conforms to the pattern observed in many female philopatric primates.

1. Introduction

Animals bias affiliative and cooperative behaviors toward kin in a wide range of animals (Archie et al., 2006; Gompper et al., 1997; Griffin and West, 2003; Guilhem et al., 2000; Hirsch et al., 2012; Kapsalis, 2004; Wahaj et al., 2004; Wilkinson, 1986). Despite the widespread presence of kin structured social networks in these animals, little is known about the process by which kin preferences develops, and whether or not the process differs between species (Rendall, 2004; Widdig, 2007). In mammals that are female philopatric (Greenwood, 1980), mothers often form long-lasting bonds with their female offspring, and these enduring bonds lead to mother-mediated familiarity among maternal female kin as they cluster around the matriarch (Chapais, 2001; Walters, 1987). As a result, mother-mediated familiarity may be the basis for maternal kin recognition in female philopatric mammals (Rendall, 2004). Paternal kin bias might also arise due to differential familiarity in species with high reproductive skew and short male tenure (Widdig, 2007), which makes it likely that natal animals of similar age are paternal siblings (Altmann, 1979; Altmann et al., 1996). Because immatures often play with others of similar age, this could lead to age-mediated familiarity among paternal siblings (Smith et al., 2003; Widdig, 2007; Widdig et al., 2001). Even in the absence of familiarity, animals may recognize kin by using phenotype matching if phenotypic similarity is correlated with relatedness (Holmes and Sherman, 1982). Phenotypic similarity in body odors (Mateo and Johnston, 2000), vocalizations (McDonald and Wright, 2011), facial features (Dal Martello and Maloney, 2006; Kazem and Widdig, 2013; Vokey et al., 2004), and pigmentation patterns (Hinz et al., 2012) may allow individuals to discriminate between familiar animals of different kinship categories (Wahaj et al., 2004) and to determine their relatedness with animals that they have not previously encountered (Holmes and Sherman, 1982).

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Most studies investigating kin recognition mechanisms have been conducted in the laboratory. Whether or not experimental findings can be generalized to wild animals is uncertain as the social conditions differ markedly from those in natural settings (Hare, 1998). At least in experimental settings, there is convincing evidence that several species of rodents use phenotype matching to recognize unfamiliar kin (*Peromyscus maniculatus*: Dewsbury, 1988; *Mus musculus*: Kareem and Barnard, 1982; *Mesocricetus auratus*: Mateo and Johnston, 2000; *Spermophilus* spp.: Schwagmeyer, 1988). However, the kin bias is often stronger toward familiar kin than unfamiliar kin, which suggests that both familiarity and phenotypic similarity are important in shaping social behaviors and partner choice in rodents (Koenig, 1994; Villavicencio et al., 2009). Experimental studies of primates are fewer, and the findings are more ambiguous. A small number of infant southern pig-tailed macaques (*Macaca nemestrina*) could discriminate kin despite no previous contact (Wu et al., 1980) while attempts to replicate this study with a larger sample size showed social preferences based on familiarity rather than phenotypic similarity (*Papio cynocephalus*: Erhart et al., 1997; *M. nemestrina*: Sackett and Fredrickson, 1987).

Studies conducted in wild animals to address these issues are often inconclusive due to the difficulties of teasing apart the effects of relatedness and familiarity. The exceptions come from species in which young are reared in nests. At the time of emergence from the nest, the young is more familiar with their littermates than other animals regardless of their relatedness, and this familiarity shapes social relationships (Hare, 1998; Wahaj et al., 2004). There is also another opportunity to decouple familiarity and relatedness when the sex that typically remains philopatric exhibits facultative dispersal. Because some animals of one sex disperse while others remain in their natal group, familiarity might not necessarily correspond to relatedness. *Colobus vellerosus* (ursine or white-thighed colobus monkey) is an African Old World monkey that shows facultative female dispersal (Teichroeb et al., 2009; Wikberg et al., 2012), and females may reside with more or less familiar female kin of different ages. Facultative female dispersal may lead to a more variable distribution of kin compared to female philopatric species, which weakens the correlation between familiarity and relatedness. If kin biased female–female social relationships leads to fitness benefits in this species, it might be necessary for females to use phenotype matching to discriminate kin from non-kin to reap these benefits.

We have previously documented that female colobus bias affiliation toward female kin (Wikberg et al., 2014). To gain insights into the possible use of familiarity and phenotype matching to discriminate kin from non-kin, this paper investigates if females discriminate between social partners (i.e. female group members) based on their co-residency status (e.g. long-term versus short-term co-residents), kinship, age-proximity, and phenotypic similarity estimated via *R*-values (i.e. dyadic estimates of relatedness). The familiarity hypothesis is supported if females distinguish between social partners depending on their co-residency status, kinship, and age-proximity (Rendall, 2004; Smith et al., 2003; Widdig, 2007; Widdig et al., 2001). The phenotype matching hypothesis is supported if females distinguish between social partners based on their *R*-values (Dewsbury, 1988; Kareem and Barnard, 1982; Mateo and Johnston, 2000; Schwagmeyer, 1988).

2. Materials and methods

2.1. Behavioral and demographic data collection

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). Between 2008 and 2009, we recorded social behaviors ad libitum and during 10-min continuous focal samples (Altmann, 1974) of 38 adult (>5 years) females residing in six groups. We have 1614 contact hours and 619 focal hours with a mean of 16 focal hours per female (range: 14–18 h/female).

We used the focal samples to calculate the proportion of time spent giving grooming and the rate of giving approaches to one meter. We standardized the proportion of time spent grooming using the *z*-transformation (Abdi, 2007). The *z*-scores were calculated separately for each female-partner combination using the following formula: $(y - \dot{X})/\mathrm{SE}$. For example, female A's *z*-score with partner B was calculated as the mean of female A's grooming across partners ($\dot{X}$), subtracted from the grooming between A and B (y), and divided by the standard error for female A's grooming across partners (SE). Partners with scores above one were categorized as preferred partners (Lehmann and Boesch, 2009).

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. The groups were observed for different number of years before the start of this study (2000: BS and WW; 2004: DA, OD, and RT; NP: 2007) and the ability to recognize individuals has increased from a few of the group members to all group members between 2004 and 2008. This allowed us to determine co-residency status, partial pedigrees, and age proximity for some of the study animals. We coded whether or not females were long-term or short-term co-residents (i.e. had resided together for at least four years versus less than four years). Females in BS group and OD group resided with both long-term and short-term co-residents, while all females in DA, NP, RT, and WW were long-term co-residents.

We knew the exact or approximate age of 12 females based on the demographic records. For the remaining females, we estimated their age-class based on their physical appearance (e.g. elongated nipples, body size, wrinkles, hair loss, and body posture). Two experienced observers independently estimated the females' ages and only in three cases did the age classification differ by more than two years. In these three cases, we used the mean estimated age. We used the exact or estimated ages to calculate the age differences between females. If their age difference was less than two years, we considered them as belonging to the same age cohort (Smith et al., 2003). Belonging to the same age cohort may be a rough estimate of the likelihood of being paternal half siblings in this population because the average male tenure is two years (Wikberg et al., 2012) and paternity is heavily skewed toward the alpha male (87.5% in one multi-male group; ECW unpublished data). In one multi-male group, 50% of the infants belonging to the same age cohort and 18% of the infants belonging to different age cohorts were paternal half siblings (ECW unpublished data). We only have access to genetic data from one uni-male group during three years of stable male group membership. All infants born in the uni-male group during this time period were paternal half siblings (ECW unpublished data).

2.2. Genotyping and calculating dyadic estimates of relatedness

We 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 and colleagues (2012). We used the software COANCESTRY (Wang, 2011) to compute *R* following a method described by Rollins and colleagues (2012). This software uses seven methods for calculating dyadic estimates of relatedness (*R*), and we investigate which of these methods is most accurate by correlating *R* with actual relatedness (*r*) using dyads with known kinship (Rollins et al., 2012). We used 105 dyads that included all study animals with known parentage, and the correlations were done using the Mantel function in the package ecodist (Goslee and Urban, 2007) in R (R Core Team, 2013). We chose to use the *R* derived from Milligan (2003) dyadic likelihood estimator because this method yielded the highest correlation between *R* and *r* ($r = 0.77$, $p = 0.001$). We used these *R* values to evaluate if females discriminate between social partners based on their phenotypic similarity.

2.3. Testing the accuracy of dyadic estimates of relatedness

A few recent studies document that dyadic estimates of relatedness (*R*) is a poor predictor of actual relatedness (*r*) due to inbreeding and sampling errors when genotyping only a small proportion of loci (Csillery et al., 2006; Van Horn et al., 2008). Due to these issues, some unrelated animals will by chance have exceptionally high *R* while some closely related animals with have low *R*. To evaluate how well *R*-values correspond to different kinship categories and to actual relatedness in our study population, we followed the methods of Van Horn and colleagues (2008) and Robinson et al. (2013). In our study population, 36 offspring had known mothers, either known from the demographic records or assigned as such in CERVUS (Kalinowski et al., 2007; Marshall et al., 1998). Only 15 of these offspring were assigned sires in the software CERVUS. These offspring and their parents made up 61 individuals all of which were genotyped at more than 10 loci. We categorized these animals as: (1) non-kin (i.e. two individuals with different parents); (2) half siblings and grandparent–grandoffspring; or (3) full siblings and parent–offspring.

First, we determined the ranges of *R* for these three kin categories using a set of reference dyads (Fig. A.1). These reference dyads only included non-kin and siblings whose mothers and sires were known. We did not include non-kin and siblings with deeper kinship (e.g. maternal half siblings that are also paternal aunt–niece), either known or suspected based on high *R* between their parents. The grandparent–grandoffspring and parent–offspring reference dyads may include some dyads with more complex kinship because the grandparent's and parent's parents remained unknown in the majority of cases. We were unable to determine the range of *R* for more distant kin because there were only a few known distant maternal kin (four aunt–niece dyads and two cousin dyads) and their paternal kinship remained unknown. The range of *R* for known non-kin (*R*: 0.00–0.06, $\dot{X} = 0$, $N = 41$), half siblings and grandparent–grandoffspring (*R*: 0.16–0.41, $\dot{X} = 0.29$, $N = 19$), and full siblings and parent–offspring (*R*: 0.43–0.76, $\dot{X} = 0.55$, $N = 49$) did not overlap (Fig. A.1).

Supplementary Fig. A.1 can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2014.04.002.

Second, we evaluated if threshold values of *R* could accurately determine kinship. As threshold values, we used the midpoint between the mean *R* of two kinship categories (Csillery et al., 2006; Van Horn et al., 2008). The threshold for distinguishing non-kin versus half siblings and grandparent–grandoffspring was $R = 0.15$, and the threshold for distinguishing half siblings and grandparent–grandoffspring versus full siblings and parent–offspring was $R = 0.42$. To evaluate the accuracy of this method, we used 105 dyads that included the 15 offspring whose mothers and sires were known or assigned. Based on the available demographic information and the parentage assignments, 89 dyads were non-kin (85%), 15 dyads were half siblings (14%), and 1 dyad consisted of full siblings (1%). Even though this is only a subset of animals in our study population, the kinship structure in this data set is similar to that reported in other wild primate populations with more complete pedigree information (Van Horn et al., 2008). Some of the dyads were most certainly more related than the kinship category that we classified them as because their parents showed a high *R* suggesting that the parents were siblings or parent–offspring. Thus, our kin categories represent the least related categories to which these dyads belonged. Of the non-kin, 89% were accurately assigned as non-kin ($N = 79$) while 9% were incorrectly assigned as half siblings ($N = 9$) or full siblings ($N = 1$) based on their *R*. Of the half siblings, 73% were correctly assigned ($N = 11$) while 27% were incorrectly assigned as full siblings ($N = 4$). The one full sibling dyad was correctly assigned as such. In total, 87% of the dyads were correctly classified based on their *R*. The remaining dyads were misclassified as belonging to a more closely related kin category that they did. These misclassified dyads do not necessarily indicate that *R* is a poor estimate of the genotypic similarity between two individuals. It may be that pedigree-based methods do not accurately reflect genotypic similarity due to chance events during Mendelian inheritance (Forstmeier et al., 2012) or that we estimated kinship based on shallow pedigrees that did not take into account deeper kinship relationship (e.g. maternal half siblings that are also more distant paternal kin). An important point to note is that although the number of kin may be overestimated if using *R* to classify kin, no close kin were misclassified as being less related than they were. It is possible that the non-kin dyads with an *R* below 0.15 were distantly related kin (e.g. half aunt–niece or cousin dyads), but no close kin (e.g. half siblings, grandparent–grandoffspring, full siblings, and parent–offspring) had such low *R*. Therefore, we conclude that *R* can be used to detect the majority of non-kin dyads while it may not accurately distinguish different categories of close kin.

Third, we investigated how well estimates of relatedness (*R*) are correlated with actual relatedness (*r*). We used the same data set as in the previous paragraph that may include dyads with deeper kinship relationships ($N = 105$ dyads). We created two matrices, one with *R* and one with *r* derived from available demography data and parentage assignments. We performed Mantel tests in the package ecodist (Goslee and Urban, 2007) in R (R Core Team, 2013). Because *R* and *r* showed a high correlation ($r = 0.77$, $p = 0.001$), we conclude that *R* is a relatively good estimator of actual relatedness in our study population.

2.4. Defining kin and non-kin

We used demographic data and kinship assignments in COLONY (Jones and Wang, 2010) to classify which females were mother–daughters, maternal siblings, and paternal siblings. COLONY uses full pedigree likelihood methods to infer parentage and sibship, and it does not require the true parents to be genotyped (Jones and Wang, 2010; Walling et al., 2010). Dyads that were not known kin from the demographic record nor assigned as kin at the 95% confidence level in COLONY were considered as non-kin if their *R* was below 0.15. The threshold $R = 0.15$ accurately distinguished the majority of non-kin dyads in our reference data set (sensu Van Horn et al., 2008) while no close kin in our reference data set had such low *R* (Fig. A.1). Kinship remained unknown for dyads that were not assigned as kin in COLONY and had an *R* above 0.15. We removed all dyads with unknown kinship from the analyses of the effect of kinship on social interactions.

2.5. Data analysis

We centered and scaled all numerical predictor variables using the *z*-transformation (Abdi, 2007; Schielzeth, 2010). We analyzed square root transformed approach rates with linear mixed models. Many of the female–female dyads never groomed each other (63/206 dyads), and to overcome the problem with zero inflated data, we created two different types of models to analyze grooming. In the first model, we excluded all dyads with no observed grooming and analyzed the square root transformed time spent grooming using a linear mixed model. In the second model, we

Table 1
The competing models' fixed effects, AIC, delta (i.e. difference in AIC between the current model and the best fitting model), and Akaike weights (i.e. relative likelihood of the model) for the analysis of approach rates of females that resided with maternal non-kin of different co-residency status. All models contained animal identity as a random effect.

Fixed effects	Approach AIC	Approach Δ	Approach Weight
–	−55.5	0.00	0.23
Co-residency	−55.1	0.46	0.18
R	−54.8	0.76	0.16
Age proximity	−53.7	1.78	0.10
Co-residency + *R*	−54.9	0.60	0.17
Co-residency + age proximity	−52.7	2.78	0.06
Co-residency + *R* + age proximity	−52.3	3.24	0.05
R + age proximity	−52.7	2.78	0.06

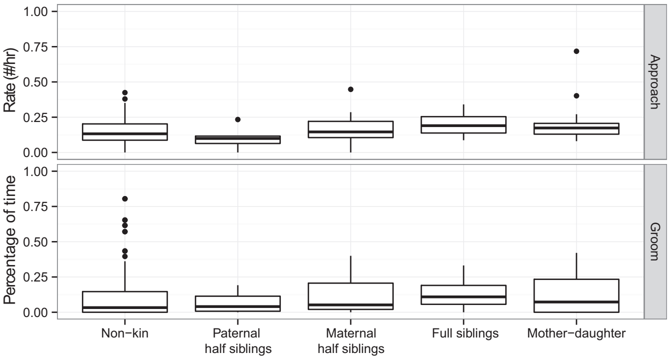

Fig. 1. Approach rates and percentage of time spent grooming in different kin categories. The box represents the 1st and 3rd quartiles and the median is marked with a horizontal bar. The whiskers represent the range of the data with the exception of outliers that are indicated with a dot.

analyzed preferred grooming partners (which is a binary variable) in the full data set with a generalized linear mixed model. Because not all females had access to female group members with different residency status, we analyzed what factors affected the partner choice using two different sets of models (Tables 1 and 2). First, we investigated individual choice of social partners in a data set that only included females with access to long-term and short-term co-resident females. We used co-residency status, *R*, and age proximity as predictor variables (Table 1). None of the females resided with both short-term and long-term co-resident kin. Therefore, we removed all kin dyads from this analysis, and we did not include kinship as a predictor variable. Second, we investigated social partner choice in a data set that only included long-term resident females with access to partners that were kin and non-kin. We included age proximity, kinship (see results for definition of kinship categories), and/or *R* as predictor variables (Table 2). Because kinship and *R* were not independent predictor variables, we only included one of these predicator variables at a time. None of the other predictor variables were correlated with each other (Fig. A.2). We used each female–partner combination as a data point and therefore included individual identities as random effects. We created a set of competing models (Tables 1 and 2), and we determined which of these models was best supported by comparing each model's Akaike Information Criterion (AIC) (Akaike, 1974). Because no model received a considerable larger amount of support than others, we took model selection uncertainty into account by averaging parameters across models (Burnham and Anderson, 2002; Grueber et al., 2011). The models were computed with the packages nlme (Pinheiro et al., 2012) and lme4 (Bates et al., 2012), and model selection and averaging of coefficients were done in the package MuMIn (Barton, 2013) in R version 2.13.2 (R Core Team, 2013).

Supplementary Fig. A.2 can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2014.04.002.

3. Results

All 38 study females resided with at least one non-kin, 15 females resided with a mother and/or daughter (range: 1–2), 4 females resided with one full sibling, 11 females resided with a maternal half sibling (range: 1–3), and 5 females resided with a paternal half sibling (range: 1–2). Paternal half siblings had the lowest median approach rates while full siblings had the highest approach rates (Fig. 1). The different kin categories did not show marked differences in the percentage of time spent grooming, and all kin categories contained dyads without any recorded grooming interactions (Fig. 1). Approximately half of the mother–daughter and full sibling dyads were preferred grooming partners while less than 25% of the non-kin, paternal half siblings, and maternal half siblings were preferred grooming partners (Fig. 2). When comparing how frequently a female interacted with her paternal half sibling and a non-kin of similar age, females did not show consistently higher interactions with their paternal half siblings (Fig. A.3). Because we had very few paternal half siblings in our dataset and they did not appear to be distinguished from non-kin, we clumped these two categories in the following analyses (i.e. non-maternal kin). We also combined mother–daughters, full siblings, and maternal half siblings into one category (i.e. maternal kin).

Supplementary Fig. A.3 can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2014.04.002.

3.1. Approaches

Females approached their female social partners at a mean of 0.16 times per hour. A few females never approached some of the available partners ($N = 8$ of 206 dyads) while others approached some of their partners up to 0.72 times per hour.

Table 2
The competing models' fixed effects, AIC, delta, and Akaike weights for the analysis of social partner choice among long-term co-residents. All models contained animal identity as a random effect.

Fixed effects	Approach			Groom			Preferred partners		
	AIC	Δ	Weight	AIC	Δ	Weight	AIC	Δ	Weight
–	−71.0	4.7	0.05	16.8	1.7	0.16	80.6	0.9	0.13
Maternal kin	−75.6	0.0	0.53	15.1	0.0	0.38	80.0	0.3	0.18
R	−71.0	4.7	0.05	16.5	1.4	0.19	79.7	0.0	0.21
Age proximity	−69.4	6.3	0.02	18.7	3.7	0.06	80.6	0.9	0.13
Maternal kin + age proximity	−74.6	1.1	0.32	16.9	1.8	0.15	80.1	0.4	0.17
R + age proximity	−69.6	6.1	0.03	18.5	3.4	0.07	79.9	0.2	0.19

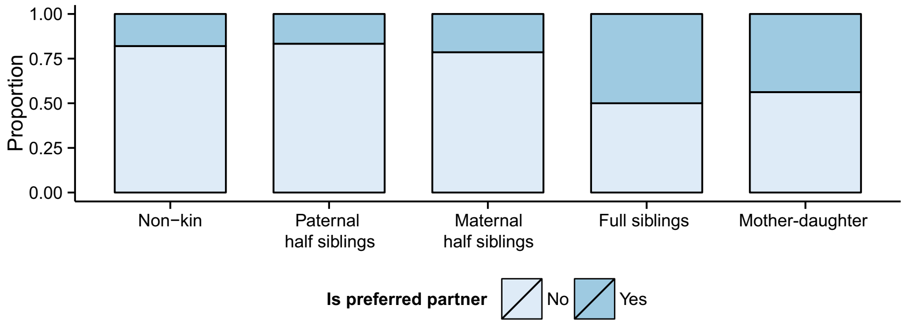

Fig. 2. Proportion of preferred and non-preferred grooming partners in different kin categories.

Only BS group and OD group contained both short-term and long-term resident females. In these two groups, three females lacked maternal kin, five females resided with long-term co-resident maternal kin, and four females resided with a short-term co-resident maternal kin that was her mother, daughter, or half sibling. Long-term co-residents had higher approach rates than short-term co-residents, and this effect was particularly pronounced among maternal kin (Fig. 3). Females approached maternal kin and non-kin of the same co-residency status at similar rates (Fig. 3). Due to the scarcity of maternal kin in the groups that contained females with different co-residency status, we analyzed approach rates in a data set that excluded all maternal kin. When investigating how co-residency status, *R*, and age proximity affected approach rates in this data set (*N* = 10 females and 40 dyads), none of the predictor variables had a consistent effect on approach rates (Fig. A.4), and the alternative models did not have a better fit than the null model (Table 1).

Supplementary Fig. A.4 can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2014.04.002.

We analyzed how maternal kinship, *R*, and age proximity affected the approach rates of 21 females that resided with long-term co-residents that were maternal kin and maternal non-kin (*N* = 72 dyads). Maternal kinship had the highest relative variable importance (0.85), and it had a relatively large positive effect on approach rates (Fig. 4). Age proximity and *R* did not have a consistent effect on approach rates (Fig. 4).

3.2. Grooming

Females spent a mean of 0.1% of their time grooming each available social partner (range: 0–2.5%). The majority of females had one preferred grooming partner (*N* = 31), and only six females had two preferred partners. One short-term resident female distributed her grooming evenly across available partners, and therefore, she did not have any preferred grooming partners and was removed from the analysis of preferred grooming partners.

Short-term co-residents spent less time grooming each other than long-term co-residents, and this difference was particularly pronounced among maternal kin with different co-residency status (Fig. 3). In the data set that contained maternal non-kin with different co-residency status, only five females groomed both short-term and long-term co-residents. Only five females had a preferred grooming partner among these females, and the preferred partner was always a long-term co-resident female. Because grooming was so rare among these maternal non-kin, we were not able to analyze the time spent grooming or the choice of preferred grooming partners in this data set.

In the data set consisting of long-term co-residents, maternal kinship had a positive effect on the time spent grooming (Fig. 5), and maternal kinship had the highest variable importance (0.53). Age proximity and *R* did not have a consistent effect on time spent grooming (Fig. 5). When analyzing preferred grooming partners among long-term co-residents, none of the predictor variables had

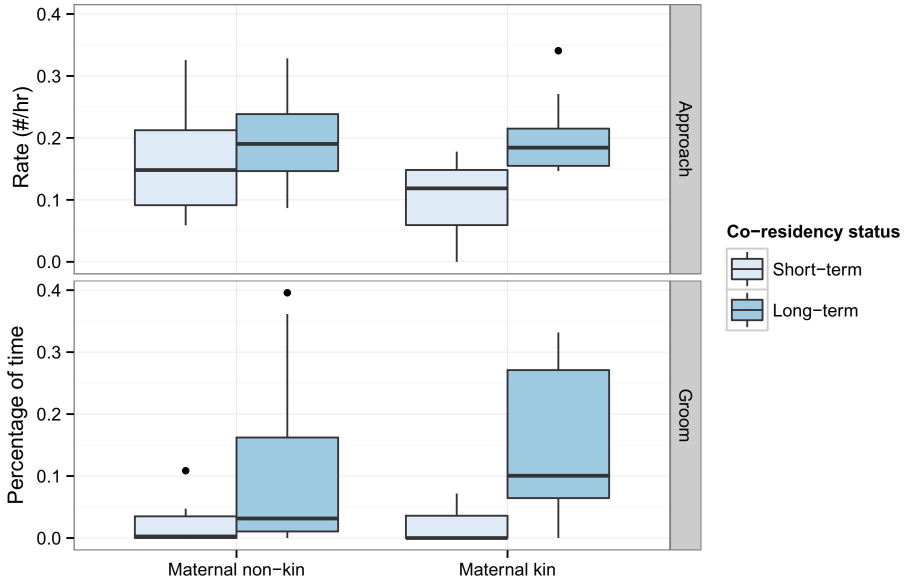

Fig. 3. Approach rates and percentage of time spent grooming short-term and long-term co-resident maternal kin and non-kin. See legend for Fig. 1 for more details.

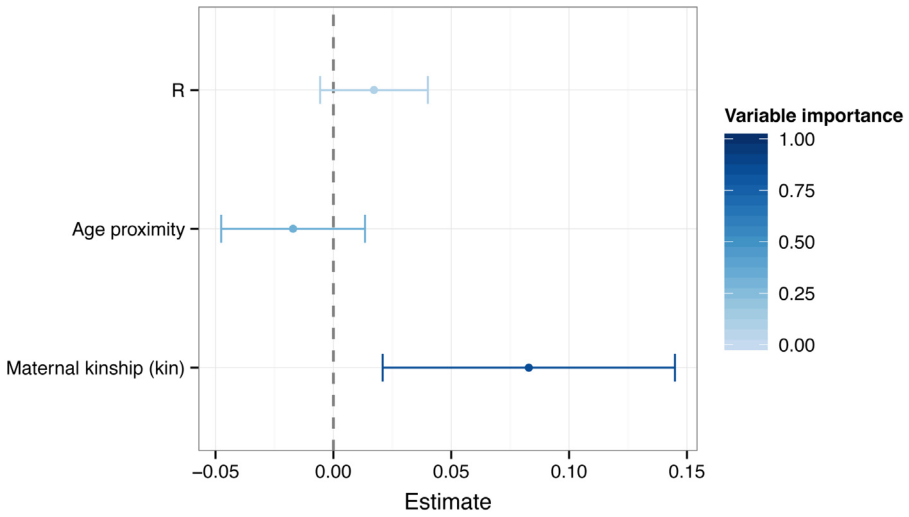

Fig. 4. Estimates and confidence intervals from the approach model that included females with access to long-term maternal kin and non-kin. *R* and age proximity are continuous variables while the effect of maternal kinship is compared to the effect of maternal non-kin.

a consistent effect on preferred grooming partners (Fig. A.5), and we did not find much stronger support for any of the alternative models compared to the null model (Table 2).

Supplementary Fig. A.5 can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2014.04.002.

4. Discussion

4.1. Familiarity

Approach rates among non-kin were not strongly affected by the time females had spent co-resident, which is similar to the association pattern in Thornicroft's giraffe (*Giraffa camelopardalis*) (Bercovitch and Berry, 2013). Although females appeared to groom long-term co-residents more than short-term co-residents, our sample size was too small for investigating if this was a statistically significant difference. Therefore, we did not find strong support for the hypothesis that affiliation is positively affected by familiarity through long co-residency although this result needs to be confirmed with a larger sample size. This finding differs from several studies of rodents (Ferkin, 1988; Ganem and Bennett, 2004; Rosell et al., 2008) and apes (Kahlenberg et al., 2008; Nishida, 1989; Robbins et al., 2005; Watts, 1991, 1994) in which animals discriminate against recent immigrants. However, our results may be explained by the fact that the immigrant females in our study had resided long enough in the groups to become integrated in the proximity network. For example, recent immigrant female gorillas (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes*) often face higher levels of aggression and are more peripheral, but become socially integrated with time (Kahlenberg et al., 2008; Nishida, 1989; Robbins et al., 2005; Watts, 1991, 1994). This increase in affiliation with longer tenure suggests that females bias friendly interactions against immigrant females based on familiarity rather than phenotypic similarity. It is possible that familiar females are more reliable social partners than less familiar females, and that females gain greater direct fitness benefits from forming affiliative relationships with familiar females (Chapais, 2001).

Among long-term co-resident females, maternal kinship (e.g. mother–daughters, full siblings and maternal half siblings) had a positive effect on approach rates and grooming durations. This finding is similar to several female philopatric species where females form the strongest bonds with close maternal kin, and it adds further support for the mother-mediated familiarity hypothesis (Archie et al., 2006; Hirsch et al., 2012; Perry et al., 2008; Silk

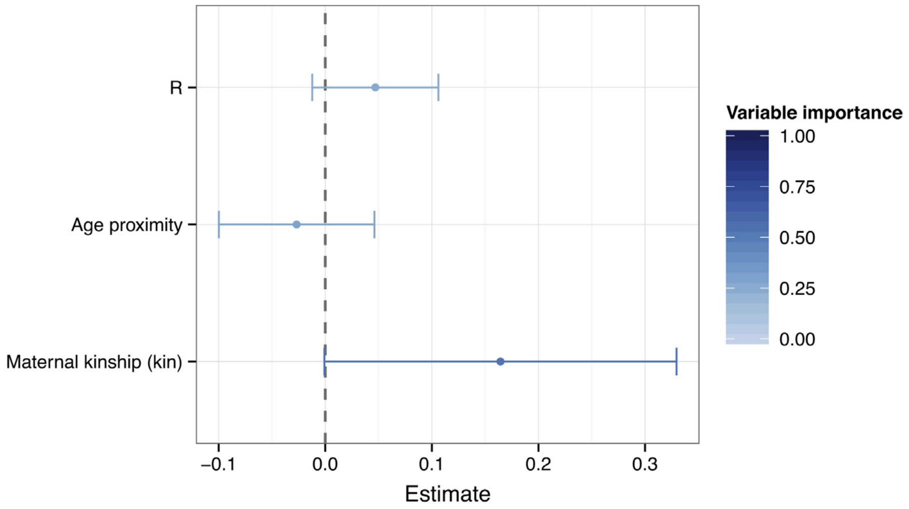

Fig. 5. Estimates and confidence intervals from the grooming model that included females with access to long-term maternal kin and non-kin. See legend for Fig. 4 for more details.

et al., 2006; Widdig et al., 2001). In contrast, maternal kinship was not a good predictor for the choice of preferred grooming partners. This surprising finding might be due to the fact that females did not spend much time grooming others, and that they typically only had one preferred grooming partner even when they resided with several maternal kin (this study; Wikberg et al., 2014). A greater proportion of mothers, daughters, and full siblings were preferred grooming partners compared to maternal half siblings, and it was only in the analysis of preferred grooming partners that estimated relatedness values had higher variable importance than maternal kinship. This leaves open the possibility that females prefer to groom more closely related maternal kin than maternal half siblings. A larger number of females with access to different types of maternal kin are required to further investigate this possibility.

We did not find any evidence that females distinguished paternal half siblings from non-kin, which is similar to a study of male chimpanzees (*Pan troglodytes*) and female white-faced capuchins (*Cebus capucinus*) (Langergraber et al., 2007; Perry et al., 2008). In contrast, female rhesus macaques (*Macaca mulatta*) and female yellow baboons (*Papio cynocephalus*) discriminate paternal half siblings from non-kin even though they form the strongest relationship with their maternal kin (Schuelke et al., 2013; Silk et al., 2006; Widdig et al., 2001). Why some primate populations but not others discriminate paternal half siblings from non-kin is still under debate (reviewed in Widdig, 2013). It may be that females form particularly strong bonds with paternal half siblings if they lack maternal kin (Silk et al., 2006). In our study, only two females resided with paternal but no maternal kin, and none of them formed strong bonds with their paternal kin (ECW unpublished data). As a matter of fact, very few of the adult females in our study resided with paternal half siblings despite a high proportion of paternal half siblings among immature animals. This suggests that a female's access to paternal half siblings decreases over time, possibly due to female dispersal and group fission along matrilines (Metheny et al., 2008; Van Horn et al., 2007; Widdig et al., 2006). Small female group sizes due to a combination of female dispersal and group fission in our study species may be the reason why females did not reside with as many paternal half siblings as female philopatric primates like macaques and baboons (Schülke and Ostner, 2012; Silk et al., 2006; Widdig et al., 2001). If female colobus rarely reside with paternal kin in comparison to maternal kin, recognizing paternal kin (i.e. kin recognition) and forming strong relationships with them (i.e. kin discrimination) may not have a significant impact on lifetime reproductive success.

Age proximity did not affect approach rates or grooming durations in our study, and we did not find any support for the age-mediated familiarity hypothesis. This is similar to a study of captive rhesus macaques (Schuelke et al., 2013) while it differs from several studies of wild or free-ranging primates (Silk et al., 2006; Smith et al., 2003; Widdig et al., 2001), ungulates (Bercovitch and Berry, 2013; Murray, 1981), and cetaceans (Ramp et al., 2010). Some of the differences in how age affects social relationships may be linked to how well age proximity corresponds to paternal sibship. In population of baboons, females show paternal kin bias, and animals belonging to the same age cohort are seven times more likely to be paternal siblings than animals from different age cohorts (Silk et al., 2006). In two primate populations without any evidence of paternal kin bias in affiliation, age proximity is a poor proxy for paternal sibship (Langergraber et al., 2007; Perry et al., 2008). Infants in one of our multi-male study group were three times more likely to be paternal siblings if they belonged to the same age cohort rather than different age cohorts. However, age proximity was not as good proxy for paternal kinship in one of our uni-male groups with a long male tenure. The accuracy of age proximity as a proxy for paternal sibship in our study population may therefore lie in the middle of the range reported for other primates. More studies are needed to systematically investigate if paternal kin discrimination is affected by the accuracy of using age-mediated familiarity as a proxy for paternal sibship (Widdig, 2013).

4.2. Phenotype matching

Female colobus that resided with short-term co-resident maternal kin did not bias affiliation toward these less familiar kin. Even though females acted as if they did not recognize these less familiar kin, one must distinguish between kin recognition and kin discrimination because the ability to recognize kin does not necessarily lead to kin discrimination as demonstrated in Belding's ground squirrels (*Spermophilus beldingi*) (Mateo, 2003) and Japanese macaques (*Macaca fuscata*) (Chapais et al., 1997). Female Japanese macaques frequently supported their nieces against lower-ranking females but not against higher-ranking females, and the occurrence of kin discrimination was linked to how costly the specific behavior was to the actor (Chapais et al., 1997). Thus, we cannot determine if female colobus were unable to recognize kin via phenotype matching, or if they simply lacked the motivation to approach and groom less familiar kin.

Estimated relatedness values did not have a strong, consistent effect on approach rates or grooming durations. Based on these findings, we conclude that females do not choose social partners based on their phenotypic similarity. The lack of evidence for partner choice based on phenotypic similarity in our study contrasts to findings from wild hyenas (Wahaj et al., 2004) and rodents in experimental settings (Dewsbury, 1988; Kareem & Barnard, 1982; Mateo and Johnston, 2000; Schwagmeyer, 1988). As a matter of fact, the evidence for phenotype matching in primates remains ambiguous (Rendall, 2004). Although rhesus macaques can distinguish paternal half siblings from non-kin regardless of their age proximity (Widdig et al., 2001), it is not clear if they use phenotype matching or father-mediated familiarity to do so.

It is also possible that the lack of a positive result in our study is due to estimated relatedness values being a poor predictor of phenotypic similarity and actual relatedness (Csillery et al., 2006). In some populations, estimated relatedness cannot accurately predict actual relatedness calculated from pedigrees (Csillery et al., 2006; Van Horn et al., 2008). This may partly be due to a high proportion of unrelated dyads, some of which have high estimated relatedness values by chance (Van Horn et al., 2008). Our preliminary results indicate that the estimated relatedness values in our study population are relatively accurate. However, further studies with larger samples sizes of known kin are required to fully evaluate how well estimated relatedness values correspond to phenotypic similarity in our study population. Future studies could also obtain more accurate estimates of overall phenotypic similarity by using massively parallel sequencing, which simultaneously genotype thousands of loci located throughout an animal's genome (Bradley and Lawler, 2011). The final methodological concern regarding the usage of short tandem repeat loci to estimate phenotypic similarity is that overall phenotypic similarity may not actually be the basis for phenotype matching. Animals may choose social or mating partners based on phenotypic similarity coded by a certain locus or a small set of loci, rather than using overall phenotypic similarity (Huchard and Pechouskova, 2014). For example, tadpoles (*Xenopus laevis*) prefer to associate with full siblings with similar rather than dissimilar major histocompatibility complex, which suggests that partner preferences in this species are based on phenotypic similarity for this particular trait (Villinger and Waldman, 2012). We know very little of the mechanisms that underlie partner choice based on phenotypic similarity in most species, and further studies are required to investigate these mechanisms.

4.3. Summary

Mother-mediated familiarity had a stronger effect than phenotypic similarity in shaping social relationships, and familiarity appeared to be a prerequisite for the formation of strong social relationships in *C. vellerosus*. This conforms to the pattern documented in female philopatric primates despite the fact that half of the females in our study population disperse, which may weaken the accuracy of using familiarity as a kin recognition mechanism. We encourage other researchers to investigate kin recognition in animals with facultative dispersal as we believe that it can be a fruitful approach to disentangle the effects of relatedness and familiarity.

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References

Abdi, H., 2007. Z-scores. In: Salkind, N.J. (Ed.), Encyclopedia of Measurement and Statistics. Thousand Oaks, Sage, pp. 1057–1058.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Automat. Control AC-19, 716–723.

Altmann, J., 1974. Observational study of behaviour: sampling methods. Behaviour 49, 223–265.

Altmann, J., 1979. Age cohorts as paternal sibships. Behav. Ecol. Sociobiol. 6, 161–164.

Altmann, J., Alberts, S.C., Haines, S.A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, D.J., Mututua, R.S., Saiyalel, S.N., Wayne, R.K., Lacy, R.C., Bruford, M.W., 1996. Behavior predicts genetic structure in a wild primate group. Proc. Natl. Acad. Sci. U.S.A. 93, 5797–5801.

Archie, E.A., Moss, C.J., Alberts, S.C., 2006. The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. Proc. R. Soc. Lond. B Biol. 273, 513–522.

Barton, K., 2013. MuMIn: Multi-Model Inference. R Package Version 1.9.5, http://CRAN.R-project.org/package=MuMIn (accessed 01.05.13).

Bates, D., Maechler, M., Bolker, B., 2012. lme4: Linear Mixed-Effects Models using S4 Classes, http://lme4.r-forge.r-project.org/ (accessed 21.09.12).

Bercovitch, F.B., Berry, P.S.M., 2013. Age proximity influences herd composition in wild giraffe. J. Zool. 290, 281–286.

Bradley, B.J., Lawler, R.R., 2011. Linking genotypes phenotypes, and fitness in wild primate populations. Evol. Anthropol. 20, 104–119.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer, New York.

Chapais, B., 2001. Primate nepotism: what is the explanatory value of kin selection? Int. J. Primatol. 22, 203–229.

Chapais, B., Gauthier, C., PrudHomme, J., Vasey, P., 1997. Relatedness threshold for nepotism in Japanese macaques. Anim. Behav. 53, 1089–1101.

Csillery, K., Johnson, T., Beraldi, D., Clutton-Brock, T., Coltman, D., Hansson, B., Spong, G., Pemberton, J.M., 2006. Performance of marker-based relatedness estimators in natural populations of outbred vertebrates. Genetics 173, 2091–2101.

Dal Martello, M.F., Maloney, L.T., 2006. Where are kin recognition signals in the human face? J. Vis. 6, 1356–1366.

Dewsbury, D.A., 1988. Kinship, familiarity, aggression, and dominance in deer mice (*Peromyscus maniculatus*) in seminatural enclosures. J. Comp. Psychol. 102, 124–128.

Erhart, E., Coelho, A.J., Bramblett, C., 1997. Kin recognition by paternal half-siblings in captive *Papio cynocephalus*. Am. J. Primatol. 43, 147–157.

Ferkin, M.H., 1988. The effect of familiarity on social interactions in meadow voles *Microtus pennsylvanicus* – a laboratory and field study. Anim. Behav. 36, 1816–1822.

Forstmeier, W., Schielzeth, H., Mueller, J.C., Ellegren, H., Kempenaers, B., 2012. Heterozygosity-fitness correlations in zebra finches: microsatellite markers can be better than their reputation. Mol. Ecol. 21, 3237–3249.

Ganem, G., Bennett, N.C., 2004. Tolerance to unfamiliar conspecifics varies with social organization in female African mole-rats. Physiol. Behav. 82, 555–562.

Gompper, M.E., Gittleman, J.L., Wayne, R.K., 1997. Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. Anim. Behav. 53, 781–797.

Goslee, S.C., Urban, D.L., 2007. The ecodist package for dissimilarity-based analysis of ecological data. J. Statist. Softw. 22, 1–19.

Greenwood, P.J., 1980. Mating systems philopatry and dispersal in birds and mammals. Anim. Behav. 28, 1140–1162.

Griffin, A.S., West, S.A., 2003. Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. Science 302, 634–636.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699–711.

Guilhem, C., Bideau, E., Gerard, J.F., Maublanc, M.L., 2000. Agonistic and proximity patterns in enclosed mouflon (*Ovis gmelini*) ewes in relation to age reproductive status and kinship. Behav. Process. 50, 101–112.

Hall, J.B., Swaine, M.D., 1981. Distribution and Ecology of Vascular Plants in a Tropical Rain Forest: Forest vegetation in Ghana. The Hague, Boston.

Hare, J.F., 1998. Juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) manifest both littermate and neighbour/stranger discrimination. Ethology 104, 991–1002.

Hinz, C., Gebhardt, K., Hartmann, A.K., Sigman, L., Gerlach, G., 2012. Influence of kinship and MHC class II genotype on visual traits in zebrafish larvae (*Danio rerio*). PLoS ONE 7.

Hirsch, B.T., Stanton, M.A., Maldonado, J.E., 2012. Kinship shapes affiliative social networks but not aggression in ring-tailed coatis. PLoS ONE 7, e37301.

Holmes, W.G., Sherman, P.W., 1982. The ontogeny of kin recognition in 2 species of ground squirrels. Am. Zool. 22, 491–517.

Huchard, E., Pechouskova, E., 2014. The major histocompatibility complex and primate behavioralecology: new tools and future questions. Int. J. Primatol. 35, 11–31.

Jones, O.R., Wang, J., 2010. COLONY: a program for parentage and sibship inference from multilocus genotype data. Mol. Ecol. Res. 10, 551–555.

Kahlenberg, S.M., Thompson, M.E., Muller, M.N., Wrangham, R.W., 2008. Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. Anim. Behav. 76, 1497–1509.

Kalinowski, S.T., Taper, M.L., Marshall, T.C., 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol. Ecol. 16, 1099–1106.

Kapsalis, E., 2004. Matrilineal kinship and primate behavior. In: Chapais, B., Berman, C.M. (Eds.), Kinship and Behavior in Primates. Oxford, Oxford University Press, pp. 153–176.

Kareem, A.M., Barnard, C.J., 1982. The importance of kinship and familiarity in social interactions between mice. Anim. Behav. 30, 594–601.

Kazem, A.J.N., Widdig, A., 2013. Visual phenotype matching: cues to paternity are present in rhesus macaque faces. PLoS ONE 8.

Koenig, B., 1994. Fitness effects of communal rearing in house mice: the role of relatedness versus familiarity. Anim. Behav. 48, 1449–1457.

Langergraber, K.E., Mitani, J.C., Vigilant, L., 2007. The limited impact of kinship on cooperation in wild chimpanzees. Proc. Natl. Acad. Sci. U.S.A. 104, 7786–7790.

Lehmann, J., Boesch, C., 2009. Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*. Anim. Behav. 77, 377–387.

Marshall, T.C., Slate, J., Kruuk, L.E.B., Pemberton, J.M., 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Mol. Ecol. 7, 639–655.

Mateo, J.M., 2003. Kin recognition in ground squirrels and other rodents. J. Mammal. 84, 1163–1181.

Mateo, J.M., Johnston, R.E., 2000. Kin recognition and the 'armpit effect': evidence of self-referent phenotype matching. Proc. R. Soc. Lond. B Biol. 267, 695–700.

McDonald, P.G., Wright, J., 2011. Bell miner provisioning calls are more similar among relatives and are used by helpers at the nest to bias their effort towards kin. Proc. R. Soc. Lond. B Biol. 278, 3403–3411.

Metheny, J.D., Kalcounis-Rueppell, M.C., Bondo, K.J., Brigham, M.R., 2008. A genetic analysis of group movement in an isolated population of tree-roosting bats. Proc. R. Soc. Lond. B Biol. 275, 2265–2272.

Milligan, B.G., 2003. Maximum-likelihood estimation of relatedness. Genetics 163, 1153–1167.

Murray, M., 1981. Structure of association in impala, *Aepyceros melampus*. Behav. Ecol. Sociobiol. 9, 23–33.

Nishida, T., 1989. Social interactions between resident and immigrant female chimpanzees. In: Heltne, P.G., Marquardt, L.A. (Eds.), Understanding Chimpanzees. Harvard University Press, Cambridge, Massachusetts, pp. 68–89.

Perry, S., Manson, J., Muniz, L., Gros-Louis, J., Vigilan, t.L., 2008. Kin-biased social behaviour in wild adult female white-faced capuchins, *Cebus capucinus*. Anim. Behav. 76, 187–199.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, t.R.D.C., 2012. nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3., pp. 1–103 (accessed 21.09.12).

R Core Team, 2013. R: A Language and Environment for Statistical Computing: R Foundation for Statistical Computing, http://www.R-project.org (accessed 01.12.13).

Ramp, C., Hagen, W., Palsbøll, P., Bérubé, M., Sears, R., 2010. Age-related multi-year associations in female humpback whales (*Megaptera novaeangliae*). Behav. Ecol. Sociobiol. 64, 1563–1576.

Rendall, D., 2004. Recognizing kin: mechanisms, media, minds, modules, and muddles. In: Chapais, B, Berman, C.M. (Eds.), Kinship and Behavior in Primates. Oxford University Press, Oxford, pp. 295–316.

Robbins, M.M., Robbins, A.M., Gerald-Steklis, N., Steklis, H.D., 2005. Long-term dominance relationships in female mountain gorillas: strength, stability and determinants of rank. Behaviour 142, 779–809.

Robinson, S.P., Simmons, L.W., Kennington, W.J., 2013. Estimating relatedness and inbreeding using molecular markers and pedigrees: the effect of demographic history. Mol. Ecol. 22, 5779–5792.

Rollins, L.A., Browning, L.E., Holleley, C.E., Savage, J.L., Russell, A.F., Griffith, S.C., 2012. Building genetic networks using relatedness information: a novel approach for the estimation of dispersal and characterization of group structure in social animals. Mol. Ecol. 21, 1727–1740.

Rosell, F., Gundersen, G., Le Galliard, J.-F., 2008. Territory ownership and familiarity status affect how much male root voles (*Microtus oeconomus*) invest in territory defence. Behav. Ecol. Sociobiol. 62, 1559–1568.

Sackett, G.P., Fredrickson, W.T., 1987. Social preferences by pigtailed macaques. Familiarity versus degree and type of kinship. Anim. Behav. 35, 603–606.

Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol. Evol. 1, 103–113.

Schuelke, O., Wenzel, S., Ostner, J., 2013. Paternal relatedness predicts the strength of social bonds among female rhesus macaques. PLoS ONE 8, e59789.

Schülke, O., Ostner, J., 2012. Ecological and social influences on sociality. In: Mitani, J., Call, J., Kappeler, P., Palombit, R., Silk, J. (Eds.), The Evolution of Primate Societies. Chicago, University of Chicago Press, pp. 193–219.

Schwagmeyer, P.L., 1988. Ground-squirrel kin recognition abilities – are there social and life-history correlates. Behav. Genet. 18, 495–510.

Silk, J.B., Altmann, J., Alberts, S.C., 2006. Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61, 183–195.

Smith, K., Alberts, S.C., Altmann, J., 2003. Wild female baboons bias their social behaviour towards paternal half-sisters. Proc. R. Soc. Lond. B Biol. 270, 503–510.

Teichroeb, J.A., Wikberg, E.C., Sicotte, P., 2009. Female dispersal patterns in six groups of ursine colobus (*Colobus vellerosus*): infanticide avoidance is important. Behaviour 146, 551–582.

Van Horn, R.C., Altmann, J., Alberts, S.C., 2008. Can't get there from here: inferring kinship from pairwise genetic relatedness. Anim. Behav. 75, 1173–1180.

Van Horn, R.C., Buchan, J.C., Altmann, J., Alberts, S.C., 2007. Divided destinies: group choice by female savannah baboons during social group fission. Behav. Ecol. Sociobiol. 61, 1823–1837.

Villavicencio, C.P., Natalia Marquez, I., Quispe, R., Vasquez, R.A., 2009. Familiarity and phenotypic similarity influence kin discrimination in the social rodent *Octodon degus*. Anim. Behav. 78, 377–384.

Villinger, J., Waldman, B., 2012. Social discrimination by quantitative assessment of immunogenetic similarity. Proc. R. Soc. Lond. B Biol. 279, 4368–4374.

Vokey, J.R., Rendall, D., Tangen, J.M., Parr, L.A., de Waal, F.B.M., 2004. Visual kin recognition and family resemblance in chimpanzees (*Pan troglodytes*). J. Comp. Psychol. 118, 194–199.

Wahaj, S.A., Van Horn, R.C., Van Horn, T.L., Dreyer, R., Hilgris, R., Schwarz, J., Holekamp, K.E., 2004. Kin discrimination in the spotted hyena (*Crocuta crocuta*): nepotism among siblings. Behav. Ecol. Sociobiol. 56, 237–247.

Walling, C.A., Pemberton, J.M., Hadfield, J.D., Kruuk, L.E.B., 2010. Comparing parentage inference software: reanalysis of a red deer pedigree. Mol. Ecol. 19, 1914–1928.

Walters, J.R., 1987. Kin recognition in non-human primates. In: Fletcher, D., Michener, C. (Eds.), Kin Recognition in Animals. John Wiley & Sons, Colchester, Essex.

Wang, J., 2011. COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. Mol. Ecol. Res. 11, 141–145.

Watts, D.P., 1991. Harassment of immigrant female mountain gorillas by resident females. Ethology. 89, 135–153.

Watts, D.P., 1994. Social relationships of immigrant and resident female mountain gorillas, II. Relatedness, residence, and relationships between females. Am. J. Primatol. 32, 13–30.

Widdig, A., 2007. Paternal kin discrimination: the evidence and likely mechanisms. Biol. Rev. 82, 319–334.

Widdig, A., 2013. The impact of male reproductive skew on kin structure and sociality in multi-male groups. Evol. Anthropol. 22, 239–250.

Widdig, A., Nurnberg, P., Bercovitch, B., Trefilov, A., Berard, J.B., Kessler, M.J., Schmidtke, J., Streich, W.J., Krawczak, M., 2006. Consequences of group fission for the patterns of relatedness among rhesus macaques. Mol. Ecol. 15, 3825–3832.

Widdig, A., Nurnberg, P., Krawczak, M., Streich, W.J., Bercovitch, F.B., 2001. Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. Proc. Natl. Acad. Sci. U.S.A. 98, 13769–13773.

Wikberg, E., Ting, N., Sicotte, P., 2014. Kinship and similarity in residency status structure female social networks in black-and-white colobus monkeys (*Colobus vellerosus*). Am. J. Phys. Anthropol. 153, 365–376.

Wikberg, E.C., Sicotte, P., Campos, F., Ting, N., 2012. Between-group variation in female dispersal, kin composition of groups, and proximity patterns in a black-and-white colobus monkey (*Colobus vellerosus*). PLoS ONE 7, e48740.

Wilkinson, G.S., 1986. Social grooming in the common vampire bat, *Desmodus rotundus*. Anim. Behav. 34, 1880–1889.

Wong, S.N.P., Sicotte, P., 2006. Population size and density of *Colobus vellerosus* at the Boabeng-Fiema Monkey Sanctuary and surrounding forest fragments in Ghana. Am. J. Primatol. 68, 465–476.

Wu, H., Holmes, W., Medina, S., Sackett, G., 1980. Kin preference in infant Macaca nemestrina. Nature 285, 225–227.