



Distribution of Affiliative Behavior Across Kin Classes and Their Fitness Consequences in Mandrills

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Received: May 29, 2012

Initial acceptance: July 23, 2012

Final acceptance: September 24, 2012

(L. Fusani)

doi: 10.1111/eth.12026

Abstract

Multimale–multifemale primate groups are ideal models to study the impact of kinship on the evolution of sociality. Indeed, the frequent combination of female philopatry and male reproductive skew produces social systems where both maternal and paternal kin are co-resident. Several primates are known to bias their behavior toward both maternal and paternal kin. Moreover, allocation of affiliation toward paternal kin has been shown to depend on the availability in maternal kin: Female baboons invest more in paternal kin after the loss of preferred maternal kin. Here, we examined how affiliation co-varies across kin classes in a multimale–multifemale society. While affiliation levels observed with the mother and with maternal half-sibs co-varied positively, especially in young females, we found that levels of affiliation among paternal half-sibs correlated negatively with levels of affiliation among individuals from the same matriline (distant kin), possibly as a result of kin availability. In addition, in social species, social bonds between individuals have been linked to differentiated fitness consequences: More socially integrated individuals generally enjoy higher fitness. We therefore also tested whether affiliation during early life impacts fitness. We showed that the global amount of affiliation during juvenescence translated into possible reproductive benefits: Females who were more socially integrated gave birth on average a year before females that were less socially integrated. However, age at first reproduction was not predicted by the amount of affiliation exchanged with any particular kin class. These results add to the growing body of evidence demonstrating differential investment in bonding and possible social adjustments among different kin categories and emphasizing once more the adaptive value of sociality.

Since its first formulation by Hamilton (Hamilton 1964), kin selection, defined as the natural selection promoting relatives, has provided a framework to explain the numerous cases of altruistic behavior observed among relatives in most animal societies. Kin selection has been proposed to play a key role in

the evolution of eusociality (Hughes et al. 2008) and to explain other striking examples of animal cooperation and sociality (Clutton-Brock 2002; Hughes et al. 2008; Hatchwell 2009; Cornwallis et al. 2010; Lukas & Clutton-Brock 2012). The Primate Order is ideally suited to study the impact of kin selection on the

evolution of sociality because most species live in highly complex, hierarchical societies often structured around elaborated social networks of kin (Silk 2009). Strong bonds between mother and offspring are established initially through lactation, followed by an extended period of juvenility (Gouzoules & Gouzoules 1987). Because many primate species exhibit female philopatry (Greenwood 1980; Pusey 1987), female maternal kin may interact with each other throughout their lifetime. Social networks in several primate species are therefore often structured around stable families of maternally related females called 'matrilines' (Gouzoules & Gouzoules 1987; Silk 2009). Maternal kin are often spatially associated and exhibit differentiated social relationships, such as increased tolerance and reconciliation, higher number of grooming interactions and lower aggression rates (Silk 2002, 2009; Berman & Chapais 2004). Nepotism among maternal kin has also been reported in non-gregarious species (e.g., Delgado & Van Schaik 2000; Kappeler et al. 2002) as well as among males in species characterized by male philopatry (e.g., Mitani 2009; and see for review: Silk 2009).

In several multimale–multifemale primate groups, reproduction is often highly skewed toward one or a few dominant males (e.g., Alberts et al. 2003; Widdig et al. 2004; Charpentier et al. 2005; Schülke & Ostner 2008; Port & Kappeler 2010). A direct consequence of such a reproductive system is that numerous individuals are genetically related through the paternal line. Moreover, fathers may also stay in the natal group of their offspring for extended periods (Widdig 2007). Consequently, in these species, individuals have the potential to interact with paternal kin. Theoretically, kin selection should act on socio-sexual relationships between paternal kin in several contexts: avoiding sexual interactions, directing paternal care, and directing beneficial behavior (Widdig 2007). While observational data on paternal biases remain limited (Widdig 2007), some studies based on several multimale–multifemale species nevertheless revealed evidence of paternal kin biases in each of these contexts. First, incest avoidance behavior has been documented in wild baboons (Alberts 1999) and in capuchin monkeys (Muniz et al. 2006). Second, male baboons are able to differentiate between their own offspring and the offspring of other males and preferentially support the former during social disputes (Buchan et al. 2003). Finally, in baboons, paternal sisters form closer affiliative bonds than non-kin (Silk et al. 2006a,b), and in rhesus macaques, females affiliate more and intervene

significantly less often against their paternal sisters compared to unrelated females (Widdig et al. 2001; 2006). In two outstanding articles, Silk and colleagues (Silk et al. 2006a,b) went beyond by studying dynamic co-variations in the distribution of affiliation across kin classes in female yellow baboons. In this species, females compensate for the absence of close maternal kin by forming strong social bonds with paternal kin. When paternal kin are also absent from the social environment, females establish social ties with non-kin (Silk et al. 2006a,b).

Studies across different animal taxa have suggested that kin bonds are adaptive. For example, in Pygmy grasshoppers (*Tetrix subulata*), individuals' survival is improved when kin are present in the group (Caesar et al. 2010). In Columbian ground squirrels (*Urocitellus columbianus*), reproductive success increases when association of philopatric female kin increases (Viblanco et al. 2010). Empirical evidence of the adaptive nature of kin bonds in primates is, however, often indirect. For example, maternal kin support is a major determinant of female rank acquisition in several species (see for review: (Silk 2009)), and female dominance rank has been shown to improve fitness in a number of species (e.g., Altmann et al. 1988; Pusey et al. 1997). In these primate societies that are structured by heritable matrilineal hierarchies, it is not obvious that individuals can also benefit from interacting with paternal kin. Although rare, empirical evidence for the fitness benefits of interacting with paternal kin has nevertheless been reported. In wild savannah baboons, the presence of the father during juvenility accelerated the timing of physiological maturation in offspring (Charpentier et al. 2008), possibly through social support from fathers during agonistic disputes involving their offspring (Buchan et al. 2003).

Here, we report on variation in affiliation patterns that occurred between juvenile mandrills (*Mandrillus sphinx*) and all members of their social group, pooled in different kin classes, as well as the fitness consequences of such behavior. Mandrill is an excellent model species to study the distribution of affiliation across kin classes. First, it is a typical matrilineal, multimale–multifemale society where strong social bonds exist among maternal kin (Charpentier et al. 2007). Second, reproduction is highly skewed among males; the alpha male generally monopolizes about 70% of reproduction (Charpentier et al. 2005). Each birth cohort therefore includes numerous paternal half-sibs. Consequently, there is high potential for paternal kin biases to develop. Third, in an earlier study, we showed that juvenile mandrills affiliated more often with paternal half-siblings and were closer to their

father than to unrelated individuals, and the intensity of affiliation observed with paternal half-sib females was of the same order of magnitude as affiliation observed with maternal half-sib females (Charpentier et al. 2007). The present analyses extend previous work in two directions. First, we investigated how affiliation levels co-vary among five defined maternal, paternal and non-kin classes. We also tested whether individual characteristics of juveniles (age, sex, or rank) may play a role in driving patterns of affiliation co-variations among kin classes. We further analyzed whether affiliation observed in a given kin class depends on kin availability in another class. Second, we examined whether affiliation during early life in mandrills has fitness consequences, in terms of growth patterns and reproduction, as shown in other species (see for review in mammals: Silk 2007). When a significant relationship was detected, we explored whether affiliation with different kin classes showed differential fitness consequences.

Methods

Study population and animals

The mandrill colony at CIRMF (Centre International de Recherches Médicales de Franceville), Gabon, was established in 1983 when 15 founder animals of both sexes were released into a large forested enclosure. Any further increase in group size has been the result of natural reproduction of these founder animals, countered by deaths and some removals for experimental purposes (see for more details on the colony: e.g., Charpentier et al. 2005, 2007). The mandrill colony has been split on several occasions to control overcrowding and to limit the spread of naturally occurring STLV and SIV viruses. In March 2002, at the beginning of this study, the colony consisted of three semi-free ranging groups living in three adjacent enclosures. This study focuses on 30 juvenile mandrills (14 females, 16 males) housed in the largest (6 ha) of the three enclosures numbering about 100 animals of both sexes and all ages. Individuals included in this study comprised mandrills that were weaned by the beginning of the behavioral observations but not yet sexually mature: Females were all nulliparous (aged 1.33–3.98 yrs) and males were younger (aged 1.39–5.30) than the youngest male known to have reproduced in this population in the presence of adult males (i.e., 5.6 yrs; Setchell et al. 2005).

Mandrills are fed twice a day with seasonal fruits and monkey chow to supplement their foraging.

Water is available *ad libitum*. Data collected for this study did not affect the daily life of the mandrills.

Behavioral observations

Behavioral observations of the 30 juveniles were carried out on a daily basis from March 2002 to January 2004, before feeding times to avoid increased aggression between group members due to feeding competition (i.e., from 10:00 to 12:00 hours and from 16:00 to 18:00 hours, see: Charpentier et al. 2007, for more details on behavioral observations performed on a subset of 22 juveniles). Data were collected using the focal sampling method (Altmann 1974) and the sequence in which animals were observed was randomized. A focal observation corresponded to a 6-min period during which one of us (MJEC) recorded all social behavior that occurred between the focal juveniles and all group members. We recorded between 26 and 67 focal observations per individual (mean \pm SD: 41.8 ± 14.4). Note that the 30 juveniles were not all observed at the same time of the study period, depending on age (some studied juveniles entered into the study later because they were still dependent offspring in March 2002) and on colony management (some studied juveniles were removed during the course of the study, see: Peignot et al. 2008). All group members were individually recognizable except for the very young animals (aged 0–2 yrs). We discarded from subsequent analyses all interactions that occurred with these very young animals as we were unable to determine their kin relationships with the juveniles. In this study, we restricted our analyses to bouts of affiliative behavior that occurred among the 30 studied juveniles and all other group members, including grooming, muzzle contact, and affiliative contact. For each juvenile, all affiliative interactions were pooled per kin class (see below).

Genetic analyses of paternity and kin classes

All CIRMF mandrills are captured annually for routine veterinary checks. Blood samples are taken on each occasion. DNA was extracted from buffy coats. The full pedigree of the mandrill colony was established in 2002–2003 using genetic paternity analyses based on eight informative microsatellite loci (for more details, see: Charpentier et al. 2005, 2007). Because all potentially reproductive males were genotyped, there is no missing information in the pedigree except for the very rare cases where some offspring died before being sampled. Paternity was

also not assigned for one adolescent male (never sampled). The few affiliative interactions involving this adolescent male were excluded from all subsequent analyses.

Five different kin classes were defined as follows: mother, maternal half-sibs, paternal half-sibs, individual belonging to the same matriline (excluding individuals from the two first classes), and 'non-kin'. Note that the individuals from the same matriline are composed of more distant maternal kin than maternal half-sibs. On rare occasions, some individuals belonged to more than one kin class (e.g., full-sibs belonged to both maternal half-sib and paternal half-sib classes). The rationale for categorizing such cases was based on our knowledge of the mandrill society: first, it is a typical matrilineal society characterized by strong social bonds among maternal kin, but second, social bonds among paternal kin are also known to occur (Charpentier et al. 2007). These observations were translated into the two following decisions: full-sibs were pooled with maternal half-sibs (seven dyads over a total of 78 maternal half-sib dyads); paternal half-sibs that also belonged to the same matriline (but were not maternal half-sibs) were grouped into the class of paternal half-sibs (54 dyads over 299 paternal half-sib dyads). All other individuals who did not belong to these four kin classes were classified as non-kin. These non-kin dyads may have included distant kin as male dispersal is limited in this mandrill population, and therefore, mean relatedness among group members is expected to be higher than in the wild. However, in most primate species, kin biases are mainly observed among closely related animals (e.g., Chapais et al. 1997). Fathers were excluded from analyses as they did not show any affiliative interactions with juveniles (but for results on spatial proximity, see: Charpentier et al. 2007). All but one juvenile still had their mother in the group and they had between 0 and 6 maternal half-sibs (mean \pm SD: 2.6 ± 2.1); between 0 and 17 paternal half-sibs (10.4 ± 5.6); between 0 and 23 individuals belonging to the same matriline (mean \pm SD: 7.7 ± 5); and between 26 and 49 non-kin (mean \pm SD: 37.7 ± 7.4).

Statistical analyses and covariates

Variations of affiliation return

Variation of affiliation across kin classes: We studied the relationships between numbers of affiliative interactions that occurred between the 30 juveniles and the members of the five kin classes. We performed a total of five regression analyses where the number of affiliative interactions within each kin class was the

response variable and the number of affiliations within each of the four other kin classes, the predictors. We used generalized linear models (proc GENMOD, SAS V9.2, Cary, NC, USA) with a negative binomial distribution and a log-link function because our response variables were count data showing over-dispersion. We did not correct for multiple testing in these analyses because the validity of such corrections has been questioned as they increase the probability of producing false negatives, especially when sample sizes are limited (Nakagawa 2004; Teriokhin et al. 2007). We weighted our analyses by the number of focal observations performed per juvenile in order to give more weight to individuals observed for a longer period of time.

When significant co-variations were detected, we performed two additional analyses. First, we added three parameters to our previous generalized linear models (juvenile's age at the beginning of the study, juvenile's sex and juvenile's matrilineal rank) as well as the interactions between each of these traits and affiliation levels with the considered kin class. This analysis aimed at examining whether the correlation of affiliation levels observed between two categories of kin depended on juvenile characteristics. For instance, individuals from high-ranking matrilineal lines may display stronger bonds than others. In juvenile mandrills, dominance rank is maternally acquired. Consequently, we considered juvenile's matrilineal rank based on approach-avoidance behavior routinely recorded in adult females since the implementation of the colony. We extracted rank data from long-term colony records, and we considered this predictor as a qualitative factor with three levels: high-, mid- and low-ranking matrilineal lines. Second, we studied whether the number of kin available in one kin class influenced the affiliation rates (number of affiliation divided by the number of focal observations) observed with the other kin class, using Pearson correlations (proc CORR, SAS V9.2). These second analyses allowed us to test whether the co-variations between affiliation levels observed were caused by kin availability.

Exploring affiliation levels among close maternal kin: Previous analyses revealed a significant positive correlation between affiliation levels observed among maternal half-sibs and affiliation levels recorded with the mother. To further explore this relationship, we studied the correlation between affiliation observed among maternal half-sibs and proximity with the mother (Pearson correlation test; proc CORR, SAS V9.2). Proximity data were obtained using scan sampling (as described in: Charpentier et al. 2007). We also studied the correlation between affiliation

levels recorded with close maternal kin (maternal half-sibs and mother) and affiliation levels recorded with all other group members (Pearson correlation test; proc CORR, SAS V9.2). This latter analysis allowed controlling whether juveniles that showed strong affiliation with close maternal kin were more social than other juveniles.

Affiliation and fitness advantages

Because growth rate has been linked to fitness correlates in primates (e.g., Johnson 2003; Altmann & Alberts 2005), we first investigated the fitness consequences of affiliation by analyzing the body mass index (BMI) in both sexes. Body mass (to the nearest 100 g) and crown-rump length (CRL, to the nearest 0.5 cm) measurements recorded from birth to adulthood were extracted from colony records for all focal animals. We obtained 83 weight and CRL data points recorded at the same time for 14 females (2–9 data points per female), and 87 weight and CRL data points recorded at the same time for 16 males (1–9 data points per male). We calculated BMI using the formula: $BMI = \text{weight (kg)} / (\text{CRL(m)})^2$. Locally weighted least squares regression (Lowess, $f = 0.4$, 10 iterations) was used to fit curves to the BMI data for each sex as a function of individual's age (Moses et al. 1992). This method is useful in that it produces an estimated average value for each age without assuming any underlying shape of the curve. 'Residuals' were computed for each data point contributing to the curves of BMI for each sex. We considered the natural logarithm of the ratio of the observed BMI value to the average value given by the Lowess curve for that age (Moses et al. 1992). We then analyzed the relationship between affiliation levels and BMI data (variable to explain) averaged over lifetime. We performed general linear models (proc GLM, SAS V9.2) as averaged BMI residuals were normally distributed. In this analysis, we studied the impact of affiliation across all kin categories divided by the total number of focal observations performed per juvenile. As the Lowess

analyses were performed on each sex separately and took into account the age at data collection, we considered only matrilineal rank as a possible confounding predictor. Because juveniles did not contribute equally to the data set, we considered the number of BMI data points collected per individual as a weighing factor.

Second, data on age at first birth in females were extracted from long-term colony records. We obtained accurate data on subsequent age at first birth of a live offspring for a subset of 12 juvenile females for whom reproductive data were available. We used a Spearman rank correlation test (Proc CORR, SAS V9.2) to determine the relationships between age at first birth and affiliation observed across all kin categories, divided by the total number of focal observations performed per juvenile female. When a significant relationship was found, we replaced the affiliation observed across all kin categories with affiliation observed within each kin class. Because this small data set did not allow examining both the impact of matrilineal rank and affiliation on age at first birth in these females, we performed an additional Spearman rank correlation test between matrilineal rank and age at first birth.

Results

Variation of affiliation across kin classes

Using generalized linear models, we first found a significant positive relationship between affiliation levels recorded among mother–offspring dyads and affiliation levels observed among maternal half-sibs (Table 1; Fig. 1a). Second, we observed a significant negative, albeit weak, relationship between affiliation levels observed among individuals from the same matriline versus paternal half-sibs (Fig. 1b). These significant relationships were consistent across analyses as we observed similar effects when the variables were either the response variables or when considered as predictors (Table 1). Finally, affiliation observed among non-kin dyads was never influenced by (as a response variable)

Table 1: Relationships between affiliation recorded across different kin classes (generalized linear models)

Predictors	Mother	Maternal hs	Matriline	Paternal hs	Non-kin
Response variable					
1. Mother	–	$\chi^2 = 5.48, p = 0.02 (+)$	$\chi^2 = 0.49, p = 0.48$	$\chi^2 = 0.79, p = 0.38$	$\chi^2 = 0.02, p = 0.89$
2. Maternal hs	$\chi^2 = 6.42, p = 0.01 (+)$	–	$\chi^2 = 0.04, p = 0.83$	$\chi^2 = 1.32, p = 0.25$	$\chi^2 = 0.38, p = 0.54$
3. Matriline	$\chi^2 = 0.17, p = 0.68$	$\chi^2 = 0.01, p = 0.90$	–	$\chi^2 = 4.30, p = 0.04 (-)$	$\chi^2 = 1.33, p = 0.25$
4. Paternal hs	$\chi^2 = 0.07, p = 0.79$	$\chi^2 = 1.26, p = 0.26$	$\chi^2 = 7.18, p < 0.01 (-)$	–	$\chi^2 = 0.08, p = 0.78$
5. Non-kin	$\chi^2 = 0.30, p = 0.59$	$\chi^2 = 0.09, p = 0.77$	$\chi^2 = 0.36, p = 0.55$	$\chi^2 = 0.32, p = 0.57$	–

For all predictors, degree of freedom: 1. Significant relationships ($p \leq 0.05$) are shown in bold. Hs: half-siblings.

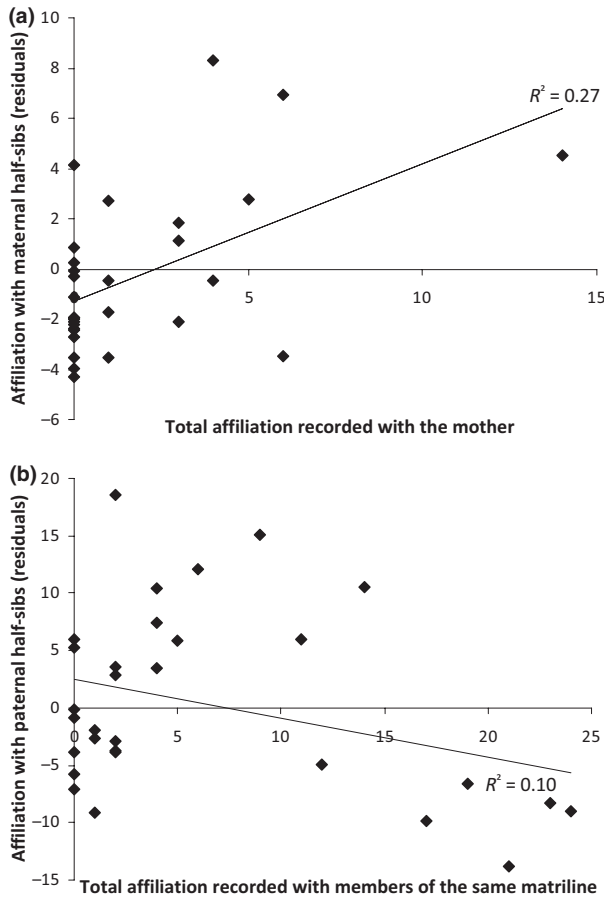


Fig. 1: Relationships between affiliation levels recorded across kin classes. (a) Mother–offspring versus maternal half-sib pairs. (b) Individuals from the same matriline versus paternal half-sibs. Residuals were obtained from the generalized linear models performed excluding the predictor of interest.

and never impacted (as a predictor) affiliation observed in all other kin classes (Table 1).

Second, we found a stronger positive relationship between levels of affiliation with both mother and maternal half-sibs in female than in male juveniles (interaction between affiliation and sex: $\chi^2 = 5.09$, $p = 0.02$; generalized linear models) but no other effect of interactions between affiliation and juvenile's rank ($\chi^2 = 2.39$, $p = 0.30$) or affiliation and age ($\chi^2 = 3.01$, $p = 0.08$). Finally, when considering affiliation levels between individuals from the same matriline and paternal half-sibs, we did not find any significant effect of the studied interactions (affiliation*sex: $\chi^2 = 1.02$, $p = 0.31$; affiliation*rank: $\chi^2 = 0.58$, $p = 0.75$; affiliation*age: $\chi^2 = 0.01$, $p = 0.92$; generalized linear models), suggesting that the initial negative relationship found was consistent across all juveniles and independent of sex, age, or rank.

Finally, we found no relationship between affiliation rates recorded among mother–offspring dyads and the number of maternal half-sibs available ($r = 0.05$, $p = 0.79$; Pearson correlation). By contrast, we found a negative relationship, albeit only marginally significant, between the number of paternal half-sibs and affiliation rates recorded among individuals from the same matriline ($r = -0.35$, $p = 0.06$; Pearson correlation). Interestingly, the reverse was not true: The number of individuals from the same matriline did not influence the affiliation rates recorded among paternal half-sibs ($r = -0.26$, $p = 0.17$), even though the relationship was still negative.

Exploring affiliation levels among close maternal kin

An examination of the relationship between the affiliation levels recorded among maternal half-sibs and the proximity to the mother showed a positive but weak and non-significant correlation (Pearson correlation, $r = 0.30$, $p = 0.10$). Moreover, juveniles showing strong affiliation with both maternal half-sibs and their mother were not, on average, more social than other juveniles because pooled affiliation with mother and maternal half-sibs did not correlate with pooled affiliation with other kin categories (Pearson correlation, $r = -0.13$, $p = 0.48$).

Affiliation and fitness advantages

Affiliation observed across all categories of kin did not influence individual's BMI (Table 2). However, affiliation positively and strongly correlated with the age at first birth in females: Juvenile females who had high affiliation across all kin categories enjoyed early onset of their reproductive careers (Table 2, Figure 2). When replacing affiliation observed across all categories of kin with affiliation observed within each kin class, we found that no single category significantly influenced age at first birth, albeit affiliation with paternal half-sibs was close to significance ($r = -0.51$, $p = 0.09$; mother: $r = 0.05$, $p = 0.88$; maternal half-sibs: $r = 0.22$, $p = 0.48$; individuals from

Table 2: Impact of affiliation on BMI in both sexes and on age at first birth in females

	Sample size	Procedure	Statistics
BMI	30	GLM	Maternal rank: $F_{2,27} = 1.97$; $p = 0.16$ Total affiliation: $F_{1,28} = 2.72$; $p = 0.11$
Age at first birth	12	Spearman correlation	$r_s = -0.68$; $p = 0.014$

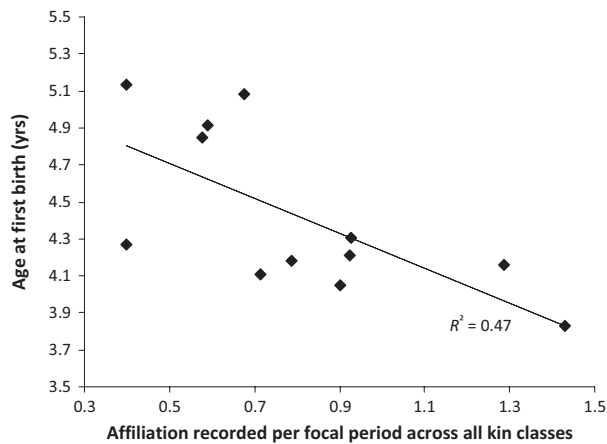


Fig. 2: Relationship between affiliation level and age at first birth in female mandrills. Affiliation observed per focal observation (6-min period) across all kin categories. R^2 is based on Spearman rho value.

the same matriline: $r = -0.27$, $p = 0.40$; non-kin: $r = -0.42$, $p = 0.17$). Age at first birth was not correlated with matrilineal rank ($r_s = 0.37$, $p = 0.23$, $N = 12$).

Discussion

Patterns of variation in affiliation among kin

In this study, we were interested to know how affiliation observed in 30 juvenile mandrills was distributed across different kin classes and how variation in affiliation during early life might affect fitness variation. Results based on affiliation data pooled across kin classes complement an earlier study based on dyadic relationships in the same population where we showed, among others, that juvenile mandrills biased their affiliative relationships toward the mother first, then toward both maternal and paternal half-sib females (Charpentier et al. 2007). Here, we have expanded these findings by showing that, in these juveniles, affiliation may co-vary across kin classes. First, using generalized linear models and a correlation test, we showed that more than a quarter of the variance in affiliation with maternal half-sibs was explained by affiliation observed among mother-offspring pairs (and *vice versa*). This positive correlation was mainly driven by juvenile females and was independent of kin availability. As suggested by others (e.g., Chapais 2001), affiliation recorded with maternal half-sibs could result from sharing a similar attraction to the mother. However, as our analyses relied on behavioral interactions rather than patterns of spatial proximity, and the studied juveniles were already independent from the mother, positive mater-

nal influence on the intensity of the bonds linking her offspring with each other should not solely arise from a passive by-product of mother-offspring spatial association. The absence of correlation between affiliation levels recorded with maternal half-sibs and proximity to the mother supported this view. Moreover, the strong positive relationship between affiliation levels recorded among close maternal kin was not driven by some particularly social juveniles. Consequently, in this mandrill population, some juveniles form strong relationship with closely maternally related individuals, independent of matrilineal rank and independent of affiliation levels recorded with other kin classes, whereas others tended to display less cohesive social bonds with their close maternal relatives, all of these results largely depending on juvenile females.

Using generalized linear models, we also found a negative, albeit weak, relationship between affiliation levels recorded among paternal half-sibs and among individuals from the same matriline (other than maternal half-sibs and mother), whatever the sex, rank, or age of studied juveniles. This relationship could suggest that less affiliation with individuals from the same matriline promoted stronger paternal kin bonds (and conversely). To explore further this result, we studied the relationship between the number of kin available in one class and affiliation rates recorded with the other class. We found some evidence that when fewer paternal half-sibs were available, juveniles affiliated more closely with individuals from their matriline. Albeit this result should be considered with caution because of marginal significance, the reverse was, however, not true: A limited availability in individuals sharing the same matriline did not increase affiliation rate toward paternal half-sibs. Further studies based on a larger data set are now needed to confirm our suggestion that the availability in paternal half-sibs is determinant in structuring social relationships among distantly related maternal kin.

From all these analyses based on co-variations of affiliation levels, we can draw a general pattern that seems to be acting in this mandrill's population. On the one hand, it seems that there are no constraints in time and energy to allocate affiliation to close maternal kin (mothers and maternal half-sibs), and some juveniles affiliate more than others to these kin, whatever their availability. On the other hand, limited availability in paternal half-sibs could possibly promote stronger bonds with individuals from the same matriline. Consequently and by contrast to the maximization of affiliation among close maternal kin, it seems that some social adjustments could

occur among other kin classes, albeit this later result needs confirmation. It is important to note that this interpretation is drawn from a semi-free ranging colony and is possibly hardly generalizable to wild populations of mandrills, for example, if they contain fewer paternal kin because of male's dispersal. While comparable behavioral data on wild populations are lacking, we can make some reasonable hypotheses. The number of paternal kin present in a group depends largely on male reproductive skew. In the studied semi-free-ranging mandrills, each birth cohort includes numerous paternal half-sibs because of high male's reproductive skew (Charpentier et al. 2005). We predict, however, that reproduction among males is highly skewed in wild mandrills because of the extreme intra-sexual competition between males and of the high costs incurred by alpha males who generally mate-guard females during sexual receptivity (MJEC pers. obs.). We therefore similarly expect that wild groups should contain many paternal half-sibs, at least in juvenile cohorts (before male's dispersal) which represent the age class our study focused on.

Deciphering the mechanisms underlying social adjustments would require monitoring changes in social networks over time to document the behavioral responses following the loss or the gain of social partners. Using such a dynamic approach, other authors have showed that in chacma baboons, females who had recently lost a close social partner compensated by extending the number of their grooming partners to maintain a stable grooming network (Engh et al. 2006). In female yellow baboons, similarly, social bonds between maternal half-sibs tend to strengthen after their mother's death (Silk et al. 2006b). Yellow baboon females are also known to form stronger bonds with their paternal half-sisters when no close maternal kin are present. And when no close maternal and paternal kin are available, female baboons direct their affiliation toward non-kin (Silk et al. 2006b). In the present study, however, variation in affiliation with close or more distant kin never translated into variation in affiliation with non-kin, as predicted by kin selection theory (Hamilton 1964).

Fitness correlates of sociality

The second part of our analyses documented a relationship between a fitness correlate and sociality: Female mandrills who received the least affiliation during juvenescence gave birth about a year later than females who benefited the most from social bonds. This study complements previous work sug-

gesting that positive relationships are valuable in primate daily life (Mitani 2009; Silk et al. 2010a) but, as for baboons where more socially integrated females enjoy enhanced offspring survival (Silk et al. 2003, 2009) and live longer (Silk et al. 2010b), no particular category of kin seems to be responsible for this effect. The important social investment in kin rather than in non-kin, observed in almost all social species, could translate into fitness benefits detectable only over the long run. The short-term nature of our study combined with a limited sample size likely precluded detecting kin-specific effects. However, this result may also be understood in the light of our results demonstrating some forms of social adjustments: It is the total amount of affiliation, rather than the affiliation level exchanged with one particular kin class, which is valuable to individual fitness. Consequently, individuals who are able to 'manage' their social relationships in order to maintain an optimal level of affiliation across kin classes may enjoy fitness benefits, including the onset of female's reproductive career.

Age at first birth is a good proxy for female primate fitness. For example, female yellow baboons who gave birth earlier exhibited higher lifetime reproductive success (Altmann et al. 1988). In several primate species, high-ranking females generally give birth at younger ages than low-ranking females (e.g., Altmann et al. 1988; Pusey et al. 1997) and are generally more socially integrated (Silk 2007). However, the relationship we report between affiliation and age at first birth in female mandrills does not seem to be caused by matrilineal rank. While the proximate mechanism linking sociality to fitness is largely unexplored, stress has been proposed as a plausible link (Silk 2007). For example, chacma baboon females who lost a close relative experienced a significant increase in stress levels in the three months following their relative's death, and simultaneously acquired new grooming partners, possibly helping them to alleviate the stress induced by this event (Engh et al. 2006).

Overall our results suggest that young mandrills carefully adjust their affiliative relationships and that the social environment experienced during early life has long-term fitness consequences. As such, this work supports previous findings that social integration has an adaptive value in primates, and possibly in other societies.

Acknowledgements

We are grateful to past and present staff at the Primate Center at CIRMF for keeping records of the colony.

M.J.E.C. is grateful to the CIRMF for permission to study the mandrill colony and for providing logistical support. The CIRMF is financed by the Gabonese government, Total Gabon, and the Ministère Français des Affaires Étrangères. This study was founded by the Laboratoire International Associé CNRS (France)/CIRMF (Gabon) – PATHOS (to M.J.E.C.) and the collaboration between M.J.E.C. and P.M.K. was supported by the Deutsche Forschungsgemeinschaft (DFG, KA 1082-20-1). During the writing-up of this manuscript, AW was supported by the DFG (WI 1808/3-1); JPR by the Volkswagen Foundation; and EH by the DFG (HU 1820/1-1).

Literature Cited

- Alberts, S. C. 1999: Paternal kin discrimination in wild baboons. *Proc Biol. Sci.* **266**, 1501–1506.
- Alberts, S. C., Watts, H. E. & Altmann, J. 2003: Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Anim. Behav.* **65**, 821–840.
- Altmann, J. 1974: Observational study of behavior - sampling methods. *Behaviour* **49**, 227–267.
- Altmann, J. & Alberts, S. C. 2005: Growth rates in a wild primate population: ecological influences and maternal effects. *Behav. Ecol. Sociobiol.* **57**, 490–501.
- Altmann, J., Hausfater, G. & Altmann, S. A. 1988: Determinants of reproductive success in savannah baboons *Papio cynocephalus*. In: *Reproductive Success*. (Clutton-Brock, T. H., ed). University of Chicago Press, Chicago. pp. 403–418.
- Berman, C. M. & Chapais, B. 2004: Kinship and behavior in primates. Oxford University Press, Oxford, UK.
- Buchan, J. C., Alberts, S. C., Silk, J. B. & Altmann, J. 2003: True paternal care in a multi-male primate society. *Nature* **425**, 179–181.
- Caesar, S., Karlsson, M. & Forsman, A. 2010: Diversity and relatedness enhance survival in colour polymorphic grasshoppers. *PLoS ONE* **5**, e10880.
- Chapais, B. 2001: Primate nepotism: what is the explanatory value of kin selection? *Int. J. Primatol.* **22**, 203–229.
- Chapais, B., Gauthier, C., Prud'homme, J. & Vasey, P. 1997: Relatedness threshold for nepotism in Japanese macaques. *Anim. Behav.* **53**, 1089–1101.
- Charpentier, M., Peignot, P., Hossaert-McKey, M., Gimenez, O., Setchell, J. M. & Wickings, E. J. 2005: Constraints on control: factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). *Behav. Ecol.* **16**, 614–623.
- Charpentier, M. J. E., Peignot, P., Hossaert-McKey, M. & Wickings, J. E. 2007: Kin discrimination in juvenile mandrills (*Mandrillus sphinx*). *Anim. Behav.* **73**, 37–45.
- Charpentier, M. J. E., Van Horn, R. C., Altmann, J. & Alberts, S. C. 2008: Paternal effects on offspring fitness in a multimale primate society. *Proc. Natl Acad. Sci. USA* **105**, 1988–1992.
- Clutton-Brock, T. H. 2002: Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69–72.
- Cornwallis, C. K., West, S. A., Davis, K. E. & Griffin, A. S. 2010: Promiscuity and the evolutionary transition to complex societies. *Nature* **466**, 969–972.
- Delgado, R. A. & Van Schaik, C. P. 2000: The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): a tale of two islands. *Evol. Anthropol.* **9**, 201–218.
- Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Seyfarth, R. M. & Cheney, D. L. 2006: Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proc Biol. Sci.* **273**, 707–712.
- Gouzoules, S. & Gouzoules, H. 1987: Kinship. In: *Primate societies*. (Smuts, B. B., Cheney, D. L., Seyfarth, R., Wrangham, R. W. & Struhsaker, T. T., eds). University of Chicago Press, Chicago. pp. 299–305.
- Greenwood, P. J. 1980: Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**, 1140–1162.
- Hamilton, W. D. 1964: The genetical evolution of social behaviour I/II. *J. Theor. Biol.* **7**, 1–52.
- Hatchwell, B. J. 2009: The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philos. Trans R Soc. Lond. B Biol. Sci.* **364**, 3217–3227.
- Hughes, W. O. H., Oldroyd, B. P., Beekman, M. & Ratnieks, F. L. W. 2008: Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* **320**, 1213–1216.
- Johnson, S. E. 2003: Life history and the competitive environment: trajectories of growth, maturation, and reproductive output among chacma baboons. *Am. J. Phys. Anthropol.* **120**, 83–98.
- Kappeler, P. M., Wimmer, B., Zinner, D. & Tautz, D. 2002: The hidden matrilineal structure of a solitary lemur: implications for primate social evolution. *Proc Biol. Sci.* **269**, 1755–1763.
- Lukas, D. & Clutton-Brock, T. 2012: Cooperative breeding and monogamy in mammalian societies. *Proc Biol. Sci.* **279**, 2151–2156.
- Mitani, J. C. 2009: Male chimpanzees form enduring and equitable social bonds. *Anim. Behav.* **77**, 633–640.
- Moses, L. E., Gale, L. C. & Altmann, J. 1992: Methods for Analysis of Unbalanced, Longitudinal, Growth Data. *Am. J. Primatol.* **28**, 49–59.
- Muniz, L., Perry, S., Manson, J. H., Gilkenson, H., Gros-Louis, J. & Vigilant, L. 2006: Father-daughter avoidance in a wild primate population. *Curr. Biol.* **16**, 156–157.

- Nakagawa, S. 2004: A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behav. Ecol.* **15**, 1044–1045.
- Peignot, P., Charpentier, M. J. E., Bout, N., Bourry, O., Massima, U., Dosimont, O., Terramorsi, R. & Wickings, E. J. 2008: Learning from the first release project of captive-bred mandrills *Mandrillus sphinx* in Gabon. *Oryx* **42**, 122–131.
- Port, M. & Kappeler, P. M. 2010: The utility of reproductive skew models in the study of male primates, a critical evaluation. *Evol. Anthropol.* **19**, 46–56.
- Pusey, A. 1987: Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol. Evol.* **2**, 295–299.
- Pusey, A., Williams, J. & Goodall, J. 1997: The influence of dominance rank on the reproductive success of female chimpanzees. *Science* **277**, 828–831.
- Schülke, O. & Ostner, J. 2008: Male reproductive skew, paternal relatedness, and female social relationships. *Am. J. Primatol.* **70**, 695–698.
- Setchell, J. M., Charpentier, M. & Wickings, E. J. 2005: Sexual selection and reproductive careers in mandrills (*Mandrillus sphinx*). *Behav. Ecol. Sociobiol.* **58**, 474–485.
- Silk, J. B. 2002: Kin selection in primate groups. *Int. J. Primatol.* **23**, 849–875.
- Silk, J. B. 2007: The adaptive value of sociality in mammalian groups. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **362**, 539–559.
- Silk, J. B. 2009: Nepotistic cooperation in non-human primate groups. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **364**, 3243–3254.
- Silk, J. B., Alberts, S. C. & Altmann, J. 2003: Social bonds of female baboons enhance infant survival. *Science* **302**, 1231–1234.
- Silk, J. B., Alberts, S. C. & Altmann, J. 2006a: Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behav. Ecol. Sociobiol.* **61**, 197–204.
- Silk, J. B., Altmann, J. & Alberts, S. C. 2006b: Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behav. Ecol. Sociobiol.* **61**, 183–195.
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2009: The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc. Biol. Sci.* **276**, 3099–3104.
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2010a: Female chacma baboons form strong, equitable, and enduring social bonds. *Behav. Ecol. Sociobiol.* **64**, 1733–1747.
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2010b: Strong and consistent social bonds enhance the longevity of female baboons. *Curr. Biol.* **20**, 1359–1361.
- Teriokhin, A. T., de Meeûs, T. & Guégan, J.-F. 2007: On the power of some binomial modifications of the Bonferroni multiple test. *Zh. Obshch. Biol.* **68**, 332–340.
- Viblanc, V. A., Arnaud, C. M., Dobson, F. S. & Murie, J. O. 2010: Kin selection in Columbian ground squirrels (*Urocitellus columbianus*): littermate kin provide individual fitness benefits. *Proc. Biol. Sci.* **277**, 989–994.
- Widdig, A. 2007: Paternal kin discrimination: the evidence and likely mechanisms. *Biol. Rev.* **82**, 319–334.
- Widdig, A., Nürnberg, 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. USA* **98**, 13769–13773.
- Widdig, A., Bercovitch, F. B., Streich, W. J., Nürnberg, P. & Krawczak, M. 2004: A longitudinal analysis of reproductive skew in male rhesus macaques. *Proc. Biol. Sci.* **271**, 819–826.
- Widdig, A., Streich, W. J., Nürnberg, P., Croucher, P. J. P., Bercovitch, F. B. & Krawczak, M. 2006: Paternal kin bias in the agonistic interventions of adult female rhesus macaques (*Macaca mulatta*). *Behav. Ecol. Sociobiol.* **61**, 205–214.