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Kin discrimination in juvenile mandrills, *Mandrillus sphinx*

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Kin selection theory predicts that the evolution of social behaviours will be promoted if these behaviours increase the inclusive fitness of the individuals that perform them, for example by positively affecting relatives. The ability to identify relatives may thus be crucial in maximizing overall fitness. In primate species, whether individuals discriminate paternal relatives and the mechanisms that might permit such discrimination are still the subject of debate. Some researchers have suggested that primates are not able to discriminate relatives in the absence of familiarity. However, recent studies have shown that paternal kin discrimination could emerge from both age proximity and phenotype matching. We investigated the effects of paternal and maternal kinship on the affiliation index of juvenile mandrills, in a semifree-ranging setting. Juveniles biased their behaviour according to kinship. First, when interacting with adult females, both paternal and maternal half-siblings showed more affiliation than unrelated dyads. Affiliation between juveniles and males was also higher among both father−offspring and maternal half-sibling dyads than among unrelated dyads. While these results suggest that juvenile mandrills are able to discriminate paternal relatives, other results do not. Maternal half-siblings had a higher affiliation index than paternal half-siblings and distant kin, the latter showing no significant differences. Finally, when the mechanisms involved in discrimination of paternal kin were analysed, we found no evidence to confirm either the phenotype-matching or the age proximity hypotheses.

Kin selection theory (Hamilton 1964) predicts that the evolution of social behaviours between relatives will be promoted if these behaviours increase the inclusive fitness of individuals, either through the reproduction of related individuals (indirect fitness) or directly through their own reproduction (direct fitness; Griffin & West 2002). The ability to discriminate kin may thus be crucial in maximizing overall fitness, for example when the ability to discriminate leads to avoidance of inbreeding. Two mechanisms for discriminating kin have been proposed as being most likely: discrimination by association, that is, identifying individuals as kin because of previous direct familiarity with each of them (Porter 1988; Halpin 1991); and phenotype matching, that is, classifying individuals as kin because they share family characteristics (Beecher 1982; Holmes & Sherman 1983; Lacy & Sherman 1983;

Porter 1988; Halpin 1991). When kin discrimination involves social cues, such as persistent affiliative associations, the ability to discriminate is most probably acquired through a learning process (reviewed in Sherman et al. 1997; in avian societies, Komdeur & Hatchwell 1999). In some animal societies, learned discrimination of relatives has been reported through association (golden hamsters, *Mesocricetus auratus*: Todrank et al. 1998; long-tailed tits, *Aegithalos caudatus*: Hatchwell et al. 2001; Russell & Hatchwell 2001) or through spatial distribution of relatives (reviewed in Komdeur & Hatchwell 1999). On the other hand, phenotype matching (reviewed in Hauber & Sherman 2001; Tang-Martinez 2001) can occur through matching of vocalizations (stripe-backed wrens, *Campylorhynchus nuchalis*: Price 1999) and odour cues (beavers, *Castor canadensis*: Sun & Müller-Schwarze 1997; golden hamsters: Heth et al. 1998; ground squirrels, *Spermophilus beldingi*: Mateo 2003), and may even be the result of a genetic recognition system (Cascades frogs, *Rana cascadae*: Blaustein & O'Hara 1981).

In primate species, the infant is continually associated with its mother from birth (Walters 1987). This bond,

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especially between a female's offspring, often endures for many years in matrilineal societies where females remain in their natal group throughout their life (Gouzoules 1984; Gouzoules & Gouzoules 1987; Walters 1987; Walters & Seyfarth 1987; Bernstein 1991). As a consequence, infants will also be in proximity to older maternal siblings and possibly other maternal relatives as well. Kin discrimination produced by familiarity because of prior association and/or spatial location has thus been cited as the most feasible mechanism for recognition of maternally related individuals (Gouzoules 1984; Walters 1987; Bernstein 1991). Indeed, several examples have been documented in primate societies, showing kin discrimination through learning processes and behavioural bias towards maternally related individuals (Gouzoules & Gouzoules 1987; Kapsalis & Berman 1996; Rendall et al. 1996; Belisle & Chapais 2001; Nakamichi & Shizawa 2003).

Conversely, less is known about the influence of paternal relatedness on shaping social relationships in primates (but see Alberts 1999; Widdig et al. 2001, 2002; Buchan et al. 2003; Smith et al. 2003), perhaps because paternity cannot be determined without genetic analyses, particularly in species where females mate with several males. In multimale primate groups with promiscuous mating systems, most fathers do not appear to treat their offspring preferentially (but see Buchan et al. 2003), which suggests that paternity is not recognized, at least individually (Bernstein 1991; Paul et al. 1992, 1996; Gust et al. 1998). Furthermore, Sackett & Frederickson (1987) and Erhart et al. (1997) found, for captive colonies, that neither pigtailed macaques, *Macaca nemestrina*, nor savannah baboons, *Papio cynocephalus*, recognized kin in the absence of maternal associations. Similarly, unfamiliar maternal and paternal relatives in a troop of Barbary macaques, *Macaca sylvanus*, showed no mating avoidance (Kuester et al. 1994). However, more recent studies on wild groups of primates found that kin discrimination arose between paternal relatives and emerged from both phenotype matching and age proximity, that is, individuals recognized their peers, born in the same birth cohort (rhesus macaques, *Macaca mulatta*: Widdig et al. 2001, 2002; savannah baboons: Alberts 1999; Smith et al. 2003).

We investigated the effects of both maternal and paternal kinship on the affiliative index of two cohorts of juvenile mandrills (Papionini; Cercopithecinae) in a semifree-ranging setting. Juvenescence is the developmental period between infancy and adolescence, defined as the period from weaning to the acquisition of sexual maturity (Pereira & Altmann 1985; Fairbanks 1993; Watts & Pusey 1993). This stage of life has been poorly studied in nonhuman primates (Walters 1987), even though it represents an important phase of apprenticeship during a primate's life span. The semifree-ranging colony of mandrills at CIRMF (Centre International de Recherches Médicales de Franceville, Gabon) has been studied for 20 years and offers the opportunity to study aspects of their mating system as well as the evolution of social behaviours, the investigation of which is still impossible in wild conditions, owing to the difficulties of studying large, itinerant groups in dense equatorial forests (Abernethy et al. 2002). Mandrills breed on a seasonal basis

(Abernethy et al. 2002; Setchell et al. 2002), females giving birth to approximately one offspring per year. Using microsatellite loci, Charpentier et al. (2005) showed that alpha males sired the majority of offspring per birth season (see also Wickings et al. 1993; Wickings 1995), suggesting that individuals born in the same cohort have a strong likelihood of being paternal half-siblings, whereas maternal half-siblings are always from different cohorts. The mandrill social system is matrilineal (Setchell 1999). Females remain in their natal group throughout their life whereas males disperse (Abernethy et al. 2002), and individuals from the same matriline interact preferentially (personal observation).

We examined in particular the affiliation index recorded for juvenile individuals. Our aims in this study were (1) to examine the effect of maternal and paternal relatedness, based on paternity analysis, on the affiliation index among dyads of juveniles and among dyads of juveniles with older males and with older females, and (2) to explore the possible mechanisms responsible for kin discrimination in mandrills.

METHODS

Animals and Husbandry

The semifree-ranging colony at CIRMF, Gabon, was established in 1983−1984 when 15 unrelated animals (eight females, seven males; Wickings 1995) of different origins were released into a 6-ha valley with natural rainforest, enclosed by an electric fence (enclosure E1). Any further increases in the group have been the result of natural reproduction of these founder animals, countered by deaths and some removals for experimental purposes. In 1994, in the face of an increasing population and to limit the spread of naturally occurring STLV and SIV viruses, the colony was separated into two groups: noninfected mandrills remained in E1 ($N = 49$), and naturally infected animals were placed in E2 (3.5 ha) with all members of their matriline ($N = 21$), in order not to break kinship associations and to conserve social units.

At the time of this study (March 2002−January 2004), the group in E1 consisted of 72−114 individuals (Table 1). Variation in group composition was due to deaths and births, and particularly to the removal of 36 individuals in October 2002 to reduce the increasing captive population. All mandrills in the colony were tattooed shortly after birth and individuals older than 2 years were given

Table 1. Composition of the mandrill colony at the beginning of the study (March 2002)

	Adults	Adolescents	Juveniles	Infants
No. of individuals				
Males	9	12	18	11
Females	20	8	15	12
Age (years)				
Males	9−15	5−8	1−3	0−1
Females	5−24	4−5	1−3	0−1

numbered and coloured ear tags for ease of recognition. All adults, adolescents and most juveniles of both sexes were individually recognizable, and their matrilineal identity was known. Those juvenile individuals (without ear tags) that could not be reliably identified until 2 years of age ($N = 2$), and all yearlings ($N = 23$), were excluded from all subsequent analyses.

The naturally rainforested enclosure has a small fenced pen, for feeding and capturing animals, overlooking an open grassy area. Mandrills are fed twice a day with seasonal fruits, vegetables and monkey chow to supplement their foraging. Water is available ad libitum. The animals are visible before, during and after the feeding, remaining on the edge of the forest for a total of approximately 2 h around each feeding period.

The study was approved by the Comité Régional d'Ethique Ile-de-France Sud. It required no change in the animals' normal daily routine.

Behavioural Observations

This study focused on 11 female and 11 male juveniles in E1, belonging to two cohorts (1999, 2001, no births occurred in 2000). Approximately 325 h of behavioural observations were carried out from March 2002 to January 2004, before feeding (1000−1100 and 1600−1800 hours) to avoid effects of feeding competition on behaviour. Data were collected with the focal method for the 22 juveniles (Altmann 1974; Martin & Bateson 1986; Lehner 1996); the sequence in which animals were observed was randomized. During a 6-min period, we noted all social behaviours (bouts) initiated and received by the focal juvenile, along with the identity of the partners. The duration of each activity was not recorded but the end of each bout corresponded to the cessation of the activity (Charpentier et al. 2004). We scored all interactions between the 22 juveniles, and between these juveniles and all other members of the mandrill colony, divided into four age and sex classes: adult and adolescent females and males (Table 1). All females that had given birth (i.e. were parous) at least once were considered as adults, even if they had not attained full adult size (Setchell et al. 2001, 2002). During behavioural observations, we recorded affiliative behaviours (grooming, muzzle contact, affiliative contact). A proximity analysis was also carried out, based on scan-time samples taken every 3 min during each sampling period and involving all neighbours within a 5-m radius. We computed a composite index of affiliation, as defined by Silk et al. (2003), for each dyad that included at least one juvenile:

$$\dfrac{\left(\dfrac{f_{\mathrm{p}}}{\bar{f}_{\mathrm{p}}}\right) + \left(\dfrac{f_{\mathrm{a}}}{\bar{f}_{\mathrm{a}}}\right)}{2},$$

where f_{p} and f_{a} represent the frequency of proximity and affiliation within a dyad, corrected for the number of focal sessions per dyad or time of coresidency (for example because of the removal of 36 individuals in October 2002) and $\bar{f}_{\mathrm{p}}$ and $\bar{f}_{\mathrm{a}}$ represent the mean frequencies of proximity and affiliation within the population.

We conducted analyses of the affiliation index at the level of the dyad. For behaviours between juveniles, since both juveniles of any dyad were focal individuals, we collapsed the affiliative bouts and proximity recorded regardless of the identity of the focal juvenile.

Paternity Analyses

All animals are captured annually. Various morphological measures (growth parameters) and blood samples are taken on each occasion. Between June 1983 and June 2002, 231 infants were born into the colony. DNA extracted from blood was available for the majority of individuals (89.4%), and in 2002, 205 offspring, as well as the 13 reproductively active founders (two founders never reproduced successfully), were genotyped. Twenty-six mandrills born in the colony could not be sampled (two were stillborn, 16 died before 1 year of age, eight were never captured). All available individuals, including all potential sires, were genotyped for eight microsatellite loci. CERVUS 2.0 (Marshall et al. 1998) and Parente (Cercueil et al. 2002) were used to assign paternity for 193 (94%) of the 205 offspring (for details of methods and paternity assignment criteria, see Charpentier et al. 2005). Of the individuals involved in social interactions with the juveniles studied, paternity could not be assigned for three individuals (two juvenile females and one adolescent male) and these were thus excluded from all subsequent analyses.

Relatedness and Kin Dyads

To investigate the effect of kinship on affiliation and proximity, we generated a coefficient of relatedness (r) and kin relationships from the pedigree obtained from paternity analyses. Degrees of relatedness, r, ranged from 0 to 0.75; however, a similar degree of relatedness did not mean only one kin class in our data set (see below). We simplified the analyses by considering only the following relationships for the analysis with adult females: nonkin, maternal half-sibling, paternal half-sibling and parent−offspring dyads; for adult males, the same categories were used, excluding paternal half-siblings as no such dyads were available. Finally, for analysis between juvenile individuals, we restricted our analysis to maternal and paternal half-siblings and what we called 'distant relatives' ($0.031 \leq r \leq 0.094$); unrelated juveniles were not available because of the reproductive skew in this colony (Wickings 1995; Charpentier et al. 2005). Note that the paternal half-sibling dyads in these analyses never came from the same matriline, to avoid confounding effects.

Since males could not emigrate from the enclosure, we had access to a range of individuals related in various ways, through both the mother and the father. Hence and to explore further the mechanisms involved in kin discrimination, we compared social interactions between dyads with comparable degrees of relatedness, but belonging to different kin classes. In this way, we carried out a final analysis testing the hypothesis of phenotype matching, by comparing the affiliation index of paternal half-siblings with that of dyads of the same degree of

relatedness (obtained from the pedigree) but sharing neither a common maternal ancestor nor the same father. These types of relatives shared distant ancestors, such as grandparents or great-grandparents.

Statistical Analyses

Repeated measures logistic regressions were used to model the relation between the response variable (affiliation index) and several explanatory variables as defined below (SAS version 9, Genmod procedure, SAS Institute, Cary, NC, U.S.A.). A logistic regression for these data is a generalized linear model with response equal to the binomial proportion N/T, where N is the affiliation index within a dyad and T the number of trials. As we obtained an affiliation index for each dyad, corresponding to a number of bouts of affiliation and proximity per focal time period (6 min), the number of trials was identical for every dyad and we chose an arbitrary value. Changing this arbitrary value had no effect on our results. The probability distribution was binomial, and the link function was a logit. The number of responses N was modelled as a binomial random variable for each combination of the explanatory variable values, with the binomial number of trials parameter equal to the number T and the binomial probability equal to the probability of a response. The repeated variable was the identity of a given juvenile and the identity of each conspecific considered within the interactions involving this juvenile. The method of generalized estimating equations was used to account for the fact that both a given juvenile and a given recipient were repeated.

First, we examined the affiliation index between juveniles and adolescent and adult females. Nonkin, maternal half-sibling, paternal half-sibling, and mother–offspring dyads were available. We considered the kin classes defined as a first explanatory variable. Several studies have shown that primates discriminate between conspecifics according to both their social status and relatedness (SantillanDoherty et al. 1991; Kuester et al. 1994; Bergman et al. 2003). Thus, we considered the interaction between a female's social rank and the rank of a juvenile's mother at the time of its birth as a second explanatory variable. We used the maternal rank in juveniles rather than estimating juvenile rank, which may vary according to circumstances (J. Wickings, personal observation). A female's rank (or maternal rank) at each birth was expressed as the percentage of all females over 3 years of age present that she dominated, to account for demographic changes over time (Cheney et al. 1988). We also considered the sex of the juvenile and the female's age class (adolescent or adult), as these factors are likely to influence behaviours.

The statistical model was as follows:

$$\text{Affiliation index} = \text{kin class} + \text{female's rank} \\ \times \text{maternal rank} + \text{juvenile's sex} \\ + \text{female's age class} + \text{constant}$$

We repeated the analysis, using the same covariables for the analysis of phenotype matching (see Results).

Second, we examined the affiliation index between juveniles and adolescent and adult males. Nevertheless, as affiliative behaviours are virtually absent between juveniles and males, we computed an affiliation index based only on the events of proximity recorded. The same kin classes as defined previously were considered, except that no paternal half-sibling dyads were available. As rank in male adolescent and adult male mandrills is defined according to competitive abilities (Setchell & Dixson 2002), and as a male's rank is always superior to that of a juvenile, we included only the juvenile's maternal rank in this analysis. The number of females in a juvenile's matriline was also taken into account to avoid by-products of proximity between adult females and males. Finally, and as for the analysis with females, we took into account the juvenile's sex and we classified males as adult or adolescent.

The second statistical model was as follows:

$$\text{Affiliation index} = \text{kin class} + \text{maternal rank} \\ + \text{number of females in the matriline} \\ + \text{juvenile's sex} + \text{male's age class} \\ + \text{constant}$$

Third, we examined the affiliation index between juveniles. We considered distant kin dyads with r ranging from 0.031 to 0.094, paternal half-siblings, and maternal half-siblings. We also used the interaction between maternal ranks within a dyad of juveniles. We also took into account the sex of the two individuals within a dyad (male–male, male–female, female–female). Finally, we used the difference in age as a last explanatory variable to detect effects of age proximity, as juveniles belonged to two cohorts (see for example Widdig et al. 2001, 2002). Juveniles were up to 2 years apart in age.

The last statistical model was as follows:

$$\text{Affiliation index} = \text{kin class} + \text{maternal rank juvenile 1} \\ \times \text{maternal rank juvenile 2} \\ + \text{sex of the juveniles within a dyad} \\ + \text{age difference} + \text{constant}$$

We used the least-squares means procedure to ordinate the different classes of kin (SAS version 9).

RESULTS

Affiliation Index With Adult and Adolescent Females

Kinship had a significant effect on the affiliation index in dyads of juveniles and females (Table 2). Table 2 also shows the effect of the other covariables. The sex of the juvenile significantly affected the affiliation index, with female juveniles always showing a greater affiliation index with older females ($\overline{X} \pm \text{SE} = 1.74 \pm 0.40$) than male juveniles did (0.39 ± 0.09). However, neither the female age class (adult or adolescent) nor the interaction between social ranks significantly influenced the affiliation index among juveniles and females.

Table 2. Effects of kinship and covariables on the affiliation index computed between 22 juvenile individuals and the different age and sex classes represented in the mandrill colony

	Affiliation index		
	χ^2	df	P
Females			
Kin type	18.40	3	<0.001
Juvenile sex	11.13	1	<0.001
Rank interaction	0.36	1	0.55
Female age class	0.03	1	0.85
Males			
Kin type	6.75	2	0.034
Juvenile sex	1.08	1	0.30
Maternal rank	0	1	0.99
Male age class	6.10	1	0.014
Matriline size	1.27	1	0.26
Juveniles			
Kin type	4.93	2	0.085
Dyad sex	18.99	2	<0.0001
Rank interaction	4.89	1	0.027
Difference in age	1.29	1	0.26

When the four kin classes were distinguished (least-squares means procedure), we found that mother−offspring dyads (i.e. the closest relatives) showed the highest affiliation index, followed by paternal half-siblings, maternal half-siblings and nonkin (Fig. 1a). First, mother−offspring dyads presented a significantly higher affiliation index than other kin classes, except paternal half-siblings (Table 3). Second, paternal half-siblings did not differ significantly from maternal half-siblings. Finally, both paternal and maternal half-siblings showed a higher affiliation index than unrelated dyads (Table 3).

Affiliation Index With Adult and Adolescent Males

The affiliation index between males and juveniles was significantly influenced by kinship (Table 2). However, neither the sex of the juveniles nor their maternal rank was correlated with proximity. We observed the same nonsignificant result for the number of females in the matriline to which the juveniles belong. Finally, the age class of males had a significant influence on the affiliation index, with adolescent male−juvenile dyads showing a higher index (1.23 ± 0.24) than dyads of adult males−juveniles (0.74 ± 0.24).

When we considered the three kin classes, we found that maternal half-siblings had the highest affiliation index, followed by father−offspring, then nonkin dyads (Fig. 1b). However, while values of the index between maternal half-siblings and father−offspring dyads were both significantly higher than those of unrelated individuals (Table 3), no significant differences were observed between these first two kin classes.

Proximity and Affiliation Between Juveniles

Finally, the affiliation index between dyads of juveniles tended to be influenced by kinship, but not significantly so (Table 2). Furthermore, the sex of the dyads was correlated
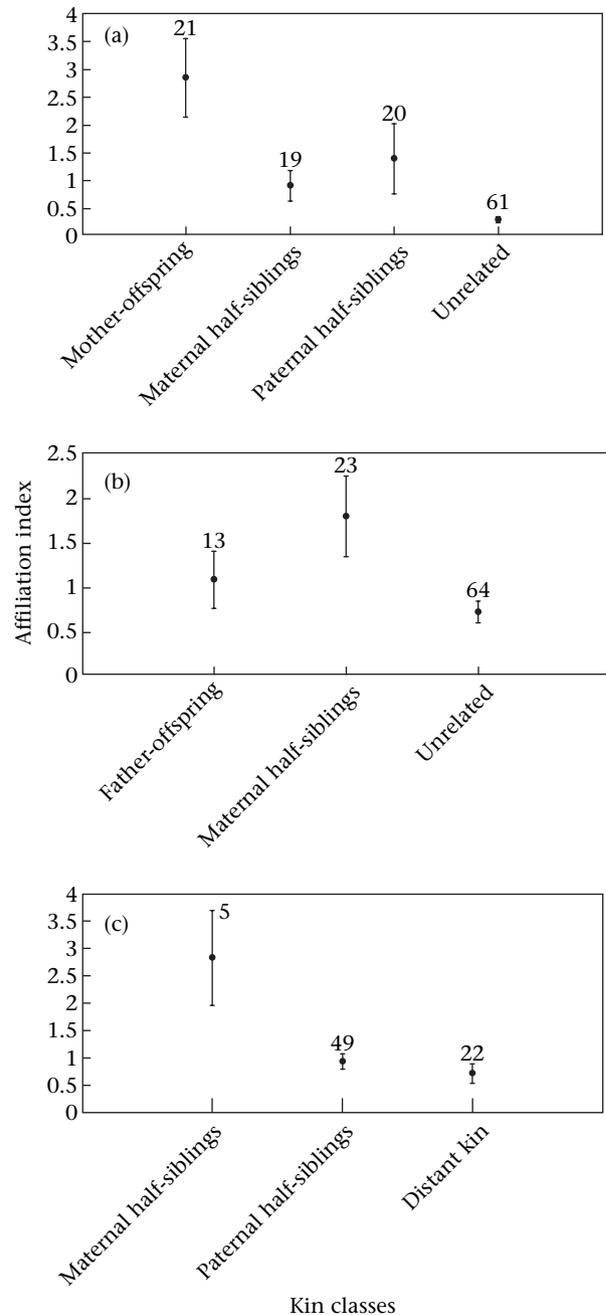

Figure 1. Kinship and affiliation index ($\overline{X} \pm$ SE) (a) between 22 juveniles and adult and adolescent female individuals, (b) between 22 juveniles and adult and adolescent male individuals and (c) within dyads of 22 juvenile individuals. Sample sizes are given with each point.

with the index, with single-sex dyads (i.e. female−female = 1.88 ± 0.54; male−male = 1.45 ± 0.20) always showing a higher affiliation index than mixed-sex dyads (i.e. male−female = 0.57 ± 0.11). Finally, while the difference in age did not correlate with affiliation, the interaction between the maternal ranks of juveniles of a given dyad influenced the affiliation index (see Appendix).

When the kin classes were considered separately, we found that maternal half-siblings showed a significantly higher affiliation index (Fig. 1c, Table 3) than the other

Table 3. Pairwise comparisons of kin classes, using differences of least-square means (SAS, version 9)

Kin classes	P
Females	
Mother–offspring/maternal half-siblings	0.012
Mother–offspring/paternal half-siblings	0.18
Mother–offspring/unrelated	<0.0001
Maternal half-siblings/paternal half-siblings	0.69
Maternal half-siblings/unrelated	<0.001
Paternal half-siblings/unrelated	0.004
Males	
Father–offspring/maternal half-siblings	0.89
Father–offspring/unrelated	0.017
Maternal half-siblings/unrelated	0.004
Juveniles	
Maternal half-siblings/paternal half-siblings	<0.001
Maternal half-siblings/unrelated	<0.0001
Paternal half-siblings/unrelated	0.92

two kin classes. Finally, no difference in the affiliation index between nonkin and paternal half-sibling dyads was recorded (Table 3).

Testing the Phenotype-matching Hypothesis

If phenotype matching occurs in mandrills, individuals related to the same degree (r equivalent), regardless of the origin of relatedness, should have an equivalent number of genes in common, and hence equivalent phenotypic cues should also be matched. We thus analysed the affiliation index between dyads of juveniles and older females for paternal half-siblings ($N = 8$) and dyads of the same degree of relatedness ($r = 0.281-0.375$), these latter sharing neither a common maternal ancestor nor the same father ($N = 26$). Paternal half-siblings had a higher affiliation index (3.10 ± 2.43) than other related dyads (0.25 ± 0.06; $\chi_1^2 = 6.11$, $P = 0.014$). No further analyses were conducted on other age and sex classes as no paternal half-siblings existed between juveniles and males and no discrimination of paternal kin was found among juveniles, as shown above.

DISCUSSION

Our study shows that juveniles behaved differently towards other individuals according to kinship, providing evidence for kin discrimination. With older individuals (adult and adolescent males and females), juveniles showed preferential treatment of both maternal (mother, maternal half-siblings) and paternal relatives (father, paternal half-siblings), compared to nonkin, with the affiliation index between juvenile and mother being the highest recorded. Furthermore, among dyads of juveniles, maternal half-siblings had the highest affiliation index, while paternal half-siblings and distant relatives did not differ. The fact that juveniles preferred paternally related adult females but not paternally related juveniles compared to nonkin remains to be explained. However, during juvenescence, a sensitive stage of life where social skills increase dramatically (Pereira & Altmann 1985; Fagen 1993), individuals may treat their congeners differently according to

the benefits involved. An alternative explanation may be that juveniles do not treat paternally related juveniles differently because the mechanisms responsible for discrimination of paternal relatives are not yet developed, whereas they are fully developed in adult and adolescent conspecifics. The bias we recorded between juveniles and older paternal half-siblings (males, females) could simply be caused by kin discrimination from adults, and not juveniles. However, an analysis of affiliative behaviour between juveniles and older females, separating initiated from received affiliation (i.e. a juvenile may initiate or receive affiliative bouts) does not confirm this hypothesis (data not shown). Indeed, juveniles initiated more affiliative behaviours towards paternal half-sibling females than towards nonkin females, showing that at this stage they are able to discriminate paternal relatives.

Our findings from the covariables analysed show that, unsurprisingly for a primate species with a matrilineal structure and female philopatry (Setchell 1999; Abernethy et al. 2002), female juveniles affiliated more with older females than did male juveniles. Among juveniles, the mixed-sex dyads showed the least affiliation. Thus male–male relationships among juveniles were as affiliative as female–female relationships. The benefits of interacting with the same sex during juvenescence, the period characterized by apprenticeship, are obvious. Females will, in any case, interact with other females throughout their lives (Gouzoules 1984; Gouzoules & Gouzoules 1987; Walters 1987; Walters & Seyfarth 1987; Bernstein 1991); in males, experience and apprenticeship for future competition can be gained, through play for example (Fagen 1993; Dolhinow 1999). However, for interactions with adult and adolescent males, the sex of the juvenile did not influence its affiliative behaviour, perhaps because few interactions occurred between these classes. While adult males engaged in few contacts with juvenile mandrills, adolescent males still interacted with them (regardless of kinship, see Charpentier et al. 2004). Finally, while social status is important in shaping relationships in primate species (SantillanDoherty et al. 1991; Kuester et al. 1994; Bergman et al. 2003), we found an effect only among juvenile mandrills, suggesting both that maternal rank still influences the social development of juveniles and that the rank of older individuals does not shape the ontogeny of young individuals.

The demonstration that discrimination of paternal relatives occurs in mandrills leads to the question of what mechanism(s) is involved in kin discrimination. Kin discrimination can arise if individuals classify relatives on the basis of frequent association patterns (familiarity) or if individuals identify relatives on the basis of shared family traits (phenotype matching; Holmes & Sherman 1983; Waldman et al. 1988). When paternity is restricted to a limited number of males per reproductive season, or skewed towards one dominant individual, which is the case in mandrills where dominant males sire 76.2% of offspring per reproductive season (Charpentier et al. 2005), individuals conceived during the same reproductive season are likely to be paternal half-siblings (Altmann 1979; Altmann et al. 1996; De Ruiter & Geffen 1998; Widdig et al. 2004). On the other hand, it is unlikely

that maternal half-siblings are born in the same birth season, as Old World monkeys rarely give birth to twins. Paternal half-siblings will thus often be from the same age cohort (peers), whereas maternal half-siblings will be at least a year apart (nonpeers). In primate species, the social experience is gained through play, with both siblings and peers (Ehardt & Bernstein 1987; Walters 1987; Fagen 1993; Watts & Pusey 1993; Dolhinow 1999), suggesting that familiarity with peers develops during ontogeny, but also that a close age proximity could be used among individuals for the identification of paternal half-siblings. Hence, a simple apprenticeship through age proximity (more familiarity between individuals born in the same year) could be used to identify paternal half-siblings. Studies have indeed shown that primates might use age proximity as a secondary cue to identify their paternal siblings (Alberts 1999; Widdig et al. 2001, 2002; Smith et al. 2003). However, we have shown that juveniles are able to discriminate paternal relatives among older individuals, and also that the difference in age between juveniles does not influence affiliation. These two findings thus provide no support for an age proximity mechanism involved in paternal kin discrimination.

In this study, we did not implicate the phenotype-matching hypothesis as a potential mechanism underlying kin discrimination in mandrills. Indeed, no differences in treatment should exist between individuals with a comparable range of relatedness, whatever the origin of relatedness, if phenotype matching occurs. The mechanism(s) responsible for discrimination of paternal relatives could thus be linked to social apprenticeship and/or to mating information transmitted maternally. Mothers could, for example, mediate affiliation between their infants as a function of shared paternity by encouraging infants to associate with offspring of females who have mated with the same male (Widdig et al. 2001). Indeed, maternal affiliation patterns partly drive the development of infant affiliation patterns among peers (Berman & Kapsalis 1999). Furthermore, and not mutually exclusive with the preceding hypothesis, mothers may also affiliate preferentially with the male with whom they have conceived. Thus, as in savannah baboons (see for example Altmann & Alberts 2003), female mandrills could have long-term bonds with males which, although not perfect predictors of paternity, are likely to be correlated with mating patterns, and could be remembered by females. These bonds place juveniles in proximity to families of other females bonded to the same males, which, especially in juveniles, could provide a (familiarity-based) mechanism to recognize paternal kin. An analysis of maternal behaviours during rearing of offspring is now required to elucidate the mechanisms involved in kin discrimination in mandrills.

Acknowledgments

Supplementary Material

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