

## Grooming Partners of Immature Blue Monkeys (*Cercopithecus mitis*) in the Kakamega Forest, Kenya

Marina Cords<sup>1</sup>

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*I report results of a 4-year study, which profiles grooming partners of immature blue monkeys in a Kenyan rain forest. The analysis focuses on the degree to which mothers and offspring were preferred grooming partners and on sex differences in grooming partners. Subjects ranged in age from 0 to 6 years and were members of one study group in which kinship relations were known from long-term study. Immatures often had their mothers as the top-ranked partner. Even more reliably, however, adult females had their offspring as top-ranked immature partners. As offspring grew older, they tended to fall in the rank ordering of their mothers' immature grooming partners, especially when younger siblings were born. Immature males had fewer grooming partners overall than female peers did. Thus, immature females diversified their partners more than males did, especially by establishing grooming relations with immature female partners. Immatures of both sexes had more female partners than expected by chance. Observed sex differences suggest that immature female blue monkeys may use grooming to cultivate relationships with long-term future benefits. It is less clear that the grooming of immature males functions in this way. Immatures of both sexes may also use grooming to maintain relationships of current value, to practice for future social exchange, and to keep clean, and some of their grooming may be in the primary interest of their partners, rather than themselves. In general, immature blue monkeys resemble the immatures of other catarrhine taxa in the way in which grooming is distributed among various partners.*

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<sup>1</sup>Anthropology Department, Columbia University, 1200 Amsterdam Avenue, MC 5529, New York, New York 10027; E-mail: mc51@columbia.edu.

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## INTRODUCTION

In studies of social development of gregarious Old World primates, grooming has emerged as one form of interaction that distinguishes a juvenile's relationships with various adults in its group and that distinguishes the social profile of juvenile males and females in ways that presage their different life histories as adults (Pereira and Altmann, 1985; Walters, 1987). The mother is a major grooming partner throughout her offspring's prereproductive life, whereas grooming with other adults seems to occur to the extent that relationships with them are or will be important to the juvenile. Sex differences in the grooming of immatures appear to reflect the degree to which males and females differ in the identity of valuable (Kummer, 1978) social partners. Such findings support the hypothesis that grooming is an important way of cultivating potentially long-term cooperative relationships with others (Cords, 1997).

As reviews of social development (Pereira and Altmann, 1985; Walters, 1987) have pointed out, the comparative method can add much to an understanding of juvenile social strategies, especially in a taxon like primates in which social systems and the social roles of adult males and females are highly variable. Interpretations of juvenile social behavior patterns are strengthened when variation in those patterns mirrors variation in the variables that supposedly cause them, and when relatively unrelated taxa are characterized by similar patterns of behavior as well as similar causal parameters. As in most studies of primate social relationships, a limited number of taxa, especially macaques and baboons, have received a disproportionate share of research. In addition, a large fraction of the data on these taxa comes from studies carried out in captivity, where the demographic and ecological situations of the subjects differ from life in the wild in ways that might well influence a social interaction like grooming. The publication of the book by Pereira and Fairbanks (1993) helped to broaden the array of primate species represented in studies that focus on juveniles and to increase the number of reports from noncaptive populations.

This paper contributes to the taxonomic diversity of data on juvenile social lives by presenting the profile of grooming relationships of juvenile blue monkeys, *Cercopithecus mitis stuhlmanni*, living under natural conditions. The guenons are a large primate radiation, with most member species inhabiting forests and living in groups of philopatric females. Males disperse

from their natal groups at puberty and enter new groups as adults. In most species, there is just one resident adult male, at least outside of the breeding season, but in a few species there are routinely several males per group year-round (Cords, in press). While loose associations may form between nonresident males from the same natal group (at least in blue monkeys, pers. obs.), it is not generally known how important male-male relationships are in this group of monkeys. Females, however, form enduring relationships with one another, and cooperate to defend a territorial boundary against neighboring groups. There have been a few studies, mostly in captivity, of juvenile social relationships in guenons, including vervets (Fairbanks and McGuire, 1985; Fairbanks, 1993; Horrocks and Hunt, 1993), talapoins (Wolfheim, 1977), and patas monkeys (Rowell and Chism, 1986). Two of the three species studied, vervets and talapoins, are atypical guenons in that their groups are usually multimale. Patas monkeys and vervets are unusual for living in savanna-woodland habitats rather than tall forests. Blue monkeys, however, share the predominantly one-male social structure and forest habitat requirements that typify most guenon species.

The goal of the present study was to examine two particular aspects of the grooming partner profiles of juvenile blue monkeys. First, to what degree was the mother a preferred grooming partner, and could mother-offspring kinship be recognized by preferential grooming? Second, are there sex differences in the profiles of grooming partners among juvenile blue monkeys, and if so, can they be interpreted in light of the social and life history differences that characterize adult males and females?

## METHODS

The subjects were immature, natal members (aged 0-6 years, born between 1992 and 1998) of the  $T_w$  group of blue monkeys, *Cercopithecus mitis*, which has been studied since 1979. They inhabit the Kakamega Forest, western Kenya, a semideciduous forest averaging just more than 2 m of rainfall per year (Cords, 1987). All individuals in the group, which totaled about 35 individuals, could be individually recognized using natural features. Age at first reproduction in this population is minimally 7 years; no female of known age has given birth at a younger age, and two males of known age that emigrated from their natal group did so at age 7 years.

Kinship between immatures and their mothers was known from long-term reproductive records and yearly monitoring of the study group. I identified infants as the offspring of particular females in the first few months of their lives, when they are carried nearly all of the time and suckle frequently. Suckling continues into the second and even third year of

life in some cases, and although infants may suckle briefly from nonmaternal adult females on rare occasions, the vast majority of suckling involves the mother only. Thus multiple observations of prolonged suckling from the same female helped me to identify immatures during the first few years of life when their physiognomy and tail hairs—the features used to identify older juveniles and adults—change the most. I used these physical features also to identify many younger juveniles.

Data reported here come from four 2–3 month field seasons (June–September, 1995–1998). In this population, most births occur between January and April, so most subjects were observed 3–6 months into each year of their lives. In the case of infants, this meant that they were usually moving independently for much of the day, but still suckled frequently, especially when their mothers rested. For analysis, I grouped the subjects into annual cohorts, with infants being <1 year old, yearlings between 1 and 2 years old, and so forth. Because my ability to recognize immatures reliably from year to year was not well developed until 1992, the sample includes fewer cohorts of older juveniles (1 cohort of 6 year olds, 2 cohorts of 5 year olds, and 3 cohorts of 4 year olds) than of infants and younger juveniles (4 cohorts of each age group from 0 to 3 years old; Table I).

The study group was followed on a daily basis by several observers (usually three), including me and university students who had been trained to recognize individuals before data collection. Whenever a grooming bout was seen, we identified the individuals. We did not record the same two subjects as participating in a new bout unless  $\geq 4$  min had elapsed; in nearly all cases, the time between bouts was considerably longer than this (on the order of hours or days). Other information, namely whether grooming was reciprocated and how long the bout lasted, was also sometimes recorded, but is not considered in this report. The main focus of our research during these study periods was mating behavior. However, in the course of taking a daily role call, monitoring sexual activity and searching

**Table I.** How individuals contributed to the data set

Birth year	Males (No.)	Females (No.)	Age cohorts in which these animals are included <sup>a</sup>
1992	3	1	3–6 year olds
1993	2	2	2–5 year olds
1994	1	1	1–4 year olds
1995	2	3	0–3 year olds
1996	3	1	0–2 year olds
1997	2	4	0–1 year olds
1998	5	3	0 year olds

<sup>a</sup>An infant is designated as zero years old.

the group's periphery for visiting adult males, each observer moved frequently through the group, and had many opportunities to see all group members. Furthermore, grooming occurred most often during midday periods of rest, when sexual activity was more infrequent (and so less distracting). Given the number of observers, their movements around the group, the diurnal patterning of behavior, and the excellent habituation of our subjects, we felt confident that our observations of different group members were reasonably representative, even though they were not made during prescheduled and timed focal samples.

The raw data for the analysis consist of matrices that specify the number of grooming interactions for each combination of individuals for each year of the study. Because many grooming bouts were discovered in progress and we were not always able to remain with grooming partners until their interaction ended, data on the directionality of grooming within each bout are incomplete. Therefore I collapsed the matrices to half-matrices, which include the total number of observed grooming bouts involving every pair of subjects, regardless of which individual actively groomed or received grooming from its partner in each one. The analysis thus focuses on the number and identity of partners with which grooming relations existed, and to some degree on the relative frequency of grooming bouts with various partners.

Because the data represent several continuous years of records, the same individuals could appear in multiple annual matrices, although they would be members of different age cohorts in different years (Table I). I carried out analyses on a per-year or per-age-cohort basis to avoid having any one individual appear more than once as a subject. I used the per-year grouping in all tests comparing the number of grooming partners because there were differences from year to year in the amount of grooming we detected, which could confound comparisons between different groups of individuals. The statistical analysis is based on the grooming profiles of individuals. I compared groups of subjects (male vs. female juveniles, adults vs. juveniles) via Mann-Whitney U tests. The *p*-values are two-tailed.

## RESULTS

### Grooming of Immatures and Their Mothers

In a given yearly observation period, we noted an average immature grooming 21.4 (s.d. = 15.2) times and with 7.3 (s.d. = 4.8, equaling about 20% of all possible) different partners ( $n = 92$  immature-years). For most

immatures, the mother was the top-ranking grooming partner (Table II). Across cohorts, the proportion of immatures that groomed most often with their mothers ranged from 100% (for yearlings) to 50% (for 6 year olds). There is no clear relationship between the age of the cohort and the proportion of individuals that groomed most often with their mothers. Although a larger proportion of males than females had their mother as top-ranked grooming partner at every age except infancy (Table II), the difference was small and not statistically significant.

Most immatures that did not have their mother as the top-ranked grooming partner ( $N = 11$  of 15 immature-years) did nevertheless groom with her sometimes, and in most cases ( $N = 9$  of 11 immature-years) she was the second-, third-, or fourth-ranked grooming partner, and differed from higher-ranked partners by only one or two grooming bouts. Over all 4 years of the study, only three females and one male were not seen to groom with their mothers in a certain year, even though grooming with other individuals occurred. More than half (9/15) of these exceptional cases (in which immatures did not have their mother as top-ranked partner in a particular year) appeared to involve certain individuals: one 1992-born female never had her mother as top-ranked partner over 4 years of sampling, and two other individuals had nonmaternal top-ranked partners for 3 of 4 and 2 of 3 years, respectively.

A preference for grooming between mothers and offspring is even more apparent when the grooming partners of mothers are considered. Although mothers did not necessarily groom with their own immature offspring more than with anyone else, they groomed with their own immature offspring more often than they groomed with any other immature group member. In each of the 4 years, all 14 adult females in the group that had immature offspring had one of them as her top-ranked immature grooming partner, with one exception and one tie with a nonoffspring for

**Table II.** The proportion of juveniles that had their mothers as top-ranked grooming partner

Age cohort	Years of data	Proportion of juvenile males that groomed most with mother(%)	Proportion of juvenile females that groomed most with mother(%)
Infants	4	9/9 (100)	10/13 (77)
Yearlings	4	8/8 (100)	9/9 (100)
2-yr olds	4	6/8 (75)	4/6 (67)
3-yr olds	4	7/8 (88)	5/6 (83)
4-yr olds	3	6/6 (100)	1/3 (33)
5-yr olds	2	4/5 (80)	1/2 (50)
6-yr olds	1	2/3 (67)	0/1 (0)

first place in 1995, and a second (7-way) tie in 1996 (Table III). Thus, overall an offspring was the top-ranked immature grooming partner in 53 of 56 female-years, and two of the three exceptions involved ties, which could be viewed as consistent with this general pattern. Females with exactly two immature offspring usually (in 22 of 26 female-years) had both of them as the top two most frequently groomed immature partners. Females with three juveniles all had one of their offspring in the top-ranked position, but only three of the five females had offspring in the top two positions, and none of them had their offspring ranked 1, 2, and 3, although one case with ties—Pet 1997—is consistent with this pattern. It thus appears that the more immature offspring a female has, the less likely she is to keep them all as her very top-ranking immature grooming partners, although one of them almost always occupies the top-ranked position.

In most cases, the top-ranking immature grooming partner of a particular female was her youngest offspring (Table III). In 20 of 22 female-years in which infants were present, they were the top-ranked immature grooming

**Table III.** The ranking of offspring among the juvenile grooming partners of adult females, according to the frequency of grooming<sup>a</sup>

Adult female	Year			
	1995	1996	1997	1998
An	<b>1</b> (2)	1 (8)	1 (6)	<b>1</b> <sup>b</sup> (3)
Ar	1 (3)	<b>1, 2</b> (12)	1, 2 (2)	<b>1</b> <sup>c</sup> (8)
Bul	1 (9)	<b>1, 2</b> (15)	2, 1 (10)	<b>1, 5–7, 2</b> (7)
Dd	<sup>c</sup> (2)	1, 3 (7)	1, 2 (2)	<b>2, 1</b> (3)
Elb	<b>1</b> (6)	1 (15)	1 (12)	<b>1, 2</b> (8)
Fle	<b>1</b> (4)	1 (11)	1 (11)	<b>1, 2</b> (5)
Gt	1 (7)	1 (12)	<b>2, 1</b> (7)	2, 1 (8)
Kam	<b>1, 2</b> (3)	—	1 (5)	1 (8)
Kit	1 (2)	<b>1, 2</b> (13)	1, 2 (5)	<b>1</b> <sup>c</sup> (5)
Pet	<b>1, 2</b> (3)	1, 2 (12)	<b>1–2, 1–2, 3–7</b> (7)	<b>1, 2, 4</b> (7)
Ray	3–6 (6)	1–7 (7)	<b>1, 2</b> (5)	1, 2 (6)
Sf	1 (6)	<b>1, 2</b> (13)	1, 2 (5)	1, 2 (6)
Sp	1 (7)	1 (8)	<b>1, 3–5</b> (5)	1 (7)
Wv	1–2 (4)	1, 2 (12)	1, 2–3, 4–12 (12)	1, 2 (10)

—: female had no surviving juvenile this year.

<sup>a</sup>A rank of 1 means that the female groomed this juvenile more than any other juvenile, 2 = second most often, etc. Ranks of all juvenile offspring of each female are given, listed in order from youngest to oldest. Ranks of infants <1 year old are in bold font. A range of ranks (x–y) is given when the grooming frequency with the offspring was tied with y–x other juveniles. The number in parentheses represents the total number of juveniles with which the adult female groomed in each year.

<sup>b</sup>Represents a juvenile offspring that was in the group but was not seen to be groomed by its mother.

<sup>c</sup>Some females had two offspring present that were not seen to be groomed.

partners. In the two exceptional cases, an infant was ranked second, after an older sibling. As offspring got older, they tended to fall in rank among the mother's immature grooming partners. Nineteen immatures were in the group for  $\geq 3$  years between 1995 and 1998, and 15 of them changed rank order among their mother's immature grooming partners. Thirteen of them ranked lower as they grew older, and the decrease in rank position was associated with the birth of a younger sibling. The two exceptions decreased in rank position in 1998 versus 1995, but it was not a monotonic decrease across all 4 years.

Sex Differences in Grooming by Immatures

Immature males and females differed in the number of grooming partners. Immature males averaged fewer total grooming partners than did immature females in every year of the study. Differences are statistically significant in 2 of the 4 years (Table IV). Although immature males and females did not differ in the number of adult female grooming partners they had, in 3 of 4 years there were sex differences in the number of immature grooming partners: females had more immature grooming partners than males did (Table IV). In particular, females had more immature female grooming partners than males (Table IV). Although the average number of immature male grooming partners was also higher for immature

**Table IV.** Sex differences in the number of grooming partners (mean with standard error given in parentheses) of juvenile blue monkeys

Year	All grooming partners <sup>a</sup>		All juvenile grooming partners <sup>b</sup>		Juvenile female grooming partners <sup>c</sup>	
	Males	Females	Males	Females	Males	Females
1995	4.0 (0.8) <i>n</i> = 8	6.6 (1.5) <i>n</i> = 7	0.8 (0.3) <i>n</i> = 8	2.3 (0.7) <i>n</i> = 7	0.6 (0.2) <i>n</i> = 8	1.1 (0.4) <i>n</i> = 7
1996	10 (1.4) <i>n</i> = 11	11.8 (1.9) <i>n</i> = 8	3.0 (0.5) <i>n</i> = 11	4.1 (1.1) <i>n</i> = 8	1.7 (0.3) <i>n</i> = 11	1.8 (0.7) <i>n</i> = 8
1997	4.8 (0.7) <i>n</i> = 12	9.3 (1.8) <i>n</i> = 12	2.0 (0.3) <i>n</i> = 12	4.7 (0.9) <i>n</i> = 12	1.2 (0.2) <i>n</i> = 12	3.2 (0.6) <i>n</i> = 12
1998	5.1 (0.8) <i>n</i> = 16	8.2 (1.2) <i>n</i> = 17	2.1 (0.4) <i>n</i> = 16	4.3 (0.6) <i>n</i> = 17	1.4 (0.3) <i>n</i> = 16	2.8 (0.4) <i>n</i> = 17

<sup>a</sup>Sex differences are statistically significant in 1996 and 1998 (Mann–Whitney U Test, *U* = 37, 80.5 respectively, two-tailed *p* < 0.05).  
<sup>b</sup>Sex differences are statistically significant in 1995, 1997, and 1998 (*U* = 13, 32, 68.5 respectively, two-tailed *p* < 0.05).  
<sup>c</sup>Sex differences are statistically significant in 1997 and 1998 (*U* = 27, 69 respectively, two-tailed *p* < 0.05).



females than for immature males in every year of the study, no difference is statistically significant.

I also checked for sex differences in the number of unrelated adult female grooming partners because previous studies of other cercopithecine species showed such differences. In no year of this study are there significant differences in the number of unrelated adult females with which juveniles groomed (1.2–5.9 for males, 2.6–6.1 for females, average values across the 4 years) or in the proportions of males vs. females that did not groom at all with unrelated females (0–31% for males, 0–18% for females, across the 4 years). However, lack of knowledge of most kinship relations among adults makes this finding tentative.

To check for overall sex biases in partner choice, I compared the proportion of female grooming partners for each individual to the proportion that would be expected if he or she had groomed randomly with respect to partner sex. The overall pattern was for both male and female immatures to groom disproportionately with female partners. The proportion of female grooming partners exceeded the random expectation in 38 of 44 immature-female-years and in 42 of 46 immature-male-years. In a given year, 63–100% of immature females and 87–100% of males had more female partners than would be expected by chance. The proportion of grooming partners that were female did not differ between immature males and females in any of the 4 years.

Differences in the Grooming Profiles of Immatures and Adults

In every year of the study, immatures averaged less than half the total number of grooming partners that adult females had (Table V; Mann–

**Table V.** Differences between juveniles and adult females in the total number of grooming partners

Year	Mean number of partners per juvenile (s.d.)	Mean number of partners per adult female (s.d.)
1995	5.2 (0.9) <i>n</i> = 15	14.0 (0.9) <i>n</i> = 14
1996	10.7 (1.1) <i>n</i> = 19	23.4 (0.8) <i>n</i> = 14
1997	7.0 (1.0) <i>n</i> = 25	16.9 (1.5) <i>n</i> = 15
1998	6.6 (0.8) <i>n</i> = 33	16.6 (0.9) <i>n</i> = 14

Whitney U test,  $p < 0.05$  in each yearly comparison). When the identity of grooming partners was broken down by age and sex class (adult females, immature males, and immature females), the difference between adults and immatures persisted and is also statistically significant in every year. These differences may partially reflect differences in observation time because our study of mating focused on adults.

Another difference between the adult and immature members of mother-offspring pairs is that an offspring is likely to have its mother as its top-ranked grooming partner, whereas a mother is more likely to have another adult as top-ranked partner (although her offspring is still likely to be the top-ranked *immature* partner). Over 56 female-years, mothers had their immature offspring as top-ranked partners in 61% of cases (34 of 56 female-years), whereas immature offspring had their mothers as top-ranked partners in 83% (72 of 87 immature-years) of cases ( $\chi^2 = 7.52$ ,  $p = 0.006$ ).

## DISCUSSION

### Grooming of Mothers and Offspring

Immature blue monkeys resemble many other primate species in maintaining important and enduring grooming relationships with their mothers. Most immatures groomed with their mothers more than with any other partner. However, with up to 17% of immatures not following this pattern, it would be inaccurate to use the ranking of an immature's grooming partners to assess maternal kinship. A much better correlate of maternal kinship comes from examining the grooming partners of adult females. Depending on how one interprets ties, in 95–98% of cases, adult females groom their own juveniles more than any other juveniles, so that it appears that one would make very few errors of classification in assigning maternity to a female's top-ranked immature grooming partner, at least with a density of data like that reported here.

Note, however, that these figures come only from females that actually have immature offspring in the group. In  $T_w$  group, there was one female, Ms, present through 1997, that had no immature offspring. She was an old female that presumably was postreproductive, for although she mated in most years, her last offspring was born in 1992 and did not survive beyond infancy. She died (and we found her carcass) early in the 1998 observation period. In two of the years when she was present, Ms groomed with juveniles. In both years, her top-ranked juvenile partners were the offspring of her two daughters. Including data from Ms, the chances of a female's top-

ranked partner being her own offspring would drop to 91–95% (again, depending on how ties are interpreted), but of course at least two of the exceptional cases still involve close kinship between a grandmother and grandoffspring.

Walters (1981) carried out a similar analysis in which he evaluated the accuracy of inferring maternal kinship from behavioral data on wild baboons with known kinship relations. His study was more extensive in that it involved behavior types other than grooming and included the directionality of the various types of social exchange, including reciprocity in grooming. He found that maternal relationships with juveniles could be distinguished behaviorally from nonmaternal relationships, even though juveniles with no mother in the group compensated for her absence by forming a close relationship with another adult female. As in my study, grooming frequency was an important variable that distinguished the mother-offspring dyads, although other aspects of behavior, such as grooming reciprocity and frequency of aggression and of agonistic interventions, had to be considered as well in order to distinguish the relationships of true mother-infant pairs from those of orphaned juveniles with compensatory attachments.

Many other researchers have highlighted preferential grooming between mothers and juvenile offspring in Old World primates; O'Brien (1993) described an exception among *Platyrrhini*. Some of them used data on the frequency of grooming bouts or episodes (Missakian, 1974; Watts and Pusey, 1993), whereas others used data on the amount of time spent grooming (Kurland, 1977; Cheney, 1978; Pereira and Altmann, 1985; Rowell and Chism, 1986; Nash, 1993; Watts and Pusey, 1993). Watts and Pusey (1993) found that the two types of data did not coincide perfectly in a study of gorillas, such that juveniles that spent most time grooming with their mothers did not necessarily have the most grooming bouts with her, and vice versa. Their study also showed that the degree to which mother-offspring grooming occurs disproportionately may depend on which partner is doing the grooming: in gorillas, grooming by the mother was more biased toward offspring than grooming by offspring was biased toward the mother. Nevertheless, the general picture from all these studies is one in which mother-offspring pairs are preferential grooming partners by at least one measure. The data from blue monkeys concur with this general pattern.

As they get older, blue monkey juveniles generally decrease their position among the rank-ordered immature grooming partners of their mothers. These decreases usually occurred in the same year that a younger sibling was born, and became the mother's top ranked immature partner. These changes may occur as mothers redirect their investment to younger, more vulnerable offspring. Several other researchers have reported changes in the amount of grooming between mothers and offspring as the offspring

grow older (Missakian, 1974; Kurland, 1977; Fairbanks and McGuire, 1985; Rowell and Chism, 1986; Nakamichi, 1989). The general pattern is for mothers to groom older offspring less than younger ones and for older offspring to groom their mothers more than younger ones do. Most of these researchers report separately the time spent grooming by the mother and by the offspring, so that the data cannot be compared directly to the results of the current study, in which directionality of grooming could not be fairly assessed and in which bouts were tallied instead of grooming time. Nakamichi (1989) presented data on total mother-offspring grooming time in Japanese macaques and found a trend seemingly opposite to the one reported here: older juveniles spent more time grooming with their mothers than younger ones did. However, it is possible that total grooming time and rank ordering of partners by bout numbers are not truly comparable measures of grooming relationships.

### **Sex Differences and the Function of Grooming of Immatures**

The degree to which one expects sex differences in the grooming of immatures depends on what one views as the main functions of their grooming. The life history differences between male and female blue monkeys might lead one to expect that immature females would begin to diversify their social network within their natal group more than immature males. Through grooming, young females could be establishing long-term cooperative relationships with other females in the group (O'Brien, 1993; O'Brien and Robinson, 1993). If this is a function of grooming by immature females, they should have a disproportionate number of female partners, and their bias toward female partners is likely to exceed any sex bias in the grooming of immature males, whose emigration at adolescence prevents them from maintaining long-term relationships with natal-group females. Immature males might be expected to develop closer relationships to same-sex peers because they may emigrate from the natal group in tandem and maintain enduring relationships after they do so (pers. obs.).

Grooming by immatures could also function to maintain social relationships that are of current value. If so, sex differences are not as clearly expected. Although the lives of juvenile blue monkeys have not been carefully studied, it seems likely that both males and females depend primarily on their mothers for protection, and on their peers for companionship and play (pers. obs.).

A third possibility is that grooming by immatures allows them to practice the social skills that they will need to negotiate their present and future relationships. Again, both males and females should benefit from

such practice because members of both sexes must cope with a similar set of social partners as immatures and with more divergent, but still demanding, social milieux as adults.

Without knowing more about how grooming can act as practice for various forms of social exchange, it is hard to predict which differences between immature males and females should occur. Both sexes groom as adults, although adult females certainly groom more often, and with a more diverse set of partners, than do adult males.

Finally, for both immature males and females, grooming may have a hygienic function. If so, sex differences in the number of partners would probably not be expected.

The various functions of grooming are articulated from the perspective of immature group members. Some grooming of immatures may occur, however, because it is primarily in the interest of their (adult) partners. For example, adults might groom immatures to increase their access to their relatives or associates or to increase the amount of grooming that they receive in reciprocation. If grooming for these reasons occurs, it is not obvious that it would lead to sex differences in partner profiles of the immatures.

My data suggest that immature female blue monkeys diversify their set of grooming partners more than males do. Young females tend to have more grooming partners than young males do. It is particularly the number of immature female grooming partners that differs between the sexes. These results are consistent with the hypothesis that the grooming of immature females relates to the development of long-term social relationships, perhaps especially with their female peers. The fact that the immature females have a disproportionate number of female grooming partners is also consistent with this hypothesis. Although the proportion of female partners is not higher for immature females than for immature males, the fact remains that young females have more female partners than young males do, apparently at least partly because they have more partners generally.

For immature males, the evidence is less convincing that grooming is related to the development of specific social relationships that will last beyond the juvenile years. The only relationships that males have in their natal groups with the potential to endure beyond the time of their emigration are ones with other immature males that are potential co-emigration partners. Across the years, however, many immature males (46–100%, depending on the year) were never seen to groom with peers close enough in age ( $< 1$  year older or younger) to emigrate in tandem, and even those that were observed grooming with male peers did so only rarely (typically only one bout). Furthermore, there was little consistency in the identity of immature male grooming partners across years, with only one dyad ap-

pearing in  $>1$  year of the study. Immature males may cultivate their relationships with one another through other types of behavior, especially play (Lee, 1983). As juveniles grow older, play becomes more and more restricted to males, and even the oldest preadolescent juvenile males play with one another (pers. obs.).

The data do not necessarily refute the other hypotheses explaining grooming in immatures. After all, there must be some explanation for the grooming relationships of juvenile males. Both young males and females may use grooming to keep clean, to solidify current social relationships and to practice social skills that are useful throughout the lifespan. The similarities in partner preferences of the two sexes, and the way that both males and females groom with a variety of partners, and especially their mothers, are consistent with these ideas. To evaluate them more deeply, however, we need much more information about the ecological and social priorities of immature blue monkeys: such information would allow more specific predictions that could differentiate this set of hypotheses. In the meanwhile, the alternative possibility remains (instead of optional) that (at least some) grooming involving immatures is not carried out in their direct interests at all; to the extent that it occurs, such grooming might obscure patterns that indicate various adaptive functions. In general, my findings agree with the picture emerging from other studies of the social life of immatures (Pereira and Altmann, 1985; Glick *et al.*, 1986; Walters, 1987; Fairbanks, 1983; O'Brien and Robinson, 1993; Watts and Pusey, 1993), which includes managing life as a nonadult, as well as preparing for life as an adult.

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## REFERENCES

- Cheney, D. L. (1978). Interactions of immature male and female baboons with adult females. *Anim. Behav.* 26: 389–408.
- Cords, M. (1987). Mixed-species association of *Cercopithecus* monkeys in the Kakamega Forest, Kenya. *University of California Publications in Zoology*, Vol. 117.
- Cords, M. (1997). Friendships, alliances, reciprocity and repair. In Whiten, A. and Byrne, R. W. (eds.), *Machiavellian Intelligence II: Extensions and Evaluations*, Cambridge University Press, Cambridge, pp. 24–49.
- Cords, M. (2000). The number of males in guenon groups. In Kappeler, P. (ed.), *Primate Males*, Cambridge University Press, Cambridge, pp. 84–96.
- Fairbanks, L. A. (1993). Juvenile vervet monkeys: Establishing relationships and practicing skills for the future. In Pereira, M. E. and Fairbanks, L. A. (eds.), *Juvenile Primates: Life History, Development and Behavior*, Oxford University Press, New York, pp. 211–227.
- Fairbanks, L. A., and McGuire, M. T. (1985). Relationships of vervet mothers with sons and daughters from one through three years of age. *Anim. Behav.* 33: 40–50.
- Glick, B. B., Eaton, G. G., Johnson, D. F., and Worlein, J. M. (1986). Development of partner preferences in Japanese macaques (*Macaca fuscata*): Effects of gender and kinship during the second year of life. *Int. J. Primatol.* 7: 467–479.
- Horrocks, J. A., and Hunte, W. (1993). Interactions between juveniles and adult males in vervets: Implications for adult male turnover. In Pereira, M. E. and Fairbanks, L. A. (eds.), *Juvenile Primates: Life History, Development and Behavior*, Oxford University Press, New York, pp. 228–239.
- Kurland, J. A. (1977). *Kin Selection in the Japanese Monkey* (Contributions to Primatology). Karger, Basel.
- Kummer, H. (1978). On the value of social relationships to nonhuman primates: A heuristic scheme. *Soc. Sci. Inf.* 17: 687–705.
- Lee, P. C. (1983). Play as a means for developing relationships. In Hinde, R. A. (ed.), *Primate Social Relationships*, Sinauer Associates, Sunderland, MA, pp. 82–89.
- Missakian, E. A. (1974). Mother-offspring grooming relations in rhesus monkeys. *Arch. Sex. Behav.* 3: 135–141.
- Nakamichi, M. (1989). Sex differences in social development during the first 4 years in a free-ranging group of Japanese monkeys, *Macaca fuscata*. *Anim. Behav.* 38: 737–748.
- Nash, L. T. 1993. Juveniles in nongregarious primates. In Pereira, M. E., and Fairbanks, L. A. (eds.), *Juvenile Primates: Life History, Development and Behavior*, Oxford University Press, New York, pp. 119–137.
- O'Brien, T. G. (1993). Asymmetries in grooming interactions between juveniles and adult female wedge-capped capuchin monkeys. *Anim. Behav.* 46: 929–938.
- O'Brien, T. G., and Robinson, J. G. (1993). Stability of social relationships in female wedge-capped capuchin monkeys. In Pereira, M. E. and Fairbanks, L. A. (eds.), *Juvenile Primates: Life History, Development and Behavior*, Oxford University Press, New York, pp. 197–210.
- Pereira, M. E., and Altmann, J. (1985). Development of social behavior in free-living nonhuman primates. In Watts, E. S. (ed.), *Nonhuman primate models for human growth and development*, Alan R. Liss, New York, pp. 217–309.
- Pereira, M. E., and Fairbanks, L. A., (eds.) (1993). *Juvenile Primates: Life History, Development and Behavior*, Oxford University Press, New York.
- Rowell, T. E., and Chism, J. B. 1986. The ontogeny of sex differences in the behavior of patas monkeys. *Int. J. Primatol.* 7: 83–107.
- Walters, J. R. (1981). Inferring kinship from behaviour: Maternity determinations in yellow baboons. *Anim. Behav.* 29: 126–136.
- Walters, J. R. (1987). Transition to adulthood. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. and Struhsaker, T. T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 358–369.

- Watts, D. P., and Pusey, A. E. (1993). Behavior of juvenile and adolescent great apes. In Pereira, M. E. and Fairbanks, L. A. (eds.), *Juvenile Primates: Life History, Development and Behavior*, Oxford University Press, New York, pp. 148–167.
- Wolfheim, J. (1977). Sex differences in behavior in a group of captive juvenile talapoin monkeys (*Miopithecus talapoin*). *Behaviour* 63: 110–128.