

Development of Mother–Infant Relationships and Infant Behavior in Wild Blue Monkeys (*Cercopithecus mitis stuhlmanni*)

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Introduction

A characteristic feature of primate life histories is the prolonged period of postnatal development in which newborns depend on adults, especially their mothers, for nutrition, transport, and protection, and develop social skills that enable them to become fully integrated members of society. Many researchers have focused on the development of infant nonhuman primates, attempting to identify factors that influence the ontogeny of

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social behavior, with strong emphasis on the mother-infant relationship (Nicolson, 1987). Studies on infant development in Old World monkeys have concentrated mainly on macaques, especially *Macaca mulatta* (Seay, 1966; Hinde and Spencer-Booth, 1967, 1971; Harlow and Harlow, 1969; Hinde, 1969; Sackett, 1972; Anderson and Mason, 1974; Berman, 1980a; Stevenson-Hinde and Simpson, 1981; Simpson, 1985). Other catarrhine taxa for which data on infant or juvenile behavioral and social development are available include *Papio* spp. (Ransom and Rowell, 1972; Nash, 1978; Altmann, 1980), *Cercopithecus aethiops*, (Struhsaker, 1971; Lee, 1984a; Fairbanks and McGuire, 1985; Fairbanks, 1989), *Erythrocebus patas*, (Chism, 1986; Loy and Loy, 1987), and a few other cercopithecines (*C. neglectus*: Chalmers, 1972; Kirkevold and Crockett, 1987; *C. mitis albobogalis*: Bramblett and Coelho, 1987).

Most of the studies were focused on terrestrial or semiterrestrial species and were carried out in captivity or with provisioned colonies. Whether their results can be generalized across the various social and ecological conditions in which cercopithecine species live in the wild is moot. Indeed, social, demographic, and ecological factors have strong and often long-lasting effects on infant and juvenile monkeys (Berman, 1980b; Johnson and Southwick, 1984; Lee, 1984b; Fairbanks and McGuire, 1987; Fairbanks, 1988; Maestripiéri, 1994a; Berman *et al.*, 1997). Accordingly, we need to extend the research on infant development to other species with different social organizations or living in different environments.

We aimed to begin filling the gap in our knowledge by providing information on infant development in a highly arboreal cercopithecine species in the wild. Blue monkeys (*Cercopithecus mitis*) differ from macaques, vervet monkeys, and baboons not only in their arboreality but also in their social organization. They live in one-male multifemale groups most of the time and have a weakly differentiated dominance hierarchy among females whose ranks seem unrelated to affiliative behavior or reproductive success (Cords, 1987a, 2000a).

We characterize behavioral development of infant blue monkeys during their first six months to assess how an infant's relationship with its mother influences its behavior, paying special attention to factors that others have found to influence various aspects of infant development, including infant sex (Mitehell, 1979; Meaney *et al.*, 1985; Brown and Dixson, 2000), infant-rearing experience of the mother (Hooley and Simpson, 1981; Maestripiéri, 1998), and maternal dominance status (Ransom and Rowell, 1972; Cheney, 1978). We also compare blue monkey infant development, especially the infant's relationship with its mother, with other cercopithecine species that are more terrestrial and have different social organizations. We evaluate the hypothesis that arboreality slows infant development because of the physical dangers of life in a three-dimensional habitat (Chalmers, 1972; Sussman, 1978).

Methods

Study Site

The study site is the Kakamega Forest (Isecheno section), western Kenya ($0^{\circ}14' \text{ N}$, $34^{\circ}52' \text{ E}$) at an altitude of *ca.* 1580 m. The indigenous vegetation of the forest is a semideciduous type of Guineo–Congolian lowland rain forest. The site included areas with some human influence, such as enrichment planting of nonindigenous trees, indigenous plantation forest, and a village area that was used on a seasonal basis by one of the study groups, though not during our study. Cords (1987b) provided a detailed description of the site.

Subjects

The blue monkey population (*Cercopithecus mitis stuhlmanni*) at Kakamega is a high-density one for the species, with *ca.* 220 individuals per km^2 (Fashing and Cords, 2000). Blue monkeys live in groups with females as permanent members. Young males leave their natal groups before reaching full bodily size at an age of about seven years. For most of the year, only one adult male is present in the group, though additional males may join the group during the mating season (Cords, 2000b). Our study took place when only one adult male was present in each study group. Females defend territories against neighboring groups, whereas males are rarely involved in intergroup aggression (Cords, 2002).

We focused on 12 infant blue monkeys from three well-habituated groups with 17–37 noninfant members, which occupied adjacent home ranges of *ca.* eight to 17 ha. We could distinguish individuals via facial and other features like the shape of tail hairs. Table I is a summary of the ages, sexes, approximate sizes at birth, and sampling durations of the subjects, and characteristics of their mothers.

Data Collection

Förster conducted focal samples of the infants between November 1999 and June 2000. He sampled each subject for 336 ± 58 minutes ($n = 60$ 2-week sample blocks) per two-week period for the first three months of life, and for an average of 148 ± 15 minutes ($n = 51$ 2-week sample blocks) for the second three months. The total duration of focal samples for each infant over the whole study period averaged 38.5 ± 10.3 hours ($n = 12$).

Predetermined sampling schedules were impractical given the dispersion of group members over several hundred meters in dense vegetation, but we distributed samples of each subject as evenly as possible over each two-week

Table I. Birthdate, Sex and Relative Size of the Subjects, the Age up to Which They Were Sampled, and Parity and Relative Rank of Their Mothers

Mother's name	Infant characteristics				Maternal characteristics	
	Sex	Birthdate (MM-DD-YY)	Relative size ^a	Maximum age (weeks)	Parity	Relative rank ^b
Fletcher	male	12-13-99	medium big	24	multiparous	medium
Tap	male	01-04-00	medium big	24	multiparous	low
Bibi	male	01-10-00	medium big	24	multiparous	low
Pody	male	02-01-00	big	20	multiparous	medium
Spanner	male	02-07-00	medium big	22	multiparous	medium
Plume	male	02-09-00	medium small	12	multiparous	low
Lolita	female	11-16-99	small	24	primiparous	medium
Dingle	female	11-26-99	medium small	24	primiparous	low
Bow	female	12-13-99	big	24	primiparous	medium
Mustache	female	01-30-00	medium small	24	multiparous	low
Angle	female	02-04-00	medium big	20	multiparous	high
Xmas	female	02-27-00	medium big	20	multiparous	high

^a Relative size of an infant was assigned to one of four classes during the first week of life.

^b Females in each group were assigned rank classes (high, medium, low) according to their position in the upper, middle, or lower third of the hierarchy. If the total number of females was not divisible by 3, the 'medium' rank class was made the largest (exception: Xmas, who was assigned high rank because of her distinct dominant behavior towards other medium ranked females and an unstable relationship with the 3rd highest ranking female).

time block. To adjust for possible diurnal differences in activity, we divided the day into three periods (0730–1100 h, 1100–1430 h, 1430–1800 h) and sampled all infants nearly equally in these three periods during the first month of the study. Older infants grew increasingly difficult to locate as focal subjects, and we could not maintain an even distribution of samples across the three periods. Therefore, from each infant's third month we combined the morning and afternoon hours as one period, which is distinguished from the midday hours when general activity levels were usually lower. Samples for all subjects are similarly distributed between these more and less active periods.

Subjects quite often disappeared from view because of the dense vegetation. If we lost a subject for <15 minutes, we extended the sample until it had been in view for about 75 minutes. If the infant remained out of view for >15 minutes, we terminated the sample at the moment of disappearance and continued at the next opportunity within the same diurnal period, usually on the same day or on the following day.

Focal samples include both point and one/zero recording methods at 30 second intervals. We noted all occurrences of approaches and leaves, as well as some other rare behavior. Table II is a list of the behavioral categories recorded and recording methods. Several qualifications should be

Table II. Behavioral Categories and Method of Recording

Behavior	Description	Recording method
On nipple	Infant has nipple in mouth (whether clinging or not)	Point and 1/0 samples
On ventrum	Infant on mother's ventrum, without nipple in mouth	Point and 1/0 samples
Clinging	Infant on mother's ventrum but it is unclear whether it is on the nipple	Point and 1/0 samples
Exploring ventrum	Infant crawling on mother's ventrum, often to her sides, with eyes open (no nipple seeking movements)	Point and 1/0 samples
Independent locomotion	Infant locomoting off mother (or caretaker)	Point samples
Explorative feeding	Handling and mouthing objects (includes gnawing) in a playful manner	Point samples
Feeding	Searching for, manipulating, and swallowing food objects	Point samples
Resting	Sitting off mother, not engaged in social interaction, nor feeding (includes sleeping)	Point samples
Playing	Social play with peers	1/0 samples
Groomed	Infant groomed by mother	Point and 1/0 samples
Approach	Moving from >1 m to <1 m	Event recording
Leave	Moving from <1 m to >1 m	Event recording
Following	Infant actively follows mother while remaining in proximity (1 m) to her	1/0 samples
Restricting	Mother prevents infant from moving away from her	1/0 samples
Retrieving	Mother approaches infant and picks it up	Event recording
Rejecting	Mother denies nipple access	Event recording

kept in mind. First, because of limited visibility, it was often unclear whether an infant was suckling or just mouthing the nipple and whether it was sleeping. Therefore, we used three categories that reflect different grades of mother-infant contact behavior and nursing (Table II). Second, we called any kind of locomotion by the infant independent locomotion, including movements during play, which we scored as independent locomotion with the point sampling method but also as play with the 1/0 sampling method. Third, we divided foraging behavior into two classes: explorative feeding (including mouthing) and feeding (ingestion and swallowing). As it was difficult to tell whether infants actually swallowed food, especially until the fourth month of life, we recorded all handling and mouthing of food objects as explorative feeding until we saw the infant actually swallowing food for the first time. From then on, feeding was usually distinguishable from explorative feeding. Fourth, both solitary object play and social play occurred, but we recorded only the latter. We could not reliably distinguish object play, which included handling and mouthing twigs, leaves or other small objects, from explorative feeding and therefore we did not record it separately. Social play was a distinctive behavioral category, involving chases or rough-and-tumble body contact. Fifth, rejection rates in our analyses represent the frequency of rejections per total sample time, not the rejection rate per number of attempted nipple contacts.

Data Analysis

We adjusted all parameters in each sample for sample duration by dividing the number of points/intervals in which the parameter was recorded by the number of points/intervals sampled. Then we averaged the time budget values for each infant over two- or four-week periods depending on the analysis.

We used repeated measure ANOVA to analyze the development of behavioral parameters over the first five months, with four-week periods as the intra-subject factor (repeated measure), while inter-subject factors include sex, parity of mother (primiparous vs. multiparous), group membership, rank of mother (high, medium, or low), and time of birth relative to birth season (early vs. late). In each group, early and late cohorts were separated by several weeks or months (Table I). For each inter-subject factor, we ran a separate repeated measures ANOVA because of the small number of subjects. We pooled data over four-week periods to achieve a normal distribution, which could not be obtained with data from two-week blocks, even with transformations. As the repeated measure procedure is sensitive to missing values, we included no data from the sixth month of life because we had sampled only eight infants through all six months. If significant main effects occurred, we usually mention them only when interactions with age

are not significant. We scrutinized all interaction effects carefully and ran follow-up one-way ANOVAs separately for each 4-week block to determine when significant differences occurred. In all analyses of temporal changes of a given measure, we searched for interindividual variation to be sure that mean values are representative. We report only statistically significant differences between individuals.

We compared the results of the repeated-measures ANOVA with linear multiple regression analyses to test for combined influences of different independent variables on a given dependent variable (usually a behavioral parameter). We entered independent variables in a stepwise procedure, with the probability of F to enter ≤ 0.05 , and the probability of F to remove ≥ 0.1 (standard setting: Sokal and Rohlf, 1981) and with pairwise exclusion of cases. We examined data points that were more than three times the standard deviation from the mean and excluded them from the model if there were reasonable explanations for their aberrant values, e.g., exceptionally short sampling time, or infant with injury. We used the Durbin–Watson statistic to assess the degree of autocorrelation between adjacent residuals, accepting values from 1.5 to 2.5. We tested the assumption of equal variances across variables by inspecting residual plots: standardized residuals against standardized predicted values. For all extracted factors we report the regression coefficient B together with its p -value and associated adjusted R^2 (or ΔR^2_{adj}) value.

In correlational analyses we used the Spearman rank correlation for two-week-block data, which were not normally distributed, or Pearson correlation for four-week-block data, which were normally distributed.

Generally, we report means and standard deviations to summarize scores; however, we use medians (and ranges) when summarizing ≤ 12 scores with outlying values.

To reduce the number of intercorrelated variables, especially in measures of mother–infant contact behavior, we ran a principal components analysis. We extracted one factor containing the following measures: clinging, time on nipple, independent locomotion, feeding/explorative feeding, resting, time off mother, time in contact to mother, time in proximity to mother, and time at a distance without other individuals in proximity. The Kaiser–Meyer–Olkin measure of validity of the model is 0.877 (maximum of 1). We estimated the factorial values via a regression procedure. For analyses involving measures included in the independence factor, we first worked with the original variables. Because of the intercorrelations, only one such variable could be analyzed at a time, so the analysis could not account for slight interactions between the variables. We usually compared the results of the separate analyses to the results when using the independence factor. If the independence factor explained more of the variance than any one of its components, we used it instead of the original measures as an independent variable in the multiple regression analysis.

Results

Mother-Infant Relationship

Nipple contact

During the first days of life, infants spent most of their time on the nipple. Primiparous mothers were generally very attentive to their infants, but sometimes had difficulty supporting them in gaining nipple access, especially while moving or foraging. This difficulty seemed to result from the infant's small size and weakness rather than the mother's experience. Two of three infants born to primiparous mothers were smaller than average and appeared

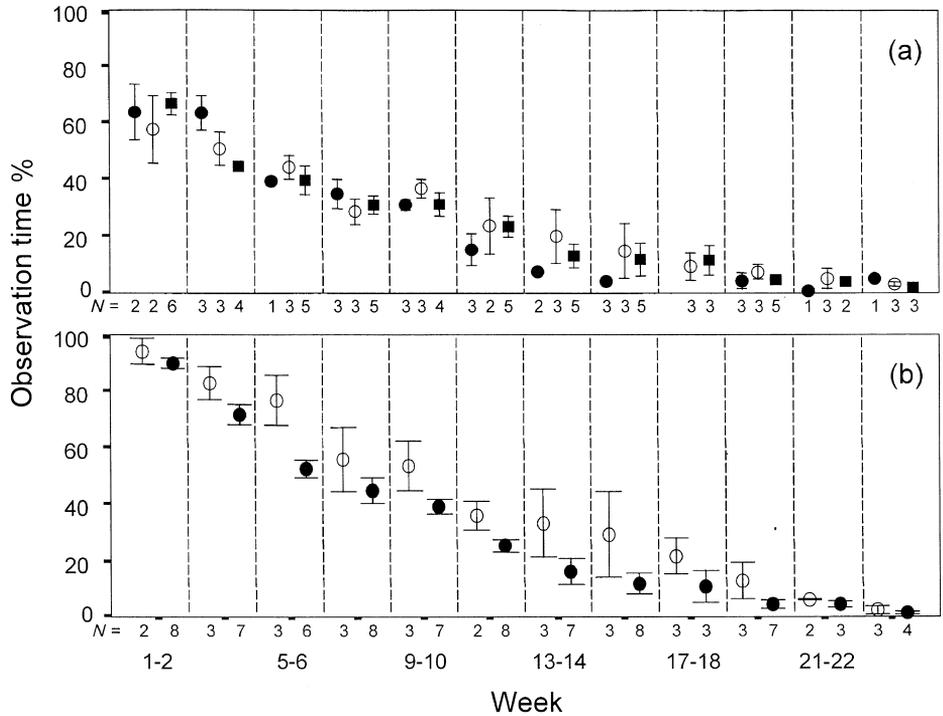


Fig. 1. Average (\pm S.E.) proportion of time infants spent in (a) nipple contact, and (b) contact to their mother, grouped by infant sex and parity of the mother. Differences in nipple contact (a) were not systematically related to infant sex or maternal parity: full circles, female infants of multiparous mothers; open circles, female infants of primiparous mothers; squares, male infants (multiparous mothers only). Infants of primiparous mothers (open circles) spent more time in contact (b) than infants of multiparous mothers (full circles; $F = 7.9$, $p < 0.05$, repeated measures ANOVA).

to be weak during their first days. Their small size, together with the still short nipples of their mothers, was obviously disadvantageous for gaining nipple access. Infants usually clung to the mothers with their hind-limbs wrapped around her hips, and a small infant could not reach the nipples from this position without maternal support. The one large infant of a primiparous mother had no problem, even from its first days, in gaining or maintaining nipple access while the mother foraged; the same was generally true of the medium to large infants of parous mothers. The two medium-small infants born to parous mothers, however, had low nipple contact rates during the first weeks of life, like the two small infants born to primiparous mothers. These comparisons show that infant size and strength are important in determining the amount of early nipple contact.

The time infants spent on the nipple decreased fairly steadily over the first six months [Fig. 1(a)], reaching <50% in weeks 5–6 ($\bar{x} = 40.1 \pm 9.4\%$, $n = 9$), and dropping below 5% during the sixth month ($\bar{x} = 2.9 \pm 1.8\%$, $n = 8$). No difference between male and female infants, infants of multiparous vs. primiparous mothers, or infants of differently ranked mothers were revealed by separate repeated measure ANOVAs.

A multiple regression with time spent on nipple as the dependent variable resulted in a different picture. Beside the independence factor ($B = -0.204$, $p < 0.001$, $R_{\text{adj}}^2 = 0.954$) and time carried by other than mother ($B = -0.478$, $p < 0.001$, $\Delta R_{\text{adj}}^2 = 0.009$), sex had an effect, with males having slightly lower rates of nipple contact than females did ($B = -0.018$, $p < 0.001$, $\Delta R_{\text{adj}}^2 = 0.007$). The fact that both the independence factor and the time infants were carried by non-mothers influenced the time an infant was on the nipple is not surprising, since they both increased fairly steadily with the infant's age, but with no significant intercorrelation between the independence factor and the amount of time non-mothers carried infants.

Spatial relationship and distance regulation

Time in contact. We calculated the time infants spent in contact with their mothers by summing up the time they spent clinging, including on nipple, on ventrum, and exploring ventrum, and the time they were off but in physical contact with their mother. Over the first six months of life, infants of primiparous mothers spent more time in contact ($41.7 \pm 1\%$, $n = 3$) than those of multiparous mother [$35.9 \pm 0.7\%$, $n = 9$; Fig. 1(b)].

A multiple regression analysis showed that age in weeks was the most important predictive variable ($B = -0.08$, $p < 0.001$, $R_{\text{adj}}^2 = 0.8$). Only parity made a small but significant additional contribution to explain differences in contact scores between infants ($B = -0.04$, $p < 0.05$, $\Delta R_{\text{adj}}^2 = 0.008$), confirming the repeated measures analysis.

Time spent off mother. Infants in their second or third day of life (median: 2.5, range = 1–5, $n = 12$) began to explore immediate surroundings

by releasing their grip on the mother while maintaining physical contact. The median age at which infants moved out of contact is five days (range = 2–14, $n = 12$). The median age at which they moved more than arm's reach from their mothers is nine days (range = 5–19, $n = 12$).

Again there is a significant difference between infants of primiparous vs. multiparous mothers ($F = 5.5$, $p < 0.05$, repeated measures ANOVA) in time spent off the mother. The average percentage for infants of primiparous mothers ($63.3 \pm 3.7\%$, $n = 3$, months 1–5) is lower than for infants of multiparous mothers ($73.4 \pm 2.3\%$, $n = 9$, months 1–5). However, multiple regression analysis did not confirm this parity effect.

The size of infants at birth significantly influenced the time they spent off their mothers [multiple regression, $B = 0.05$, $p < 0.01$; $\Delta R^2_{\text{adj}} = 0.035$; Fig. 2(a)]. Larger infants tended to spend more time off their mothers than smaller infants did, especially during the first four weeks of life. The correlation between size of the infant at birth and overall percentage of time spent off the mother across the first six months ($r = 0.16$, $n = 12$) is not significant however.

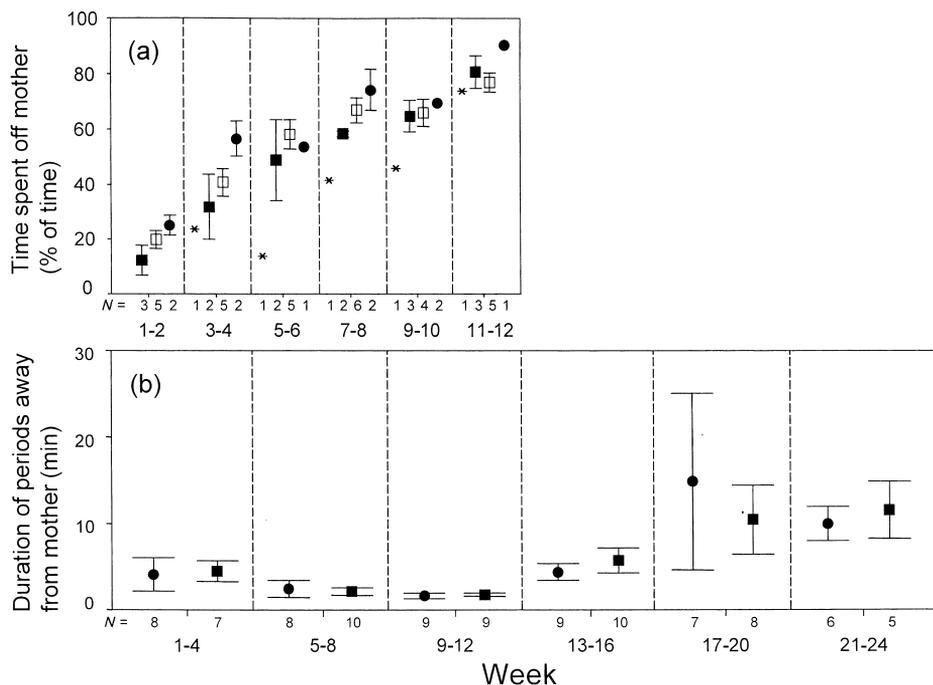


Fig. 2. Time spent off mother (a) and duration of periods away (>1 m) from mother (b), means (\pm S.E.). In (a), asterisk = small, full square = medium-small, open square = medium-big, full circle = big infant. In (b), circles = female and squares = male infants.

Duration of periods away from the mother. The average duration of periods away (>1 m) from the mother did not increase steadily with age [Fig. 2(b)]. Slightly higher values in the first month vs. months two and three were probably caused by the infant's inability to keep up with the mother when she decided to leave. Once an infant began to locomote steadily, it would follow its mother when she left, which led to a decrease in the average length of separation up to the third month. From the third month onward, infants spent ever-longer periods away from their mothers. Average values are probably underestimates, especially for the last two months when infants were often away from their mothers for the entire 75-minutes sample period.

Repeated measures ANOVA revealed no main effect. A multiple regression revealed that aside from age, the rejection rate and the time being carried by others influenced the duration of periods away from the mother ($B = -9.6$, $p < 0.05$, $\Delta R^2_{\text{adj}} = 0.047$, and $B = 69.1$, $p < 0.05$, $\Delta R^2_{\text{adj}} = 0.040$, for rejection rate and time carried by others, respectively). A higher rejection rate resulted in a decrease in the average duration of periods away from the mother.

Regulation of proximity between mother and infant. There was no overall main effect of sex, parity, rank, size, or time of birth on how proximity between mother and infant was regulated, measured either with the proximity index of Hinde and Atkinson (1970), or as the average number of approaches and leaves. The degree to which the infant was responsible for remaining in proximity to its mother as measured by the proximity index increased more or less steadily with age, whereas especially the number of leaves made by the mother as well as the number of leaves and approaches made by the infant reached a peak between weeks 11 and 14 (Fig. 3).

The overall pattern shows that infants generally were primarily responsible for maintaining proximity to their mothers, as evidenced by the usually higher number of approaches and lower number of leaves by infants vs. mothers and also from the positive proximity index scores from the very beginning of infancy (Fig. 3). Only one infant showed a negative proximity index in the first month. She tried to get away from her mother as often as possible during the fourth week of life, though the mother tried to prevent her escape, and therefore approached her infant more often than the infant approached her.

In the sixth month there was a marked increase in the number of approaches and leaves by male infants. The proportion of leaves by infants is significantly different for males vs. females at 21–22 weeks ($73 \pm 3\%$, $n = 2$, vs. $39 \pm 14\%$, $n = 4$, respectively, $F = 11.1$, $p < 0.05$) and at 23–24 weeks ($70 \pm 5\%$, $n = 3$, vs. $37 \pm 13\%$, $n = 4$, respectively, $F = 16.4$, $p < 0.05$). Significant differences in the same measure (proportion of leaves by the infant) for infants of primiparous vs. multiparous mothers occurred in weeks 5–6 ($6 \pm 10\%$, $n = 3$, vs. $35 \pm 12\%$, $n = 6$, respectively, $F = 13.5$, $p < 0.01$) and 23–24 ($32 \pm 12\%$, $n = 3$, vs. $65 \pm 11\%$, $n = 4$, $F = 14.5$, $p < 0.05$).

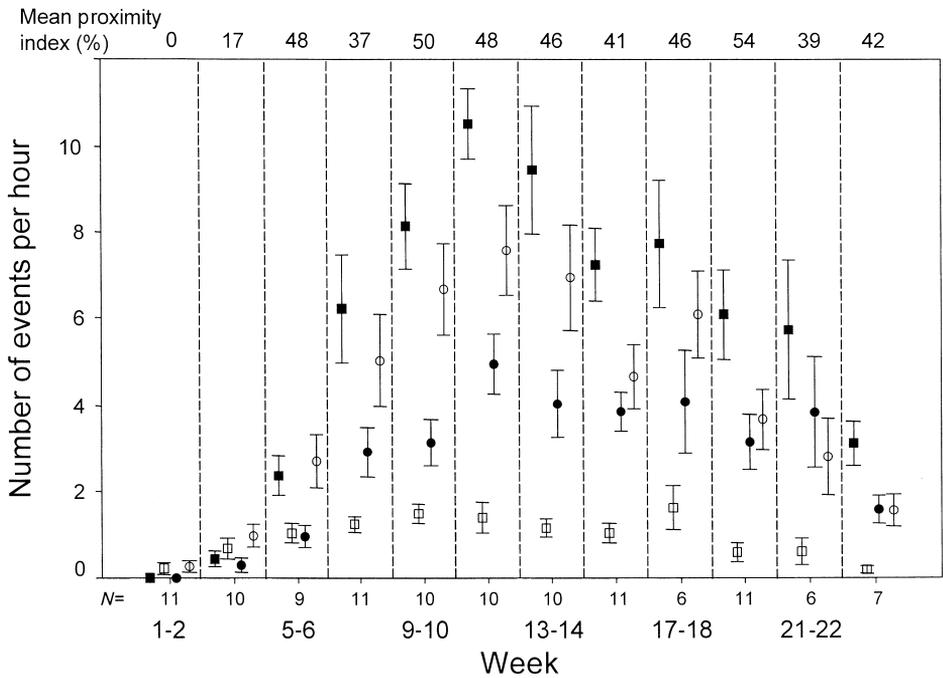


Fig. 3. Proximity regulation between mother and infant, expressed as the average (\pm S.E.) number of approaches and leaves per hour. Full squares = approaches by infant, open squares = approaches by mother, full circles = leaves by infant, and open circles = leaves by mother. The Hinde and Atkinson (1970) proximity index is the proportion of approaches made by the infant less the proportion of leaves made by the infant, averaged across infants for each period.

The maximum number of transitions occurred in weeks 11–12 for males and weeks 13–14 for females. During this period, mothers would usually leave and infants would try to keep up with them. If an infant had problems catching up, the mother usually waited until it came near again, and then either picked it up or repeated the procedure, i.e., moving ahead and waiting.

Across the entire study period, the number of leaves by mothers is correlated with the proportion of 30-second intervals when infants followed their mothers within a distance of 1 m ($r_s = 0.78$, $p < 0.001$, $n = 97$ 2-week periods, all infants combined), which underscores the predominant responsibility of infants to remain close to their mothers.

Restriction

Mothers restricted their infants from moving out of contact only during the first few weeks. They did so by holding a limb or tail, or by forcing it into

ventroventral contact. If others were nearby, mothers frequently shielded clinging infants by embracing them and turning away from other individuals.

By the third to fourth week, restriction was fairly infrequent, occurring in <1% of sampling intervals (Fig. 4). Mothers allowed older infants to move away freely, but would still often pick them up if other individuals approached or if there were other signs of disturbance or danger, e.g., a predator alarm, intergroup encounter, observer, or loud calls by the resident adult male. After the third month, maternal protective behavior was far less frequent, partly because the infants spent much time away from their mothers. When infants were far from their mothers, however, other individuals, especially adult and subadult females, usually offered protection.

Although multiparous mothers tended to restrict their infants far less than primiparous mothers did, and high-ranking mothers were generally least restrictive, the small sample sizes prevent either difference from reaching statistical significance. Mothers of early-born infants, however, showed higher restriction rates during the first three months than mothers of later-born infants (Fig. 4).

Maternal rejection

Rejections occurred infrequently and never exceeded an average of three events per hour for a given infant over a two-week period. Most rejections

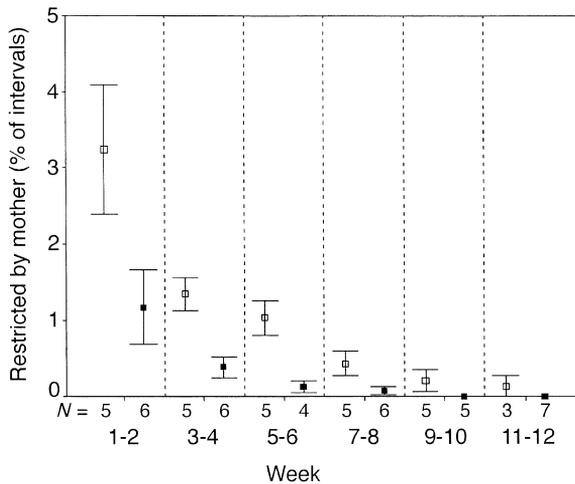


Fig. 4. Average (\pm S.E.) proportion of half-minute periods in which early- (open squares) and late-born (filled squares) infants were restricted by their mothers from moving out of contact. The difference between early- and late-born infants was significant during the first three months ($F = 17$, $p < 0.01$, repeated measures ANOVA).

were subtle, without overt aggression by the mother. They include pushing or grooming the infant off the nipple, stretching the torso so that the infant lost nipple contact, blocking access to the nipple with the forelimbs or by turning around, and only occasionally hitting or (mock) biting the infant.

Infants sometimes threw tantrums in response to maternal rejections, shrieking loudly while making jerking body movements. After such tantrums mothers usually promptly allowed the infant to suckle. Similar exaggerated reactions occurred even more frequently in response to denied riding opportunities and also resulted in prompt ventroventral contact initiated by the mother. A few prolonged tantrums, to which the mother did not respond positively, resulted in the infant falling out of the tree because of its jerking movements.

The first peak in rejection frequency occurred during weeks 7-8 for mothers with female infants, and about two weeks later for mothers with male infants (Fig. 5). This pattern is independent of parity: both multiparous and primiparous mothers began to prevent their female infants from gaining nipple access earlier than (multiparous) mothers with male infants did. There was, however, considerable variation across individuals, which is masked by mean values: two infants were rejected at an early stage only, two others showed an early peak in rejection frequency as well as a less pronounced peak in the second three months of life, while three others were not rejected at all until the second three months of life. Two infants experienced a rejection rate

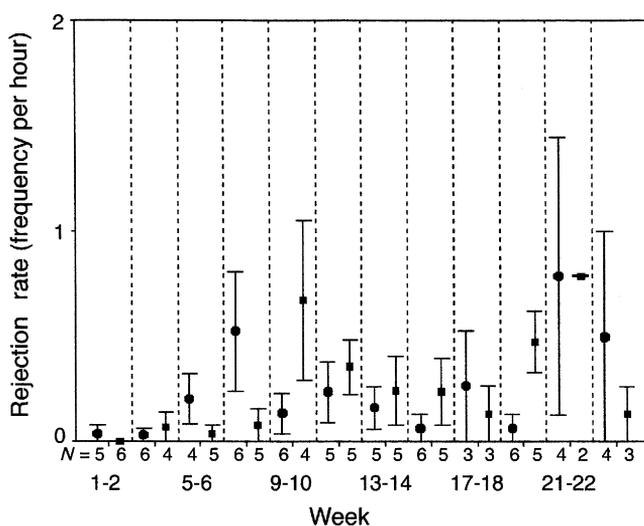


Fig. 5. Average (\pm S.E.) frequency of maternal rejections from accessing the nipple. Circles = female, squares = male infants.

that increased rather steadily with age, and two infants received relatively low rejection rates throughout the first six months, with no obvious peak.

Neither infant sex or size at birth nor maternal parity or rank had significant influences on the rejection frequency in a factorwise repeated measures ANOVA. A multiple regression model showed the number of leaves mothers made per hour ($B = 0.05$, $p < 0.001$, $R_{\text{adj}}^2 = 0.13$) as the only useful predictive variable. This measure is highly correlated with the number of approaches per hour made by the infant ($r_s = 0.916$, $p < 0.001$, $n = 112$ two-week time blocks across all infants).

Maternal grooming

For all infants over all ages through the fifth month, neither infant sex nor maternal parity or rank influenced the relative amount of maternal grooming, i.e., grooming time per time spent in contact (repeated measures ANOVA, Fig. 6). In the sixth month, however, mothers groomed their female infants much more than their male infants ($40.7 \pm 22.8\%$ of contact time for females vs. $2.8 \pm 4.8\%$ for males, Fig. 6).

A multiple regression using data from all infants revealed that in addition to the infant's age ($B = 0.017$, $p < 0.05$, $R_{\text{adj}}^2 = 0.117$), the frequency of rejections ($B = 0.105$, $p < 0.05$, $\Delta R_{\text{adj}}^2 = 0.035$) and infant sex ($B = -0.035$, $p < 0.05$, $\Delta R_{\text{adj}}^2 = 0.026$) played a significant role in determining the relative

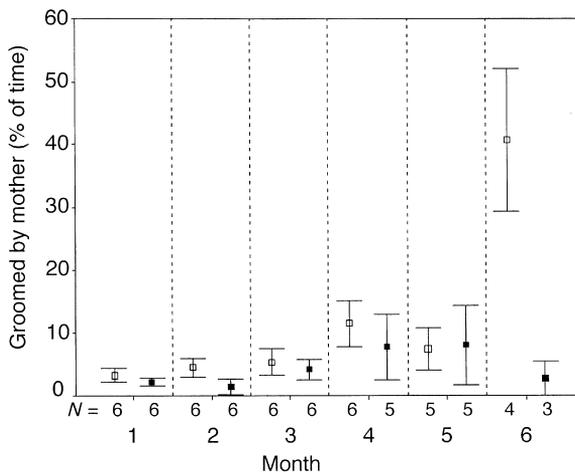


Fig. 6. Average (\pm S.E.) proportion of time male and female infants were groomed by their mothers, expressed as a percentage of time spent in contact with the mother. Circles = female, squares = male infants. The sex difference in month six was significant ($F = 7.7$, $p < 0.05$, repeated measures ANOVA).

amount of maternal grooming. Thus at periods with higher rejection frequencies, infants were generally groomed for a higher proportion of time than at periods with lower rejection frequencies, and, accounting for the differences in the previous two variables (age and rejection frequency), female infants were generally groomed for a higher proportion of time than male infants were.

Because sex apparently had some influence on maternal grooming, we carried out separate regressions for male and female infants to see whether these factors were equally important for both sexes. The results for both sexes combined held only for female infants. For males, the mother's rank class was the most important independent variable influencing maternal grooming ($B = 0.08$, $p < 0.05$, $\Delta R^2_{\text{adj}} = 0.097$), followed by the independence factor ($B = 0.03$, $p < 0.05$, $\Delta R^2_{\text{adj}} = 0.062$), the latter being highly correlated with the infant's age ($r_s = 0.954$, $p < 0.001$, $n = 51$ two-week time blocks across all male infants).

Infant Behavior

Mouthing and feeding

Although we observed infants mouthing objects as early as the fourth day of life, we observed them first swallowing food from the fifth week onward (mean: day 44 ± 15 , $n = 7$ infants that we monitored sufficiently closely during this period for confident assessment). In the repeated measure analysis, the first month had to be excluded because for some of the first-born infants, feeding behavior was not included in the sampling protocol. Female infants

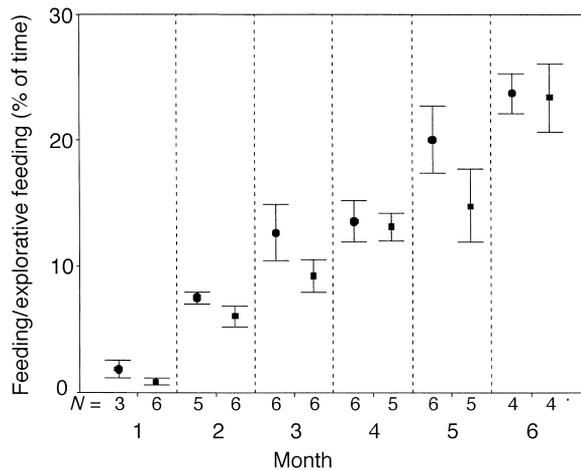


Fig. 7. Average (\pm S.E.) proportion of time male and female infants spent manipulating or eating food objects. Females (circles) had significantly higher scores than males (squares; $F = 6.6$, $p < 0.05$, repeated measures ANOVA).

had higher average scores for mouthing and feeding ($14 \pm 1\%$ of observation time, $n = 5$) than males ($11 \pm 1\%$, $n = 5$). This sex difference is consistent over time (Fig. 7) and is supported by multiple regression analysis. Age (in months) and sex accounted for 77.1% of the variance in time spent mouthing or feeding ($B = 0.038$, $p < 0.001$, $R_{\text{adj}}^2 = 0.718$, and $B = -0.017$, $p < 0.01$, $\Delta R_{\text{adj}}^2 = 0.044$ respectively).

Independent locomotion and general activity measures

Because the time spent moving independently is significantly correlated with the total time spent off the mother ($r = 0.845$, $p < 0.001$, $n = 66$ four-week time blocks, all infants combined), we used the measure time spent locomoting independently when off the mother for the ANOVA. Strikingly there are no significant interindividual differences in the proportion of time spent in independent locomotion when off the mother and there is no significant change with age in the time off mother allocated to independent locomotion. Similarly, multiple regression analysis failed to identify factors that made significant contributions in explaining the proportion of time spent in independent locomotion when off the mother.

Discussion

Several factors influence the development of mother–infant relationships and infant behavior in blue monkeys. Table III is a summary of the effects of the main group factors—infant sex, maternal parity, maternal rank, birth order, and size of the infant at birth—on five independent variables.

Spatial Relationship Between Mother and Infant

The early spatial relationship between infants and their mothers was characterized by interindividual differences in mothering styles. Some of the differences seemed to derive from the mother's prior experience rearing infants and from her rank. Primiparous mothers spent more time than multiparous mothers in contact with and in proximity to their infants throughout most of the first six months. It is not clear whether primiparous mothers or their infants were primarily responsible for this difference relative to multiparous mothers, though primiparous mothers tended to be more responsible for approaches than multiparous mothers were throughout the study period. Infants of primiparous mothers had a significantly lower responsibility for leaves than infants of multiparous mothers did in weeks 5–6 and 23–24.

Similar influences of parity on proximity measures occur in other species. Brown and Dixson (2000) observed that in captive rhesus macaques, infants of

Table III. Summary Table for Effects of Different Group Factors on Variables Representing Development of Infant Behavior and Mother-Infant Relationships in Blue Monkey Infants During Their First Six Months of Life^a

Factor Variable	Sex (M males, F females)	Parity (P primiparous, M multiparous)	Rank	Birth order	Size
Time off mother		Lower for P mothers			Increasing with size in first three months
Explorative feeding/feeding	F more than M, significant after third month				
Restriction		Tendency of higher values for P mothers	Tended to increase with decreasing rank	Higher for early born infants than for later borns	
Rejection	Tended to happen earlier at relatively high levels in F	Tended to be later in infants of P mothers			Tended to be latest in small, and earliest in big infants
Maternal grooming	F were groomed more per contact time in month 6		Tended to increase with rank in M		

^aTendencies indicate non-significant but consistent differences over time, or effects seen in the majority of subjects (but where sample size usually prevented the differences from reaching statistical significance). Blanks indicate no discernible effects.

primiparous mothers spent significantly more time in ventroventral contact than infants of multiparous mothers did. Hooley and Simpson (1981) found that primiparous rhesus macaque mothers tended both to approach and to leave their infants more often than multiparous mothers did. These findings together with our results for blue monkeys are consistent with other features of maternal style that characterize primiparous mothers such as their generally greater anxiousness and protectiveness or their lower confidence (Seay, 1966; Mitchell and Stevens, 1969; Ransom and Rowell, 1972, Hooley, 1983; Berman, 1984; Tanaka, 1989; Maestripieri, 1998).

Because the responsibility for maintaining proximity is an important aspect of the mother–infant relationship, Hinde and Atkinson (1970) proposed an index, defined as the percentage of approaches by the infant less the percentage of leaves by the infant, to represent the contribution of each partner to the maintenance of proximity between them. In Kakamega blue monkeys, the proximity index was positive throughout the study period for all but one infant, indicating that from the first weeks of life infants had a greater responsibility to maintain proximity to their mothers than vice versa. This finding contrasts with those for group-living rhesus macaques (Hinde and Spencer-Booth, 1967; Nash, 1978; Berman, 1980b; Johnson and Southwick, 1984) and baboons (Altmann, 1980), in which the proximity index is negative in the first weeks of life, becoming positive only when infants reached ages of five to 12 weeks.

Differences among species in the responsibility for proximity maintenance may relate to the dangers that infants face in different environments and social situations. The few cases in which positive proximity indices were recorded from the very beginning of an infant's life involved species or environments wherein intra-group aggression rates were low (Chism, 1986: captive patas monkeys; Hinde and Atkinson, 1970: isolated rhesus macaque mother–infant pairs). In wild blue monkeys, rates of intra-group aggression (Cords, 2000a), especially aggression directed towards infants (Cords, pers. obs.), were also extremely low, whereas most studies that have addressed proximity regulation involve species with relatively high intra-group aggression rates like rhesus macaques or baboons (Chism, 2000). When aggression rates are low, the danger of infant harassment, including potentially fatal kidnapping (Maestripieri, 1994b) by other group members, is reduced; mothers can afford to be less vigilant toward infants and may profit from spending more time foraging or engaging in social interactions that they might otherwise forego in order to maintain vigilance over their offspring.

Protective Actions by the Mother

Maternal restriction of an infant is a way that mothers can directly ensure that their infants stay nearby and safe. Mothers that birthed earliest in a group restricted the movements of their infants more than mothers that birthed

later. This seemed to be an immediate result of the higher rates of handling that early-born infants received from other group members, especially adult and large juvenile females that often tried to investigate newborns (Förster & Cords, in prep.). To prevent an infant from being carried too often and for too long, the mother usually restricted its movements as soon as other individuals came close. Mothers that birthed later, however, received much less attention from other group members, and thus the danger of excessive infant handling was lower.

There are also individual differences in the degree of protectiveness, some of which relate to infant size and strength. Mothers with bigger infants generally were less protective and allowed other individuals to hold them earlier than mothers of smaller infants did. Also, big infants were left far behind earlier than small infants were. Other systematic factors that could account for individual differences in mothering behavior include the early experience of the mother when she was an infant herself (Fairbanks, 1989; Berman, 1990) or her rank.

Indeed, in blue monkeys, restrictiveness tended to be related to rank, but the risk of aggression from others did not seem to drive this relationship because aggression was so rare. Probably low-ranking mothers increased restrictiveness to ensure access to their infants. High-ranking mothers had few problems retrieving their infants from caretakers, and reduced restrictiveness seemed advantageous for them. A more relaxed behavioral style by high-ranking mothers could allow them to increase their foraging efficiency, by spending more time and more uninterrupted time. Carrying an infant is energetically costly and can reduce a mother's feeding efficiency (Altmann, 1980; Whitten, 1982 cited in Altmann and Samuels, 1992; Johnson, 1986; Stanford, 1992). The effect of maternal rank on restrictiveness, while weak, is one of the few ways in which rank affects any aspect of non-agonistic social behavior in this species.

Mother-Infant Distance Regulation

The relative role of mother and infant in the development of infant independence is an extensively debated issue (Nicolson, 1987). The proximity index of Hinde and Atkinson (1970) has been used to describe the increasing independence of the infant by relating it to measures such as time spent off or at a distance from the mother (Hinde and Spencer-Booth, 1967; Berman, 1980b). In our study, the proximity index is not significantly related to any behavioral measures, and it did not explain significant amounts of variance in the data set in any of our regression analyses. The absolute number of approaches and leaves, as well as the responsibility for approaches and leaves considered separately, were much more useful to characterize mother-infant relationships.

Maternal Rejection and Its Effects on the Development of Independence

The mother's role in the infant's growing independence is often measured by the rate of rejection infants receive from their mothers when attempting to suckle or to seek contact. There is disagreement about whether maternal rejection promotes infant independence (Nicolson, 1987), but most researchers see rejection as directly responsible for an increase in independence, usually expressed as the time infants spend off or at a distance from their mothers (Hinde and Spencer-Booth, 1967; Altmann, 1980; Berman, 1980b; Rijt-Plooij and Plooij, 1987). In our study, rejection rate correlates with no distance measure. Instead, the rejection frequency is positively related to the number of leaves by mothers. There is no obvious causal connection between these measures. Rejections were seldom followed by leaves, either by mother or infant, but the period of high rejection frequency coincided with a period when it was primarily mothers rather than infants that initiated an increase in distance between them. There is also a correlation between the number of leaves by mothers and the number of approaches by infants. It seems that mothers were trying to promote infant independence by rejecting attempts to get on the nipple and by encouraging independent locomotion with the leave-and-wait game described earlier (Altmann, 1980; Maestriperri, 1995). However, the outcome of this period of maternal rejection was apparently a temporary decrease in infant independence because the higher number of maternal leaves is correlated with a higher number of infant approaches, and not by infants staying away as would be expected if independence were increasing. Indeed, although most infants were already quite independently mobile, as expressed by measures of the mother-infant spatial relationship, when they experienced the highest rates of rejection they seemed to become more attracted to the mother. However, after a period of adjustment to the sudden negative behavior of their mothers, during which infants seemed to learn when and how often they could approach their mothers to suckle, infants shifted their activities away from the mother again, actively increasing their own independence.

Interindividual differences in rejection behaviour were related to maternal parity and infant sex. Two of three primiparous mothers rejected their infants at a later point in life than multiparous mothers did. This difference is consistent with the higher contact and proximity scores for primiparous mothers and their infants, which indicate a closer relationship and a reduced (and delayed) tendency of primiparous mothers to encourage infant independence. There is some evidence, however, that mothers might have simply responded to different abilities of their infants rather than to their own internal motivational states, since the two infants that were rejected latest were the smallest, and the infants that were rejected at high rates earliest in life were

the two largest infants. Maestriperi (1995) showed that rhesus macaque mothers adjust their behavior to the competence of the infant.

Like free-living vervet monkeys (Lee, 1984a), the majority of female blue monkey infants were rejected earlier than males were. This sex difference might relate to parental investment theory, which predicts that maternal investment is generally highest in the sex with the most variable reproductive success, i.e., males for most mammals (Trivers, 1972; Altmann, 1980). Because suckling is energetically demanding and suppresses future reproduction, it is generally considered to be a clear form of maternal investment. Rejection, however, is not a direct measurement of the termination of investment, and since there is no sex difference in time spent on the nipple, the existence of a sex difference in actual suckling investment is questionable. Future studies that measure milk consumption could resolve this issue.

Maternal Grooming

In late infancy especially, infant female blue monkeys were groomed much more than the males were. One of the more commonly assumed functions of social grooming is the establishment of long-term cooperative relationships (O'Brien and Robinson, 1993; Cords, 1997). In many cercopithecine species, the relationships are established preferentially with kin (Silk, 1987). For philopatric female blue monkeys, it should be advantageous for both high and low-ranking mothers and their daughters to establish close affiliative and cooperative relationships, which are maintained and manifested by social grooming. These close relationships among female blue monkeys are important for effectively defending home ranges and food resources from neighboring groups (Cords, 2002).

There are very few comparable data on infant grooming and a similar preference for female over male infants as grooming partners of mothers has been reported only for captive patas monkeys (Loy and Loy, 1987), though it was absent in another captive patas monkey group (Rowell and Chism, 1986). A preference for grooming infants of either sex is not apparent in rhesus monkey infants, even though they show a matrifocal social system similar to that of blue monkeys (Hinde and Spencer-Booth, 1967; Brown and Dixson, 2000). Taken together with our results, these studies do not indicate clearly whether or how maternal grooming of infants is used to cement mother-offspring relationships.

Development of Nutritional and Locomotor Independence

There was no major difference among infants in the proportion of time they spent locomoting off their mothers, and there was no major change in such independent locomotion with age. This suggests that the overall activity

levels were similar for all infants regardless of sex, size, or mothers' characteristics.

However, some differences occurred in activity budgets, with female infants spending more time than male infants interacting with food objects. Female infants also spent less time playing (Förster & Cords, in prep.), and given similar overall activity levels for both sexes, it would be expected that female infants engaged in other activities more than male infants did. Foraging, i.e., explorative feeding and feeding, was apparently the only activity to which female infants devoted more time than infant males did.

Harrison (1983), Terborgh (1983), van Noordwijk *et al.* (1993), and Nakagawa (2000) reported that sex differences in foraging behavior of juveniles were related to sex differences in foraging behavior of adults, with males usually feeding more and/or using more high-calorie food than females. In adult blue monkeys, males are more frugivorous and less insectivorous than females are (Cords, 1986), but no information is available about sex differences in the time adult blue monkeys spend foraging. Thus a functional explanation for the finding that female infants spent more time feeding than male infants cannot be derived from our data.

Arboreality and Infant Development

The time infants spend in contact with their mothers is a frequently used measure of infant dependence among primates, and it varies both within and among cercopithecine species (Struhsaker, 1971; Altmann, 1980; Chism, 1986; Kirkevold and Crockett, 1987; Maestripietri, 1994a). Chalmers (1972) suggested that arboreality, and especially the risk of falling from trees, might be an important factor influencing the rate at which infants gain independence. However, correlations across species between the degree of terrestriality and the rate at which infants reduce contact with their mothers are not obvious among data from captive and free-living groups (Kirkevold and Crockett, 1987). Regarding only free-ranging groups, Karssemeijer *et al.* (1990) found that arboreal long-tailed macaques developed independence later in life than more terrestrial, similarly-sized species like rhesus macaques or vervet monkeys; however, they used limited comparative data to evaluate the differences among species. Considering data from a larger number of studies in the wild or under natural conditions, we could not discern the contrast they emphasized. For instance, free-living, largely terrestrial patas monkey infants spend more time in contact with the mother at every age during the first six months than infant blue monkeys (Chism, 1986; Loy and Loy, 1987). Our study of wild blue monkey infants does not support the view that infants develop independence more slowly in more arboreal cercopithecines.

Moreover, there is no evidence that the risk of injury from falling from trees is significant. We witnessed infants falling out of trees 20 times from

heights of 3–15 m (median: 9.5 m for 16 measured falls), especially between months 2–4. Falls occurred when they tried to keep up with their mothers, while playing with peers, and while throwing tantrums. No falling infant sustained injuries: they either sat motionless until retrieved by their mothers, or climbed up independently. Even after falling from 15 m, infants quickly moved normally.

We suggest that the risks of falling from trees are relatively unimportant in influencing the rate at which primate infants develop independence, even for arboreal species. Infants are also at risk for being prey, or being a victim of aggression or abuse by groupmates. Predation risk may decrease with increasing height above the ground (van Schaik *et al.*, 1983; Boinski *et al.*, 2000), and this effect may counteract the risk of injury from falls, which would increase with greater height, and lead to no discernable relationship between arboreality and the rate at which infants attain independence from their mothers.

Karssemeijer *et al.* (1990) provide data on mother–infant contact in long-tailed macaques, another arboreal species inhabiting forest habitats. Infant long-tailed macaques are considerably slower to break contact with the mother than are infant blue monkeys. The difference between them probably does not reflect differences in the risk of injury from falls, but is likely to result from differences in the risk of predation or infant harassment by groupmates. We cannot quantitatively compare predation risk at the two sites, but note that predation rates on blue monkeys seem very low. Most infants (*ca.* 80–100%) survive to 12 months, and group members are often very dispersed; group spreads of several hundred meters regularly occur. In addition, the risk of infants receiving conspecific aggression, whether as direct targets or as bystanders, seems very low in blue monkeys, which show very low rates of aggression compared to that in macaques (Cords, 2000). In a low-risk environment, blue monkey mothers may be able to afford relaxed behavior toward their infants, which would promote development of the motor skills and independent movements that are especially important in the highly diverse, three-dimensional environment in which they live.

Summary

We studied 12 blue monkey (*Cercopithecus mitis stuhlmanni*) infants in a wild population during the first six months of their lives, with the goals of (1) identifying factors that explain interindividual differences in the various aspects of the mother–infant relationship and infant behavior, and (2) evaluating the hypothesis that arboreality slows the rate at which infants become independent from their mothers. Infants spent more time in contact with primiparous than multiparous mothers throughout the first six months of

life. In addition, primiparous mothers tended to reject their infants at a later stage than multiparous mothers did. A comparison of the time course of development of independence with the timing of maternal rejection suggests that rejection by mothers did not play the major role in the infants' achieving independence. Mothers who gave birth earliest in their groups were more restrictive during the first weeks of the infant's life than mothers who gave birth later. Mothers groomed female infants increasingly more than male infants, suggesting the formation of bonds between mothers and daughters in this matrifocal species at a very early stage in life. The rate at which blue monkey infants attained independence from their mothers resembled that of similar sized terrestrial species, but was faster than the few arboreal cercopithecine species that have been studied to date. We suggest that the development of infant independence in blue monkeys reflects the risks of intra-group aggression and predation more than arboreality.

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