

RESEARCH ARTICLE

Sex and Age Differences in Juvenile Social Priorities in Female Philopatric, Nondespotic Blue Monkeys

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Juveniles should choose social partners on the basis of both current and future utility. Where one sex is philopatric, one expects members of that sex to develop greater and sex-typical social integration with group-mates over the juvenile period. Where a partner's position in a dominance hierarchy is not associated with services it can provide, one would not expect juveniles to choose partners based on rank, nor sex differences in rank-based preferences. We tested these ideas on 39 wild juvenile (3.2–7.4 years) blue monkeys (*Cercopithecus mitis stuhlmanni*), cercopithecines with strict female philopatry and muted hierarchies. We made focal animal observations over 6 months, and computed observed:expected amounts of proximity time, approaches and grooming given to various social partners. Overall, our results agree with the hypothesis that juvenile blue monkeys target social partners strategically. Spatial proximity, approaches and active grooming showed similar patterns regarding juvenile social preferences. Females were far more sociable than males, groomed more partners, reciprocated grooming more frequently, and preferred—while males avoided—infants as partners. Older juveniles (5–7 years) spent more time than younger juveniles (3–4 years) near others, and older females were especially attracted to infants. Close kin, especially mothers and less consistently adult sisters, were attractive to both male and female juveniles, regardless of age. Both sexes also preferred same-sex juveniles as social partners while avoiding opposite-sex peers. Juveniles of both sexes and ages generally neither preferred nor avoided nonmaternal adult females, but all juveniles avoided adult males. Partner's rank had no consistent effect on juveniles' preference, as expected for a species in which dominance plays a weak role. Juveniles' social preferences likely reflect both future and current benefits, including having tolerant adult kin to protect them against predators and conspecifics, same-sex play partners, and, for females, infants on which to practice mothering skills. *Am. J. Primatol.* 72:193–205, 2010. © 2009 Wiley-Liss, Inc.

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INTRODUCTION

Primate life histories include a prolonged period of juvenility. The social lives of juveniles should, in principle, both facilitate survival of this life stage in which small body size and limited experience make them vulnerable, and prepare them for social life as an adult [Maestriperi & Roney, 2006; Pereira, 1988]. Several studies of juvenile primate social behavior have focused on spatial and affiliative relations, finding sex differences in immatures that match the patterns characteristic of adults of the species. For example, in female-bonded long-tailed macaques, juvenile females have both adult and other juvenile females as neighbors more than juvenile males do [van Noordwijk et al., 2002]. In male-bonded muriquis, juvenile males associate with one another more than juvenile females do [Strier, 2002]. Although studies of the social lives of juvenile primates are still

few, it appears that species-typical sex differences in spacing and affiliation can emerge as early as the first year or two of life [e.g. Rowell & Chism, 1986]. To the extent that they result from adaptive partner choice [Dugatkin & Sih, 1998], these differentiated social relationships may benefit juveniles as such

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[Fairbanks & Bird, 1978; Pereira, 1988], or may represent developing social “investments” for advantages realized in or nearer to adulthood [Cords, 2000a; Rowell & Chism, 1986; van Noordwijk et al., 2002].

In the cercopithecines in which juvenile social behavior has been relatively well studied (vervets, baboons, mangabeys, and long-tailed, rhesus and bonnet macaques), matrilineal dominance hierarchies and advantages of high rank are marked. With female philopatry characteristic of these monkeys, one would expect that females, more than males, should try to develop amicable relations with higher-ranking female group-mates [Cheney, 1978; Fairbanks, 2002; Pereira, 1988; Range, 2006; Silk et al., 1981], whether to benefit from contingent agonistic support from powerful allies [Ehardt & Bernstein, 1987; Fairbanks, 2002; Schino, 2007; Seyfarth, 1977], to reduce the chance of direct competition while feeding, or to ensure tolerance in a spatial position in the group in which predation risk is minimized [Fairbanks, 1993; O’Brien, 1993; Pereira, 1988]. Where hierarchies are marked, one expects higher-ranked females to control access by subordinates to these benefits; subordinates may increase benefits received, both immediately and later, by ensuring amicable relations with familiar higher-ranked partners. Because rank may affect competition for social access to higher-ranking partners, however, low-ranked females may be constrained in their ability to foster the bonds that would most benefit them [Fairbanks, 2002; Range, 2006; Seyfarth, 1977].

In many female-bonded societies, female rank hierarchies are matrilineal, such that members of a single family rank near each other in the group [Wrangham, 1980]. Female juveniles in these social systems depend on agonistic support from their highest ranking kin to achieve their adult rank positions, and one would predict that they develop social relations resulting in such support [Chapais, 1996; Ehardt & Bernstein, 1987; O’Brien, 1993; Pereira, 1988]. Relations with more powerful kin may, however, bring other more immediate benefits as well, including tolerance around resources or in safe proximity to group-mates when avoiding predation.

Blue monkeys (*Cercopithecus mitis stuhlmanni*), like other cercopithecines, are characterized by female philopatry, with males leaving their natal groups permanently when they are about 7 years old and approaching the age of puberty [Ekernas & Cords, 2007] and females remaining for life. As adults, females cooperate to defend a group territory [Cords, 2002, 2007], whereas adult males—who live alone or, rarely, in loose association with a few other males before taking over a group—cooperate rarely if ever. As a result, we expected sex differences in general social integration, and we have documented such differences in juveniles nearing the dispersal

age of males and reproductive age of females [Ekernas & Cords, 2007]. Here, we examine sex differences in social behavior of a larger set of juveniles, aged 3–7 years. We expected to see that juvenile females focused social interaction on other females, with whom they would live together for life, and we expected these patterns to become more marked for older juveniles approaching adulthood.

Unlike other well-studied cercopithecines, blue monkeys lack a steep dominance hierarchy and the advantages of high rank seem minimal [Cords, 2000b; Pazol & Cords, 2005]. In addition, rates of aggression are low and coalitions are rare [Cords, 2000b]. We therefore expected to see little evidence that juveniles, and especially philopatric females, jockey for advantageous social positions as they do in societies with stronger power differentials. Particularly, we expected to find little evidence that female juveniles are especially motivated to develop affiliative and potentially strategic relations with relatively high-ranking adult female group-mates. Although we did expect an attraction to close adult female kin, simply because such individuals should be relatively tolerant of young relatives seeking safety or a feeding site nearby [Pereira, 1988], we did not anticipate sex differences in social attraction to such partners. In contrast to papionins, where juvenile females develop their adult position in the group’s hierarchy with the support of close adult female kin [Chapais, 1996; Pereira, 1995; Schino et al., 2007], it is unclear for blue monkeys that a similar mechanism is operating [Cords, 2000b]; in addition, as noted above, the benefits of high rank appear muted relative to other cercopithecines.

We aimed to characterize spatial relations, approach patterns, grooming and received agonism for 39 juvenile subjects, to examine sex differences in light of normative adult patterns in the species, and to evaluate the evidence that juveniles invest in relations with higher-ranking or related group-mates according to the predictions outlined above. Although previous research indicates that juveniles behave strategically in the context of strongly rank-stratified social systems, our study considers the inverse of this hypothesis, namely that juvenile social priorities will not be based on partner rank in societies where rank is less important.

METHODS

Study Site and Subjects

The study population inhabited the Isecheno research site of the Kakamega Forest, Kenya (0°19’N, 34°52’E, 1650 m), the eastern-most fragment [85 km²; Lung, 2004] of the Guineo-Congolese rainforest in central Africa. Annual rainfall totals about 2,000 mm, and is seasonally variable [Fashing et al., 2004]. The study area supports a high density

of blue monkeys [170–220 individuals/km²; Fashing & Cords, 2000]. At the time of this study, May–November 2004, there were three neighboring study groups (Table I), all of which had been monitored for at least 10 years, allowing precise knowledge about the subjects' ages and kinship relations.

Our subjects were all 24 “younger” juveniles (11 females, 13 males) aged 3.2–4.6 years and all 15 “older” juveniles (6 females, 9 males) aged 5.3–7.4 years in the study groups. Unlike even younger blue monkeys (≤ 2 years), none of our subjects was ever observed to suckle. Blue monkey males disperse from their natal groups as adolescents at an average age of 7.25 years [range: 5.9–8.1; Ekernas & Cords, 2007], but all our subjects still lived in their natal groups. Females may first give birth as early as their fifth year [Cords & Chowdhury, in preparation], but all our female subjects were prereproductive. Two younger juveniles had no living mother.

We did not mark individuals, but recognized them using natural features. The two observers were not equally proficient at identifying the youngest animals (aged < 5 years); we comment explicitly where this situation may have influenced our results. Our research was approved by Columbia University's IACUC, and adhered to the laws of Kenya.

Data Collection

As part of two originally separate studies, M. J. S. conducted 30 min focal samples on the 25 youngest juveniles from July–November 2004, averaging $9.2 \pm \text{SD } 0.3$ hr per subject, whereas L. S. E. conducted 40 min focal samples on the 14 oldest juveniles from June–September 2004, averaging $6.5 \pm \text{SD } 0.7$ hr per subject. We misidentified the oldest animal in the younger group at the time of data collection, when we temporarily confused her with a younger individual who had died: as her true age was closer to those in the older group, we included her records among the older juveniles in our analyses.

Given the difficulty of locating particular widely spaced individuals in the forested environment, we did not sample focal subjects on a predetermined schedule. Instead, we chose subjects trying to ensure that sampling was approximately equally distributed among individuals of each age class, across the months of the study period and throughout the hours of the day. We never sampled a monkey more

than once per day. Some samples did not reach our target length because the subject went out of sight: we did not continue the sample if time out-of-sight exceeded 7.3 min (younger juveniles) or 10 min (older juveniles). We included all aborted samples in our data summaries for older subjects, but for younger subjects they were included only if they lasted ≥ 10 min. Samples less than 10 min long accounted for 1.8% of total sampling time for older subjects.

We collected behavioral observations on check-sheets using instantaneous recording. Every 20 sec, we noted the identity of all group-mates that were in proximity (≤ 3 m away), henceforth “neighbors,” and any grooming of or by the subject. A grooming partner was by definition also a neighbor. Observation conditions sometimes prevented us from identifying every neighbor; in such cases, we omitted the record/s from consideration of partner preferences, but not when analyzing the proportion of time a subject spent within 3 m of others. We recorded all occurrences of the subject making close approaches (to ≤ 1 m) to group-mates. We also recorded all occurrences of agonistic behavior directed by or toward the subject, including avoids (avoided animal > 1 m away but coming nearer), supplants (supplanting animal comes within 1 m before partner leaves to > 1 m), threats (growls, stares), chases and contact aggression.

Data for determining dominance rank derived from long-term population monitoring. Our team noted all observed occurrences of agonism, even outside of focal samples, including aggressive acts (threats, chases, contact aggression), submissive acts (cowering, flight, trills, geckers, screams) and approach–retreat interactions (avoids and supplants, definitions above).

Data Analysis

Because total amounts of focal sampling varied among subjects, we expressed spatial relations and grooming activity as proportions of total sample points and approaches as rates per unit time observed. To evaluate proximity relations, grooming and approaches with different partners, we analyzed observed:expected ratios, where we based expected values on the assumption of random association with the class of social partners under consideration. For example, to assess whether a particular subject spent time in proximity (≤ 3 m) with certain partners (or

TABLE I. Age/Sex Class Composition of the Three Study Groups

Group	Year first observed	Infants (< 12 mos)	Juvenile females ^a	Juvenile males ^a	Adult females	Adult males	Total
GN	1993	1	9	12	10	1	33
GS	1993	6	12	14	19	1	52
TW	1979	3	14	19	23	5	64

^aIn addition to our subjects, the juvenile age class included younger animals aged 1–3 years.

classes of partner) disproportionately relative to their abundance in its group, we computed an association index

$$AI = \frac{(\% \text{ neighbor records with } X)}{(\% \text{ of groupmates constituted by } X)}$$

where X is the partner individual or age–sex class of interest. A neighbor record represented any record of a particular monkey within 3 m of the subject: two such records were scored if the subject had two neighbors simultaneously. An AI of 1 indicates that a subject interacted with a given partner or partner class at chance levels, whereas lower and higher values indicate avoidance or attraction, respectively. We calculated similar ratios to evaluate the degree to which subjects approached and groomed with various partners relative to a random expectation.

We defined partner classes demographically (e.g. juvenile males), sometimes including information on social rank (see below) or matrilineal kinship relative to the subject. Matrilineal kinship (mother, sisters) was known from pedigree records. Random expectations for interaction with particular partner classes were always specific to each individual subject.

We determined rank relations of our subjects from pairwise agonistic interactions in which only one partner showed signs of submission. We used the program Matman [Noldus; deVries, 1995] to compute rankings for the adult females in each group based on input data from 2004 only. The hierarchies in 2004 were significantly linear (Matman linearity test, two-tailed $P = 0.0001$ for all groups), the directional consistency index was high (Gn 0.90, Gs 0.91, Tw 0.94) and the percentage of interactions that went against the hierarchy was low (Gn 2.1%, Gs 3.5%, Tw 2.1%). When incorporating dominance rank as a variable in our analyses, we sometimes used a dichotomous rank classification, distinguishing adult females (excluding the mother) in the top half of the hierarchy from those in the bottom half. In other analyses, we used a standardized rank with values of 0–100, representing the percentage of other group members that the individual outranked. For example, the top-ranked individual was always ranked 100, and a female with a rank of 50 outranked 50% of the other adult females in her group. This way of expressing rank allowed us to combine data across groups.

Each analysis of variance (ANOVA) used sex, age class (younger vs. older), group and their interactions as factors that could explain observed:expected ratios. All tests were two tailed. We report means along with their associated standard errors. To streamline presentation, we report statistical results only for factors that contributed significantly ($P < 0.05$) to our models, and sample size only when it deviated from the total number of subjects given above.

RESULTS

Spatial Association Patterns

On average, juvenile females had neighbors within 3 m four times more often than juvenile males did (Fig. 1; $F_{1,38} = 80.46$, $P < 0.0001$). In addition, older juveniles had neighbors slightly but significantly more often than younger juveniles (7.3 ± 0.9 SE vs. 6.2 ± 0.7 SE% of the time; ANOVA, $F_{1,38} = 40.16$, $P < 0.041$). There was a significant age–sex interaction (ANOVA, $F_{1,38} = 5.54$, $P = 0.026$) such that older females had neighbors more often (14.9 ± 2.6 SE% of time) than younger females did (9.7 ± 1.1 SE), whereas male juveniles showed lower proportions of times with neighbors than females and no differences with age (older males, 2.3 ± 0.5 SE, younger males 3.2 ± 0.7 SE; Tukey's HSD, $P < 0.05$).

The size of the neighbor network, i.e. the number of individuals that were nearby at least once, did not differ for males and females (Fig. 1, younger juveniles, ANOVA $F_{1,23} = 2.05$, $P = 0.17$; older juveniles $F_{1,14} = .08$, $P = 0.79$) but individuals in larger groups had a longer list of neighbors (younger juveniles, ANOVA, $F_{2,22} = 11.70$, $P = 0.0006$; older juveniles $F_{2,13} = 18.35$, $P = 0.007$). For younger juveniles, the number of neighbors ranged from 15.3 ± 2.4 SE ($N = 6$) in Gn, to 18.9 ± 1.7 SE ($N = 12$) in Gs to 30.1 ± 2.1 SE ($N = 6$) in Tw; for older juveniles, the same trend was generally evident (Gn, 10.6 ± 2.0 SE, $N = 7$; Gs 10.0 ± 3.4 SE, $N = 2$; Tw

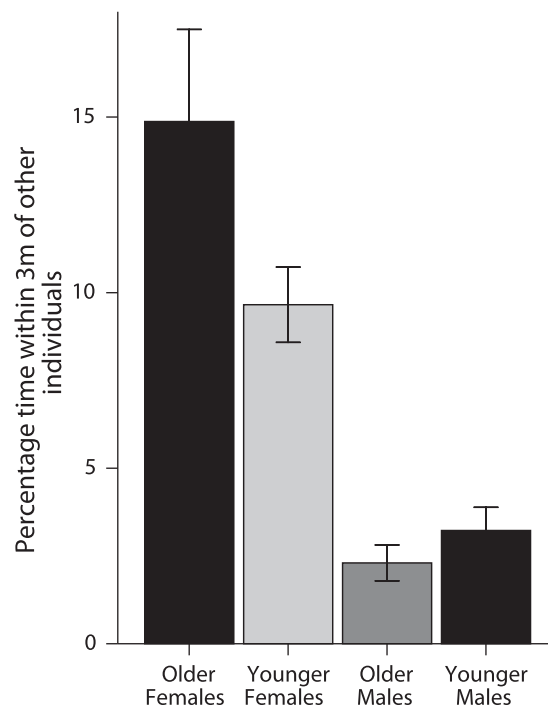


Fig. 1. Sex and age differences in proximity to group-mates (mean ± standard error). Sex, age and age–sex interactions were all significant ($P < 0.05$, see text for details).

26.0 ± 1.9 SE, N = 6), although numbers were lower, most likely reflecting the less complete identification of younger juvenile neighbors for these subjects.

In the context of all group members acting as possible social partners, all juvenile subjects associated disproportionately with their own mothers (Fig. 2A): association indices with mothers were

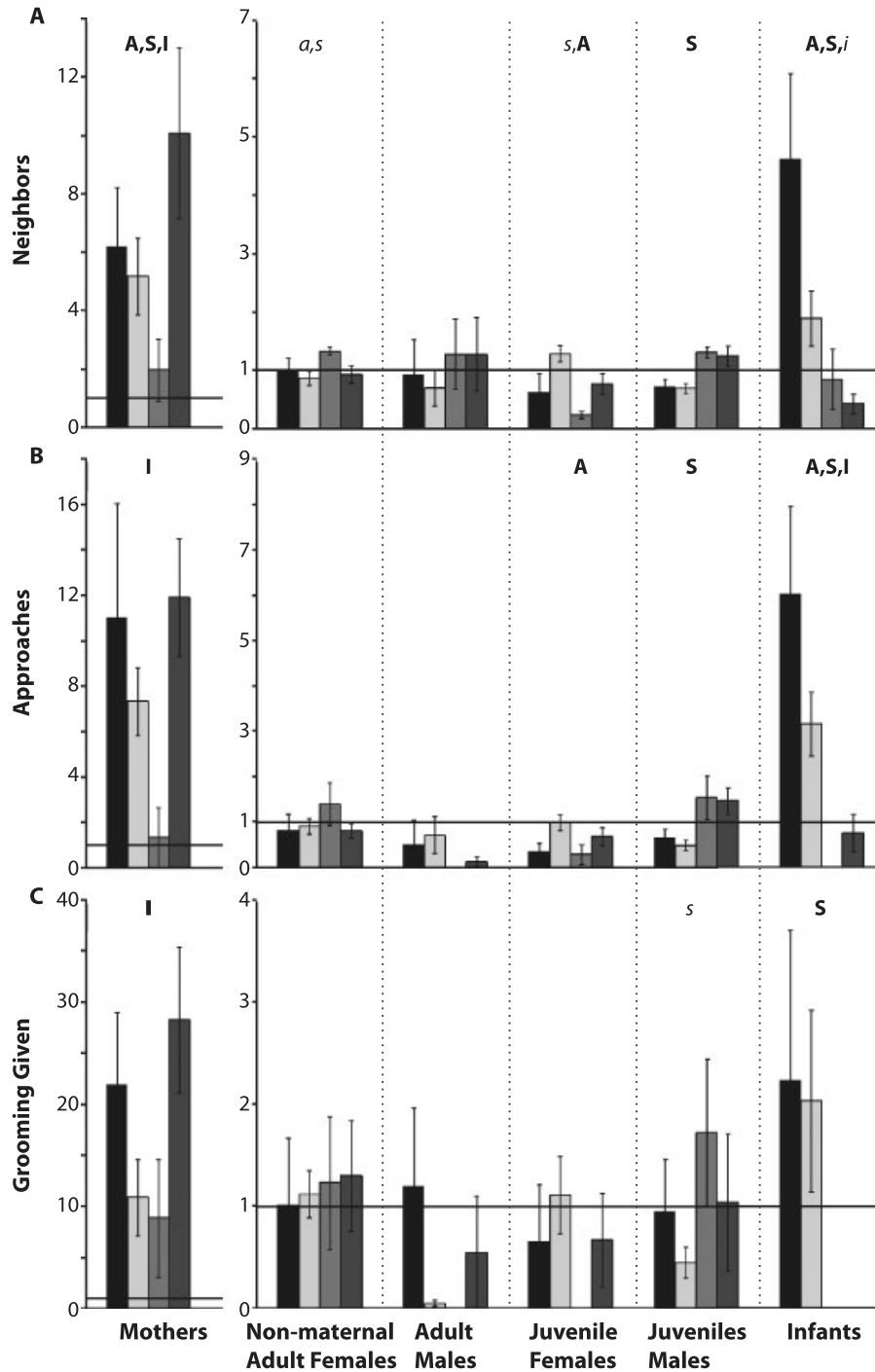


Fig. 2. Observed:expected interaction ratios for juveniles (A) neighboring, (B) approaching and (C) giving grooming to different social partners. Each bar shows mean ± SE (N = 11 younger, 6 older females, and 13 younger, 9 older males; for grooming, N = 6 younger, 7 older males) for each category of partner. Ratios above or below the solid line (i.e. > 1) indicate preference or avoidance, respectively. Calculations for mothers included all group-mates. Calculations for partners in all other age-sex classes excluded the mother (see text). Within each group of bars, the age-sex class of subjects from left to right is: older females (black bars), younger females (lightest gray bars), older males (medium gray bars) and younger males (darkest gray bars). Letters denote significant differences among groups: A = age, S = sex, I = age*sex interaction. Uppercase letters indicate a significance level of $P < 0.05$. Italicized lower case letters indicate a significance level of $P < 0.08$.

highest by far (young juveniles, 7.8 ± 1.7 SE, $N = 22$; older juveniles 3.6 ± 2.2 SE, $N = 15$), whereas index values for most other classes of partner were less than 1, indicating less-than-random association. The one exception involved juvenile females whose average affiliation index with infants (1.98 ± 0.30 SE) also indicated preferential association with these group members. There were no significant effects of sex, age or group on association indices with the mother.

Because the mother was so overwhelmingly preferred as a spatial association partner, we recalculated affiliation indices for nonmaternal partners omitting her from consideration (Fig. 2A). This adjustment increased association indices with other partner classes as expected, and revealed several sex and age differences. Both sex and age influenced affiliation indices for infant partners, with females associating preferentially with infants to a significantly greater extent than males, who tended to avoid them ($F_{1,38} = 14.36$, $P = 0.0008$). Older juveniles had greater preferences for infants than younger juveniles ($F_{1,38} = 5.11$, $P = 0.032$). Male subjects associated preferentially with other juvenile males, whereas females avoided associating with them ($F_{1,38} = 11.57$, $P = 0.002$). There was a weak sex difference in association with juvenile females, with males avoiding these partners, whereas females generally interacted with them at near random levels ($F_{1,38} = 3.87$, $P = 0.059$). The association index for juvenile female partners showed a significant age effect, however, with older juveniles avoiding these partners, whereas younger juveniles interacted with them at random levels ($F_{1,38} = 10.65$, $P = 0.003$). Comparisons of each subject's AI values for male vs. female peers confirmed that both females (*paired* $t = 2.0$, *two-tailed* $P = 0.060$) and males (*paired* $t = 5.5$, *two-tailed* $P = 0.022$) preferred same-sexed peers to opposite-sexed peers. Associations with adults, both nonmaternal adult females and adult males, were not clearly differentiated by age or sex. All subjects associated with nonmaternal adult females at least sometimes, but many of our subjects (4 of 11 younger females, 4 of 6 older females, 7 of 13 younger males, 3 of 9 older males) were never observed within 3 m of adult males.

The strong attraction of juveniles to associate with the mother was noted above. We also examined attraction to adult sisters, but were limited to 11 subjects that had at least one adult sister in the group. The average juvenile associated with its adult female sisters 4.60 ± 1.89 SE times more often than expected by chance. However, 5 of the 11—including 3 of 4 female subjects—were never recorded in proximity to their adult sisters. We could not detect any age (Mann Whitney $U = 21$, *two-tailed* $P = 0.736$) or sex ($U = 22$, *two-tailed* $P = 0.676$) difference in attraction to adult sisters.

Approaches by Juveniles

Juveniles approached their mothers at rates that exceeded random expectations by a factor of 7.3 ± 1.2 SE ($N = 37$; Fig. 2B). When we included the mother in analyses of approach rates, juveniles approached most other group members less often on average than one would randomly expect: exceptions included juvenile females that approached infants 3.7 ± 0.8 SE times more than expected (a significant difference from juveniles males that avoided approaches to infants, $F_{1,38} = 42.11$, $P < 0.0001$), juvenile males that approached other juvenile males 1.3 ± 0.2 SE times the random expectation (a significant difference from juvenile females that avoided juvenile males, $F_{1,38} = 11.87$, $P = 0.0019$), and older juvenile males that were the only juvenile age-sex class to approach nonmaternal adult females disproportionately (1.4 ± 0.5 SE times random expectation, $F_{3,36} = 4.98$, $P = 0.034$).

Because the mother so dominated juvenile approach patterns, we again reanalyzed the data removing her from consideration (Fig. 2B). Generally, this adjustment strengthened the apparent preferences for approaches to certain classes of partners without changing the overall patterns reported above. In particular, female juveniles showed a strong preference for approaching infants whereas males avoided them ($F_{1,38} = 45.60$, $P < 0.0001$). Older juveniles showed a stronger preference for approaching infants than did younger juveniles ($F_{1,38} = 4.28$, $P = 0.048$). The age-by-sex interaction was significant ($F_{3,36} = 8.85$, $P = 0.006$), with older females showing the largest departure from random expectations, whereas older males never approached infants, and younger juveniles showed more muted responses similar to those of their older same-sexed peers. Male juveniles approached other male juveniles more than expected by chance, whereas female juveniles avoided them ($F_{1,38} = 9.73$, $P = 0.004$). Juveniles generally avoided approaching female peers, with a significantly stronger avoidance for older vs. younger juveniles ($F_{1,38} = 8.44$, $P = 0.007$). Juveniles generally approached nonmaternal adult females at approximately chance levels, and avoided adult males. There were neither age nor sex effects in the observed:expected ratios for approaches to adults.

On average, juveniles approached adult sisters 9.5 ± 4.1 SE ($N = 11$) times more often than expected by chance. Again, however, three of four female juveniles and two of seven males never approached their adult sisters. There were neither age nor sex differences in the observed:expected ratios.

Results from analysis of approaches generally matched those from proximity durations, suggesting that these measures similarly reflect juvenile social priorities with regard to spacing.

Grooming

Grooming partners represent a particular subset of neighbors with whom there is direct behavioral exchange that may indicate more clearly than mere proximity or even approaches the social priorities of the animals involved. Compared with males, female juveniles both actively groomed more partners (ANOVA, $F_{1,38} = 18.55$, $P = 0.0002$) and were groomed by more partners (ANOVA, $F_{1,38} = 8.46$, $P = 0.0072$; Fig. 3A). Moreover, females groomed more partners than groomed them (*paired t* = 3.23, *two-tailed P* = 0.0052), whereas males did not show this same discrepancy. Although we observed all female subjects both groom and receive grooming from others, 5 of 13 younger males and 2 of 9 older males were never observed to take the active role of groomer (Fisher Exact test on overall sex difference, *two-tailed P* = 0.012). In fact, one of the younger males and two of the older males were not observed to receive grooming either. Overall, females groomed more reciprocally than males (Fig. 3B; ANOVA, $F_{1,35} = 13.59$, $P = 0.0011$; three males that neither gave nor received grooming were excluded here).

All juveniles groomed their mothers much more than expected by chance (Fig. 2C), although there was a significant age–sex interaction ($F_{3,34} = 8.65$, $P = 0.009$; analysis limited to eight younger male, ten younger female, six older male and six older female juveniles that actively groomed their mothers). Preference for grooming the mother was so strong that nearly all other group members were apparently avoided, so again we repeated the analyses without the mother (Fig. 2C). The strongest average preference for a grooming target was exhibited by female juveniles when grooming infants; females differed in this preference from males ($F_{1,27} = 5.71$, $P = 0.029$), none of whom ever groomed infants (vs. 8 of 17

females who did so; Fisher Exact Test, *two-tailed P* < 0.01; test included 11 males who actively groomed at least one partner). Juveniles of different age and/or sex classes generally avoided female peers as grooming targets, and showed no age or sex differences in the degree of avoidance. We observed more females (11 of 17) than males (1 of 11 that actively groomed anyone) grooming female peers (Fisher Exact Test, *two-tailed P* < 0.006). Male juveniles tended to prefer grooming their male peers, whereas females avoided them (Fig. 2C, $F_{1,27} = 4.34$, $P = 0.054$). There were no sex or age differences in the fraction of subjects that groomed male peers. Juveniles generally groomed nonmaternal adult females in proportion to their abundance, and there were no sex or age differences in the degree to which juveniles preferred to groom these partners. The fractions of male and female juveniles (8 of 11 males vs. 11 of 17 females) and of old vs. young juveniles (5 of 11 old, 14 of 17 young) that ever groomed nonmaternal adult females were also indistinguishable (Fisher Exact Test, *two-tailed P* > 0.09). Adult males were generally avoided as grooming targets, regardless of the subject's age or sex. Only 5 juveniles of 31 that took the role of groomer at least once groomed adult males.

Sisters were, on average, attractive grooming partners for juveniles. Juveniles groomed their sisters 7.6 ± 6.1 SE ($N = 8$ who actively groomed anyone) times more than expected by chance. Sample sizes were small, however, and individual results heterogeneous. Of the eight active groomers we could examine, five individuals never groomed an adult sister.

Grooming and Approaching Nonmaternal Adult Females: Rank Effects?

To evaluate whether juveniles interacted with nonmaternal adult females according to their rank,

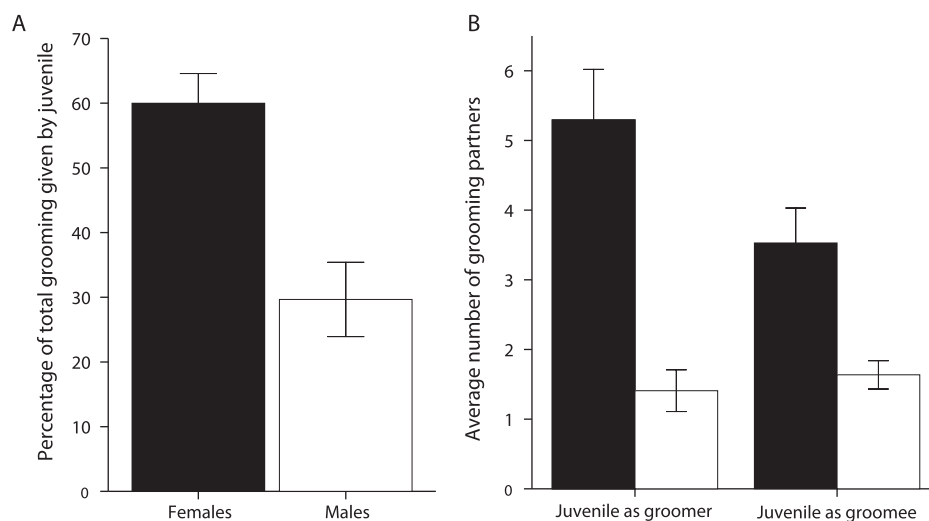


Fig. 3. Compared with males (white bars), female (black bars) juveniles (A) take the role of active groomer more often, and (B) engage in grooming bouts with more partners both as groomer and recipient. Mean \pm standard errors shown.

we limited our analysis to younger juvenile females for grooming, and to younger males and females for approaching, as other juveniles did not interact with these partners sufficiently often for inclusion. The nine younger juvenile females that actively groomed nonmaternal adult females groomed those in the lower half of the hierarchy about three times more often (0.63 ± 0.20 SE min/hr) than those in the upper half of the hierarchy (0.18 ± 0.06 SE min/hr; Wilcoxon matched pairs signed rank, $Z = 17.5$, $N = 11$, two-tailed $P = 0.039$). Results were similar when we considered the partner's rank relative to that of the juvenile female's mother: on average, young female juveniles groomed higher-ranking nonmaternal adult females considerably less often than expected by

chance (0.60 ± 0.60 SE times the random expectations) and only two of nine subjects groomed them preferentially. These two females each groomed only one nonmaternal adult female partner, however, and were themselves low ranking; together, these facts may account for their apparent preference for higher-ranking grooming partners.

Young juvenile females showed no difference in the frequency of approaches to nonmaternal adult females in the top half (1.63 ± 0.38 SE approaches) vs. bottom half (2.81 ± 0.52 SE approaches) of the hierarchy (Wilcoxon Matched Pairs Signed Ranks Test, $Z = 19.5$, $N = 11$, two-tailed $P = 0.10$). On average, they approached nonmaternal adult females that outranked their mothers slightly less often than

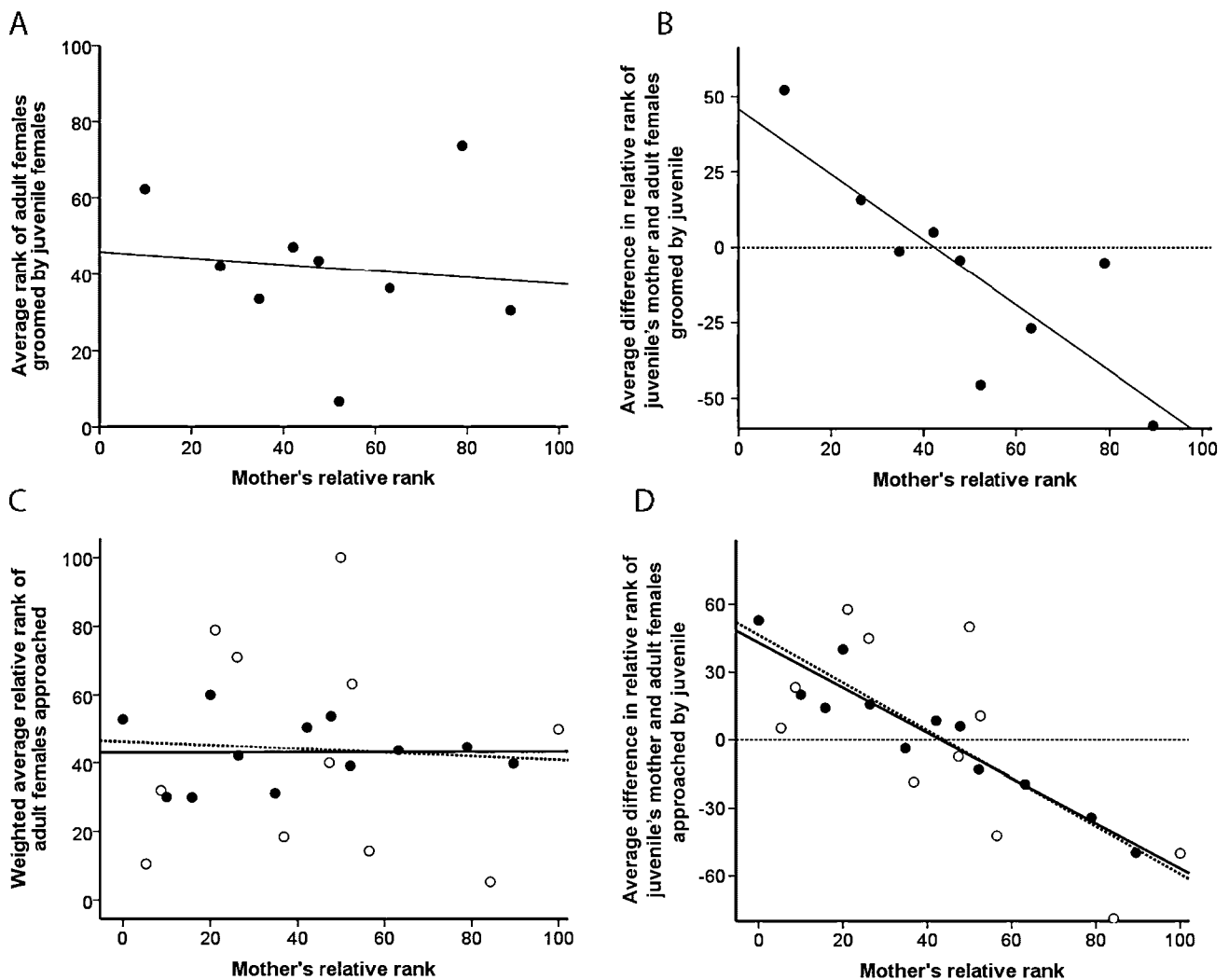


Fig. 4. Relationship between young juvenile maternal rank (x -axis) and ranks of the nonmaternal adult females groomed (top row) and approached (bottom row). Rank is expressed on a 0–100 scale, reflecting the percentage of group-mates that a given adult female outranked. (A) Average rank of adult females groomed by young female juveniles, weighted by the proportion of grooming given. (B) Difference between average rank of adult females groomed by the young female juvenile subjects and subject's maternal rank. (C) Average rank of adult females approached by the young juveniles (filled circles = females, open circles = males), weighted by the proportion of approaches given. (D) Difference between the average rank of adult females approached by young juvenile subject and that subject's maternal rank. For (C) and (D), values greater than zero indicate grooming/approaching up the hierarchy, whereas values less than zero indicate grooming/approaching down the hierarchy. Lines show least squares fit.

expected by chance (0.84 ± 0.49 SE times the expected value, 4 of 11 showing a value > 1). Similarly, on average, young juvenile males showed no preference for approaching adult females that outranked their mother (0.73 ± 0.6 SE times the expected value, with 6 of 10 showing a value > 1).

Although juveniles as a whole clearly did not prefer to groom or approach higher-ranking adult females, there was variation among them, leading us to investigate whether a juvenile's (maternal) rank influenced its preference. For the nine young juvenile females that groomed nonmaternal adult females, the average rank of the partners they groomed, weighted by the amount of grooming given, did not differ as a function of the juvenile's maternal rank (linear regression, $r^2 = -0.12$, $F_{1,7} = 0.84$, *two-tailed* $P = 0.78$, Fig. 4A and B). However, juveniles with the lowest ranking mothers groomed up the hierarchy to the greatest extent, whereas those with the highest ranking mothers tended to groom down the hierarchy (linear regression, $r^2 = -0.62$, $F_{1,7} = 14.25$, *two-tailed* $P = 0.007$, Fig. 4B). In effect, juveniles seemed to focus their grooming on mid-ranking nonmaternal adult females. We examined partner identities, but found them idiosyncratic: that is, there were no particular adult females shared as favored targets of juvenile grooming.

Approaches to nonmaternal adult females by young juvenile females and young juvenile males followed similar patterns. The average rank of nonmaternal adult females approached by young female and male juveniles, weighted by the proportion of approaches, showed no relationship to the juvenile's maternal rank (Fig. 4C and D; females: linear regression, $r^2 = 0.00$, $F_{1,10} = 0.001$, *two-tailed* $P = 0.98$; males: linear regression, $r^2 = 0.003$, $F_{1,9} = 0.024$, *two-tailed* $P = 0.88$). Among young juveniles of both sexes, those with the lowest ranking mothers approached up the hierarchy to the greatest extent, whereas juveniles of the highest ranking mothers tended to approach lower-ranking adult females (Fig. 4C and D, females: linear regression, $r^2 = 0.89$, $F_{1,10} = 78.07$, *two-tailed* $P < 0.0001$; males: linear regression, $r^2 = 0.50$, $F_{1,9} = 8.88$, *two-tailed* $P = 0.015$).

Agonism Received

Overall, males and females yielded in agonistic contexts (i.e. received aggression, were supplanted or avoided others) at indistinguishable rates (0.34 ± 0.05 SE acts/hr, $N = 22$ males vs. 0.30 ± 0.06 SE acts/hr, $N = 17$ females). There were also no differences for older (0.29 ± 0.07 SE, $N = 15$) vs. younger (0.34 ± 0.05 SE, $N = 24$) juveniles. However, there was a group effect ($F_{2,36} = 14.23$, $P < 0.001$), with juveniles in the largest group yielding in agonistic contexts more often (0.58 ± 0.06 SE per hour, $N = 12$, Tw) than individuals in the two smaller groups

(0.28 ± 0.08 SE, $N = 14$, Gs; 0.13 ± 0.07 SE, $N = 13$, Gn; ANOVA, $F_{2,38} = 14.04$, $P < 0.0001$; Tukey's HSD, $P < 0.05$), suggesting that group size may increase the rate of receiving aggression from or yielding to others. Overall, juveniles yielded in agonistic encounters (0.31 ± 0.04 SE, $N = 39$) about 1.2–1.5 times more often than has been reported for adult females [values ranging 0.20–0.27 per hour; Cords, 2000b; Pazol & Cords, 2005] in this same population.

DISCUSSION

Social Integration and Partners

The social relations of 3- to 7-year-old juvenile blue monkeys are clearly transitional between infant and adult patterns. On the one hand, these juveniles, like many other cercopithecines [Fairbanks, 2002], still approach and spend highly disproportionate amounts of time in proximity to their mothers, which remain their single most important social partners. On the other hand, when we consider relations with nonmaternal group-mates, many adult-like patterns are obvious. Most notably, and as we predicted based on the matrilineal social system, juvenile females spend much more time than juvenile males in proximity to other group-mates, and older females are more sociable than younger ones. In addition, although females do not have a larger number of proximity partners than male peers, they do have a larger set of partners with whom they groom. They more often take the role of active groomer, and groom more reciprocally with their partners. In these ways, it seems that juvenile females are actively establishing a network of bonds within the group where they will remain for life, whereas males—which invariably leave their natal groups at puberty—are less so inclined.

The patterns of juvenile social interaction with different classes of partner also resemble those of adults and sub-adults in certain ways. First, juvenile females develop an increasingly strong attraction to infants, which are avoided by juvenile males. As adults, males interact with infants very rarely [Cords, personal observation], in contrast to females. A previous study of infants in this species identified only females (younger and older juveniles as well as adults) as allomaternal caretakers [Förster & Cords, 2005]. Second, as we expected, and as reported in other matrilineal monkeys [Charpentier et al., 2007; Ehardt & Bernstein, 1987; Nakamichi, 1989; Robinson, 1981; van Noordwijk et al., 2002], juvenile females and males differed in their preference for social interactions with peers on the basis of sex. Overall, juvenile females showed a neutral to slightly attracted relationship to their female peers, while avoiding interactions with male peers. In contrast, juvenile males were attracted to male peers, but avoided interactions with female peers. The attraction between juvenile males may reflect the

fact that blue monkey males sometimes disperse from their natal groups together with a peer, and may remain with former group-mates as they begin to live apart from females [Cords, unpublished]. Thus, their bonds with male peers before emigration may be preparatory to their lives as sub-adults, as suggested by van Noordwijk et al. [2002] for long-tailed macaques and Jack and Fedigan [2004] for white-faced capuchins. In addition, however, juvenile males usually play with male peers [personal observation], and their association with male peers may facilitate such play interactions, and thus have a more immediate benefit [Ehardt & Bernstein, 1987]. Females, in contrast, interact rarely as adults with the resident male/s in their group (except when mating) and are unlikely to live together with natal males again during their lifetimes. Their avoidance of male peers as social partners matches these adult tendencies.

Regardless of sex, juveniles generally interacted at close-to-chance levels with unrelated adults, and avoided adult males the most. In blue monkeys, adult males are infrequent social partners for all group members, a pattern that juveniles seem to adopt early [and in contrast to some other primate species, e.g. Agostini & Visalberghi, 2005; Horrocks & Hunte, 2002; Watts & Pusey, 2002]. Nonmaternal adult females, while likely to become important allies in territorial defense [Cords, 2007], may respond less predictably than related adults or young animals to the social overtures of juveniles. Like other Cercopithecines [Charpentier et al., 2007; Fairbanks, 2002; Pereira, 1988; Range, 2006], our subjects showed a strong preference for adult sisters as partners, but it was independent of sex or age; however, there was considerable inter-individual variation in relations with adult sisters. This variation did not appear to relate to whether the sister had her own infant, which might have limited her availability for a younger sibling. The causes of such variation merit further study.

Others have noted the similarity of juveniles' spatial and social patterning relative to conspecific adults [e.g. Robinson, 1981; Watts & Pusey, 2002]. Among female-bonded monkeys, it is commonly found that female juveniles are generally more sociable than male peers, where sociability is measured in terms of time spent in proximity, approach rate, grooming time or ratio of grooming given relative to grooming received [Bramblett & Coelho, 1987; Ehardt & Bernstein, 1987; Nakamichi, 1989; Nikolei & Borries, 1997; Pereira, 1988; Raleigh et al., 1979; Range, 2006; Rowell & Chism, 1986; Wolfheim, 1977]. These patterns contrast with male-bonded muriquis [Strier, 2002] in which male juveniles are in proximity to group-mates more often than female peers. Although such social similarities between juveniles and adults might suggest that juvenile social patterns are preparatory to adult life,

only longitudinal studies of juveniles variably exhibiting adult-typical behavior could allow a firm conclusion. Sex differences in other aspects of juvenile social behavior, such as the frequency and nature of play and aggressiveness, seem *not* to anticipate adult patterns as regularly across taxa [Fagen, 2002; Raleigh et al., 1979; Wolfheim, 1977; but see Paukner & Suomi, 2008]. Such discrepancies may serve as a reminder that juvenile behavior has more immediate consequences in an animal's life than those realized years later in adulthood. In blue monkeys, females may simply be the generally more sociable sex, even when they are young.

Determining whether differences in juvenile sociability influence differences in adult behavior raises the question of how those differences originate. Do young juveniles of the more sociable, philopatric sex receive different social cues from groupmates, or do they spontaneously develop a stronger motivation for mutual interaction? Observational studies are unlikely to answer this question definitively, but some suggest that sex differences in sociability can begin to emerge during the first year or two [Glick et al., 1986; Nakamichi, 1989], which means that environmental effects would have to act prenatally or very early in life [e.g. Eaton et al., 1985] if sex differences are not genetically encoded. In our study population, for example, infant females aged only 3–6 months and away from their mothers spent more time in proximity to nonmaternal adult females than did their male peers [Förster & Cords, 2005]. Milton [2002] reported the assembly of species-typical social and spatial patterns among spider monkeys (*Ateles geoffroyi*) on Barro Colorado Island, where humans seeded the population only with very young individuals: in particular, sons of the original female founders developed species-typical (male–male) association patterns without any models present. Her study suggests intrinsic sex differences for young male and female spider monkeys, a view shared by Roney and Maestripieri [2003] in their review of primate social development.

Rank Effects

Although we expected blue monkey juveniles to show sex differences characteristic of other cercopithecines, we predicted that rank—either of the partner or the juvenile—would account for little variation in juvenile social behavior relative to its role in other species, even closely related ones, with more salient hierarchies. Although hierarchical dominance relations are discernable among female blue monkeys, advantages of high rank on behavior and life history appear minimal [Cords, 2000b, 2002; Pazol & Cords, 2005] and coalitions are rare [Cords, 2000b]. The value of developing amicable relations with high-ranking adult females in the group is unclear for a juvenile blue monkey, relative to

baboons, vervets and some macaques, in which such individuals are important alliance partners as a juvenile acquires its own adult rank [Fairbanks, 2002; Pereira, 1988; Range, 2006]. As expected, the dominance rank of nonmaternal adult females appeared to have little effect on social patterns (i.e. grooming and approaching) of young juvenile blue monkeys, the only subjects that interacted often enough to be included in the analysis. Furthermore, there was no sex difference in the degree to which higher-ranking nonmaternal adult females were preferred as approach partners. This result, in conjunction with the presence of rank effects in taxa with more salient hierarchies, supports the hypothesis that juvenile social priorities are related to future benefits: juveniles seem to cultivate friendly relations with higher-ranking adult females only in species in which those adults are important social partners. Nikolei and Borries [1997] came to a similar conclusion by comparing juvenile female *Semnopithecus entellus*, which lack matrilineal rank hierarchies and avoid interacting with adult female group-mates, with cercopithecine species in which an attraction to adult females is consistent with their value as social partners as adult ranks are acquired. Our comparison of species within the Cercopitheciinae adds a better control for phylogenetic differences to the overall conclusion. Furthermore, it supports from the perspective of *juvenile* grooming the findings of Schino et al. [2009], who reported that adult female capuchins did *not* groom up the hierarchy in a captive group where grooming was *not* exchanged for rank-related benefits.

Our observations not only discounted the importance of higher-ranked social partners, but even suggested that juveniles may generally prefer nonmaternal adult females in the *lower* part of the hierarchy and *avoid* those higher up. It is possible that juveniles learn to avoid higher-ranking females if they are more intolerant of the juveniles' proximity. Unlike Pereira [1988], who found that juvenile female baboons approached higher-ranking adult females selectively when the group was resting, we did not limit our analysis to periods of group rest. Our data collection occurred during all kinds of group activity, including feeding. Feeding accounts for a large fraction of an adult female's time budget [33 ± 1 SE%, Pazol & Cords, 2005], and agonism in blue monkeys occurs disproportionately in the feeding context [Cords, 2000b; Pazol & Cords, 2005]. Juveniles may adjust the group-mates they approach in these circumstances, avoiding those higher up in the hierarchy. The same explanation cannot hold, however, when our subjects are compared with juvenile female vervet monkeys: Fairbanks [2002] found a preference for approaching high-ranked adult female group-mates even though she did not limit her analysis to particular kinds of group activity.

The fact that young juveniles' maternal rank did not predict the rank of their adult female social partners in a consistent way, either for females or males, suggests that juveniles are not competing to groom up the hierarchy. Again, these findings are consistent with a view that juvenile blue monkeys differ in their social priorities from other closely related species in which rank is both matrilineal and important [reviewed for cercopithecines in Fairbanks, 2002; also Perry, 1996 for a noncercopithecine example]. Instead, it seemed that juveniles, especially females, groomed and approached nonmaternal adult females in the middle of the hierarchy, so that the offspring of high-ranked mothers groomed down the hierarchy, whereas those of low-ranked mothers groomed up the hierarchy. This pattern was not driven by a shared attraction to particular grooming partners in any of the groups; rather, partner choices by juveniles were idiosyncratic.

Some researchers have emphasized a juvenile's attraction to related adult females as part of a strategy to ensure agonistic support when the juvenile acquires her adult rank [Fairbanks, 2002; Pereira, 1988]. Like others, we found our juvenile subjects were socially attracted to mothers and, less universally, to adult sisters, associating with, approaching and grooming them disproportionately. Given a lack of sex differences, the fact that partner's rank was unimportant in directing younger juvenile's grooming and approach behavior, and the fact that hierarchies appear generally muted in blue monkeys, we are inclined to view the social preference for close adult female kin as reflecting the tolerance of these adults toward related youngsters. As Pereira [1988] noted, juveniles are likely more vulnerable to predators because of their small size, so should be motivated to stay near adults that will tolerate their proximity. Feeding near kin may also reduce resource competition for juveniles, whose small size again makes them vulnerable.

CONCLUSION

Overall, our results are consistent with the hypothesis that juveniles target social partners that are likely to be important in their adult lives. In a female-bonded species, such important partners for females include other females, and especially close kin, whereas males may benefit from associations with male peers during cases of parallel dispersal. Our findings with regard to sex differences in social priorities and kin preference resemble those of other cercopithecine species, which are also female bonded. The fact that blue monkey juveniles do not target partners on the basis of rank, in contrast to juvenile baboons and vervets, further supports the general idea that their social priorities are related to adult life, given species differences in agonistic behavior.

We would not discount, however, the possibility that juvenile social behavior reflects contemporary priorities as well: proximity to close adult kin may provide protection against predators and conspecifics alike for vulnerable juveniles, attraction to same-sex peers facilitates play, and female attraction to infants may provide opportunities to learn. Indeed, older juvenile females showed social patterns most like those of same-sexed adults.

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