Effects of age and sex on intra-group spacing behaviour in juvenile savannah baboons, *Papio cynocephalus cynocephalus*

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Abstract. Twenty juvenile members of known genealogies in two baboon groups were studied over a 16-month period to evaluate a number of predictions about juvenile spacing behaviour based on the natural history of savannah baboons. Young juveniles (1–2.5 years old) approached more frequently and spent more time in proximity to other group members than did old juveniles (3–5.5 years old). In particular, young juveniles associated more closely with their mothers, particular adult males (possible fathers) and age-peers than did old juveniles. Approaches of young juveniles towards unrelated, high-ranking adults were more likely to occur during feeding than were those of old juveniles. Also, following such an approach, young juveniles were more likely than old juveniles to begin feeding immediately. The overall rates of feeding of old juveniles were depressed when they were in proximity to unrelated, high-ranking adults, whereas the feeding rates of young juveniles were not. Juvenile males approached adult males more often than did juvenile females. Juvenile females approached unrelated adult females more often than did juvenile males. Sex differences also existed in juveniles' choices of unrelated adult female neighbours. Juvenile females associated most often with lactating females, whereas juvenile males associated primarily with cycling females. During group resting, juvenile females approached adult females from higher-ranking matriline more often than they approached adult females from lower-ranking matriline. Juvenile males did not exhibit this attraction. Also, among old juveniles, females associated closely with their mothers, whereas males did not. Taken together, the results support the hypotheses that juvenile baboons associate with group members in ways that (1) enhance the probability of surviving an early period of high mortality, (2) create opportunities for social learning of sex-typical behaviours/skills, and, for females, (3) facilitate acquisition of familial dominance status.

Information on inter-individual spacing behaviour is fundamental to developmental studies of social relations (Kummer 1968). Relationships are founded upon series of social interactions (Hinde 1976) and interactions require proximity between participants. Group-living animals commonly employ behavioural tactics that enhance their chances of encountering some group members and reduce their chances of encountering others. These spacing tactics underlie the continuing development of social relations among individuals (Deputte 1983). To date, patterns of approaching and departing between group-living animals have been examined primarily in studies of mother–infant relations (e.g. Altmann 1980; Taber & Thomas 1982; Lickliter 1984). A few excellent non-mother–infant studies (Harcourt 1979; Smuts 1983a; Stein 1984; Colvin & Tossier 1985), however, have shown that collection of such data in other studies of social relations would contribute substantially to the knowledge of how primates value

(sensu Kummer 1978) different social relationships.

Among primates, juveniles are particularly important subjects for the study of developing spatial relations. (Pereira & Altmann 1985 reviewed the literature on primate behavioural development, noted great confusion in terminology, and argued that the term 'juvenile' should be reserved for prepubertal immatures whose survival does not depend on that of their mothers.) An infant primate is carried by and, later, follows its mother into proximity with her associates (Altmann 1980; Berman 1982a, b). As juveniles, immatures begin a lifetime of independent association and interaction with surrounding members of their group or population. In many species (e.g. baboons, *Papio* spp., macaques, *Macaca* spp., ringtailed lemurs, *Lemur catta*), juveniles must select partners for the development of particular relationships from many diverse individuals. In Amboseli, juvenile baboons associate indepen-

dently for 3 (some females) to 5 years (some females, most males) before reaching puberty (Altmann et al. 1981; Pereira & Altmann 1985). Satisfactory information is not available for any primate species concerning which group members are sought by young and old, male and female juveniles for association and interaction (Pereira & Altmann 1985; Caine 1986; see also Cheney 1977, 1978a, b; Silk et al. 1981; Colvin & Tissier 1985; Fairbanks & McGuire 1985).

Predictions

The behaviour of immature animals is likely to be dually adaptive, functioning both to promote survival during immaturity and to prepare developing individuals, through experience, for lives as reproductive members of their sex and species (Bekoff 1977; Mason 1979). In the present study, it was expected that juvenile baboons would associate with other group members in ways that promoted survival and provided experience with species- and sex-typical adult behaviour. Survival is not a challenge of equal magnitude for young versus older juveniles. In Amboseli, baboons aged between 1 and 3 years (hereafter, 'young juveniles') experience much higher rates of mortality than do those aged 3–6 years (hereafter, 'old juveniles'), whose mortality rates are as low as those of adolescents and young adults (J. Altmann, S. Altmann & G. Hausfater, unpublished data). Because young juveniles are very small, weak and behaviourally inexperienced in comparison to old juveniles, they are more vulnerable to several medium-sized predators (e.g. eagles, *Stephanoaetus coronatus*, *Polemaetus bellicosus*, *Aquila rapax*, pythons, *Python sebae*, and cats, *Felis* spp.; see Coelho 1985 for data on baboon growth schedules). Circumstantial evidence strongly suggests that much of the mortality that occurs during the early juvenile period is due to predation (J. Altmann, S. Altmann & G. Hausfater, unpublished data). Because juveniles that associate frequently with other group members should experience mitigated rates of predation for a number of reasons (Hamilton 1971; Pulliam 1973), it was predicted that young juveniles would approach more frequently and spend more time near other group members than would old juveniles.

Social learning of foraging techniques and feeding competition were also expected to influence differentially the spacing behaviour of young and

old juveniles. Immature primates need to acquire skills in foraging and food processing in order to obtain adequate nourishment and avoid toxins (see Glander 1982; Watts 1985; Whitehead 1986). Recent research suggests that immatures that associate often with tolerant group members benefit from frequent opportunities for social learning of foraging techniques (Watts 1985; Whitehead 1986). Because it was expected that young juveniles would be most tolerated and also most frequently agonistically supported by their mothers and probable fathers (see Altmann 1980; Stein 1984), I predicted that young juveniles would associate more strongly with their mothers and probable fathers than with unrelated adult group members. Differential maternal tolerance towards juvenile offspring by sex was not predicted (cf. Dittus 1979); however, it was expected that mothers would become less important sources of agonistic support for sons than for daughters as juvenile offspring aged (see below; Pereira 1984, 1986; note: known fathers of old juveniles did not exist in either group). Consequently, I predicted that the rates of filial association of young juveniles would exceed those of old juvenile males but not females.

With age, juveniles undoubtedly become progressively more important foraging competitors for adults. The sizes of the food items that they select increase along with their foraging efficiency and metabolic needs. As the frequency and intensity of agonistic interactions of juveniles with adults increase (Pereira 1984), so do the risks of associating with adults during group foraging. Consequently, it was predicted that old juveniles would approach unrelated, higher-ranking adults during feeding less frequently than young juveniles would, and feed less than young juveniles while in proximity to such feeding adults. I also predicted that, when foraging in proximity to unrelated adult females, old juvenile females would forage primarily near females from matriline ranking lower than their own. Familial dominance status was not expected to affect choice of adult female neighbours during foraging by either young juveniles or old juvenile males because young juveniles are probably insignificant food competitors for adults, and old juvenile males gradually become agonistically dominant to all adult female members of their groups (Lee & Oliver 1979; Pereira 1984).

Life-history considerations led to several other predictions concerning sex differences in juvenile patterns of association. For example, it was

expected that old juvenile females would associate with their mothers and adult sisters more than would male age-peers (see also Ehardt-Seward & Bramblett 1980; Handen & Rodman 1980; Fairbanks & McGuire 1985). Cercopithecine juvenile females receive support from female kin during fights with unrelated adult females from lower-ranking matriline (Cheney 1977; Walters 1980; Horrocks & Hunte 1983; Bernstein & Ehardt 1985). This support is thought to assist juvenile females in acquiring familial dominance status (Cheney 1977; Fairbanks & McGuire 1986). By maintaining proximity to older kin, juvenile females would increase the likelihood of receiving support during these fights. Previous research also indicates that support from unrelated females from higher-ranking matriline is important to the efforts of juvenile females to acquire familial dominance status (Walters 1980; Horrocks & Hunte 1983). In contrast, adult females do not provide much agonistic support to unrelated juvenile males (Pereira 1984, 1986). Therefore, I predicted that old juvenile females would approach high-ranking adult females during group resting more often than they would approach low-ranking adult females, whereas old juvenile males were expected not to exhibit selective association based on adult female rank.

Old juvenile males and females were also expected to be attracted to unrelated females of different reproductive states: I predicted that old juvenile females would associate most often with lactating females, whereas old juvenile males would associate primarily with menstrually cycling females. Immature female primates may learn important mothering skills by practising handling infants, competing to handle infants, and watching mothers and their infants interact (Struhsaker 1971; Lancaster 1972; Cheney 1978b; Altmann 1983; Pereira & Altmann 1985). By associating with cycling females, juvenile males would gain opportunities to copulate and develop sexual skills essential to their chances of reproducing during adolescence and adulthood.

Finally, I predicted that juvenile males would associate with adult males more than would juvenile females and that females would associate with unrelated adult females more than would males. Time spent observing the social interactions of same-sex adults may be critical for sex-typing in non-human primates as it seems to be for humans (e.g. Maccoby & Wilson 1957; Slaby & Frey 1975).

Observation of same-sex adults may improve the expression of sex-typical behaviour of juveniles and familiarize juveniles with the types of social interactions in which they will participate as adults. The rate and fidelity of information transfer during social learning can be expected to increase with increases in frequency or duration of proximity between the model and learner.

METHODS

Study Groups

Two free-ranging groups of yellow baboons, *Papio c. cynocephalus*, were studied in Amboseli National Park, Kenya, over a period of 16 months (see Altmann & Altmann 1970 and Western & Van Praet 1973 for descriptions of the Amboseli baboons and their ecosystem). One group, Alto's Group, ranged in size between 45 and 53 members during the study, including 18 adult females, six adult males, five adolescent males, and 15 infants, 10 of which were born during the latter half of the study (see juvenile composition below). Each group member was visually recognizable and all matrilineal kin relationships were known except for possible relationships among the oldest adult females (greater than 10 years old) and among the adult males, all of whom had migrated into Alto's Group as adults. Hook's Group was the other large baboon group in Amboseli for which considerable longitudinal data were available when I arrived. This group had often been censused between 1971 and 1977, and about monthly from 1977 until the time of my study (1981). Consequently, the mothers of all juveniles in Hook's Group were known, as were some of the juveniles' nulliparous adult female kin. Hook's Group ranged in size between 28 and 33 members during the study, including 12 adult females, four–six adult males, two adolescent males, and six infants born throughout the study.

Throughout this report, references to 'unrelated adult females' mean adult females that were neither the mothers nor the adult sisters of juveniles. In Hook's Group, the identities of two adult sisters were known. Another female was considered a juvenile's adult sister if she occupied a dominance rank immediately adjacent to the juvenile's mother, frequently groomed the juvenile (see Pereira & Altmann 1985 for descriptions of the grooming

relations of juveniles with related versus unrelated adult females), was one of the mother's two most frequent adult female grooming partners, and often supported both the juvenile and its mother during agonistic interactions (see Walters 1981). These criteria categorized one adult female as 'sister' for one juvenile in Hook's Group and identified the two known sisters in that group.

Study Subjects

Table I displays the subjects' ages, the maternal ranks, and the numbers of hours of sampling. Whereas baboons do not breed seasonally in Amboseli (Altmann 1980), both social groups that I studied fortuitously contained discrete cohorts of young and old juveniles; i.e. no juvenile survived whose age spanned these two age-classes during the study. Only one of the two oldest females experienced menarche; data from this female (Tatu) are excluded from all analyses. Lona experienced menarche about 1 month prior to the conclusion of the study (age: 49 months). Because less than 3% of her data were gathered following menarche, they were analysed uniformly along with the rest.

Sampling Methods

Focal-animal samples of 16 min were conducted on the hour and the half-hour from 0700 to 1730 hours inclusive, excluding the noon hour. For each day, a morning and an afternoon sample were scheduled for each subject using random assignment without replacement. If a subject could not be located at the beginning of a sampling period, the animal was sampled for 16 min upon location or only until the end of the assigned half-hour, whichever occurred first. Comparable amounts of each subject's data were gathered during each sampling 'time-slot' and each month of study. To minimize the effect of my presence on rates and qualities of interactions but to maintain excellent observation conditions (see Altmann 1980), I tried to conduct all sampling while standing at least 10 m from all animals.

The identities of all group members within 3 m of focal subjects were recorded 1 min after the onset of each focal sample. The nearest of these 'neighbours' was also recorded. In certain situations, it was sometimes impossible to collect these point samples (Altmann 1974) and still maintain a continuous record of a focal animal's behaviour (e.g.

during group running or foraging in a dense bush or tree). To guard against over-representation of easily collected data (e.g. 'no neighbours' and older, larger neighbours) point samples were never collected in such situations.

Throughout focal samples, all non-interactive approaches (Altmann 1980) involving focal subjects were recorded. Approaches were scored whenever one baboon moved more than 1 m towards one or more stationary group members and came to rest or feed within 3 m of them for at least 5 s. If either the approacher or approachee departed (beyond 3 m) within those first 5 s, an approach was not scored between those two animals. No approaches were scored when a potential approacher initiated any other form of interaction with any potential approachee. Thus, these data provide information about group members' voluntary initiations of simple association with others, apart from strong inclinations to initiate (or risk) displacement, grooming, or other dispersive or cohesive interactions. Finally, the behaviour assumed by the approacher immediately following each approach and the continuing behaviour of all approachees were recorded. To facilitate the recording of many other types of interactions, departures between group members were not recorded (Pereira 1984). Consequently, unequivocal analyses of the relative roles of dyad members in the maintenance of proximity were not possible (Hinde & Atkinson 1970). To identify partners likely to have been primarily responsible for proximity maintenance, correlations between rates of approach by dyad members and time spent in proximity by those dyads were examined.

Statistical Analyses

Throughout this paper, classes of juveniles are compared using single scores from each individual and non-parametric statistical tests of two sample medians. The Mann-Whitney *T*-test (Mosteller & Rourke 1973) was used to evaluate differences between medians of age, sex, or age-sex classes. Sign or Wilcoxon tests (Mosteller & Rourke 1973) were used to evaluate paired or dichotomous data. Wherever class average and variability within a class are represented in the text, values are presented as follows: median (range). Simple correlations were used as explained at the end of the previous section, and multiple regressions were performed for one analysis to help illustrate graphi-

Table I. Study subjects: ages, group membership, mothers' ranks and time spent sampling (h)*

Name	Age at beginning of study (months)	Age at end of study	Group	Mother's rank among females	Focal sampling time (h)
Old juveniles					
Males					
Hodi	45	56	A	15	56.68
Spike	42	53	A	11	58.56
Peanut	42	53	A	16	55.02
Nami	34	45	H	12	49.40
Females					
Vixen	40	51	A	7	54.63
Oreo	54	65	A	13	54.88
Lona	39	50	H	4	49.15
Kupima	39	50	H	6	50.42
Lamu	36	47	H	9	50.51
Tatu	60?	71	H	?	47.90
Young juveniles					
Males					
Putz	17	28	A	16	54.78
Sluggo	7	18	A	15	28.25
Rasta	17	28	H	?	47.55
Females					
Siku	16	27	A	1	54.83
Pichka	17	28	A	9	54.55
Scherzo	8	19	A	11	27.52
Poco	13	24	H	1	49.93
Whiskey	5	16	H	3	16.39
Kanga	18	..	H	6	33.69
Sybil	16	27	H	11	49.45

* Tatu's date of birth is unknown; however, her age was estimated annually throughout juvenescence by comparing her body size with juveniles of known ages in Alto's Group. All other animals' birthdates are known at least to within a period of 2 weeks. There were 18 adult females in Alto's Group (A) and 12 adult females in Hook's Group (H). Tatu's mother was not living in Hook's Group during the study. Rasta's mother died before her precise dominance status among females could be determined. She was mid-ranking. Kanga disappeared 6 months after the start of the study, having reached 24 months of age. Sampling on Sluggo and Scherzo began 4 months after the start of the study and sampling on Whiskey began 7 months after the start of the study. All young juvenile subjects rarely or never suckled during the day.

cally the effect of juvenile sex beyond the effect of age. Because age and sex were slightly associated in my sample (Table I), sex differences were evaluated separately within age classes. Two-by-two analyses of variance were not used to investigate potential effects of age and sex on behavioural variables because exploratory analyses (Pereira 1984) in several instances indicated greater variance in data from age-sex classes with fewer representatives. Under these conditions, the results of ANOVAs become particularly vulnerable to spurious rejec-

tions of null hypotheses (Type I error). To guard additionally against Type I error, all statistical tests were two-tailed (α -level = 0.05), even though directional predictions were advanced prior to data collection for most comparisons. When comparisons between two very small classes (e.g. young versus old juvenile males) yielded complete separation, the exact two-tailed *P*-values (between 0.05 and 0.10) are given. For all comparisons using data from both social groups, patterns within each group were first ascertained to be the same.

Table II. Frequency of juvenile association among seven age-sex classes of neighbours

	Neighbours								
	Adult males	Adult females	Adolescent males	Old juveniles	Young juveniles	Rising juveniles*	Infants	Total	χ^2 †
Old juvenile males									
Observed	114	296	179	192	206	79	163	1229	279.76
Expected	173.40	489.71	121.91	123.12	103.34	50.95	166.93		
Chi-squared	20.35	76.62	26.74	38.54	101.98	15.44	0.09		
Old juvenile females									
Observed	104	470	93	197	236	80	244	1424	185.61
Expected	214.30	560.71	117.05	163.76	144.45	52.34	172.30		
Chi-squared	56.77	14.67	4.94	6.75	58.02	14.62	29.84		
Young juvenile males									
Observed	74	234	110	145	134	70	137	904	219.05
Expected	128.54	353.95	83.29	117.33	60.96	30.24	130.02		
Chi-squared	23.14	40.65	8.57	6.53	87.51	52.28	0.37		
Young juvenile females									
Observed	160	572	160	323	290	155	347	2007	449.82
Expected	297.08	787.52	170.79	279.13	147.25	58.77	266.87		
Chi-squared	63.25	58.98	0.68	6.89	138.39	157.57	24.06		

* Infants at the start that became juveniles before the end of the study.

† χ^2 values exceeding 12.6 attain the 0.05 level of significance.

RESULTS

Basic Demographic Patterns in Juvenile Association Neighbours

To describe its fundamental pattern of social association, each juvenile's distribution of neighbours among seven age-sex classes was examined. If juveniles associated with other group members without regard to the age or sex of potential neighbours, the distributions would simply reflect the number of individuals in each class of neighbours (Altmann 1962). Every subject's distribution of neighbours, however, differed significantly from values expected from neighbour class representations ($31 < \chi^2 < 176$; all 19 P -values < 0.001). Because juveniles within age-sex classes exhibited similar patterns of association and non-association (see Pereira 1984), data within juvenile classes were pooled to illuminate important patterns (Table II).

Juveniles spent less time near adults and more near juveniles and rising juveniles (infants that became juveniles by the end of the study) than expected by chance (sign tests, $N=19$, all P -values < 0.01 ; see also large contributions of cells to χ^2 -statistics in the rows of Table II). Greater proportions of the neighbours of old juvenile males

than of those of old juvenile females were adult males (Mann-Whitney test, $N, M=4, 5, T=29$, $P < 0.04$), and greater proportions of the neighbours of old juvenile females than of those of old juvenile males were adult females ($N, M=4, 5, T=10$, $P < 0.02$). Also, old juvenile males spent more time near adolescent males than expected, whereas old juvenile females associated with adolescent males less than expected ($N, M=4, 5, T=30$, $P < 0.02$). Finally, old juvenile females were found in proximity to infants more frequently than were their male age-peers ($N, M=4, 5, T=10$, $P < 0.02$). Significant sex differences did not exist between young juveniles for any of these four comparisons.

Nearest neighbours

Next, I identified those group members that were more or less likely to be nearest neighbours than expected from their rates of association within 3 m (see also Pereira et al., in press). Expected values were derived from each subject's observed distribution of neighbours. Old juvenile males and young juveniles of both sexes had adult males as their nearest neighbours as often as expected by chance (Table III). In contrast, all five old juvenile females

Table III. Patterns of association among neighbours: nearest neighbours

	Nearest neighbours								
	Adult males	Adult females	Adolescent males	Old juveniles	Young juveniles	Rising juveniles*	Infants	Total	χ^2 †
Old juvenile males									
Observed	37	107	79	86	78	23	29	439	24.00
Expected	40.86	105.64	65	68.74	72.25	27.92	58.59		
Chi-squared	0.36	0.02	3.02	4.33	0.46	0.87	14.94		
Old juvenile females									
Observed	25	198	31	90	98	35	37	514	46.71
Expected	37.27	168.69	34.88	71.67	84.77	29.12	87.58		
Chi-squared	4.04	5.09	0.43	4.69	2.06	1.19	29.21		
Young juvenile males									
Observed	25	96	44	52	48	28	41	334	3.64
Expected	27.40	86.58	40.77	53.90	48.81	25.76	50.77		
Chi-squared	0.21	1.02	0.26	0.07	0.01	0.19	1.88		
Young juvenile females									
Observed	43	234	52	139	108	52	83	711	27.88
Expected	56.35	201.66	57.67	114.57	102.11	55.24	123.40		
Chi-squared	3.16	5.19	0.56	5.21	0.34	0.19	13.23		

* Infants at the start that became juveniles before the end of the study.

† χ^2 values exceeding 12.6 attain the 0.05 level of significance.

had adult males as their nearest neighbours less often than expected by chance (sex difference, old juveniles: $N, M=4, 5, T=29, P<0.04$). Also, six of the seven juvenile males had adolescent males as nearest neighbours more frequently than expected by chance, whereas only four of the 12 juvenile females did so. Five of the seven males had adult females as their nearest neighbours as or more often than expected, while all 12 females did so. Finally, old juveniles were nearest neighbours more often than expected for all nine old juvenile subjects (sign test, $P<0.005$).

Two strong departures from expected values represented neither age nor sex effects (Table III). First, all juveniles had infants as nearest neighbours less often than expected. This was due at least partly to a sampling convention: the adult female was scored as nearest neighbour whenever a mother and infant in ventro-ventral contact were nearest during a point sample. Second, kinship accounted for the disproportionate representation of old juveniles as nearest neighbours for young juvenile females: one female in each group had an old juvenile sibling; they contributed 17 of the 24 observations in excess of expected values, and both

females were most frequently nearest to their siblings when they were scored as being near to old juveniles.

Time Alone and Juvenile Rates of Approach

Young juveniles spent less time alone than did old juveniles (percentage point samples with no neighbours, medians (ranges); old juveniles: 39 (33–44), young juveniles: 29 (22–38); Mann-Whitney test, $N, M=9, 10, T=129, P<0.001$). No significant sex differences in rates of association were evident for either juvenile age-class. A tendency for the juveniles of the larger group (Alto's) to spend more time near other group members than juveniles in the smaller group failed to reach significance. No age, sex, or group differences were evident in the sizes of neighbour groups with which juveniles tended to associate (numbers of neighbours during periods of association, young juvenile males: 2.6 (2.5–2.7), young juvenile females: 2.9 (2.4–3.1), old juvenile males: 2.6 (2.6–2.9), old juvenile females: 2.6 (2.3–3.0)).

The patterns of movement of juveniles within their social groups contributed strongly to the age-

Figure 1. Differences in rates of approaching young versus old juveniles. Each subject's median number of approaches towards old juvenile individuals per 100 instances of locomotion was subtracted from its median number of approaches towards young juveniles per 100 instances of locomotion. The mean ages of subjects in months during their periods of observation were used to order data within age classes, left to right, by increasing subject age (see also Table I).

differentiated pattern of association. Young juveniles approached other group members more often per instance of locomotion than did old juveniles (young juveniles: 13.5% (11–18), old juveniles: 9% (9–11); Mann–Whitney test, $N, M=9, 10, T=46, P<0.001$). Moreover, a significant decline with age in rates of approaching was found among young juveniles (young juveniles: Pearson $r^2=0.45, P<0.03$; old juveniles: Pearson $r^2=0.20, NS$). Between 12 and 24 months of age, progressively fewer instances of locomotion by young juveniles resulted in approaches towards other group members, and the rates of approach by juveniles remained low after 24 months of age.

Young and old juvenile cohorts

Young juveniles in both groups formed more cohesive age-cohorts than did old juveniles: young juveniles approached age-peers more frequently than did old juveniles ($N, M=9, 10, T=50, P<0.001$), and approached age-peers more frequently than they approached old juveniles (Fig. 1; Wilcoxon test of matched pairs, $N=10, P<0.01$). Overall, young and old juveniles approached one another at comparable rates (Mann–Whitney test, $N, M=9, 10, T=75.5, P<0.26$); but the three very young juveniles approached old juveniles more frequently than they were approached by them (sign test of dyads, $N=14, P<0.002$).

Feeding Competition and Juvenile Spatial Relations

I examined three variables to evaluate the effects of juvenile age and sex on feeding and spatial relations with adolescents and adults: (1) the

proportion of juvenile approaches that occurred while the older approachees were feeding, (2) the proportion of approaches towards feeding adolescents and adults following which juveniles immediately began to feed, and (3) the proportion of the total time spent in proximity to adolescents and adults that was spent feeding relative to the proportion of time spent feeding over all social contexts.

Feeding and proximity relations with adult and adolescent males

Smaller proportions of the approaches of old juvenile males than of those of young juvenile males towards adult males occurred while adult males were feeding (Mann–Whitney test, $N, M=3, 4, T=18, P=0.056$). Following such approaches, old juveniles of both sexes were less likely than young juveniles to begin feeding immediately (Mann–Whitney tests, males: $N, M=3, 4, T=18, P=0.056$; females: $N, M=5, 6, T=16, P=0.01$). Overall, proximity to adult males was associated with depressed rates of feeding for old juveniles but not for young juveniles (Fig. 2; $N, M=9, 10, T=61, P<0.02$).

Proximity to adult males may have a slightly more depressive effect on the feeding of females than of males among old juveniles. Old juvenile males approached adult males that were feeding more often than did old juvenile females (Mann–Whitney test, $N, M=4, 5, T=30, P<0.02$), and, following such approaches, old juvenile males more often began feeding ($N, M=4, 5, T=29, P<0.04$). But, overall, juvenile males and females of the same age tended to spend comparable

Figure 2. Effect of proximity to adult males on time spent feeding by juveniles. For each subject the proportion of time in proximity to adult males spent feeding divided by the proportion of time spent feeding over all social contexts is plotted. The mean ages of subjects in months during their periods of observation were used to order data within age-sex classes, left to right, by increasing subject age.

proportions of their time near adult males feeding (Fig. 2; sex differences in both age-classes were non-significant).

No depression of the rates of feeding of juveniles occurred with proximity to adolescent males. Thirteen of the 19 juveniles fed less near adolescent males than over all contexts combined; sign test, $P < 0.20$, and little of the variation among juveniles is explained by juvenile age or sex. Also, no significant age-sex differences existed in the rates at which juveniles approached feeding adolescent males nor in the probabilities of feeding immediately after approaching feeding adolescent males.

Feeding and proximity relations with unrelated adult females

Young juveniles approached unrelated adult females from matriline higher-ranking and lower-ranking than their own at comparable rates during adult feeding, and they began feeding following similar proportions of their approaches to the two classes of feeding females (Fig. 3). Old juvenile females more often approached unrelated adult females from lower-ranking families than unrelated adult females from higher-ranking families during feeding, and every old juvenile more often began feeding when the females they approached were members of lower-ranking families (Fig. 3; age difference for latter comparison, $N, M = 7, 8, T = 32, P < 0.005$).

The relative familial dominance status of un-

related adult females, however, most strongly and consistently influenced the spacing and feeding behaviour of old juvenile females. Smaller proportions of the approaches of old juvenile females towards unrelated adult females from higher-ranking families than towards females from lower-ranking families occurred during feeding by approachees, whereas this was not true for any other class of juveniles (Fig. 3). Also, the differences in the tendencies of old juvenile females to begin feeding after approaching the two classes of feeding adult females exceeded those of any other class of juveniles (sex difference, old juveniles: $N, M = 3, 5, T = 6, P < 0.04$; Fig. 3). Finally, four of the five old juvenile females spent considerably smaller proportions of time feeding while they were in proximity to adult females from higher-ranking families than they did over all contexts combined, whereas all four old juvenile males and six of the seven young juveniles eligible for analysis (see legend to Fig. 3) spent as much or more time feeding near adult females from higher-ranking families as they did over all social contexts. No age- or sex-differentiated patterns were evident in the proportions of time spent feeding by juveniles while in proximity to unrelated adult females from lower-ranking families (Pereira 1984).

Feeding and proximity relations among juveniles

Finally, potential effects of competition on spacing behaviour among juveniles were investigated.

Figure 3. Effects of familial dominance status, age and sex on the spatial relations of juveniles with unrelated adult females during feeding. (A) For each subject, percentages of approaches towards unrelated adult females that occurred while the adults were feeding are shown. Each subject's median percentage of approaches towards females from lower-ranking families (UFL) was subtracted from its median percentage of approaches towards females from higher-ranking families (UFH). For example, for the subject whose mother ranked above five unrelated adult females and below nine others, the third greatest percentage of approaches that occurred towards UFL during feeding was subtracted from the fifth greatest percentage of approaches that occurred towards UFH during feeding. (B) The difference between the percentages of approaches towards feeding UFH and UFL following which the juvenile immediately began to feed (% to UFH - % to UFL) are shown for each subject. Median scores for each class of adult females were used as described above. (C) The percentages of time in proximity to UFH spent feeding divided by the percentages of time spent feeding over all social contexts ($\times 100$). Bars extending above the abscissa indicate subjects that were more likely to feed while in proximity to UFH than over all contexts combined; bars extending below indicate subjects that were less likely to feed while in proximity to UFH than over all contexts combined. Again, median scores were used to characterize each subject's interaction with each of the two classes of females. In each panel, data from subjects within age-sex classes are ordered, left to right, by increasing subject age (see legend of Fig. 2). These analyses were not applicable (see NA in C) to data from the young juvenile daughters of each group's top-ranking adult female (Poco and Siku; no UFH). The old juvenile son (Nami) of Hook's Group's lowest-ranking female was not eligible for the first two analyses (no UFL), and young juvenile male Rasta was omitted from all analyses because his family rank was unknown (see Table I).

Approaches during which approachees were feeding and after which the approaching individuals began feeding are considered here. If competition among juveniles, mediated by dominance status, affects spacing behaviour during feeding, dominant individuals could be expected to approach and begin feeding near feeding subordinates more frequently than vice versa. During my study, this was true only among old juveniles. In 12 of 16 dyads (seven of 10 in Alto's Group and five of six in Hook's Group), dominant dyad members more frequently approached to feed near feeding subordinates than vice versa (Wilcoxon test, $N=16$, $P<0.01$). In neither young nor mixed-age juvenile dyads did dominant or subordinate members con-

sistently perform the majority of approaches-to-feed during feeding by approachees (dominance relations were characterized using the techniques of Hausfater 1975 and Walters 1980; see Pereira 1984 for additional information).

Association with Kin versus Non-kin

Adult female kin

Young juveniles spent more time in proximity to their mothers than did old juvenile males and spent more non-grooming time near their mothers than did old juveniles of either sex (Table IV; old juvenile females spent much time near their mothers grooming with them; see Pereira & Alt-

Table IV. Association with kin versus with unrelated group members

	Young juveniles			Old juveniles			Prediction	Result
	Males (N=2)	Females (N=7)	Total (N=9)	Males (N=4)	Females (N=4)	Total (N=8)		
% Time in proximity to mother (median individual's score)	12	9	9	2.5	9	4.5	YJ > OJ OF > OM	NS *
% Non-grooming time in proximity to mother	11	9	9	2.5	6	3.5	YJ > OJ OF > OM	* *
% Non-grooming time in proximity to adult sister	—	6	6	4	5.5	5	YJ > OJ OF > OM	† †
% Non-grooming time in proximity to unrelated adult females (per caput)	2	2	2	2	3	2	(for females) < with mother OF > OM	* NS
% Non-grooming time in proximity to immature sibling	11	10	11	9	7.5	9		
% Non-grooming time in proximity to sibling's age-sex peers (per caput)	8	6	6	6	4.5	6	< with sibling	*

Median individuals' scores are presented in all cells; no young juvenile males had adult female sisters.

* Significant difference; two-tailed Mann-Whitney test, $P < 0.05$; NS = not significant.

† Direction of results supports prediction; insufficient subjects to test statistically.

mann 1985). This is not simply because young juveniles spent more time near all group members: although young juveniles approached unrelated adult females more frequently than did old juveniles (see Fig. 5), they did not spend significantly more non-grooming time in proximity to unrelated adult females than did old juveniles (Table IV).

Young juveniles had their mothers as nearest neighbours for significantly larger proportions of proximity time than was true for old juveniles (young juveniles: 81% (35–90), old juveniles: 55% (48–73); $N, M = 8, 9, T = 50, P < 0.04$). Despite this large age difference, all old as well as young juveniles had their mothers as nearest neighbours more often than expected by chance: every subject had their mother as their nearest neighbour for a proportion of time that exceeded $1/N$, where N equals the average number of neighbours the subject had during periods of association (sign tests, $N = 9, N = 10$, both $P < 0.005$).

Old juvenile females spent significantly more total and non-grooming time near their mothers and adult female sisters than did old juvenile males (Table IV). Moreover, four of the five old juvenile females spent more total time near their mothers than near any unrelated adult female, and twice as much non-grooming time near their mothers as they spent near unrelated adult females per caput.

In contrast, old juvenile males spent comparable amounts of time in proximity to their mothers and unrelated adult females. This sex difference was not evident in young juveniles.

Rates of approach by juveniles were correlated significantly with time spent in proximity to their mother (Pearson $r^2 = 0.38, P < 0.01$), whereas rates of approach by mothers towards juvenile offspring were not (Pearson $r^2 = 0.10, P > 0.10$). This suggests that the juveniles, rather than their mothers, were primarily responsible for maintaining mother-offspring proximity relations.

Probable fathers

The prediction that juveniles are most attracted to their probable fathers among the adult males could be tested only for the young juveniles of Alto's Group (probable fathers = males that consorted or copulated with the juveniles' mothers 5–1 days prior to detumescence of sex skins during cycles in which juveniles were conceived; see also Hausfater 1975; Altmann 1980; Stein 1984). None of the probable fathers of old juveniles still resided in that group, and records of previous consortships were inadequate to identify probable fathers for any juvenile of Hook's Group.

All five young juveniles in Alto's Group asso-

Figure 4. Probabilities ($\times 100$) of approaching a recent immigrant given an approach towards an adult male as estimated by percentages of approaches towards adult males that were towards immigrant males. Dashed lines indicate expected values based on the representation of resident versus immigrant males during the observation period for each subject. Data are ordered within age classes, left to right, by increasing subject age.

ciated most closely with a possible father among the adult males (a male present at the time of their conception; for every young juvenile, the same three of the six adult males present throughout the study were possible fathers). Three of the five approached their probable fathers as or more frequently than they approached any of the other five available adult males, and spent more total time near their probable fathers than near any of the other males. All five young juveniles in Hook's Group approached the same long-term resident adult male most frequently, a male known to have joined this group no less than eight and no more than 16 months prior to their earliest conceptions. This male was also the primary adult male associate (*sensu* Altmann 1980) of Whiskey throughout her infancy (Pereira, unpublished data). Generally, young juveniles associated closely with adult males who had been present since the juveniles' births and avoided adult males who had immigrated since then (Fig. 4). In contrast, old juveniles in both

groups approached recent immigrants at rates much closer to those expected on the basis of the immigrants' representation among adult males (age difference in each group, $N, M = 5, 5$, $P < 0.01$).

The rates of approaching by juveniles explain 23% more of the variance in the time spent by juveniles near adult males than do the rates of approaching juveniles by adult males (juvenile approach rates: Pearson $r^2 = 0.64$, $P < 0.001$; adult male approach rates: Pearson $r^2 = 0.41$, $P < 0.01$). This suggests that the movement patterns of juveniles were primarily responsible for age, sex and potential kinship-related differences in the proximity relations of juveniles with adult males.

Immature kin

Both male and female juveniles associated more regularly with juvenile and adolescent siblings than with unrelated individuals of the same age-sex classes. In each of nine untied comparisons, involving subjects from each of the four juvenile age-sex classes, proximity scores with juvenile or adolescent siblings exceed per caput scores for association with the unrelated age-sex peers of siblings (see Table IV). Too few juveniles had immature siblings to test predictions concerning age or sex differences in patterns of sibling association (*cf.* Colvin & Tissier 1985).

Differential Attractiveness of Unrelated Adult Females

Relative dominance status

The potential attraction of juveniles to be near unrelated adult females from higher-ranking families *per se* (versus attraction to groom with them) could only be expressed in contexts of group resting because old juvenile females often received aggression in feeding contexts from higher-ranking females but not from lower-ranking females (Pereira 1984, 1986, unpublished data). As a probable consequence, old juvenile females approached unrelated adult females from higher-ranking families less often than they approached adult females from lower-ranking families during adult feeding, and spent more time resting (not feeding) while near adult females from higher-ranking families than while near those from lower-ranking families (see above). Considered here are approaches to-

Figure 5. Sex differences in juvenile attraction towards unrelated adult females from higher-ranking families. Approaches towards resting adult females following which juveniles themselves began resting are shown (see text for explanation). For each subject, the median number of approaches made per hour towards unrelated adult females from lower-ranking families is subtracted from the median number of approaches made per hour towards unrelated adult females from higher-ranking families. Y denotes young juvenile; O denotes old juvenile. Data within age-sex classes are ordered, left to right, by increasing subject age (see legend of Fig. 2). Rasta, Nami, Siku and Poco were ineligible for analysis (see legend of Fig. 3). Young juvenile female Whiskey was also omitted from the analysis (see text for explanation).

wards resting adult females following which juveniles themselves began to rest. Figure 5 shows that, in this resting context, all 10 juvenile females eligible for analysis (see legend) more often approached adult females from higher-ranking families than they approached adult females from lower-ranking families (sign test, $P < 0.005$). In contrast, only two of the five eligible juvenile males showed this pattern.

The datum from young juvenile female Whiskey was omitted from Fig. 5 because it was far out of line with the others. In the resting context, she approached adult females higher-ranking than her mother three times as often as she approached females lower-ranking than her mother. Her data may be unusual because they were gathered during only the last quarter of the study (see Table I). It is also possible that the two adult females that outranked her mother were her mother's mother and sister; these relationships were unknown. No other subject except the daughter of the top-ranking female in Alto's Group was known or was likely to have had an aunt or a grandmother in their group (Siku was accompanied by two aunts, and family rank rendered her ineligible for this analysis). Whiskey's data did not stand out so radically in other analyses concerning the relations of juveniles with 'unrelated' adult females. Each of those

Table V. Numbers of approaches towards unrelated females of three reproductive states

Juvenile age-sex class	Female reproductive state		
	Cycling	Pregnant	Lactating
Old juvenile males	205(129)	241(286)	189(220)
Young juvenile males	160(126)	214(250)	217(215)
Old juvenile females	284(252)	244(343)	323(258)
Young juvenile females	334(328)	380(475)	496(407)

Expected values appear in parentheses. For each subject and its period of observation (see Table I), the number of female-months represented by unrelated adult female group members in each of the three reproductive states was determined; to attain the expected number of approaches, the proportion of total female-months represented by a given state was multiplied by the subject's total number of approaches toward unrelated adult females. Numbers of approaches (observed and expected) were summed within age-sex classes.

analyses, however, was conducted both with and without Whiskey's datum, to ensure that its omission or inclusion did not unduly affect the results and their interpretation.

Reproductive states

For each subject, the number of approaches towards unrelated adult females in each reproductive state was compared to the number that would have occurred if approaches towards adult females had occurred without regard to reproductive condition. Table V displays the data pooled for each juvenile age-sex class. Eighteen of the 19 juveniles approached unrelated pregnant females less often than expected by chance. Consequently, juvenile attraction towards cycling and lactating females could be treated as a binomial probability. If juveniles were uniformly averse towards, or evaded by, pregnant females, roughly equal numbers would have more often approached cycling and lactating females. In fact, all seven juvenile males approached cycling females more often than expected by chance (sign test, $P < 0.02$), whereas 10 of the 12 juvenile females approached unrelated lactating females more often than expected (sign test, $P < 0.04$). The attraction of juvenile females towards high-ranking resting adult females is un-

Figure 6. Probabilities of approaching adults as estimated by the number of adults approached per 100 instances of locomotion. (A) The number of adult males approached per 100 instances of locomotion. The least squares regression line that results when juvenile approach rate is regressed on juvenile age in months is shown. Identification of juvenile sex illustrates the importance of juvenile sex as the second variable in the two-variable regression model. (B) The number of unrelated adult females approached per 100 instances of locomotion.

likely to account for their attraction towards lactating females: for five of the nine juvenile females concerned, data were gathered while adult females from higher-ranking families cared for infants for only one-third as many mother-months as did adult females from lower-ranking families. Age differences in the attraction of juveniles towards cycling and lactating females were not detectable.

Sex of Adult and Juvenile Rates of Approach

The age and sex of juveniles influenced the rates at which they approached adults of the two sexes. First, the rates of approach by juveniles towards adult males and females declined significantly with age (Fig. 6). In addition, the males of each juvenile age-class approached adult males more frequently than did their female age-peers. Adding the factor

of juvenile sex to the regression analysis explains an additional 10% of the variance in the rates of approach by juveniles towards adult males. Juvenile females tended to approach adult females more frequently than did their male age-peers. Adding juvenile sex to the regression model explains an additional 5% of the variance in rates of approach towards adult females. Among old juveniles, the greater reluctance of females to approach high-ranking adult females that were feeding (60%–80% of the day in Amboseli; see Altmann 1980; Post 1981) reduced this sex difference.

Group differences in the rates of approaching adolescent males by young juveniles precluded pooling the data of all juveniles. Separate analyses, however, confirmed the importance of the age and sex of juveniles as variables influencing rates of approach. First, young juveniles approached adolescent males more frequently than did same-sex old juveniles (Mann–Whitney tests; juvenile males: $N = 3, 4, T = 17.5, P = 0.088$; juvenile females: $N = 5, 7, T = 60, P < 0.02$). Second, juvenile males in both groups approached adolescent males more frequently than did their female age-peers (sign test of young juvenile dyads within groups: $N = 10, P < 0.02$; Mann–Whitney test for old juveniles; $N = 4, 5, T = 29, P < 0.04$).

DISCUSSION

A juvenile baboon's age, sex and familial dominance status strongly influenced its spacing behaviour within its social group. Age-related changes in spacing behaviour appear to be fundamental to the extent that many sex-related differences and effects of dominance appeared only among old juveniles. The data presented here support the hypotheses that juvenile baboons associate with group members in ways that enhance the probability of surviving an early period of high mortality, create opportunities for social learning of sex-typical behaviour/skills, and, for females, facilitate acquisition of familial dominance status.

Changes with Age

The vulnerability of young juveniles to predation and starvation has probably led to the evolution of behavioural tactics that decrease the likelihood of death by these causes. One possible tactic is to spend much time in association with other group

members. Time spent near age-peers reduces the probability that a given juvenile will be selected by a predator (Hamilton 1971; Pulliam 1973). Time spent near adult group members probably also provides direct shielding against some predators like eagles, *Stephanoaetus coronatus*, *Polemaetus bellicosus*, *Aquila rapax* (see Seyfarth & Cheney 1986), servals, *Felis serval*, and jackals, *Canis aureus*, *C. mesomelas*. Even young juveniles situated centrally within a baboon group on the savannah remain vulnerable to eagles while they are without proximate neighbours. Diurnal predation attempts by raptors on immature baboons (J. Altmann, personal communication) and on vervet monkeys (*Cercopithecus aethiops*; Seyfarth & Cheney 1986) have been observed in Amboseli. I expect that, partly for these reasons (see below), young juveniles become progressively more likely to approach other group members as periods of relative solitude continue. This could be tested using survival analysis (e.g. Post 1981).

Two young juvenile subjects, Kanga and Poco, disappeared near the end of my study. Six of the other nine young juveniles spent more time in association with other group members than did Kanga; Poco associated with group members less than any other young juvenile. The menarcheal female, Tatu, also disappeared shortly after my study; she associated with other group members less than any of the 19 juveniles. All three disappeared, without previously exhibiting noticeable signs of illness or injury, during short periods in which observers were not working with Hook's Group. The present data support the hypothesis that diurnal predators, like eagles, present a considerable threat to juveniles that do not associate closely with other group members. It remains to be determined, however, whether diurnal patterns of association also reflect differential vulnerability to nocturnal predation.

Natural selection is also likely to favour gregarious young juveniles because gregariousness promotes social learning. Substantial evidence indicates that for birds, primates and other mammals learning of predator/danger signals and foraging techniques is facilitated by or depends on observation of the performance of conspecifics (Hinde & Fisher 1951; Hall 1963, 1968; Tsumori 1967; John et al. 1968; Mineka et al. 1984; Palameta & Lefebvre 1985; Watts 1985; Seyfarth & Cheney 1986; Whitehead 1986). Avoidance of both predators and toxic secondary compounds can be

acquired by trial-and-error learning only with the risk of dying. Juveniles gain optimal opportunities to learn about signals of caution and alarm used for predators (see Mineka et al. 1984) and about what and how to eat (see Watts 1985; Whitehead 1986) by associating with older group members. Their mother and adult male associates are the best choice of neighbours for young juveniles because they are most familiar (predictable), most likely to tolerate these young juveniles foraging nearby, and most likely to support them in the event of aggression from others or the appearance of a predator (Pereira 1984). In contrast to old juveniles, each young juvenile spent more time near its mother than near any other adult female in its social group, and had its mother as its nearest neighbour for most of that time. Also, young juveniles associated more frequently with adult males, despite associating with smaller proportions of the available adult males (primarily with possible fathers). Young juveniles rarely interacted overtly with these neighbours, but glanced often to watch their methods of processing foods such as *Sporobolus* grass corms and *Trianthema ceratosepala* buds.

By feeding with adult male associates, young juveniles probably also gained access to high-quality food patches (Post 1981) and avoided competition with old juveniles. Old juveniles spent relatively little time near adult males, spent smaller proportions of their proximity time feeding, and commonly received adult male aggression if they harassed young juveniles (Pereira 1984, 1986). By tolerating the proximity of young juveniles and shielding them from predation and aggression, adult males enhance the probability that the youngsters will survive a life stage of high mortality. In doing so, adult males often promote the survival of their offspring: many primary adult male associates are the probable fathers of young juveniles; most are possible fathers. The protective behaviour of adult males towards familiar young juveniles might also evolve if such behaviour increases their future chances of mating with the juveniles' mothers (Smuts 1983b).

Juvenile growth leads to increases in both foraging proficiency and need. Concurrently, the spatial relations of juveniles with adults are influenced by intensifying dominance relations with adults (Pereira 1984). Most aggression by adults towards old juveniles occurred during juvenile feeding (Pereira, unpublished data). As the risks of feeding near

high-ranking adults increased, juveniles became progressively less willing to do so. Several observations, however, suggest that decreasing tolerance from older group members does not entirely account for the decreasing association of juveniles with age. Most importantly, the significant decline with age in the approach rates of young juveniles was not associated with a complementary increase in rates of displacement by and submission to adults (Pereira 1984). Also, while young juveniles approached their mothers and adolescent males more frequently than did old juveniles, these approachees did not direct more aggression towards old juveniles than towards young juveniles per unit of time spent in proximity (Pereira 1984).

I suggest that young juveniles spend less time in close proximity with other group members as they become more 'confident' as independent members of their group. Growth of confidence, beginning during infancy, is likely to be a function of increasing proficiency in foraging and food processing, as well as increasing familiarity with dangerous aspects of their environment. Later, the growing intolerance of adults for proximity with juveniles in certain foraging situations amplifies this age-related change in the propensities of juveniles to associate. With age, dominance relations among juveniles also begin to mediate competition during foraging, which probably accentuates a continuing decline in association among juveniles caused by sex-differentiation of social behaviour: males engage in considerable play with male age-peers and associate with adolescent and adult males, while females associate and interact primarily with adult females and their infants (Pereira 1984; Pereira & Altmann 1985).

Association with Adult Females

Juvenile male and female patterns of association with adult females are importantly related to fundamental differences in the life histories of male and female baboons. By maintaining proximity to older kin, for example, juvenile females increase the likelihood of receiving support during agonistic interactions with females from lower-ranking matriline. Missakian (1972, 1974), Cheney (1977) and others have suggested that for immature female Cercopithecinae close affiliation with adult female kin is important for the acquisition of familial dominance status (see also Massey 1977; Kaplan 1978; Walters 1980; Horrocks & Hunte 1983; Fairbanks & McGuire 1985, 1986; also Sade

1965; Miller et al. 1973; Kurland 1977; Nash 1978; and Ehardt-Seward & Bramblett 1980 document affinity among cercopithecine female kin).

In contrast to females, juvenile male baboons grow to associate at comparable rates with related and unrelated adult females (see also Fairbanks & McGuire 1985). Immature male baboons eventually rise in rank above all adult females in their natal groups (see Lee & Oliver 1979; Pereira 1984) and typically emigrate prior to reproducing (Packer 1979). Consequently, a male's adult status and reproductive success is unlikely to benefit from reciprocally supportive relations with female kin. Males may, in fact, benefit from solo fighting and rank reversal with many unrelated adult females if this experience helps to improve fighting skills, which partly determine relative dominance status and, perhaps, reproductive success among young adult males (Hausfater 1975; Packer 1979). Juvenile males in Amboseli seek and receive little assistance during their fights with adult females, whereas old juvenile females often solicit and receive support from unrelated higher-ranking females and from female kin (Pereira 1984, 1986).

Affinitive interaction with a wide variety of unrelated adult females may also provide experience to facilitate the future attempts of males to reproduce. The juvenile males that I studied sought proximity primarily with cycling adult females, whereas juvenile females more frequently associated with lactating females (see also Cheney 1978a; Pereira 1984 for sex-differentiated patterns of grooming with adult females). Interaction with oestrous females facilitates the development of sexual competence in immature male primates (Hanby & Brown 1974; Owens 1976; Wolfe 1978, 1979; Hopf 1979; Rostal & Eaton 1982). Juvenile males that develop competence in their sexual behavioural repertoire are more likely to reproduce as adolescents and young adults than are males that do not.

The attraction of juvenile females to lactating adult females also creates opportunities to learn behaviour directly related to future chances of reproduction. Virtually the entire burden of infant care rests with adult females in cercopithecine species (Altmann 1980, 1983). Studies of callitricid monkeys have presented data that implicate juvenile interaction with infants or exposure to mother-infant-other interactions for the development of adequate parenting skills (Epplé 1975; Epplé & Katz 1980; Hoage 1977). In the present study, juvenile females were strongly attracted to mothers

and infants, often without any further degree of interaction. Also, the vast majority of the interactions of juvenile females with infants were brief and seemed not to threaten the infants' health (Pereira 1984, unpublished data; see also Cheney 1978b). Data from these studies support the long-standing hypothesis that the attraction of juvenile females towards mothers and infants functions to facilitate interactive and observational learning of care behaviour (Struhsaker 1971; Lancaster 1972; Pereira & Altmann 1985). To evaluate the possible importance of observational learning, it would be valuable to determine whether juvenile females are most likely to watch infants if they are on or near their mothers (Pereira & Altmann 1985).

Rank-related Attraction and Agonistic Support

Juveniles exploited likely sources of support by associating with appropriate group members during periods of frequent or imminent agonistic interaction. For example, young juveniles commonly ran into proximity with their adult male associates when they were harassed by other group members. These adult males agonistically supported young juveniles virtually every time youngsters solicited support from them and many times in the absence of solicitation behaviours per se (Pereira 1984, 1986). An interesting exception to this pattern was that adult males sometimes seemed reluctant to attack adult females on behalf of a young juvenile. Instead, during rare protracted episodes of adult female aggression towards young juveniles, adult males sometimes redirected their aggressive 'support' towards nearby juveniles, adolescents and human observers.

Just as resident adult males support young juveniles almost unconditionally, adult female baboons appear to be ever-ready to support an unrelated female against another from a family ranking lower than both of theirs (Walters 1980; personal observation; see also Horrocks & Hunte 1983). Juvenile females associated with unrelated adult females in a way that increased the availability of this source of agonistic support. When they approached unrelated adult females outside of feeding contexts, they most often approached females from matriline higher-ranking than their own. The two old juvenile females (Lona and Kupima) who were most active in attempting to become dominant to particular adult females from lower-ranking families (Pereira 1984) were those

that associated strongly with adult females from higher-ranking families. The other three old juvenile females exhibited more stable relations with females from lower-ranking families and their attractions towards high-ranking adult females were less remarkable (Fig. 5). Old juvenile males infrequently sought support during fights with unrelated adult females (Pereira 1984, 1986) and did not exhibit clear association preferences for high-ranking females.

An important advantage may accrue for high-ranking adult females who frequently support the efforts of all juvenile females to assume familial dominance status. Their support probably abbreviates the period during which the dominance relations of juvenile females with adult females are unsettled (Pereira 1986). By abbreviating this period, adult females may increase the chance that dominance relations among matriline will remain unchanged (see Samuels & Henrickson 1983; Samuels et al. 1987).

Sex-typical Behaviour, Observational Learning and Behavioural Development

The present data are the first to quantify differential attraction towards same-sex adults in both male and female juvenile non-human primates (but see also Pusey 1983). Whereas cercopithecine juvenile females are known to be attracted towards females with new infants (e.g. Caine & Mitchell 1980), the spacing data presented here reveal an overall attraction of juvenile females towards adult females that exceeds that of juvenile males (cf. Cheney 1978a; Clarke 1978; Handen & Rodman 1980), and an attraction of juvenile males towards adolescent and adult males that has as yet gone undocumented in free-ranging primates (but see Ehardt-Seward & Bramblett 1980; Handen & Rodman 1980).

The social processes that augment and extend possible inherent behavioural sex differences in juvenile non-human primates (see e.g. Young et al. 1982) remain virtually unknown (Pereira & Altmann 1985). The present data support the 'sex-typing' hypothesis that selective attention towards same-sex adults and their interactions is an important component of the development of sex-typical repertoires of social behaviour in baboons, as appears to be true for children (see e.g. Maccoby & Wilson 1957; Maccoby et al. 1958; Slaby & Frey 1975). Juveniles create opportunities to observe

and learn sex-specific behaviour by selectively associating with same-sex adults. Clear instances of juveniles watching same-sex adolescents and adults are often observed during field work with baboons (see also DeBenedictis 1973). For example, I observed a young and an old juvenile male (Sluggo and Spike) watch an adolescent male approach an adult female and rise up to greet her by grasping her hips and lipsmacking. As soon as the adolescent moved off, the young juvenile male ran and approached the adult female to greet her in a manner that was strikingly similar to that used by the adolescent. The old juvenile male watched this greeting as well, and then moved off to feed. Immature primates may tend not only to watch different adults, but also to perceive different aspects of the adult behaviour that surrounds them. Human females, for example, tend not to notice or retain details of aggressive interactions between adult males to the extent that males do (see e.g. Maccoby & Wilson 1957; Kagan & Moss 1962; Bandura 1965; Moore 1966).

The sex-typing hypothesis also helps to explain a puzzling observation concerning cercopithecine adult male relations with juveniles of the two sexes. In this study, adult males tended to displace and elicit submissive behaviour from juvenile females more frequently than from juvenile males per unit of time in proximity (Pereira 1984). Also, old juvenile females approached to feed near feeding adult males less often than did old juvenile males. Dittus (1979) discussed similar results in toque macaques, *Macaca sinica*, and suggested that adult males are selected to favour sons over daughters partly because this would help to prepare sons to survive dispersal and attain mating success in their new social groups. If fathers rarely still reside in groups containing old juvenile offspring, however (as in this study; see also Altmann et al., in press) adult males could not benefit in this way by being less tolerant of females among old juveniles. The sex-typing hypothesis suggests that juvenile male primates are more percipient observers of adult males than are juvenile females. If so, juvenile males probably better anticipate displacement and aggression from adult males and more frequently avoid such interactions. This, in turn, would presumably allow juvenile males to behave more boldly than females around adult males during foraging.

Animals are predisposed to learn particular

types of behaviour (Hinde & Stevenson-Hinde 1973; Pulliam & Dunford 1980), and behavioural ontogeny functions, in part, to facilitate this selective learning and ensure that certain early social experiences are virtually inevitable (Hall 1968; Mason 1979). Over 20 years ago, Hall (1963) and Jolly (1966) suggested social learning as an important mechanism for the development of both social and feeding behaviour in primates, and called for a 'sustained observational and experimental attack' (Hall 1968, page 224) to illuminate the most important factors involved in natural social learning. Only recently, however, have data been collected from natural primate social groups and interpreted with primary regard to the importance of social learning during development (Cambefort 1981; Watts 1985; Whitehead 1986; see also Mineka et al. 1984).

Unequivocal demonstration of the fundamental importance of observational learning in primate development has not yet been accomplished (but see Epple & Katz 1980). The possibility remains, for example, that whereas considerable variability exists in the degree to which juveniles associate as described in this paper, the differential experience attained thereby has no differential effect on survivorship or reproduction. In particular, strong selection pressure may favour immatures that observe and imitate one aspect of the behaviour of similar-looking elders (say, foraging, food selection and processing), while no selective advantage or disadvantage accrues among juveniles in whom this propensity to imitate extends into other domains of behaviour, such as sexual interaction.

Future investigators of development in social behaviour should design studies that can evaluate the potential importance of social learning as a mechanism in behavioural development. An appropriate beginning for non-interventive studies would be to determine whether juvenile males and females selectively watch not only different adult group members but also different types of social interactions, irrespective of the sexes of the participants. Also, many important predictions remain to be evaluated concerning the scheduling of changes in foci of social attention during pre-reproductive development. For example, perhaps young juvenile females are generally attracted to infants, regardless of the infants' proximity to their mothers, but spend little available time gazing at infants from afar (Garipey, Pereira & Strayer, unpublished data,

discuss distant, proximate and interactive visual attention in primates). In contrast, old juvenile females may exhibit strong tendencies not only to interact but also to watch from a distance infants that are near their mothers, and this interest may be particularly strong when third parties initiate interactions with those pairs. By addressing predictions such as these, studies of juvenile visual attention in the field, together with appropriate experimental work, could provide substantial insight into the roles of observational learning in primate behavioural development.

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