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INTERACTIONS OF IMMATURE MALE AND FEMALE BABOONS WITH ADULT FEMALES

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Abstract. Immature males interacted at lower rates than immature females both with their mothers and with unrelated adult females. Immature males interacted with unrelated adult females primarily when the females were sexually cycling, whereas immature females interacted with adult females primarily during lactation. Immature males tended both to groom and to copulate with adult females who ranked lower than their mothers. In contrast, immature females generally groomed and interacted with the infants of adult females who ranked higher than their mothers. It is postulated that some of the differences in the behaviour of immature males and females may be related to differences in the ways in which members of each sex potentially benefit as adults from bonds formed with high-ranking adult females in their natal troops.

At present, more is known about the behaviour of male and female monkeys as adults than about their social development. It is probable, however, that some of the factors which appear to affect the social interactions of male and female monkeys as adults can be shown to be related to the behaviour of each sex as immatures. In this paper, the interactions of free-ranging juvenile and sub-adult baboons with adult females are discussed, and an attempt is made to compare the behaviour of males and females during ontogeny with their behaviour as adults.

In those species of Old World Monkeys such as baboons and macaques that live in multi-male groups, the adult female social structure is usually characterized by a stable, linear dominance hierarchy in which members of the same genealogy share similar ranks. Daughters assume ranks similar to those of their mothers, with younger daughters ranking higher than older daughters (Kawai 1958; Kawamura 1958; Yamada 1963, 1966; Sade 1965, 1967, 1972; Koyama 1967; Missakian 1972; Moore, 1977. Social interactions occur primarily among members of the same matriline, a structural pattern which appears to result from bonds which develop during ontogeny. In addition to the close bonds between related females, however, females often compete among themselves to interact with high-ranking females and their infants, with the result that such 'attractive' high-ranking females usually receive more grooming and interact with a larger number of individuals than do their lower-ranking peers (Gouzoules 1975; Seyfarth 1976, 1977; see also Bernstein & Sharpe 1966; Ok & Maeda 1973).

Close social relationships between related females may be regarded functionally in terms of each individual's inclusive fitness (Hamilton 1964; Alexander 1974), and may be especially adaptive in species where a parent invests heavily in a limited number of offspring, and where the social development of such offspring appears to benefit from the presence of peers and a relatively stable social environment (Harlow & Harlow 1965; Kaufmann 1966; Harlow 1969; Rudran 1973). In addition to selecting for close bonds between blood relations, it is also possible that natural selection confers an advantage on those females who are able to attain high rank. High-ranking female rhesus macaques, for example, raise more offspring to maturity than do their lower-ranking peers (Drickamer 1974).

In contrast, the reproductive success of male monkeys is more variable than that of females. Among multi-male groups of baboons and macaques, males generally emigrate from their natal troops, and may rise and fall in rank several times during adulthood (Kawanaka 1973; Packer 1975, 1977b; Sugiyama 1976). Although access to oestrous females is often positively correlated with rank (Altmann 1962; Hall & DeVore 1965; Kaufmann 1965; Struhsaker 1967, 1975; Hausfater 1975; Bernstein 1976), adult male rank appears to be less stable than female rank, and to depend less upon maternal rank than upon such factors as age, length of stay in the troop, and the ability to form coalitions with other males (Mizuhara 1964; Hall & DeVore 1965; Yamada 1966; Lindburg 1969; Saayman 1971; Boelkins &

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Wilson 1972; Kawanaka 1973; Norikoshi & Koyama 1975; Sugiyama 1976; Bernstein 1976; Packer 1977a). Data on dominance, group transfer, and the nature of bonds between close blood relations therefore suggest that the social behaviour of adult male and female monkeys is fundamentally different. As a result, it might be predicted that members of each sex will show dissimilar propensities to interact with individuals of particular age/sex classes during development.

Methods

A troop of free-ranging baboons (*Papio cynocephalus ursinus*, Thorington & Groves 1970) was observed in the Mountain Zebra National Park, South Africa for 15 months, using instantaneous, focal animal, and behaviour dependent sampling (Altmann 1974). The study area and full details of methods of observation are described in Seyfarth (1976). During the study period, the troop consisted of between 24 and 30 individuals, depending upon births, deaths, and the emigration of sub-adult males. It always included the same two adult males and eight adult females. All seven infants born during the study period were males. Although it was not possible to determine the blood relations of the adults, the mothers and siblings of all but two of the immatures were known.

The adult females in the study troop could be arranged in a stable, linear dominance hierarchy, based on the direction of approach–retreat interactions (Seyfarth 1976). Ranks of immature animals could be predicted on the basis of relative age and maternal rank (Cheney 1977). This paper concerns differences in the behaviour of males and females among the six sub-adults in the troop (five males and one female, estimated ages between 36 and 48 months at the beginning of the study) and the six juveniles (three males and three females, aged between 16 and 20 months). Because the number of juveniles and sub-adults was small, data suggest only some tentative generalizations concerning the social development of members of each sex.

Results: I. Relationships with the Mother

Among macaques, interactions between mothers and their immature daughters usually occur more frequently than those between mothers and their immature sons (Sade 1965; Oki & Maeda 1973). Mother–daughter grooming has also been found to be more reciprocal (i.e. more equally distributed between partners) than mother–son grooming. An immature female's relationships with the female members of her immediate family appear to provide the basis upon which all her other relationships with adult females develop. Familial relationships also affect the social development of immature males. Although males usually emigrate from their natal troops, and therefore do not interact regularly with their blood relations as adults, most of their interactions with individuals in their natal troops occur either with their peers or with members of their immediate families (Miller et al. 1973).

In this section, the relations of juveniles and sub-adults with their mothers are discussed, in order to provide a framework within which interactions between immatures and unrelated (non-maternal) adult females may subsequently be considered.

Grooming

Adult females rarely groomed juveniles and sub-adults other than their offspring (Fig. 1): 91% of all grooming of immatures by adult females involved the grooming of offspring. The exception to this rule was the lowest-ranking adult female (Pat in Fig. 1), who did not appear to have any offspring and regularly groomed apparently unrelated sub-adult males (see below). Immature males and females received grooming from their mothers at rates comparable to each other (Table I). There appeared to be no relation between the frequency with which mothers groomed their

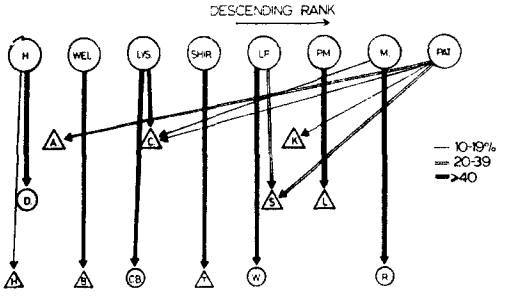

Fig. 1. The proportion of each adult female's total grooming of juveniles and sub-adults which was given to particular individuals. Adult females are arranged at the top of the figure, from 1. to r. in descending rank order. Offspring are arranged vertically beneath their mothers, according to their relative ages: first level (reading down) = older sub-adults, second level = young sub-adults, third level = juveniles. Triangles represent males, circles represent females. Ranks of two of the older sub-adult males (A and K), whose mothers were not known, have been approximated. Data based on instantaneous sampling.

offspring and maternal rank: the two highest-ranking adult females, for example, groomed their juvenile sons the least and the most of all mothers, respectively.

The rate at which each immature animal groomed its mother was higher than the mean rate at which it groomed other, unrelated adult females (Table I). Thus grooming by both adult females and immatures was largely restricted to immediate family members. Mothers with daughters, however, tended to be groomed at higher rates than mothers with sons. Immature females were tested against immature males using a Mann–Whitney *U*-test on the null hypothesis that there was no difference in the rates at which members of each sex groomed their mothers. Results indicated that immature females groomed their mothers at significantly higher rates than did immature males (two-tailed test, $P < 0{\cdot}01$).

Sexual cycling and the formation of sexual consortships by adult males and females did not appear to disrupt rates of grooming between mothers and their offspring (Seyfarth 1978a). Similarly, there did not seem to be any relation between the emigration of sub-adult males and the rate at which their mothers groomed them in the months prior to their departure. The mothers of two of the sub-adult males who emigrated from the troop were known: these mothers groomed their sons neither the least nor the most of all mothers who had sons (Table I).

Friendly Gestures

Eight of the ten immatures whose mothers could be identified received more friendly gestures (touches, hugs, kisses) from their mothers than from unrelated adult females (Table II). Immature males and females received friendly gestures from their mothers at comparable rates. Similarly, seven of the ten immatures gave more friendly gestures to their mothers than to other adult females, and individuals of both sexes gave such gestures to their mothers at similar rates (Table II).

Grooming Solicitations

Among many species of monkeys, the orientation of the flank toward another individual often elicits grooming, and is generally interpreted as a 'solicitation' to receive grooming (Rowell 1972). Juveniles and sub-adults solicited grooming from their mothers more than from other adult females (Table III). Eight of the ten immatures were also more likely to be groomed when they solicited grooming from their mothers than when they did so from unrelated females (Table III).

Although based on a small sample, in eight of ten cases adult females solicited grooming from their offspring more than might have been expected had they solicited grooming equally from the 12 immature animals (Table IV). Immature females received a larger proportion of their mothers' grooming solicitations than

Table I. The Monthly Rates at which Immature Males and Females were Groomed By and Groomed Their Mothers and Unrelated Adult Females. Figures Represent the Mean Number of Instantaneous Samples Per Month, Based on 240 Samples on Each Dyad Each Month. Sub-adult Males Who Emigrated From the Troop are Marked with Asterisks. Two Sub-adult Males (A and K) Whose Mothers Were Not Known Have Been Excluded From Analysis

		Mean monthly rate of grooming received from:		Mean monthly rate of grooming given to:	
	Mother's rank (1 = highest)	mother	each other adult ♀	mother	each other adult ♀
Imm. ♂♂					
H	1	2·1	0·13	0·1	0·03
B	2	16·7	0·02	0·5	0·05
C*	3	8·5	0·55	1·1	0·20
T	4	10·3	0·07	0·3	0·03
S*	5	8·6	0·27	1·2	0·28
L	6	11·3	0·10	0·7	0·20
Imm. ♀♀					
D	1	11·2	0·10	2·3	0·30
CB	3	10·5	0·10	2·1	0·90
W	5	13·1	0·01	2·7	0·04
R	7	8·1	0·15	1·8	1·10

Table II. The Mean Number of Friendly Gestures Received and Given by Immature Males and Females to their Mothers and to Unrelated Adult Females Each Month. Two Sub-adult Males whose Mothers Were Not Known Have Been Excluded From Analysis. Data Based on Focal Animal Plus Behaviour Dependent Sampling

		Mean monthly no. of fr. gest. received from:		Mean monthly no. of fr. gest. given to:	
	Mother's rank (1 = highest)	mother	each other adult ♀	mother	each other adult ♀
Imm. ♂♂					
H	1	0·4	0·2	0·1	0·4
B	2	0·7	0·2	1·1	0·2
C	3	0·2	0·3	0·3	0·8
T	4	0·8	0·2	0·6	0·1
S	5	0·2	0·1	0·6	0·4
L	6	0·5	0·1	0·7	0·4
Imm. ♀♀					
D	1	0·4	0·3	0·7	0·6
CB	3	0·6	0·6	0·8	0·6
W	5	0·6	0·4	0·4	0·1
R	7	0·7	0·5	0·2	0·5

Table III. The Proportion of Immature Grooming Solicitations Given to Mothers, and the Proportion of Solicitations Resulting in Grooming. Two Sub-adult Males Whose Mothers Were Not Known Have Been Excluded From Analysis. Data Based on Focal Animal Plus Behaviour Dependent Sampling

			% of solic. resulting in gr. when given to:	
	N = total gr. solic.	% of gr. solic. given to mother	mother	other adult ♀♀
Imm. ♂♂				
H	19	74	79	60
B	42	98	85	0
C	29	86	84	75
T	38	92	100	67
S	34	85	86	80
L	46	98	91	100
Imm. ♀♀				
D	64	83	94	82
CB	39	79	90	75
W	71	99	81	100
R	43	62	91	75

did immature males. Data on grooming solicitations were therefore comparable to those on grooming, suggesting that affinitive interactions occurred predominantly between family members, and that immature females interacted more with their mothers than did immature males.

Interactions with Infant Siblings

Nine of the 12 juveniles and sub-adults had infant siblings who were observed during their first 18 weeks of life. For all nine immatures, the rate of friendly gestures given to infant siblings was higher than the mean rate of friendly gestures given to unrelated infants of their siblings' age (Table V). Immature females interacted more with their infant siblings than did immature males.

No mother was ever observed to avoid her own offspring when her offspring attempted to interact with her infant, although mothers did avoid many of the friendly gestures of other juveniles and sub-adults (see below).

Table IV. The Proportion of Each Adult Female's Grooming Solicitations Given to Her Offspring. Expected Values Represent the Proportion of Solicitations that Offspring Would have Received if Females Had Distributed their Solicitations Equally Among the 12 Immatures. Data Based on Focal Animal Plus Behaviour Dependent Sampling

Adult ♀♀	N = total gr. solic.	% of grooming solicitations given to offspring			
		To daughters		To sons	
		Obs.	Expected	Obs.	Expected
H	4	100	8·3	0	8·3
Wel	13	—	—	15	8·3
Lys	6	33	8·3	17	8·3
Shi	5	—	—	0	8·3
LP	16	25	8·3	19	8·3
PM	4	—	—	50	8·3
M	7	14	8·3	—	—

Discussion

Within families, the behaviour of mothers appeared to be an important factor contributing to the high rate of interaction between immatures of both sexes and their infant siblings. While mothers of young infants often avoid the approaches of juveniles and sub-adults (Lancaster 1971; Ransom & Rowell 1972; Breuggeman 1973), both Kaufmann (1966) and Spencer-Booth (1968) have observed that rhesus monkey mothers avoid their own offspring less than other immatures. Mothers in the study troop were never observed to avoid their offspring, even though they often avoided unrelated immatures.

In the case of immature females, data on intrafamilial interactions may provide some evidence of the means by which females are gradually integrated into the adult female social structure. The higher rates of interaction between mothers and daughters, as opposed to mothers and sons, probably contribute to the formation and maintenance of close social bonds among adult females of the same matriline (Sade 1965; Oki & Maeda 1973; Fox 1975).

In contrast, all immature males, including those juveniles who would probably remain in their natal troop for two or more years, interacted less often and in a less reciprocal manner with their mothers and infant siblings than did females. It is possible, therefore, that the relatively infrequent interactions between immature males and their mothers may have been not only illustrative of, but also causal to, the gradual process of male peripheralization from the natal troop (see also Breuggeman 1973).

Itoigawa (1975) could predict when male Japanese macaques would become peripheral to the social group by the frequency with which they associated with their mothers up to two years preceding their departure from the central part of the troop: males who interacted infrequently with their mothers became peripheral before peers who interacted with their mothers regularly. Moreover, the sons of low-ranking females generally became peripheral before the sons of high-ranking females (see also Yamada 1966). Although the present study was of shorter duration than Itoigawa's, sub-adult male baboons who emigrated from the troop did not appear to receive less maternal grooming than males who remained, nor did any evidence suggest that low-ranking males left the troop before their higher-ranking peers. On the contrary, the relationships of emigrant males with their

Table V. The Number of Friendly Gestures Given by Immatures to Infant Siblings and to Other Infants. Figures Represent the Total Number of Friendly Gestures Given to Infants in Their First 18 Weeks of Life. Only Those Individuals Whose Infant Siblings Were Observed Throughout Their First 18 Weeks of Life are Included in the Analysis. Data Based on Focal Animal Plus Behaviour Dependent Sampling

Imm. ♂♂	N = total fr. gest. to infs.	No. of fr. gest. to inf. siblings	Mean no. of fr. gest. to each other inf.
Imm ♂♂			
H	19	7	2·0
B	12	8	0·7
C	17	5	2·0
T	14	7	1·2
S	12	10	0·3
L	26	10	2·7
Imm. ♀♀			
D	201	75	21·0
CB	307	75	38·7
W	72	32	6·7

mothers did not appear to differ from those of males who remained, an observation also supported by data on some groups of Japanese and rhesus macaques (Drickamer & Vessey 1973; Sugiyama 1976). It is probable, therefore, that factors related to male emigration are to be sought also in the nature of adolescent males' relationships with individuals other than the mother.

Results: II. Relationships with Unrelated Adult Females

The Frequency of Interactions

(1) Presenting and grooming solicitations.

Presenting, or orienting the rump towards another individual, is generally considered to contain motivational elements of submission or conciliation on the part of the presenter (Rowell

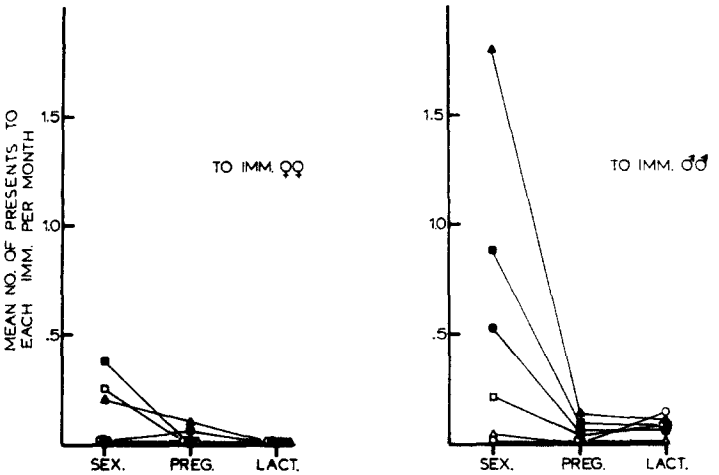

Fig. 2(a)

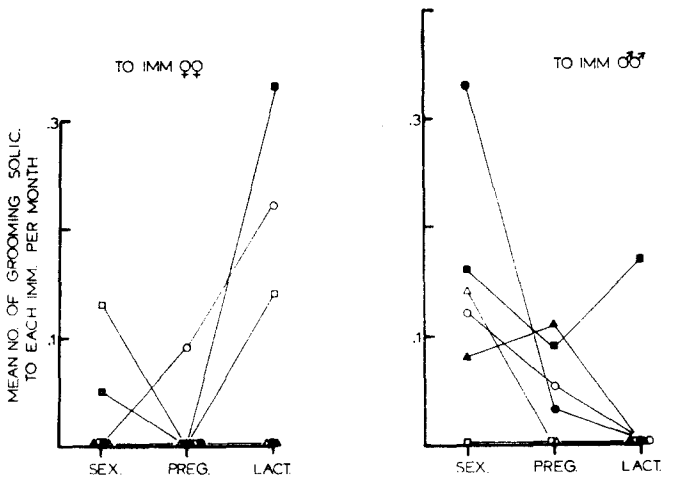

Fig. 2(b)

Fig. 2. Mean monthly rates at which six adult females (a) presented to, and (b) solicited grooming from each unrelated immature male and female while sexually cycling, pregnant, and lactating. All adult females included in the analysis spent approximately equal lengths of time in each reproductive state. Data based on the 11 months preceding the emigration of four sub-adult males, and on focal animal plus behaviour dependent sampling.

1972). If the presenting individual is a sexually receptive female, the behaviour is usually interpreted as a sexual invitation (Marler 1965; Rowell 1972). Adult females in the study troop presented primarily to immature males rather than to immature females, and they did so at the highest rate while sexually cycling (Fig. 2(a)).

Adult females also solicited grooming from immature males at the highest rate while sexually cycling (Fig. 2(b)). They solicited grooming from immature females, however, primarily during lactation. Adult females therefore appeared to initiate interactions with unrelated immature males and females differently, according to changes in their reproductive state.

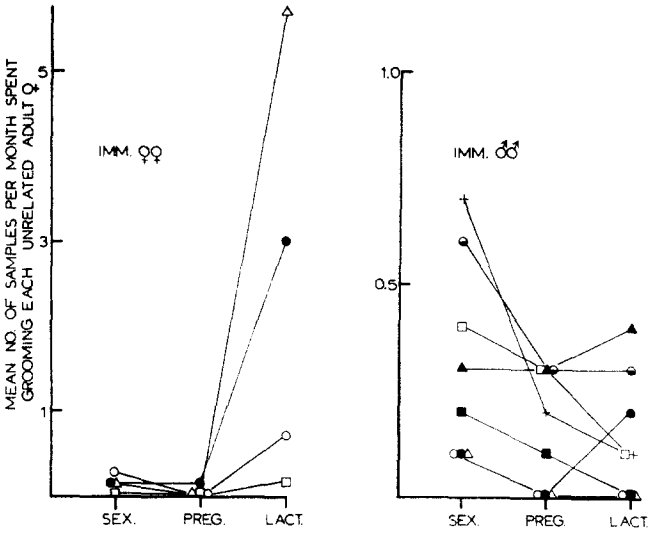

Fig. 3(a)

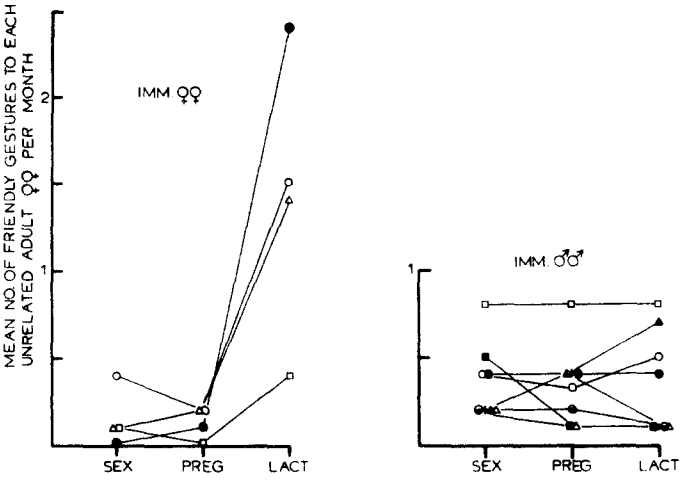

Fig. 3(b)

Fig. 3. Mean monthly rates at which immature males and females (a) groomed and (b) gave friendly gestures to each of six unrelated adult females while the females were sexually cycling, pregnant, or lactating. Legend as in Fig. 2. (a) Based on instantaneous sampling, and (b) based on focal animal plus behaviour dependent sampling.

(2) Grooming. Three of the four immature females groomed adult females other than their mothers at a higher rate than did all immature males (Table I). Changes in the reproductive state of adult females also appeared to affect the frequency with which immature males and females groomed unrelated adult females. Most males groomed adult females primarily when the females were sexually cycling, while immature females groomed adult females almost entirely during lactation (Fig. 3(a)).

(3) Friendly gestures. While immature males and females gave friendly gestures to unrelated adult females at comparable rates (Table II), the occurrence of such gestures appeared to vary depending on the adult female's reproductive state. While most immature males gave friendly gestures to adult females other than their mothers at approximately the same rate in all reproductive states, immature females gave the majority of their friendly gestures to adult females when the females were lactating (Fig. 3(b)). In this respect, the behaviour of immature females resembled that of adult females, who gave 88% of their friendly gestures to lactating females (Seyfarth 1976).

Interactions with Individual Adult Females

Immature males and females differed markedly in the distribution of their grooming among unrelated adult females. All immature females gave a larger proportion of grooming to the adult females who ranked higher than their own mothers than to those who ranked lower than their own mothers (Fig. 4). In contrast, all immature males gave a larger proportion of their grooming to the adult females who ranked lower than their own mothers (Fig. 4).

The discrepancy in the behaviour of immature males and females becomes more apparent when other patterns of behaviour related to the distribution of grooming are considered. Immature males not only groomed, but also copulated, with adult females of low rank more than with those of high rank (Fig. 5). This was especially the case for the two lowest-ranking adult females (M and Pat in Fig. 5). Even though all females spent a similar amount of time sexually cycling, 65% of all observed copulations by immature males occurred with these two females. Moreover, 71% of all non-maternal grooming by immature males was given to these two females. The same females were also the only two adult females who regularly groomed sub-adult males other than their offspring (Fig. 1). Thus the largest proportion of immature male grooming was given to sexually cycling females, and such females tended to be low-ranking females with whom the males also copulated.

In contrast, immature females groomed unrelated adult females predominantly during lactation, and gave the majority of their non-maternal grooming to individuals to whose infants they also gave friendly gestures (Fig. 6). These adult females were usually either females who ranked higher than the immatures' own mothers, and/or females who ranked adjacent to their mothers and with whom their mothers most often interacted (Seyfarth 1976).

Fig. 4. Mean proportion of each immature animal's total grooming of unrelated adult females which was given to each female who ranked higher or lower than the immature's own mother. The son and daughter of the highest-ranking adult female have been excluded from analysis. Data based on instantaneous sampling.

The Distribution of Immature Male Grooming and Copulation

(1) Competition from other males. Immature males both groomed and copulated more with adult females who ranked lower than their own mothers than with higher-ranking females. Although competition from other individuals did not obviously appear to restrict the access of immature males to adult females, there was indirect evidence that the presence of adult males inhibited the ability of immature males to copulate, and perhaps also to groom, with particular adult females.

In this study, copulations were defined as mounts with insertion. This definition therefore included mounts by juvenile males, who were probably not yet capable of ejaculation. Both sub-adult and juvenile males not only copulated less than adult males but were also less likely to copulate when conceptions were most likely. The troop's two adult males accounted for 49% and 15% of the 658 observed copulations, with over 95% of all copulations by each male occurring with fully swollen oestrous females. In contrast, no immature male accounted for more than 10% of all copulations, with only 69% of all sub-adult male and 54% of all juvenile male copulations occurring during the females' swollen stage.

There was little overt competition between adult and immature males for access to oestrous females: such interactions comprised only 5% of all agonistic interactions between adult and immature males. Despite the absence of overt competition, two sorts of data indicated that the access of immature males to sexually receptive females was restricted by adult males. First, only a small proportion of copulations by immature males involved the adult females with whom the alpha male most often interacted: the third-ranking adult female (Lys in Fig. 5), and, to a lesser extent, the fourth- and fifth-ranking adult females (Shi and LP in Fig. 5)

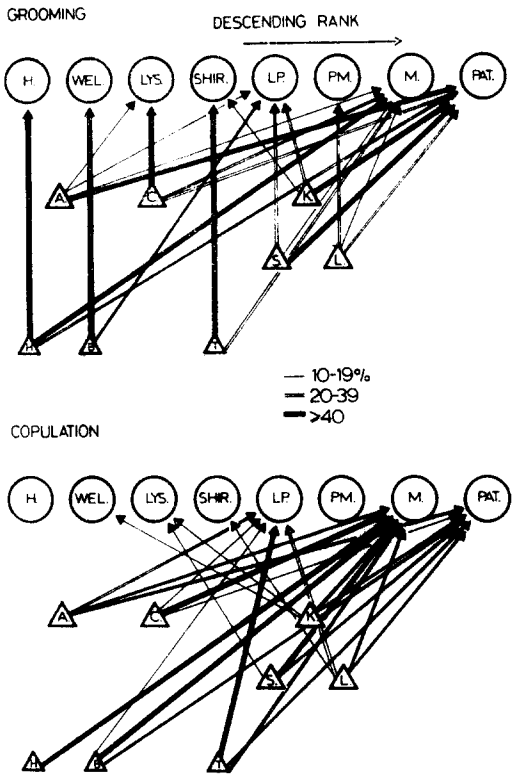

Fig. 5. The proportion of each immature male's total grooming of adult females which was given to particular individuals, and the proportion of each male's total copulations with adult females that occurred with particular individuals. Legend as in Fig. 1. Grooming based on instantaneous sampling, copulations based on focal animal plus behaviour dependent sampling.

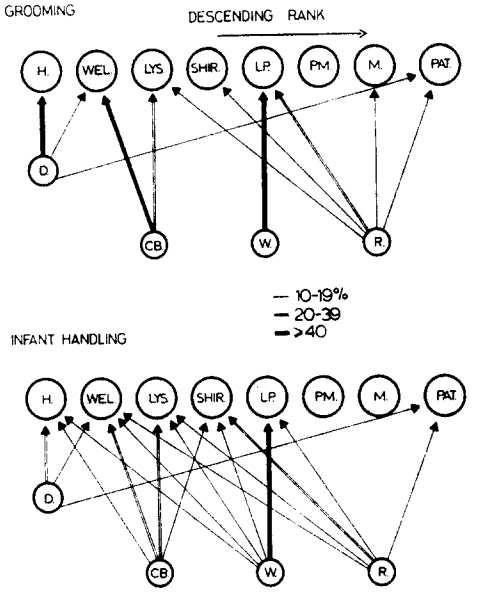

Fig. 6. The proportion of each immature female's total grooming of adult females which was given to particular individuals, and the proportion of each immature female's total friendly gestures to infants aged 18 weeks or less which was given to the infant of each adult female. Legend as in Fig. 1. Grooming based on instantaneous sampling, friendly gestures based on focal animal plus behaviour dependent sampling.

(Seyfarth 1978b). Second, of the 238 copulations by immature males, only 11% occurred after one of the two adult males had copulated even once with the oestrous female concerned, and no copulations by immature males were ever observed after either adult male had established a sexual consortship.

Throughout the study, competition from high-ranking adult females appeared to limit the access of low-ranking females to the troop's alpha male (Seyfarth 1978b). Perhaps as a result, low-ranking adult females presented to immature males while sexually cycling at a higher rate than did high-ranking adult females (Table VI). Thus competition from adult males did not solely determine the distribution of immature male interactions with adult females; many of the interactions between immature males and low-ranking females were initiated by the females themselves.

(2) The rate at which immature males copulated. By calculating the number of days that each female was observed while fully swollen, it was possible to determine the rate at which each immature male copulated per swollen female-day, when conception was most likely to have occurred. Mothers were excluded from the analysis, since no copulations between mothers and sons were ever observed in this study (see also Sade 1968; Missakian 1973).

Although the rate at which immature males copulated was not significantly correlated with rank, all three of the high-ranking, older sub-adult males copulated at a higher rate than did other immature males (Table VII). Data on the immature males' rates of copulations therefore partially support data on adult male baboons collected by Hausfater (1975), and they suggest that, even among immatures, copulation rates may be positively correlated with rank.

Table VI. Mean Monthly Rates at Which Adult Females Presented to Immature Males while Sexually Cycling. Spearman Correlation Illustrates the Extent to which Rates of Female Presenting Were Inversely Correlated With Female Rank. Only Those Females Who Spent Approximately Equal Lengths of Time Sexually Cycling During the 11 Months Preceding the Emigration of Sub-adult Males Are Included in the Analysis. Data based on Focal Animal Plus Behaviour Dependent Sampling

Adult ♀♀	Rank (1 = highest)	Monthly rate of presenting to immature ♂♂ while sexually cycling
Wel	2	0
Lys	3	0·3
Shi	4	1·5
LP	5	3·7
M	7	14·4
Pat	8	7·0

$r_s = -0.943$; $P < 0.02$ (two-tailed).

The Interactions of Immature Females with Adult Females and Their Infants

The attraction of immature females to infants appeared to be the primary factor causing them to interact with adult females other than their mothers (see above). Among most non-human primate species, nulliparous females are more attracted than males to infants, and often spend large portions of time attempting to carry, hug, groom, or play with them, Such care-giving behaviour, termed 'aunt' behaviour by Rowell et al. (1964), occurs among macaques (Sade 1965; Kaufmann 1966; Spencer-Booth 1968; Rosenblum 1971; Breuggeman 1973), langurs (Jay 1965), black and white colobus monkeys (Leskes & Acheson 1971; Hill 1972; Struhsaker & Oates 1975), vervets (Struhsaker 1971; Lancaster 1971), baboons (DeVore 1963; Ransom & Rowell 1972; Owens 1975), chimpanzees (Goodall 1968), and gorillas (Fossey 1976).

Immature female interactions with infants carry potential benefits to both females and infants. For immature females, such interactions provide practice in care-giving behaviour before they produce infants of their own, while for infants interactions with individuals other than the mother probably facilitate the development of independence in a gradual, relaxed manner (Kaufmann 1966; Harlow 1969; Rudran 1973). Regular interactions between nulliparous females and infants are likely to be especially adaptive to both infants and females if the immature care-givers are related to the infants (Hamilton 1964; Hrdy 1976), and in the study troop, as among most primates, immature females interacted more with their infant siblings than with other infants (see above; see also Kaufmann 1966; Spencer-Booth 1968; Goodall 1968; Ransom & Rowell 1972; Breuggeman 1973).

In addition to the attraction of immature females to infant siblings, data from the present study suggested that immature females attempted to interact with the infants of high-ranking adult females more than with those of low-ranking adult females. As discussed below, such interactions may have permitted immature females to establish relationships with the members of high-ranking families, thereby potentially deriv-

Table VII. The Rate at Which Immature Males Copulated as a Function of the Availability of Oestrous Females in the Troop. Spearman Correlation Illustrates the Extent to Which Copulation Rates Were Positively Correlated With Immature Male Rank. Data Based on Focal Animal Plus Behaviour Dependent Sampling

Imm. ♂♂		Rank (1 = highest)	N = no. of swollen ♀-days	Daily rate of copulation
Older sub-adults	A	1	202	0·30
	C	2	161	0·17
	K	3	202	0·10
Younger sub-adults	S	4	170	0·05
	L	5	202	0·03
Juveniles	H	6	202	0·04
	B	7	179	0·07
	T	8	188	0·05

$r_s = 0{\cdot}671$ NS

ing some of the benefits associated with high rank.

(1) Interactions with infants and their mothers. Immature females differed from immature males in the number of friendly gestures they gave to infants; every immature female gave more friendly gestures to infants than every immature male (Fig. 7; Mann–Whitney U-test, two-tailed, $P < 0{\cdot}004$). Interactions between immature females and infants not only occurred more often but also were qualitatively different from those between immature males and infants. These differences are best considered by examining the interactions of immature males and females with mothers and infants of particular rank.

Kaufmann (1966), observing rhesus monkeys, and Struhsaker (1971), studying vervets, found few correlations between a mother's rank and the number of friendly approaches she and her infant received from other animals. If anything, low-ranking mothers and their infants were approached more often than others, possibly because low-ranking mothers were less likely

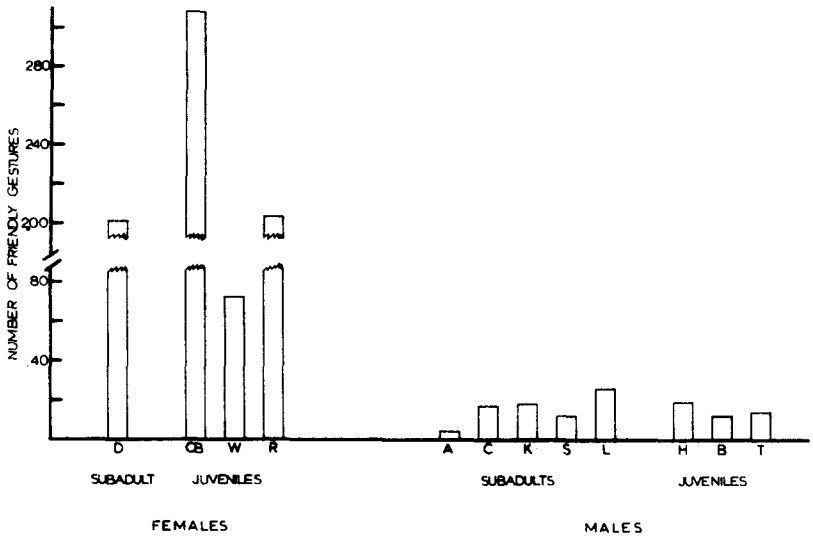

Fig. 7. The total number of friendly gestures given by each immature male and female to seven infants in their first 18 weeks of life. Data based on focal animal plus behaviour dependent sampling.

than their higher-ranking peers to avoid immature animals. Although the number of immature females in this study was small, data suggest that, contrary to the observations of Kaufmann and Struhsaker, immature female baboons were attracted to the infants of high-ranking, rather than low-ranking, adult females. When interacting with infants other than their siblings, immature females gave most friendly gestures to the infants of adult females who ranked higher than their mothers, while immature males showed no preference for infants of high-ranking adult females as opposed to others (Fig. 8).

Interactions with infants also tended to bring immature females, more than immature males, into direct contact with unrelated adult females. During their infants' first 18 weeks of life, unrelated mothers avoided 9% of immature male, and 9% of immature female, friendly gestures to their infants. Despite the fact that immature males and females were avoided at similar rates, immature females generally 'appeased' unrelated mothers (by touching, grooming, or presenting to them when they handled their infants) at higher rates than did immature males (Table VIII; see also Struhsaker 1971; Lancaster 1971; Breuggeman 1973). Thus immature females were more likely than immature males to interact with the mothers of infants. Furthermore, during the infants' first 6 weeks of life, immature females appeased mothers who ranked higher than their own mothers at a higher rate than they appeased lower-ranking mothers (Table IX). There was no correlation between rates of immature male appeasement gestures and the ranks of infants' mothers, nor was there any relationship between a mother's rank and the frequency with which she avoided immature animals.

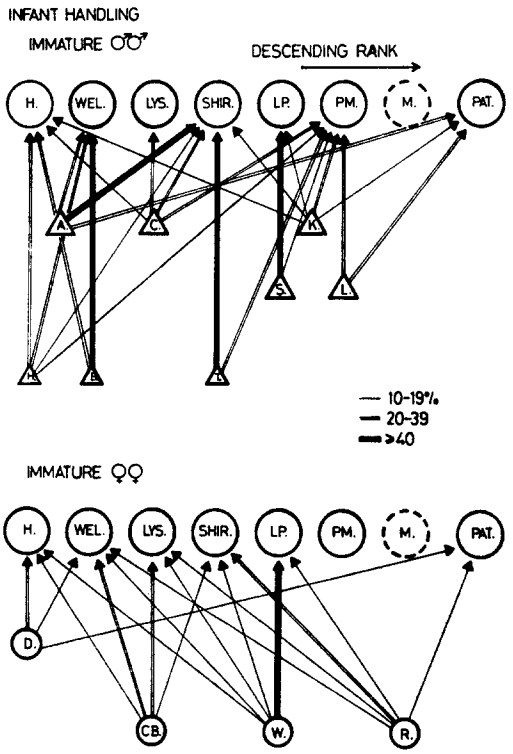

Fig. 8. The proportion of each immature male's and each immature female's friendly gestures to infants which was given to the infants of particular adult females. Legend as in Fig. 1. Data based on focal animal plus behaviour dependent sampling.

(2) Agonistic interactions over access to mothers and infants. While the ranks of juveniles and sub-adults appeared to be dependent upon relative age and maternal rank rather than sex (Cheney 1977), immature females were involved in more agonistic interactions with other immature females than with immature males, and vice versa (Table X). This may have been due in part to the fact that agonistic interactions

Table VIII. The Rate at Which Immatures Appeased Unrelated Mothers When Giving Friendly Gestures to Infants Under 18 Weeks. Rate of Appeasement was Calculated as follows:

No. of friendly gestures to infants accompanied by grooming, friendly gestures, or presenting to infants' mothers

Total no. of friendly gestures to infants

Data Based on Focal Animal Plus Behaviour Dependent Sampling

	N = no. of fr. gest. to unrelated infs.	Mean rate of appeasement of unrelated mothers
Imm. ♂♂		
H	12	8%
B	4	0
C	12	8
T	7	0
S	2	0
L	16	19
Imm. ♀♀		
D	126	16
CB	232	20
W	40	20
R	203	33

Table IX. The Rate at Which Immature Females Appeased Mothers Higher- and Lower-Ranking Than Their Own During Infants' First Six Weeks of Life. Legend as in Table VIII. The Daughter of the Highest-ranking Adult Female is Excluded From Analysis

Imm. ♀♀	No. of fr. gest. to infants of: higher-ranking mothers	No. of fr. gest. to infants of: lower-ranking mothers	Mean rate of appeasement: higher-ranking mothers	Mean rate of appeasement: lower-ranking mothers
CB	30	30	0·50	0·23
W	3	2	0·67	0·50
R	45	11	0·33	0·27

involving the members of each sex occurred in different social contexts.

The social context of an agonistic interaction was defined in terms of the behaviour of the two individuals involved immediately prior to the interaction and the presence of other individuals during the interaction. Table XI lists the most common contexts of agonistic interactions involving immatures. A high proportion of agonistic interactions involving immature females occurred as they competed with others over access to mothers and infants. In this respect, the behaviour of immature females resembled that of adult females, whose agonistic interactions most often concerned access to mothers and infants (Seyfarth 1976). While only a small proportion of the agonistic interactions of immature males occurred in this context, more male than female agonistic behaviour occurred during play. Agonistic interactions between immature and adult females usually concerned either access to mothers and infants or the aiding of the recipient of an aggressive act. In contrast, agonistic interactions involving adult females and immature males seldom concerned access to social objects.

Table X. The Mean Number of Each Immature's Agonistic Interactions Which Involved Immature Males and Females. Data Based on Focal Animal Plus Behaviour Dependent Sampling

	Mean number of agonistic interactions with each: imm. ♂	imm. ♀
Imm. ♂♂		
A	20·7	8·8
C	15·1	12·8
K	17·4	8·0
S	12·4	7·8
L	23·9	23·0
H	18·1	14·3
B	13·9	11·3
T	15·3	10·3
Imm. ♀♀		
D	11·9	31·0
CB	11·3	28·3
W	13·9	27·7
R	11·0	15·0

(3) Competition over access to high-ranking mothers and infants. Although a large proportion of the agonistic interactions involving immature females concerned access to mothers and infants, competition from peers appeared to affect the access of high-ranking immature females less than that of low-ranking immature females. For example, R, daughter of the seventh-ranking adult female, was threatened and supplanted from infants and their mothers by her peers more often than was CB, daughter of the third-ranking adult female (Fig. 9). Possibly as a result, R gave fewer friendly gestures to infants than did CB. Moreover, since R was threatened and supplanted from some infants more than others, competition seemed to affect the distribution of her friendly gestures. Although both R and CB were threatened and supplanted most from the infants of the two highest-ranking mothers, for CB such agonistic interactions occurred only rarely relative to the total number of friendly gestures she gave to the infants. In contrast, R gave most friendly gestures to the infant from whom she was threatened and supplanted least. In other words, competition met by R when she attempted to interact with particular infants appeared to limit her interactions with them, and she consequently gave such infants fewer friendly gestures than she gave to infants to whom access was relatively unrestricted.

It is difficult to determine how frequently an individual must be threatened or supplanted from a resource before such behaviour causes the individual to attempt to gain access to an alternative resource, although even a single interaction may potentially alter the course of

Table XI. The Three Most Common Contexts of Agonistic Interactions Involving Immatures. Data Exclude Agonistic Interactions With Adult Males, and Are Based on Focal Animal Plus Behaviour Dependent Sampling

Actor	Recipient	N = total agon. inter.	Aiding others	Over access to M. & inf.	In play
Sub-adult ♂♂		615	4%	7%	13%
Juvenile ♂♂	Other	178	2	15	15
Sub-adult ♀	Immatures	139	8	41	12
Juvenile ♀♀		84	5	44	11
Sub-adult ♂♂		198	12	1	4
Juvenile ♂♂	Adult ♀♀	25	—	4	24
Sub-adult ♀		92	40	13	4
Juvenile ♀♀		45	58	10	4
Adult ♀♀	Immature ♂♂	289	30	22	2
	Immature ♀♀	272	10	62	4

future interactions (Simpson 1973). The significance of the total threats and supplants received by R as opposed to CB is therefore difficult to measure precisely. It seems clear, however, that immature females did attempt to interact with the infants of high-ranking mothers, that each was occasionally constrained by competition from her peers, and that the social interactions of low-ranking immature females were therefore more restricted than those of their higher-ranking peers.

(4) The distribution of friendly gestures among infants: a hypothetical model. The data presented above indicate, at the very least, that the access of low-ranking individuals to other animals may be constrained by their higher-ranking peers. Taking the argument one step further, it is possible to hypothesize that in any group of monkeys competition among animals for access to particular individuals will result in a predictable distribution of social interactions. This hypothesis is developed further below.

Among the adult females in the study troop, both an individual's 'attractiveness' (as measured by the total amount of grooming received) and her access to others were positively correlated with rank (Seyfarth 1976). As a result, when a female distributed grooming among those ranking lower than herself, she received little competition, and groomed them in direct relationship to their ranks. When she attempted to gain access to higher-ranking females, however, she appeared to meet the most competition for the highest-ranking female, and the least competition for the female ranking immediately above herself. Thus preference for high-ranking females and the social constraints which limited the expression of these preferences combined to perpetuate grooming between females of adjacent rank, and to inhibit the formation of bonds between females of widely disparate ranks (see also Seyfarth 1977). Since females of adjacent rank are often close blood relations (Sade 1965, 1967, 1972; Koyama 1967; Missakian 1972; Moore 1977), the combination of competition and the attractiveness of high rank may also reinforce and contribute to the persistence of close bonds between members of the same genealogy.

A similar combination of rank-related attractiveness and restricted access may have influenced the behaviour of immature females when they interacted with infants. If such factors did affect the distribution of immature female friendly gestures, the following pattern of interactions might be expected to emerge. First, because of the close bonds that existed between mothers and their offspring, and because immature animals were never avoided by their mothers, immature females might be expected to interact most often with their infant siblings. Second, since the infants of high-ranking mothers appeared to be most attractive, immature females might be expected to interact more with the infants of adult females who ranked higher than their mothers than with the infants of lower-ranking adult females. Third, however, for some immature females access to the infants of high-ranking mothers might be expected to be restricted by competition from other females. Immature females might therefore be expected to meet most competition when attempting to interact with the infant of the highest-ranking mother, and least when attempting to interact

with the infant of the mother ranking immediately above their own mothers. As a result, immature females might be expected to interact with infants of mothers higher ranking than their own in inverse relationship to the ranks of the infants' mothers. Finally, all infants of mothers lower-ranking than the immature females' own mothers might be expected to receive fewer friendly gestures than all infants of higher-ranking mothers. Such infants, however, would probably be attractive in direct relationship to their mothers' ranks, and friendly gestures to them might therefore be expected to be distributed accordingly.

Given these assumptions, Fig. 10 illustrates the predicted distribution of friendly gestures among infants by two hypothetical juvenile females, the daughters of the third- and fifth-ranking adult females in a troop including six adult females and their infants.

Figure 11 compares the actual distribution of immature friendly gestures among five infants with the distribution predicted by the model. Of the four females only one, the daughter of the highest ranking adult female, failed to behave as predicted by the model, and then only because she interacted more than was predicted with the infant of the lowest-ranking adult female. In contrast, immature males distributed their friendly gestures to infants in no discernable pattern. Unless the infants were their siblings, males did not seem to be attracted to the infants of high-ranking mothers, and did not compete for access to them.

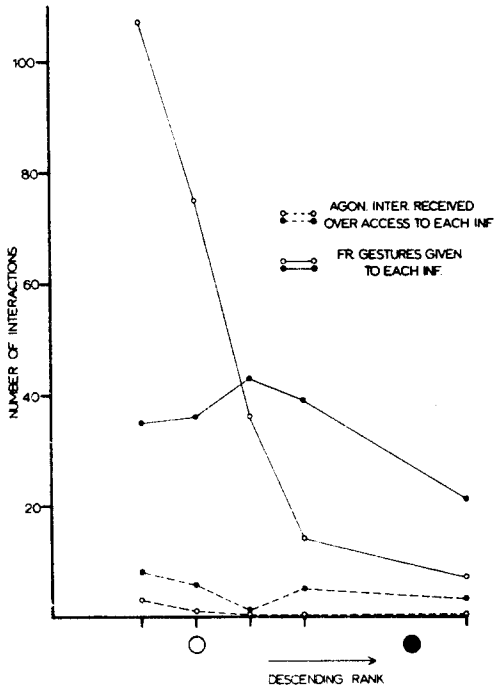

Fig. 9. The number of friendly gestures given by two juvenile females to each of five infants (solid line), and the number of times that each female was threatened or supplanted by her peers from each of the infants (broken line) during the infants' first 18 weeks. Reading from l. to r., marks on the *X*-axis represent infants of the second, third-, fourth-, fifth-, and eighth-ranking adult females. All infants were born within two months of each other. Each juvenile female is represented by a circle, placed immediately below the *X*-axis according to the rank of her mother. Daughter of the third-ranking adult female is represented by open circles; daughter of the seventh-ranking adult female by closed circles. Data based on focal animal plus behaviour dependent sampling.

Discussion

(1) The role of infants in the formation of social relationships. For both immature and adult females, infants appear to constitute a major mechanism for the formation of social relationships. While the attraction of adult females to infants creates opportunities for mothers to interact with high-ranking females (Weisbard & Goy 1976; Seyfarth 1976), the attraction of

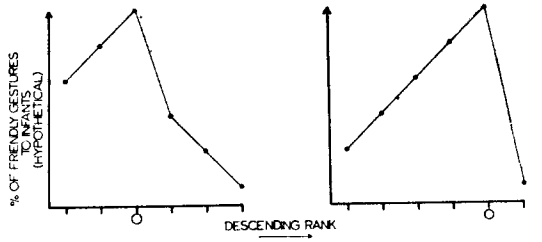

Fig. 10. A theoretical distribution of friendly gestures by two juvenile females, daughters of the third- and fifth-ranking adult females in a troop containing six infants. The distribution assumes that (a) immature females will give most friendly gestures to their infant siblings, (b) they will give friendly gestures to the infants of adult females who rank higher than their own mothers in inverse relationship to the infants' mothers' ranks, and (c) while all infants of adult females ranking lower than the immature females' own mothers will receive fewer friendly gestures than the infants of higher-ranking adult females, immature females will give friendly gestures to such infants in direct relationship to their mothers' ranks. Each mark on the *X*-axis represents an infant, arranged from l. to r. in descending maternal rank order. Each juvenile female is represented by a circle, arranged on the *X*-axis according to the rank of her mother.

immature females to infants brings them into regular contact with unrelated adult females and may facilitate their integration into the adult female social structure. Infants may therefore promote interactions between females who might not otherwise associate regularly, and may permit individuals to establish relationships with high-ranking females which persist even after infants mature (Weisbard & Goy 1976).

In species of Old World Monkeys where males assume an active role in group formation and maintenance, males may also take an active role in the care of infants. Young adult male hamadryas baboons 'adopt' juvenile females, and provide a focal point for infant play (Kummer 1968). Among gelada baboons, bachelor groups are often a focus of activity for immature animals from one-male units, and much carrying of infants is done by males (Bernstein 1975). Such care-giving behaviour should be distinguished from 'agonistic buffering' (Deag & Crook 1971), since the latter has been defined only in terms of specialized behavioural contexts. Presumably it permits males to develop bonds with infants, and perhaps also with the infants' mothers, and may facilitate the recruitment of females to young adult males (see also Ransom & Ransom (1971) and Seyfarth (1978b) for discussions of the relationships between adult male cynocephalus baboons and infants.

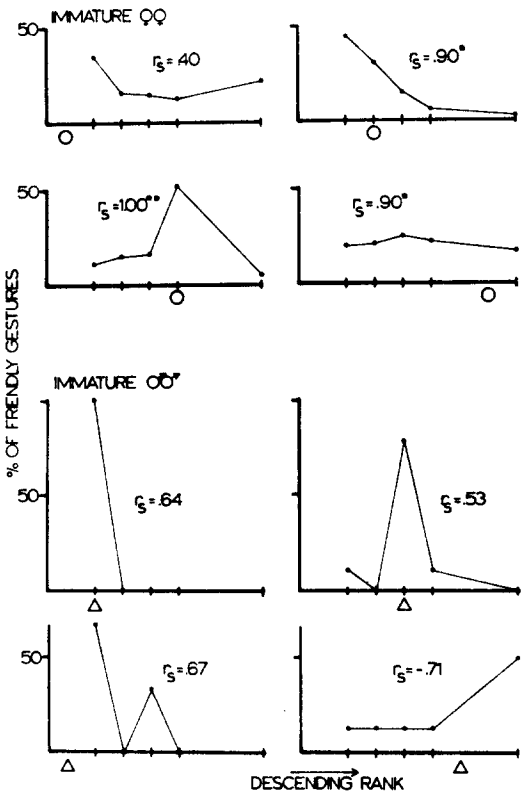

Fig. 11. The proportion of four immature females' and four immature males' friendly gestures to five infants which was given to particular individuals. Spearman correlations illustrate the extent to which the actual distribution of each immature's friendly gestures was correlated with the theoretical distribution illustrated in Fig. 10. * = $P < 0{\cdot}05$, ** = $P < 0{\cdot}01$, one-tailed. Data based on friendly gestures to infants 18 weeks old or younger, all born within two months of each other. Reading l. to r., marks on the *X*-axis represent infants of the second-, third-, fourth-, fifth-, and eighth-ranking adult females. Each immature is represented by a triangle (males) or circle (females), arranged beneath the *X*-axis according to the rank of his or her mother. Data exclude the immature males who emigrated from the troop.

For both males and females, therefore, infants may provide a means by which groups are established, and by which the stability of a group's social structure may be perpetuated across generations. Interactions with infants appear to be particularly important for the members of that sex which, as adults, provides the stable core of the social group, or which contributes to the group's formation and maintenance.

(2) The attractiveness of high rank. Among baboons and macaques, most social interactions occur among related individuals who share similar ranks. Kin-based preferences, however, also occur in conjunction with preferences for those of high rank. As adults, the members of high-ranking families not only compete more successfully than others for access to scarce resources but also often receive more affinitive behaviour from others (Seyfarth 1977; see also Bernstein & Sharpe 1966; Oki & Maeda 1973). Even the infants of high-ranking females appear to interact more often, and with a larger number of individuals, than the infants of low-ranking females (Gouzoules 1975; Berman, in prep.). For the members of high-ranking families, therefore, the attractiveness of high rank probably reinforces bonds that develop among related individuals during ontogeny. In contrast, attraction to high-ranking animals may inhibit the formation of close bonds among the members of low-ranking families. As a result, the members of high-ranking genealogies may develop closer relationships with each other than the members of low-ranking

genealogies (see also Fady 1969; Yamada 1963; Seyfarth 1977; Cheney 1977).

Immature males not only interacted less often with unrelated adult females than did immature females, but, unlike their female peers, also did not appear to compete for access to high-ranking adult females and their infants. Possible explanations for the different behaviour of males and females may be sought by considering the different ways in which males and females may benefit as adults from their social relationships with individuals of particular age/sex classes.

Unlike males, females usually retain ranks similar to those of their mothers throughout their lives, maintaining close bonds with the members of their matriline. The adult female social structure is therefore more stable than that of males, and a female's reproductive success probably depends largely on rank, close bonds with her relatives, and the formation of bonds with high-ranking females. If it can be assumed that high-ranking females are more fit than others, females may be selected to learn to behave in such a way that they derive some of the benefits associated with high rank, even if they do not actually rise in rank themselves. Thus females may attempt to interact regularly with their higher-ranking peers, since such interactions may lead to close relationships with high-ranking individuals, and therefore to increased access to scarce resources (for evidence to support this point, see Maslow 1936; Varley & Symmes 1966; Weisbard & Goy 1976).

Females who attempt to interact with high-ranking individuals as immatures may be especially likely to benefit, for two reasons: first, because the ranks of immatures may be more flexible than those of adults (Bernstein & Draper 1964); and second, because social interactions in any small population of individuals may be affected by such demographic factors as a skewed sex ratio in one age class. At any given time, for example, there may be fewer immature females than adult females with infants in the troop, and low-ranking immature females may be able to maximize their opportunities to develop bonds with those of high rank. In this study, the daughter of the seventh-ranking adult female had to compete with only three higher-ranking peers, while her mother had to compete with six other adults. Clearly, infant birth patterns and the sex ratio among immatures will not always be conducive to the formation of bonds between the members of high-ranking families and low-ranking immature females. The point to be made, however, is that by behaving according to the attractiveness of high rank during both development and adulthood females may be able to take advantage of all opportunities to establish bonds with high-ranking individuals.

In this respect, differences in the context of agonistic interactions of immature males and females can also be related to differences in the pattern of each sex's social relationships with others in the troop, and to the manner in which members of each sex may be able to 'exploit' social relationships to their own potential benefit. Thus it is perhaps indicative of their gradual integration into the adult female social structure that immature female agonistic behaviour so resembled that of adult females.

Males generally emigrate from their natal troops, and as adults probably interact only rarely with the adult females with whom they have matured. Consequently, since immature males, unlike their female peers, will probably not benefit as adults from relationships formed with the high-ranking adult females of their natal troops, they may be less attracted than immature females to such individuals during development. Furthermore, although it is possible that in their adopted groups adult males prefer to interact with high-ranking rather than low-ranking females (see below), their ability to gain access to such individuals probably depends not only upon their relationships with the females but also upon such factors as age, length of stay in the troop, and the ability to form coalitions with other adult males.

An additional factor affecting the distribution of immature male interactions with particular adult females in their natal troops may be competition from adult males. In this study, immature males and females did not appear to receive differential amounts of competition when they attempted to groom high-ranking adult females. It is nevertheless possible that competition from adult males indirectly prevented immature males from copulating with high-ranking females, and that this competition also affected their grooming distribution. Competition from dominant adult males often prevents subordinate males from copulating with oestrous females (Altmann 1962; Kaufmann 1965; Struhsaker 1967, 1975; Alexander & Bowers 1969; Hanby & Brown 1974; Hausfater 1975), particularly those of high rank (Kaufmann 1967; Stephenson 1975; Fujii 1975; Enomoto 1975). Thus although immature males, unlike

immature females, never competed with each other to groom adult females of high rank, they also appeared to be unable to compete successfully with adult males to copulate with such females. It therefore seems likely that competition, in combination with a relative lack of attraction to high-ranking adult females, produced a pattern of interaction with low-ranking adult females, and may also have contributed to the emigration of sub-adult males from the troop.

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