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Hierarchy, kinship and social interaction among Japanese monkeys (*Macaca fuscata*)

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Abstract. The study reports the relationship between hierarchy, genetic relatedness and social interaction in captive Japanese macaques. Grooming and proximity were found to be positively related to both dominance rank and degrees of relatedness. Ranks also positively correlated with threats while no relationship was observed between genetic relationships and agonistic interactions. The removal of α-male tightened the male hierarchy while the female hierarchy became relatively loose. Affiliative behaviour became more correlated with ranks than degrees of genetic relatedness. In the absence of α-male, the next dominant male avoided involvement in either agonistic or afliliative interactions with reintroduced animals and group females.

Keywords. Agonistic: groom; hierarchy; kinship; *Macaca fuscata*

1. Introduction

Since the introduction of the concept of inclusive fitness' (Hamilton 1964) and a synthesis by Wilson (1975), researchers in the field of animal behaviour have evinced a keen interest in the determination of the relationship between genetic relatedness and social interactions in a wide range of species. While the phenomenon is recognized in Hymenoptera beyond doubt, the occurrence of kin recognition and kin preference has also been observed in sessile cnidarians (Grosberg and James 1989), fish (Olsen 1989), frogs (Cornell *et al* 1989), birds (Emlen and Wrege 1988; Payne *et al* 1988), New World monkeys (Harrison and Tardif 1988) and Old World monkeys (Mehlman and Chapais 1988; Lopez-Vergara *et al* 1989). Due to the relative simplicity of behaviour, such relations may be easily evident in lower organisms, but in higher mammals, especially the non-human primates, the multiplicity of factors such as hierarchy, demography, local habitat conditions, niche specificity etc., influence social behaviour strongly, thus making the genetic and behavioural relations obscure and uncertain. Although in recent years, quite a few studies have been reported in the literature on ranks, relationships and social behaviour, the concern is still current as far as non-human primates are concerned. Furthermore, in free-ranging animals, the determination of genetic relatedness among individuals is nearly impossible. The non-human primates, maintained in social groups in captivity for long periods, assume immense importance for such investigations. The present study deals with such a group of Japanese macaques where the genealogy and hierarchical positions of all animals were determined to the best possible extent of accuracy. The range of relationships (r) among the animals varied from 0 through 0·13, 0·25, 0·31, 0·38, 0·41, 0·45. 0·5, 0·57

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to 0·75. The study is an attempt to establish quantitative relationships between hierarchy and social behaviour on the one hand and genetic relatedness and social interactions on the other in the stable and disturbed dominance and social structure.

2. Subjects

The present study was conducted on a group of Japanese monkeys housed in an outdoor colony measuring 12×12×3·7m in length, breadth and height respectively, at Bucknell University, Pennsylvania, USA (for details, see Candland *et al* 1972). During the first four months of study, the group consisted of 6 adult males, 5 adult females and 3 infants. Three adult males (Hal, the α-male and Sam and Oliver, the lowest ranks), and two adult females (Bertha and Victoria, the lowest ranking among females) were removed from the group for some other experiments at the end of 4 months of observations, and the observations were continued on the remaining 3 adult males, females and infants each for a period of another 3 months. All monkeys were individually identified and their complete genealogy, hierarchical position and age were known. Table 1 presents the information on the ranks (of adults only), identities, sex and age as well as the degree of genetic relatedness among all monkeys at the beginning of this study.

The hierarchical position of the animals was determined on the basis of directional, one-to-one interactions at the beginning of the study. Due to the restricted presence of adult males in the colony, the parentage was known in each case, and so, the degree of relatedness among animals was determined on the basis of shared genes using the method of 'path analysis' (Wilson 1975). Figure 1 presents the familial tree of the monkeys existing in the colony at the time of observations.

3. Methods and procedure

The observations were made from the beginning of October 1986 till the end of March 1987. The method of one–zero sampling by selecting a focal animal was employed to collect data. An observation session lasted for 10 min divided into 30 intervals of 20 s each. During each interval, all behaviours of the focal animal, including the identity of interacting animals, were recorded and the recurrence of any behaviour during the same interval was ignored. A single observer made all the observations throughout the study. Equal amounts of time were spent on the observation of each animal at each hour from 8·00 a.m. to 5 p.m. One hundred and sixty eight hours consisting of 1008 sessions and 70·5 h consisting of 423 sessions of observation made during the first and the second phases of the study respectively amounted to a total of 238·5 h of quantitatively recorded observations. *Ad lib* notes were maintained for more than 100 h on the behaviour of monkeys when they were not being observed through one–zero sampling.

The first part of the analysis in this paper deals with the determination of the relationship among hierarchical position, degrees of genetic relatedness and various types of social interactions. For the sake of availability of a number of ranks and varied degrees of relatedness, the data collected during the first 4 months only is used for this purpose, because all animals were present in the group at that time.

Table 1. Ranks, identities, sex, age and degree of genetic relationships among monkeys.

Rank	Name	Sex	Age	Degrees of relatedness													
				Hal	Eros	Ursula	Quip	Bertha	Victoria	Ripley	Maxwell	Taipei	Sam	Oliver	Xiaowen	Yaz	Zip
1	Hal	M	17y?	1	0	0·50	0·50	0	0·50	0·50	0·50	0·50	0·50	0·50	0·75	0·50	0·75
2	Eros	F	15y 4m	0	1	0·50	0	0·50	0·25	0·25	0·13	0	0·50	0·50	0·25	0·50	0
3	Ursula	F	5y 4m	0·50	0·50	1	0·25	0·25	0·38	0·38	0·31	0·25	0·50	0·50	0·75	0·50	0·38
4	Quip	F	7y 3m	0·50	0	0·25	1	0	0·25	0·25	0·25	0·50	0·25	0·25	0·38	0·25	0·75
5	Bertha	F	20y?	0	0·50	0·25	0	1	0·50	0·50	0	0	0·25	0·25	0·13	0·25	0
6	Vicky	F	4y 6m	0·50	0·25	0·38	0·25	0·50	1	0·50	0·25	0·25	0·38	0·38	0·45	0·38	0·38
7	Ripley	M	6y 5m	0·50	0·25	0·38	0·25	0·50	0·50	1	0·25	0·25	0·38	0·38	0·45	0·38	0·38
8	Max	M	9y 4m	0·50	0·13	0·31	0·25	0	0·25	0·25	1	0·25	0·31	0·31	0·41	0·31	0·38
9	Taipei	M	6y 4m	0·50	0	0·25	0·50	0	0·25	0·25	0·25	1	0·25	0·25	0·50	0·25	0·50
10	Sam	M	6y 4m	0·50	0·50	0·50	0·25	0·25	0·38	0·38	0·31	0·25	1	0·50	0·50	0·50	0·38
11	Oliver	M	8y 5m	0·50	0·50	0·50	0·25	0·25	0·38	0·38	0·31	0·25	0·50	1	0·50	0·50	0·38
	Xia	M	1y 4m	0·75	0·25	0·75	0·38	0·13	0·45	0·45	0·41	0·50	0·50	0·50	1	0·50	0·57
	Yaz	M	1y 4m	0·50	0·50	0·50	0·25	0·25	0·38	0·38	0·31	0·25	0·50	0·50	0·50	1	0·50
	Zip	F	5m	0·75	0	0·38	0·75	0	0·38	0·38	0·38	0·50	0·38	0·38	0·57	0·50	1

M, Male; F, female; y, years; m, months.

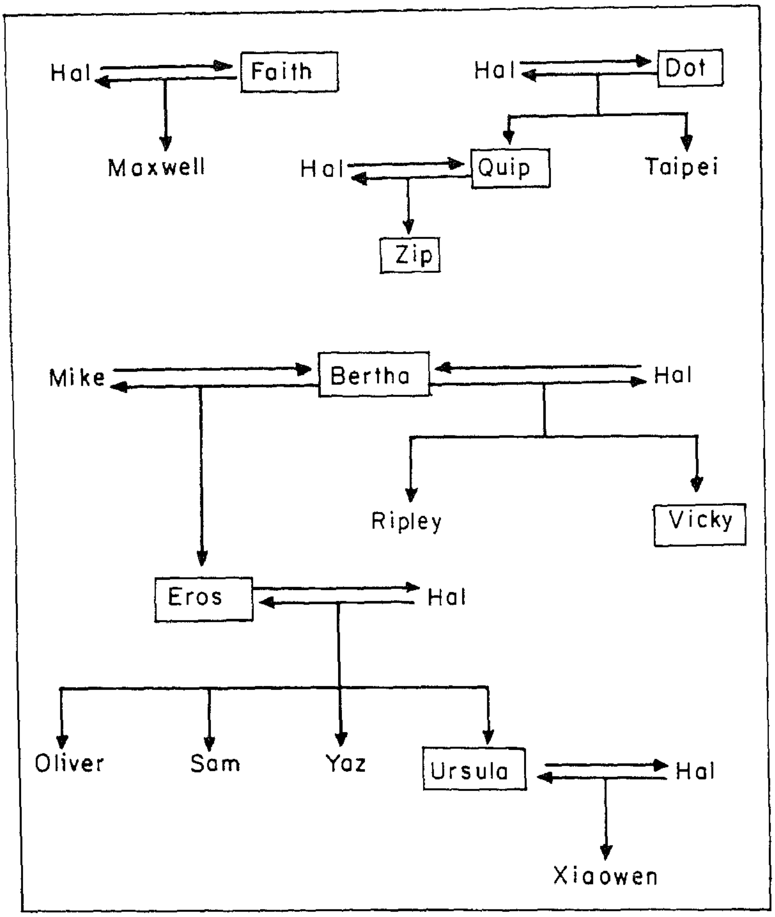

Figure 1. Familial tree of the animals existing in the colony at the time of this study. Double arrows indicate 'mating between' and single arrows indicate offspring. Females are enclosed in rectangles.

Rates of behaviour were calculated per individual (in the case of ranks) and per pair (in the case of degrees of relatedness). The second part of the analysis deals with the strength of dominance hierarchy and social interaction patterns of each individual during the presence and absence of α-male. Social interactions were analysed for all individuals as well as for the adult monkeys alone since the infants cannot be placed in the dominance hierarchy of adults.

The strength of dominance hierarchy was calculated by a modification of the method suggested by Landau (1951). Landau proposed the following formula for the measurement of hierarchical strength of a group.

$$h = \frac{12}{n^3 - n} \sum_{a=1}^{n} \left[V_a - \frac{n-1}{2} \right]^2$$

In Landau's equation, n refers to the number of animals and V_a refers to the number of group members a th animal dominates. Our long term observations indicated that an animal may not dominate another animal all the time, and hence, the above equation was modified as follows:

$$h = \frac{12}{n^3 - n} \sum_{a=1}^{n} \left[d_a - \frac{n-1}{2} \right]^2$$

where $d_a = \sum_{a=1}^{n} P_a$

(P_a representing the proportion of the encounters won against Bath animal). In the above equation, the value of h may range from 0 to 1 indicating no hierarchy to perfectly linear hierarchy, respectively.

4. Results

4.1 *Ranks, relationships and social interactions*

Table 2 presents the correlation of different behaviour patterns with degrees of relatedness and dominance ranks both during the presence and absence of α-male

Table 2. Behaviour correlations with ranks and degrees of relatedness during the presence (Pre) and absence (Post) of a- male.

Interaction category	Correlation (R) Pre	Post
Rank and grooming received	0·69*	0·68*
Rank and grooming given	0·58	0·62*
Degrees of relatedness and grooming among (all individuals)	0·61	0·04
Degrees of relatedness and grooming among (adults alone)	0·56	0·14
Rank and threats made	0·79*	0·81*
Rank and threats received	−0·78*	−0·91*
Degress of relatedness and threats among (adults alone)	0·06	−0·65*
Rank and proximity with others	0·87*	0·30
Degrees of relatedness and proximity among (all individuals)	0·61	0·75*
Degrees of relatedness and proximity among (adults alone)	0·37	−0·23
Rank and approached by others	0·38	0·15
Degrees of relatedness and approaches among (adults alone)	0·20	−0·25

*Significant at 95%.

The amount of grooming received decreased significantly (figure 2) with a decrease in the rank (r= 0·69; P = 0·05) and the reciprocal grooming increased (r= 0·61) with an increased degree of genetic relatedness (figure 3) among individuals. Figure 3 further illustrates that with higher degrees of relatedness (beyond 0·41), the increase in reciprocal grooming was more or less linear. However, the analysis run for adults only, resulted in a decreased correlation (r = 0·56). An

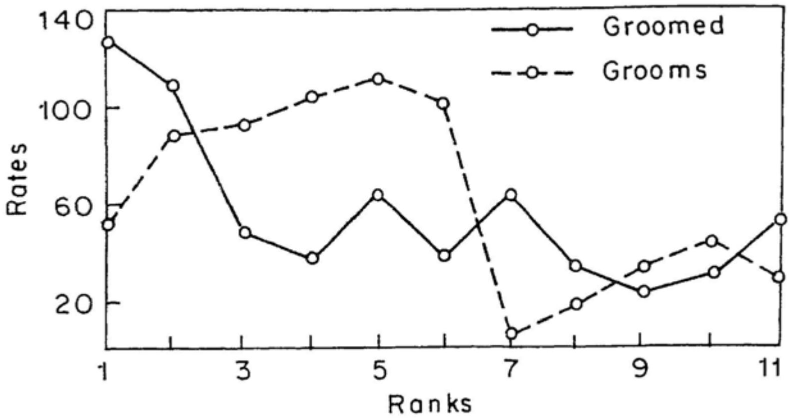

Figure 2. The relationship between ranks and grooming. X- and Y-axis depict ranks and rates of behaviour per individual respectively.

observation of figure 2 indicates that most of the grooming was received only by the first 3 high ranking individuals, and the rates for all other animals were almost the same. The disturbed conditions caused by the removal of α-male did not influence the pattern of relationships between ranks and grooming but the correlation between degrees of relatedness and reciprocal grooming became almost nil (table 2).

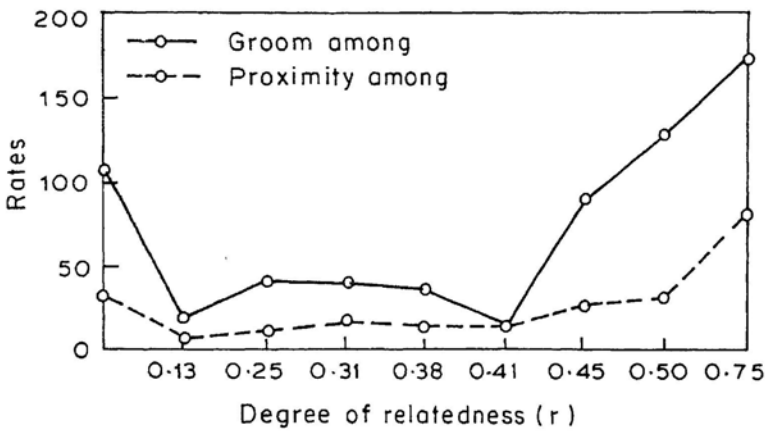

Figure 3. The relationship between degrees of relatedness, reciprocal grooming and proximity. X- and Y-axis depict degrees of relatednens and rates of behaviour per pair respectively.

So far as agonistic interactions were concerned, the results indicated that higher the rank (figure 4), higher was the number of threats made (r= 0·79; P= 0·05) and as the rank lowered, the number of threats received increased (r= –0·78; P= 0·05). On the other hand, no relationship was observed between agonistic interactions and degrees of genetic relatedness (figure 5, table 2).

High ranking individuals were found more in proximity with other animals (figure 6) than the lower ranking ones (r = 0·87; P=0·05). The proximity was also

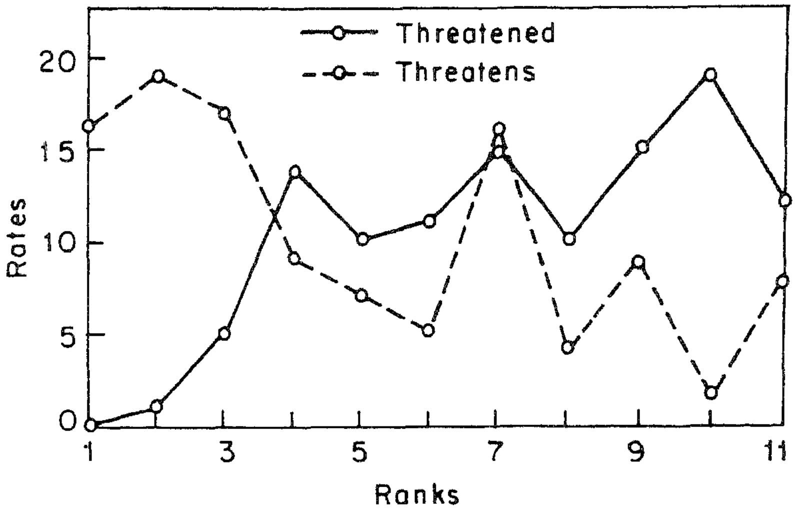

Figure 4. The relationship between ranks and agonistic interactions. X- and Y-axis depict ranks and rates of behaviour per individual respectively.

high among individuals which had a higher degree of genetic relatedness (figure 3; r =0·61). Here again, the removal of proximity values for mother-infant dyads and the analysis run for adults only resulted in a sharply reduced correlation (r=0·37) between relatedness and proximity. The most striking observation here was that

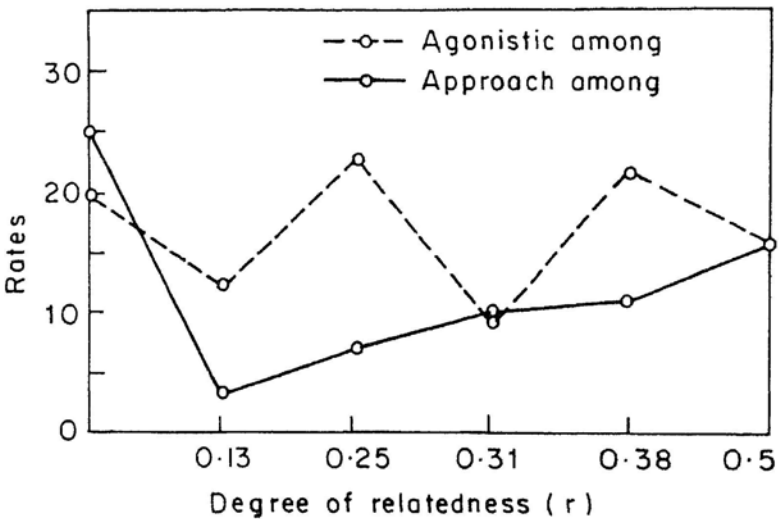

Figure 5. The relationship between degrees of relatedness, agonistic interactions and reciprocal approach. X- and Y-axis depict degrees of relatedness and rates of behaviour per pair respectively.

during the absence of α-male the relationship between rank and proximity reduced to non-significance (r = 0·30) whereas between proximity and degrees of relatedness, it further increased (r=0·75; P = 0·05). Since this relationship was observed only in the case of 'all individuals' analysis, it indicated higher protectiveness of the young during disturbed social conditions.

The relationship between reciprocal approaches made by individuals with varying degrees of relatedness (figure 5) and individuals approached in relation to their ranks (figure 6) was found to be statistically non-significant.

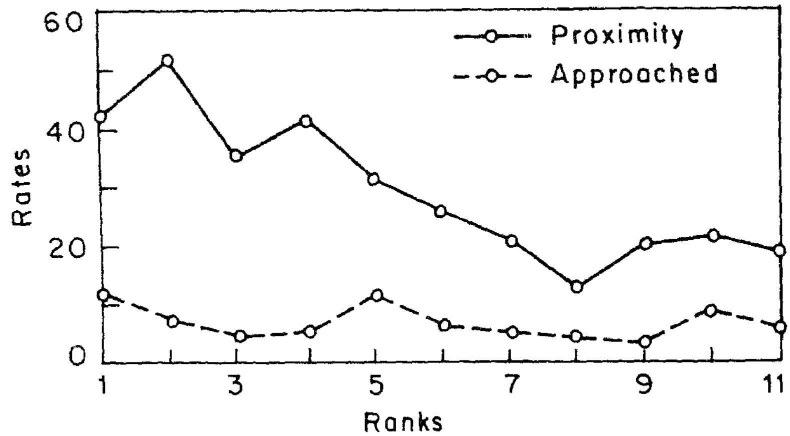

Figure 6. The relationship between ranks, proximity with others and approaches by others. X- and Y-axis depict ranks and rate of behaviour per individual respectively.

4.2 *Strength of dominance hierarchy*

During the presence of the cc-male (first four months of the study), the value of h (see modified Landau's equation in § 3) for the overall strength of hierarchy in the group was 0·86, and it was 0·95 and 0·97 for males and females respectively. During the following three months, when the α-male was absent, the overall strength of hierarchy slightly increased (h=0·91) but it became perfectly linear among the males (h= 1) and relatively loose among females (h=0·80)

4.3 *Ranks, kinship and behavioural correlates in the presence and absence of α-male*

Ranks and kinship correlates with behaviour during the presence and absence of α-male are presented in table 2. As far as grooming was concerned, the correlation with degree of genetic relatedness reduced to non-significance during the absence of α-male, whereas the correlation with dominance ranks persisted. The same pattern to some extent was also observed in the case of proximity. The correlation between agonistic behaviour and ranks remained the same during the presence and absence of α-male, however, the highly significant correlation of aggression (R=–0·65) with degrees of genetic relatedness indicated low agonistic interactions among closely related individuals.

4.4 *Interaction patterns of individual animals*

An attempt was further made to delineate the interaction patterns of each individual during the two phases of the study. The interaction rate per individual for each animal during the two phases of the study for various behaviour patterns is presented in table 3.

An overview of table 3 reveals that the most striking changes took place in the interaction patterns of Maxwell, the second rank among the males during the absence of α-male. Grooming increased significantly only in the case of Maxwell. A further analysis of the interactions of Maxwell showed that the significant increase in grooming was only by the females (χ^2=28·3; P=0·01). There was a significant increase in the rates of grooming by Eros and Quip (table 3) which, the further analysis showed, was directed only towards Maxwell. The increased rate of grooming by Maxwell was also found to be directed only towards the females (χ^2=33·43; P = 0·01. Furthermore, the values in table 3 indicate that the proximity of Maxwell to other males significantly decreased, whereas, to the females, it showed a multi-fold increase. Interestingly, no change was observed in the interaction patterns of Ripley, the highest ranking among the males in the absence of the α-male, except for the significant reduction in proximity to the females. Though statistically non-significant, overall aggression during the absence of α-male, surprisingly, reduced.

5. Discussion

In non-human primates, the dominance hierarchy plays a very significant role in the regulation of social interactions. Messeri and Giacoma (1986), in a study of female pigtail Macaques, found that except grooming, many other social behaviours such as displacement, present, attack, mount and threat were linearly related to hierarchy. Seyfarth (1977), however, discussed that in a number of different species, high ranking adult females received more grooming and he proposed a theoretical model to explain the functional significance of the pattern. The present study revealed that the dominance ranks were positively related to being groomed, threatening others and being in proximity with others. At the same time, genetic relationships, which were positively correlated with grooming and proximity, also emerged as an important factor regulating these behaviours.

Mehlman and Chapais (1988) found that in Japanese monkey females, most of the grooming was directed towards kin during the non-mating season, and towards kin or heterosexual/homosexual partners during the mating season. The analysis of individual interactions during the present study revealed that in the absence of α-male, a female Eros, who became the most dominant animal in the group, directed most of her grooming towards Quip, a relatively lower ranking female, and with a zero degree of relatedness with Eros. Interestingly, Eros was sexually receptive, and was observed to be frequently mounted and rubbed genitally by Quip, instigated by Eros herself, mostly through threats. Lopez-Vergara *et al* (1989) also reported that stump-tailed macaques lacking relatives were rarely chosen as groomees, and they mostly involved themselves in self-grooming.

Although the relationship between dominance and grooming is often found to be significant, Loy and Harnois (1988), after a study on patas monkeys, concluded that dominance probably was not a reliable structural variable and kinship was considered to be a major organizing feature affecting allogrooming and other affiliative interactions. On the other hand, Ehardt (1988), in a study on adult female sooty mangabeys, reported that affiliative interactions were more than expected

Table 3. Per individual rates of social interactions among monkeys during the presence (Pre) and absence (Post) of α-male.

Animal	Groomed		Grooms		Threatened		Threatens		Proximity-M		Promixity-F		Breaks contact		Contact broken	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Hal	98·54	–	39·38	–	0	–	16·2	–	30·6	–	343·8	–	12·7	–	7·4	–
Eros	83·92	103·28	68·08	134·45*	0·9	0	18·7	24·48	107·83	97·92	284·75	192·78*	7·8	5·93	14·8	6·5
Ursula	36·77	50·87	71·92	34·23*	5·2	8·16	17·3	6·73	91	99·45	95·25	84·15	5·1	3·83	5·2	5·74
Quip	27·92	37·48	80·31	133·3*	14·3	9·49	9·3	11·02	83	174·9*	179·75	131·6*	9·1	4·4	5·4	2·68
Bertha	49·92	–	86·00	–	10·1	–	6·9	–	112·67	–	140·25	–	9·8	–	10·3	–
Victoria	29·08	–	78·23	–	10·3	–	5·1	–	135·67	–	111·5	–	7·7	–	8·6	–
Ripley	49·61	67·13	4·31	3·06	15·1	12·85	16·4	16·23	75·2	82·11	63	13·3*	4·1	2·68	4·4	3·64
Maxwell	26·54	58·9**	12·77	29·3*	9·5	11·63	3·9	2·75	107	31·4*	83·2	359·1*	3·9	7·07	3·6	2·87
Taipei	16·77	7·08	26	74·1*	14·6	22·03	9	0*	113·8	107·1	1·2	0	4·1	3·82	3·1	2·1
Sam	22·85	–	34·23	–	18·6	–	1·5	–	172·8	–	39·6	–	6·5	–	4·1	–
Oliver	41·46	–	21·92	–	11·5	–	0·8	–	105·4	–	105·5	–	3·3	–	7·2	–

* χ^2 values significant at 99%; M- to male; F- to female.

among kin when all kin were included in the analysis. The removal of just mother-infant dyads rendered all the correlations non-significant among adults and Ehardt (1988) suggested to review the role of kinship in affiliative behaviour of non-human primates. In the present study also, when the analysis for grooming and proximity was done for adults alone, the correlation between genetic relatedness and grooming was found to be somewhat reduced and it became non-significant in the case of proximity. It has been reported in bonnet monkeys that the juveniles become independent after their mothers give birth to new babies (Singh and Sachdeva 1977), but the mothers continue to 'invest' in the older offspring in ways such as grooming that would not 'cost' them in terms of future reproduction (Singh *et al* 1987). It can be argued that the lactating females are forced to spend more time with, and take care of, their infants, and they may not have enough time to spend with adult kins. We suggest that the analysis for 'adults alone' should be done not by removing the values for mother-infant dyads but only in those groups where there are no infants present.

In the present study, no relationship was observed between degrees of relatedness and aggression. However, many investigators have previously reported the lack of or reduced aggression among kin. Cheney and Seyfarth (1987) reported that in vervets over 3 years in age, an individual was more likely to threaten another if the kin of the two were previously involved in a fight. The preference for kin males has also been observed in marmosets and tamarins who exhibited decreased frequency of agonistic behaviours in the presence of kin males over novel males (Harrison and Tardif 1988). The agonistic behaviour in the present study was found to be significantly related only to the dominance ranks. Such a relationship has also been observed in baboons (Chalyan and Meishvili 1987).

Unlike in natural groups where the α-male loses dominance through a prolonged process of explicit and implicit contests, the sudden removal of α-male in captive groups may lead to a variety of unpredictable reactions among the group members. Oswald and Erwin (1976) reported that the experimental removal of resident males increased the violence among females more than ten-fold. In the present study, there was an overall reduction in aggression after the removal of α-male and some other animals. The reason probably is that in the absence of α-male, a female, Eros, became the most dominant animal, and even after 3 months, hardly any affiliative or aggressive interactions were observed between her and Ripley, the most dominant among the males. The affiliative interactions of Eros significantly increased towards Maxwell, a male below the rank of Ripley. The need for allies to maintain rank in Japanese female macaques has also been reported by Chapais (1988). In another paper, Chapais (1985), describing rank changes in female Japanese monkeys, concluded that females do not ally with subordinates but with an individual ranking above the target. The alliance of Eros with the second rank among the males in the present study could only be explained as protection of her own rank and antagonism towards Ripley, the male ranking above Maxwell.

In the present study, the changed pattern of correlations for affiliative and agonistic interactions with ranks and genetic relationships indicated an interesting aspect of sociality. It may be hypothesized that the abrupt absence of α-male would result in an abrupt change in dominance hierarchy and social structure which in turn would influence social behaviour in different ways. We propose that affiliative behaviours would show high correlations with degrees of relatedness in stable groups with an established hierarchical structure, but in an abruptly disturbed social structure, affiliative and appeasing behaviours would be regulated more by the ranks or struggle for ranks than the genetic relationships.

In the absence of α-male, the increased affiliative interactions of females with the now second ranking among the males, and the avoidance of any kind of contact with the females by the most dominant of the males was the most dramatic impact of the removal of α-male. It may be mentioned that after 3 months, the α-male and the other removed animals were re-introduced to the group. This situation resulted in an enormous increase in aggression by the resident monkeys. Interestingly, all the attacks were initiated by the lower ranking males, and Ripley, the most dominant of the males did not make the first attack on the re-introduced animals even once. He participated in attacks only after the re-introduced animal was completely overpowered and subdued by other males. It may be conjectured that the sudden removal of α-male may influence the behaviour of the next ranking male in ways that he would avoid all kinds of agonistic encounters, including attacking the re-introduced α-male, because even one withdrawal may result in the loss of his high rank, and hence, the chance of establishing himself as the new α-male. The lower ranking animals, on the other hand, only stand to gain from such aggressive encounters and have 'nothing to lose' in terms of their ranks.

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