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GROUP HISTORY AND SOCIAL STYLE: THE CASE OF CRAB-EATING MONKEYS

ABSTRACT: *Two groups of crab-eating monkeys, one formed of individuals whose mothers were high-ranking, another comprising animals whose mothers' status was low, are used to test the hypothesis of a between-group systemic variation of social relationships within a species. Using a multivariate analysis of 17 variables it is demonstrated that rank by birth affects several inter-related traits of aggressive, affiliative, and cooperative behaviour of animals regardless of their actual rank. Females whose inborn status was high exhibited a more masculine, assertive, and dominant behavioural style, were more individualistic and less dependent on other group members. Our results suggest that group history can produce a systemic effect on social relationships in conspecific populations.*

KEY WORDS: *Macaques – Birth-rank – Dominance – Aggression – Affiliation*

INTRODUCTION

Factors underlying inter-specific differences in social behaviour have been widely debated over the recent years (Thierry 1985, de Waal, Luttrell 1989, de Waal, Ren 1988, van Schaik 1989, Wrangham 1980). Studies in primate socioecology suggest that species having superficially similar systems of dominance relationships (for instance, a relatively linear hierarchy) can be quite dissimilar in terms of aggressive, post-conflict, affiliative, and spatial behaviour both within and between the sexes and thus have different dominance styles (de Waal 1989, Thierry 1988, Butovskaya 1993a,b, 1994, de Waal 1993). These differences are apparently affected by adaptation to specific habitats. Social predisposition of individuals may be shaped by selection (Williams 1966, Lott 1984).

Studies into dominance styles shown by various species of macaques indicate that intergroup relationships can be different even in closely related species with a similar matrilinear structure (Aureli *et al.* 1989, Waal, Yoshihara 1983, Waal 1993, Thierry 1988, Petit, Thierry 1994,

Butovskaya 1993a,b, 1994). It has also been demonstrated that species-specific social relationships (first and foremost their asymmetry) are practiced both under natural conditions and in captivity (Aureli *et al.* 1989, Aureli 1992). According to some writers, group differences in behavioural style are based on the principle of systemic variation: groups differ in complexes of coadapted traits rather than in separate parameters (Thierry 1993, Castles *et al.*, in print). Specifically, characteristics of social tolerance should be inter-correlated.

The objective of this article is to test the hypothesis of systemic variation using two groups of crab-eating monkeys (*Macaca fascicularis*) having different histories. One was formed of animals whose mothers were high-ranking, the other of animals whose mothers had a low status. The additional hypothesis tested by us was that in matrilinear species (like macaques in general), the increased proportion of adult females high-ranking by birth should result in an increase of social tension within the group, while the larger number of females low-ranking by birth should shift within group relationships towards greater flexibility and cooperation.

SUBJECTS AND METHODS

The two groups of macaques were observed over a three-months' period from November 1992 to February 1993 at the Primatological Station of the Kassel University, Germany. The first group (H) was composed of animals whose mothers were high-ranking, the second one (L) consisted of those whose mothers were low-ranking (see Butovskaya *et al.* 1995, for more information). Conflict and postconflict behaviour was recorded by means of the scan method. Ninety-four 30-min scans were made for group H, and 100 such scans for group L. Other behavioural patterns were recorded using the focal sampling method. Sixty-four 5-min samples were collected for each adult individual in group H, and 66 such samples in group L (Altmann 1974, Dunbar 1976, Bernstein 1991). The statistical evaluation of data was performed using the software package written by B. A. Kozintsev (Butovskaya *et al.* 1994). The correlation between the behavioural variables was assessed both at the level of individual characteristics averaged over all the animal's partners, and at the level of all pairwise interactions. In the first case, the correlation structure was evaluated using the principal components analysis, and in the second case, matrix permutation tests were applied, each test being based on 500 permutations (Hemelrijk 1990, Butovskaya *et al.* 1994). Thirty patterns of social behaviour were used for comparing the two groups, including dominance vs. submission (teeth baring, avoidance, ritual biting), noncontact aggression (threat display, chasing, etc.), and contact aggression (slapping, pinching, pushing, beating, etc.). Frequencies of dyadic and nondyadic aggression of both types were calculated. Nondyadic aggression included attacks performed by two or more animals against a single victim or by a single individual against several victims simultaneously. Also, we registered alliances (cooperation in attacks), quarrels (mutual aggression between groups), support of aggressors, defence of victims, redirected aggression, number of wounds received in clashes, as well as affiliative behaviour (initiation of spatial proximity, sitting close together, grooming), friendly behaviour (touching, embracing, presenting, friendly vocalization, tails-in-twine).

RESULTS

Frequencies of behavioural patterns are presented in Table 1. Landau's linearity index (Lehner 1979) calculated for the pairwise submission matrix equals 0.87 in group H, and 0.82 in group L, indicating moderate degree of linearity (Table 2). As demonstrated by the permutation tests, a significant positive correlation between the initiation of spatial proximity and submission existed in group H ($p < 0.001$, Table 3). No such correlation was observed in group L. While in group H, affiliative relationships were initiated only by individuals of a higher rank, no effect of

status on such relationships was detected in group L. The frequency of pairwise noncontact aggression in group L was 1.5 times lower than in group H (Table 4). Landau's linearity index for this variable equals 0.98 in group H, but only 0.84 in group L. In group L, the frequency of aggressive alliances was 4 times higher than in group H. The frequency of contact aggression, too, was twice as high in group L than in group H, and the same is true of collective contact aggression (Tables 1, 5). Landau's linearity index equals 0.64 and 1.13, respectively, apparently suggesting that despite a higher level of aggression (especially its contact variety) in group L, aggressive relationships in group H were much more rigid. Permutation tests applied to matrices of aggression in group H (Kendall's $K = -41$, $p = 1.000$, for the contact variety, and $K = -44$, $p < 0.980$, for the noncontact variety) support the above conclusion: aggression in this group was directed mainly down the hierarchy. The same tests applied to aggression matrices in group L suggest that in this group, in contrast to group H, low-ranking animals were not afraid to resist, moreover, they occasionally directed aggression (both contact and noncontact) against higher-ranking animals ($K = -24$, $p = 0.808$, and $K = -16$, $p = 0.628$, insignificant). Over the observation period, episodes of aggression in group L had never resulted in injuries. In group H, 26 cases of injuries were registered (Table 1, Mann-Whitney's $U = 4.5$, $p < 0.01$). In group H, a distinct polarization of relationships was observed. While most aggressive actions were performed by three female relatives (Heda and her two daughters), other females rarely demonstrated aggression. Nearly all aggressive coalitions were formed by these three relatives (Table 6). The hypothesis about the equal probability of all members of group H to enter into alliances is rejected at the 0.1% level (chi-squared = 210.1, d.f. = 9). Most often (20 times), alliances occurred between the two sisters, Hanna and Herta. Those between their mother Heda and both her daughters had occurred 12 times, and those between Heda and her younger daughter Herta, six times. The correlation between the matrix of alliances and that of differences in dominance ranks (based on submission) in group H is negative but insignificant ($K = -14$, $p = 0.826$), the probable explanation being that only high-ranking individuals entered into coalitions. In group L, the distribution of aggressive alliances was more uniform. There were two conflicting parties. The more dominant one consisted of the male, Theo, and three females, Maria, Sonia, and Jutta. The second party, headed by Julia, also included Christa, Kora, and Elke. Like in group H, individuals in groups L differed in their predisposition to form alliances (chi-squared = 377.0, d.f. = 9, $p < 0.001$). Those most predisposed were Maria, Sonja, and Jutta. Alliances in this group were more frequent than in group H and much more variable in composition. Each of them was mainly formed of individuals belonging to one of the opposing parties, but in some instances, females from different parties joined for aggression (Table 6). The hypothesis of nonselectivity

in alliances is rejected at the 0.1% level (chi-squared = 305.8, alliance between Julia, Christa, and Kora accounting for half of this value). A significant negative correlation was observed between the matrix of alliances and that of differences of dominance ranks ($K = -101$, $p < 0.990$), suggesting that all individuals close in dominance status tended to form coalitions.

To evaluate the relationships between the group members, several criteria suggested by other writers were used (Watts 1994). The relationships in a dyad were considered to be good if they met the following criteria: (1) the level of affiliative (specifically friendly) relationships, initiation of spatial proximity, and sitting close together, was above median, (2) the level of agonistic relationships was below median, and (3) the frequency of grooming between members of the dyad was above median. Also, we used four indicators of friendly behaviour (friendly contacts, sitting close together, initiation of spatial proximity, and grooming) and two indicators of agonistic behaviour (contact and noncontact aggression). Frequencies of each behavioural pattern were scored as either 0 (below median for friendly behaviour and above median for aggression) or 1 in the opposite case (Table 7).

According to these criteria, the dyads with the best relationships in group H were Carmen and Charlotte, Carmen and Laura, Laura and Meike, as well as those which included the male (Majo) and each of the three females, Meike, Carmen, and Laura. The worst were Hanna's relationships with Charlotte, Meike, and Laura, Herta's with Meike and Laura, and Majo's with Hanna and Herta. A negative correlation was found between the matrix of relationships and that of alliances ($K = 28$, $p = 0.032$). In group H, then, mostly those individuals supported one another who maintained good relationships with each other.

In group L, the best were Christa's relationships with Sophie, Kora, and Julia, Else's with Sophie and Jutta, and Kora's with Elke and Julia. The worst relationships were practised in the dyads Maria vs. Kora, Sonia vs. Julia, Elke vs. Jutta, Christa vs. Else, and Theo vs. Else, Julia, and Jutta. The relationships between Sonia, on the one hand, Maria and Elke, on another, combined friendliness with a high level of aggression. Unlike group H, no correlation between the matrix of relationships and that of alliances was found here ($K = 32$, $p = 0.172$), and thus the tendency to form coalitions was unrelated to the quality of relationships between the partners.

To assess the overall pattern of social structure in the two groups with reference to the principal strategies of dominant and subordinate individuals, the principal components (PC) analysis was used. Thirty standardized variables of social behaviour were analyzed (Table 8). The first two PCs account for nearly two thirds (62 %) of the total variation (Table 9, Figure 1). The variables with the highest positive loadings on PC1, accounting for 36 % of the variation, are performed aggression (contact and noncontact), participation in aggressive blocs, support of aggression (both performed and received), received

submission and received avoidance. The trait with the highest negative loading on this PC is the avoidance demonstrated by the individual itself to other group members. PC1, then, describes the contrast between the behaviour of dominant and subordinate individuals. Within the groups, PC1 scores are positively correlated with Zumpe-Michael's dominance index ($r = 0.86$ in group H, and 0.84 in group L, $p < 0.001$ in both cases). However, the loading of received submission on PC1 is not especially high, and the order of individuals according to PC1 scores differs from that according to the dominance index. Specifically, neither of the two alpha males has the highest PC1 scores in his respective group. The first places on this variable are occupied by Hanna and Herta in group H and Maria in group L, the assertive high-ranking females who terrorized other females, were able to get support of other group members in their aggressive actions, and helped other aggressors. However, because they often demonstrated submission (first and foremost to the males), their dominance indices are not the highest. The low-ranking females have the lowest PC1 scores.

PC2, which accounts for 26 % of the variance, is most tightly linked with friendly contact behaviour (both performed and received), sitting in close proximity, participation in quarrels, received ritual biting, and performed redirected aggression. All these patterns, except for the last one, significantly differentiate the two groups (see above), all of them having higher frequencies in group L. As seen from Figure 1, PC2 scores, too, are significantly different in the two groups. Females are set apart without overlap. A very small total overlap is due to the fact that the male in group L falls in the same part of the variation range as do the females of group H. The male of group H deviates from the females of his group in the same direction as does his counterpart in group L. In other words, the following sequence is observed: (1) male of group H, (2) females of group H and male of group L, (3) females of group L (Figure 1). The behaviour of the male in group H, then, accentuates the principal features of the behavioural style of this group, while in group L the reverse tendency is observed.

DISCUSSION

Group history has a notable effect on female dominance structure in matrilinear species (Datta 1989). Significant differences in social relationships were observed between the two groups studied by us, although they were housed under identical conditions and contained a nearly equal number of adult animals. When one group is formed only of individuals high-ranking by birth, another of those whose mothers were low-ranking, the behavioural contrast between the two can attain the level of inter-specific differences. The systemic variation hypothesis (Castles *et al.*, in print) predicts that the groups should differ in a complex of coadaptive traits. This is what is actually

TABLE 1. Average frequencies of behavioural variables in two groups of crab-eating monkeys.

Variables	Group H (females)			Group L (females)			Group H	Group L
	x	s	sx	x	s	sx	(male)	(male)
1	2	3	4	5	6	7	8	9
Contact aggression, r.	22.57	29.52	11.16	40.00	47.64	15.88	32	42
Contact aggression, p.	27.71	12.47	4.71	44.44	23.47	7.82	0	2
Noncontact aggression, p.	149.29	164.50	62.18	211.11	234.79	78.26	164	294
Noncontact aggression, r.	172.43	101.68	38.43	240.67	144.26	48.09	2	28
Submission, p.	776.86	277.89	105.03	1060.78	357.79	119.26	188	109
Submission, r.	549.14	666.20	251.80	624.11	717.99	239.33	1781	4036
Initiation of spatial proximity, p.	219.71	128.48	48.56	303.00	195.84	65.28	188	127
Initiation of spatial proximity, r.	217.00	162.68	61.49	307.11	201.73	67.24	206	91
Grooming, p.	4165.29	1179.57	445.84	2761.78	1618.47	539.49	8344	636
Grooming, r.	4328.71	2704.90	1022.36	2786.00	1963.29	654.43	7200	418
Friendly contacts, p.	115.29	90.94	34.37	553.33	501.61	167.20	150	145
Friendly contacts, r.	126.14	103.09	38.96	551.33	334.40	111.47	75	164
Scratching	115.14	56.71	21.43	56.56	33.51	11.17	113	55
Sitting close	2285.00	726.84	274.72	19745.44	7835.52	2611.84	2494	909
Victim's request for help, p.	19.00	20.40	7.71	7.56	9.15	3.05	0	0
Victim's request for help, r.	1.43	2.23	0.84	6.89	8.95	2.98	123	6
Running away, p.	60.00	36.67	13.86	78.22	43.19	14.40	0	0
Running away, r.	54.43	63.27	23.91	61.56	75.07	25.02	40	150
Going away, p.	9.29	5.31	2.01	14.89	11.14	3.71	0	0
Going away, r.	8.14	8.19	3.10	14.00	25.00	8.33	6	8
Quarrels between blocs, p.	0.00	0.00	0.00	32.22	21.99	7.33	0	14
Quarrels between blocs, r.	0.00	0.00	0.00	30.22	22.01	7.34	0	32
Ritual biting, p.	0.00	0.00	0.00	6.67	12.49	4.16	4	0
Ritual biting, r.	0.00	0.00	0.00	6.67	7.42	2.47	0	0
Support of aggressor, p.	14.29	15.89	6.01	28.44	29.07	9.69	13	56
Support of aggressor, r.	14.43	17.77	6.71	29.11	33.96	11.32	13	50
Redirected aggression, p.	6.86	7.71	2.91	13.78	18.21	6.07	0	0
Redirected aggression, r.	7.14	6.26	2.36	13.78	14.30	4.77	0	0
Alliances	39.14	48.73	18.42	107.11	100.84	33.61	2	116
Injuries per individual	3.71	3.20	1.21	0.00	0.00	0.00	0	0

Note: p., performed by the focal individual; r., received by focal individual;

Frequencies are standardized per individual per one hour of observation.

Only interactions with females are registered. x, mean; s, standard deviation, sx, standard error.

Focal observations are standardized per 5.33 hours in group H, and per 5.5 hours in group L;

scan observations, per 47 and 50 hours, respectively. Numbers of injuries are not standardized.

observed, especially with respect to characters related to within-group social tolerance. The differences between groups H and L and those of quality rather than of quantity. In group H, the dominance vs. submission relationships were more predictable. The dominant individuals more often initiated aggression, as might be expected in a species with a rigid, despotic dominance style (Waal, Luttrell 1989, Butovskaya 1993b, Chaffin *et al.* 1995). While ritual forms of aggression, especially between the most apparent opponents, were rare, injuries were frequent, and the victims did not try to resist. Support was offered when the aggressor was obviously stronger than the victim. The subordinate females actively avoided spatial proximity or affiliative contacts with the high-ranking ones. They escaped when the dominants approached them, and they

never showed disobedience or tried to challenge their status. In short, they presented no real threat to the dominants. Evidently, for the high-ranking females in group H, aggression was the principal way of maintaining social bonds. Injuries to the low-ranking females were inflicted not because the latter resisted, but rather because the dominants were strongly motivated for self-assertion.

In group L, the dominant females preferred noncontact and ritual aggression, especially in clashes with their antagonists. The subordinates resisted attacks and formed coalitions against the dominants. The leading party and the opposing bloc, which comprised medium- and low-ranking females, were engaged in quarrels. Compared to group H, the approach of the dominants much less frequently caused avoidance reaction from the side of the

TABLE 2. Frequencies of submission demonstrations (focal observations, pairwise interactions).

a) Group H										
	Ch	M	C	L	He	Ha	Hr	Mj	DI	Rank
Ch	-	0	0	0	3	4	5	8	0,452	5
M	3	-	3	0	5	20	4	9	0,017	8
C	1	0	-	1	3	20	25	14	0,266	6
L	4	0	2	-	6	12	6	5	0,103	7
He	0	0	0	0	-	27	20	6	0,626	4
Ha	0	0	3	0	6	-	0	36	0,833	2
Hr	1	0	0	0	5	6	-	17	0,662	3
Mj	0	1	1	2	0	6	0	-	0,915	1

Ch, Charlotte; M, Meike; C, Carmen; L, Laura; He, Heda; Ha, Hanna; Hr, Herta; Mj, Majo; DI, dominance index.

b) Group L												
	Ch	M	Sn	Sp	I	E	C	Jl	Jt	T	DI	Rank
Ch	-	12	1	0	0	2	0	1	1	12	0,308	7
M	1	-	18	6	0	0	0	2	1	23	0,767	3
Sn	0	14	-	0	0	2	0	0	0	9	0,840	2
Sp	2	14	2	-	0	6	1	4	6	34	0,194	8
I	0	20	6	0	-	4	4	0	2	34	0,043	10
E	2	17	18	2	1	-	0	9	0	16	0,531	4
C	0	13	4	2	0	9	-	5	14	15	0,174	9
Jl	0	26	4	2	0	12	0	-	1	30	0,508	5
Jt	1	11	7	0	0	3	0	9	-	49	0,409	6
T	1	0	1	0	2	1	1	0	0	-	0,961	1

Ch, Christa; M, Maria; Sn, Sonja; Sp, Sophie; I, Ilse; E, Elke; C, Cora; Jl, Julia; Jt, Jutta; T, Theo.

TABLE 3. Initiation of spatial proximity (focal observations, all interactions).

a) Group H								
	Ch	M	C	L	He	Ha	Ht	Mj
Ch	-	16	2	1	0	0	0	1
M	0	-	4	5	0	0	0	7
C	2	4	-	3	0	0	0	4
L	1	0	1	-	0	0	0	1
He	0	0	2	0	-	3	0	1
Ha	1	0	4	0	10	-	1	0
Ht	5	1	2	0	12	2	-	0
Mj	2	6	3	0	0	0	1	-

b) Group L										
	Ch	M	Sn	C	I	E	Sp	Jl	Jt	T
Ch	-	0	0	2	2	2	2	2	1	0
M	15	-	19	8	13	6	22	15	1	3
Sn	10	5	-	4	4	8	8	7	2	2
C	7	0	1	-	1	4	1	5	0	0
I	5	2	2	2	-	3	9	3	1	0
E	13	0	7	2	5	-	9	5	2	1
Sp	3	2	4	0	2	2	-	2	3	0
Jl	11	1	1	5	5	3	12	-	2	1
Jt	5	2	0	7	7	1	5	4	-	0
T	2	2	9	0	0	3	1	0	0	-

TABLE 4. Frequencies of noncontact aggression events (scan observations, all interactions).

a) Group H								
	Ch	M	C	L	He	Ha	Hr	Mj
Ch	-	16	4	12	0	0	1	0
M	0	-	0	6	0	0	0	0
C	1	20	-	9	0	1	1	0
L	0	1	0	-	0	0	0	0
He	13	15	20	14	-	0	0	0
Ha	19	30	62	24	16	-	10	1
Ht	29	37	71	25	33	0	-	0
Mj	3	3	6	1	8	32	24	-

b) Group L										
	Ch	M	Sn	Sp	I	E	C	Jl	Jt	T
Ch	–	2	3	14	10	9	3	0	3	1
M	36	–	7	23	16	61	80	102	29	4
Sn	22	14	–	11	15	27	35	59	29	0
Sp	0	0	0	–	0	0	1	0	0	0
I	0	0	0	2	–	0	1	0	0	0
E	0	7	4	13	11	–	4	1	6	1
C	0	4	2	12	4	1	–	0	6	1
Jl	0	7	7	40	9	19	7	–	30	5
Jt	10	0	2	3	5	11	65	32	–	2
T	15	10	5	10	11	14	21	48	13	–

TABLE 5. Frequencies of contact aggression events (scan observations, all interactions).

a) Group H								
	Ch	M	C	L	He	Ha	Ht	Mj
Ch	-	2	1	2	0	0	1	0
M	0	-	0	0	0	0	0	0
C	0	1	-	0	0	0	0	0
L	0	0	0	-	0	0	0	0
He	3	2	1	0	-	0	0	0
Ha	6	4	4	7	8	-	2	0
Ht	5	6	6	4	9	0	-	0
Mj	4	2	3	1	1	5	1	-

b) Group L										
	Ch	M	Sn	Sp	I	E	C	Jl	Jt	T
Ch	-	0	0	0	0	3	0	1	0	0
M	9	-	1	13	4	21	11	17	0	0
Sn	0	2	-	1	0	7	1	5	7	0
Sp	1	0	0	-	0	0	1	0	1	0
I	0	0	0	0	-	0	0	0	0	0
E	1	1	0	1	2	-	0	0	4	0
C	1	0	1	1	3	0	-	0	2	0
Jl	0	1	1	9	3	3	2	-	14	0
Jt	1	0	0	1	0	1	12	8	-	1
T	1	3	3	0	4	3	3	2	2	-

TABLE 6. Frequencies of alliances in aggressive interactions (scan observations, all interactions).

a) Group H	
Members of alliances	Frequency
Hanna, Herta, Heda	12
Hanna, Herta	20
Heda, Herta	6
Majo, Carmen	1
Hanna, Carmen	2

b) Group L	
Members of alliances	Frequency
Cora, Christa, Elke, Julia	3
Ilse, Maria, Sonja, Julia	1
Cora, Christa, Julia, Jutta	1
Cora, Christa, Julia	6
Cora, Elke, Julia	1
Cora, Julia	11
Christa, Julia	2
Maria, Sonja, Theo, Jutta	6
Maria, Sonja, Theo	9
Maria, Sonja, Elke	1
Maria, Sonja, Julia	1
Maria, Sonja, Jutta	12
Maria, Sonja	34
Maria, Theo, Jutta	3
Maria, Theo	3
Maria, Elke	1
Maria, Julia, Jutta	2
Maria, Julia	2
Maria, Jutta	23
Sonja, Theo, Jutta	1
Sonja, Theo	10
Sonja, Elke	1
Sonja, Julia	3
Sonja, Jutta	3
Sophie, Jutta	1
Theo, Elke	1
Elke, Julia	2
Elke, Jutta	1

subordinates. The victims were helped both by dominants and by subordinates. In the latter case, help was offered not only by relatives, but also by unrelated females whose status was lower than the aggressor's. No "dictatorship" of high-ranking females was observed in this group. On the contrary, the dominants were evidently interested in affiliative contacts with the subordinates, and practised several forms of such contacts other than grooming (initiation of spatial proximity, sitting close together, hugging, naso-nasal sniffing, touching, friendly vocalization, etc.). Overall, the dominance style of group L may be described as flexible, egalitarian, and largely similar to that practised by stump-tailed and tonkean macaques (Thierry 1985, Waal 1989, Butovskaya 1993a,b, 1994).

In group H, a positive correlation was observed between the nature of interindividual relationships and the tendency to form coalitions, suggesting that the typical strategy of

TABLE 7. Level of relationships between the group members (based on 4 affiliative and 2 agonistic criteria). 6 – best; 0 – worst.

a) Group H							
	Ch	M	C	L	He	Ha	Ht
M	4						
C	6	4					
L	2	5	6				
He	2	2	3	2			
Ha	0	1	3	0	4		
Ht	4	0	2	1	4	3	
Mj	3	5	5	5	4	1	0

b) Group L									
	Ch	M	Sn	Sp	I	E	C	Jl	Jt
M	2								
Sn	5	4							
Sp	6	3	4						
I	1	2	2	6					
E	3	3	4	4	4				
C	5	0	2	3	2	5			
Jl	6	2	1	3	4	2	5		
Jt	3	2	1	4	5	1	2	3	
T	3	2	4	2	1	4	2	1	1

daughters of the high-ranking mothers is to enter into coalitions with friendly individuals, primarily relatives. An attempt to establish a connecting bond with the alpha male made by a medium-ranking female Carmen had not resulted in an enhancement of her status, although, according to some writers, such alliances can be crucial for rank reversal between the macaque matriline (Chance *et al.* 1977, Chapais *et al.* 1991). The strategies of social behaviour in group L indicate that apart from personal preferences towards members of their blocs, the females tended to develop a network of affiliative bonds with other group members. The capacity for forming coalitions was higher in females of the high-ranking bloc. However, marked preferences in alliances were shown only by subordinate females. No correlation between the matrices of relationships and those of alliances was observed in group L, implying that friendly ties were not crucial for the establishment of alliances. Similarity in status was more important in this respect.

The strategies of the two alpha males, too, were different. The leader of group H supported subordinate females and often threatened the dominant female Hanna and her relatives. The male did not establish friendly bonds with Hanna, implying that the relationships between these individuals were antagonistic.

We have no direct evidence suggesting that the male competed with the alpha female for the dominance status, as was the case in Japanese macaques. However, the fact that the interference of the male on the side of the victims often failed to prevent aggression implies that some threat for him did exist. This interference should not be regarded as a manifestation of altruism. More likely, the male acted

TABLE 8. Standardized frequencies of behavioural variables (interactions with males included).

Group H		1p	1r	2p	2r	3p	3r	4p	4r	5p	5r	6p	6r	7	8	9p	9r	10p	10r	11p	11r	12p	12r	13p	13r	14p	14r	15p	15r	16	17
Mj	36	0	164	2	188	1781	188	206	8344	7200	150	75	113	2494	0	123	0	40	0	6	0	0	0	4	0	13	13	0	0	2	0
Ha	66	11	345	70	844	1781	263	75	4444	2100	263	19	56	1913	0	6	6	98	0	19	0	0	0	0	0	45	36	6	0	98	3
Ht	64	9	415	77	544	1125	375	19	4519	2438	150	169	113	1969	0	0	17	177	4	19	0	0	0	0	0	19	43	21	2	106	3
He	13	38	132	121	994	525	75	394	2719	7425	75	319	56	1913	15	0	66	47	15	4	0	0	0	0	2	21	11	2	15	64	1
Ch	13	38	70	138	375	169	356	131	5700	2006	150	150	75	2775	6	2	57	34	13	11	0	0	0	0	0	6	2	13	0	0	0
C	2	32	68	347	1200	169	150	319	5081	8775	150	113	150	2756	55	2	91	21	11	2	0	0	0	0	0	9	9	6	11	6	7
L	0	30	2	194	656	56	56	150	4219	3788	0	94	150	1256	21	0	79	0	11	0	0	0	0	0	2	0	0	0	11	0	3
M	0	36	13	260	825	19	263	431	2475	3769	19	19	206	3413	36	0	104	4	11	2	0	0	0	0	0	0	0	0	11	0	9

Group L		1p	1r	2p	2r	3p	3r	4p	4r	5p	5r	6p	6r	7	8	9p	9r	10p	10r	11p	11r	12p	12r	13p	13r	14p	14r	15p	15r	16	17
Th	42	2	294	28	109	4036	127	91	636	418	145	145	164	55	909	0	6	0	150	0	8	14	32	0	0	56	50	0	0	116	0
Sn	46	12	424	60	455	1109	327	400	5473	2982	273	291	91	11109	0	14	8	138	2	14	32	38	0	0	2	80	36	8	0	236	0
M	152	14	716	88	909	2309	709	164	2655	6364	891	145	91	10382	0	12	20	226	2	78	50	44	38	2	6	72	90	12	2	280	0
E	18	76	94	284	1182	709	455	400	1255	1655	127	636	18	9691	6	4	90	36	26	0	24	14	2	6	12	20	16	28	42	0	0
Jl	66	66	248	484	1364	545	327	127	2982	5691	1745	945	18	28891	2	26	120	68	30	20	64	66	10	22	28	24	60	0	108	0	0
Jr	48	60	260	232	1455	436	255	73	2073	1309	436	291	73	19673	14	0	80	50	2	8	52	46	10	6	28	80	8	8	170	0	0
Ch	8	28	90	166	527	127	91	545	1600	1836	400	509	18	25345	2	6	48	18	26	2	34	32	0	4	8	8	6	10	52	0	0
Sp	6	52	2	256	1255	218	145	655	636	709	145	1127	36	29782	12	0	118	0	18	0	0	0	0	0	16	2	0	0	42	2	0
Co	16	60	60	434	1127	109	91	200	4927	1855	436	291	73	19618	28	0	120	18	16	4	34	32	0	2	26	4	14	12	74	0	0
I	0	32	6	162	1273	55	327	200	3255	2673	527	727	91	23218	4	0	100	0	12	0	0	0	0	0	0	0	0	0	22	0	0

Note: 1, contact aggression; 2, noncontact aggression; 3, submission; 4, initiation of spatial proximity; 5, grooming; 6, friendly contacts; 7, scratching; 8, sitting close; 9, request for help; 10, running away; 11, going away; 12, quarrels; 13, ritual biting; 14, support of aggressor; 15, redirected aggression; 16, aggressive alliances; 17, injuries (nonstandardized); p, performed; r, received.

TABLE 9. Loadings on principal components, based on 30 behavioural variables

Variables	PC1	PC2	PC3	PC4	PC5
Contact aggression, p.	0.912	0.278	0.149	0.054	0.158
Contact aggression, r.	-0.560	0.688	0.148	0.106	-0.118
Noncontact aggression, p.	0.960	0.129	0.065	0.122	0.062
Noncontact aggression, r.	-0.536	0.628	0.459	-0.037	-0.217
Submission, p.	-0.368	0.651	0.357	0.297	0.098
Submission, r.	0.753	-0.197	-0.313	0.020	-0.054
Initiation of spatial proximity, p.	0.592	0.292	0.203	0.185	0.352
Initiation of spatial proximity, r.	-0.528	0.123	-0.245	0.224	0.442
Grooming, p.	0.136	-0.487	0.331	-0.633	0.049
Grooming, r.	0.092	-0.141	0.654	-0.326	0.433
Friendly contacts, p.	0.303	0.795	0.245	-0.341	-0.009
Friendly contacts, r.	-0.388	0.750	-0.361	-0.052	0.259
Scratching	-0.077	-0.628	0.624	0.143	0.037
Sitting close	-0.258	0.814	-0.212	-0.049	0.095
Request for help, p.	-0.556	-0.192	0.658	0.262	-0.117
Request for help, r.	0.220	-0.221	-0.035	-0.739	0.379
Running away, p.	-0.757	0.512	0.317	0.121	-0.017
Running away, r.	0.931	0.018	-0.027	0.157	-0.009
Going away, p.	-0.608	0.614	-0.022	-0.166	0.046
Going away, r.	0.823	0.236	0.266	0.147	0.297
Quarrels, p.	0.403	0.796	0.117	-0.066	-0.212
Quarrels, r.	0.458	0.731	0.036	-0.102	-0.316
Ritual biting, p.	0.665	0.402	0.323	0.156	0.385
Ritual biting, r.	-0.193	0.831	-0.071	-0.193	0.097
Support of aggressor, p.	0.848	0.126	-0.083	0.131	-0.143
Support of aggressor, r.	0.848	0.222	0.047	0.305	-0.085
Redirected aggression, p.	0.170	0.698	0.277	-0.421	-0.208
Redirected aggression, r.	-0.686	0.252	-0.255	0.416	0.405
Alliances	0.843	0.331	0.028	0.237	-0.104
Injuries	-0.278	-0.456	0.636	0.275	-0.064
Percent of variation	34.823	25.905	10.115	7.416	4.964

Note: see Table 1 for abbreviations.

in his own interests. The situation was profitable for him, since the risk that someone (the alpha female or her relatives) would challenge his leadership was thereby eliminated (Bercovich 1988, Chapais *et al.* 1991).

The male leader of group L usually took the side of the dominant females against Julia, who headed the second bloc. The male's affiliative bonds with the females (members of his coalition and those of the rival bloc alike) were much weaker than those of his counterpart in group H. The strategy of cooperation and alliances with several high-ranking female partners could have been aimed at enhancing the male's dominant status. Possibly, the sense of insecurity and the need for cooperating with others in conflict situations are distinctive features of sons of low-ranking mothers. These features make quite difficult for them to acquire a dominant status after having migrated from their native group to a new one.

There is abundant evidence suggesting that in matrilinear species only close relatives dare to support each other in clashes with dominant individuals while

distant relatives and unrelated animals tend to support high-ranking females against those whose mothers' status was low (Silk 1982, Netto, Hooff 1986, Pereira 1989, Chapais *et al.* 1991). This is precisely what happened in group H. In group L, however, there were many exceptions to this rule: in 30% of alliances in which the low-ranking females took part, they supported victims who were not their close relatives against the aggressors whose status was higher than that of the supporters.

The principal strategy of females in group H was to keep as far as possible from unrelated individuals. Irrespective of their actual rank, then, these females tended to disperse in space. This is a typical strategy of unrelated high-ranking macaques (Bernstein, Ehhardt 1986). The use of canines in clashes between the females indicates that the relationships in group H were unstable (Kaplan *et al.* 1980). Regardless of their actual status, females born of high-ranking mothers tend to be less flexible in their relationships with other animals.

Position of individuals in groups H and L on the 2nd and 3rd principal components based on 30 behavioural parameters (60.7% of variation).

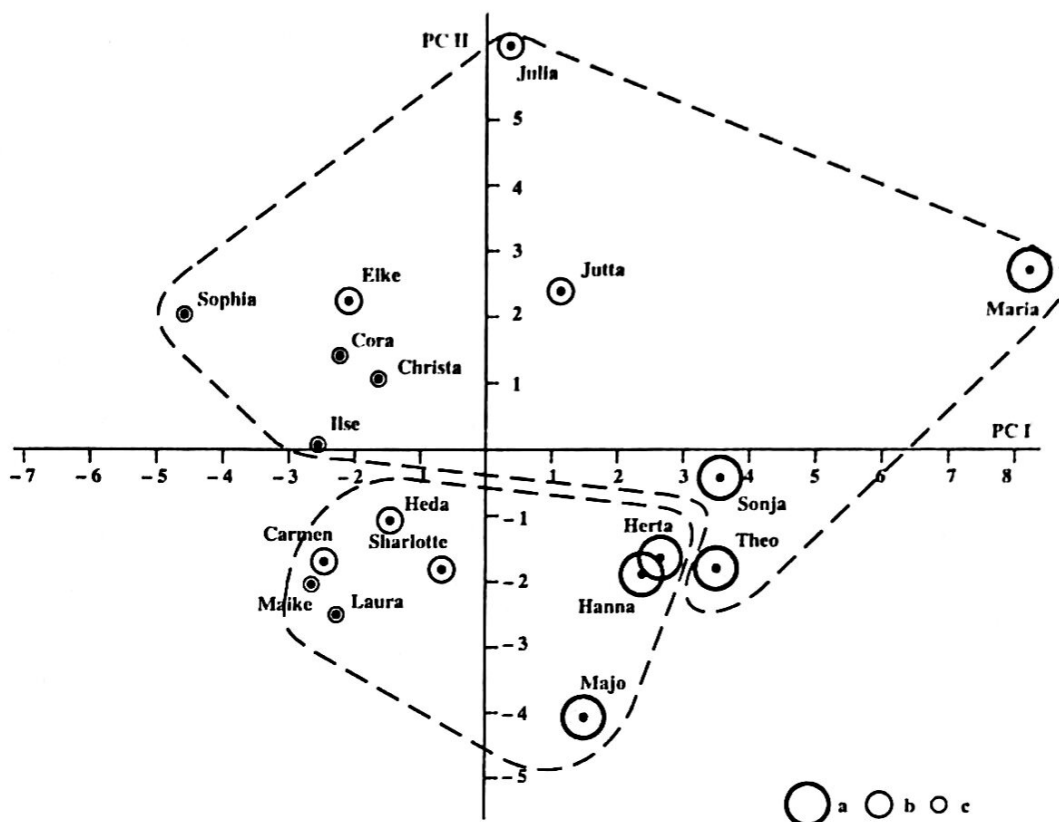


FIGURE 1. Similarities in principal behavioural strategies of individuals from two groups, expressed in the space of PC I and PC 2 coordinates. Dominance status of individuals within their own group: a – high; b – medium; c – low; black figures – males, plain figures – females.

In group L, the principal function of aggression was to enhance social structure (Bernstein, Ehardt 1986, Waal, Luttrell 1989). By entering into alliances and cooperating in attacks the females strengthened their bonds and increased the stability of the group. The greater social adaptability of females with a low inborn status and their ability to form stable groups are important survival strategies for low-ranking matriline in species with a despotic dominance style since these matriline are the first to emigrate from the natal groups.

These conclusions are confirmed by the results of the principal components analysis. While PC1 differentiates all the animals according to their actual ranks, PC2 (which is uncorrelated with PC1) sets them apart according to group membership. This means that, irrespective of their actual rank, animals whose inborn rank was high differed from those whose inborn rank was low in a number of features of social behaviour. Because the two groups differ in the same way as do the males and the females within each of the groups, the behavioural style of the females in group H may be described as more masculine, dominant, assertive, and independent.

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REFERENCES

- ALTMANN J., 1974: Observational study of behaviour: Sampling methods. *Behaviour* 49: 227-267.
- AURELI F., 1992: Post-conflict behaviour among wild long-tailed macaques (*Macaca fascicularis*). *Behavioural Ecology and Sociobiology* 31: 329-337.
- AURELI F., SCHAIK C. van, HOOFF A. R. A. M. van, 1989: Functional aspects of reconciliation among captive long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology* 19: 39-51.
- BERCOVICH F. B., 1988: Coalitions, cooperation and reproductive tactics among adult male baboons. *Animal Behaviour* 36: 1198-1209.

- BERNSTEIN I. S., 1991: An empirical comparison of focal and ad libitum scoring with commentary on instantaneous scans, all occurrence and one-zero techniques. *Animal Behaviour* 42: 721-728.
- BERNSTEIN I. S., EHARDT C. L., 1986: The influence of kinship and socialization on aggressive behaviour in rhesus monkeys (*Macaca mulatta*). *Animal Behaviour* 34: 739-747.
- BUTOVSKAYA M. L., 1993: Kinship and different dominance styles in groups of three species of the Genus *Macaca* (*M. arctoides*, *M. mulatta*, *M. fascicularis*). *Folia Primatologica* 60: 210-224.
- BUTOVSKAYA M. L., 1993b: Intrusion into agonistic encounters in 3 species of the Genus *Macaca* (*Macaca arctoides*, *M. mulatta*, *M. fascicularis*) with reference to different dominance styles. *Primate Report* 37: 41-50.
- BUTOVSKAYA M. L., 1994: Towards a social psychology of personal behavior: Attachments in four species of the Genus *Macaca*. *Current Primatology* 2: 119-126.
- BUTOVSKAYA M. L., KOZINTSEV A. G., KOZINTSEV B. A., 1994: The structure of affiliative relations in a primate community: Allogrooming in stump-tail macaques (*Macaca arctoides*). *Hum. Evol.* 9: 11-23.
- BUTOVSKAYA M. L., KOZINTSEV A. G., WELKER C., 1995: Grooming and social rank by birth: The case of *Macaca fascicularis*. *Folia Primatologica* 65: 30-33.
- BUTOVSKAYA M. L., LADYGINA O. N., 1989: Support and cooperation in agonistic encounters of stump-tail macaques (*Macaca arctoides*). *Anthropologie* 27: 73-81.
- CASTLES D. L., AURELI F., WAAL F. B. M. de: Variation in conciliatory tendency and relationship quality across groups of pigtail macaques. *Animal Behaviour* (in print).
- CHAFFIN C. L., FRIEDLEN K., WAAL F. B. M. de, 1995: Dominance style of the Japanese macaques compared with rhesus and stump-tail macaques. *American Journal of Primatology* 35: 103-116.
- CHANCE M. R. A., EMORY G. R., PAYNE R. G., 1977: Status referents in long-tailed macaques (*Macaca fascicularis*): Precursors and effects of a female rebellion. *Primates* 18: 611-632.
- CHAPAIS B., 1995: An experimental analysis of a mother-daughter rank reversal in Japanese macaques (*Macaca fuscata*). *Primates* 26: 407-423.
- CHAPAIS B., MIGNAULT C., 1991: Homosexual incest avoidance among females in captive Japanese macaques. *American Journal of Primatology* 23: 171-183.
- DATTA S. B., 1989: Demographic influences on dominance structure among female primates. In: V. Standen and R. A. Foley (Eds.): *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals*. Pp. 265-284. Oxford.
- DUNBAR R. I. M., 1976: Some aspects of research design and their implications in the observational study of behaviour. *Behaviour* 58: 78-98.
- HEMELRIJK C. K., 1990: Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Animal Behaviour* 39: 1013-1029.
- KAPLAN J. R., MANNING P., ZUCKER E., 1980: Reduction of mortality due to fighting in a colony of rhesus monkeys (*Macaca mulatta*). *Laboratory Animal Science* 6: 565-570.
- LEHNER P. N., 1979: *Handbook of Ethological Methods*. New York.
- LOTT D. F., 1984: Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88: 266-325.
- NETTO W. J., HOOFF J. A. R. A. M. van, 1986: Conflict interference and the development of dominant relationships in immature *Macaca fascicularis*. In: J. G. Else and P. C. Lee (Eds.): *Primate Ontogeny, Cognition and Social Behaviour*. Pp. 291-300. Cambridge.
- PEREIRA M. E., 1989: Agonistic interactions of juvenile savanna baboons. II. Agonistic support and rank acquisition. *Ethology* 80: 152-171.
- PETIT O., THIERRY B., 1994: Reconciliation in a group of black macaques. *Dodo Journal of Wildlife Preservation Trusts* 30: 89-95.
- SCHAIK C. P. van, 1989: The ecology of social relationships amongst female primates. In: V. Standen and R. A. Foley (Eds.): *Comparative Socioecology: The Behavioural Ecology of Humans and Other Animals*. Pp. 195-218. Oxford.
- SILK J. B., 1982: Altruism among female *Macaca radiata*: Explanations and analysis of patterns of grooming and coalition formation. *Behaviour* 79: 162-188.
- THIERRY B., 1985: Patterns of agonistic interactions in three species of macaques (*Macaca mulatta*, *M. fascicularis*, *M. tonkeana*). *Aggressive Behavior* 11: 223-233.
- THIERRY B., 1988: A comparative study of aggression and response to aggression in three species of macaques. In: J. Else and P. C. Lee (Eds.): *Primate Ontogeny, Cognition, and Social Behaviour*. Vol. 3. Pp. 307-313. Cambridge.
- THIERRY B., 1993: Emergent constraints condition the action of ultimate causes. *Journal of Theoretical Biology* 160: 403-405.
- WAAL F. B. M. de, 1989: Dominance "style" and primate social organization. In: V. Standen and R. A. Foley (Eds.): *Comparative Socioecology: The Behavioural Ecology of Humans and Other Animals*. Pp. 243-263. Oxford.
- WAAL F. B. M. de, 1993: Reconciliation among primates: A review of empirical evidence and unresolved issues. In: W. A. Mason and S. P. Mendoza (Eds.): *Primate Social Conflict*. Pp. 111-144. New York.
- WAAL F. B. M. de, LUTTRELL L. M., 1989: Towards a comparative socioecology of the genus *Macaca*: Different dominance styles in rhesus and stump-tail monkeys. *American Journal of Primatology* 19: 83-109.
- WAAL F. B. M. de, REN R. M., 1988: Comparison of the reconciliation behavior of stump-tail and rhesus macaques. *Ethology* 78: 129-142.
- WAAL F. B. M. de, YOSHIHARA D., 1983: Reconciliation and redirected affection in rhesus monkeys. *Behaviour* 85: 224-241.
- WATTS D. P., 1994: Social relationships of immigrant and resident female mountain gorillas. *American Journal of Primatology* 32: 13-30.
- WILLIAMS G. C., 1966: *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton.
- WRANGHAM R. W., 1980: An ecological model of female-bonded primate groups. *Behaviour* 75: 262-300.

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