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**The structure of affiliative relations in
a primate community: allogrooming in
stumptailed macaques (*Macaca arctoides*)**

Social grooming in 19 adult stumptailed macaques (a dominant male and 18 females) was studied by focal sampling and scanning methods. Significant individual differences were found with respect to both active and passive grooming intensity, active grooming being a more variable parameter. Individual preferences in partner choice are very strong, but among the factors examined, age was the only one influencing these preferences. Neither social rank nor kinship were significant. The proportion of active and passive contacts shows marked individual differences. Yet, there is a positive association between performed and received grooming. The "extortion hypothesis" is not supported by our results: high-ranking individuals performed on the average more, and received relatively less grooming than low-ranking ones. High grooming performance of the dominants may secure group integrity in species with a "soft" dominance style.

Key words: Primates, social structure,
grooming.

Introduction

Allogrooming, or social grooming, one of the most frequent types of affiliative behavior in primates, is traditionally regarded as an indicator of group integration aimed at establishing closer social links, reducing tension, and preventing aggression (Carpenter, 1964; Hausfater & Sutherland, 1984; Easley et al., 1989). Being a means of removing ectoparasites, grooming has purely hygienic functions as well. In a number of works, both social and hygienic aspects of grooming were analyzed (McKenna, 1978; Boccia, 1989; Thierry et al., 1990), while some investigators focused on the relations between allogrooming and other social parameters, most importantly, dominance status (e.g. Seyfarth, 1983; de Waal & Luttrell, 1986; Dunbar, 1988; Easley et al., 1989).

According to a wide-spread belief, grooming is more useful for the recipient than for the performer. This postulate provides a basis for Silk's extortion hypothesis which states that high-ranking animals can, and do, receive more grooming than they perform (Silk, 1982). There is a growing amount of data, however, indicating that relations between grooming and dominance are more complex, and that they may be different even in various populations of the same species (Altmann, 1980; de Waal & Luttrell, 1986; Dunbar, 1988).

The objective of the present paper is to analyze the structure of grooming ties in a group of stumptailed macaques and to examine the relation of grooming to dominance and other characteristics of social behavior.

Materials and Methods

A group of stump-tailed macaques was observed in summer and autumn 1986 at the Tamysk division of the Sukhumi Primate Research Center, Republic of Georgia. The group comprised 19 adult animals, including a dominant male (C-1) and 18 females (Figure 1). The animals were kept in a 600 m² outdoor corral with inside sections for sleep and feeding. All animals were identified, and their kinship relations were known. Observations on dominance/submission, individual activity, non-contact friendly behavior, and aggression were performed using the focal animal sampling. For grooming and spatial proximity, the whole group scanning from left to right was used. Ten scannings, 3 minutes in duration each, were made per one observation series lasting 30 minutes. The total observation time was 190 hours, and 742 grooming bouts were observed.

A grooming matrix was constructed (Table 1) whose element on the intersection of *i*-th row with *j*-th column is the number of instances (g_{ij}) when *i*-th animal groomed *j*-th, and the element on the intersection of *j*-th row with *i*-th column, the number of cases (g_{ji}) when the reverse was true. Cases in which one animal groomed another without receiving grooming from it either during the same bout or later, were regarded as one-way grooming. Cases in which one animal groomed another and did receive grooming from it either at the same time or later, were regarded as two-way grooming.

On the basis of dominance and submission behavior (Butovskaya & Ladygina, 1989, 1990), dominance index was calculated (Zumpe & Michael, 1986). Landau's linearity index could not be calculated because of missing observations.

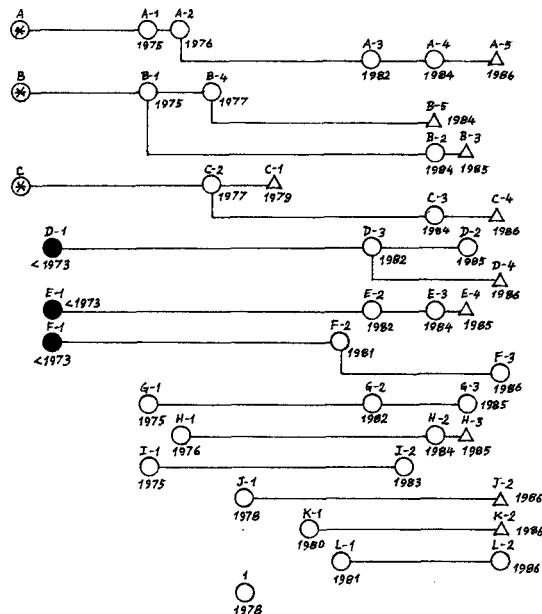


Figure 1 - The composition of the group. Circles denote females, triangles, males. Year of birth is given for each individual. A, B, and C, marked by asterisks, are founders of the matriline (all of them have died). D-1, E-1, and F-1 (shown by black circles) were brought from Thailand in 1973. The group stems from a fission of the primary population in 1983.

Following null hypotheses were tested:

Ho1) Both active and passive grooming contacts of each animal are random and follow the Poisson distribution. To test this hypothesis, the coefficient of dispersal, CD (the variance divided by the mean) was calculated for each row and each column of the grooming matrix (Sokal and Rohlf, 1969; Easley et al., 1989). Because the variance of the Poisson distribution equals the mean, CD must be close to 1 if Ho1 is true. The significance of deviations from randomness was tested with the χ^2 -test, using the formula $\chi^2 = 17CD$, 17 being the number of degrees of freedom with 18 possible partners.

Ho2) The animals do not differ either in their overall grooming performance or in their overall attractiveness as grooming objects. To test this hypothesis, CD was applied to the distribution of row totals and column totals (n_a and n_p), taken separately, and the results were assessed using the formula $\chi^2 = 18CD$, 18 being the number of degrees of freedom with 19 individuals. The same was done with the distribution of animals with respect to the number of active and passive partners (also taken separately) each of them had.

Ho3) There are no individual preferences in partner choice. That is, if A grooms B more often than it grooms C, this is due, not to any peculiar dispositions of A, but to the fact that B is generally (i.e. for other animals as well) a more attractive object than C. If, on the other hand, A grooms B more often than C does, this is due, not to any specific features of B, but to A's being generally more active than C. In short, Ho1 may be false only because Ho2 is false. To test this hypothesis, expected frequencies for each cell of the grooming matrix were calculated using Wagner's iterative algorithm (Wagner, 1970). After that, the χ^2 -test with $k(k-3)+1$ degrees of freedom was applied.

Ho4) There are no individual differences in the relative amount of active and passive grooming. (The absolute amount may be different, that is, Ho2 may be false). To test this hypothesis, the numbers of active contacts and passive partners various animals had were compared with the numbers of their passive contacts and active partners, respectively, using Stuart's multivariate method (Stuart, 1955). Also, the binomial test was applied to each pair of symmetrical elements of the grooming matrix. It was impossible to generalize this test for the entire matrix because the expected values were too small.

Ho5) There is no relation between active and passive grooming. This hypothesis was tested by means of the Spearman's rank correlation coefficient applied to marginal totals of the grooming matrix. Beside that, the random permutation tests based on Spearman's (R-method) and Kendall's (K-method) approaches (Dietz, 1983; Dow & Cheverud, 1985; Hemelrijk, 1990) were used to see if the original and the transposed grooming matrices are correlated. We performed 500 random permutations, and each time the elements of the two matrices were ranked and compared within each row and each column (that is, only connected pairs were taken into account). The significance level was $(L+1)/(M+1)$, L being the number of permutations in which the test value was equal to, or larger than, the original value, and M, the total number of permutations.

Ho6) There is no relation between grooming and other social parameters. Same methods as those described in the preceding paragraph were used to test this hypothesis.

For assessing the structure of grooming relations, two multivariate methods, cluster analysis and non-metrical multidimensional scaling, were employed (Easley et al., 1990).

Results

Before testing the null hypotheses, the overall intensity of grooming relations must be evaluated. As can be seen from Table 1, not a single animal was excluded from grooming contacts with others, the minimal number of partners being 7, the minimal number of contacts, 24. Also, not a single animal had grooming relations with all others; the maximal number of partners was 16 out of 18 possible, the maximal number of contacts, 169. The differences in the number of partners are insignificant ($CD=0.6$), the average number being 11.9, including 6.8 one-way partners (3.4 perform-only and 3.4 receive-only) and 5.1 two-way partners. The differences in the contact frequency are highly significant ($CD=18.7$, $P<0.001$), the average frequency being 78.1, or 39 active and 39 passive.

CD_a and CD_p values for various animals (Table 1) are always larger than 1 and sometimes reach 22, indicating strongly nonrandom distribution. In 34 cases out of 38, the χ^2 values are significant (30 of them, at the 0.1% level), and in only four cases (active contacts of L-1 and G-2; passive contacts of F-2 and G-2) they do not reach significance level, probably because each of these animals had very few contacts with others.

So for the vast majority of individuals both active and passive contacts with various partners are not equally probable, and H_01 must be rejected. What is the reason for that?

Let us test H_02 . The variation of the total active grooming frequency is very large, from 5 to 106, CD equalling 19.8. The variation of the total passive grooming frequency is considerably less (17-79), with CD almost three times lower (6.9), although also highly significant. There is an even stronger contrast between the variation in the number of passive partners (2-16, $CD=1.6$, $P<0.05$) and active partners (6-13, $CD=0.5$, meaning that the variation is significantly reduced). Thus H_02 is also rejected, the overall grooming performance being much more variable than the overall attractiveness.

As to H_03 , it should first be noted that only 2/3 of the possible number of grooming dyads were observed (113 out of 171, or 66%). Among these, less than a half (48) were two-way dyads, while 65 were one-way dyads. Comparing observed and expected frequencies in the reduced grooming matrix 9x9 (ten animals having theoretical frequencies below 1 had to be excluded) yielded a χ^2 value of 618.3 (d.f.=55, $P<0.001$). Almost 3/4 of this value is accounted for by following two-way dyads: C-1 and C-2; F-1 and B-4; A-1 and I-1; D-1 and C-2. The contacts within these dyads occurred much more frequently than could be expected if no individual preferences existed. In the first dyad, the excess was caused mainly by the increased activity of the female (C-2) directed at the male (C-1); in other dyads, bidirectional excess was observed.

The inspection of normalized residuals in the original grooming matrix 19x19 revealed three more dyads with excessive intensity of contacts: E-1 and D-3; B-1 and J-1; I and K-1. In all these dyads, the excess was bidirectional and the expected frequencies were not too low. Overall, individual preferences are so marked that H_03 should also be rejected. The opposite phenomenon, avoidance, could not be discerned in our sample because the expected frequencies are too low for that purpose.

Turning to H_04 we see that in 8 dyads the asymmetry of active and passive grooming was statistically significant according to the binomial test. Taking into consideration the significance level (5% in six dyads, 1% in two) and the total number of possible dyads (171), this result could be ascribed to chance. However, Stuart's test value ($Q=101.4$, d.f.=18) indicates that the difference between the animals in the proportion of active and passive contacts is highly significant. Consequently, despite the fact that differences in the proportion of passive and active partners are insignificant ($Q=15.2$), H_04 can not be accepted.

TABLE 1 - Frequencies of grooming in stumptailed macaques.

Active partners	Passive partners														Dominance												
	C-1	F-1	A-1	G-1	D-1	I-1	E-1	B-1	A-2	H-1	B-4	C-2	1	J-1	K-1	F-2	L-1	D-3	G-2	n _a	x _a	s _a	CD _a	P	PP	Status	Rank
C-1	-	4	5	0	1	11	6	9	7	12	4	21	0	5	3	2	8	4	4	106	5.9	5.1	4.4	16	6	100.0	1
F-1	0	-	0	5	0	0	1	1	6	0	23	0	0	0	0	0	0	3	0	39	2.2	5.5	14.0	6	2	0.0	17.5
A-1	0	1	-	0	0	12	0	3	4	13	0	5	0	0	2	0	2	3	0	45	2.5	4.0	6.3	9	4	87.5	2
G-1	0	5	0	-	1	0	0	3	2	0	1	2	0	0	0	0	0	0	3	17	0.9	1.5	2.3	7	3	62.5	5
D-1	2	0	0	0	-	4	1	0	5	2	0	25	0	0	0	0	0	1	0	40	2.2	5.9	15.5	7	2	52.8	9
I-1	8	0	14	0	1	-	7	0	4	3	0	0	0	2	3	0	1	3	3	49	2.7	3.7	5.0	11	3	81.8	3
E-1	3	0	2	0	0	1	-	0	0	0	0	1	0	0	1	2	2	11	0	23	1.3	2.6	5.3	8	4	66.7	4
B-1	3	0	0	2	0	1	0	-	1	0	2	0	1	13	0	2	0	1	0	26	1.4	3.0	6.4	9	4	34.8	11
A-2	0	3	2	0	3	1	0	0	-	6	2	0	0	3	3	1	0	0	0	24	1.3	1.7	2.2	9	1	31.8	12
H-1	18	9	9	1	15	0	0	4	12	-	2	10	3	5	4	1	3	5	0	101	5.6	5.4	5.2	15	9	53.2	8
B-4	1	22	0	6	2	1	0	10	8	0	-	2	2	5	7	5	0	0	2	73	4.1	5.5	7.3	13	8	25.0	13.5
C-2	22	0	0	0	15	0	0	2	2	1	0	-	0	0	0	3	0	0	0	45	2.5	6.0	14.5	6	2	58.3	6.5
1	0	0	0	0	0	0	0	0	0	0	0	0	-	0	25	0	1	0	2	28	1.6	5.9	22.2	3	1	0.0	17.5
J-1	1	0	0	0	0	1	0	10	3	0	0	0	1	-	2	3	0	0	0	21	1.2	2.4	5.1	7	2	0.0	17.5
K-1	0	0	0	0	0	0	0	0	3	0	0	5	10	3	-	0	4	5	0	30	1.7	2.8	4.7	6	1	58.3	6.5
F-2	0	0	0	0	0	4	0	1	0	0	0	0	0	0	0	-	0	0	0	5	0.3	1.0	3.3	2	1	12.5	15
L-1	1	0	3	0	1	1	1	1	1	0	0	4	0	0	0	3	-	3	0	19	1.1	1.3	1.6	10	5	46.4	10
D-3	4	2	2	2	0	0	10	0	0	5	0	4	0	1	3	5	3	-	3	44	2.4	2.6	2.8	12	5	25.0	13.5
G-2	0	0	1	2	0	1	0	0	0	0	0	0	2	0	0	0	1	0	-	7	0.4	0.7	1.3	5	2	0.0	17.5
n _p	63	46	38	18	39	38	26	44	58	42	34	79	19	37	56	24	25	39	17	742	-	-	-	-	-	-	-
x _p	3.5	2.6	2.1	1.0	2.2	2.1	1.4	2.4	3.2	2.3	1.9	4.4	1.1	2.1	3.1	1.3	1.4	2.2	0.9	-	-	-	-	-	-	-	-
s _p	6.4	5.4	3.8	1.8	4.7	3.6	3.0	3.6	3.4	4.1	5.4	7.3	2.4	3.4	5.8	1.7	2.1	2.9	1.4	-	-	-	-	-	-	-	-
CD _p	11.6	11.6	6.8	3.3	10.4	6.2	6.1	5.2	3.5	7.3	15.4	12.2	5.5	5.5	10.8	2.2	3.1	3.8	2.2	-	-	-	-	-	-	-	-
n _i	169	85	83	35	79	87	49	70	82	143	107	124	47	58	86	29	44	83	24	-	-	-	-	-	-	-	-
x _i	9.4	4.7	4.6	1.9	4.4	4.8	2.7	3.9	4.6	7.9	5.9	6.9	2.6	3.2	4.8	1.6	2.4	4.6	1.3	-	-	-	-	-	-	-	-
s _i	11.1	10.7	7.4	2.9	9.8	6.9	5.3	6.0	4.8	8.6	10.4	13.0	8.2	5.5	8.1	1.8	2.5	5.1	1.8	-	-	-	-	-	-	-	-
CD _i	13.0	24.0	11.9	4.4	22.1	9.8	10.2	9.3	5.0	9.3	18.1	24.4	25.6	9.3	13.6	2.1	2.5	5.6	2.5	-	-	-	-	-	-	-	-
A	10	7	8	6	8	11	6	10	13	7	6	10	6	8	11	9	9	10	6	-	-	-	-	161	-	-	-
AA	0	3	3	2	3	3	2	5	5	1	1	6	4	3	6	8	4	3	3	-	-	-	-	-	65	-	-
T	16	9	12	9	10	14	10	14	14	16	14	12	7	10	12	10	14	15	8	-	-	-	-	-	-	-	-
Status	23.5	52.5	44.0	46.2	51.7	44.6	43.5	56.8	73.0	19.0	20.1	72.1	68.4	61.7	69.7	86.7	49.7	45.7	60.6	-	-	-	-	-	-	-	-
Rank	17	9	15	12	10	14	16	8	2	19	18	3	5	6	4	1	11	13	7	-	-	-	-	-	-	-	-

n_a, x_a, s_a and CD_a are total number, mean, standard deviation, and coefficient of dispersal of the number of active contacts, n_p, x_p, s_p and CD_p, n_i, x_i, s_i and CD_i same for passive and total number of contacts; A is number of active partners, AA, number of perform-only partners, P and PP, numbers of passive and receive-only partners, respectively, T, total number of partners. Indexes of grooming and dominance status are given as percentages.

Once the existence of asymmetry in active and passive grooming has been established, it is possible to propose an index which is formally identical to Zumpe and Michael's dominance index (Zumpe & Michael, 1986) but aims at evaluating the relative status of a given animal, not as a subject, but as an object. It measures the share of received grooming in the total number of grooming contacts. Let us define the grooming status of the i -th animal against the j -th as the ratio $g_{ji}/g_{ij} + g_{ji}$. The unweighted average of this ratio over all i -th animal's partners provides a measure of this animal's overall grooming status and is perfectly suited to test the extortion hypothesis (see above).

As we see from Table 1, the index of grooming status varies from 19.0% in H-1 (if the strategy "receive more and perform less" is actually practiced, this should be regarded as the lowest status) to 86.7% in F-2 ("highest status"). The index shows strong negative correlation with active grooming, that is, frequency of active contacts ($r_s = -0.58$) and number of passive partners ($r_s = -0.77$), but little if any correlation with passive grooming (0.05 and 0.32, respectively).

Ho5 must also be rejected. The coefficient of Spearman's rank correlation between the frequency of active and passive contacts (n_a and n_p) equals 0.60; as the test with 1000 random permutations showed, the significance level is 4.2% in this case. It becomes even higher ($P=0.2\%$) if we consider not only the marginal totals but all pairwise contacts and apply the permutation test for a correlation between the original grooming matrix and its transpose (Table 2). Thus active groomers have more chances to receive grooming from others. However, the correlation between the number of passive and active partners is insignificant ($r_s = 0.23$).

As Tables 2 and 3 demonstrate, Ho6 is false as well since grooming is correlated with some parameters of group behavior. Specifically, the higher the dominance status, the higher the grooming performance (frequency of active contacts, number of passive partners) and, consequently, the lower the grooming status ($r_s = -0.48$, $P < 0.05$). The dominant male had a maximal number of active grooming contacts and passive partners, and his grooming status ranks 17th (one of the lowest). The opposite extreme (lowest grooming performance and highest grooming status is occupied by F-2, a young female with a very low dominance rank (15). Not a single animal has high ranks on both scales, dominance and grooming. Opposite cases (low rank on both scales) do exist and they disturb the general tendency; this is especially true of the female B-4.

Passive grooming is not correlated with either dominance or submission. Thus dominance status apparently has no effect upon the attractiveness of an animal as a grooming object and probably as a social partner in general.

As follows from Table 2, grooming contacts between animals usually spending time in close proximity were on the average more intensive than between others. Animals which more often became objects of non-contact friendly actions were groomed more often (Table 3). Neither performed nor received grooming depends on age or individual activity. The correlations of grooming parameters with aggression status (the share of aggressive actions performed by the animal in the total number of its agonistic contacts) are of the same direction as those with dominance status, but lower (Table 3).

Presently we shall analyze the structure of grooming relations by means of multivariate methods following the approach used by Easley et al. (1990). To do this, we shall introduce the concept of grooming distance and calculate the distance index, d_{ij} , between i -th and j -th animals as $d_{ij} = 1 - n_{ij}/n_{\max}$ where $n_{ij} = g_{ij} + g_{ji}$ (total number of grooming bouts between i -th and j -th animals), and n_{\max} is the maximal number of bouts among all dyads. Essentially, this dissimilarity measure is the standardized form of the measure used by Easley et al., (1990). The standardization, that is, division of $(n_{\max} - n_{ij})$ by n_{\max} , is introduced to ensure that d_{ij} has not only a lower limit, zero (if i -th and j -th individuals were the dyad with the highest number of bouts), but also an

TABLE 2 - Correlation between grooming and other parameters: results of 500 random permutation tests.

Parameters	K	P	R	P
1. Active grooming vs. passive grooming (correlation between the original grooming matrix and its transpose)	740*	0.002	34099.25*	0.002
2. Grooming vs. dominance				
a) Both matrices original				
Active grooming vs. dominance	229*	0.008	31885.5*	0.020
Passive grooming vs. submission	96	0.110	31321.5	0.068
Total	325*	0.014	-	-
b) One of the matrices transposed				
Active grooming vs. submission	-7	0.517	30831.25	0.517
Passive grooming vs. dominance	115	0.072	31408.25	0.066
Total	108	0.208	-	-
c) Grooming distance vs. difference in dominance status	187	0.130	31733.5	0.094
3. Grooming distance vs. difference in age	374*	0.006	32649.0*	0.012
4. Grooming vs. spatial proximity				
Active grooming	1048*	0.002	35356.0*	0.002
Passive grooming	1062*	0.002	35356.0*	0.002
Total	2110*	0.002	-	-
5. Grooming distance vs. difference in grooming status	-221	0.912	29872.5	0.910

K is the unnormalized Kendall's tau statistic for connected pairs (i.e. those having one individual in common), and R is the unnormalized Spearman's rho statistic based on ranks within rows and within columns of the matrices. P is the significance level (see methods). Values significant at the 2% or higher level are marked with asterisks.

TABLE 3 - Spearman's rank correlation coefficients between grooming and other parameters.

Parameters	x_a	P	x_p	A	x_t	T	Grooming status
Dominance status	0.44	0.46*	0.31	0.29	0.43	0.42	-0.48*
Age	0.21	0.08	0.16	-0.20	0.16	-0.16	-0.30
Individual activity	0.10	0.32	0.07	0.14	0.25	0.26	-0.14
Friendly non-contact acts (performed)	0.22	0.22	0.07	0.01	0.23	0.24	-0.24
Friendly non-contact acts (received)	0.08	0.04	0.52*	0.60**	0.22	0.30	0.33
Aggression status	0.26	0.44	0.30	0.18	0.32	0.38	-0.44

The grooming parameters are denoted as in Table 1.

* $P < 0.05$ ** $P < 0.01$

upper limit, 1 (if these animals had no contacts). This may provide an advantage when between-group comparisons are made.

The clustering of the (d_{ij}) matrix performed with the use of the unweighted pair-group average-linkage method (Sneath and Sokal, 1973) yielded a dendrogram shown in Figure 2. To increase the informative contents of the graph, one more axis, dominance status, was added above the upper (zero) level so that the height of the terminal point of a branch shows the individual's position in the group hierarchy.

The cophenetic correlation coefficient between d_{ij} and the distance separating the respective animals on the dendrogram (level of the nearest common branching-point) is sufficiently high (0.86), indicating that the tree-like scheme provides a fairly good representation of the original data.

The structure of grooming relations in the group studied is rather amorphous. Two loosely defined clusters are seen in Figure 2. The larger one comprises 9 animals (C-1 to L-1), including all four high-ranking ones (C-1, A-1, I-1, E-1), as well as four middle-ranking and only one low-ranking. The opposite is true of their grooming status: it is low in most of these animals (five), medium in three, and high in one only. The second cluster consists of six animals (F-1 to J-1), including five females with a low dominance rank and one medium-ranking. Their grooming status, on the contrary, is high or medium with only one exception. There is also one isolated dyad comprising a medium-ranking animal (K-1) and a low-ranking one (1), both having a high grooming status. Two young females with a low dominance rank (F-2 and G-2) are very isolated and may be regarded as separate units.

As Table 2 demonstrates, there is a positive correlation between grooming distance and difference in dominance status, but this correlation is insignificant. The correlation between grooming distance and difference in age is also positive and significant, that is, grooming partners were on the average closer in age than could be expected by chance. The correlation between grooming

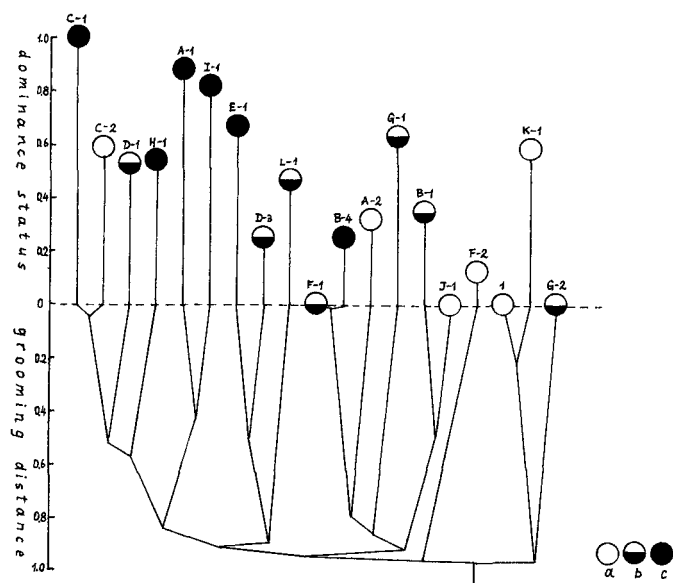


Figure 2 - Dendrogram based on the results of clustering of grooming distances between the animals. Categories of grooming ranks according to the extortion hypothesis: a — high (1-6), b — medium (7-13), c — low (14-19). See text for explanations.

distance and grooming status is negative, which means that animals differing in grooming performance became partners more often than those who were equally active, but this tendency falls a little short of the significance level.

As to the kinship relations, only one pair of relatives, the dominant male (C-1) and his sister (C-2) had an excessive number of grooming contacts, the excess being due mainly to the sister's activity directed at the brother. Members of other matriline (B-1 and B-4; D-1 and D-3), although belonging to the same grooming space in the broad sense, did not display strong mutual preferences, and in some cases (A-1 and A-2; G-1 and G-2; F-1 and F-2) members of one matriline even belong to different grooming clusters (Figure 2). The clustering of another dissimilarity matrix, based on normalized residuals (or "pure" preferences/avoidances), the individual variation in the total number of contacts being excluded, makes some relatives closer to each other in the grooming space, but even with this approach it is not possible to regard kinship as a crucial factor influencing partner choice.

The second method we used was the non-metrical multi-dimensional scaling (NMDS) which was already employed to analyze social relations in baboons (Easley et al., 1990). The matrix of grooming distances was scaled in two dimensions. We did not introduce the third dimension because three-dimensional graphs are difficult to visualize. The starting configuration was obtained by means of the Torgerson's method, and Guttman's algorithm was used at the non-metrical stage (Davison, 1983).

In morphometrical analysis, NMDS usually allows to reproduce the original distance structure with less distortion than the cluster analysis does because two or three dimensions are used instead of only one dimension inherent in the dendrogram. In our case, however, the result turned out to be worse: the cophenetic correlation coefficient between (d_{ij}) and the Euclidean distances separating the respective points in the space of two new coordinates is only 0.52. The probable reason is that the distribution of grooming distances has a strong negative skewness due to a predominance of pairs with very few or no contacts. This is more in accord with the structure of the dendrogram where large (between-cluster) distances may predominate over small (within-cluster) ones, than with the bidimensional model generated by NMDS where the distribution of distances is always positively skewed.

The logarithmic transformation of ($n_{ij}+1$) values results in a certain improvement, the cophenetic correlation coefficient rising up to 0.65. Although this is still below the value obtained with the cluster analysis, NMDS has some important advantages (Figure 3). Firstly, it is not based on the a priori assumption of a discrete hierarchical structure of the community and can detect animals whose position is intermediate. Secondly, pairwise relations are more evident on a bidimensional graph. Using arrows to show dyads with significantly asymmetrical grooming relations, as revealed by the binomial test, we see that in some of them (C-1 and A-2; C-1 and L-1; H-1 and F-1; H-1 and D-1) the activity was directed mainly from animals of a higher dominance rank to lower-ranking ones, while in others (B-4 and B-1; B-4 and K-1; 1 and K-1; H-1 and C-2) the opposite was true. Some of these dyads (C-1 and A-2; H-1 and F-1; B-4 and K-1) functioned as connecting links between the clusters.

The analysis of mutual preferences indicates that some animals show close attachment towards each other, including the dyads C-1 and C-2 (brother and sister), A-1 and I-1 (both high-ranking), D-1 and C-2 (both medium-ranked), B-4 and F-1, B-1 and J-1 (all of them low-ranked). However, there were also cases of *mésalliance*, like E-1 (an old high-ranking female) and D-3 (a young adult low-ranking one), or K-1 (medium-ranked) and 1 (low-ranked). The latter dyad displayed an exceptional degree of mutual affection.

So neither kinship nor social status appear to be the principal parameters affecting the structure of grooming ties. And, although age similarity did influence partner choice, this factor also does not appear to be crucial. The same pertains to the sex of animals. Evidently, stump-tailed

macaques can develop strong individual preferences. Without further investigations it is not possible to make any specific comments concerning the factors responsible for this selectivity.

Discussion

Contrary to data on chacma baboons (Seyfarth, 1977) and hamadryas baboons (Stammback & Kummer, 1982) indicating that high-ranking animals receive more grooming than low-ranking ones, our results reveal no correlation between the reception of grooming and social status. At the same time, the performance of grooming is positively correlated with social status. Due to this correlation, the share of received grooming in the total amount of grooming contacts is significantly diminishing with increasing social status. Consequently the extortion hypothesis is not supported by data on the stump-tailed macaques: rather than trying to receive more grooming from lower-ranking group members, the high-ranking animals were themselves engaged in intensive grooming activity. This could probably be considered an important strategy aimed at achieving and maintaining dominant status in populations of this macaque species known for its mild dominance style (de Waal, Luttrell, 1988). In certain cases, high grooming performance may indicate that the animal's social status is about to rise. This is what actually happened with H-1, one of the most active groomers, which, a year after having been observed by us, attained a very high position in the group's hierarchy.

However, the influence of social rank upon the choice of grooming partners could not be

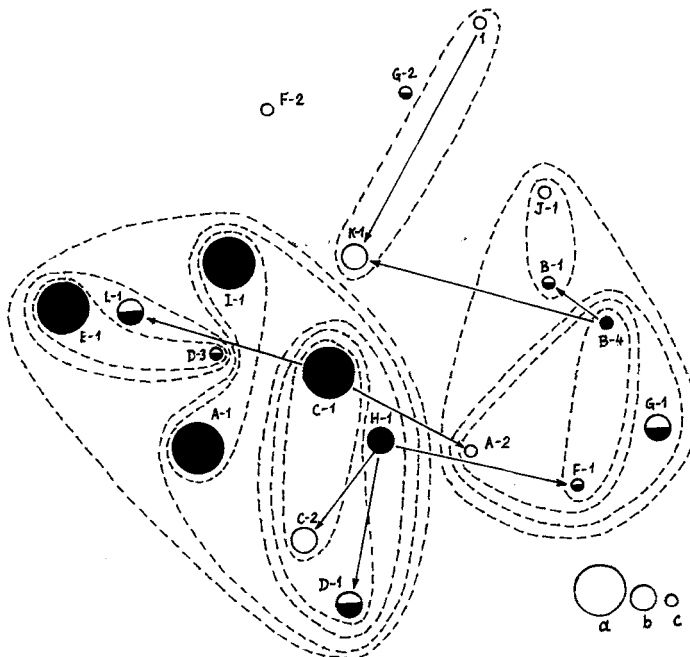


Figure 3 - Results of multidimensional non-metric scaling of grooming distances (based on the log-transformed number of contacts). Categories of dominance ranks: a — high (1-4), b — medium (5-10), c — low (11-17.5). Categories of grooming ranks are marked as in Fig. 2. Arrows show significant asymmetry of grooming contacts and are directed from the more active partner to the more passive one. Closed dash curves show the same clusters as in Fig. 2.

detected in our sample. Kinship was not an important factor either, same as for Tonkean macaques (Thierry et al., 1990) and anubis baboons (Ransom & Ransom, 1971). This could make grooming an important social activity in egalitarian communities which are open for newcomers and comprise not only relatives but unrelated animals as well. The ability to establish affiliative bonds between non-relatives may provide a means for securing integrity of such groups. It was shown, however, that in *Macaca arctoides*, grooming bouts in related dyads are generally longer than in non-related ones (Lopez-Vergara et al., 1989).

The high grooming performance of the male is evidently due to the specifics of group formation in macaques: as soon as males attain maturity, they have to leave their group for another one and, without wasting much time, gain the favor of adult females and their offspring. Females, who are the resident sex, begin to establish affiliative bonds with other females already in their early years (because of the importance of matrilinearity) and with several males.

Despite the fact that the distribution of grooming relations was definitely nonrandom, it was not possible to discern well-defined clusters of individuals in our sample. The most isolated were the young adults which were probably not yet fully integrated into the social grooming network. Their contacts like those of infants, were still maintained mostly through social play.

Thus along with the tolerance shown by the dominant group members toward the subordinate ones and the considerable degree of freedom the latter enjoy, the model of grooming described in this paper may be regarded as a characteristic feature of the egalitarian, or "soft", style of dominance (see de Waal & Luttrell, 1988).

The low grooming performance of the subordinate animals is apparently explained by their low overall level of social activity. In spite of the freedom enjoyed by the subordinates, they still find it safer to keep away from the dominants rather than trying to establish ties with them.

The "average individual" of our sample maintained grooming contacts with 12 others, thus having no contacts with each third of its potential partners. Although we are as yet unable to detect avoidance behavior, preferences are so evident that it is very unlikely that all possible dyads would ever be observed even if the observation time increased indefinitely. Other researchers expressed the same view (Easley et al., 1989). Possibly, primate species having a softer and more flexible dominance system and a greater intensity of friendly contacts, like Tonkean and stumptailed macaques, have a larger average number of "friends" per individual than species with a rigid social hierarchy, like rhesus and crab-eating macaques.

If we regard grooming as a principal source of evidence concerning friendship in primates (Smuts, 1985), then it should be admitted that, so far, most of the social and psychological factors affecting individual sympathies can not be detected. The ability and desire to maintain longlasting friendly bonds with unrelated group members of the same sex, females in our case, males in the case of anubis baboons (Easley et al., 1989), is an important manifestation of individuality in anthropoids living in complex multi-male communities. Stumptailed macaques are apparently one of the species in which individual affections may be an even more important factor of group cohesion than dominance/submission or kinship.

Primate species having a soft dominance style (Tonkean and stumptailed macaques, chimpanzees, bonobos) tend to display a scattered distribution of social and material benefits. In chimpanzees, grooming is related to food sharing, and the partner who grooms more actively receives on the average more food from the recipient than vice versa (de Waal, 1989). It was suggested that such species may provide good models for early hominid social evolution (Butovskaya, 1987; Butovskaya & Ladygina, 1989; de Waal, 1989). The results of the present study make it possible to hypothesize that the individualization of social contacts and the dominant members' striving for support from subordinates could be among the important principles securing the viability of early hominid communities.

Grooming data may also shed light upon the social significance of the tactile forms of friendly behavior, like touching, tapping, embracing, kissing, and others, which had succeeded grooming in the course of evolution. Finally, these data have some bearing on the development of reciprocal altruism in relation to social status since, in our sample, the dominant group members not merely enjoyed privileges but spared no efforts to gain support of the subordinates. It may be speculated that in early hominid groups these efforts went beyond symbolic manifestations of patronage and included food sharing.

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