
Dominance hierarchy and social grooming in female lion-tailed macaques (*Macaca silenus*) in the Western Ghats, India

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This article reports the structure of dominance and its relationship with social grooming in wild lion-tailed macaque females. The strength of dominance hierarchy was 0.79 on a scale of 0 to 1 indicating a moderate linearity in the ranking system. Dominance scores were converted into an ordinal as well as an interval scale. Grooming scores were also converted into interval scales using standard scores. Grooming received and grooming given correlated positively and negatively respectively with dominance ranks indicating that high ranking females received more and gave less grooming. Grooming was also positively related to encounter rates for dyads of females. More grooming among adjacent ranks, and grooming being more reciprocal, occurred only in the case of dominant females. The grooming patterns, therefore, appeared to be more of despotic than egalitarian nature. While ranking macaques into different Grades of social systems ranging from despotic to egalitarian, Thierry (2004) has placed lion-tailed macaques in Grade 3 corresponding to the 'relaxed' social system. Our results indicate that the grooming and dominance relationships in this species are more despotic, and hence, the Grade for this species requires to be shifted toward 2 or 1.

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1. Introduction

Due to the presence of 21 species in the genus *Macaca*, inhabitation of a variety of habitats ranging from deserts to climax rainforests, and considerable variety in social relationships, this genus has proved to be a model for the study of social organization (Thierry *et al* 2004). A key factor that helps understand social organization is the dominance relationships among individuals of a group of primates. de Waal and Luttrell (1989) introduced the concept of "dominance styles" that referred to the species-typical patterns of asymmetrical outcomes in agonistic interactions. van Schaik (1989) and Sterck *et al* (1997) considered that resource competition among females was the source of such asymmetrical relationships. On the other hand, de Waal (1986) and Thierry (1985) showed that the power asymmetries covary with relation to severity of conflict, pattern of post-conflict resolution

and grooming relationships, and this analysis indicated a strong phylogenetic bias in the 'Grades' (Thierry 2000). Such outcomes could be largely unidirectional or bi-directional. On the basis of dominance styles of a species, macaques were classified into four categories including 'despotic', 'tolerant', 'relaxed' and 'egalitarian' (Flack and de Waal 2004). Thierry (2004) reviewed the literature on 14 behavioural characters of macaques and classified 19 macaque species into four 'Grades' roughly corresponding to the four categories mentioned above. The lion-tailed macaque (*Macaca silenus*) was placed in Grade 3 indicating more egalitarian than despotic nature of social relationships in the species.

One aspect of social behaviour in nonhuman primates that has shown a strong relationship with dominance is social grooming. Grooming may have a primitive function of cleansing the fur and removing ectoparasites (Tanaka and Takefushi 1993), but it has also acquired a social function

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in terms of establishment of social bonds and affiliation in systems that are often regulated by aggression (Terry 1970). Grooming also provides hedonistic benefits (Keverne *et al* 1989). Food is the limiting resource in nature that would lead to the establishment of a dominance hierarchy. However, in an established hierarchical system, access to dominant females to solicit agonistic support itself becomes a limiting resource, and the subordinate females try to achieve this by grooming dominants (Seyfarth 1977). In macaques, grooming therefore is upward in the hierarchy. However, this pattern is not universal in primates. In some species of New World monkeys (e.g. *Cebus apella*), more grooming is directed down the hierarchy (Parr *et al* 1997). Hemelrijk (2004) included the concept of spatial centrality, i.e. the dominant individuals remaining in the centre and the subordinates in the periphery of the group, into dominance and grooming relationships. According to her hypothesis, the central individuals meet each other more often, and hence, they should get more grooming than the subordinates who are less likely to meet each other in the periphery. Further, grooming should be more among similar ranks. A species with the above pattern of grooming with grooming being related to the encounter rates would be classified as more despotic than egalitarian.

We have checked the above hypotheses in the lion-tailed macaques (*M. silenus*), a species that holds a unique position among macaques due to their patterns of spatial distribution. In the forests of the Western Ghats in south India, an individual member of a group of lion-tailed macaques is found 'alone' (i.e. at a distance of more than six metres from the nearest neighbour) in 94.4% of the scans (Jeyraj 2003) as against only 1.8% of the scans in the bonnet macaques (Prashanth 2003) in nearby forests. Likewise, an individual lion-tailed macaque is found in 'proximity' of another (at a distance less than three metres) only in 2.9% of scans (Jeyraj 2003) as against 61.9% for bonnet macaques (Prashanth 2003). The inter-individual distance in lion-tailed macaques is even more while foraging and ranging which take up more than 76% of the time of a day (Sushma 2004). A group even might split into subgroups with an inter-subgroup distance of more than 100 metres (Sakthivelou and Kumar 1998) and sleep at different places in the night (unpublished data). In such a situation, the animals cannot be meaningfully considered 'central' or 'peripheral' as the likelihood of one encountering another is little most of the time. However, the lion-tailed macaques live in a resource-limited environment (Kumar 1987; Sushma 2004) where the resource competition, especially among females, is always high. We, therefore, propose that the necessity of spatial centrality notwithstanding, the lion-tailed macaque females should have a strong and stable dominance hierarchy. Since grooming is considered a commodity in a biological market (Noe and Hammerstein

1995) that can be exchanged for food (de Waal 1997), coalitional support (Seyfarth and Cheney 1984) or just for tolerance (Henzi and Barrett 1999), high-ranking females should get more grooming than low-ranking females, and grooming should be positively related to aggressive encounter rates in dyads of females. If the hierarchical system is considerably linear, then grooming among adjacent ranks and reciprocal grooming should occur only in dominant females. The low-ranking females tending to groom higher-ranking females should have more of distant rank and nonreciprocal grooming.

2. Methods

The present study was carried out from February 2002 to June 2005. The study animals comprised of a group of lion-tailed macaques (*M. silenus*) inhabiting a rainforest fragment in a privately owned tea/coffee garden called Puthuthotam Estate in the Anaimalai Hills of the Western Ghats in the state of Tamilnadu. This forest fragment is inhabited by two groups of lion-tailed macaques called PT1 and PT2, and our study was carried out on PT1. For other details about this habitat and the surrounding Anaimalai Hills, see Singh *et al* (1997, 2001, 2002). In February 2002, the group comprised of 56 animals including four adult males, 17 adult females, 13 subadults and 22 immatures. By June 2005, the group size had increased to 82 animals including five adult males, 20 adult females, 10 subadults and 47 immatures. The study was conducted on adult females only since lion-tailed macaque groups usually have only one adult male, and if there are two or more than two adult males in a group, they rarely indulge in social interactions.

For the purpose of determining dominance ranks, dominance behaviours included threat, chase, attack, mount and displacement, and subordinate behaviours included present for mount (showing back to another individual), lip smack, bared-teeth display (shown during an agonistic encounter) and avoidance between dyads of females. In case both individuals showed aggressive behaviour, the final outcome where one individual ultimately withdraws was taken into account. These behaviours were recorded *ad libitum*. Since the study spanned over a long period, we considered only dyadic aggressive encounters which occurred in sufficient numbers for analysis of dominance since involvement of more than two individuals in a fight makes the determination of outcome difficult. The data on social grooming were collected through focal-animal one-zero sampling. During a session of observations on a focal animal, a period of 10 min was divided into 30 intervals of 20 s each. Each behavior that occurred during an interval was recorded, and no behaviour was recorded twice even if it occurred. Grooming was counted as one bout if it occurred in a 20 s interval.

The analysis of dominance data and the determination of dominance ranks was based on Singh *et al* (1992, 2003), a modification of Landau's index (Landau 1951a,b, 1953), that allows the calculation of strength of dominance hierarchy as well as the placement of dominance ranks on an interval scale; i.e.

$$h = [12/(n^3-n)] \sum_{\alpha=1}^n [d_{\alpha} - (n-1)/2]^2. \quad (1)$$

$$\text{Here, } d_{\alpha} = \sum_{\alpha=1}^n P_{\alpha}, \quad (2)$$

in which h is the strength of hierarchy that ranges between 0 and 1, and p_{α} is the proportion of winning in pair-wise encounters.

The dominance ranks of all individuals were placed on an interval scale to mark the distance between ranks. A constant value of 0.5 was added to d_{α} values of each female so that p_{α} , which is otherwise d_{α}/n , remains above zero and less than one. Standard scores were obtained for each P value. The least standard score was converted into an arbitrary zero and it was added to all other z scores. This provided an interval scale for dominance hierarchy, which indicates not only the dominance rank for each individual but also the distance between ranks. The social grooming data for each individual was the number of "grooming received" (groomed by others) and "grooming given" (grooming others) episodes obtained from one-zero sampling data sheets. Groomed and grooming values were also converted into interval scales using standard scores (z) for each individual so that all interval scales could become comparable. The lowest standard score was arbitrarily labelled zero and this score was added to the standard score of each individual. Since "grooming given" and "grooming received" were expected to correlate negatively, the scale scores for "grooming given" were inversed so that the individual giving least grooming got the highest standard score.

Analysis was first carried out for the data collected between February 2002 and May 2004 (Period One). In May 2004, the most dominant female, F1, disappeared from the group, and it led to a rank reversal in some group members. The second similar analysis was carried out for the data collected between June 2004 and June 2005 (Period Two).

For the purpose of this analysis, we have used the data only on 16 adult females who were present from the beginning to the end of this study. Of the 17 adult females, one female, F11, was eliminated from data analysis since this female hardly ever interacted with other females and was mostly seen in the periphery of the group throughout this study. Since all analysis is based on social interactions, the inclusion of this female in data analysis would have disrupted all the patterns among the routinely interacting

all other females. In order to divide the females into rank classes, we clubbed five top-ranking females as High Ranks, the next five as Middle Ranks and the remaining as Low Ranks.

3. Results

3.1 Dominance ranks and grooming between 2002 and 2004 (Period One)

We observed 2,484 dyadic dominance-submission interactions from February 2002 to May 2004 (table 1). Using the modified Landau Index for dyadic dominance interactions, we determined ranks of females on an ordinal as well as an interval scale. F1 and F13 were the highest ranking females and F6 and F15 were the lowest ranking. Figure 1a depicts dominance ranks and distance between ranks on an interval scale. Individuals appeared to form clusters on the interval scale. The strength of dominance hierarchy (h) was found to be 0.79 indicating a considerable linearity in hierarchy. Table 1 also presents the data on grooming received and grooming given and interval scales for both. We observed a total of 5,461 instances of grooming. Figure 1b,c show the placement of females for grooming received and grooming given next to the interval scale for dominance. The dispersal of individuals on the three scales largely corresponded to each other. In order to display the direction of this relationship, we scatter-plotted the actual scores of grooming received and grooming given against ranks on the ordinal scale (figure 2a,b). The relationship between dominance ranks and grooming received (Spearman's rho: $r = -0.95$) was significant ($N=16$; $P < 0.01$), indicating that the high-ranking females (depicted by a lower number on the ordinal scale) received more grooming and the low-ranking received less grooming. The relationship between dominance ranks and grooming given (Spearman's rho: $r = 0.85$) was also significant ($N=16$; $P < 0.01$), indicating that the high-ranking females gave less grooming and the low-ranking gave more grooming. The difference for grooming received (Kruskal-Wallis test: $\chi^2=10.55$; $df=2$; $P < 0.01$) and grooming given (Kruskal-Wallis test: $\chi^2=7.73$; $df=2$; $P < 0.02$) by the rank classes (figure 3) was significant. The relationship between encounter rate and grooming (Pearson-Product Moment Correlation: $r=0.20$) in dyads was significant ($N=120$; $P < 0.05$) indicating that more were the encounters between any two females, more was grooming between them.

3.2 Dominance ranks and grooming between June 2004 and June 2005 (Period Two)

We observed 1,605 dyadic dominance-submission interactions between June 2004 and June 2005 (table 2). We

Table 1. Scores on fights and grooming between February 2002 and May 2004 in female lion-tailed macaques.

Female identity	Fights won	Fights lost	Rank on ordinal scale	Score on interval scale	Grooming received	Interval scale score for grooming received	Grooming given	Interval scale score for grooming given*
F1	362	18	1	2.75	907	3.21	0	3.37
F13	334	23	2	2.64	847	2.98	30	3.23
F7	247	67	3	2.18	609	2.08	146	2.73
F8	200	89	4	1.93	582	1.98	124	2.82
F5	235	107	5	1.85	372	1.19	300	2.05
F10	143	82	6	1.72	266	0.79	272	2.17
F9	139	79	7	1.66	345	1.08	364	1.77
F14	178	117	8	1.64	372	1.19	146	2.73
F12	112	79	9	1.51	229	0.65	358	1.80
F17	110	196	10	1.05	103	0.17	697	0.31
F4	92	219	11	0.94	208	0.57	444	1.42
F16	102	212	12	0.91	199	0.53	249	2.27
F2	104	254	13	0.86	159	0.38	473	1.29
F3	72	271	14	0.67	144	0.33	480	1.26
F15	29	353	15	0.13	58	0	768	0
F6	25	318	16	0	61	0.01	610	0.69

*Lowest value gets the highest score on the interval scale, and vice versa. See text for details.

followed the similar procedure for analysis as for the first period from February 2002 to May 2004. F17 and F13 were the highest ranking females and F2 and F6 were the lowest ranking. The strength of dominance hierarchy (h) was found to be 0.78 which was almost the same as between 2002 and 2004. Figure 1d depicts dominance ranks and distance between ranks on an interval scale. Once again, the individuals appeared to form clusters on the interval scale. Table 2 also presents the data on grooming received and grooming given and interval scales for both. We observed a total of 4,266 instances of grooming. Figure 1e,f show the placement of females for grooming received and grooming given next to the interval scale for dominance. The dispersal of individuals on the three scales once again largely corresponded to each other. In order to display the direction of this relationship, we scatter-plotted the actual scores of grooming received and grooming given against ranks on the ordinal scale (Figure 2c,d). The relationship between dominance ranks and grooming received (Spearman's rho: $r = -0.82$) was significant ($N=15$; $P < 0.01$), indicating that the high-ranking females received more grooming and the low-ranking received less grooming. The relationship between dominance ranks and grooming given (Spearman's rho:

$r = 0.87$) was also significant ($N=15$; $P < 0.01$), indicating that the high-ranking females gave less grooming and the low-ranking gave more grooming. The difference for grooming received (Kruskal-Wallis Test: $\chi^2 = 11.01$; $df = 2$; $P < 0.01$) and grooming given (Kruskal-Wallis Test: $\chi^2 = 9.60$; $df = 2$; $P < 0.01$) by the rank classes (figure 3) was significant. The relationship between encounter rate and grooming (Pearson-Product Moment Correlation: $r = 0.32$) in dyads was significant ($N=115$; $P < 0.01$), indicating that more were the encounters between any two females, and more was grooming between them.

3.3 Rank classes and other grooming patterns

Of the 1,402 grooming bouts by the high-ranking females, about 74%, 16% and 10% were directed towards high-, middle- and low-ranking females respectively (figure 4a). The middle ranking females directed about 72%, 18% and 10% of their grooming ($N=3,081$) towards high, middle and low ranking females respectively. The low ranking females directed about 55%, 29% and 16% of their grooming ($N=5,244$) towards high-, middle- and low-ranking females

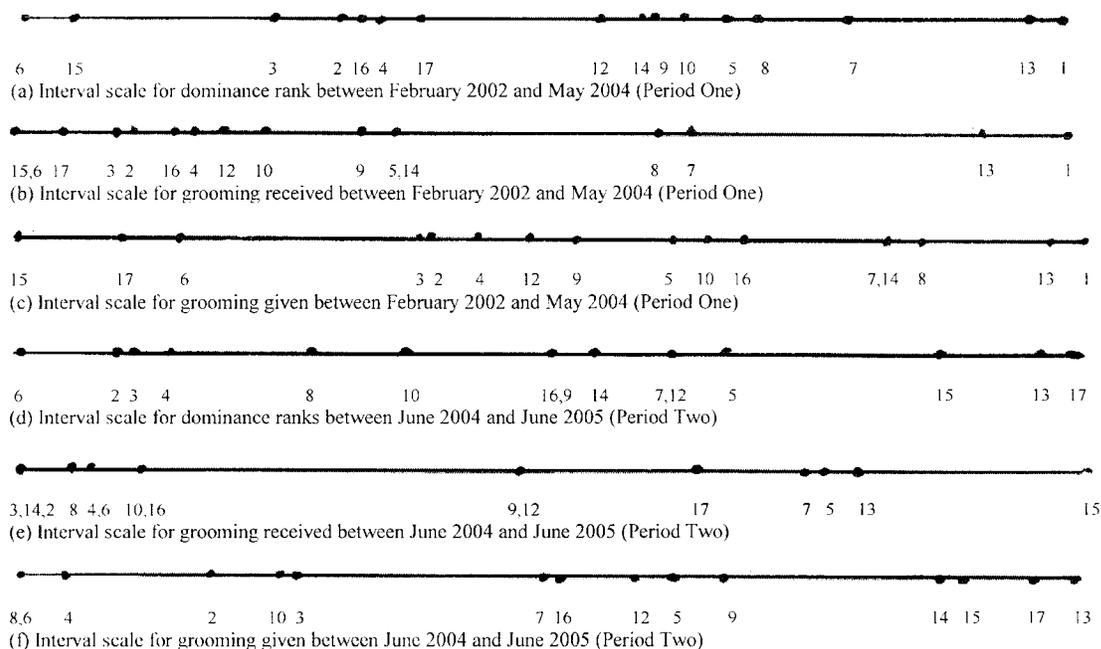


Figure 1. (a) Placement of females on interval scale for dominance scores during Period One. Higher ranks start from right to left. (b) Placement of females on interval scale for scores on grooming received during Period One. (c) Placement of females on interval scale for scores on grooming given during Period One. (d) Placement of females on interval scale for dominance scores during Period Two. (e) Placement of females on interval scale for scores on grooming received during Period Two. (f) Placement of females on interval scale for scores on grooming given during Period Two.

respectively. We also calculated grooming of females of the adjacent ranks (mean of two individuals on either side of a female of each rank) and females of the distant ranks (mean for all other individuals for each female). The high-ranking females directed a mean of about 13 and 9 bouts towards females of adjacent and distant ranks respectively (figure 4b). The middle-ranking females directed a mean of about 19 and 21 towards females of adjacent and distant ranks respectively. The low ranking females directed a mean of about 14 and 36 bouts towards females of adjacent and distant ranks respectively. We also analysed the total grooming bouts to check whether grooming occurs more between grooming partners as reciprocal grooming. The analysis showed that grooming was largely reciprocal among high rank females whereas grooming by middle- and low-rank females was largely nonreciprocal (figure 4c).

4. Discussion

During this study, we had an opportunity to verify the stability of the patterns of dominance and its relationship with social grooming even when there was a reversal in the ranks of few females. The strength of dominance hierarchy was 0.79 and 0.78 during the two periods. Similarly, the

relationship between dominance ranks grooming received and grooming given remained the same in the two periods. The relationship between encounter rates and grooming in dyads of females was positive and significant in both periods. These observations indicated not only the stability of these patterns but also provided an internal validity to the results.

The strength of dominance hierarchy of the lion-tailed macaque females indicated a moderate linearity. Measured using the same method, this value of linearity is close to bonnet macaques who show a strength of 0.76 (Prashanth 2003) and far below the value of 0.95 for males and 0.97 for females in Japanese snow monkeys (Singh *et al* 1992). This aspect of the sociality of the lion-tailed macaque confirms Thierry's classification (Thierry 2004) that this species has a more 'relaxed' dominance system. As mentioned earlier, the individuals of a group of lion-tailed macaques are usually wide spread and spatial centrality has no meaning in such a situation. With the relaxed dominance system and the wide spread of group members, the grooming relationships among individuals are expected to be more of the egalitarian than despotic type.

In the present study, grooming was related to the dominance ranks as well as rates of encounter in dyads of females. In the egalitarian society of Tonkean macaques,

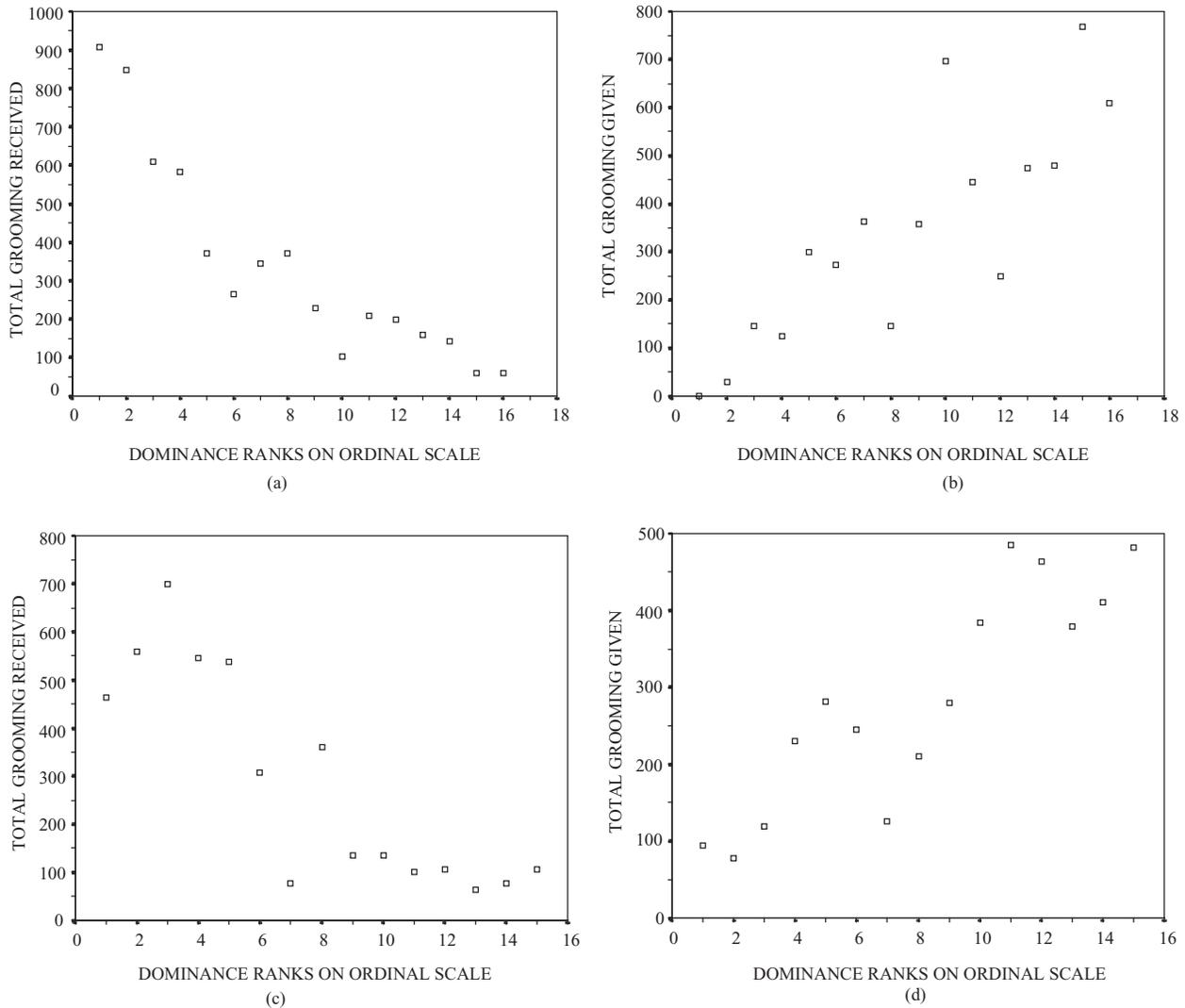


Figure 2. Scatter-plot for dominance ranks on ordinal, and on (a) grooming received during Period One, (b) grooming given during Period One, (c) grooming received during Period Two, and (d) grooming given during Period Two in lion-tailed macaque females.

grooming is not dominance-related (Thierry *et al* 1990). On the other hand, grooming is significantly dominance-related in the despotic rhesus (Sade 1972; de Waal and Luttrell 1986) and Japanese (Mehlman and Chapais 1988) macaques. In lion-tailed macaques, grooming was upward in the hierarchy. The high-ranking females during the first period of the study gave little grooming and the most dominant female never groomed anyone. During the second period after a rank reversal, two females F17 and F15 who were low-ranking during the first period and gave highest grooming, showed the least grooming score after achieving high ranks. Our data also revealed that F17 and F15 during the first period of the study gave maximum grooming to the two highest ranking females one of which, F1, disappeared. This observation also indicates coalitional

nature of social relationships in which low-ranking females could attain higher ranks by having high ranking females as grooming partners. The high-ranking females received grooming from all ranks, whereas the middle- and low-ranking females largely received their grooming from the low-ranking females. The view that more grooming occurs between closely ranked dyads than between distant dyads (Parr *et al* 1997) was true in the case of the high-ranking and the middle-ranking lion-tailed macaque females where the low-ranking females largely groomed distant ranks. The view that grooming is reciprocal in macaques (de Waal and Luttrell 1986; de Waal 1991) was true only for high-ranking females as the middle- and the low-ranking females were observed to groom more unidirectionally than reciprocally. The grooming patterns of the lion-tailed macaque females,

Table 2. Scores on fights and grooming between June 2004 and June 2005 in female lion-tailed macaques.

Female identity	Fights won	Fights lost	Rank on ordinal scale	Score on interval scale	Grooming received	Interval scale score for grooming received	Grooming given	Interval scale score for grooming given*
F17	228	17	1	2.41	464	1.80	94	2.73
F13	229	19	2	2.36	558	2.22	77	2.85
F15	211	19	3	2.13	700	2.85	119	2.55
F5	147	59	4	1.62	545	2.16	230	1.78
F7	177	90	5	1.51	537	2.12	282	1.42
F12	135	36	6	1.51	306	1.33	245	1.67
F14	65	47	7	1.33	76	0.06	126	2.50
F9	136	109	8	1.23	360	1.33	210	1.92
F16	60	102	9	1.23	136	0.33	279	1.44
F10	49	96	10	0.90	134	0.32	384	0.71
F8	56	126	11	0.68	100	0.16	485	0
F4	35	171	12	0.37	105	0.19	464	0.15
F3	32	191	13	0.26	63	0	379	0.74
F2	28	258	14	0.23	76	0.06	410	0.52
F6	17	265	15	0	106	.019	482	0.02

*Lowest value gets the highest score on the interval scale, and vice versa. See text for details.

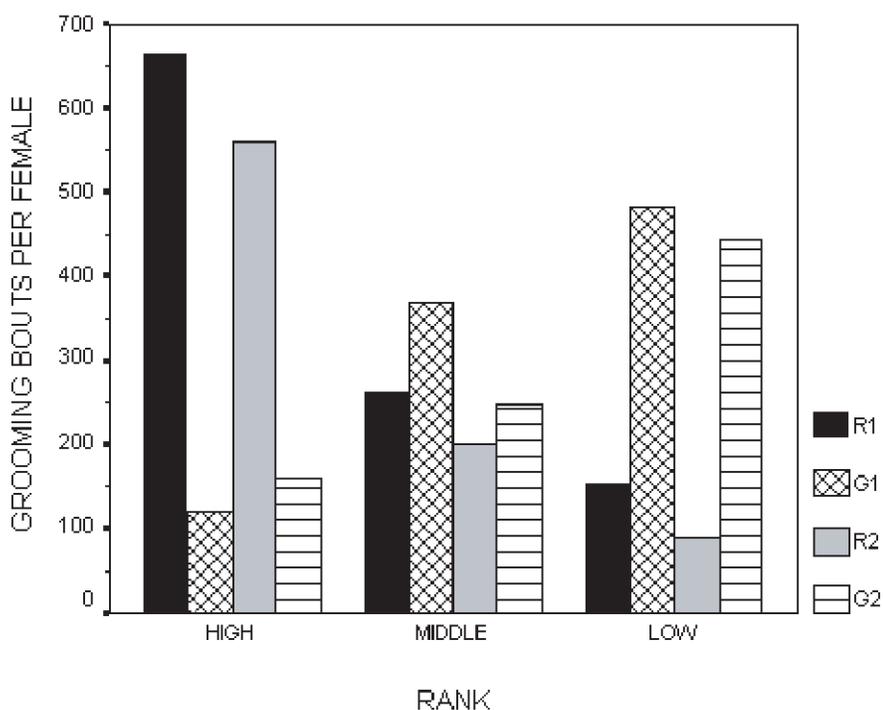


Figure 3. Dominance rank classes and grooming by female lion-tailed macaques. R1, Grooming received during Period One; G1, grooming given during Period One; R2, grooming received during Period Two; G2, grooming given during Period Two.

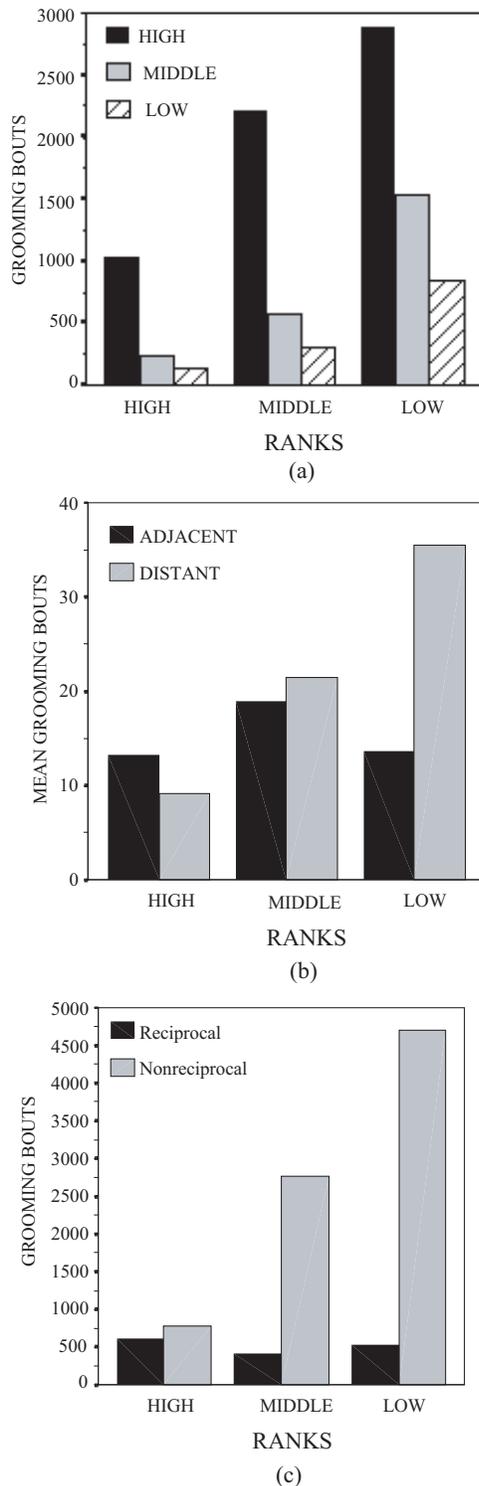


Figure 4. (a) Bouts of grooming given to high-, middle- and low-ranking females by females of different rank classes; (b) mean grooming given bouts by females if high, middle and low rank classes towards adjacent and distant ranks; and (c) reciprocal and nonreciprocal grooming bouts by females if high-, middle- and low-rank classes.

therefore, point to a more despotic than a relaxed system. We propose that spatial centrality and individual proximity are not the so much necessary conditions for more despotic social interactions. The classification of macaque social system by Thierry (2004) may require a revision and the lion-tailed macaques could be ranked more towards Grades 2 or 1 from Grade 3.

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