



Social Grooming in Tonkean Macaques (*Macaca tonkeana*)

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*The distribution, form, and contexts of occurrence of social grooming were studied in two captive groups of Tonkean macaques (*Macaca tonkeana*), using interaction-dependent sampling. The social events surrounding grooming had little influence on its form, the participants' behavior being shaped mainly by physical constraints. Adult females were most often involved in grooming interactions. Grooming between adult females appeared more intimate than that between adult males and females. Kinship and dominance had no effect on the form or distribution of social grooming among adult females. It is concluded that social systems that are characterized by mild dominance relations allow individuals the freedom to interact in the way and with whom they wish.*

KEY WORDS: communication; conciliation; social grooming; gender; dominance; kinship; macaque.

INTRODUCTION

Judging by the amount of time allocated to social grooming among Old World monkeys, it is an important activity; accordingly many observers have investigated its functions. Most have been concerned with social functions. They looked at the identity of grooming partners and measured frequency and duration of interactions, finding that the distribution of social groom-

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ing is influenced by factors such as gender, age, kinship, dominance rank, reproductive state, and behavioral context (Poirier, 1970; Sade, 1972; Lindburg, 1973; Drickamer, 1976; Defler, 1978; Kurland, 1977; Seyfarth, 1977; Silk, 1982; Seyfarth and Cheney, 1984; Goy *et al.*, 1988). On the other hand, some authors have examined the cleaning function of grooming. They compared social and autogrooming with regard to body sites groomed, generally showing that individuals involved in the second kind of activity concentrate their attention mainly on easily accessible regions (Poirier, 1970; Hutchins and Barash, 1979; Freeland, 1981; Barton, 1985; but see Boccia, 1983).

In this context, systematic studies that integrate both physical and social characteristics of grooming interactions are rare (McKenna, 1978; Boccia *et al.*, 1982; Boccia, 1986, 1989; Barton, 1983). However, a number of facts support the idea that the physical aspects of grooming reflect the social situation. It is a common observation that subordinates that initiate grooming with higher-ranking individuals display behaviors that express a lack of confidence [*Erythrocebus patas* (Hall *et al.*, 1965); *Miopithecus talapoin* (Dixon *et al.*, 1975); *Macaca fuscata* (Turillazi *et al.*, 1982)]; it has been claimed that grooming interactions among kin look more peaceful than those between unrelated individuals or that lower-ranking individuals are less relaxed in their postures and acts than their dominant partners are during grooming [*Macaca radiata* (Rosenblum *et al.*, 1965); *M. mulatta* (Reynolds; cited by Sparks, 1967); *M. arctoides* (Bertrand, 1969); *M. fuscata* (Oki and Maeda, 1973)]. When there is tension in the group, the initial brushing of the partner's fur is performed with rapid and rough movements [*Macaca radiata* (Rosenblum *et al.*, 1966); *M. arctoides* (Bertrand, 1969); *M. mulatta* (de Waal and Yoshihara, 1983)]. In Indian langurs (*Presbytis entellus*) (McKenna, 1978) and black macaques (*Macaca nigra*) (Barton, 1983), grooming started with the receiver facing away from the performer more frequently than usual when it was preceded by an intense social interaction. Grooming bouts lasted longer among kin [*Macaca arctoides* (Lopez-Vergara *et al.*, 1989)] or when the recipient was the most dominant individual of the dyad [*Presbytis johnii* (Poirier, 1970); *Papio hamadryas* (Coelho *et al.*, 1983); *Macaca mulatta* (Boccia *et al.*, 1982; de Waal and Luttrell, 1986)]. Further, in Japanese macaques (*Macaca fuscata*), reciprocal interactions occurred mainly between near-ranking mates (Turillazi *et al.*, 1982). Other results indicate that the body sites that are groomed, as well as postures and relative orientations of interactants, might be influenced by gender and dominance status (Boccia *et al.*, 1982; Barton, 1983). Finally, interspecific differences exist in the form of grooming; for instance, bonnet females (*Macaca radiata*) were found more frequently placed in front of or obliquely to their partners, while pigtail females (*Macaca nemestrina*) more often face the partner's back (Boccia, 1989).

We studied grooming in two captive groups of Tonkean macaques (*Macaca tonkeana*), which are one of the seven primate species inhabiting the island of Sulawesi. By testing the influence of gender, dominance, and kinship on the distribution, form, and context of grooming interactions occurring among Tonkean macaques, we aimed to understand the mechanisms of social grooming and relate them to the social system peculiar to the species.

METHODS

Subjects

Two groups of *Macaca tonkeana* were studied. The first group (A) was semi-free-ranging in a wooded park of approximately 0.5 ha. The second group (B) was housed in a cage of approximately 120 m², and 4 m high, containing various supports. The composition of each group and kinship relations are shown in Table I. Individuals at least 4 years old were classified as adults. Kinship is represented by the relations linking siblings (or maternal half-siblings), mother and offspring, and grandmother and grandchild. Relations involving more tenuous relatedness were not considered in the analysis. Further information about the groups' history is given by Herrenschmidt (1977) and Thierry (1984). Monkey commercial diet and water were available ad libitum; fruits and vegetables were also distributed, but not during observations.

Data Collection

Observations were conducted during a two-month period, between 0800 and 1500 hr. Since the group B was in a zoo, observations took place on weekdays, the time of least disturbance by the public. One observer (C.G.) accumulated 118 hr of observation on group A, while another (P.P.) totaled 97 hr on group B. Social grooming was collected using interaction-dependent sampling (see Altmann, 1974), with paper and pencil. If two grooming interactions began simultaneously, the one involving the individuals less frequently sampled was chosen. A break of 10 sec in grooming was used as the criterion for the end of a bout. A grooming bout was defined as a part of a grooming interaction within which a participant continues to play the same role, either as performer or as recipient. The observers recorded the subjects involved, the duration of grooming of each body site (using a stopwatch), the frequency of postures and orientations of partners, the frequency of invitations, and the occurrence of contexts before and after grooming. For the

Table I. Identity, Age, and Kin Relations in Groups A and B^a

Group A						
MAM						
♀ (27)	┌───────────┐					
	JUL	MAR				
	♀ 8	♀ 5				
	└───────────┘					
					JUS	JIM
					♀ 3	♂ 1
VER	┌───────────┐					
♀ (17)	BOU	VEO	VAL	VAN	VEN	
	♀ 9	♀ 5	♀ 4	♂ 2	♂ 1	
	└───────────┘					
MOU			BOG	BEA		
♂ 11			♂ 4	♀ 3		
Group B						
TIK						
♀ (23)	┌───────────┐					
	GAU				TON	
	♀ 13				♀ 4	
	└───────────┘					
					GAL	GIS
					♂ 5	♀ 4
MIG	┌───────────┐					
♀ (19)	TIN	MIC	MIN	MIK		
	♂ 8	♂ 7	♀ 5	♂ 4		
	└───────────┘					

^aAges are expressed in years. Parentheses indicate estimated ages for subjects born in the wild. All other subjects were born in captivity.

analysis, we retained only grooming interactions which were fully observed from the preceding context until the following one. This led to 690 bouts sampled in group A (17 hr 14 min of social grooming, of which 12 hr 34 min was performed by adult females) and 869 bouts in group B (23 hr 45 min, of which 21 hr 19 min by adult females).

Definition of sites of grooming, postures, and orientations of partners mostly followed Boccia *et al.* (1982). The body was divided into nine regions: *face* (hairless area), *head* (area other than the face, including ears and neck), *back* (from the base of the neck to the base of the tail), *ventrum* (chest and abdominal area, including genitals in males), *rump* (including ischial callosities, genitals in females, and the tail, which is a few centimeters long), *thigh*, *leg* (and *foot*), and *arm*, *forearm* (and *hand*). There were two categories of recipient's posture: *up* (sitting or standing) and *down* (lying). There were three possible groomer's orientations, according to the area of the recipient's body which faced the groomer: *front*, *side*, and *back* (in cases when the recipient adopted a somewhat complicated posture, the relative orientation of partner was based on the direction of the groomee's head). An *invitation* was

defined as a clear presentation of a part of the body (often the chest or the side) before a grooming bout.

Eight contexts were defined according to behavioral events occurring in the 10 sec preceding or following the grooming bout: *social grooming*, *proximity* (partners were at a distance equal or less than 50 cm of each other and did not interact), *distance* (partners were at a distance of more than 50 cm and did not interact), *social play*, *affiliation* (including clasping, grunting, lip-smacking, and silent bared-teeth display), *mount*, *agonism* (including threatening, charging, screeching, slapping and grabbing, and avoiding), and *interference* (a grooming bout stopped because of the behavior of a third individual: in *supplantation* this individual became involved in grooming; in *interruption* it did not).

Two additional measures were taken. First, partners in social grooming were recorded using scan sampling at intervals of 30 min. Second, agonistic interactions were collected ad libitum to determine agonistic rank orders. For group A, additional data on agonistic interactions were taken from another study conducted by the senior author during the same period. As most contests are bidirectional in Tonkean macaques (Thierry, 1986), it was not possible to determine dominance relationships from the outcome of agonistic interactions. However, *inducing aggression* (i.e., provoking an aggression or aggressing without having been provoked) was shown to be a reliable indicator of dominance (Desportes *et al.*, 1989), and this criterion was applied in the present study; while this criterion may appear unusual, it does not depart markedly from usual measures of dominance since individuals inducing aggression are also the winners in unidirectional interactions.

Statistical Tests

Comparisons used the chi-square test, the Spearman rank correlation coefficient test, and analyses of variance (ANOVAs). In repeated-measures ANOVAs, grooming interactions of each individual were compared in two conditions which represent the repeated measure. The ANOVAs generally showed no difference between groups; exceptions to this are stated in the text. No interaction between factors was found. Alpha was set at 0.05.

RESULTS

Distribution of Social Grooming

Data used in the analysis of distribution were those collected by scan sampling (106 samples were recorded in group A, 104 in group B). The influence of kinship and dominance was tested only in adult females because

Table II. Distribution of Social Grooming as a Function of Age and Sex Classes^a

Group A				
Groomer	Groomee			Row total
	Adult males	Adult Females	Juveniles	
Adult males				
OF	2	23	1	26
EF	0.6	8.2	5.8	14.6
Adult females				
OF	18	35	20	73
EF	8.2	24.5	20.4	53.1
Juveniles				
OF	3	3	1	7
EF	5.8	20.4	11.6	37.8
				$\chi^2 = 27.5$ (2 df, $P < 0.001$)
Column total				
OF	23	61	22	$\chi^2 = 6.6$ (2 df, $P < 0.05$)
EF	14.6	53.1	37.8	
Group B				
Groomer	Groomee		Row total	
	Adult males	Adult females		
Adult males				
OF	1	14	15	
EF	17.3	28.9	46.2	
Adult females				
OF	47	42	89	
EF	28.9	28.9	57.8	
			$\chi^2 = 22.5$ (1 df, $P < 0.001$)	
Column total				
OF	48	56	$\chi^2 = 0.1$ (1 df, NS)	
EF	46.2	57.8		

^aExpected frequencies of grooming were calculated on the basis of the proportion of dyads represented by each age-sex combination. OF, observed frequencies; EF, expected frequencies.

this was the only class represented by enough individuals for statistical analysis ($N = 12$).

Age and Gender. The observed and expected distributions of grooming among the different classes of individuals were compared using the chi-square test (Rao, 1973). Results presented in Table II show that grooming distributions differed from random. The majority of interactions occurred among adult females or between adult males and females. In group A,

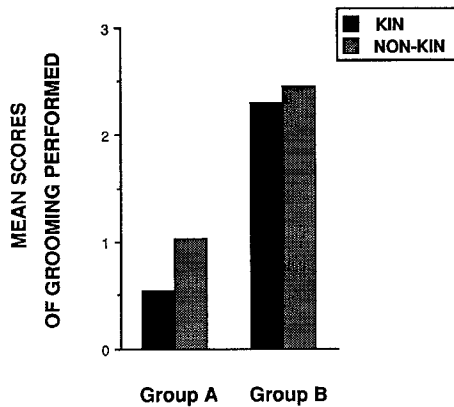


Fig. 1. Lack of kinship effect on the distribution of grooming among adult females. Scores represent the amount of grooming divided by the number of potential partners.

juveniles were rarely involved except when groomed by adult females. In group B, interactions were rare among adult males.

Kinship. The amount of grooming performed by each adult female toward kin and nonkin was calculated after correcting data for the number of potential partners (i.e., dividing the sums of bouts by the number of potential partners). Comparison using repeated-measures ANOVA ($F_{1, 10}$) showed no effect of kinship; however, numbers were higher in group B than in group A ($P = 0.031$) (Fig. 1).

Dominance. In each group, females were ranked according to the ratio of grooming received to grooming performed. This order was compared to dominance rank order using the Sperman rank test: correlation coefficients were $+0.34$ (group A) and -0.20 (group B), neither reaching statistical significance (Fig. 2). In a second analysis, amounts of grooming received from females of adjacent rank and those more than one rank distant were compared, with data corrected for the number of potential partners (repeated-measures ANOVA; $F_{1, 10}$), giving no significant difference (apart from the difference between group A and group B, obtained earlier in the analysis of the effect of kinship).

Form of Social Grooming

The influence of gender, kinship, and dominance was tested for the following parameters: total duration of grooming bouts, duration of groom-

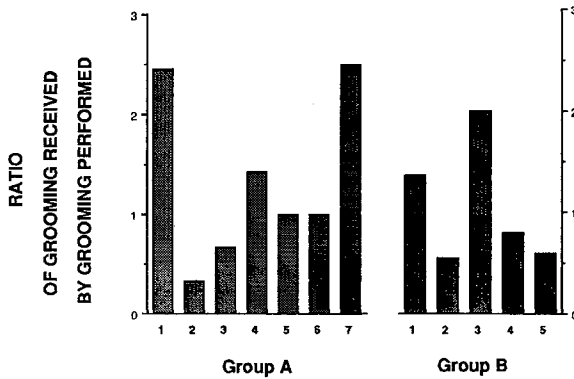


Fig. 2. Lack of dominance effect on the distribution of grooming among adult females. Individuals were ranked from the highest (1) to the lowest dominance position (7 or 5).

ing for each part of the body, frequency of groomee's postures, and groomer's orientations. Adult females were taken as focal individuals ($N = 12$), and their scores (as performer or receiver) were compared according to the factor tested.

Gender. Comparisons were made between interactions involving an adult male and an unrelated adult female and those involving two unrelated adult females (repeated-measures ANOVA). Grooming bouts performed by adult males were shorter than those by adult females (Table III). Compared to adult females, adult males exhibited a preference for grooming the back; they frequently faced the backs, and less often the sides, of their female partners. Conversely, females were more often groomed on the head by other females, and they chose to be in front of them more frequently than males did (Table III). Finally, a difference in lying position was found between group A and group B (groomer, $P < 0.036$; groomee, $P < 0.026$) (Table III). (Such a group effect might be related to variations in the physical environment: in the sunny conditions at the zoo, monkeys might seek the coolness of the concrete, in contrast to the shaded wood inhabited by group A.)

Kinship. Social grooming directed by adult females toward related and unrelated adult females was compared for each body site, posture, and orientation. A repeated-measures ANOVA ($F_{1, 10}$) showed no differences.

Dominance. The comparison of scores of dominant and subordinate adult females on each of the above parameters, using ANOVA ($F_{1, 8}$), revealed no significant effect.

Table III. Influence of Gender on Form of Social Grooming^a

	Group	Groomer ^b			Groomee ^b		
		Male	Female	<i>P</i>	Male	Female	<i>P</i>
Duration (seconds)							
Total bout	A	68.6	122.2	0.015	111.0	102.6	0.722
	B	47.2	118.5		122.0	106.0	
Face	A	0.7	1.9	0.070	0.7	1.8	0.121
	B	0	0.7		0.3	0.9	
Head	A	16.5	20.5	0.944	15.8	24.3	0.115
	B	27.3	23.0		13.9	21.7	
Ventrum	A	10.0	22.8	0.413	16.4	17.9	0.146
	B	24.7	21.2		12.5	23.1	
Back	A	51.2	20.8	0.018	34.2	26.2	0.083
	B	34.5	34.0		30.5	28.7	
Rump	A	16.4	12.9	0.990	8.4	13.2	0.176
	B	5.3	34.0		2.3	8.6	
Thigh	A	1.0	8.9	0.208	7.2	7.2	0.703
	B	7.7	7.2		9.9	7.4	
Leg and foot	A	0	4.1	0.391	2.8	2.8	0.841
	B	0	2.4		2.2	2.9	
Arm	A	2.4	2.4	0.698	8.9	1.3	0.090
	B	4.0	6.2		9.6	8.1	
Forearm and hand	A	0.2	0.3	0.430	2.2	1.9	0.594
	B	2.0	0.6		1.7	0.6	
Frequency (percentage)							
Lying position	A	21.4	24.7	0.927	24.5	24.7	0.256
	B	45.8	42.6		30.5	42.6	
Front orientation	A	21.7	30.1	0.246	24.6	38.6	0.043
	B	26.2	23.9		21.4	25.5	
Side orientation	A	26.4	46.3	0.011	28.8	37.4	0.131
	B	24.9	37.1		27.7	33.2	
Back orientation	A	52.0	23.8	0.028	46.4	24.0	0.118
	B	49.3	41.4		48.6	41.3	

^aAnalysis compared grooming interactions occurring between an adult male and an adult female with those observed between adult females, using repeated-measures ANOVAs ($F_{1, 10}$). Figures represent means for groups A and B. *P* gives the probability calculated from the *F* value.

^bGroomer means an individual grooming an adult female; groomee, an individual groomed by an adult female.

Context of Social Grooming

Frequencies of occurrence before and after grooming were compared for each social context using repeated-measures ANOVA ($F_{1, 16}$) (Fig. 3). Most grooming interactions were not preceded by a particular event: either

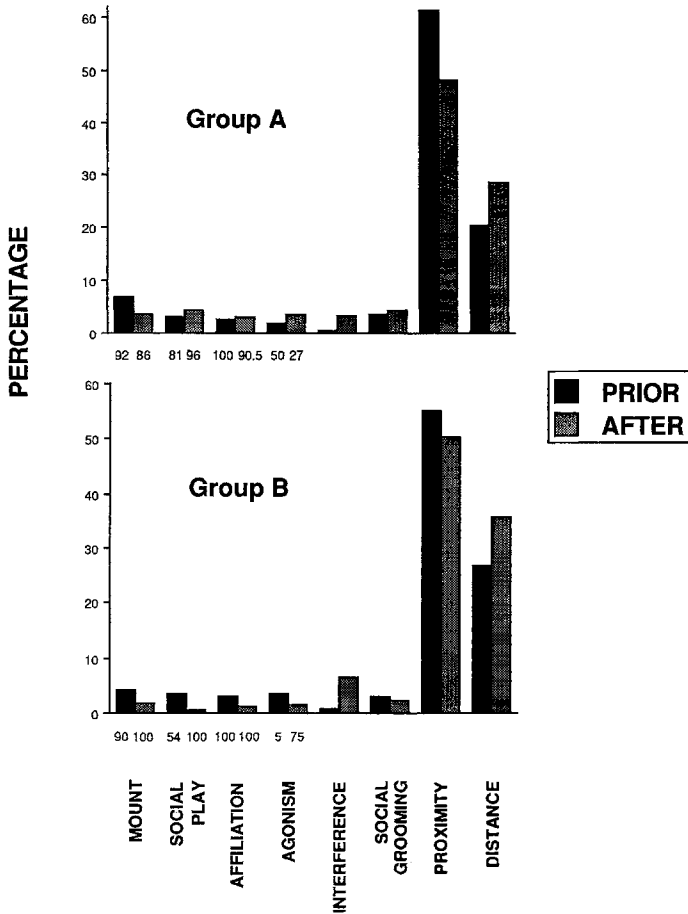


Fig. 3. Behavioral events occurring before and after grooming interactions. Figures represent mean percentages calculated from data collected for mature individuals recorded as groomers (group A, $N = 9$; group B, $N = 9$). For mount, social play, and affiliation, the proportion of instances where both members of the grooming dyad were involved is designated by the numbers displayed under bars. For agonism, numbers indicate the proportion of instances in which members of the dyad were adversaries.

individuals were in proximity or one individual approached another. “Proximity” was more frequent before grooming than after it ($P = 0.001$), while “distance” showed the converse trend ($P = 0.004$) (Fig. 3): partners tended to disperse after the interaction. Invitations to be groomed were not frequent: only 2.6% of instances. Interruption defines the end of a bout, and therefore, interference was more frequent after grooming ($P = 0.003$). Mounts

more often occurred before than after the interaction ($P = 0.014$) (Fig. 1), all being performed by males. With regard to other contexts, there were no significant differences before and after grooming (Fig. 3).

When *one* of the grooming partners was previously involved in an agonistic interaction, it was generally that individual which initiated grooming (A, 100%; B, 72%). Aggression between grooming partners was rare (Fig. 3) and appeared to be induced mostly by (inadvertent?) hair plucking.

Over both groups, a total of 77 instances of interference was recorded, including 48 instances of interruption and 29 of supplantation. Interruptions appeared not to reflect direct social competition: some were induced by disturbance in the vicinity of the interactants or by affiliative behavior directed toward one of the grooming partners (lip-smacking, mounting, playing, handling an immature groomed by mother) (A, 45%; B, 36%); in most other instances, the intervener simply approached and sometimes contacted the grooming pair. In only two cases, an intervener approached grooming individuals and threatened one of them. Most instances of interruption were not followed by dispersal of the interactants (A, 70%; B, 57%).

With respect to supplantation, the intervener generally contacted the grooming pair to groom or to be groomed, and one of the partners left. With regard to the relative ranks of the Supplanting, Targeted, and Leaving individuals, all six possible combinations were observed: $S > L > T$ (9 cases), $S > T > L$ (9), $T > S > L$ (5), $L > S > T$ (3), $L > T > S$ (2), and $T > L > S$ (1) (total number of cases over both groups). The supplanting individual was likely to be dominant over the other two interactants. However, subordinates did not appear to compete for access to high-ranking partners, the overall level of competition being very low. Targets were virtually always (28 of 29) adult females, which also represented the individuals most often performing grooming. All females in the groups appeared to be equally attractive as grooming partners since no factor (rank, age, kinship) emerged as being most important in the choice of supplanting individuals; however, the lack of data precluded us from testing this statistically.

Relation Between Form and Context of Social Grooming

For each group, data from all individuals were necessarily pooled in the following analyses.

Relation Between Context and First and Last Site Groomed. This analysis asked whether certain regions were more frequently groomed at the start or the end of a bout, depending on the situation. Contingency tables were established for each group: one for the sites groomed at the start of bouts, another for the sites at the end. For analysis, categories had to be regrouped as follows: for social contexts, *positive context* (mount, play, and affilia-

tion), *negative context* (agonism and supplantation), and *neutral context* (social grooming, proximity, and separation); and for body sites, *head* (face and head), *ventrum*, *back*, and *rump/limbs*. Observed and expected frequencies were compared using the chi-square test (Rao, 1973). There was no significant departure from randomness. To test specifically whether the back was more often groomed after aggression, as suggested by data from the literature, a further test was made using different categories: aggression *versus* other contexts and back *versus* other body sites. While in group B, the back was more frequently groomed following an agonistic interaction (8/241 compared to 4/616; $\chi^2 = 6.8$, 1 df, $P < 0.05$), no effect appeared in group A (4/148 compared to 6/532; $\chi^2 = 1.0$, 1 df, NS). Therefore, on the whole, the social context generally appeared to have no influence upon most grooming interactions.

Body Sites Starting and Terminating Social Grooming. Regardless of the context, certain regions might be more frequently groomed at the beginning or the end of the bout. To test for such an effect, frequencies of grooming were calculated for each body site, according to the stage of the grooming sequence: *start*, *middle*, or *end*. The three values obtained for each body site were compared with expected numbers using the chi-square test [general χ^2 followed by partitioning into three 2×2 tables to test the origin of the effects: Brunden's method, described by Everitt (1977)] (Fig. 4). The analysis showed that limbs (and face in group B) were generally groomed in the middle of a grooming bout. Opposite trends were found with respect to back and rump, which were more frequently groomed at the start and end of grooming (Fig. 4). Most comparisons between start and termination were nonsignificant; however, the head was more often groomed at the start ($P < 0.05$) in group A, and the lower arm at the end ($P < 0.05$) in group B (Fig. 4).

Grooming Sequence. A transition matrix was made describing the progression of grooming from one region of the body to another (Table IV). It showed that (1) grooming advanced according to continuity of body sites, with the exception of forearms and legs, which often occurred following the head or ventrum; (2) grooming tended to progress from the proximal parts of limbs toward the distal ones; and (3) the most frequent direction of grooming was the following: ventrum \rightarrow head \rightarrow back or arm; however, the reverse was also common.

Post Hoc Test. Since there were differences in the body sites groomed, including those tended at the start and end of bouts, the gender effect previously found in the analysis of postures and orientations of partners might be attributed to the fact that adult males groomed for shorter durations than adult females. Therefore, short grooming bouts (i.e., those lasting less than 1 min) were reanalyzed, using the parameters previously showing differences and for which values were sufficient to use statistical tests (repeated-measures

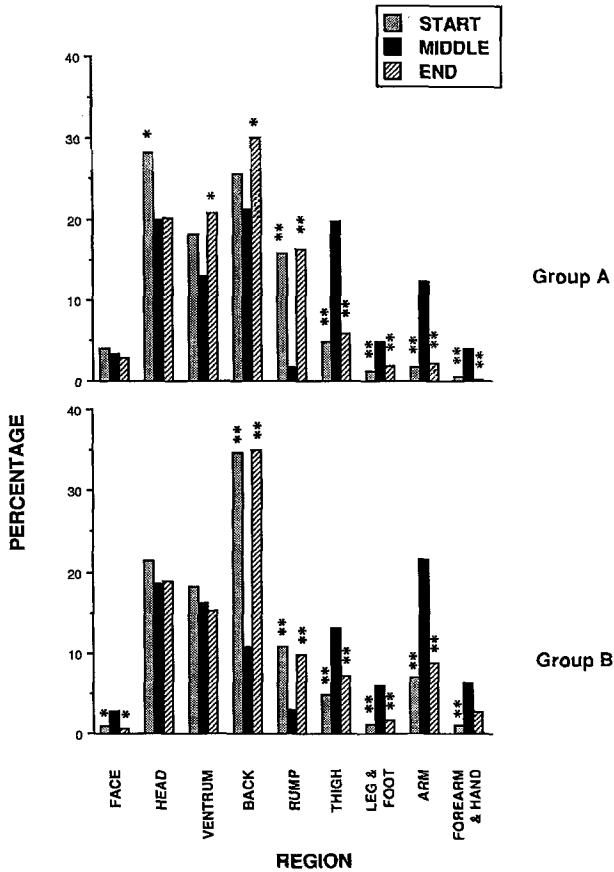


Fig. 4. Relation between parts of the body and progression of the grooming sequence. Values were expressed for every stage (start, middle, end) as proportions of the total frequency of body sites groomed. Significant results of statistical comparisons either between start and middle or between middle and end are indicated above the bars. Chi-square test: (*) $P < 0.05$; (**) $P < 0.01$.

ANOVA): durations of back grooming and the three possible orientations. The results were identical to those obtained in the first analysis. The effect was therefore not dependent from the grooming duration.

DISCUSSION

In our study, grooming sometimes followed affiliative interactions or agonistic interactions, which is consistent with the view that social groom-

Table IV. Transition Matrix Showing the Progression of Grooming from One Body Site to Another^a

Preceding body site	Following body site									
	Face	Head	Ventrum	Back	Rump	Thigh	Leg & foot	Arm	Forearm & hand	
Face	—	30/29	5/4	1/4	0/0	2/1	2/0	2/5	—	.1/1
Head	20/16	—	54/75	161/219	15/6	5/6	4/2	28/127	—	3/5
Ventrum	7/9	63/106	—	34/50	19/11	34/61	11/12	17/97	—	1/24
Back	5/7	83/133	66/92	—	60/51	44/62	2/8	15/83	—	1/6
Rump	0/0	6/8	15/21	62/50	—	30/46	3/2	1/5	—	2/0
Thigh	1/1	13/20	37/41	32/41	24/47	—	11/43	6/17	—	2/4
Leg & foot	0/2	6/23	7/14	2/7	2/6	10/19	—	2/9	—	2/7
Arm	3/5	21/89	15/81	14/69	0/2	5/28	3/9	—	—	8/57
Forearm & hand	0/2	11/21	5/15	1/6	0/0	3/9	0/15	2/19	—	—

^aFigures indicate frequencies observed in groups A and B, respectively (A/B).

ing may be used to regulate social tension within a group (Terry, 1970; Lindburg, 1973; McKenna, 1978; de Waal and Yoshihara, 1983). However, most grooming bouts were not preceded or followed by a special event. This may be accounted for by the other roles of social grooming: either its long-term function, of establishing and reinforcing bonds between individuals (Bertrand, 1969; Silk, 1982; Seyfarth and Cheney, 1984), or, more immediately, body cleaning (Sparks, 1967; Hutchins and Barash, 1976; Kurland, 1977). However, whatever the function of social grooming and its context of occurrence, the participants' behavior appeared to be constrained mainly by factors internal to the interaction. As a rule, easily accessible and not very intimate regions such as the back and rump were frequently chosen to start or terminate grooming, while limbs were groomed during the course of a bout. There was little relation between context and the order in which body sites were groomed. The sequence of grooming was bounded by physical factors, for example, depending on the continuity of body sites, or progressing from proximal to distal parts. Data from a similar study in rhesus macaques (Boccia *et al.*, 1982; Boccia, 1986) are concordant with our results. The body being the focus of the interaction, it is consistent that physical parameters govern most of the course of social grooming. This does not detract from the function of grooming in formation of alliances and conciliation between Tonkean macaques, but it may mean that, usually, short-term constraints from the social milieu on the individuals are not severe.

Whereas context was not an important intervening factor, gender strongly affected grooming. Comparing interactions involving two adult females with those occurring between an adult male and an adult female showed that, between adult females, bouts were longer and grooming was more often directed toward the head. While females preferred to face their partners, males were more often front to back. It may be said that grooming interactions were more "intimate" between females than between males and females. In rhesus macaques, a similar gender effect was found by Boccia *et al.* (1982).

The analysis revealed little influence of dominance and kinship on the form of social grooming. While the distribution of grooming depended on age and sex of individuals, which is a common finding among primates (Mitchell and Tokunaga, 1976; Goosen, 1987), it was not affected by dominance or kinship among adult females. This contrasts with observations from many species. In matrilineally structured groups, related individuals are preferentially chosen as grooming partners (Gouzoules and Gouzoules, 1987). The influence of the relative social ranks on grooming is well documented, especially among adult female macaques [*Macaca arctoides* (Estrada *et al.*, 1977; O'Keefe *et al.*, 1983; Nieuwenhuijsen *et al.*, 1988; Lopez-Vergara *et al.*, 1989); *M. mulatta* (Sade, 1972; Lindburg, 1973; de Waal and Luttrell, 1986); *M. fuscata* (Oki and Maeda, 1973; Mori, 1975; Ando, 1982, 1988;

Mehlman and Chapais, 1988)]. Although it is conceivable that some effects of kinship or dominance may be detected in a study of larger groups of Tonkean macaques, the present data indicate that such factors are not as important in them as in several other species of *Macaca*.

Although higher-ranking individuals appeared to choose their partners more easily, the overall level of competition was particularly low. This is in accordance with previous findings in Tonkean macaques, including a marked symmetry in contests, an elevated frequency of appeasement behaviors, and a great diversity of social contacts, with little influence of kinship relations (Thierry, 1984, 1985, 1986). The uniformity of social grooming in the Tonkean macaque reflects a weak gradient of asymmetry between individuals and a high degree of openness of matriline vis-à-vis unrelated conspecifics (Desportes and Thierry, in preparation). Such findings are reminiscent of what is known about the social relationships of bonnet macaques. In comparison to rhesus or pigtail macaques, bonnet macaques present little rigidity in their social relationships, individuals' behaviors being less constrained by dominance and kinship (Rosenblum, 1971; Glick, 1978; Caine and Mitchell, 1980; Silk *et al.*, 1981), and this is especially true for social grooming (Sugiyama, 1971; Defler, 1978; Silk, 1982). Also, while Boccia (1989) showed some dominance effects in bonnet females, she found that they less frequently faced their partners' backs than pigtail females did, and her data on relative orientations of interactants are comparable to those found for Tonkean macaques.

In several species, high-ranking individuals receive more grooming than others do, and those of adjacent rank tend to groom each other more than expected. Seyfarth (1977) hypothesized that these are effects of competition over access to higher-ranking individuals. However, as the subjects of the competition often do not outrank the competitors, competition alone appears insufficient to account for the phenomenon. Other authors (Colvin, 1983; de Waal and Luttrell, 1986) have proposed that, instead of preference for higher-ranking partners, it is the propensity to establish bonds with conspecifics much like oneself which is the root of the phenomenon. However, this hypothesis cannot explain the preference of individuals for higher-ranking partners. In addition, Seyfarth's model may still stand providing a closer examination of the consequences of strong hierarchies. A great asymmetry in dominance between individuals may often prevent them from establishing close relations. The consequence is that individuals form bonds with others, with which they *may* interact, i.e., those most familiar and nearer in rank. It is a common observation that subordinates may be reluctant to be in proximity with high-ranking individuals and, conversely, that the latter may threaten low-ranking ones that approach. In species with marked differences of status between individuals, the difficulty of individuals of widely separated

ranks in achieving proximity, combined with subordinates' avoidance of eventual competitors, may hinder the occurrence of affiliative interactions. On the contrary, where there are weak barriers in terms of rank and relatedness, as in bonnet and Tonkean macaques, the effects of these factors are correspondingly weaker: there may be neither a strong impetus to compete for access to high-ranking individuals nor potent factors preventing interactions between potential partners.

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REFERENCES

- Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour* 49: 227-267.
- Ando, A. (1982). Analysis of grooming relationships in a free-ranging group of Japanese macaques (*Macaca fuscata*). *Ann. Anim. Psychol.* 32: 60-71.
- Ando, A. (1980). Grooming relationships of the transplanted Arashiyama A group of Japanese macaques (*Macaca fuscata*). *Res. Rep. Arashiyama W. E. Groups Jap. Monkeys*, pp. 41-49.
- Barton, R. A. (1983). A comparative study of grooming interactions in primates. *Dodo J. Jersey Wildl. Preserv. Trust* 20: 26-36.
- Barton, R. (1985). Grooming site preferences in primates and their functional implications. *Int. J. Primatol.* 6: 519-532.
- Bertrand, M. (1969). *The Behavioral Repertoire of the Stumptail Macaque*, Karger, Basel.
- Boccia, M. L., Rockwood, B., and Novak, M. A. (1982). The influence of behavioral context and social characteristics on the physical aspects of social grooming in rhesus monkeys. *Int. J. Primatol.* 3: 91-108.
- Boccia, M. L. (1983). A functional analysis of social grooming patterns through direct comparison with self-grooming in rhesus monkeys. *Int. J. Primatol.* 4: 399-418.
- Boccia, M. L. (1986). Grooming site preferences as a form of tactile communication and their role in the social relations of rhesus monkeys. In Taub, D. M., and King, F. A. (eds.), *Current Perspectives in Primate Social Dynamics*, Van Nostrand Reinhold, New York, pp. 505-518.
- Boccia, M. L. (1989). Comparison of the physical characteristics of grooming in two species of macaques (*Macaca nemestrina* and *M. radiata*). *J. Comp. Psychol.* 103: 177-183.
- Caine, N. G., and Mitchell, G. (1980). Species differences in the interest shown in infants by juvenile female macaques (*Macaca radiata* and *M. mulatta*). *Int. J. Primatol.* 1: 323-332.
- Coelho, A., Turner, S., and Bramblett, C. (1983). Allogrooming and social status: An assessment of the contributions of female behavior to the social organization of hamadryas baboons (*Papio hamadryas*). *Primates* 24: 184-197.
- Colvin, J. (1983). Familiarity, rank and the structure of rhesus male peer networks. In Hinde, R. A., *Primate Social Relationships*, Blaxwell Scientific, Oxford, pp. 190-200.
- Defler, T. R. (1978). Allogrooming in two species of macaque (*Macaca nemestrina* and *Macaca radiata*). *Primates* 19: 153-167.

- Desportes, C., Demaria, C., and Thierry, D. (1989). Measures of dominance in a semi-free ranging group of Tonkean macaques. Communication to the *21st Int. Ethol. Conf., Aug. 9-17, Utrecht, The Netherlands*.
- de Waal, F. B. M., and Luttrell, L. M. (1986). The similarity principle underlying social bonding among female rhesus monkeys. *Folia Primatol.* 46: 215-234.
- de Waal, F. B. M., and Yoshihara, D. (1983). Reconciliation and redirected affection in rhesus monkeys. *Behaviour* 85: 224-241.
- Dixon, A. F., Scruton, D. M., and Herbert, J. (1975). Behaviour of the talapoin monkey (*Miopithecus talapoin*) studied in groups, in the laboratory. *J. Zool. Lond.* 176: 177-210.
- Drickamer, L. C. (1976). Quantitative observations of grooming behavior in free-ranging *Macaca mulatta*. *Primates* 17: 323-335.
- Everitt, B. S. (1977). *The Analysis of Contingency Tables*, Chapman and Hall, London.
- Freeland, W. J. (1981). Functional aspects of primate grooming. *Ohio J. Sci.* 81: 173-177.
- Glick, B. (1978). Kin relations and the social network of adolescent bonnet macaques (*Macaca radiata*). *Am. J. Phys. Anthropol.* 48: 398.
- Goosen, C. (1987). Social grooming in primates. In Mitchell, G., and Erwin, J. (Eds.), *Comparative Primate Biology, Vol. 2B. Behavior, Cognition, and Motivation*, Alan R. Liss, New York, pp. 107-131.
- Goy, R. W., Kraemer, G., and Goldfoot, D. (1988). Biological influences on grooming in non-human primates. *Ann. N. Y. Acad.* 525: 56-68.
- Gouzoules, S., and Gouzoules, H. (1987). Kinship. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 299-305.
- Hutchins, M., and Barash, D. P. (1976). Grooming in primates: Implications for its utilitarian function. *Primates* 17: 145-150.
- Kurland, J. A. (1977). *Kin Selection in the Japanese Monkey*, Karger, Basel.
- Lindburg, D. G. (1973). Grooming as a regulator of social interactions in rhesus monkeys. In Carpenter, C. R. (ed.), *Behavioral Regulators of Behavior in Primates*, Bucknell University Press, Lewisburg, pp. 124-148.
- Lopez-Vergara, L., Santillan-Doherty, A. M., Mayagoitia, L., and Mondragon-Ceballos, R. (1989). Self and social grooming in stump-tailed macaques: Effects of kin presence or absence within the group. *Behav. Proc.* 18: 99-106.
- McKenna, J. J. (1978). Biosocial functions of grooming among the common Indian langur monkey (*Presbytis entellus*). *Am. J. Phys. Anthropol.* 48: 503-510.
- Mehlman, P. T., and Chapais, B. (1988). Differential effects of kinship, dominance, and the mating season on female allogrooming in a captive group of *Macaca fuscata*. *Primates* 29: 195-217.
- Mitchell, G., and Tokunaga, D. H. (1976). Sex differences in nonhuman primate grooming. *Behav. Proc.* 1: 335-345.
- Mori, A. (1975). Signals found in the grooming interactions of wild Japanese monkeys of the Koshima troop. *Primates*, 16: 107-140.
- Nieuwenhuijsen, K., Slob, A. K., and van der Werff ten Bosch, J. J. (1988). Gender-related behaviors in group-living stump-tail macaques. *Psychobiol.* 16: 357-571.
- Oki, J., and Maeda, Y. (1973). Grooming as a regulator of behavior in Japanese macaques. In Carpenter, C. R. (ed.), *Behavior Regulators of Behavior in Primates*, Bucknell University, Lewisburg, pp. 149-163.
- Poirier, F. E. (1970). The Nilgiri langur (*Presbytis johnii*) of South India. In Rosenblum, L. A. (ed.), *Primate Behavior. Developments in Field and Laboratory Research, Vol. 1*, Academic Press, New York, pp. 251-383.
- Rao, C. R. (1973). *Linear Statistical Inference and Its Application*, Wiley, New York.
- Rosenblum, L. A. (1971). Kinship interaction patterns in pigtail and bonnet macaques. In Kummer, H. (ed.), *Proc. 3rd Int. Congr. Primatol., Zurich, 1970. Vol. 3*, Karger, Basel, pp. 79-84.
- Sade, D. S. (1972). Sociometrics of *Macaca mulatta*. I. Linkages and cliques in grooming matrices. *Folia Primatol.* 18: 196-223.
- Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *J. Theor. Biol.* 65: 671-692.

- Silk, J. B. (1982). Altruism among female *Macaca radiata*: Explanations and analysis of patterns of grooming and coalition formation. *Behaviour* 79: 162-188.
- Silk, J. B., Samuels, A., and Rodman, P. S. (1981). Hierarchical organization of female *Macaca radiata* in captivity. *Primates* 22: 84-95.
- Sparks, J. (1967). Allogrooming in primates: A review. In Morris, D. (ed.), *Primate ethology*, Weidenfeld and Nicholson, London, pp. 148-175.
- Sugiyama, Y. (1972). Characteristics of the social life of bonnet macaques (*Macaca radiata*). *Primates* 12: 247-266.
- Terry, R. L. (1970). Primate grooming as a tension reduction mechanism. *J. Psychol.* 76: 129-136.
- Thierry, B. (1984). Clasping behaviour in *Macaca tonkeana*. *Behaviour* 89: 1-28.
- Thierry, B. (1985). Social development in three species of macaque (*Macaca mulatta*, *M. fascicularis*, *M. tonkeana*): A preliminary report on the first ten weeks of life. *Behav. Proc.* 11: 89-95.
- Thierry, B. (1986). A comparative study of aggression and response to aggression in three species of macaque. In Else, J. G., and Lee, P. C. (eds.), *Primate Ontogeny, Cognition and Social Behaviour*, Cambridge University Press, Cambridge, pp. 307-313.
- Turillazzi, P. G., Marchini, S., Alessandrini, P., Baldo, N., Campanella, C., and Trucchi, D. (1982). Social grooming in *Macaca fuscata*. *Ann. Ist. Super. Sanità* 18: 239-250.