PRIMATES, 39(3): 365–374, July 1998

Comparative Study of Grooming Relationships among Wild Japanese Macaques in Kinkazan A Troop and Yakushima M Troop

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ABSTRACT. The influences of socionomic sex ratio (SSR; adult males/adult female) and troop size upon male-male, female-female, and male-female grooming relationships were examined and compared between two wild Japanese macaque troops (Kinkazan A and Yakushima M troops) in Japan. The Yakushima M troop was smaller and had a higher-SSR than the Kinkazan A troop. Between the troops, (1) the male-male grooming frequency and number of partners were greater in the Yakushima M troop than in the Kinkazan A troop; (2) the female-female grooming frequency and number of partners were not different; and (3) the male-female grooming frequency and number of partners were not different. Based on these features, the patterns of female-female and male-female grooming relationships appear to be independent of SSR and troop size variations. In contrast, male-male grooming relationships are influenced by both factors, especially SSR. Frequent grooming interactions among males may be useful for the continued coexistence of relatively many males especially in a higher-SSR troop.

Key Words: *Macaca fuscata*; Grooming relationships; Socionomic sex ratio; Troop size; Non-provisioning.

INTRODUCTION

In primate societies, there may be considerable intra-species variations in social relationships. Such intra-species variation in Japanese macaques (*Macaca fuscata*) has been discussed mainly from the viewpoint of provisioning (IZAWA, 1982; FURUICHI, 1983, 1984, 1985; YAMAGIWA, 1985).

HILL (1994) found that troop size and socionomic sex ratio (SSR; number of adult males per female) may influence the nature of the relationships between males: males tend to show affiliative behaviors more in small-sized non-provisioned troops with a high-SSR than in large-sized provisioned troops with a low-SSR. However, provisioning is associated with an increased group size and a skewed SSR (reviewed in ASQUITH, 1989). Moreover, it may enhance competition between animals, because the artificial food resources are limited in space and time. Provisioning may thus inhibit the occurrence of male-male affiliative behaviors (HILL, 1994). Comparative studies on non-provisioned troops of Japanese macaques are therefore required in order to exclude the potential influence of provisioning.

This paper compares the affiliative behavior (grooming) of a troop of *M. fuscata fuscata* on Kinkazan Island with that of a troop of *M. fuscata yakui*. Both troops were non-provisioned, but differed in their troop sizes and SSR; the Kinkazan troop is known to be larger in size with a lower-SSR compared to the Yakushima troop (SPRAGUE et al., 1998). The Japanese macaque is one of the most studied primate species. However, comparable data on grooming in non-provisioned troops are rare. The present study may therefore provide a good opportunity to test HILL's

findings by analyzing the male-male, female-female, and male-female grooming relationships. Following HILL's findings, male-male grooming is predicted to be more frequent in the Yakushima troop than in the Kinkazan troop.

METHODS

Data were obtained from two non-provisioned populations of Japanese macaques: (1) the Kinkazan A troop, and (2) the Yakushima M troop. The Kinkazan A troop was studied from January 9 to March 31, 1993, in the non-mating season. The troop contained 45 animals including 7 adult males and 20 adult females, giving an SSR of 0.35. The 7 adult males and 14 parous females were traced for 600 min each by the focal animal sampling method (ALTMANN, 1974). However, the two lowest-ranking males were in fact followed for a short amount of time, because they emigrated from the study troop during the above period (see TAKAHASHI, 1997a).

The Yakushima M troop was studied from April 13 to May 18, 1981, in the non-mating season. The troop contained 27 animals including 6 adult males and 7 adult females, giving an SSR of 0.86. All adult males and adult females were traced for 600 min each by the focal animal sampling method (see FURUICHI, 1985).

In the Kinkazan A troop, the numbers of possible dyads among focal animals were 21 between males, 91 between females, and 98 between males and females. In the Yakushima M troop, the corresponding numbers were 15, 21, and 42, respectively.

Social behaviors which involved the focal animal were recorded at 1-min intervals in the Yakushima M troop (FURUICHI, 1985) and at 30-sec intervals in the Kinkazan A troop (TAKAHASHI, 1997a). Each record was counted as one observation unit (OU). In both troops, the grooming behaviors among male-male, female-female, and male-female dyads were recorded (for data on grooming OUs in the Yakushima M troop, see FURUICHI, 1985, Table 4). In order to standardize the data on grooming, a grooming index was adopted as follows: the grooming indices between individuals *A* and *B* can be expressed by $[f_A(B)\times 100]/[F(A)+F(B)]$ and $[f_B(A)\times 100]/[F(A)+F(B)]$, where $F(A)$ or $F(B)$ is the total number of OUs of *A* or *B*, $f_A(B)$ is the total number of OUs in which individual *A* groomed *B* while *A* or *B* was followed, and $f_B(A)$ is the total number of OUs in which *B* groomed *A* while *A* or *B* was followed. However, the Kinkazan A troop often split into several sub-groups during the study period (TAKAHASHI, unpubl. data). Thus, $F(A)$ or $F(B)$ of the Kinkazan A troop is defined as the total number of OUs when *A* and *B* were identified in the same sub-group or a troop which did not split. Grooming indices for both troops are presented in Table 1. Dyads which were not observed to show grooming interactions were excluded from the statistics.

All statistical tests were non-parametric and two-tailed unless otherwise stated.

RESULTS

MALE-MALE RELATIONSHIPS

The Kinkazan A troop was larger and had a lower-SSR than the Yakushima M troop, and male-male grooming occurred more frequently in the Yakushima M troop than in the Kinkazan A troop (Fig. 1 and Table 1).

In the Kinkazan A troop, grooming among the seven males was observed in 10 (47.6%) of the 21 possible male-male dyads (Table 1a), while that among the six males in the Yakushima

Table 1a. Distribution of grooming index in the Kinkazan A troop.[1)]

		Groomee																			
	Groomer	*AR*	*IS*	*PR*	*CR*	*NT*	*KD*	*RS*	*Hr*	*Sr*	*Ob*	*Mk*	*Be*	*Er*	*Kb*	*Dk*	*Hn*	*Mg*	*Su*	*Mn*	*Mr*	*Sh*
Males	*AR*	–		0.30	0.75	0.31	0.45			2.07				1.40		0.75		1.23		1.03*		0.05
	IS		–	0.38*	1.45					0.51	0.05	1.08		0.15								
	PR	0.20		–		0.44				0.5		0.21			0.04			0.10	0.86			1.80
	CR	1.94*	2.33		–	4.14*																
	NT	0.13		1.73*	2.83	–						0.98										
	KD	0.71					–	3.81*			0.22		0.08			0.94			1.46*			
	RS	0.57					0.52	–														0.17
Females	*Hr*								–	2.55	0.38											
	Sr	2.05	1.47*	0.44					7.34*	–		0.44							0.40	0.38		
	Ob		0.26						0.19		–	0.54	5.18*			0.36				1.54		
	Mk	0.57*	1.58	0.31		0.98				0.16	0.21	–	0.04			0.44			0.54	0.17		
	Be										3.62	0.13	–	0.48								
	Er	4.77*	1.12*										0.24	–	0.07	5.40						
	Kb													0.07	–	2.13*	0.04		0.07			
	Dk	0.90					0.57				0.41	0.55		2.25	0.39	–	8.30*					
	Hn															3.90	–		1.29*	1.38*		
	Mg	2.24*																–				
	Su		0.09	1.14			0.26			0.30		0.49		0.05				0.48*	–		0.29	
	Mn	0.36								0.26	1.84	0.11						1.32*		–	5.26*	
	Mr																		0.76	2.41	–	
	Sh	0.05		1.50												0.06						–

Table 1b. Distribution of grooming index in the Yakushima M troop.[1)]

		Groomee												
	Groomer	*NU*	*AH*	*PL*	*MC*	*E*	*J*	*Ak*	*Ks*	*Sd*	*Ao*	*Aj*	*It*	*Sk*
Males	*NU*	–	5.42*	2.92*	0.75	0.83		2.67*		1.00*		2.08*		
	AH	3.83	–	1.00		2.75	0.92	1.83	0.17	0.50			0.42	0.25
	PL	1.67	2.42*	–		1.75	1.25							
	MC	1.67			–	2.83*	1.67							
	E	0.58*	2.67	2.33	1.33	–	1.17						0.25	
	J		0.83	1.50	2.92*	2.58*	–							
Females	*Ak*	1.25	1.33					–	3.92	0.08			0.67	
	Ks					0.08		6.17*	–	1.67	0.25			0.83
	Sd	0.33	1.00					0.08	2.33	–				0.17
	Ao							0.42	0.17		–	8.17		
	Aj	0.83	0.42*								8.42	–	0.08	0.08
	It		0.67			0.25		0.17		0.08		0.17	–	5.00
	Sk	0.17	0.33						0.50				3.42	–

1) For calculation of the grooming index, see text. The dyad cells in squares are kin-related. Asterisks indicate that the index is significantly more than that in the opposite direction in the same dyads, on calculation of OUs by the binomial test ($p<0.05$). Blank cells represent those in which grooming interactions were not observed.

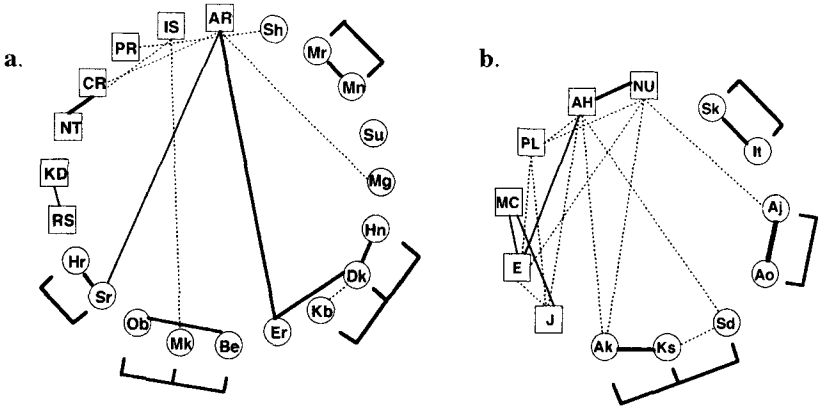

Fig. 1. Grooming networks in **a**. the Kinkazan A troop and **b**. the Yakushima M troop. Only indices greater than the mean ($\overline{X}$) are shown in each troop. Scale: Dotted line$<\overline{X}+SD$; $\overline{X}+SD\leqq$thin line$<\overline{X}+2SD$; $\overline{X}+2SD\leqq$thick line$<\overline{X}+3SD$; $\overline{X}+3SD\leqq$bold line. Squares represent males, and circles represent females. Adult males are arranged in descending rank order, counter-clockwise from *AR* in the Kinkazan A troop and from *NU* in the Yakushima M troop. Adult females are arranged in descending rank order, counter-clockwise from *Hr* in the Kinkazan A troop and from *Ak* in the Yakushima M troop. Kin-related individuals are indicated for each network (outer brackets).

M troop was observed in 12 (80%) of the 15 possible male-male dyads (Table 1b). The number of grooming partners and the grooming indices were larger in the Yakushima M troop than in the Kinkazan A troop. The number of male grooming partners per male was significant greater in the Yakushima M troop (4.0) than in the Kinkazan A troop (2.9) (Mann-Whitney *U*-test, $N1=6$, $N2=7$, $U=7$, $p<0.05$). The mean male-male grooming index calculated for the total GOUs in each dyad was significant higher in the Yakushima M troop (3.97, S.D.=2.06) than in the Kinkazan A troop (2.30, S.D.=2.19) ($N1=12$, $N2=10$, $U=30$, $p<0.05$).

Dominance relationships did not influence the direction of grooming in either troop. The grooming indices in which dominants groomed subordinates were not significantly different from those in which subordinates groomed dominants (Wilcoxon matched pairs signed rank test: Yakushima M troop, $Z_{cal}=0.157$, N.S.; Kinkazan A troop, $Z_{cal}=0.152$, N.S.).

FEMALE-FEMALE RELATIONSHIPS

Although the number of dyads in which grooming was observed differed between the troops, the number of grooming partners and frequency of grooming interactions were not different between the two troops. Grooming interactions were observed in only 28 (30.8%) of the 91 possible female-female dyads of the Kinkazan A troop (Table 1a), but 13 (61.9%) of the 21 possible female-female dyads of the Yakushima M troop (Table 1b). The number of female grooming partners per female was 4.0 in the Kinkazan A troop and 3.4 in the Yakushima M troop (Mann-Whitney *U*-test, $N1=14$, $N2=7$, $U=40$, N.S.). The mean female-female grooming index calculated for the total GOUs in each dyad was 2.33 (S.D.=3.44) in the Kinkazan A troop, and 3.30 (S.D.=5.21) in the Yakushima M troop ($N1=28$, $N2=13$, $U=176$, N.S.).

Kin dyads exhibited frequent grooming interactions in both the Kinkazan A troop and the Yakushima M troop (Fig. 1, Table 1). In both troops, grooming interactions occurred in all kin dyads. In contrast, grooming interactions occurred in only 20 (24.1%) of the 83 possible non-kin dyads of the Kinkazan A troop (Table 1a), and in 8 (50%) of the 16 possible non-kin dyads of the Yakushima M troop (Table 1b).

There were no significant differences in grooming indices between the troops for either all kin dyads ($N1=8$, $N2=5$, $U=15$, N.S.) or all non-kin dyads ($N1=20$, $N2=8$, $U=53$, N.S.). In both troops, the mean grooming indices calculated for the total GOUs in each dyad were greater among kin dyads (Kinkazan A troop, mean index=5.26, S.D.=4.91; Yakushima M troop, mean index=7.86, S.D.=6.24) than among non-kin dyads (Kinkazan A troop, mean index=1.16, S.D.=1.69; Yakushima M troop, mean index=0.45, S.D.=0.43). This difference was significant in the case of the Yakushima M troop ($N1=5$, $N2=8$, $U=6$, $p<0.05$). On the other hand, no significant difference was found in the grooming indices between kin and non-kin dyads in the Kinkazan A troop ($N1=8$, $N2=20$, $U=47.5$, N.S.). However, when the lowest grooming index for one kin dyad (*Kb-Hn*, total grooming index=0.04, Table 1a) was excluded, the difference between kin and non-kin dyads was also significant in the Kinkazan A troop ($N1=7$, $N2=20$, $U=27.5$, $p<0.05$).

Dominance relationships did not influence the direction of grooming in either troop. The grooming indices among non-kin dyads in which dominants groomed subordinates were not significantly different from those in which subordinates groomed dominants (Wilcoxon matched pairs signed rank test: Kinkazan A troop, $Z_{cal}=0.785$, N.S.; Yakushima M troop, $Z_{cal}=0.703$, N.S.).

Male-female Relationships

As shown in Figure 1, higher-ranking males tended to exhibit frequent grooming interactions with females in both the Kinkazan A and Yakushima M troops. The male-female grooming indices between the troops were not different. Grooming interactions were observed in 24 (24.5%) of the 98 possible male-female dyads in the Kinkazan A troop (Table 1a), and in 12 (28.6%) of the 42 possible male-female dyads in the Yakushima M troop (Table 1b).

The number of grooming partners did not differ between the troops. The number of female grooming partners per male was 3.4 in the Kinkazan A troop and 2.0 in the Yakushima M troop (Mann-Whitney U-test, $N1=7$, $N2=6$, $U=12.5$, N.S.). The number of male grooming partners per female was 1.7 in the Kinkazan A troop and 1.6 in the Yakushima M troop ($N1=14$, $N2=7$, $U=46$, N.S.).

The frequency of male-female grooming interactions was not different. The mean male-female grooming index calculated for the total GOUs in each dyad was 1.51 (S.D.=1.54) in the Kinkazan A troop, and 1.32 (S.D.=1.31) in the Yakushima M troop ($N1=24$, $N2=12$, $U=136.5$, N.S.).

The grooming indices in which males groomed females were not significantly different from those in which females groomed males in either troop (Wilcoxon matched pairs signed rank test: Kinkazan A troop, $Z_{cal}=0.811$, N.S.; Yakushima M troop, $Z_{cal}=0.712$, N.S.).

DISCUSSION

Features of Grooming Relationships Common to Both the Kinkazan A and Yakushima M Troops

Agetsuma and Nakagawa (1998) have demonstrated that differences exist between the Kinkazan and Yakushima populations in terms of the activity time budgets of the individuals. Those in the Yakushima population spent more time in grooming interactions than did those of Kinkazan. However, there was no significant difference between the grooming indices of the Kinkazan A troop and Yakushima M troop (mean grooming index for the Kinkazan A troop= 2.01, S.D.=2.64; for the Yakushima M troop=2.87, S.D.=3.48, Table 1a and 1b; Mann-Whitney U-test, $N1=37$, $N2=62$, $U=960.5$, N.S.).

Although the Kinkazan A and Yakushima M troops differed in their troop size and SSR, the following common features of the grooming relationships were found. First, dominance relationships did not influence the direction of male-male, female-female, or male-female grooming interactions. These tendencies were quite different from those reported for provisioned Japanese macaque troops and other species, in which subordinate individuals tended to groom dominant ones unilaterally (e.g. FURUYA, 1957; KAUFMANN, 1967; Sade, 1972; OKI & MAEDA, 1973; DRICKAMMER, 1976; SEYFARTH, 1977; TAKAHATA, 1982). Such tendencies might be related to the fact that closer relationships with dominant individuals could have an advantageous effect for subordinate individuals in severe competitive situations such as at artificial feeding sites of provisioned troops, as discussed previously by KAWAI (1958), KITAMURA (1977), WATANABE (1979), and SEYFARTH (1983). On the other hand, affiliative behaviors in non-provisioned troops may be less influenced by dominance relationships, since competition for food resources is generally not severe in non-provisioned situations (IZAWA, 1982; FURUICHI, 1986).

Second, in female-female dyads, kin dyads exchanged the most frequent grooming interactions. This finding is consistent with a kin-selection hypothesis. A similar tendency has been reported in both provisioned and non-provisioned Japanese macaque troops (FURUYA, 1957; YAMADA, 1963; KOYAMA, 1977; FURUICHI, 1984) and in other species (e.g. *M. mulatta*: SADE, 1972; *M. nemestrina*: DEFLER, 1978).

Third, in male-female dyads, higher-ranking males tended to have frequent grooming interactions with females in both the Kinkazan A and Yakushima M troops. This tendency has been observed in both a large-sized provisioned troop with a low SSR (TAKAHATA, 1982) and a small, non-provisioned troop with a high-SSR (HILL, 1991, 1994). It appears that affiliative relationships between higher-ranking males and females may be common in both provisioned and non-provisioned troops independent of troop size and SSR.

DIFFERENCES IN FEATURES OF GROOMING RELATIONSHIPS BETWEEN THE KINKAZAN A AND YAKUSHIMA M TROOPS

The male-male grooming relationships were quite different between the Kinkazan A and Yakushima M troops. Grooming among males occurred more frequently in the Yakushima M troop than in the Kinkazan A troop.

In general, SSR and troop size are correlated in the genus *Macaca* (HILL, 1994), and these factors may not influence the social relationships independently. Taking this into consideration, HILL (1994) suggested that the SSR is the more important of the two factors for male-male affiliative behaviors. The difference of male-male grooming interactions found in the present study seems to support this proposition.

Table 2 shows variations in the troop size, SSR, and grooming behaviors of several non-provisioned Japanese macaque troops in the non-mating season. The data indicate that male-male grooming tends to occur more frequently than male-female grooming in higher-SSR troops. The grooming sex ratio (GSR), i.e. the total frequency of male-male grooming interactions divided by the total frequency of male-female grooming interactions, was significantly correlated with the SSR (Kendall's rank correlation coefficient, $N=12$, $\tau=0.573$, $p<0.01$), but not with troop size ($N=12$, $\tau=-0.276$, N.S.). Whereas the SSR predicts the possibility for males to have social interactions with males and females, the troop size does not. The SSR is thus a more important factor for male-male affiliative interactions than troop size in non-provisioned troops.

FURUICHI (1985) and HILL (1994) stated that troop males form relationships with other troop males when female partners are not available. This situation will tend to occur more in higher-

Table 2. Variations of grooming behaviors, socionomic sex ratio, and troop size in non-provisioned Japanese macaque troops in the non-mating season.

Study troop	Study period	Sampling method[2)]	Sex of focal animals	Troop size	Socionomic sex ratio	Grooming sex ratio[3)]	Source
Yakushima M	Feb. 1980	Scanning (scan number)	–	25	1.14	3.92	FURUICHI, 1985
Yakushima M	Apr.–May 1981	Focal (OU)	Male & female	27	0.86	2.54	FURUICHI, 1985
Yakushima A[1)]	Mar.–Sep. 1986	Focal (Time)	Male	38	0.86	0.31	TSUKAHARA, 1990
Yakushima P	Dec. 1987–May 1989	Focal (Time)	Male	15	0.80	0.58	HILL, 1994
Kinkazan B1	Mar. 1995	Focal (OU)	Male	30	0.56	1.52	TAKAHASHI, unpubl.
Yakushima M	Apr.–May 1980	Ad lib (Time)	–	22	0.5	1.15	FURUICHI, 1985
Kinkazan A	Jan.–Mar. 1993	Focal (OU)	Male & female	45	0.35	0.58	TAKAHASHI, 1997b
Kinkazan A	Apr.–May 1993	Focal (OU)	Male	40	0.25	0.07	TAKAHASHI, 1997b
Kinkazan A	Feb.–Mar. 1995	Focal (OU)	Male	52	0.2	0.19	TAKAHASHI, 1997b
Kinkazan A	Apr.–May 1996	Focal (OU)	Male	53	0.17	0.63	TAKAHASHI, 1997b
Kinkazan A	Feb.–Mar. 1994	Focal (OU)	Male	38	0.15	0	TAKAHASHI, 1997b
Kinkazan A	Apr.–May 1994	Focal (OU)	Male	51	0.15	0.17	TAKAHASHI, 1997b

1) Four of 13 males were selected as focal animals; 2) the details in parentheses indicate the sampling scale of grooming interactions; 3) grooming sex ratio is given by the total frequency of grooming interactions between males divided by that between males and females.

SSR troops such as the Yakushima M troop than in lower-SSR troops such as the Kinkazan A troop. However, the male-female grooming index and numbers of female grooming partners for males did not differ between the two troops. This finding failed to support FURUICHI's and HILL's hypothesis.

The question then arises as to why the male-male grooming index and number of male grooming partners for males should be greater in high-SSR troops. Male-male potential competition for access to females is more severe in higher-SSR troops than in lower-SSR troops. To coexist in higher-SSR troops, it is considered that males may take steps to reduce the social tension among themselves that arises from the potential competition for access to females. In this context, frequent grooming interactions among many males could help to reduce social tensions among them and may be useful for maintaining coexistence in higher-SSR troops such as the Yakushima M troop.

Further, the inter-group relationships need to be considered in order to understand the variations in male-male relationships. HILL and VAN HOOFF (1994) pointed out that increased competition between groups might enhance cooperation between individuals within a group. Inter-group encounters were observed more frequently, and males were more aggressive, in the Yakushima troop than in the Kinkazan troop (SAITO et al., 1998; SAITO et al., in prep.). Troop extinction, which could be influenced by inter-troop competition, is known not to be a rare phenomenon in the study area of Yakushima Island (MARUHASHI, 1992; TAKAHATA et al., 1994). Thus, the close male-male relationships occurring in the Yakushima M troop may reflect the existence of severe inter-group relationships.

Acknowledgments. We are grateful to Prof. T. NISHIDA, Dr. H. IHOBE, and the members of the Laboratory of Human Evolution Studies, Kyoto University, for their guidance and suggesting regarding this study. Special thanks are accorded to T. KANO, H. ISHIDA, Y. TAKAHATA, D.A. HILL, J. YAMAGIWA, D.S. SPRAGUE, N. NAKAGAWA, C. SAITO, H. SUGIURA, and the anonymous referees for their critical reading and correction of the manuscript; and to T. MARUHASHI, N. AGETSUMA, and T. TANAKA for their helpful criticisms. We thank Prof. K. IZAWA and many colleagues at both the Kinkazan and Yakushima study sites for their invaluable help and provision of excellent facilities. This study was financed in part by the Cooperative Research Fund of the Primate Research Institute, Kyoto University, and a Grant-in-Aid for Encouragement of Junior Scientists (No. 3104) from the Japanese Ministry of Education, Science, Culture, and Sports.

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—— Received: *November 25, 1996*; Accepted: *November 11, 1997*

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