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Effects of Troop Size on Social Relations among Male Formosan Macaques, *Macaca cyclopis*

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Tai-Jung Lin, Govindasamy Agoramoorthy, Chih-Chien Huang, and Minna J. Hsu (2008) Effects of troop size on social relations among male Formosan macaques, *Macaca cyclopis*. *Zoological Studies* **47**(3): 237-246. We investigated the effects of troop size on differences in grooming and agonistic behaviors among adult males (AMs) and adult females (AFs) of Formosan macaques (*Macaca cyclopis*) during mating and non-mating seasons. Data were recorded for a total of 1248.8 h in 2 free-ranging social groups from Aug. 2000 to Feb. 2003 at Mt. Longevity, Kaohsiung, southern Taiwan. The socionomic sex ratios of these 2 social groups were similar during the mating seasons (AM: AF = 1: 1.8). Both troop and peripheral males had significantly higher frequencies of social grooming with AFs in the mating than in non-mating seasons. The types of males and social groups, however, had significant effects on the allogrooming frequency among AMs in the mating seasons but not in the non-mating seasons. Moreover, troop males had higher numbers of grooming partners than did peripheral males. Major grooming partners of troop males were adult females regardless of the seasons. Nonetheless, peripheral AMs had more male grooming partners seemingly to enhance male affiliative relations. Subordinate males were mostly receivers in grooming dyads with dominant males in the mating seasons, but the relationships changed during the non-mating seasons. Agonistic interactions occurred mainly during the mating seasons, and their frequency among peripheral males was 1.8 times that of troop males ($p < 0.05$). Formosan macaque AMs employ complex strategies to balance competition and affiliative relations and ultimately achieve reproductive success. http://zoolstud.sinica.edu.tw/Journals/47.3/237.pdf

Key words: *Macaca cyclopis*, Affiliation, Grooming, Agonistic behavior, Mating season.

In primates, grooming is a major social activity by which individuals that live in proximity can bond and reinforce social structures by regulating group life and promoting cohesion within social groups (Lindburg 1973). Social grooming is also used as a form of reconciliation and a means to resolve conflicts in some species. The matrilineal organization of macaques' society is characterized by kinship and frequent social grooming, especially among females (Goosen 1987, Thierry et al. 1990, Butovskaya and Kozintsev 1996, Copper and Bernstein 2000).

The matrilineal societies of macaques are known to have closer affiliations of females with higher frequency of allogrooming than among males (Copper and Bernstein 2000). Social grooming is a good index for measuring affiliative relations of female primates, but competition for grooming partners also exists in addition to attraction towards kin-related and high-ranking individuals (Seyfarth 1977). However, a greater variation in male-male relationships occurs in non-human primates (van Hooff and van Schaik 1994).

Male macaques are known to disperse from their natal groups and frequently move from 1 group to another (Suzuki et al. 1998, van Noordwijk and Schaik 2001, Mori and Watanabe 2003). Therefore, affiliative behavior among adult males

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(AMs) in the genus *Macaca* has been reported to be rare or not observed in some species such as rhesus macaques (*M. mulatta*) (Lindburg 1973, Drickamer 1976), Japanese macaques (*M. fuscata*) (Koyama 1991), and crab-eating macaques (*M. fascicularis*) (Wheatley 1982). However, after thoroughly reviewing the published literature on macaques, Hill (1994) reported that affiliative behavior among AMs is more widespread than previously thought, and it may be related to troop size and the adult sex ratio. Detailed comparative studies are therefore needed to substantiate the role of troop size and the adult sex ratio in influencing affiliative behaviors among AM macaques.

The Formosan macaque (*M. cyclopis*) is the only non-human primate endemic to the island of Taiwan. Earlier studies of Formosan macaques mainly focused on their morphology, physiology, and anatomy (Pryor and Raulston. 1969). Population ecology and behavior have been emphasized only in recent years (Wu and Lin 1993, Lee and Lin 1995, Hsu and Lin 2001). A long-term field study of Formosan macaques at Mt. Longevity, southern Taiwan has been conducted since 1993 to collect data on demographics, behavior, and ecology (Hsu and Lin 2001, Hsu et al. 2001 2002 2005 2006). Although a previous study reported the patterns of adult affiliations among Formosan macaques (Birky and Su 2005), quantitative data on the relations and behavioral differences among adult males are so far not available.

Suzuki et al. (1998) found that larger troops have a greater proportion of young males than smaller troops, but the inter-troop transfer of male Japanese macaques maintained an age-graded dominance rank order among non-natal males irrespective of variations in troop size. Furthermore, the sex ratio among social troops, rates of inter-troop encounters, number of non-troop males, troop sizes, and habitat preferences noticeably affected the frequency of male-male grooming patterns (Takahashi and Furuichi 1998, Horiuchi 2007). However, data on the function and seasonal variation of male-male affiliations and the frequency of agonistic interactions among Formosan macaques are still lacking.

In this paper, we provide data for the first time on social interactions among male Formosan macaques at Mt. Longevity. We compared and discussed grooming and agonistic behavioral interactions among troop males and peripheral males during mating and non-mating seasons in relation to troop sizes.

MATERIALS AND METHODS

The study area is located at Mt. Longevity (22°39'N, 120°15'E), Kaohsiung, southern Taiwan, which is adjacent to the Taiwan Strait. The highest peak is about 354 m. A long-term field study to investigate the behavioral ecology of Formosan macaques at Mt. Longevity began in July 1993 (see Hsu et al. 2000, Hsu and Lin 2001 for study site details). Mt. Longevity is located in an area with a southwesterly prevailing wind in summer, and is occasionally passed by typhoons in July and Aug. According to records of the Central Weather Bureau in Kaohsiung, the average annual precipitation between 2000 and 2003 was 1622 ± 660 mm, which was concentrated from May to Sept. The average annual temperature is about 25.3 ± 0.2°C.

A field study to record data on the social behaviors of Formosan macaques was conducted from July 2000 to Feb. 2003, mainly (for 88.5% of the observation time) on a multi-male/multi-female group (C) and its splinter group (Cd). Field data were collected for 1-3 d/wk from dawn to dusk, whenever it was possible to track the groups. We followed the broad age classification of (1) infants (< 1 yr); (2) juveniles (1-4 yr); and (3) adults (≥ 5 yr). Adult males (AMs) are non-natal, immigrate from other troops, and can be divided into 2 distinctive types: troop AMs and peripheral AMs. Troop AMs who belong to stable troop members remain within 5 m of females and juveniles most of time during both mating and non-mating seasons. Peripheral AMs frequently remain at a distance from the bisexual group, often at the periphery or even a distance away from the troop, but follow the same troop almost daily for a few weeks or longer even in the non-mating season. We have excluded AMs that appeared near our study groups for a brief time (a few hours), since we had no interaction records of them with our study groups. All adult macaques mentioned in this paper are individually identifiable due to the availability of long-term demographic, genealogical, and photographic (video/still) documentation since 1993 (Hsu and Lin 2001, Hsu et al. 2006).

Troop C consisted of 46-61 individuals, including 2 or 3 AMs and 13-19 adult females (AFs) plus juveniles (Js) and infants (Is). Additionally, 4-10 AMs followed the group during the mating seasons and some even in the non-mating seasons, and these were categorized as peripheral AMs. A splinter troop (Cd) was established in Dec. 2000 (4 AFs, 3 Js, 3 Is, and 1 peripheral AM from C). During this study, troop Cd consisted of 11-18 individuals (1-3 AMs and 4 or 5 AFs plus 1 or 2 peripheral AMs).

We used focal animal sampling and scan sampling to record data on social interactions and activity patterns (Altmann 1974). We rotated focal animals during every 20 min focal period, which included 13 AMs and 18 AFs (troop C), and 6 AMs and 4 AFs (troop Cd), respectively. We used behavior terminology following Horiuchi (2005). Data collection commenced when the appearance of the observers no longer caused any obvious change in the group activity of the macaques.

We followed the definition of a grooming bout as beginning from the hands of a groomer touching the body of the receiver and ended when the two ceased contact for more than 90 s (Horiuchi 2005). Within a bout, 2 individuals might take turns grooming each other. When a grooming dyad separated for longer than 90 s or one groomed another, this was regarded the end of the previous grooming bout. An agonistic interaction included a series of fights, chases, and bites during close encounters, which was also counted as an agonistic bout (event). We used winner-loser or uncertainty to establish a dominance hierarchy (Lehner 1996).

Behavioral data were recorded from study groups for a total of 1248.8 h. The duration of an AM stay was calculated from our long-term demographic records (Hsu and Lin 2001, Hsu et al. 2001 2002 2005 2006, Lin unpubl. data). The socionomic sex ratio (SSR) was calculated as number of AMs divided by the number of AFs monthly between Aug. 2000 and Feb. 2003.

All statistical analyses were conducted with Statistical Analysis System software (SAS Institute, 2000). We used analysis of variance (ANOVA, F-test) to test the effects of independent variables (categories: mating or non-mating season, troop or peripheral AMs, and troops C or Cd) on dependent variables (grooming interactions, grooming partners, and agonistic frequency). Duncan's multiple-range tests were used to test the similarity among the 4 types of AM (troop and peripheral males within the 2 groups) following the ANOVA tests. All mean values are presented as ± 1 standard deviation (SD). The X^2 goodness of fit test was used to test the frequency of participating in allogrooming in the 4 age/sex groups (AM, AF, J, and I) compared to the number of individuals in each group. Significant differences of means between categories were tested using Wilcoxon rank tests. Paired t-tests were used to examine the difference between the frequencies of animals which gave and received grooming of each adult male individual.

We used the allogrooming and agonistic bouts of each AM, adjusted by the total observation period toward each individual during mating/non-mating periods as the allogrooming and agonistic frequencies. We followed the definition of the grooming active index used in a recent study of male Japanese macaques (Horiuchi 2005). We calculated the average duration of allogrooming records, which lasted more than 2 min (131.7 ± 184.28 s, $n = 1501$). Then, we chose allogrooming

Table 1. Comparisons of the duration of stay and behaviors of troop and peripheral adult males (AMs) during the mating and non-mating seasons in troops C and Cd of Formosan macaques at Mt. Longevity, Taiwan

	Troop C		Troop Cd		ANOVA F-test		
	Troop AMs	Peripheral AMs	Troop AMs	Peripheral AMs	Group	Type	Interaction
Sample size	3	10	4	2			
Duration of stay (mo)	38.1 ± 16.9 a	10.8 ± 6.0 b	9.9 ± 6.6 b	4.6 ± 0.6 b	**	ns	ns
Mating season							
Allogrooming bouts/h	2.29 ± 1.65 a	0.42 ± 0.30 b	0.79 ± 0.54 b	0.17 ± 0.25 b	*	**	ns
Grooming partners	15.3 ± 2.08 a	1.40 ± 0.70 bc	3.00 ± 1.63 b	0.50 ± 0.71 c	***	***	***
Non-mating season							
Allogrooming bouts/h	0.09 ± 0.06 a	0.01 ± 0.01 a	0.64 ± 0.81 a	0.00 ± 0.00 a	ns	ns	ns
Grooming partners	3.67 ± 2.31 a	0.20 ± 0.42 b	1.25 ± 1.26 b	0.00 ± 0.00 b	*	***	ns

Probability of ANOVA tests: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns not significant. a, b, c, d are from Duncan's multiple-range tests for 4 variables. Different letters indicate that a significant difference exists ($p < 0.05$).

bouts of dyads of ≥ 6 min and calculated the pair-grooming index for each bout as the duration of time (A) groomed (B), divided by the duration of the grooming bout. An index value of > 0.5 indicated that the male was a groomer of the dyad who spent more time grooming his partner. On the contrary, a value of this index of < 0.5 indicated that the male was a groomee (receiver), who spent less time grooming the partner. Subsequently, we calculated the average and standard deviation (average ± SD) of the grooming active index of troop and peripheral males to females or to dominant males during the mating and non-mating seasons.

RESULTS

Two Formosan macaque troops (C and Cd) were observed for 188 d in the field to record a total of 1248.8 h of behavioral data. The observation period of adult males in troop C (n = 13) averaged 34.68 ± 34.58 h and for troop Cd (n = 6) averaged 14.97 ± 11.71 h. Troop size had a significant effect on the duration of stay of AMs in the social groups ($p < 0.01$), but not between the types of males (troop and peripheral, Table 1). In Aug. 2000, there were 12 AMs (3 troop males, 9 peripheral males) and 18 AFs in troop C. At the end of Dec. 2000, a peripheral AM (PAM-1) led some members of the main troop C (4 AFs, 2 juveniles, and 4 infants) to form a new splinter group (Cd). Within a year, 3 adult males (1 troop and 2 peripheral males) had left the main troop C and immigrated into or appeared near troop Cd (PAM-3 in Jan., CAM-2 in Aug., and PAM-8 in Nov. 2001). Subsequently, PAM-3 became a troop male while PAM-8 became the alpha male of the newly established troop Cd. During Oct.-Nov. 2001, two AMs from other troops appeared near Cd troop; one became a peripheral male (CdAM-3) while the other (CdAM-4) became a troop male. On the other hand, 1 AF disappeared in May (CAF-6) and 1 AM in Oct. 2002 (CAM-1).

Troop AMs of C stayed significantly longer than peripheral AMs, but in the smaller troop Cd, the difference in the length of stay between the 2 types of males was not significant (Table 1). The mean duration of stay of AMs was 38.1 (± 16.9; range, 8.1-56.7) mo in troop C, but that was 9.9 (± 6.6; range, 1.0-16.8) mo in troop Cd. Replacement of the alpha male was more frequent in troop Cd than in troop C. In troop C, gaining an alpha-male status involved 34.3 mo. On the contrary, the alpha male status of troop Cd was achieved in 2 cases immediately through troop fission or take-over, while in a 3rd case, a troop male took about 6 mo to raise his rank to the top.

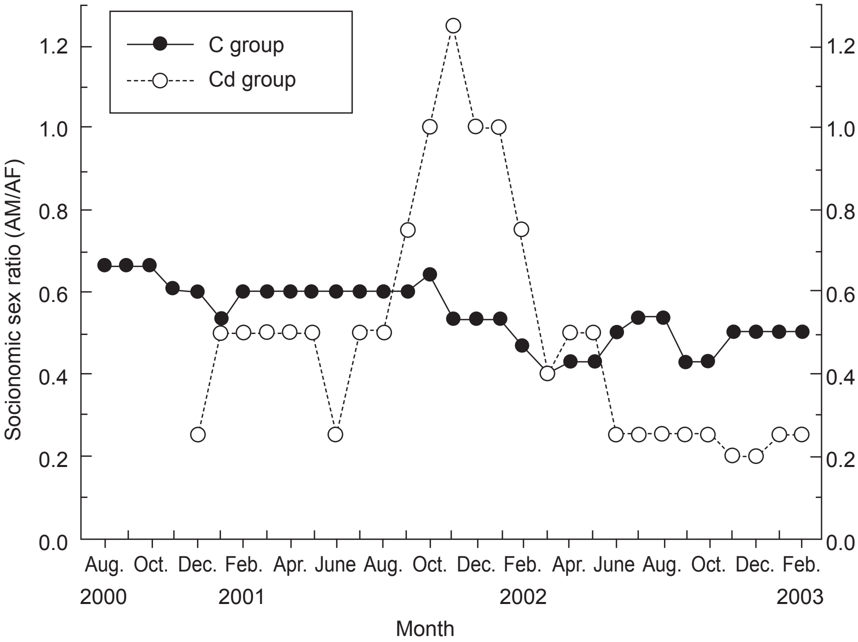

Fig. 1. Socionomic sex ratio of adult males (AMs) to adult females (AFs) in troops C and Cd of Formosan macaques at Mt. Longevity, Taiwan.

Four peripheral males changed their status during mating seasons (Sept.-Feb.) and became troop males in troop C or Cd. In total, 12 peripheral AMs were identified, and the average focal sampling time for them was 20.3 ± 22.7 h, and the focal sampling time for 7 troop males averaged 42.4 ± 38.4 h. The average age of peripheral males was 9.7 ± 4.0 yr, which did not significantly differ from that of troop males (12.3 ± 4.1 yr, $p > 0.05$, Wilcoxon test).

The average sex ratio (troop AMs/AFs) of troop C during the mating season was 0.13 ± 0.05 (range, 0.07-0.2), while in Cd it was 0.39 ± 0.19 (range, 0.2-0.75). However, after including peripheral AMs, the average SSR during the mating seasons reached 0.55 ± 0.07 in troop C, which was nearly identical to that of troop Cd (0.56 ± 0.37, $p > 0.5$). The average SSR of troop C reached 0.54 ± 0.07 for the entire study period (Fig. 1), which was significantly higher than that of troop Cd (0.49 ± 0.29, $p < 0.05$, Wilcoxon rank test). Seasonal changes in the SSR were not significant in either troop C ($p > 0.8$) or troop Cd ($p > 0.6$). However, the average SSR of troop Cd slightly decreased to 0.41 ± 0.12 during the non-mating seasons.

Behavioral patterns

Behavioral patterns of AMs differed from those of AFs (Fig. 2). In both troops (C and Cd), the most frequent behavior of AMs was resting followed by moving and affiliative behaviors (Fig. 2). Allogrooming participation of AMs was the lowest among the 4 age/sex groups examined. Allogrooming accounted for 9.54% ± 0.08% (n = 13) of AM daytime activities in troop C, which was significantly lower than that for AFs (26.53% ± 0.14%, n = 18). A similar trend was observed in troop Cd (8.05% ± 6.7%, n = 4, and 21.87% ± 5.7%, n = 4, respectively; Fig. 2). The average frequency of grooming among AMs in troop C was 0.61 ± 0.45 bouts/h (n = 13), significantly less than that for AFs (2.77 ± 0.84 bouts/h, n = 18). A similar trend was found in troop Cd (0.80 ± 0.83 and 2.17 ± 0.15 bouts/h, respectively).

In regard to providing and receiving grooming services among AMs, no significant difference was found in either troop C (t = -1.61, $p > 0.1$, Fig. 3) or troop Cd (t = 1.97, $p > 0.1$). Nevertheless, the major partner grooming AMs was AFs, which accounted for 72% and 63% of total AM allogrooming (Fig. 3). In the smaller troop Cd, however, AMs received more-frequent grooming from AFs than they groomed AFs, which was contrary to troop C.

Seasonal variations and troop size effects

The types of males and troop sizes had significant effects on the allogrooming frequency of AMs only during mating ($p < 0.05$) but not during non-mating seasons ($p > 0.05$, Table 1). Troop males of C had the highest grooming frequency (2.29 ± 1.65 bouts/h) among all male types/groups during the mating seasons (Duncan's multiple-range tests, $p < 0.05$, Table 1). This model explained the significant variations in grooming frequency of males in the mating seasons ($F_{3,\ 15}$ = 6.20, R^2 = 0.55, $p < 0.01$, Table 1).

The allogrooming frequency between troop AM dyads and troop-peripheral male dyads did not significantly change between the mating and non-mating seasons. On the contrary, a seasonal variation in grooming interactions was found within peripheral males, being significantly higher during the mating seasons (0.24 ± 0.30 bouts/h, n = 12) than during non-mating seasons (0.01 ± 0.01 bouts/h).

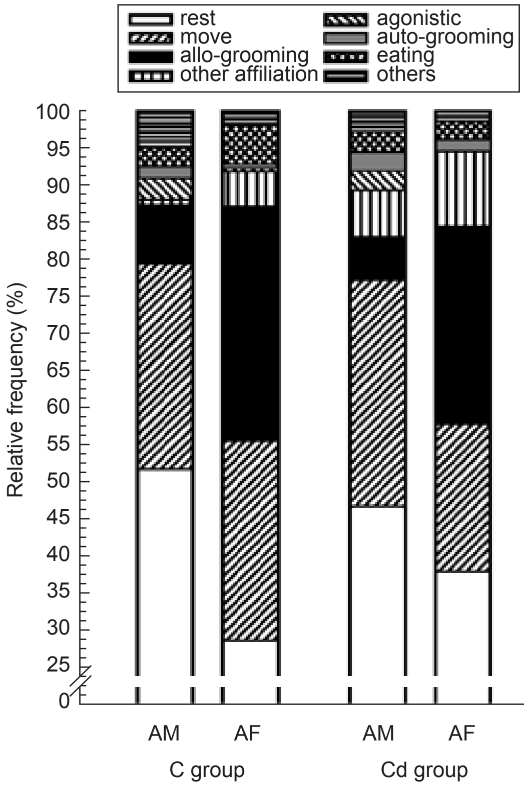

Fig. 2. Relative frequency of 8 behavioral catalogues in adult males (AMs) and adult females (AFs) between troops C and Cd of Formosan macaques at Mt. Longevity, Taiwan.

The frequency of allogrooming was slightly higher among peripheral males of troop C during the mating season (0.28 ± 0.31 grooming bouts/h, Fig. 4A) than among troop males (0.05 ± 0.04 bouts/h), but the difference was not significant ($p > 0.3$). During the mating season, peripheral males were actively involved in grooming troop males in Cd (0.17 ± 0.24 grooming bouts/h, Fig. 4B). In contrast, troop males of Cd during the non-mating season had a slightly higher frequency of affiliation (0.28 ± 0.36 grooming bouts/h, Fig. 4D) than did those of troop C (0.00 ± 0.00, $p > 0.1$, Fig. 4C). There were no grooming interactions among peripheral males and AFs in the non-mating seasons (Fig. 4).

Different patterns of male-male and male-female reciprocal grooming encounters occurred between troops C and Cd. During the mating seasons, 12.20% of instances of allogrooming were reciprocated in male-male grooming in troop C, but none was observed in troop Cd. Although the frequency of reciprocal grooming of heterosexual dyads was higher in the mating seasons than in the non-mating seasons in both troops, it only occurred in troop Cd in the non-mating season. In addition, the rate of reciprocal grooming of heterosexual allogrooming in the mating seasons was 37.5% in troop Cd, slightly higher than the 24.79% observed in troop C. During the non-mating seasons, no reciprocal grooming was observed in troop C; neither among males nor among heterosexual allogrooming dyads. On the other hand, 15.39% of instances of allogrooming were reciprocated for heterosexual encounters compared to 33.3% among male-male grooming dyads in troop Cd.

Grooming partners

Types of AMs and groups significantly explained variations in the average number of grooming partners of males in the mating ($F_{3,15}$ = 111.5, R^2 = 0.96, $p < 0.001$) and non-mating seasons ($F_{3,15}$ = 8.79, R^2 = 0.64, $p < 0.005$, Table 1). Troop males had higher numbers of grooming partners than peripheral males in both study groups, but the interaction was only significant during the mating seasons ($F_{1,15}$ = 76.8, $p < 0.001$), which indicated that the effect of male type was not similar between the 2 groups.

Troop males of C had the highest number of grooming partners compared to other male type/groups in both seasons (Duncan's multiple-range tests, $p < 0.05$, Table 1). The number of grooming partners in troop males of C averaged 15.30 ±

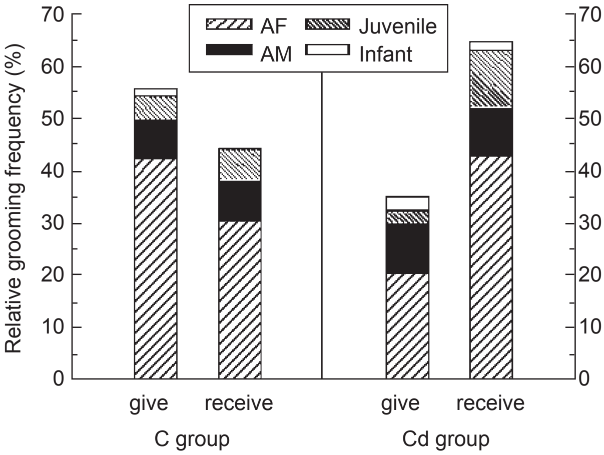

Fig. 3. Relative percentages of grooming frequency of adult males (AMs) grooming or receiving grooming from adult females (AFs), juveniles, and infants in troops C and Cd of Formosan macaques at Mt. Longevity, Taiwan.

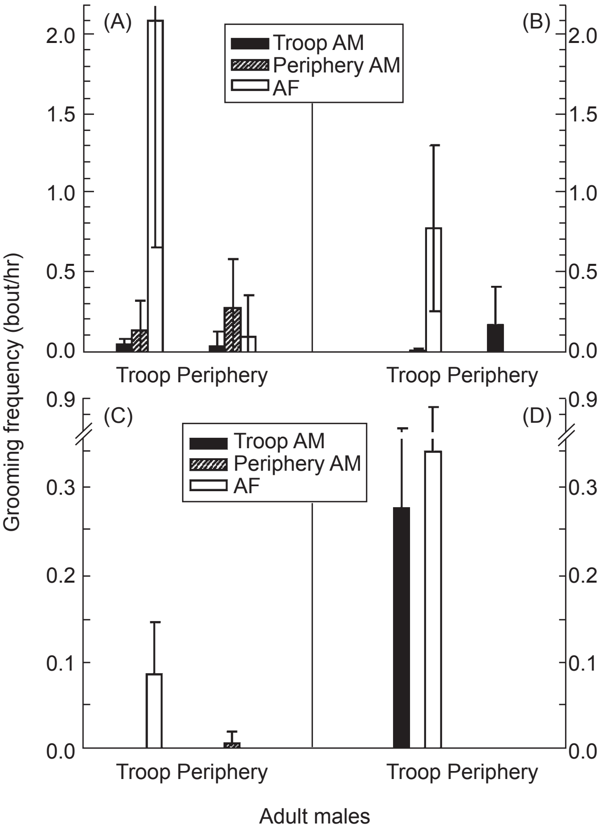

Fig. 4. Grooming bouts by troop and peripheral adult males with females, other troop males, or peripheral males during the mating seasons in (A) troop C and (B) troop Cd and during the non-mating seasons in (C) troop C and (D) troop Cd of Formosan macaques on Mt. Longevity, Taiwan.

2.08 ($n = 3$) during the mating seasons, which was significantly greater than that of peripheral males (1.40 ± 0.70, $n = 10$, Table 1). The major allogrooming partner of troop males was AFs regardless of the season. They accounted for 85% (13.0 ± 3.0 in troop C) to 92% (2.75 ± 1.3 in troop Cd) of grooming partners in the mating seasons. Therefore, the major grooming partner of peripheral males in troop C was peripheral males, which accounted for 57% of instances during the mating seasons, but that increased to 100% during the non-mating seasons. During the non-mating seasons, the average numbers of grooming partners in the 4 male types/groups all decreased, and the differences were also reduced (Table 1). Troop males of C had the highest number of grooming partners (3.67 ± 2.31) compared to the other male type/groups (Duncan's multiple-range tests, $p < 0.05$, Table 1).

Grooming active index

The grooming active index of troop and peripheral males to dominant males in troop C did not significantly differ during the mating seasons ($Z = -0.20$, $p > 0.1$). They were both ≥ 0.5 (0.50 ± 0.71, $n = 2$ and 0.77 ± 0.23, $n = 5$, respectively). Even during the non-mating seasons, the grooming active index of troop males in Cd and peripheral males in C to dominant males were both ≥ 0.5 . Nevertheless, there was no allogrooming interaction between troop males and dominant males or between peripheral males and females of troop C during the non-mating seasons. Peripheral males of troop Cd were rarely seen to be involved in allogrooming.

Aggression

Different patterns of agonistic interactions were found between troops and seasons. The agonistic interactions were only observed in troop C during the mating seasons. During the mating seasons, the agonistic frequency among peripheral males of troop C was 0.45 ± 1.06 bouts/10 h ($n = 10$), nearly 1.8 times that among the troop males (0.25 ± 0.23 bouts/10 h, $n = 3$, $p < 0.05$). In addition, both troop and peripheral males expressed agonistic behaviors toward AFs (0.85 ± 0.91 and 0.25 ± 0.57 bouts/10 h, respectively). There were no agonistic interactions observed among troop males and peripheral males during the non-mating seasons in either troop.

DISCUSSION

Troop size played important roles in influencing the social relations of troop males and peripheral males of Formosan macaques. According to Hill (1994), a strong association can be seen among AMs' affiliative behavior, adult sex ratio, and troop size in the Genus *Macaca*. Hill (1994) found affiliative behaviors of AMs to be rare or not observed in 13 troops of 4 species such as rhesus macaque, Japanese macaques, crab-eating macaques and pig-tailed macaques (*M. nemestrina*). The average troop size was 71.9 ± 54.4 ($n = 4$) with a relatively high adult (AF/AM) sex ratio (4.9 ± 2.1; range, 2.3-10.5). However, affiliative behavior between AMs was not rare in 17 groups of 7 species including rhesus macaques, Japanese macaques, and crab-eating macaques (Hill 1994). The average troop size for those 7 species was small (37.2 ± 17.4) with a relatively low adult sex ratio of 1.8 ± 0.6.

In this study, we recorded the formation of a new troop as a result of fission during the mating season. The fission was initiated by a peripheral male who established consort relations with estrous females, which is similar to troop fission recorded in Japanese macaques (Yamagiwa 1985). Other factors, including the availability of a large number of peripheral males and a short supply of troop males, might have also contributed to troop fission (Yamagiwa 1985).

The average sex ratio (AM/AF) during the mating season was 0.13 (troop C), which was 1/3 that of the splinter troop (Cd). After including peripheral males, the average SSR of the 2 groups (C and Cd) were nearly identical, which indicated peripheral males were balancing the SSRs between the groups. The average sex ratio and SSR of troop C were both lower than those reported for Japanese macaques on Kinkazan Island (0.17 ± 0.06 and 0.71 ± 0.25, respectively, Takahashi 2001). In addition, the SSR in the smaller troop Cd changed to a large extent, compared to the relatively stable SSR of the larger troop C. This may have been due to the small size and a combination of 1 male group conditions of troop Cd most of the time which lacked socially stability even after the fission process. Frequent alpha male replacement and troop male transfer were also documented in Japanese macaques (Yamagiwa 1985).

The mean duration of stay by troop males in the larger troop C was longer than that of the smaller troop Cd. Males attaining the top ranking alpha-male status in C involved a long process. However, it was immediately achieved through group fission or group take-over in the smaller splinter troop, which is similar to that reported for Japanese macaques (Yamagiwa 1985, Sprague et al. 1996). In addition, the food supply and group size influencing the patterns of associations of resident males might have also played a role (Yamagiwa and Hill 1998).

We found different effects of troop and seasons on the affiliative behavior and reciprocity among AM Formosan macaques. The frequency of male-male allogrooming encounters during the mating seasons was slightly higher among peripheral males than among troop males of the larger troop C; this may have been due to the former having a lower number of heterosexual grooming partners than troop males. However, peripheral males of the smaller troop Cd were actively involved in allogrooming with troop males in the mating seasons. On the other hand, troop males of the smaller troop Cd during the non-mating seasons exhibited a higher frequency of grooming affiliation and reciprocity than did those of the larger troop C. This situation is similar to that reported in previous studies by Takahashi and Furuichi (1998) and Horiuchi (2007).

The active grooming index of troop and peripheral males to dominant males (troop C) were both ≥ 0.5, which indicated that subordinate males were actively grooming dominant males; they were often the groomers in grooming dyads with dominant males. Even during the non-mating seasons, subordinate troop males actively groomed dominant males while peripheral males and dominant males took turns as groomers in the dyads. In Japanese macaques of Yakushima I., grooming interactions among troop males were far more frequent during the non-mating than mating seasons, which may compensate for less-frequent grooming by AFs during the non-mating season (Furuichi 1985). On the contrary, the difference in allogrooming frequency among troop males between the mating and non-mating seasons was not significant in our study. However, Horiuchi (2005) reported that the reason for Japanese macaque's grooming behavior among troop males was to ensure that they had a steady social relationship for the entire year probably to prevent peripheral male invasion and harassment. Moreover, Takahashi and Furuichi (1998) suggested the proximate cause of mutual grooming among troop males may influence long-term alliances to prevent peripheral males from invading troops and mating with females.

Troop size and season also influenced the social relations of AMs with AFs in Formosan macaques. Reciprocal allogrooming of heterosexual dyads during the non-mating seasons existed only in the smaller splinter troop, but not in the larger main troop. This suggests that AFs in the small troop might be trying to recruit AMs in order to prevail in inter-troop encounters (Wrangham 1980, Saito et al. 1998). However, in Assamese macaques (*M. assamensis*), male-female grooming cannot be accounted for in terms of reciprocity since it is not a simple function of dominance (Cooper and Bernstein 2000). Social grooming interactions between male and female Formosan macaques were much higher during the mating than non-mating seasons, which was similar to an earlier study conducted at different sites in Taiwan (Birky and Su 2005). In non-mating seasons, very few heterosexual affiliative interactions occurred. This also caused the allogrooming partners of troop males to dramatically decrease during the non-mating seasons especially for the larger group.

More agonistic interactions of male Formosan macaques occurred in the larger social group than in the smaller social group during the mating seasons. This may have been due to less-intense competition among males in small social groups (Hemelrijk and Luteijn 1998), which is also consistent with the hypothesis that affiliative behavior among males of a small group with an SSR of 0.5 would be more frequent than in a large group with a scrambled SSR in the genus *Macaca* (Hill 1994). A significantly higher grooming interaction was found during the mating seasons among peripheral male Formosan macaques, which indicated higher affiliation for reducing tension or competition among low-ranking AMs. However, in wild Japanese macaques, non-troop males were reported to exhibit frequent affiliative behavior toward troop males only during the non-mating seasons (Horiuchi 2005).

Male mating competition and conflicts mainly occurred during the mating seasons, and Formosan macaque troop males expressed agonistic behaviors toward AFs and all types of males. These interactions were less frequent in Japanese macaques (Horiuchi 2005). Although some peripheral male Formosan macaques were accepted and groomed with troop males or females during the mating seasons, conflicts and agonistic interactions still prevailed. This phenomenon was reported in wild Japanese macaques, and peripheral males sometimes became the target of coordinated attacks by troop males (Horiuchi 2005). Therefore, it was important for troop males to establish close affiliations in the smaller social group that is vulnerable to frequent male replacements even during the non-mating seasons.

Takahashi and Furuichi (1998) compared 2 groups of Japanese macaques and found that affiliative behavior between males of a small group with a high SSR was more frequent than in the large group with a low SSR, which is similar to the Formosan macaque small troop (Cd) which had a high SSR and higher affiliation among males. We found that AFs often served as groomers in grooming dyads mainly with troop males during the mating seasons in the small troop (Cd). This might have been due to the higher turnover rate of adult males in small social groups leading to AFs actively sourcing affiliative relationships to maintain social bonds with AMs. In addition, peripheral males of the small social group also actively groomed troop males during the mating seasons. This might augment coalition establishment with troop males and increase access to females in estrous, ultimately leading to them becoming troop males as reported in Japanese macaques (Horiuchi 2005). However, participation in coalitions did not consistently influence the ranks of male bonnet macaques (*M. radiata*) in captivity (Silk 1993).

Social grooming can promote the formation of coalitions in adult macaques (Nakagawa 1998). Macaques achieve coalition formation through the support of kinship, reciprocity, and cooperation (Widdig et al. 2000). From a functional perspective, mutual selfishness provides a better explanation than reciprocal altruism, since the possibility that both groomers and supporters derive immediate net benefits cannot be excluded (Chapais et al. 1995). However, Manson et al. (2004) found that only 5%-7% of macaque grooming bouts were reciprocated, and the allogrooming of males and females might be related to the male's mating strategy toward the female. On the other hand, the purpose of allogrooming between males is probably coalition formation.

The cause for frequent affiliative behaviors in Japanese macaques was reported to prevent peripheral males from invading social groups and mating with females, and as a result, troop males cooperate to form alliances to oppose peripheral male invasions (Horiuchi 2005). Data presented in this paper suggest that troop males groomed each other more frequently and attacked peripheral males more than vice versa during the mating seasons, whereas no agonistic behavior occurred between troop and peripheral males during the non-mating seasons. Hence, we suggest that an alliance of defense can occur during the mating season among troop males of Formosan macaques at Mt. Longevity while peripheral males are most likely to reduce tension and possibly form coalitions from affiliated allogrooming. This sort of coalition among peripheral males may possibly arise due to resource sharing or to gain fighting support with a relatively low cooperative mating strategy towards sexually active females. Further research is required to examine this aspect and support this prediction.

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