



Postconflict Behavior Among Male Japanese Macaques

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Received November 25, 2003; revision April 12, 2004; accepted May 17, 2004

*Reconciliation was first described more than 20 years ago. Since then, it has been observed in many mammals (mainly primates) but data on postconflict behavior among males are still scarce because they usually aggressively compete for mating partners, rarely maintain amicable relationships with one another. Accordingly, reconciliation is expected to occur at low rates. Although this is true for Japanese macaque males, the subspecies on Yakushima Island (*Macaca fuscata yakui*) seems to represent an exception as grooming among males occurs often. We analyzed postconflict behavior among them and discuss the possible factors that may favor the occurrence of grooming and reconciliation. Selective attraction between former opponents—reconciliation—occurred soon after conflicts. Consolation—affiliative interactions between a focal animal and group members other than the former opponents occurring earlier in PCs than in MCs—was absent among males. Conciliatory tendency is higher for Yakushima macaque males (0.31) versus that in studies on the other subspecies *Macaca fuscata*. We discuss differences in the behavioral ecology of the 2 subspecies, the ecological and social factors that may favor the occurrence of reconciliation, and the possible benefits that males gain from grooming exchange and reconciliation.*

KEY WORDS: Japanese macaque; male behavior; postconflict behavior; reconciliation; Yakushima.

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INTRODUCTION

Since it was first described in chimpanzees by de Waal and van Roosmalen (1979) reconciliation—the postconflict friendly reunion of former opponents that restores their social relationship disturbed by the conflict (Aureli and de Waal, 2000, p. 387)—has been documented in many primates and other social mammals (domestic goats, *Capra hircus*: Schino, 1998; whales and dolphins: Samuels and Flaherty, 2000). Based on these studies, the valuable relationship hypothesis states that reconciliation evolved to restore tolerance and the relationship between former opponents; it exists whenever the quality of individual relationships is important for the fitness of the animals (Aureli *et al.*, 1989; Kappeler and van Schaik, 1992). Because reconciliation reduces the chance of future conflicts and restores the tolerance between former opponents, victims and aggressors show an increase of stress-related behavior when reconciliation does not take place (Maestripieri *et al.*, 1992; Schino *et al.*, 1996).

Males and females of many species usually differ in their strategies to maximise inclusive fitness. Trivers (1972) once postulated that the sexes may be considered different as 2 species in this respect. Female reproductive success mainly depends on her ability to acquire the food sources necessary for her survival and reproduction, whereas male reproductive success is mainly dependent on access to females and mating opportunities. Because food sources can be shared under certain circumstances, while competition over mating partners can only have a win or lose result, cooperation and amicable interactions are expected to occur more often among females. Contrarily, interactions among males, are usually characterized by aggressive competition and there are many documented examples, e.g., harbour seals, *Phoca vitulina* (Neumann, 1999) and Japanese medakas, *Oryzias latipes* (Grant and Foam, 2002). Indeed, competition among males was first observed by Darwin (1871) and was also emphasised by Zuckermann (1932). The phenomenon occurs in macaque societies and Japanese macaques in particular (Melnick and Pearl, 1987; Preuschoft and Paul, 2000). Group males are usually unrelated to one another because they disperse at adulthood and join different groups during their life times (Melnick and Hoelzer, 1996; Suzuki *et al.*, 1998). Moreover, Japanese macaque males rarely engage in cooperative acts, e.g., 2 males joining forces against a third, dominant male (Enomoto, 1981; Noë, 1994; Silk, 1992; Watanabe, 1979) while they aggressively compete for mating partners (Soltis *et al.*, 1997). All these factors strongly reduce the importance of inclusive fitness or reciprocal altruism or both to affect male behavior

(Hamilton, 1964; Kurland, 1977; Trivers, 1971). Therefore, unlike females, the males have no particular reason or time to establish long-lasting amicable relationships (Matsumura, 1996). This is the reason why grooming, which is the main behavioral indicator of a valuable relationship among primates (Dunbar, 1991) is often exchanged among cercopithecine females but rarely among males.

Given that Japanese macaque males, like males of many mammalian species, often aggressively compete with one another, reconciliation is expected to occur at low levels. Accordingly, except in chimpanzees (*Pan troglodytes*; Wittig and Boesch, 2003), male postconflict behavior had not been specifically analyzed. *Macaca fuscata yakui* represents an exception because grooming among males is frequent in comparison to populations on the mainland: *Macaca fuscata fuscata* (Nakagawa, 1998; Takahashi and Furuichi, 1998). The number of males per female in a group is higher among Yakushima macaques than in the mainland macaques (Sprague *et al.*, 1998), though it is unclear whether the difference has a genetic basis or is due to different mortality of the sexes. Intergroup encounters are more frequent among Yakushima macaques (Saito *et al.*, 1998; Sugiura *et al.*, 2000), and they often involve aggressive participation of males (Majolo *et al.*, in press).

If the valuable relationship hypothesis applies to Japanese macaque males one would expect to find higher levels of reconciliation in Yakushima macaques than in the other subspecies. Moreover, affiliative interactions or cooperative acts or both among males are predicted to occur when group males share a common interest under certain circumstances (Hill and van Hooff, 1994; Mc Donald and Potts, 1994; Nunn, 2000; Nunn and Lewis, 2002; van Hooff, 2001). One circumstance is when group males defend their females or food sources or both from foreign males. Therefore, during intergroup encounters, males might cooperate to defend group-females aggressively and avoid male immigration into the group.

Cooperative acts often occur among animals that maintain amicable relationship via grooming exchange, though grooming interactions do not always imply cooperation (van Hooff, 2001). Accordingly, frequency of intergroup encounters may affect grooming interactions among males and possibly also reconciliation.

We analyzed postconflict behavior among Yakushima males and variation in the occurrence of reconciliation in relation to context of conflict and season aiming to determine whether grooming and reconciliation among group males were related to male behavior during intergroup encounters. We collected data on postconflict behavior, social interactions—grooming and aggression—and intergroup encounters.

METHODS

Study Area and Subjects

The study area is on the volcanic island of Yakushima (31°N, 131°E), which is *ca.* 500 km² and located 60 km south of Kyushu, Japan (Agetsuma and Nakagawa, 1998). No troop relies on provisioned food and no predator is present. The subjects were 13 males (≥ 4 years) in a troop composed, at the beginning of the data collection, of 25 monkeys (13 males, 8 adult females, 3 yearling, and 1 infant).

Data Collection

We collected data continuously from 22 June, 2001 to 4 May, 2002 with only one interruption from December 20, 2001 to January 23, 2002. We collected data on postconflict behavior via the postconflict-matched-control (PC-MC) method (de Waal and Yoshihara, 1983). Observation sessions began ≤ 30 sec after conflicts involving ≥ 2 males, and we collected data on the victim or the aggressor for 5 min. The session stopped if the conflict started again ≤ 30 sec. On the next possible day we collected a matched-control observation on the same monkey. We postponed the session for ≥ 10 min if the focal-animal was involved in an agonistic interaction ≤ 3 min before a planned MC (Aureli *et al.*, 1993). In the field it is particularly difficult to collect matched-control observations under conditions, e.g., time of day or distance between former opponents, that perfectly resemble those of postconflict observations. The conditions may greatly affect the result of statistical analyses run via the PC-MC method (Call, 1999; Call *et al.*, 1999). We decided to give prior importance to context, i.e., conflicts occurring during grooming, foraging, play or moving, or over mating partners, and distance between former opponents when the observations were to be collected, starting the sessions when the conditions were similar to postconflict observations. If the conditions were not met within one week from the conflict we discarded the PC. For each aggressive interaction we recorded the identity of the monkeys involved, the intensity of the attack, i.e. threat, slap, chase, and bite, and the context of the conflict. Moreover, we recorded whether the conflict was decided or not. A conflict is decided only if one monkey showed clear submission towards the other individual involved.

We used 10-min focal animal sampling to record social interactions among males. Observations sessions were distributed evenly throughout the day for each monkey and we obtained a total of 155.3 hrs. of

observations. We calculated monthly percentage of grooming among males from 661 scans collected every hour. We recorded data *ad libitum* on all the agonistic interactions with a clear-cut result to determine the hierarchical status of the study males. Moreover, we recorded *ad libitum* all the occurrences of intergroup encounters involving the focal troop. We then divided the number of intergroup encounters by contact time with the troop to obtain monthly frequencies of encounters.

We recorded grooming interactions, aggressive and stress-related, i.e. self-scratching, self-grooming, yawning, and body-shake behavior via all occurrence sampling (Altmann, 1974; Martin and Bateson, 1993). During PC-MC observations, we also recorded the time elapsed from the beginning of the session and the first affiliative interaction between the focal animal and the former opponent or other group members.

Data Analysis

We analyzed data on postconflict behavior via 2 methods. To analyze the occurrence of reconciliation we first determined in which minute an affiliative interaction between former opponents occurred. We analyzed the distribution of the interactions over time in the PCs and MCs—the time-rule method (Aureli *et al.*, 1989)—via the Kolmogorov-Smirnov test. Moreover, we compared the occurrence of affiliative interactions between former opponents between PCs and MCs at the individual level—the PC-MC method (de Waal and Yoshihara, 1983)—via the Wilcoxon matched-pairs signed-rank test. We used the same procedure to determine the occurrence of consolation, i.e. the occurrence of an affiliative contact between the focal animal and a group member other than the former opponent earlier in the PCs than in the MCs, and the distribution and frequency of stress-related behaviors.

When we used the PC-MC method, we could assign each PC-MC pair to one of 3 different groups (de Waal and Yoshihara, 1983): 1) when an affiliative interaction between former opponents occurred earlier or only in the PC than in the MC the pair was attracted; 2) the pair was dispersed when an affiliative interaction occurred later in the PC than in the MC (or only in the MC); and 3) a pair was neutral when no affiliative interaction occurred in the PC and the MC. Following this division, we measured conciliatory tendency per individual or per dyad via the formula (Veenema *et al.*, 1994):

$$(\text{attracted pairs} - \text{dispersed pairs}) / \text{total PC-MC pairs}$$

we only measured conciliatory tendency for individuals or dyads for which at ≥ 2 PCs-MCs were available. To analyze the relationships between

monthly frequency of intergroup encounters, grooming and conciliatory tendency we considered only months for which enough data were available.

RESULTS

We obtained a total of 128 PC-MC pairs (9.8 ± 2.7 mean number of PC-MC pairs per male \pm SE), 79 in the mating season and 49 in the nonmating season. The relatively low sample size for a one-year study is due to the steepness of the habitat, which made it difficult to collect data. Among the 128 PC-MC pairs, 11.7% involved >2 males, while the remaining 88.3% were dyadic conflicts; 89.1% of conflicts had a clear-cut result, whereas 10.9% of conflicts were undecided. Further, 52.3% of conflicts were characterized by a threat directed from the aggressor to the victim, 38.4% by a chase, 7.0% by a slap, and 2.3% by a bite.

The Occurrence of Reconciliation

We compared the distribution of the first affiliative contact between former opponents between PCs and MCs (see Fig. 1). Affiliative contacts were more frequent in the first minute after the conflict than in the control (Kolmogorov-Smirnov test: $D = 1.27$, $p < 0.05$). Per analysis at the individual level, the percentage of attracted pairs was significantly higher than that of dispersed pairs attracted pairs: $30.41 (\pm 5.82$ mean percentage \pm SE; dispersed pairs: 1.54 ± 1.35 ; Wilcoxon signed ranks test: $T = 66$,

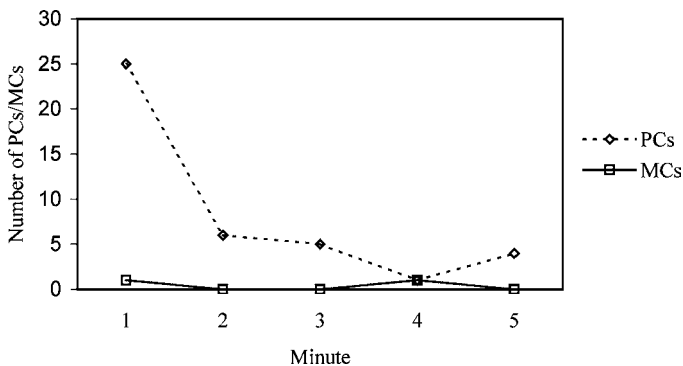


Fig. 1. Number of PCs and MCs with an affiliative contact between former opponents in each minute.

$N = 11, p < 0.01$), indicating that affiliative contacts between former opponents did not occur by chance but instead were due to selective attraction, i.e., reconciliation.

All the affiliative behaviors were used by males, though at different proportions, as the first affiliative behavior exchanged between former opponents (grooming = 61.0%; mounting = 21.9%; sitting in contact = 7.3%; playing = 4.9%; muzzle-contact = 2.5%; bidirectional lip-smacking = 2.4%). The aggressors took the initiative to reconcile in 29.3% of the 41 attracted PCs-MCs; the victim did so in 51.2%; and in 19.5% of attracted pairs both the former opponents took the initiative to reconcile. We also analyzed the intensity of aggression in the 41 attracted pairs. A simple threat characterized 58.2% of the attracted pairs; the aggressor chased the victim in 34.5% of conflicts, a slap occurred in 4.9% of conflicts, and a bite occurred in 2.4% of them.

The Occurrence of Consolation

The distribution over time of first affiliative contacts between the focal animal and group members other than the former opponent is not significantly different between PCs and MCs ($D = 0.63, NS$; see Fig. 2). The percentage of PCs and MCs showing an affiliative contact between the focal animal and group members other than the former opponent was also analyzed at the individual level using two Wilcoxon matched-pairs signed-rank tests. No significant difference was found between PCs and MCs (PCs: 32.55 ± 8.30 mean percentage \pm SE; MCs: 57.21 ± 9.46 ; $T = 43.5, N = 11$,

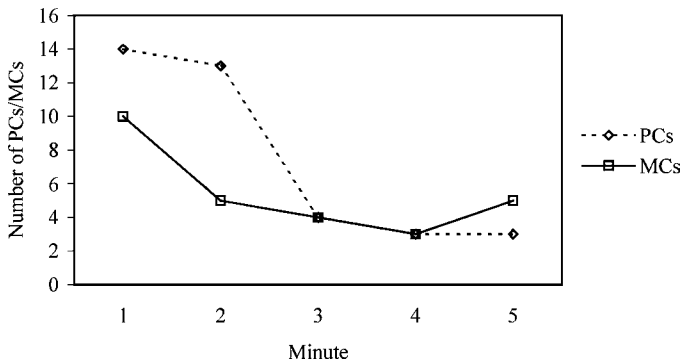


Fig. 2. Number of PCs and MCs with an affiliative contact between the focal animal and group members other than the former opponent in each minute.

NS) and the result remained basically unchanged ($T = 43.0$, $N = 11$, NS) when all the MCs in which the focal animal was already involved in affiliative contacts with other group members at the beginning of the MC were excluded from the analysis.

Redirection, Further Aggression from the Former Opponent and Stress-Related Behaviors

The victim of aggression was aggressive towards group members other than the former aggressor in 4.7% of PCs and 0.8% of MCs. Moreover, the victim of aggression was the subject of further aggression from the former aggressor or from other group members in 9.4% of PCs and 2.3% of MCs. Small sample size precludes establishing whether redirection and further aggression from the former opponent took place following conflicts among males.

In order to test whether the frequency of stress-related behaviors increased in the minutes after conflicts we selected all the neutral and with a clear-cut result PCs-MCs pairs in which redirection and further aggression from the former opponent did not occur ($n = 63$) because they may decrease and increase, respectively, the frequency of stress-related behaviors (Aureli, 1997). First, we compared the distribution over time of the frequency of self-scratching between PCs and MCs; there is no difference ($D = 0.95$, NS; see Fig. 3). We also compared at the individual level the frequency of self-scratching in PCs and MCs and the difference was not significant (PCs: 0.52 ± 0.11 mean events per minute \pm SE; MCs: 0.43 ± 0.09 ; $T = 27.5$, $N = 9$, NS). The same analyses on the percentage of time that the monkeys spent self-grooming indicate no difference in the distribution of self-grooming over time in PCs and MCs ($D = 0.95$, NS; Fig. 4).

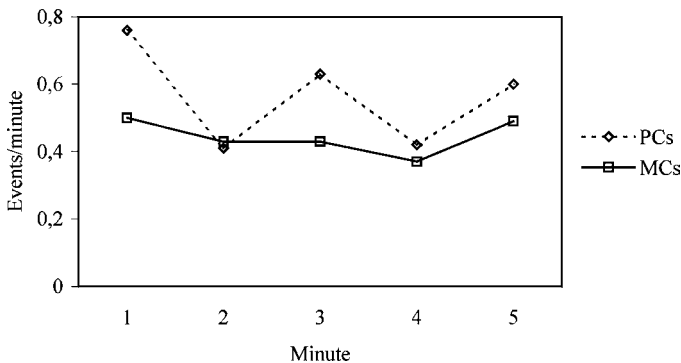


Fig. 3. Frequency of self-scratching in each minute.

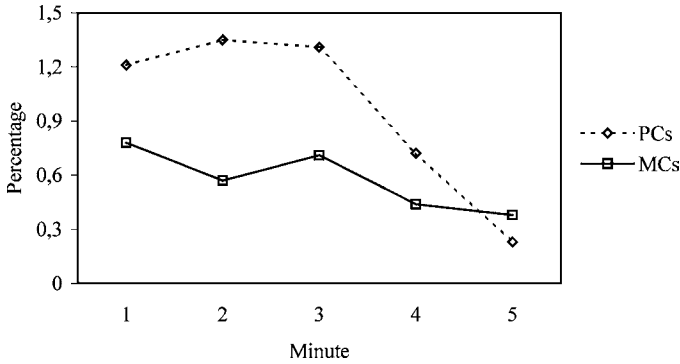


Fig. 4. Percentage of time spent self-grooming.

Self-grooming was higher during neutral PC observations than during MCs per analyses at the individual level (PCs: 6.21 ± 1.52 mean percentage \pm SE; MCs: 2.99 ± 1.06 ; $T = 38.0$, $N = 9$, $p < 0.05$). We did not analyze data on yawning and body-shake because they occurred at low rates.

Variation in Conciliatory Tendency in Relation to Context of the Conflict, Season, and Among Dyads

The overall conciliatory tendency (Veenema *et al.*, 1994) is 0.31. Reconciliation was relatively rare following conflicts over mating partners (0.04) and over food (0.13), but it was more frequent after conflicts occurring during grooming or play sessions (0.41). Moreover, conciliatory tendency was significantly lower during the mating season (0.16 ± 0.07) than during the nonmating season (0.53 ± 0.08 ; $T = 54$, $N = 10$, $p < 0.01$).

The valuable relationship hypothesis predicts that conciliatory tendency should be higher among monkeys that frequently exchange affiliative behaviours (mainly grooming) than among ones that rarely do so. In order to test whether the hypothesis applies to Japanese macaque males we ran a Spearman correlation to analyze the relationship between conciliatory tendency and grooming exchanged per dyad. Conciliatory tendency is positively correlated to the quality of the relationship between former opponents (Spearman rank correlation: $r_s = 0.52$, $N = 22$, $p < 0.05$).

The Effects of Intergroup Encounters on Grooming and Reconciliation

We observed 28 intergroup encounters, one every 5.13 ± 0.91 observation days. We ran a series of analyses to determine whether the conciliatory

tendency was related to intergroup encounters. Two Spearman rank correlations showed no significant relationship between monthly frequencies of intergroup encounters, grooming, and conciliatory tendency (frequency of intergroup encounters \times grooming: $r_s = -0.5$, $N = 10$, NS; frequency of intergroup encounters \times conciliatory tendency: $r_s = 0.12$, $N = 10$, NS.). To test whether intergroup encounters had any short-term effects on the occurrence of reconciliation we divided all the PCs-MCs pairs into 2 groups: ones occurring within a given time-window after an intergroup encounter and ones occurring outside the time-window. According to the average interval of days between 2 successive intergroup encounters and in order to have a relatively balanced number of PCs-MCs pairs in the 2 periods, we used a time-window of 3 days in the analysis, i.e., we compared all the PCs-MCs pairs occurring within 3 days following an intergroup encounter to all the PCs-MCs pairs occurring outside the time-window. We obtained a total of 12 dyads for which ≥ 2 PC-MC pairs were available for each period. The analysis is based on 30 PC-MC pairs for the period after the intergroup encounters and 63 PC-MC pairs for the period outside it. A Wilcoxon matched-pairs signed-rank test showed that conciliatory tendency in the 2 periods was very similar (≤ 3 days from an encounter: 0.40 ± 0.13 mean conciliatory tendency \pm SE, outside this period: 0.42 ± 0.11 ; $T = 8.0$, $N = 12$, NS).

DISCUSSION

The Occurrence of Reconciliation

Two different methodological approaches demonstrated the occurrence of reconciliation. Postconflict behavior among Japanese macaque males follows similar patterns to that among females; affiliative contacts between former opponents occurred mostly during the first minute after conflicts and grooming was the most used behavior for reconciliation. Victims took the initiative to reconcile more often than aggressors did. The result may be related to the low percentage of PCs in which the victim received further aggression, suggesting that the low risk of being attacked may make it easier for victims to approach the former aggressor in order to reconcile. However, possibly aggressors vocally communicated an intention to reconcile favoring the victims' approach.

The Occurrence of Consolation

Unsurprisingly, the study failed to demonstrate the occurrence of consolation. While consolation occurs in chimpanzees (de Waal and

van Roosmalen, 1979), no study on the phenomenon in macaques (*Macaca fuscata*: Aureli *et al.*, 1993; *M. fascicularis*: Aureli and van Schaik, 1991; *M. nemestrina*: Judge, 1991; *M. sylvanus*: Aureli *et al.*, 1994) provided evidence of consolation. Accordingly, consolation probably does not occur in *Macaca*, perhaps because they lack the cognitive abilities—empathy and mind-reading—for consolation (de Waal and Aureli, 1996).

Redirection, Further Aggression from the Former Opponent and Stress-Related Behaviors

The study showed no conclusive evidence for an increase of stress-related behavior following non-reconciled conflicts. Almost all the studies on this topic have demonstrated that stress-related behavior increases in nonreconciled conflicts whereas it drops almost immediately to baseline levels after reconciliation (Aureli, 1997; Aureli and van Schaik, 1991; Maestripieri *et al.*, 1992; Schino *et al.*, 1996). Reconciliation reduces the chance of further aggression from the former aggressor or other group members and restores the tolerance between former opponents, which lower the level of anxiety of an animal (Aureli, 1992a; Kappeler and van Schaik, 1992). Redirection is also a factor that may help to reduce stress-related behavior to baseline levels after conflicts (Aureli, 1992b). In light of these observations the results of the study are not surprising. Males do not frequently support other males fighting (Watanabe, 1979). Indeed, the percentage of polyadic conflicts in our study was low. If the risk of further aggression from the former opponent is low, then the level of anxiety may not increase. This consideration helps to understand why stress-related behavior was partly unaffected by the occurrence of the conflicts.

Variation in Conciliatory Tendency in Relation to Context of the Conflict, Season, and Among Dyads

Reconciliation was more frequent following conflicts occurring in a grooming context than those over mating partners or food, which supports the view that reconciliation is rarely observed when primates are competing over food (Aureli, 1992a; Koyama, 2001; Verbeek, 1997). Perhaps social relationships might not be endangered by food competition as food-related aggression would be limited to the displacement from the food sources, not disrupting the relationship between the opponents (Aureli, 1992a).

The results show that reconciliation rarely occurs after conflicts over resources that cannot be shared by the 2 contestants, be they food items or mating partners. This is confirmed by the lower conciliatory tendency observed during the mating season than during the nonmating season. Clearly,

Table I. Conciliatory tendency of Japanese macaque males from different studies

Conciliatory tendency	Number of males	Condition of study	Reference
0.31	13	Wild	This study
0.13	20	Provisioned	Kutsukake, pers. comm.
0.30	7	Captivity	Petit <i>et al.</i> , 1997
0.09	32	Captivity	Schino <i>et al.</i> , 1998

conflicts over these primary resources can only have a clear-cut result—win or lose—whereas no room is left for negotiation (van Hooff, 2001). An exception is when reciprocal altruism or inclusive fitness is at work (Hamilton, 1964; Trivers, 1971), but they usually do not apply to Japanese macaque males (Kurland, 1977). Therefore, the mating season represents a period of intense male competition during which social relationships with other males become less important and consequently reconciliation occurs at low rates. Schino *et al.* (1998) reached the same conclusion from a study in captivity.

Conciliatory tendency is positively correlated to the quality of the relationship existing among opponents. Accordingly, the data support the valuable relationship hypothesis and confirm that reconciliation may be predicted to occur among animals that maintain amicable relationships regardless their sex or kinship (Aureli *et al.*, 2002). The results contradict the general view predicting that male Japanese macaques usually compete with one another and rarely exchange amicable behavior. Beside the scarcity of data for male monkeys, conciliatory tendency was higher in Yakushima male macaques than it was in other studies (Table I). Moreover, the conciliatory tendency of the Yakushima macaque males is higher than that among females of the group (0.25; Majolo, in prep.).

Effects of Intergroup Encounters on Grooming and Reconciliation

There is no significant relationship between the occurrence of intergroup encounters, grooming among males, and the frequency of reconciliation. However, the results may be due to the lack of variation in the data as the intervals between 2 successive encounters were too small to affect the quality of social relationships among males in a short period of time. Indeed, researchers who tried to analyze the relation between intergroup interactions and social relationships within groups have given contrasting results (Cheney, 1981, 1992).

The behavioral ecology of Yakushima macaques differs for many aspects from the other subspecies of Japanese macaque inhabiting the mainland. A comparison of grooming distribution, frequency of reconciliation and of intergroup encounters in groups of different size would clarify if a

cause-effect relationship exists between competition among groups and social interactions within a group. Because the data are still unavailable the possible benefits that grooming and reconciliation may give to group males remain to be tested.

ACKNOWLEDGMENTS

We thank the Yakushima District Forestry Office for permission to carry on the study. Drs. S. Suzuki and D.S. Hill and students at the Kyoto University Yakushima Station kindly helped us in many ways during the study, for which we are extremely grateful. We also thank Filippo Aureli, Nobuyuki Kutsukake, Gabriele Schino, and 2 anonymous referees for useful discussion and comments on the manuscript. Majolo and Ventura were funded by University bursaries.

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