International Journal of Primatology, Vol. 27, No. 3, June 2006 (© 2006)
DOI: 10.1007/s10764-006-9039-y

Postconflict Affiliation Between Former Opponents in *Macaca thibetana* on Mt. Huangshan, China

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Received May 9, 2004; revision January 21, 2005; 2nd revision April 29, 2005; accepted June 6, 2005; Published Online July 26, 2006

We describe basic patterns of postconflict affiliation between former opponents within a group of wild, provisioned Tibetan macaques (Macaca thibetana) *on Mt. Huangshan, China. Like most primates studied to date, Tibetan macaques reconciled, i.e., overall they engaged in affiliative interaction with opponents at higher rates immediately after an aggressive conflict than at other times. Probabilities of affiliation were enhanced* ≤ 30 *s after the end of hostilities. However when we examined sex partner combinations separately, we found unequivocal evidence for reconciliation only for male-male dyads. Tolerant interaction among other partner combinations apparently was not disrupted after a conflict, presumably obviating the need to reconcile. One aspect of reconciliation among males was consistent with other indications of a despotic dominance style: aggressors initiated a higher proportion of affiliative interactions after a conflict than at other times. Another aspect of reconciliation was more typical of relaxed dominance styles: males used specialized behaviors (embraces and same-sex mounts) disproportionately to reconcile. We also found inconsistent evidence for the valuable relationship hypothesis; probabilities of reconciliation were enhanced for male-male dyads with the closest affiliative relationships, but not for those that displayed the most tolerance or mutual agonistic support. We discuss reconciliation and other aspects of conflict management among males in the*

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context of a group with nearly even sex ratios and high male-male mating competition.

KEY WORDS: conflict management; dominance style; *Macaca thibetana*; postconflict affiliation.

INTRODUCTION

Conflict management among nonhuman primates involves social patterns hypothesized to be related to conflict prevention; conflict moderation; and postconflict signaling, stress reduction, and relationship repair (Aureli and de Waal, 2000; Cords and Killen, 1998). They include agonistic buffering (Deag, 1980); preventative affiliation or sexual behavior (Koyama, 2000; de Waal, 1987); and postconflict affiliation, redirection, and consolation (de Waal and van Roosmalen, 1979). Postconflict affiliation between former opponents (reconciliation) is the best studied pattern. It refers to the increased probability of opponents to engage in affiliative interaction after a conflict than at other times, and is hypothesized to signal the end of hostilities (Silk, 1996), restore tolerance (Cords, 1992), reduce stress, or repair damaged relationships (Koyama, 2001). It remains a cornerstone in the study of conflict management for a number of reasons, including its widespread occurrence among both primate and nonprimate mammals (de Waal, 2000; Schino 2000), its association with indicators of stress reduction (Aureli and Schino, 2004; Aureli and Smucny, 2000) and relationship quality (Cords and Aureli, 2000; Cords and Thurnheer, 1993), as well as its central use as an indicator of dominance style (de Waal, 1989; Thierry, 2000; but see Flack and de Waal, 2004).

We have published an initial assessment of dominance style in wild, provisioned Tibetan monkeys (*Macaca thibetana*) on Mt. Huangshan, China, that included a preliminary documentation of reconciliation (Berman *et al.*, 2004). We used the postconflict-matched control (PC-MC) method (de Waal and Yoshihara, 1983) and calculated the index of Veenema *et al.* (1994) to establish that conciliatory tendencies were low compared with those of other macaques. Here we focus on reconciliation in Tibetan macaques by further validating its occurrence via the time-rule methods (Aureli *et al.*, 1989; Veenema *et al.*, 1994) and additional controls, and by describing basic patterns of postconflict affiliation between former opponents in detail, as a next step in describing conflict management patterns. How quickly does reconciliation occur after the end of hostilities? Do opponents show increased tendencies to affiliate specifically with one another? What behaviors, if any, do contestants use preferentially to reconcile? To what extent is reconciliation initiated primarily by attackers or targets? Do all sex partner combinations reconcile?

In our preliminary study (Berman *et al.*, 2004), we found strong evidence for reconciliation only for male-male dyads. However, most conflicts took place in the provisioning area where conflicts over food were common and may have been less likely to be reconciled than others (Aureli, 1992; Castles and Whiten, 1998; Matsumura, 1996; Verbeek and de Waal, 1997). Thus our inability to demonstrate reconciliation in female-female and male-female dyads may have been an artifact of the location of conflicts.

Here we confirm the absence of reconciliation in female-female and male-female dyads by reanalyzing data from conflicts in the forest where conflicts over food were rare. Because reconciliation is expected only where relationships are disrupted by conflict (Aureli *et al.*, 2002), we investigate the extent to which positive interaction among female-female and male-female dyads is disrupted by conflicts. Finally, we use multiple logistic regression to examine the independent and combined influences of several independent factors on reconciliation in male-male dyads: location (provisioning area vs. forest), intensity (contact vs. noncontact), and nature (dyadic vs. polyadic) of the aggression between the opponents, and the nature of the relationship between the opponents (kinship, quality, rank distance), thereby testing predictions for conflict management and dominance style theory.

First, the valuable relationship hypothesis (de Waal and van Roosmalen, 1979; Cords and Aureli, 2000) posits that reconciliation should be biased toward relationships that provide valuable benefits for the partners. Dyads with strong affiliative, tolerant, and supportive relationships should reconcile more readily than those with poorer relationships. In the focal group, closely ranked males, in particular, displayed more tolerance for one another in the form of cofeeding than distantly ranked males (Ionica, 2005). Thus we predict higher conciliatory tendencies for closely ranked than for distantly ranked male-male dyads. Finally, Berman *et al.* (2004) suggesting that female but not found high degrees of kin bias in affiliation and tolerance among females but not among males, male kin may provide valuable benefits to each other. Accordingly, we do not predict kin bias in conciliatory tendencies among male-male dyads.

Second, the pattern of findings in Berman *et al.* (2004) suggested that the group displayed a despotic dominance style; in addition to low conciliatory tendencies, the macaques consistently displayed highly asymmetric patterns of aggression and little counteraggression. Briefly stated, the dominance style concept posits that species covary systematically in many aspects of social relationships, particularly intensity of aggression, consistent enforcement of dominance status, and tolerance around limited resources. In despotic societies, dominant individuals show intense and asymmetric aggression, little tolerance, and little reconciliation, whereas more relaxed societies show the opposite tendencies. More specifically, the systematic variation hypothesis (Castles *et al.*, 1996; Thierry, 1985) posits that species displaying ≥ 1 despotic characteristics should consistently display other despotic characteristics. Thus we expect initiations of reconciliation to be biased toward winners, i.e., for winners to initiate affiliative interaction after conflict more often than they do at other times. The prediction is based on the assumption that victims of aggression in despotic societies should be more inhibited from initiating interaction with opponents after conflicts than those in relaxed societies because of the high possibility of a renewed attack (de Waal, 1993). Conversely, attackers in despotic societies may be more likely to initiate interaction after a conflict than those in relaxed societies because they are less likely to experience retaliation from victims (Silk, 1996). In addition, we do not expect to find explicit forms of reconciliation, i.e., specific affiliative behaviors specialized for conflict management (de Waal and Ren, 1988). Instead we expect behaviors used for reconciliation to occur frequently in other contexts as well.

METHODS

Study Species and Site

The study took place at Mt. Huangshan, Anhui Province, China, between August 1, 2000 and July 27, 2002. Mt. Huangshan (118.3E, 30.2N, elevation 1841 m) is a scenic area and tourist destination in east-central China that consists of steep, sparsely treed peaks at high elevations and mixed deciduous and evergreen forests in the middle and lower elevations. Several groups of Tibetan monkeys live in the forested areas, feed on a variety of plant species (Wada *et al.*, 1987), and maintain apparently nonoverlapping home ranges. They have been protected from hunting and trapping since the 1940s, and the area does not contain any known large predator.

Like other macaques, Tibetan macaques display female philopatry, male dispersal, and linear dominance hierarchies (Berman *et al.*, 2004; Deng and Zhao, 1987; Li *et al.*, 1996a; Li and Wang, 1996; Zhao, 1996). Though they are most closely related genetically to Assamese macaques (*Macaca assamensis*; Delson, 1980; Hoelzer and Melnick, 1996), they closely resemble Barbary macaques (*Macaca sylvanus*) ecologically and demographically; both species live in montane habitats near the subtropical/temperate boundary, have similar diets, are the 2 largest macaque species, and live in groups with relatively even male to female ratios, short tenures of α males, and large proportions of natal adult males.

Chinese researchers had monitored our study group, Yulingkeng A1, since 1986. We thus knew the individual identities and maternal kinship relationships of the natal adults. In 1992, the local government drove the group about 1 km from its natural range to an unoccupied adjacent area where tourists could easily view them (Berman and Li, 2002). Wardens restricted the group's movement away from the artificial feeding area, reducing its range from *ca.* 7.75 km^2 to <3 km^2 (Li *et al.*, 1996b).

The group initially consisted of *ca.* 52 individuals: 7 adult males ($\geq$8 yr), 12 adult females ($\geq$6 yr), 2 subadult males (7 yr), 1 subadult female (5 yr), 12 juvenile males (2–6 yr), 7 juvenile females (2–4 yr), 2 yearling males, 2 yearling females, and 7 infants (<1 yr). During the summer of 2001, the group fissioned and the smaller fission product left the area, reducing the total number to 37. By the end of the study it totaled 35 individuals. In 2000 and 2001, wardens provisioned the monkeys with corn 3–4 × /d on a set schedule in an open area by a stream where tourists could view them for 30–60 min at a time. When not feeding, the macaques spent most of the time in the forest. In 2002, however, wardens prevented the macaques from returning to the forest between feedings.

Data Collection

The subjects (Table I) included all adults or subadults at the beginning of the study, for a total of 13 females and 11 males. In March 2001, we began observing an additional subadult male (HH) to replace an adult male (GS) that left the group. In the summer of 2001, 1 male immigrated into the group (PN), and 2 adult males (ZM and HZ) and 2 adult females (HU and HR) left with the smaller fission product. One adult female died in December 2001.

We used focal-individual sampling (Altmann, 1974) to record affiliative, tolerant, supportive, and aggressive interaction between focal subjects and other adults or subadults. We observed each focal individual for at $\geq$2 15-min sessions/wk, 1 in the provisioning area and 1 in the surrounding forest. We recorded a total of 1200 h of focal-individual data (median = 59.1 h/subject, interquartile range = 42.5–60.6) over the 2-yr period.

To examine postconflict affiliation, we also recorded 5-min postconflict (PC) and matched control (MC) samples (de Waal and Yoshihara, 1983). We began PC sessions when we observed moderate (long lunge, chase, slap, hit, grab) or intense (bite) aggression (Table II) between the subjects and other adults or subadults, either during or between focal-individual

Table I. Focal subjects

Males			Females		
Name	Age[a]	Mother	Name	Age[a]	Mother
CW	13	Zhi[b]	BH	14	Gan[b]
GS	?	?[c]	BX	9	BH
HG	11	HU	CL	15	Ye[b]
HH	6	HU	ES	13	Ye[b]
HL	8	HU	FM	15	Gen[b]
HZ	?	?[c]	FT	9	FM
PN	?	?[c]	FY	5	FM
SX	15	Gan[b]	HR	10	HU
TY	7	Teng[b]	HU	17	Gen[b]
ZL	7	Zhi[b]	TG	14	Ye[b]
ZM	11	Zhi[b]	TT	9	TG
			YM	10	Ye[b]
			YZ	8	Ye[b]

[a] Age of subject at the beginning of the study.
[b] The mother was not in the group during the study.
[c] Immigrant to the group; age and mother were unknown, but appeared fully adult.

sessions. The PC session began as soon as aggression ceased between the 2 opponents. If aggression between the opponents reoccurred or a third party attacked either opponent ≤2 min of the PC, we aborted the session and restarted immediately after aggression ceased again. During dyadic PCs, we followed the target (instead of the attacker) of the aggression, when possible. We considered the conflict polyadic rather than dyadic if 1) third parties aided either opponent during the initial conflict or 2) the target redirected aggression to another macaque. In polyadic conflicts involving >1 target, we followed the final target, when possible. If >1 individual attacked the target, we considered the attacker directing the most intense aggression as the opponent. During PCs, we recorded all aggressive, tolerant, supportive, and affiliative interaction involving the focal individual, along with the identities of the partners, the directions of interaction, and the times of occurrence.

We recorded an MC sample on the same focal individual, via the same procedure as during the PC on the next possible observation day, provided the 2 opponents were ≤10 m of one another and in a similar location: provisioning area or forest. We used the proximity criterion because interopponent distance is an important factor affecting PC-MC analyses (Call, 1999), but we were unable to match exact distances between opponents. Neither were we able to match times of day because we could not reliably locate individuals at predetermined times. We recorded a total of 574 PC-MC pairs meeting the criteria, 133 (23.2%) of which involved polyadic aggression in the PC. The median number of days between PCs and MCs was 3 (interquartile range = 1–7, range = 1–30).

Ionica, Berman, and several assistants collected the data. Each observer achieved levels of interobserver reliability with Ionica of ≥85%, as determined by the κ coefficient (Cohen, 1960). We used Psion handheld computers and Noldus Observer 3.0 software to record data during the first 4 mo, but later switched to tape recorders to increase accuracy during quick interaction. We subsequently transcribed the tapes into files that were compatible with Noldus Observer 3.0 tabulation software. We used both the software and visual basic programs Ionica wrote to tabulate the data.

Data Analysis

To examine postconflict affiliation, we compared the lengths of time from the beginning of a session until the first occurrence of any criterion affiliative behavior (Table II) between former opponents in the PCs and in its corresponding MCS. We defined attracted, dispersed, and neutral PC-MC pairs as in de Waal and Yoshihara (1983). We used Wilcoxon matched pairs signed ranks tests to compare proportions of attracted and dispersed PC-MC pairs at an individual level to determine whether the macaques reconciled, unlike Berman *et al.* (2004), who used sign tests on numbers of attracted vs. dispersed pairs. We separately analyzed individuals with all opponents and for separate sex partner combinations. We described the extent to which monkeys reconciled by calculating the mean conciliatory index (number of attracted pairs minus the number of dispersed pairs over the total number of pairs) over all individuals (Veenema *et al.*, 1994). In Berman *et al.* (2004), the calculations were based on pooled data.

We used time rule analysis to determine how soon reconciliation took place after the cessation of a conflict (*cf.* Aureli *et al.*, 1989). We graphically compared the distributions of time until the first affiliative interaction between opponents in the PCs and in the MCs to identify a time window during which the rate of affiliation in the PCs exceeded that in the MCs. We then used Wilcoxon tests to compare the proportions of first affiliative interactions that fell within this window during PCs and MCs for individual subjects with at ≥2 PCs and MCs that included affiliative interactions. Subsequent analyses were based on the time window as the operational criterion for reconciliation; if an affiliative interaction occurred in the PC within the window, we considered the conflict reconciled.

We investigated whether conflict disturbed positive interaction between opponents via methods adapted from Schaffner *et al.* (2005). Focusing on conflicts that broke out while the opponents were either sitting or

Table II. Behavioral definitions

Aggressive interaction triggering a PC:

1. Long lunge: An individual directs a lunge of ≥ 2 body lengths to another individual but does not go into a full chase
2. Chase: An individual runs after another individual at great speed
3. Slow grab: An individual seizes another individual slowly and holds while staring
4. Slap: An individual slaps or hits another individual
5. Grab: An individual roughly and quickly seizes another individual and holds for at least a few seconds
6. Bite: An individual bites hard, either releasing the victim quickly or hanging on for several seconds. (Soft bites were seen in the context of embracing or play and were not counted as aggression.)

Criterion affiliative interaction used in PC-MC analysis:

1. Lipsmack: Slightly puckered lips are rapidly opened and closed, sometimes producing a smacking sound
2. Teeth-chatter: Clicking sounds are made with the teeth by rapidly moving the jaw up and down. Eyelids are lowered, the chin is raised, and the tongue may move rapidly across the teeth. Often the corners of the mouth are retracted as in the silent bared-teeth display
3. Embrace: One individual approaches another and 1 or both individuals hold each other and may lightly bite one another
4. Touch: One individual lightly touches another usually on the head, shoulders, or back
5. Present: One individual displays his/her bottom to another
6. Social mount: One individual approaches another from behind and mounts. A full ankle clasp may be used but there is no thrusting or evidence of intromission
7. Penis display: A male lifts his leg and presents his penis to another, often from a reclining position
8. Penis suck: One individual sucks the penis of another
9. Genital inspection: One individual touches, licks, or sniffs the genitals of another
10. Groom: One individual orally or manually manipulates the fur of another
11. Bridge: A complex sequence of behavior in which an individual approaches another, alternating glances at the receiver and an infant that is carried by either the approacher or the approached. The pair holds the infant between them and simultaneously licks the infant's genitals or body while teeth-chattering vigorously (Ogawa, 1995)
12. Hold bottom: One individual approaches another and holds or embraces his/her bottom for a few seconds

cofeeding ≤ 1 m of one another, we compared the proportion of conflicts in which the same tolerant interactions resumed during the PC with the proportion of MCs in which they occurred at all, using Wilcoxon tests at an individual level.

To determine whether either attackers or targets were more likely to initiate affiliative interaction after a conflict than at other times, we identified the initiator of the first affiliative interaction in each PC and MC, and compared the distributions of attacker-initiated vs. target-initiated affiliations in PCs and in MCs, using χ^2 tests. When both opponents simultaneously initiated the first affiliative interaction, e.g., when they mutually embraced, we counted initiations by both partners. We performed analyses for all PCs vs. all MCs and for reconciled conflicts vs. all MCs.

We investigated the extent to which former opponents affiliated specifically with one another via Wilcoxon matched-pairs signed-ranks tests to ask 1) whether the number of affiliative partners was greater in each PC than in its matched control and 2) whether the proportion of total affiliative interactions that were directed toward the former opponent was greater in the PCs than in the MCs. We used χ^2 analysis to determine what affiliative behaviors, if any, the individuals used preferentially to reconcile, by comparing distributions of each criterion behavior in the PCs vs. the MCs, separately for whole PCs vs. whole MCs and for the first 30 s of each PCs vs. whole MCs.

We used backward stepwise multiple logistic regression analysis to investigate the independent and combined effects of several factors on probabilities of reconciliation: location (provisioning area vs. forest), kinship (close kin vs. other), rank distance (1 or 2 vs. other), intensity of aggression (noncontact vs. contact), dyadic vs. polyadic aggression, and relationship quality. Because the logistic regression analyses were at the level of individual conflicts, we also calculated conciliatory tendencies (Veenema *et al.*, 1994) for each individual and used Wilcoxon tests to compare them across each factor at the individual level.

Because there were several rank changes among both males and females and a period of rank instability when the group fissioned, we also investigated whether hierarchical instability may have affected reconciliation. We coded each PC-MC pair by whether or not it occurred during 1 of 3 sustained time periods when dominance relationships, inferred from the direction of submissive interactions between pairs of individuals (Berman *et al.*, 2004), were linear and stable: 1) August 1, 2000–January 28, 2001, 2) February 27, 2001–May 29, 2001, and 3) December 9, 2001–July 25, 2002. The first period took place primarily during the mating season, and the second and third periods primarily during the birth season. We then compared proportions of reconciled conflicts during stable and unstable periods at an individual level via Wilcoxon tests.

We classified kin by degree of relatedness through maternal lines. Close kin were related by ≥ 0.25 (e.g., as much as half siblings). We considered all others nonkin. We had 6 pairs of adult brothers because male Tibetan macaques typically delay dispersing from their natal groups until they are young adults. We thus had the opportunity to test for kin bias among males as well as females. We measured rank distance only for PC-MC pairs that took place within the 3 stable time periods.

We measured 3 forms of relationship quality—support, affiliation, and tolerance—separately within each of the 3 stable time periods. We classified dyads in which mutual aiding occurred (i.e., in which each partner gave and received aid at least once) during focal samples, PC-MC samples, or *ad libitum* observations as allies and contrasted them with all other dyads. For affiliation, we calculated rates of grooming and sitting $\leq$1 m during focal samples for each dyad and converted them into standard scores [(dyadic rate minus mean rate)/standard deviation)]. We calculated mean standard scores over the 2 measures. We classified dyads with mean standard scores in the top quartile as most affiliative and contrasted them with all other dyads. For tolerance, we calculated rates of cofeeding $\leq$1 m during focal samples for each dyad, classified dyads with scores in the top quartile as tolerant, and contrasted them with all others. For affiliation and tolerance, we calculated quartiles in 2 ways: relative to all dyads and to each individual. Both methods yielded similar results in the logistic regression analyses, so for simplicity's sake, we report results only for all dyads here. All statistical tests are 2-tailed, and probabilities $\leq$0.05 are significant.

RESULTS

As reported in Berman *et al.* (2004), of the 574 PC-MC pairs, 73 were attracted, 36 were dispersed, and 465 were neutral, which yielded a mean ± SE conciliatory tendency (CT) of (7.9 ± 2.8%). Fourteen focal subjects had higher proportions of attracted pairs (mean ± SE = 12.9 ± 2.6%) than dispersed pairs (mean ± SE = 5.5 ± 1.0%), 3 had lower proportions, and 6 had equal proportions ($Z = 2.68$, $n = 17$ individuals plus 6 ties, $p = 0.007$, Wilcoxon test). Thus overall, opponents engaged in affiliation with one another at higher rates after aggression than at other times.

The temporal distribution of first affiliative interactions between opponents over 30-s intervals during PCs and MCs is in Fig. 1. Most (50/77 or 65.8%) affiliative responses in the PCs took place within the first 30 s, whereas this was the case for only 15/41 (36.6%) affiliative interactions in the MCs. After 30 s the 2 distributions were similar. Proportions of affiliative responses that occurred during the first 30 s were greater in the PCs (mean ± SE = 80.1 ± 10.7%) than in the MCs (mean ± SE = 20.1 ± 7.7%) ($T = 1$, $n = 7$ individuals with no ties, $p < 0.032$, Wilcoxon test). We thus considered conflicts followed by affiliation in $\leq$30 s to be reconciled.

We investigated whether approaching behavior should be considered affiliative behavior for purposes of reconciliation by comparing conciliatory tendencies when approaches were counted as a criterion affiliative behavior in addition to the ones in Table II. We consequently found a slightly lower conciliatory tendency; of the 574 PC-MC pairs, 118 were attracted, 84 were dispersed, and 372 were neutral, yielding a mean ± SE conciliatory tendency of (7.1 ± 3.5%) and a Wilcoxon test that fell short of significance

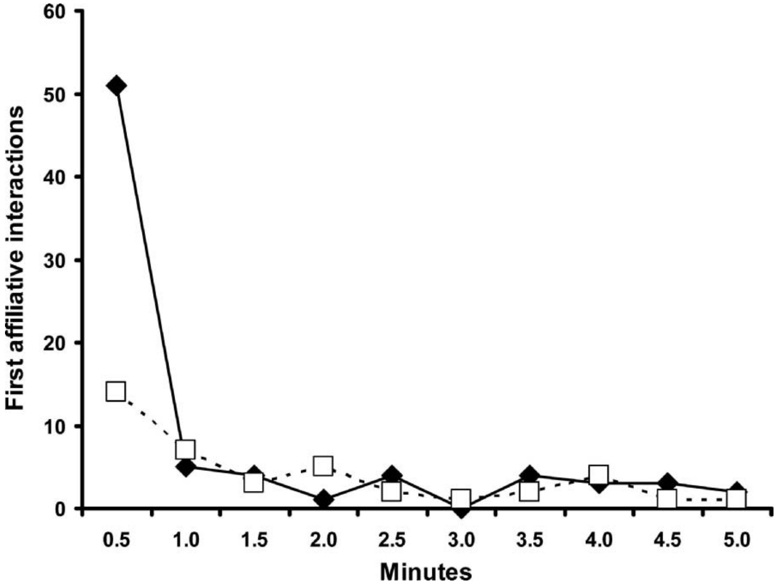

Fig. 1. Frequency of first affiliative interactions by time elapsed from the beginning of postconflict (◆) and matched-control (☐) sessions.

($Z = 1.87$, $n = 22$ individuals plus one tie, $p = 0.062$), which tentatively suggested that macaques did not use approaches to reconcile. We confirmed the result by examining approaches only; we found 99 attracted pairs, 79 dispersed pairs, and 394 neutral pairs; a mean ± SE conciliatory tendency of (3.6 ± 3.0%); and a nonsignificant Wilcoxon test ($Z = 1.14$, $n = 20$ individuals plus 3 ties, $p = 0.26$). Thirty-three of 91 (36.3%) first approaches occurred within the first 30 s of the MC, a figure virtually identical to that for other affiliative behaviors (36.6%). However, first approaches appeared to be distributed more evenly than other affiliative behaviors after conflict; 45 of 107 (42.1%) approaches vs. 65.8% of other affiliative behaviors occurred within the first 30 s of the PC.

Some MC samples were delayed by as much as 30 d because it was difficult to find the 2 opponents in the same location—provisioning area vs. forest—and $\leq$10 m of one another. To investigate whether delayed MCs may have produced biased control samples, we calculated conciliatory tendencies separately for PC-MC pairs that were delayed by >7 d (delayed MCs, $n = 142$) and by $\leq$7 d (quick MCs, $n = 432$). Among the quick PC-MC pairs, proportions of attracted pairs (mean ± SE = 14.6 ± 3.1%) were significantly greater than proportions of dispersed pairs (mean ± SE = 6.4 ± 1.2%) ($Z = 2.46$, $n = 16$ individuals plus 7 ties, $p = 0.014$, Wilcoxon test). In contrast, the same analysis for delayed PC-MC pairs yielded a mean ± SE proportion of attracted pairs of 12.9 ± 4.9%, a mean ± SE proportion of dispersed pairs of 2.9 ± 1.3%, and a marginally nonsignificant Wilcoxon test ($T = 11.5$, $n = 11$ individuals plus 12 ties, $p < 0.08$). However, further analysis suggested that delayed MCs did not differ from quick MCs; times to first affiliative responses were similar ($Z = -1.19$, $n = 16$ individuals plus 5 ties, ns, Wilcoxon test). Instead, first affiliative responses occurred earlier in PCs followed by quick than delayed MCs is ($Z = -2.05$, $n = 19$ individuals plus 2 ties, $p = 0.04$, Wilcoxon test). The finding suggests either that reconciliation occurred more readily in dyads that were together frequently, or that dyads that failed to reconcile subsequently avoided one another.

Partner Combination

Berman *et al.* (2004) found evidence for reconciliation in male-male dyads, but not for female-female dyads or male-female dyads. Our data confirm the finding: at an individual level, male-male dyads (mean CT = 19.1 ± 4.5%) had significantly higher proportions of attracted (mean ± SE = 25.4 ± 4.9%) than dispersed pairs (mean ± SE = 6.3 ± 1.9%) ($T = 0$, $n = 10$ individuals plus 1 tie, $p = 0.005$, Wilcoxon test), but other partner combinations did not [female-female dyads (mean proportion of attracted pairs ± SE = 10.8 ± 3.2%, mean proportion of dispersed pairs ± SE = 4.0 ± 1.4%) ($T = 14.5$, $n = 11$ females, plus 2 ties, ns, Wilcoxon test)] [male-female dyads (mean proportion of attracted pairs ± SE = 6.2 ± 1.9%, mean proportion of dispersed pairs ± SE = 5.5 ± 1.8%) ($T = 29$, $n = 11$ individuals plus 12 ties, ns, Wilcoxon test)].

The reason for our inability to demonstrate reconciliation in female-female and male-female dyads may be that we recorded most PC-MC pairs (498 of 574, or 86.8%) in the provisioning area where conflicts over food were common. To test the hypothesis, we reanalyzed data for each partner combination using only PC-MC pairs recorded in the forest ($n = 76$) where conflicts over food were rare. The results were similar to those for the full sample of PC-MC pairs. At an individual level, male-male dyads (mean CT ± SE = 31.4 ± 11.6%) had significantly higher proportions of attracted (mean = 38.9 ± 7.3%) than dispersed (mean = 7.4 ± 4.9%) PC-MC pairs ($T = 4.5$, $n = 9$ males with no tie, $p < 0.04$, Wilcoxon test). This was not the case for either female-female dyads (mean proportion of attracted pairs = 46.3 ± 15.7%, mean proportion of dispersed pairs = 29.6 ± 15.2%) ($T = 14.5$, $n = 8$ females plus 1 tie, ns, Wilcoxon test) or male-female dyads (mean proportion of attracted pairs = 9.0 ± 4.9%, mean proportion of dispersed pairs = 19.2 ± 10.7%) ($T = 6.5$, $n = 6$

individuals plus 7 ties, ns, Wilcoxon test), supporting the suggestion of Berman *et al.* (2004) that only male-male dyads reconcile.

Because reconciliation is expected only for relationships disrupted by conflict (Aureli *et al.*, 2002), we next investigated the extent to which conflicts among female-female and male-female dyads disrupted positive interaction. Opponents were never engaged in overt affiliative interaction such as grooming or embracing at the outbreak of a conflict. Opponents engaged in tolerant interaction (sitting or cofeeding ≤ 1 m of one another) before a conflict in a minority of cases (female-female: 22 of 165, or 13.3% of PCs; male-female: 17 of 257, or 6.6% of PCs). Nevertheless, in most cases (female-female: 13 of 22, or 59.1%; male-female: 10 of 17, or 58.8%), the opponents resumed their tolerant interaction during the PC, i.e., ≤ 5 min after the end of the conflict. When we compared the proportion of PCs in which tolerant interaction was resumed with the proportion of cases in which tolerant interaction took place any time during MCs, we found no evidence that tolerant interaction was disrupted after conflicts. Individual females were actually more likely to resume sitting near or cofeeding with another female after a conflict than to engage in these activities with the same partner during an MC ($T = 0$, $n = 11$ females with no ties, $p < 0.01$, Wilcoxon test). Males and females were equally likely to resume sitting near or cofeeding with opposite-sex opponents after a conflict as they were to engage in the activities with the same partner during an MC ($T = 10$, $n = 9$ individuals plus 1 tie, ns, Wilcoxon test). Cases in which macaques resumed tolerance more often involved coalitionary allies ($p = 0.02$, $n = 28$ conflicts, Fisher's exact test) and close affiliates ($p = 0.035$, $n = 28$ conflicts, Fisher's exact test) than those that were not resumed, but were not more likely to involve kin ($p = 0.262$, $n = 39$ conflicts, Fisher's exact test) or otherwise highly tolerant pairs ($p = 0.364$, $n = 28$ conflicts, Fisher's exact test).

Who Initiates Postconflict Affiliation?

Given the lack of evidence for reconciliation among female-female and male-female dyads, in subsequent analyses of reconciliation we focus on male-male dyads. Among male-male dyads, targets initiated about half the first affiliative interactions during PCs (all conflicts: 22/43 = 51.2%, reconciled conflicts: 14/31 = 45.2%), but they initiated nearly all (14/15 = 93.3%) first affiliative responses during MCs, yielding highly significant differences between distributions (all conflicts MCs vs. all MCs: $\chi^2 = 8.40$, df = 1, $p = 0.004$; reconciled conflicts vs. all MCs: $\chi^2 = 9.85$, df = 1,

$p = 0.002$). Thus among male-male dyads, attackers were more likely to initiate affiliative behavior with former opponents after conflicts than at other times.

Is Postconflict Affiliation Specific to Former Opponents?

Males engaged in affiliative interaction with more partners during PCs than during MCs, suggesting a generally increased propensity to affiliate. Male opponents interacted affiliatively with a mean ± SE of 0.63 ± 0.08 partners during each PCs compared with 0.36 ± 0.06 in each MC, yielding a significant difference ($Z = 2.36$, $n = 79$ PC-MC pairs plus 73 ties, $p = 0.018$, Wilcoxon test). At an individual level, 10 males affiliated with more partners in the PCs than MCs, 1 with fewer, none with the same number ($T = 7, n = 11$ males, $p < 0.02$, Wilcoxon test).

Though males may have been motivated to affiliate with more partners after a conflict, they nevertheless directed higher proportions of their affiliative interaction toward their former male opponents after a conflict than otherwise. We compared proportions of total affiliative responses directed toward former male opponents during the first 30 s of PCs vs. entire MCs. Because opponents engaged in no affiliative interaction during many PCs and MCs, it was not possible to compare each individual PC with its matching MC. We therefore calculated proportions of affiliative interaction with opponents for each focal individual by dividing the total number of interactions it had with its opponents by the total number of affiliative interactions it had with any partner, separately for all its PCs and all its MCs. About one-half (mean ± SE = 0.53 ± 0.12) of affiliative interactions were with former opponents during PCs compared with about one-quarter (mean ± SE = 0.25 ± 0.10) during MCs. Seven males had higher scores in the PCs than MCs, none had higher scores in the MCs, and 3 had equal scores or no affiliation in MCs ($T = 0, n = 7$ males, $p = 0.016$, Wilcoxon test).

Specific Behaviors Used in Reconciliation

We observed no particular kind of affiliative behavior among male-male pairs exclusively during PCs (either in the first 30 s of PCs or in entire PCs) rather than MCs. Nevertheless, distributions of different affiliative behaviors differed between PCs and MCs (entire PCs vs. entire MCs: $\chi^2 = 30.8$, df = 6, $p < 0.0001$: first 30 s of PCs vs. entire MCs: $\chi^2 = 37.6$, df = 6, $p < 0.0001$). Adjusted residuals indicate that embraces, grooming, and, to a lesser extent, same-sex mounts and various rare

Table III. Distributions of specific affiliative behaviors involving males during PCs and MCs

Behavior	PC First 30 s (1)	PC Whole (2)	MC Whole (3)	Adjusted residuals[a] (1) vs. (3)	Adjusted residuals[a] (2) vs. (3)
Groom	1 (2.6)	4 (6.3)	29 (32.2)	− 3.7	− 3.8
Embrace	9 (23.1)	10 (15.9)	1 (1.1)	+ 4.3	+ 3.5
Same-sex mount	12 (30.8)	18 (28.6)	10 (11.1)	+ 2.7	+ 2.8
Bridge	2 (5.1)	7 (11.1)	6 (6.7)	− 0.3	+ 1.0
Touch	4 (10.3)	5 (7.9)	9 (10)	0.0	− 0.4
Present	9 (23.1)	10 (15.9)	17 (18.9)	+ 0.5	− 0.5
Miscellaneous[b]	2 (5.1)	9 (14.3)	18 (20.0)	− 2.1	− 0.9
Total	39	63	90		

Note. The value in parenthesis are in percent.

[a] Adjusted residuals describe the degree to which each behavior contributed to the overall χ^2 value tests and the direction of deviation (+ or −) from the expected values during PC.

[b] We lumped rare affiliative behaviors to meet the assumptions of the χ^2 analysis: teeth-chatter, genital inspection, show penis, suck penis, hold bottom.

miscellaneous behaviors (teeth chatter, genital inspection, show penis, suck penis, and hold bottom) contributed most to the results (Table III). During PCs, embraces and same-sex mounts occurred more than expected, whereas grooming and the miscellaneous behaviors occurred less than expected.

Sources of Variation

The proportion of reconciled conflicts (followed by affiliation in $\leq$30 s) for male-male dyads was 31/152 (20.4%). The mean ± SE percentage across the 11 individual males is 21.1 ± 5.1. To examine the independent and combined influences of each variable on probabilities of reconciliation, we entered all the variables except hierarchical stability into a backward stepwise logistic regression. We excluded hierarchical stability because we could reliably measure 4 other variables—rank distance, affiliation, tolerance, and support—only during stable periods. A model based on rank distance ($\beta = -2.0$, exp (β) $= 0.14$, Wald $= 7.2$, df $= 1$, $p = 0.007$), affiliation ($\beta = 1.6$, exp (β) $= 5.0$, Wald $= 4.9$, df $= 1$, $p = 0.027$) and location ($\beta = 1.1$, exp (β) $= 2.9$, Wald $= 2.9$, df $= 1$, $p = 0.09$) produced the best result (model $\chi^2 = 15.3$, df $= 3$, $p < 0.002$, -2 log likelihood $= 90.9$). The addition of interaction terms did not improve the model. The results for affiliation were sustained when we examined the data for conciliatory tendencies (Veenema *et al.*, 1994) at the level of individual focal males ($T = 3$, $n = 8$ males with 1 tie, $p = 0.039$, Wilcoxon test), but those for rank distance ($T = 6$, $n = 7$ with no ties, ns, Wilcoxon test) and location ($T = 14$, $n = 10$ males with no ties, ns, Wilcoxon test) were not. Because we could not evaluate hierarchical stability in the multiple logistic regression we examined it only at the individual level. Individual males had significantly higher conciliatory tendencies during periods of hierarchical stability than instability ($T = 1$, $n = 9$ males plus one tie, $p < 0.008$, Wilcoxon test). There were no significant differences in conciliatory tendencies at an individual level for any other factor (Table IV).

DISCUSSION

Like most primates studied to date, Tibetan macaques engage in affiliative interaction with opponents at higher rates immediately after an aggressive conflict than at others times. We found significant overall tendencies to reconcile via both the PC-MC (de Waal and Yoshihara, 1983) and the time-rule methods (Aureli *et al.*, 1989). The latter method also demonstrated that most reconciliation takes place remarkably quickly; probabilities of affiliation after a conflict were enhanced only during the first 30 s after the end of hostilities. However, unlike most primate species studied to date, only male-male dyads appear to reconcile. Confirming and extending our preliminary findings (Berman *et al.*, 2004), we demonstrated reconciliation for male-male dyads, but not for female-female or male-female dyads, both when we examined all PC-MC pairs together and only those recorded in the forest. By examining data only from the forest (where disputes over food were rare), we eliminated the possibility that our lack of evidence for reconciliation in female-female and male-female dyads was due to the fact that many conflicts were over food.

Male opponents directed higher proportions of their affiliative interaction toward former male opponents than they did at other times, suggesting that they had enhanced tendencies to affiliate specifically with former opponents instead of with whichever individuals were nearby. Males also affiliated with a larger number of partners after a conflict than at other times, raising the possibility that they may also engage in other postconflict strategies or management patterns with uninvolved third parties such as substitute or third-party reconciliation, consolation, encouragement, or support-recruitment (Das, 2000; Watts *et al.*, 2000).

Table IV. Conciliatory tendencies (mean percent ± SE) for male-male dyads

Independent variable[a]	Conciliatory tendencies	Total conflicts	Mean (range) conflicts per male	N (males)
Kin vs. nonkin	26.2 ± 11.2 vs. 21.5 ± 6.7	35 vs. 117	5.8 (2–7) vs. 10.6 (4–20)	6 vs. 11
Provisioning area vs. forest	13.6 ± 6.0 vs. 38.3 ± 12.4	121 vs. 31	11 (4–31) vs. 3.1 (1–6)	11 vs. 10
Stable vs. unstable hierarchy	24.4 ± 4.9 vs. 0.7 ± 8.6**	120 vs. 32	10.9 (4–31) vs. 3.2 (1–6)	11 vs. 10
Dyadic vs. polyadic aggression	16.2 ± 5.1 vs. 24.0 ± 8.9	102 vs. 50	9.3 (3–12) vs. 4.5 (1–9)	11 vs. 11
Contact vs. noncontact aggression	17.5 ± 6.5 vs. 19.7 ± 7.9	69 vs. 83	6.3 (2–13) vs. 7.5 (2–24)	11 vs. 11
Close vs. distant in rank	17.7 ± 7.8 vs. 39.7 ± 10.7	45 vs. 48	5.6 (3–15) vs. 5.3 (2–11)	8 vs. 9
Relationship quality:				
Most affiliative vs. others	53.6 ± 12.1 vs. 15.6 ± 6.0*	40 vs. 53	4.8 (1–17) vs. 5.5 (2–10)	8 vs. 10
Most tolerant vs. others	19.5 ± 6.7 vs. 29.4 ± 6.2	32 vs. 61	4 (1–14) vs. 6.1 (2–12)	8 vs. 10
Supportive vs. not supportive	32.4 ± 6.3 vs. 23.4 ± 7.0	30 vs. 63	5 (2–9) vs. 6.3 (1–17)	6 vs. 10

[a] Criteria for classification of variables are in Methods.

*$p < 0.05$, **$p < 0.01$, Wilcoxon matched pairs signed rank test on individual males.

Postconflict Tolerance in Female-Female and Male-Female Dyads

Aureli *et al.* (2002) predicted that reconciliation may be absent in relationships undisturbed by conflict because there would be no need to repair them. Our finding that conflicts did not tend to disrupt tolerant interaction between female-female and male-female opponents is consistent with the prediction. Nevertheless, understanding why conflicts between the partner combinations may not be disturbed by conflict requires more research. Cords and Aureli (2000) suggested that highly secure relationships, e.g., among kin or characterized by highly table rank relationships, are unlikely to be disturbed after conflicts. However, the explanation does not appear to apply to our social group, given that rank changes among both sexes were frequent and conflicts were equally likely to lead to disruptions of tolerant interaction among kin and nonkin. That conflict was less likely to disrupt tolerant interaction when opponents were coalitionary allies and close affiliates than when they were not suggests that highly compatible mutual protectors may have been more motivated than others to maintain access to one another despite their conflict. Alternatively, the finding that females were actually more likely to resume tolerant interaction with their opponents after a conflict than at other times raises the possibility that they may have used subtle behaviors to reconcile, e.g., soft vocalizations, that we did not record.

Conciliatory Tendencies: Comparisons with Other Macaques

Berman *et al.* (2004) compared the overall conciliatory tendency for Yulingkeng A1 with comparable values for other macaques with better known dominance styles, finding it was low even for macaques with despotic dominance styles. However, given marked differences between partner combinations, we now suggest that the use of an overall conciliatory tendency may be misleading for the species. We now favor the use of separate figures for each partner combination, and suggest that they remain useful for comparison with other species even for partner combinations that do not necessarily reconcile. We further caution against use of overall conciliatory tendencies for other species without first checking for differences between partner classes. Because most studies exclude conflicts over food, we also conservatively suggest using figures for PC-MC pairs recorded outside the provisioning area, even though we did not find significant differences in the probabilities of reconciliation for male-male dyads according to location.

Given the aforementioned criteria, conciliatory tendencies still resembled those for other despotic macaques (Fig. 2). Mean conciliatory tendencies for nonkin female-female dyads (8%) are within the range for other macaques with despotic dominance styles (1–32%) and below the range for those with more relaxed styles (22–48%). The figure for male-female dyads (−10%) is lower than that for both other despotic macaques (2.5–16%) and relaxed macaques (18–67%). Only 3 studies of male-male dyads were available for comparison, all for despotic species: Petit *et al.* (1997) and Majolo *et al.* (2005) found values of 30% and 31%, respectively, among Japanese macaques (*Macaca fuscata*), and Cooper (1999) found a value of 12% among Assamese macaques (*M. assamensis*). The corresponding value for the Tibetan male monkeys in Yulingkeng A1 (31%) could be considered moderate, but was nevertheless similar to those for Japanese macaques.

Systematic Variation Hypothesis

Given that Yulingkeng A1 displayed several characteristics of despotic species (low-moderate conciliatory tendencies, highly asymmetric patterns of aggression, little counter-aggression and high kin bias among females in affiliative and tolerant interactions; Berman *et al.*, 2004), the systematic variation hypothesis predicts the display of additional indicators of despotism. One finding supports the prediction. Though attackers and targets initiated reconciliation in equal proportions, attackers in male-male dyads initiated more affiliative exchanges with former opponents after a conflict than they did at other times. The behavior is consistent with the hypothesis that targets in despotic societies may be more inclined to avoid attackers after conflict than those in more relaxed societies because of higher chances of renewed aggression. Similarly, attackers in despotic societies may be more likely to attempt to reconcile with a former opponent than those in relaxed societies because they are less likely to receive retaliation.

Another finding does not support the systematic variation hypothesis. Though we found no affiliative behaviors used exclusively in reconciliation, macaques were more likely to use 2 conspicuous behaviors—embracing and same-sex mounting—after conflicts than at other times. Specialized and conspicuous reconciliation behaviors are associated with more relaxed dominance styles, whereas implicit forms of reconciliation are more common in despotic societies (de Waal and Ren, 1988). Though the incidence of same-sex mounting and embracing was low during the MCs, we commonly observed these behaviors during other tense situations, such as immediately after the staff signaled the imminent arrival of provisioned food (Ionica, 2005). Hence, their use in both situations points to a more general stress reduction/conflict management function.

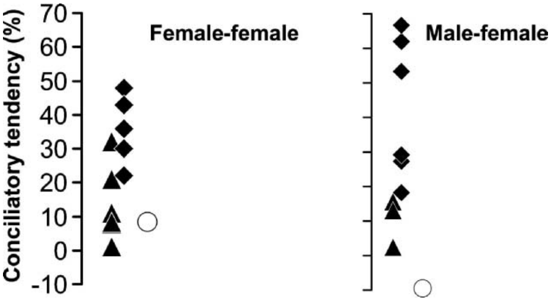

Fig. 2. Conciliatory tendencies for Tibetan monkeys in the forest (circles) are compared with published data for despotic macaques (triangles) and relaxed macaques (diamonds). Left: Females with nonkin females: published data for highest to lowest values are from: Tonkeana (Demaria and Thierry, 2001), lion-tailed (Abegg *et al.*, 1996), stump-tailed (Call, 1999), pig-tailed (Castles *et al.*, 1996), Barbary (Aureli *et al.*, 1997), black crested (Petit *et al.*, 1997), Japanese (Aureli *et al.*, 1997), rhesus (Demaria and Thierry, 2001), rhesus (Call, 1999), Japanese (Petit *et al.*, 1997), long-tailed (Aureli *et al.*, 1997). Right: Males with females: published data for highest to lowest values are from: lion-tailed (Abegg *et al.*, 1996), Tonkeana (Demaria and Thierry, 2001), lion-tailed (Abegg *et al.*, 1996), black crested (Petit *et al.*, 1997), moor (Matsumura, 1996), lion-tailed (Abegg *et al.*, 1996), Japanese (Petit *et al.*, 1997), rhesus (Demaria and Thierry, 2001), Assamese (Cooper, 1999). Note: Means of individual scores were plotted except for moor macaques (Matsumura, 1996) for which they were not available. We limited comparisons to published data on adults of well-established groups that used similar data collection methods, behavioral measures, partner combinations, and definitions of kin with the following exceptions: Abegg *et al.* (1996) and Petit *et al.* (1997) used all-occurrence sampling (Altmann, 1974) rather than focal-individual sampling.

Valuable Relationship Hypothesis

Many studies of nonhuman primates have found enhanced probabilities of reconciliation among dyads with high-quality relationships (Cords and Aureli, 2000), but only a few have controlled for both kinship and rank distance (Call *et al.*, 1999). Most defined high-quality relationships primarily or exclusively in terms of affiliative or agonistic interaction or both, and their findings suggest that reconciliation is more common among partners that are highly compatible and accessible to one another (Cords and Aureli, 2000; Silk, 2002). Our findings are consistent with them; males were more likely to reconcile conflicts with opponents with which they had strong affiliative relationships. Among great apes, partner combinations that rely on each other for coalitionary support tend to reconcile more than those that do not (Boesch and Boesch-Achermann, 2000; Watts, 1995). However, so far evidence for an association between support and reconciliation at the dyadic level is inconsistent. Wittig and Boesch (2003) and Cooper *et al.* (2005) found positive evidence in wild chimpanzees (*Pan troglodytes*) and female Assamese macaques, respectively, but other researchers have not (chimpanzees: Arnold and Whiten, 2001; Preuschoft *et al.*, 2002; long-tailed macaques (*Macaca fascicularis*): Cords and Aureli, 1993; male Assamese macaques: Cooper *et al.*, 2005). Like the latter studies, we found no evidence that Tibetan macaque males reconciled more with opponents with which they exchanged more tangible benefits; probabilities of reconciliation were similar among dyads that varied in mutual agonistic support and tolerance around resources. Similarly, reconciliation was not more likely among closely ranked males than distantly ranked males in spite of their high cofeeding rates (Ionica, 2005). Some researchers attributed such negative results to the rarity of aiding or the asymmetrical exchange of benefits during tolerance and some support (Cords and Aureli, 1993; Preuschoft *et al.*, 2002). However, rates of aiding among males were moderate in Yulingkeng A1 (*ca.* once per 6.8 focal observation hours, or on average 1–2 × /male per 12-h d), and some degree of mutual aiding was reasonably widespread (in $12/43 = 27.9\%$ of the male-male dyads for which we had PC-MC data). Hence, at this point our results can offer only limited support for the valuable relationship hypothesis; male partners appear to reconcile preferentially with opponents that are compatible and accessible, but are not necessarily sources of more concrete benefits.

Conflict Management Among Males

Though many researchers discuss the use of specific conflict management patterns, particularly reconciliation, at a specific level and compare them with those for other species, it is becoming increasing clear that conflict management patterns may differ within species, particularly for different partner combinations. For example, among wild mountain gorillas (*Gorilla gorilla*) only opposite-sex adult dyads reconcile (Watts, 1995); among white-faced capuchins (*Cebus capucinus*) only kin and nonkin male-female dyads reconcile (Leca *et al.*, 2002); and among captive (de Waal, 1986), but not necessarily wild (Arnold and Whiten, 2001; Goodall, 1986; Kutsukake and Castles, 2004; Muller, 2002; Wittig and Boesch, 2003) chimpanzees, male-male dyads are more likely to reconcile than female-female dyads. In many cases, the reconciling partner classes represent those that form frequent alliances and hence valuable social partners. Among Barbary macaques, male-male relationships are more egalitarian than those of females with either males or other females (Preuschoft *et al.*, 1998). Preuschoft *et al.* (1998) hypothesized that relative male-male egalitarianism in Barbary macaques is the result of standoffs between highly competitive males that bear powerful weapons and that benefit by avoiding conflict with one another. Male Tibetan macaques also appear to engage more frequently and in a wider range of conflict management patterns with one another than other partner combinations. In addition to reconciling, males engage frequently in a number of ritualized affiliative interactions with one another, including bridging, that reduce tension, facilitate friendly interaction, and prevent aggression (Deng, 1993; Ionica, 2005; Ogawa, 1995).

Ogawa (1995) described a number of parallels between the forms and functions of bridging in Tibetan macaques and triadic interactions in Barbary macaques, and suggested that both may be associated with nearly even sex ratios. The mean adult male/female ratio in Yulingkeng A1 from 1985 to 1992 was 0.94 (Wada and Xiong, 1996), and 0.58–0.82 during the study. The ratios are among the highest in macaques (Caldecott, 1986). Ogawa (1995) hypothesized that nearly even adult sex ratios lead to both high levels of male-male competition and enhanced mechanisms to cope with potential and actual conflict. Nearly even sex ratios and high tolerance among males also co-occur among *Macaca radiata*, *M. assamensis*, and *M. fuscata yakui* (Cooper and Bernstein, 2002; Hill, 1994; Majolo *et al.*, 2005; Silk, 1994). Preuschoft and Paul (2000) predicted that nearly even sex ratios and the high levels of male-male competition they engender lead to tolerance and active conflict management patterns when 1) there is a substantial scramble component to competition, 2) high-ranking males require the aid of lower-ranking males to achieve high mating success, or 3) individual differences in male resource-holding power are small. In the last case, the possession of dangerous weapons, e.g., canine teeth, could lead to stalemates in which males ignore challenges from one another to avoid direct conflict.

Though more data are needed, we suggest that Tibetan macaque males display indications of both contest and scramble competition with one another that might account for the display of a diversity of conflict management patterns, including moderate conciliatory tendencies, alongside highly asymmetric patterns of aggression. One indirect indication that males engage in mating contest competition is their high degree of sexual dimorphism in size (Zhao, 1994a). In addition, the 2 or 3 highest ranking males mate and form consortships more frequently than lower-ranking males, which are rarely able to complete matings in their presence (Li, 1999; Zhao, 1993). Zhao (1996) explicitly linked contest competition between males to sex ratios; at Mt. Emei, Tibetan macaque groups displayed a range of sex ratios, and low-ranking males mated within view of α males only in groups with relatively low male/female ratios.

Despite evidence of contest competition, Tibetan males also exhibit a substantial scramble component in male-male competition for mating, perhaps associated with female reproductive patterns. Tibetan macaques are seasonal breeders, concentrating complete matings in the second half of the year (Li *et al.*, 2005; Zhao, 1994b). Though we do not know whether female cycles are well synchronized, females display few visible or behavioral signs pinpointing probable days of ovulation, and some mate more or less continuously throughout the peak of the mating season (Li *et al.*, 2005). Thus it may be difficult for high-ranking males to confine their mating effort to females when they are most likely to conceive (*cf.* van Schaik *et al.*, 2000). The highest-ranking males may then use a mixed mating strategy, attempting to mate opportunistically with receptive females even during consortships with other sexually active females. Lower-ranking males primarily scramble, pursuing opportunistic matings out of their sight (Li, 1999). Other indications that scramble competition is substantial in Yulingkeng A1 are that males have proportionally large testicles (de Waal, 2001) and are single-mount ejaculators (Xiong and Wang, 1991), though multiple-mount ejaculation occurs at Mt. Emei (Zhao, 1996). Large testicles and single-mount ejaculation are hypothesized to be related to high levels of sperm competition, a form of scramble competition, among a variety of primate species (Harcourt, 1997).

Finally, there is evidence that high-ranking males rely on each other to maintain their ranks and to garner high mating success (Li, 1999). The α males have short tenures (mean = 10.4 mo) and most changes take place just before or in the early part of the mating season (Li and Wang, 1996). Often, they are replaced by young natal adult males that rise rapidly from their previous low ranks as subadults. Between rank changes, the α male, β male, and, to a lesser extent, γ male (often an older former α male) display unusually low levels of agonistic interaction, and high levels of tolerance, ritualized affiliation, and agonistic support for one another against lower-ranking males. In Yulingkeng A1, these dyads appeared to be so adept at avoiding conflict that we could not collect enough PC-MC samples on them to compare their conciliatory tendencies reliably to those of other dyads. During the mating season, the β male, and to a lesser extent the γ male, are the only males able to mate regularly in the presence of the α male. Though further data are needed, these observations suggest that high-ranking males cooperate in the midst of intense competition from other males, particularly young adults, to garner a large proportion of the matings within the group. Though males possess formidable canines and also actively avoid conflict with one another (Ionica, 2005), at this point we have no evidence that male-male interaction in general represents a stalemate; individual differences in size and strength were clear to observers, male-male dyads were no more likely to ignore challenges than other sex combinations were, and subordinates responded to most challenges with fearful or submissive behavior (Berman *et al.*, 2004).

ACKNOWLEDGMENTS

We thank the Huangshan Monkey Management Center and the Huangshan Garden Forest Bureau for permission to carry out research at Mt. Huangshan. We received financial support from the Leakey Foundation, the Wenner-Gren Foundation, the National Geographic Society, National Natural Science Foundation of China, Key Teacher Program of the Ministry of Education of China, and the Excellent Youth Foundation of Anhui. We thank May Lee Gong, Krista Jones, Stephan Menu, Stephanie Pieddesaux, Justin Sloan, and Lei Zhang for field assistance. We also thank Lei Zhang and Akie Yanagi for translating Chinese and Japanese works into English. We benefited greatly from discussions with Hideshi Ogawa and from comments of 2 anonymous reviewers. Finally, we give special thanks to Xinming Chen and his family for taking us into their home and making us feel so welcome in China.

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