

## **Dominance Style Among *Macaca thibetana* on Mt. Huangshan, China**

**Carol M. Berman,<sup>1,3</sup> Consuel S. Ionica,<sup>1</sup> and Jinhua Li<sup>2</sup>**

*Received February 9, 2004; accepted March 1, 2004*

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*The dominance style concept has proven useful for understanding covariation patterns in relationship qualities, particularly among macaques. However, the dominance styles of many macaques, including Tibetan macaques (*Macaca thibetana*), have not been examined in detail. We describe patterns of bidirectionality of aggression, postconflict affiliation and kin bias in a group of wild, but provisioned Tibetan macaques over a 2-yr period in order make an initial assessment of their dominance style. Bidirectional aggression, including percentage of counteraggression (1.9%), and conciliatory tendencies (6.4%) were consistently low across partner combinations, seasons and locations (forest vs. provisioning area). In addition, females consistently displayed high levels of kin bias in affiliation and tolerance. Compared with macaque species with better known dominance styles, the Tibetan data generally fell within the range for despotic species and outside the range for relaxed species. Although other researchers have tentatively classified them as tolerant or relaxed, we conclude that Tibetan macaques display a despotic dominance style. This conclusion poses complications to explanations based both on phylogenetic inertia and socio-ecological models.*

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**KEY WORDS:** *Macaca thibetana*; dominance style; kin bias; reconciliation; aggression.

<sup>1</sup>Department of Anthropology, State University of New York, Buffalo, New York 14261.

<sup>2</sup>School of Life Sciences, Anhui University, Hefei, Anhui Province, People's Republic of China.

<sup>3</sup>To whom correspondence should be addressed; e-mail: cberman@buffalo.edu.

## INTRODUCTION

A major challenge facing primate behavior today is to explain how and why social systems vary so widely from species to species. Even when species have similar group compositions and associative patterns, species vary in the nature of social relationships among group members. Macaques offer a good example. Macaques typically live in groups with multiple females and males, female philopatry, male dispersal and linear dominance hierarchies. However, individual macaque species vary in several ways, including the extent to which dominant individuals consistently enforce their status and the ways in which they manage conflict. Interestingly, the variation is not random. Researchers have documented the tendency for many aspects of social behavior, particularly aggression patterns, to covary with one another among macaque species (Thierry, 2000). De Waal (1989) coined the term dominance style to describe the covariation. According to the dominance style concept, despotic macaque species are at one end of a continuum, or graded series (Thierry, 2000) and tolerant or relaxed species are at the other end. Among despotic species, dominant individuals show intense and highly asymmetrical patterns of aggression, display little tolerance around resources, and reconcile infrequently, whereas relaxed or tolerant species show opposite tendencies. On a broader level, dominance style is associated with other aspects of social structure. Relatively relaxed species show low or moderate levels of kin bias in affiliative, tolerant and supportive interactions, strong group cohesion, and maternal tolerance for infant handling by other group members.

There are several models to explain variations in dominance style, the best known being the socio-ecological model (Sterck *et al.*, 1997), in which despotic societies are the result of intragroup competition for monopolizable resources. They represent adaptations by individuals, particularly females and their kin, to improve their access to resources. However, relaxed societies occur when groups rely on collective efforts to prevent predation or when group females cooperate to compete with conspecific groups for resources. In contrast, various epigenetic models view differences in dominance style as emergent properties of self-organizing social systems (Hemelrijk, 1999; Thierry, 1990a). Differences between despotic and relaxed societies are driven by species-specific variations in nepotistic tendencies or intensities of aggression, and each strategy may represent an evolutionary stable strategy (ESS), making it somewhat independent of current ecological conditions (Matsumura and Kobayashi, 1998).

The terms relaxed, tolerant and egalitarian are sometimes used interchangeably. We use relaxed or tolerant to avoid confusion with use of

egalitarian by Sterck *et al.*'s (1997) for species that have low levels of intra-group competition and lack decided dominance relationships.

It has been difficult to test the ecological basis of dominance style in macaques because researchers lack much of the necessary relevant ecological data on wild populations. Available data are inconsistent. For example, evidence of strong intergroup competition involving female aggression occurs in both despotic and relaxed macaques, and does not characterize all relaxed macaques (Cheney, 1992; Okamoto and Matsumura, 2002). Conversely, Matsumura (1999) used indirect evidence of strong phylogenetic inertia to bolster the ESS argument and the epigenetic model in turn. Of the macaque species studied in detail, those of the *fascicularis* lineage (Delson, 1980; Fooden, 1980) are all despotic, while species in the other 3 lineages appear to be more relaxed with 2 exceptions: pigtailed macaques (*Macaca nemestrina*: Castles *et al.*, 1996; Judge, 1991) and Assamese macaques (*M. assamensis*: Cooper and Bernstein, 2002). However, only about half of the species from the 3 other lineages, have been studied in enough detail to make more than tentative judgments (Thierry, 2000).

We describe several measures related to dominance style in wild Tibetan macaques (*Macaca thibetana*), one of the understudied species from the *sinica* lineage (Delson, 1980; Fooden, 1980). Tibetan monkeys show social characteristics typical of better-studied macaques: female philopatry, male dispersal and linear dominance hierarchies (Li *et al.*, 1996a; Li and Wang, 1996; Zhao, 1996). However, no research had been done specifically on dominance style or its hypothesized covariates. Thus, we aim to make an initial assessment of the dominance style of the species by examining patterns of bidirectionality of aggression, conciliatory tendencies, and kin bias in affiliation and tolerance. Where possible, we also compare our results to those published for macaques with better known dominance styles.

We originally hypothesized that Tibetan monkeys would show a relaxed dominance style. First, previous studies (Deng, 1993; Ogawa, 1995) document a few behavioral indicators of relaxed dominance. For example, males frequently engage in ritualized greetings in which they mount, embrace or touch each other's genitalia. In addition, both sexes engage in frequent bridging, i.e., ritualistic triadic interactions, with infants whose mothers appear to be tolerant of infant handling by a wide range of group members. Second, as members of the *sinica* lineage, a relaxed dominance style is predicted on phylogenetic grounds (Matsumura, 1999; Thierry, 2000). Hence we predicted that, compared with macaque species with better studied dominance styles, we would find relatively high rates of bidirectional aggression, including counteraggression, high rates of reconciliation, and low levels of kin bias in reconciliation, affiliation and tolerance.

## METHODS

### Study Species and Site

We conducted the study between August 1, 2000 and July 25, 2002, at Mt. Huangshan, Anhui Province, China. Mt. Huangshan (118.3E, 30.2N, elevation 1841 m) is a scenic area and tourist destination in east-central China that contains no large predators. It consists of steep, sparsely treed peaks at high elevations and mixed deciduous and evergreen forests in the middle and lower elevations. The forested areas are home to several groups of Tibetan macaques that maintain apparently nonoverlapping home ranges and feed on a variety of plant species (Wada *et al.*, 1987). The population has been protected from hunting and trapping since the 1940's.

Tibetan macaques are most closely related genetically to Assamese macaques (Hoelzer and Melnick, 1996), although they resemble stump-tailed macaques (*Macaca arctoides*) closely in appearance (de Waal, 2001). Ecologically and demographically, they resemble Barbary macaques (*Macaca sylvanus*); 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 and large proportions of natal adult males.

Our study group, Yulingkeng A1 had been monitored by Chinese researchers since 1986. As a result, we knew individual identities and maternal kinship relationships of the adults. In 1992, the local government drove the group about 1 km from its natural range to an unoccupied area where it could be viewed easily by tourists (Berman and Li, 2002). Wardens provisioned the group daily in the new area and restricted their movement away from the artificial feeding area. Thus the group range decreased from *ca.* 7.75 km<sup>2</sup> to <3.0 km<sup>2</sup> (Li *et al.*, 1996b).

At the beginning of our study, the group consisted of *ca.* 52 individuals (Table I). During summer 2001, the group fissioned; the smaller group left the area and some juveniles disappeared, reducing the remaining group to 37. By the end of the study it totaled 35 individuals. During 2000 and 2001, the monkeys received corn 3–4 times a day on a set schedule in an open area by a stream where they could be viewed by tourists for 30–60 min. When not being fed, they spent most time in the forest. However, during 2002, they were often prevented from returning to the forest between feedings.

### Data Collection

Ionica collected most of the data. Berman and several assistants also contributed data. Each observer achieved levels of interobserver reliability

**Table I.** Group composition at the beginning of each data analytic period<sup>a</sup>

	August 1, 2000– January 28, 2001 <sup>b</sup>	February 27, 2001– May 29, 2001 <sup>b</sup>	December 9, 2001– July 25, 2002 <sup>c</sup>
Adult males ( $\geq 8$ yrs)	7	8	8
Adult females ( $\geq 6$ yrs)	12	13	11 <sup>d</sup>
Subadult males (7 yrs)	2	1	1
Subadult females (5 yrs)	1	3	1
Juvenile males (2–6 yrs)	12	13	5
Juvenile females (2–4 yrs)	7	5	2
Yearling males (1 yr)	2	5	4
Yearling females (1 yr)	2	1	1
Infant males (<1 yr)	6	1	3
Infant females (<1 yr)	1	4 <sup>e</sup>	1
Total	52	54	37

<sup>a</sup>Total data collection period was 8/1/2000 to 7/25/2002.

<sup>b</sup>Numbers of juveniles and yearlings are approximate until 9/30/2001 when we were able to mark them.

<sup>c</sup>The group fissioned and the smaller fission product left the area between the second and third data collection periods.

<sup>d</sup>Data for one adult female that disappeared 2 days after this period began were not analyzed.

<sup>e</sup>This number includes one infant whose sex is unknown.

with Ionica of  $\geq 85\%$ , as determined by the Kappa coefficient (Cohen, 1960). We began by using Psion handheld computers and Noldus Observer 3.0 software to record the data, but by December 2000, we found that we got more accurate data using tape recorders. We transcribed the tapes into files that were compatible with Noldus Observer 3.0 tabulation software. We used both the software and visual basic programs written by Ionica to tabulate the data.

We used focal-animal sampling (Altmann, 1974) to record affiliative, tolerant, and aggressive interaction between all group members that were adults (males:  $\geq 8$  yr, females:  $\geq 6$  yr) or subadults (males: 7 yr, females: 5 yr) at the beginning of the study, for a total of 13 females and 11 males. In March 2001, we began to observe an additional subadult male (HH) replacing an adult male (GS) that left the group. During the summer of 2001, one male (PN) immigrated into the group, and 2 adult males (ZM and HZ) and 2 adult females (HU and HR) left with the smaller fission product. Finally, one adult female died in December 2001. Definitions of the behaviors we analyzed are in Table II. Details on all subjects are in Table III.

We observed each focal subject for  $\geq 2$  15-min sessions per week, one in the provisioning area and one in the surrounding forest. We recorded the identities of the interactors and the directions of interaction chronologically, along with the time of occurrence. At the beginning of each focal-animal session, and at 3-min intervals throughout the session, we also recorded the main activity of the focal subject and the identities of all adults

**Table II.** Behavioral definitions and measures

## Measures of proximity, affiliation and tolerance:

1. *% Time within 5 m*: Percentage of point time samples in which a focal subject was  $\leq 5$  m of another individual.
2. *Grooming bout rate*: Frequency per h that a focal subject initiated or received a bout of grooming (oral or manual manipulation of fur) from another individual.
3. *Approach rate*: Frequency per h that a focal subject came from beyond to  $\leq 1$  m of another individual, or vice versa.
4. *Sit near bout rate*: Frequency per h that a focal subject sat down or lay down  $\leq 1$  m of another individual, or vice versa. The partners could have been in physical contact but not in any other kind of affiliative or tolerant interaction, e.g., grooming, play, cofeeding.
5. *Cofeeding bout rate*: Frequency per h that a focal subject and another individual begin to feed  $\leq 1$  m of one another.

## Criterion affiliative interaction used in PC-MC analysis:

1. *Lipsmack*: Slightly puckered lips are rapidly opened and closed, sometimes producing and smacking sound.
2. *Teeth-chattering*: 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 one 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 or her rump to another.
6. *Social mount*: One individual approaches 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 lick the infant's genitals or body while teeth-chattering vigorously (Ogawa, 1995).
12. *Hold bottom*: One individual approaches another and holds or embraces his or her rump for a few sec.

## Submissive or fearful interaction:

1. *Fear grin or silent bared-teeth display*: A grimace in which the corners of the mouth and lips are laterally retracted, the jaws are partly open and the teeth are visible (Preuschoft and van Hooff, 1995). No vocalization, lip-smacking or teeth-chattering is included.
2. *Cower*: A lateral flexion of the spine away from another individual.
3. *Mock leave*: One individual turns his or her body away from the receiver, as if preparing to leave, while displaying a horrified facial expression: jaws partly open, and lips partly retracted forming a square opening.
4. *Avoid*: One individual moves out of the way from another, either walking or running, but remains  $\leq 5$  m. This differs from a displacement in that the other individual need not approach the performer.
5. *Displace*: One individual immediately withdraws from the approach of another. The approacher takes the exact place of the displaced individual.

**Table II.** Continued

- 6. *Grooming displace*: An individual that is grooming another stops grooming and yields to a third individual that takes over grooming the same individual. The displaced individual does not necessary leave.
- 7. *Flee*: One individual runs from another at a moderate or fast pace to a position  $\geq 5$  m away.
- 8. *Scream*: A high pitched vocalization, often accompanied by grimacing and soliciting for support.

Aggressive interaction:

- 1. *Threat*: An individual directs an open mouth threat gesture or any of its components, e.g., stare, raised eyebrows, lowered jaw, ground slap, to another individual.
- 2. *Short lunge*: An individual directs a lunge  $< 2$  body lengths to another individual.
- 3. *Long lunge*: An individual directs a lunge  $> 2$  body lengths to another individual but does not go into a full chase.
- 4. *Chase*: An individual runs rapidly after another individual.
- 5. *Slow grab*: An individual seizes another individual slowly and holds while staring.
- 6. *Slap*: An individual slaps or hits another individual.
- 7. *Grab*: An individual roughly and quickly seizes another individual and holds for at least a few sec.
- 8. *Bite*: An individual grabs and bites hard, either releasing the victim quickly or hanging on for several sec. Soft bites occurred in the context of embracing or play and were not counted as aggression.

and subadults  $\leq 1$  m and between 1 and 5 m of the focal individual. We recorded a total of 1200 h of focal-animal data (median = 59.10 h per subject, interquartile range = 42.5–60.6) over the 2 yr period.

In order to examine conciliatory tendencies, we also recorded 5-min postconflict (PC) samples and matched control (MC) samples (De Waal

**Table III.** Focal subjects: Name, sex, age at beginning of the study, and mother’s identity

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

<sup>a</sup>The mother was not in the group during the study.

<sup>b</sup>Immigrant to the group; age and mother were unknown, but appeared fully adult.

and Yoshihara, 1983). PC sessions were initiated when moderate (long lunge, chase, slap, hit, grab) or intense (bite) aggression occurred either during or between focal-animal sessions. The PC session began as soon as aggression ceased between the 2 opponents. If aggression reoccurred within the first 2 min of the PC, the session was aborted and restarted immediately after aggression ceased again. During the PC, we followed the target (rather than the attacker) of the aggression, when possible. During the PC, we recorded all aggressive, tolerant, supportive and affiliative interaction involving the focal subject, along with the identities of the partners, the directions of interaction and the time of occurrence.

We recorded an MC sample on the same focal subject using the same procedure as during the PC on the next possible observation day, provided the 2 opponents were  $\leq 10$  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). We could not match times of day because we could not reliably locate individuals at predetermined times. We recorded a total of 574 PC-MC pairs meeting our criteria. The median number of days between PC's and MC's was 3.0 (interquartile range = 1–7, range = 1–30).

### Data Analysis

Typically for the species (Li and Wang, 1996; Ogawa, 1999; Zhao, 1996), there were several rank changes among both males and females over the course of the study. In addition, rank relationships were unstable during the summer and fall of 2001 when the group fissioned. To avoid exaggerating rates of bidirectionality of aggression that occur when rank reversals take place, we restricted our analyses of it to focal data collected during 3 sustained time periods when dominance relationships, inferred from the direction of submissive interactions between pairs of individuals, were linear and stable: 1) August 1, 2000, to January 28, 2001; 2) February 27, 2001, to May 29, 2001, and; 3) December 9, 2001, to July 25, 2002. The first period took place primarily during the 2000 mating season (August 2000–January 2001), whereas the second and third periods took place primarily during the 2001 (January 2001–August 2001) and 2002 (November 2001–June 2002) birth seasons. When possible, we further restricted our analyses of kin bias to the first period and excluded data collected after the birth of the first infant on January 10, 2001. This allowed us to examine kin bias while both controlling for variations in rank distance and avoiding possible distortions caused by the presence of attractive newborn infants (Hinde and Proctor, 1977). For all analyses, we examined interactions in the forest and in the provisioning area separately whenever possible.



We constructed dominance hierarchies (Appendix) from the directions of all submissive interaction between subjects during each stable period using Matman 1.0 (Noldus Information Technology, 1998). We calculated the linearity index  $h'$ , an index based on Landau's index but corrected for unknown relationships (De Vries, 1995). To describe the extent to which submissive interaction was asymmetric within dyads, we calculated the directional inconsistency index (DII) as the percentage of all submissive interactions that were directed in the less frequent direction within dyads (de Waal, 1977; modified from Rowell, 1966). We also examined the direction and asymmetry of one interaction alone—the silent bared-teeth display—because it is directed almost exclusively from subordinates to dominants in despotic macaques, but is bidirectional in some relaxed macaques (Preuschoft and van Hooff, 1995; Thierry *et al.*, 1989).

We used 3 indices to calculate the degree to which aggression is bidirectional: 1) the directional inconsistency index applied to aggressive interaction: the percentage of total aggressive interactions that were directed in the less frequent direction within dyads, 2) the dyads-up index: the percentage of dyads for which the main direction of aggression was up the dominance hierarchy; and, 3) the percentage of counter-aggression: the percentage of instances of aggression of any kind to which the target responded with aggression of any kind. For the last index, we included cases in which the response was aggressive, fearful, avoidant, affiliative or redirected, but not ones in which the target apparently ignored or did not notice the aggressive act. For all 3 indices, aggressive interaction included all forms from mild threats to intense biting (Table II).

To examine postconflict affiliation, we defined attracted, dispersed and neutral PC-MC pairs per de Waal and Yoshihara (1983). We determined whether the monkeys reconciled by comparing 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 PC and in its matching MC, via Wilcoxon-matched pairs signed ranks tests. We calculated the extent to which they reconciled using Veenema *et al.*'s (1994) conciliatory index: the number of attracted pairs minus the number of dispersed pairs over the total number of pairs. We ascertained whether the results were due to only a few individuals using Sign tests that compare numbers of attracted and dispersed PC-MC pairs at an individual level. A more complete examination of postconflict interaction is in Berman *et al.* (manuscript in preparation).

We used partial Kr tests (Hemelrijk, 1990) with 2000 permutations to detect significant kin preferences in rates of proximity, affiliation (grooming, approaching, sitting  $\leq 1$  m) and tolerance (cofeeding  $\leq 1$  m). Because maternal degrees of relatedness among females are correlated with rank

distances (Kendall's tau =  $-0.52$ ,  $n = 13$ ,  $p = 0.0005$ ), we controlled for the possible effects of rank distance. The partial Kr test is a row-wise, distribution-free matrix permutation correlation technique based on the Kendall correlation test that uses data in all cells of a social interaction matrix, i.e., from all pairs of animals in a matrix, while avoiding problems of their interdependence. We classified kin by degree of relatedness through maternal lines—mother-offspring: 0.50; grandmothers, grand-offspring, half siblings: 0.25; aunts, uncles, nephews and nieces: 0.125; first cousins, great aunts, great uncles, great nieces, great nephews: 0.063. Since males of the species typically delay dispersing from natal groups until they are young adults, we could test for kin bias among both males and females (same-sex pairs) and between males and female (opposite-sex pairs). To detect significant kin preferences in reconciliation, we compared the proportions of PC samples in which affiliation did and did not take place within the first min for close kin ( $r \geq 0.25$ ) and others ( $r < 0.25$ ), using two-sample Chi-square tests. We used the 1-min time window as an operational criterion for reconciliation in individual conflicts, based on results of a time-rule analysis (*cf.* Aureli *et al.*, 1989) of all PC-MC pairs. Rates of affiliative interaction in the PC exceeded those in the MC during this time window but not beyond it (Berman *et al.*, manuscript in preparation). Accordingly, we considered conflicts in which the opponents engaged in affiliation within 1 min reconciled, whereas all others were unreconciled. All statistical tests are two-tailed, and we considered probabilities  $\leq 0.05$  to be significant.

When possible, we compared our results to those in published studies of macaques with better known dominance styles. To facilitate comparison, we limited them to published studies of well-established groups that had similar data collection methods, behavioral measures, partner combinations and definitions of kin. Major exceptions are noted. We confined our comparisons of the intensity of kin bias to published data collected outside the birth season. Since females in large groups tend to display more intense kin bias than ones in small groups (Berman *et al.*, 1997), we used published data from macaque groups with roughly the same number of adult females ( $13 \pm 5$ ) as the Tibetan group. When comparing conciliatory tendencies, we only used the corrected measure of Veenema *et al.* (1994). In some cases, we calculated conciliatory tendencies and kin bias intensities from raw published data. Because the details of methodology inevitably varied to some extent among the studies and because we were not able to match all the conditions of our study with those in others, we did not attempt to make statistical comparisons. Instead, we asked more generally whether the data for Tibetan macaques fall within the range of values for relaxed or despotic macaque species.

RESULTS

Submissive Interaction

We recorded a total of 3250 submissive or fearful interactions via focal-animal sampling during the 3 analytic periods. The dominance hierarchies constructed from them (Appendix) were significantly linear during each period (Table IVa). This was the case for both single-sex and mixed-sex hierarchies and for interaction in the forest and at the provisioning area. Although the highest ranks were held by adult males, some adult females outranked some adult males. With one exception (HH), adults outranked subadults. In 2 of 5 (40%) mother-daughter dyads, daughters outranked their mothers: FT and FM in all time periods, and TT and TG in the second and third time periods. In both cases, the mothers were past prime age  $\geq 15$  when the reversal occurred. In 13 of 28 (46%) cases, older sisters outranked younger adult sisters.

Of the 3250 interactions, only 55 (DII = 1.7%) were directed in the less common direction within dyads, suggesting highly asymmetric patterns of submission (Table IVb). The direction and asymmetry of silent bared-teeth displays, when examined alone, were almost always (514 of 519, or 99% the same direction as other fearful and submissive interactions, and they were at least as asymmetrically distributed within dyads as all fearful and submissive interactions combined (DII =  $3/519 = 0.6\%$  overall data periods and partner combinations, and 1.9%, 0.6% and 0% in the first, second and third data analysis periods, respectively).

**Table IV.** Landau’s modified index of linearity ( $h'$ ) and the directional inconsistency index (DII) for dominance hierarchies based on submissive and fearful interactions

	8/1/00–1/28/01	2/27/01–5/29/01	12/9/01–7/25/02
<b>A. Landau’s Modified Index</b>			
All partner combinations	0.69****	0.64****	0.77****
Male–male dyads	0.69*	0.65*	0.90**
Female–female dyads	0.79****	0.76****	0.90****
Forest	0.27**	0.23*	0.46****
Provisioning area	0.60****	0.58****	0.74****
<b>B. Directional Inconsistency Index</b>			
All partner combinations	20/858 (2.3%)	13/871 (1.5%)	22/1521 (1.4%)
Male–male dyads	2/122 (1.6%)	2/89 (2.2%)	2/189 (1.1%)
Female–female dyads	11/263 (4.2%)	4/379 (1.1%)	9/428 (2.1%)
Male–female dyads	7/473 (1.5%)	7.403 (1.7%)	7/904 (0.7%)
Forest	1/145 (0.7%)	0.169 (0%)	2/216 (0.9%)
Provisioning area	16/713 (2.2%)	12/709 (1.7%)	18/1305 (1.4%)

\* $p \leq 0.05$ ; \*\* $p \leq 0.01$ ; \*\*\* $p \leq 0.001$ ; \*\*\*\* $p \leq 0.0001$ .

**Table V.** Bi directionality of aggression during each of three data analytic periods

	8/1/00–1/28/01	2/27/01–5/29/01	12/9/01–7/25/02
<b>A Directional Inconsistency Index</b>			
All partner combinations	11/323 (3.4%)	10/314 (3.2%)	17/701 (2.4%)
Male–male dyads	3/583 (5.2%)	2/50 (4.0%)	2/108 (1.9%)
Female–female dyads	6/160 (3.8%)	3/166 (1.8%)	4/243 (1.6%)
Male–female dyads	2/105 (1.9%)	5/98 (5.1%)	11/350 (3.1%)
Forest	0/27 (0.0%)	0/40 (0.0%)	0/69 (0.0%)
Provisioning area	11/296 (3.7%)	10/274 (3.6%)	17/632 (2.7%)
<b>B. Dyads Up Index</b>			
All partner combinations	8/231 (3.5%)	4/231 (1.7%)	1/153 (0.7%)
Male–male dyads	1/36 (2.8%)	2/36 (5.6%)	0/28 (0.0%)
Female–female dyads	3/78 (3.8%)	1/78 (1.3%)	0/45 (0.0%)
Male–female dyads	4/117 (3.4%)	2/117 (1.7%)	1/80 (1.3%)
Forest	0/231 (0.0%)	1/231 (0.4%)	0/153 (0.0%)
Provisioning area	8/231 (3.5%)	4/232 (1.7%)	1/153 (0.7%)
<b>C. Percent Counteraggression</b>			
All partner combinations	3/218 (1.5%)	6/234 (2.6%)	10/528 (1.9%)
Male–male dyads	3/37 (8.1%)	0/33 (0.0%)	0/73 (0.0%)
Female–female dyads	0/97 (0.0%)	4/114 (3.5%)	6/157 (3.8%)
Male–female dyads	0/84 (0.0%)	2/87 (2.3%)	4/298 (1.3%)
Forest	0/14 (0.0%)	0/35 (0.0%)	1/39 (2.6%)
Provisioning area	3/204 (1.5%)	6/199 (3.0%)	9/489 (1.8%)

### Bidirectionality of Aggression

All 3 indices of bidirectionality of aggression suggest that aggression was also highly asymmetric (Table V). We recorded a total of 1338 aggressive interactions using focal-animal sampling during the 3 periods. Thirty-eight (DII = 2.8%) of them were directed in the less common direction within dyads. Low DII's (0–5.2%) were consistent in each period, for each partner combination and in each location (Table Va). Similarly, few dyads directed aggression primarily up the hierarchy (mean = 2.0% of dyads,  $n = 3$  data analytic periods). Since the hierarchies were constructed from submissive interactions, this suggests that partners that displayed submissive behavior to another individual rarely directed aggression towards that individual. Low scores for the dyads-up index (0–5.6%) were also consistent across time periods, partner combinations and locations (Table Vb). Finally, percentages of counteraggression were low; 980 instances of aggression were followed by a clear response from the target. Nineteen (1.9%) of them were followed by aggression from the original target to the original aggressor. Low percentages of counteraggression were consistent (0–8.1%) across time periods, partner combinations and locations (Table Vc).

**Table VI.** Conciliatory tendencies (CI), using Veenema *et al.*'s (1994) formula

	Attracted	Dispersed	Neutral	Total	CI
All partner combinations	73	36	465	574	6.4%***
Male–male dyads	42	12	98	152	19.7%***
Female–female dyads	16	9	140	165	4.2%(*)
Male–female dyads	15	15	227	257	0%
Forest	20	10	47	77	13.0%(*)
Provisioning area	53	26	418	497	5.4%***

\*\*\* $p < 0.001$ ; (\*) $p = 0.08$ , Wilcoxon matched-pairs signed-ranks test.

### Reconciliation

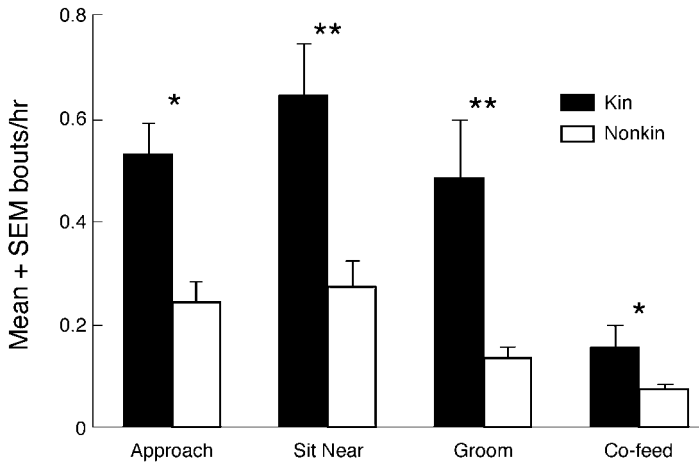
Seventy-three of the 574 PC-MC pairs were attracted, 36 were dispersed and 465 were neutral, yielding a conciliatory index of 37/574 (6.4%) and a significant Wilcoxon test ( $Z = 4.23, p < 0.001$ ). At an individual level, 14 focal subjects had more attracted pairs than dispersed pairs, 3 had fewer, and 6 had equal numbers ( $p = 0.013, n = 23$  individuals, Sign test). Thus overall, opponents engaged in affiliation at higher rates following aggression than at other times. However, when we examined conciliatory tendencies separately for each partner combination, significant results were sustained only for male-male dyads (Table VI). Similarly, at an individual level, male-male dyads had significantly more attracted than dispersed pairs (10 vs. 0 with 1 tie,  $p = 0.002$ , Sign test), but other partner combinations did not (female-female dyads: 7 vs 4 with 2 ties,  $p = 0.55$ ; male-female dyads: 6 vs. 5 with 12 ties,  $p = .99$ , Sign test).

Significant results were sustained for conflicts that took place in the provisioning area, but results for the forest were somewhat inconsistent; although conciliatory tendencies appeared to be greater in the forest than in the provisioning area (13.0% vs. 5.4%), the Wilcoxon test for the forest was no longer significant, perhaps because the sample of PC-MC pairs recorded in the forest was small. Indeed, when we compared the distribution of reconciled (affiliation  $\leq 1$  min) and unreconciled (no affiliation  $\leq 1$  min) conflicts by location, we found that reconciliation was more likely to take place in the forest than in the provisioning area ( $\chi^2 = 15.9, df = 1, n = 574$  conflicts,  $p < 0.001$ ).

### Kin Bias

#### *Proximity, Affiliation and Tolerance*

Figure 1 shows mean rates of affiliative and tolerant interaction of females with close female kin ( $r \geq 0.25$ : mothers, daughters, half sisters,



**Fig. 1.** Affiliative and tolerant interaction with kin and nonkin: mean + SEM bouts per h of approaches, sitting near, grooming and cofeeding between focal females ( $n = 13$ ). \* $p < 0.05$ , \*\* $p < 0.01$ , partial Kr test, controlling for rank distance.

granddaughters and grandmothers) and with other females ( $r < 0.25$ ) during the first data analytic period. Partial Kr correlation matrix tests suggest that females not only spent significantly more time  $\leq 5$  m of close kin but also groomed, sat near, approached and cofed with them more than with nonkin, even when variations in rank distance were controlled (Table VII). Results were similar for analyses of the data over the whole study, without controlling for rank distance. In contrast, males showed few signs of kin bias in any measure of interaction with either females or with other males (Table VII). When we examined female-female interaction separately in the provisioning area and in the forest, results were similar with one exception: there was no kin bias for time spent near one another in

**Table VII.** Kin bias among Tibetan macaques during the mating season: Partial Kr coefficients between interaction rates and degree of relatedness, controlling for rank distance

Partner combination <sup>a</sup>	% Time w/in 5 m	Grooming	Sit near	Approaches	Co-feed
♀-♀	0.16*	0.22**	0.25**	0.24*	0.18*
♂-♂	-0.14	0.13	-0.17(*)	-0.17	-0.14
♂-♀	0.01	-0.04	-0.13(*)	-0.05	-0.02
♀-♂	-0.08	-0.02	-0.14	-0.11	-0.10

<sup>a</sup>The first symbol represents the sex of the focal subject, and the second symbol represents the sex of the partner, e.g., ♀-♂ represents interaction between focal females and their male interactors.

(\*)  $p < 0.1$ ; \* $p \leq 0.05$ ; \*\* $p \leq 0.01$ .

**Table VIII.** Kin bias among female Tibetan macaques during the mating season by location and per unit of time spent  $\leq 5$  m: Partial Kr coefficients between interaction rates and degree of relatedness, controlling for rank distance

	% Time w/in 5 m	Grooming	Sit near	Approaches	Co-feed
Provisioning	0.09	0.26***	0.23*	0.25*	0.18*
Forest	0.15*	0.15*	0.22**	0.22**	— <sup>a</sup>
Per hr spent $\leq 5$ m	—	0.21**	0.28***	0.19*	0.12(*)

<sup>a</sup>Rates of co-feeding in the forest were too low for analysis.

(\*) $p = 0.09$ ; \* $p \leq 0.05$ ; \*\* $p \leq 0.01$ ; \*\*\* $p \leq 0.001$ .

the provisioning area (Table VIII). The results were also similar when we examined rates of affiliation and tolerance per hour of time that each pair of females spent  $\leq 5$  m of each other (Table VIII), although they fell short of significance for cofeeding. Overall, the results suggest that females (but not males) were actively attracted to kin and did not randomly interact with individuals nearby.

### Conciliatory Tendencies

Unfortunately sample sizes did not permit us to restrict our analyses of kin bias in conciliatory tendencies to the mating period. When all partner combinations over the whole study were considered, conciliatory tendencies (CT) calculated separately for kin and nonkin were both significant (kin: CT = 10.3%,  $n = 87$  PC-MC pairs,  $p = 0.021$ , Wilcoxon test; nonkin: CT = 5.7%,  $n = 487$  PC-MC pairs,  $p < 0.001$ , Wilcoxon test), and distributions of reconciled conflicts differed significantly between kin and nonkin ( $\chi^2 = 5.0$ ,  $df = 1$ ,  $n = 574$  conflicts,  $p = 0.025$ ), suggesting that kin were more likely to reconcile than nonkin. However, the results were not sustained when we examined each partner combination separately. Among male-male pairs, kin and nonkin had similarly significant conciliatory tendencies (kin vs. nonkin = 20.0% vs. 19.6%) and similar distributions of reconciled and unreconciled conflicts ( $\chi^2 = 1.5$ ,  $df = 1$ ,  $n = 152$  conflicts,  $p = 0.21$ ). Female-female pairs had nonsignificant conciliatory tendencies for kin vs. nonkin of 4.8% vs. 4.1%, respectively, and similar distributions of reconciled and unreconciled conflicts ( $p = 0.35$ ,  $n = 165$  conflicts, Fisher’s exact test). Finally, for mixed-sex pairs, conciliatory tendencies for kin vs. nonkin were both 0, and distributions of reconciled and unreconciled conflicts were similar ( $p = 1.0$ ,  $n = 257$  conflicts, Fisher’s exact test).

### Intensity of Kin Bias

Given that females affiliated with female kin more than with unrelated females, we next examined the intensity of their kin preferences. Do

females show strong preferences for kin typical of despotic macaques or only moderate preferences typical of relaxed macaques? To facilitate comparisons with other species, we measured the intensity of kin bias as the ratio of observed to expected grooming between kin. Expected amounts were based on the null hypothesis that grooming bouts were distributed evenly among females. Thus we calculated the expected amount of grooming as the total number of grooming bouts given and received by a female during her focal sessions multiplied by the proportion of females in the group that were related by  $\geq 0.25$ . The mean  $\pm$  SE ratio of observed to expected grooming bouts was  $2.7 \pm 0.7$  ( $n = 13$  females), indicating that females groomed their close kin nearly 3 times more than expected by chance.

### Comparisons with Other Macaques

#### *Bidirectionality of Aggression*

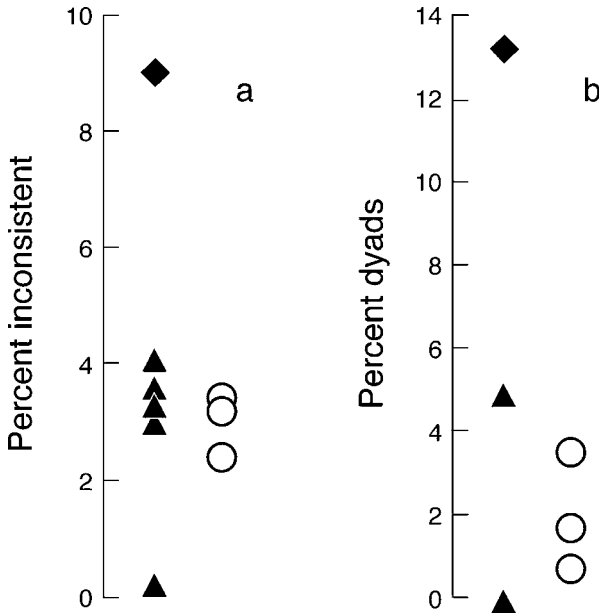
Most comparable published data for the directional inconsistency index and for the dyads-up index are for all adult partner combinations together. In Fig. 2a, we compare these data for the DII with data from each of our data analytic periods. Five published values, ranging from 0.7% to 4.1%, are available for 3 species typically classified as despotic: rhesus, long-tailed and Japanese macaques. One value (9.0%) is available for stumptailed macaques, a species typically classified as relatively relaxed. All 3 data points for Tibetan macaques fall within the range for the despotic macaques, and are considerably lower than the one for stumptailed macaques. Similarly, all 3 data points for Tibetan macaques for the dyads-up index fall within the range for despotic rhesus (4.9%) and long-tailed (0%) macaques and considerably below the value for stumptailed macaques (13.2%; Figure 2b).

Most comparable published data for percentage of counteraggression are for unrelated dyads and separate partner combinations (Fig. 3). For each partner combination, values for 3 despotic macaque species (rhesus, long-tailed and two for Japanese) are below those for 2 relaxed species (Tonkean and black crested Macaques) and values for Tibetan macaques are within or below the range of values for the despotic species.

#### *Reconciliation*

Two sets of comparable published data are available for conciliatory tendencies: 1) all partner combinations and degrees of relatedness combined; and 2) unrelated female-female partners. With one exception—unrelated pigtailed macaque females—the values for despotic species are less than the values for relaxed species (Fig. 4). In both sets of data,



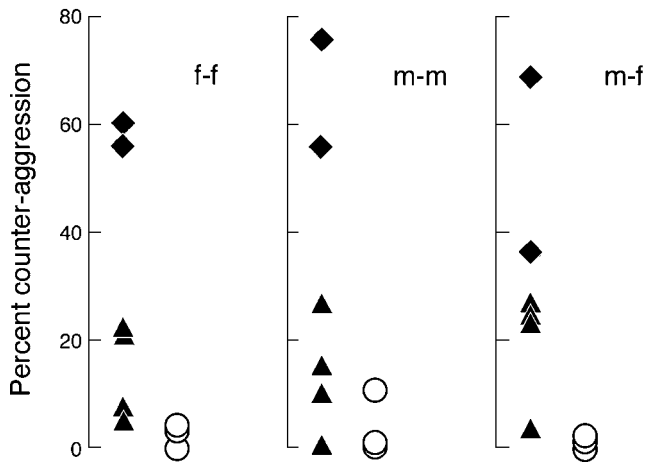


**Fig. 2.** Bidirectionality of aggression: All partner combinations are shown together. Data for Tibetan macaques (circles) from each data analytic period are compared with published data for despotic macaques (triangles) and relaxed macaques (diamonds). A) directional inconsistency index; published data for highest to lowest values are from: stumptailed (de Waal and Luttrell, 1989), long-tailed (de Waal, 1977), rhesus (De Waal and Luttrell, 1985), Japanese (Chaffin *et al.*, 1995), rhesus (de Waal and Luttrell, 1989), long-tailed (de Waal, 1977). B) Dyads up index (percentage of dyads in which the primary direction of aggression is up the hierarchy); published data for highest to lowest values are from: stumptailed (de Waal and Luttrell, 1989), rhesus (de Waal and Luttrell, 1989), long-tailed (de Waal, 1977).

conciliatory tendencies for Tibetan macaques are relatively low even compared to values for despotic macaques. Unfortunately, there is only one study with comparable data for male-male partners, the partner combination with the highest conciliatory tendencies among the Tibetan macaques. Petit *et al.* (1997) found a conciliatory tendency among unrelated despotic Japanese males of 30.3%, a higher value than that found for unrelated Tibetan males (19.6%).

*Intensity of Kin Bias*

Ratios of observed to expected amounts of grooming are available for 2 despotic macaque species—rhesus (Sade, 1972) and Japanese macaques



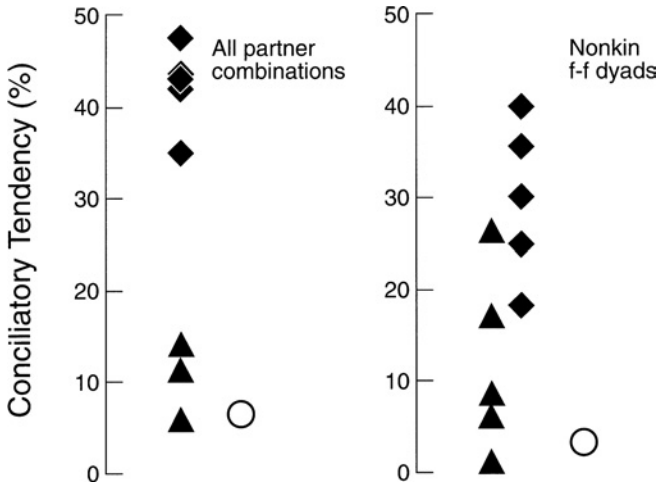
**Fig. 3.** Counteraggression: percentage of aggression to which the unrelated target responds with aggression. Data for Tibetan monkeys (circles) from each data analytic period are compared with published data for despot macaques (triangles) and relaxed macaques (diamonds). F-f: female-female interaction; m-m: male-male interaction; m-f: male-female interaction. For female-female partners, published data for highest to lowest values are from: Tonkeana (Thierry, 1985), black crested (Petit *et al.*, 1997), Japanese (Thierry, 1990b), Japanese (Petit *et al.*, 1997), longtailed (Thierry, 1985), rhesus (Thierry, 1985). For other partner combinations, the order is the same except that the data points for Japanese macaques are reversed. Note: Thierry (1985, 1990b) used behavior-dependent sampling (Altmann, 1974), and Petit *et al.* (1997) used all-occurrence sampling (Altmann, 1974).

(Mehlman and Chapais, 1988)—and for one relaxed macaque species—stumptailed (Butovskaya *et al.*, 1994). The value for Tibetan females (2.7) is similar to those for 2 despotic species—rhesus: 2.6; Japanese macaques: 2.3—and higher than that for relaxed stumptailed macaques (1.3). Sade (1972) used sampling *ad libitum* corrected for observability, and Mehlman and Chapais (1988) used grooming durations rather than grooming bouts.

## DISCUSSION

### Dominance Hierarchies

Like other macaques, adult Tibetan macaques on Mt. Huangshan display strong linear dominance hierarchies based on the directions of submissive interaction. Like Tibetan macaques at Mt. Emei (Deng and Zhao, 1987), males at Mt. Huangshan occupied the top ranks, but females



**Fig. 4.** Conciliatory tendencies: Veenema *et al.* (1994). Data for Tibetan macaques (circles) from each data analytic period are compared with published data for despotic macaques (triangles) and relaxed macaques (diamonds). Left: All partner combinations, kin and nonkin dyads together: published data for highest to lowest values are from: lion-tailed (Abegg *et al.*, 1996), lion-tailed (Abegg *et al.*, 1996), Moor (Matsumura, 1996), lion-tailed (Abegg *et al.*, 1996), stumptailed (Call *et al.*, 1999), Japanese (Kutsukake and Castles, 2001), Assamese (Cooper and Bernstein, 2000), Japanese (Schino *et al.*, 1998). Right: Females with nonkin females: published data for highest to lowest values are from: Tonkeana (Thierry, 1985), lion-tailed (Abegg *et al.*, 1996), stumptailed (Call, 1999), pigtailed (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). Note: Data for Call *et al.* (1999) and Kutsukake and Call (2001) include juveniles, but conciliatory tendencies were unaffected by variations in the ages of partners in these studies. Thierry (1985) used behavior-dependent sampling (Altmann, 1974), and Abegg *et al.* (1996) and Petit *et al.* (1997) used all-occurrence sampling (Altmann, 1974).

outranked some males, particularly older males and subadults. Finally, as in previous studies (Li and Wang, 1996; Ogawa, 1999; Zhao, 1996), we observed several rank changes among both males and females and several exceptions to Kawamura's (1965) principles, e.g., mother-daughter rank reversals and instances of older sisters outranking younger adult sisters.

### Dominance Style

Previous studies tentatively suggested that Tibetan macaques had a relaxed dominance style (Matsumura, 1999; Thierry, 2000) based on reports of frequent ritualistic affiliative interactions among males, the bidirectional

use of the silent bared-teeth display, triadic interactions involving infant handling and tolerant responses to handling by mothers (Deng, 1993; Ogawa, 1995). Accordingly, we predicted that we would find more direct indicators of relaxed dominance style, including high rates of bidirectional aggression and reconciliation, and low levels of kin bias in affiliation, reconciliation and tolerance. However, our results suggest that Tibetan macaques are more despotic than previously suspected. First, all 3 measures of bidirectional aggression occurred at rates similar to typically despotic macaque species and well below those for relaxed macaques. Second, their conciliatory tendencies were low compared with those of other macaque species, even several despotic species. Indeed, significant tendencies to reconcile occurred only among males and not among females or between males and females. Third, females exhibited significant preferences for female kin in proximity relationships, approaching, sitting near, grooming and cofeeding, and the intensity of their grooming preferences, at least in the mating season, was comparable to ones for typically despotic species living in comparably-sized groups. Fourth, the silent bared-teeth display was almost exclusively directed from subordinates to dominants, suggesting that it is a reliable indicator of relative status and is not used by higher-ranking individuals to reassure lower-ranking individuals as it is in some relaxed species (Preuschoft and van Hooff, 1995; Thierry *et al.*, 1989). Previous reports that it is bidirectional may have included instances of teeth-chattering, a bidirectional gesture in which performers typically retract the corners of the mouth in a manner similar to the silent bared-teeth display.

Thus, contrary to our expectations, several direct indicators suggest a despotic dominance style for *Macaca thibetana*. Moreover, the indicators are consistent across partner combinations, time periods—hence reproductive seasons—and locations. The consistency of results indicating a despotic dominance style across locations is particularly noteworthy because it suggests that the results are not due merely to the fact that many interactions in the provisioning area occurred in a feeding context or in proximity to tourists. Several researchers have found reduced conciliatory tendencies in conflicts over food (Aureli, 1992; Castles and Whiten, 1998; Matsumura, 1996; Verbeek and de Waal, 1997), and in harmony with this, we found a higher proportion of reconciled conflicts in the forest, where feeding conflicts were rare, than in the provisioning area. Nevertheless, conciliatory tendencies in the forest (13%) are within the range for despotic species and well below those in relaxed species (Fig. 4a).

The only clear indicator we found that is inconsistent with a despotic dominance style is an apparently weak kin bias in tendencies to reconcile, as indicated by significant results over all conflicts, but not for those of separate partner combinations. As such, this result argues against the necessary covariation of this characteristic with other dominance style

indicators. We also found frequent exceptions to Kawamura's (1965) principles. Although such exceptions are associated more commonly with relaxed than despotic dominance styles (Thierry, 2000), they are not exclusive to them. For example, mother-daughter reversals are common among despotic rhesus and Japanese macaques when mothers are past their primes, as they were in the Tibetan macaque group (Missakian, 1972; Nakamichi, 1984; Nakamichi *et al.*, 1995), and older sisters routinely outrank younger sisters in some wild Japanese macaque groups (Hill and Okayasu, 1995). Because the extent to which groups conform to Kawamura's principles may vary with factors associated not only with dominance style, e.g., resource distribution, intragroup competition, kin bias in alliances, but also reproductive value (Chapais and Schulman, 1980; Combes and Altmann, 2001) and demography (Datta and Beauchamp, 1991), conformity to those principles may be a less useful indicator of dominance style than are bidirectional aggression or conciliatory tendency.

### Possible Explanations

If Tibetan macaques indeed exhibit a despotic dominance style, they represent a complication for explanations based on phylogenetic inertia. Tibetan macaques appear to represent a third exception to the generalization that despotic species are confined to the *fascicularis* lineage of macaques, and the second example of a despotic macaque within the *sinica* lineage. Both captive pigtailed macaques of the *silenus-sylvanus* lineage (Castles *et al.*, 1996; Judge, 1991) and Assamese macaques of the *sinica* lineage (Cooper and Bernstein, 2002) display several characteristics associated with despotism. The extent to which the new exception seriously undermines the phylogenetic hypothesis is uncertain and depends to some extent on the phylogenetic model one uses.

Delson's (1980) reconstruction, based on morphology, places Tibetan and Assamese macaques as sister species with a recent common ancestor. Accordingly, a single reversal of dominance styles from the ancestral relaxed style to a more despotic style in their common ancestor could account for both exceptions in the lineage. In contrast, the model of Hoelzer *et al.* (1992), based on mitochondrial DNA, divides Assamese macaques into 2 subspecies—eastern and western—and only the eastern subspecies is close to Tibetan macaques. The western subspecies, studied by Cooper and Bernstein in India, is hypothesized by Hoelzer & Melnick (1996) to be a remnant population of bonnet macaques (*Macaca radiata*) that subsequently hybridized with Assamese males. Because there are no data on the dominance styles of eastern Assamese macaques, it is difficult to hypothesize about the number of reversals that may have occurred within the lineage.

It is also difficult to evaluate the results from a socioecological perspective. The natural diet of Tibetan macaques relies heavily on foliage and structural plant parts (Zhao *et al.*, 1991), a diet associated with moderate levels of intragroup competition in other species, and the population has been exposed historically to predators to which group members responded collectively (Xiong, 1984; cited in Fooden, 1986). Although no or few predators are present, historically moderate levels of intragroup competition and collective predation defense might predict the evolution of a relaxed dominance style (Sterck *et al.*, 1997). Clearly this is not supported by our data. Conversely, we observed no evidence of high intergroup competition. We occasionally observed another social group at the boundary of the group's range, but interaction between them was limited to peering and nonaggressive contact calling, particularly by subadult males (but see Zhao, 1997). Low intergroup competition in combination with intragroup competition is hypothesized to lead to a despotic dominance style.

Another possibility is that our results represent responses of a normally relaxed species to human management. During the past decade, the group has not only been provisioned in a small open area with a viewing platform for tourists but also its range has been restricted by frequent herding. Although results vary, many studies support the notion that provisioning (Asquith, 1989) and long-term crowding (Judge, 2000) can increase aggression and intragroup competition for resources in a variety of species. Such responses might be considered consistent with flexible interpretations of both the socio-ecological model (Sterck *et al.*, 1997) and a self-organizing model based on levels of aggression (Hemelrijk, 1999). One piece of evidence possibly favoring this explanation is that females in the study group showed no kin bias in grooming or huddling during observations conducted before the group was used for tourism (Ogawa and Takahashi, 2003). However, because kin bias is sensitive to group size (Berman *et al.*, 1997) and because the number of females in the group was smaller than in the current study (7 vs. 13), it is difficult to compare the results directly. Moreover, during Ogawa's (personal communication) study, there was little bidirectional aggression among females when dominance relationships were stable. Hence, it would be premature to conclude that the group displayed a more relaxed dominance style in the past.

Clearly, we cannot rule out the possibility that the group has changed its dominance style over time until we are able to assess dominance style indicators in a comparably-sized, undisturbed group. Nevertheless, published findings argue against it. Most simply, relaxed dominance styles occur in captive macaques, so provisioning and range restriction cannot provide a full explanation for our results. Moreover, dominance styles in other species do not vary greatly across environments. For example, there is generally good agreement among captive studies of the same species carried out in

different settings (Thierry, 2000). In addition, a small number of studies of wild or free-ranging populations have shown similar patterns of postconflict behavior to those in captivity (Aureli, 1992; Balcomb *et al.*, 1993; Judge and de Waal, 1997; Kutsukake and Duncan, 2001). Finally, studies specifically designed to describe the range of intraspecific variation in dominance style indicators with environmental conditions found some variation with ontogenetic experience and group composition (Butovskaya *et al.*, 1996; Castles *et al.*, 1996; de Waal and Johanowicz, 1993), but little with reproductive season (Abegg *et al.*, 2003; *cf.* Schino *et al.*, 1998) or spatial density (Demaria and Thierry, 1989; Judge and de Waal, 1997).

### CONCLUSION

In conclusion, the preponderance of evidence supports a despotic dominance style for Tibetan macaques. Although they display some characteristics of moderately relaxed species (e.g., maternal tolerance for infant handling, weak kin biases in reconciliation), low rates of counter-aggression and low conciliatory tendencies, particularly among females, are considered particularly reliable criteria for despotism, as indicated by the weight they are given in Thierry's (2000) four grade scale. If we were to consider the low scores for counter-aggression and reconciliation alone, we would be inclined to place Tibetan macaques at the extreme despotic end of the dominance style continuum (e.g., grade 1 of Thierry's four grade scale). However, given the presence of some relaxed qualities, we suggest that the second grade of the scale may be more appropriate.

### ACKNOWLEDGMENTS

We are grateful to the Huangshan Monkey Management Center and to 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 Piedesaux, Justin Sloan and Lei Zhang for field assistance, and Mark Bender, Meredith Dorner, Monique Fortunato, Aviva Kugel, Beth Lake, Stephanie Miller and Nicole Schiro for assistance in data analysis. We are grateful to Lei Zhang and Akie Yanagi for translating Chinese and Japanese works into English. We also benefited greatly from discussions with Hideshi Ogawa. 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.

APPENDIX

Dominance matrices for the 3 stable data analytic periods: Cells contain total numbers of submissive and fearful interactions received by focal subjects (rows) from their interactors (columns) during focal observations. Male names are in bold; female names are in italics. Subadults are underlined.

A. First data analysis period: August 2000-January 2001

	<b>HL</b>	<b>CW</b>	<b>SX</b>	<b>HZ</b>	<b>BH</b>	<b>GS</b>	<b>ZM</b>	<b>BX</b>	<b>TG</b>	<b>TT</b>	<b>HG</b>	<b>YM</b>	<b>ES</b>	<b>YZ</b>	<b>CL</b>	<b>FT</b>	<b>HU</b>	<b>FM</b>	<b>HR</b>	<b>ZL</b>	<b>TY</b>	<b>FY</b>	<b>Total</b>	
<b>HL</b>	*	3	0	10	14	1	7	4	16	7	0	15	16	11	3	4	2	7	4	2	0	0	7	133
<b>CW</b>	0	*	2	8	12	1	13	7	10	11	4	19	21	19	6	16	7	21	12	6	2	4	2	201
<b>SX</b>	0	0	*	2	2	1	10	8	9	1	12	18	8	3	5	3	13	2	3	0	1	0	1	102
<b>HZ</b>	0	0	0	*	0	2	2	1	4	4	1	0	2	5	4	4	4	0	6	2	4	5	50	
<b>BH</b>	0	0	0	0	*	0	4	7	8	0	6	6	8	2	1	1	5	0	1	0	1	0	1	50
<b>GS</b>	0	0	0	1	0	*	3	0	1	1	1	1	0	0	0	0	2	1	3	6	0	0	1	21
<b>ZM</b>	0	0	0	0	0	0	*	1	0	1	4	0	0	0	0	0	4	0	4	4	1	4	4	23
<b>BX</b>	0	0	0	0	0	0	0	*	2	0	0	8	4	2	4	0	5	1	2	0	1	1	1	30
<b>TG</b>	0	0	0	0	0	0	0	0	*	4	0	3	5	2	1	3	1	1	0	1	0	0	3	24
<b>TT</b>	0	0	0	0	0	0	0	0	0	*	0	2	11	5	5	2	2	5	3	1	0	2	0	38
<b>HG</b>	0	0	0	0	0	0	0	0	0	0	*	0	0	3	0	1	1	0	1	0	1	0	2	27
<b>YM</b>	0	0	0	0	0	0	0	0	0	0	0	*	8	3	5	3	0	2	1	0	0	0	4	27
<b>ES</b>	0	0	0	1	0	0	1	0	0	0	0	0	*	5	0	3	3	3	0	0	0	0	3	19
<b>YZ</b>	0	1	0	0	0	0	3	0	0	0	0	0	4	*	3	4	6	1	0	0	0	0	2	30
<b>CL</b>	0	0	0	0	0	0	0	0	0	0	0	0	4	0	*	2	0	7	4	2	1	1	1	21
<b>FT</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	3	1	6	2	0	0	7	19
<b>HU</b>	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	*	2	1	2	2	2	3	13
<b>FM</b>	0	0	0	0	0	0	0	0	0	1	0	0	3	1	0	0	0	0	2	1	0	0	2	10
<b>HR</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	4	1	4	9	
<b>ZL</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	*	6	1	8	
<b>TY</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<b>FY</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	*	0	0	
<b>Total</b>	0	5	2	22	28	5	32	27	49	46	11	66	102	73	36	48	44	75	53	46	28	60	858	



B. Second data analysis period: February 2001-May 2001

	HL	CW	SX	HZ	YZ	BH	ZM	TT	BX	HG	TG	YM	CL	ES	FT	HH	HU	HR	FM	ZL	TY	FY	Total
HL	*	0	1	1	14	12	0	12	3	0	12	9	1	12	19	3	1	10	10	4	2	2	128
CW	0	*	3	3	13	22	3	10	3	3	5	8	2	8	8	2	11	7	16	3	0	11	141
SX	0	0	*	2	7	4	1	5	9	0	10	4	0	4	9	4	2	10	7	0	1	0	79
HZ	0	0	0	*	1	5	2	0	3	3	0	0	0	3	2	6	3	3	1	4	1	2	41
YZ	0	0	0	0	*	29	0	6	14	0	18	18	3	5	9	5	0	3	4	0	0	7	121
BH	0	0	0	0	0	*	1	14	11	0	23	7	4	3	13	5	11	10	4	1	3	5	115
ZM	0	0	0	0	0	0	*	0	1	1	0	0	1	0	2	0	6	1	1	0	0	3	16
TT	0	0	0	0	0	0	0	*	0	0	0	4	4	1	2	0	2	4	7	0	1	11	36
BX	0	0	0	0	0	0	0	0	*	1	2	1	5	2	2	2	1	0	9	0	0	4	29
HG	0	0	0	0	0	0	0	0	0	*	0	1	0	0	0	1	5	1	2	8	6	0	24
TG	0	0	0	0	0	0	0	0	0	0	*	2	4	0	1	1	11	0	6	0	0	0	25
YM	0	0	0	0	0	0	0	0	0	0	0	*	1	0	0	0	3	0	4	0	0	4	12
CL	0	0	0	0	0	0	0	0	0	0	0	0	*	2	0	0	3	6	0	0	0	0	11
ES	0	0	0	0	0	0	0	0	0	0	0	0	0	*	4	1	2	1	0	1	0	1	10
FT	0	0	1	0	0	0	1	0	0	0	0	0	0	0	*	1	5	4	1	3	0	4	20
HH	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	2	2	0	0	3	0	8
HU	0	0	0	0	0	0	2	1	0	0	1	0	0	0	0	0	*	1	3	2	1	0	11
HR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	*	1	1	0	19	22
FM	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	*	1	0	0	2
ZL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	*	15	0	18
TY	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*	0	0
FY	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	*	2
Total	1	0	5	6	35	72	10	48	44	10	71	54	27	40	72	33	69	64	76	28	33	73	871

C. Third data analysis period: December 2001-July 2002

	ZL	CW	SX	YZ	TT	HL	HG	TG	YM	BH	BX	ES	FT	FM	FY	HH	PN	TY	Total
ZL	*	1	2	26	28	4	6	38	31	27	21	28	56	27	19	8	5	1	328
CW	0	*	1	22	26	12	14	14	29	21	23	6	33	37	7	8	5	2	260
SX	0	0	*	37	34	18	8	19	40	28	24	21	17	3	3	7	1	0	260
YZ	0	0	0	*	24	2	0	36	19	22	25	11	27	5	10	5	0	0	186
TT	0	0	0	0	*	1	0	10	13	20	6	6	7	8	5	5	1	0	82
HL	0	0	0	0	0	*	7	3	1	3	3	4	17	1	22	19	4	3	87
HG	0	0	0	1	0	0	*	2	1	0	1	4	21	4	12	22	7	1	76
TG	0	0	0	3	0	2	0	*	7	4	5	4	4	5	1	0	5	0	40
YM	0	0	0	0	0	0	0	0	*	5	8	5	8	4	9	2	2	0	43
BH	0	0	0	0	0	0	1	2	0	*	10	3	19	5	4	6	0	0	50
BX	0	0	0	0	0	0	0	0	0	0	*	8	10	0	9	1	0	0	28
ES	0	0	0	0	1	2	7	0	0	0	0	*	7	2	1	2	0	0	22
FT	0	0	0	2	0	0	1	0	0	0	0	0	*	4	12	4	0	0	23
FM	0	0	0	0	0	0	0	0	0	0	0	0	0	*	2	4	1	0	7
FY	0	0	0	0	0	0	0	1	0	0	0	0	0	0	*	2	0	0	3
HH	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	*	2	6	9
PN	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	*	13
TY	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	*	2
Total	0	1	3	91	113	41	44	125	141	130	126	101	226	106	117	95	35	26	1521

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