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Bridging Behavior and Other Affiliative Interactions Among Male Tibetan Macaques (*Macaca thibetana*)

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*I describe bridging behavior and social relationships between adult males and infants in a free-ranging group of Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan, China. The subjects performed bridging in which two adult males simultaneously lifted up an infant, sucked or touched its genitalia, and then groomed each other in nonagonistic contexts. Males also expressed social behaviors with other males, such as mounting, penis-sucking, and embracing while touching each other's penes. Males also employ bridging while exploiting an infant as a social tool, not only to reduce the probability of an aggressive response from dominant males (agonistic buffering), but also to develop and to maintain affiliative social relationships with other males. Use of male infants in bridging contributed to frequent male–infant interactions such as holding, grooming, and penis-sucking. Although these interactions might not have a positive influence on infant survival, they may facilitate the maintenance of affiliative relationships with adult males until they reach maturity. The development of bridging might have a close relation to the high socionomic sex ratio (adult male/adult female) and frequent affiliative interactions between males, especially among the adolescents and adults.*

KEY WORDS: bridging behavior; Tibetan macaque; agonistic buffering; male preference; penis-sucking.

INTRODUCTION

In nonhuman primates, male–infant relationships vary with the social structure of the species (Whitten, 1987). In monogamous species—marmo-

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sets, tamarins, and titis—adult males carry their own offspring and provide benefits for the infant (Epple, 1975; Kleiman, 1977). However, in multimale multifemale groups of macaques and baboons, males interact with infants less frequently (Alexander, 1970; Estrada, 1984; Hiraiwa, 1981; Packer, 1980; Ransom and Ransom, 1971; Smith and Whitten, 1988; Smuts, 1985; Stein, 1984; Vessey and Meikle, 1984). This is partly because the paternity of infants is uncertain (Kurland and Gaulin, 1984). These males increase their reproductive success by mating with as many estrous females as possible, while females do so by investing care-taking in their offspring (Trivers, 1972).

In contrast, frequent affiliative male–infant interactions have been observed in multimale, multifemale groups of Tibetan macaques (*Macaca thibetana*). Male Tibetan macaques occasionally show social behavior in which two individuals simultaneously lift up an infant (Deng, 1993). This bridging behavior is like that of *Macaca arctoides* (Estrada, 1984; Estrada and Sandoval, 1977). Male Barbary macaques (*Macaca sylvanus*) perform similar behavior and have frequent interactions with infants (Deag, 1980; Deag and Crook, 1971; Kuester and Paul, 1986; Smith and Peffer-Smith, 1982; Taub, 1980a). Deag and Crook (1971) proposed an agonistic buffering hypothesis to explain bridging among Barbary macaques: subordinate males may handle an infant to reduce the likelihood of aggression from dominant males. On the other hand, Taub (1980a, 1984) proposed an enforced baby-sitting hypothesis. Related males—matrilineal siblings—may use a related infant to bridge between themselves, thereby informing one another which infant is their relative and developing a special care-taking relationship with the infant. Anecdotal reports imply bridging in *Macaca fascicularis* (de Waal *et al.*, 1976) and *M. assamensis* (Kawamoto, personal communication).

Similar triadic male–infant interactions occur in baboons (*Papio cynocephalus, P. anubis, Theropithecus gelada*). Male baboons may carry an infant during agonistic male–male encounters in order to reduce the probability of being threatened and to increase their rank (Dunbar, 1984; Packer, 1980; Ransom and Ransom, 1971; Smith and Whitten, 1988; Smuts, 1985; Stein, 1984; Strum, 1984). Male baboons also protected their presumed offspring from aggression by immigrant males (Busse and Hamilton, 1981). During agonistic interactions, a male may solicit support of the infant's mother and develop a social relationship with her (Dunbar, 1984; Smith and Whitten, 1988; Smuts, 1985); Stein, 1984).

I examined bridging among male Tibetan macaques in order to discern its functions and to test the agonistic buffering and the enforced baby-sitting hypotheses.

The agonistic buffering hypothesis predicts that (1) males that have a higher probability of being attacked will handle an infant more frequently, (2) males will handle an infant in situations in which they are more likely to be attacked, and (3) males will be less likely to be attacked while handling an infant. The enforced baby-sitting hypothesis predicts that (1) males use infant relatives for bridging and have affiliative interactions with them, and (2) males provide benefits to them.

I will compare bridging in male Tibetan macaques to triadic male–infant interactions of other nonhuman primates and will discuss it vis-à-vis the social structure of Tibetan macaques.

MATERIALS

The study site is Mt. Huangshan (30°29′N, 118°11′W) in Anhui province, China. Nine groups of wild Tibetan macaques inhabit Mt. Huangshan. Wada *et al.* (1987) have studied the "Yulingkeng" group extensively since 1985. All individuals of the study group are identified via physical characteristics. The group is provisioned only during the study periods to facilitate observations. The monkeys received corn four times a day at a feeding station. Matrilineal kinship and population changes of the study group caused by birth, death, and male transfer are known since 1985 (Wada and Xiong, 1995). Table I shows the age–sex composition of the study group. Tibetan macaques live in stable multimale, multifemale groups. Males emigrate from their natal group after sexual maturity, while females remain in the natal group throughout their lives. Females mature at 5 years of age and males at 6–7 years. Infants are born mainly between early January and early May (Deng and Zhao, 1987; Zhao and Deng, 1988a–c).

METHODS

I collected data during four mating seasons (September–January) and one birth season (March–April) from 1989 to 1992 (Table I). Total observation time is 1,173 hr. I observed the monkeys at the feeding station and in the forest.

While individuals fed at the feeding station, I employed all-occurrences behavior sampling (Altmann, 1974). Supplanting behavior there showed that the adult males are ranked in a linear hierarchy.

In the forest, I used focal-animal sampling (Altmann, 1974) during study periods 1, 4, and 5. Mean focal sampling time on 12 immatures is 14.1 (range, 9.4–24.5) hr. During focal sampling, I also recorded all

Table I. The Age-Sex Composition of the Study Group for Each Study Period[a]

Age class	Age (yr)	Period 1, 12/5 89–1/21/90 (227 hr)[b]		Period 2,[c] 11/18/90–1/11/91 (298 hr)		Period 3,[d] 3/30/91–4/23/91 (134 hr)		Period 4,[e] 12/5/91–1/15/92 (226 hr)		Period 5, 9/16/92–11/4/92 (283 hr)	
		Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Adult	Male: ≥ 8 Female: ≥ 5	6	5	5	7	5	7	5	8	9	9
Subadult	Male: ≥ 6–7	0	—	1	—	1	—	2	—	1	—
Adolescent	Male: 4–5 Female: 4	2	2	1	2	1	2	6	1	5	2
Old juvenile	3	0	2	1	1	1	1	4	2	2	1
Young juvenile	2	1	1	1	2	1	2	2	1	1	4
Old infant	1	1	2	2	1	2	1	1	4	0	3
Young infant	<1	2	1	1	4	1	4	0	3	4	1
Total		12	13	12	17	12	17	20	19	22	20

[a] Sixteen infants were born between 1989 and 1992. Fourteen males immigrated into and seven males emigrated from the group from 1989 to 1992.

[b] Observation time in parentheses.

[c] One adult female died in period 2.

[d] Composition in period 3 was same as in period 2. Although one female infant was born on the last day of period 3, it is not included in the table.

[e] One adult, five adolescent, and three juvenile males immigrated into the group in period 4. However, two adolescent males and one juvenile male emigrated from the group, and one juvenile male died in period 4.

occurrences of male-infant interactions ad libitum (Altmann, 1974): holding infants by males, males grooming infants, genital sucking of infants by males, and male use of an infant in bridging. During periods 2 and 3, when male-male encounters were focal, I recorded the entire sequence of the male-male interaction until one of the males left the other. I analyzed the data to reveal the proximate effects of social behavior on subsequent male-male interactions. During mating seasons, males formed consortships with particular females. A consortship is defined as a male-female dyad that maintains prolonged proximity due mainly to the male frequently following the female. I recorded these consortships each day.

The social behaviors that I recorded during the observations include the following.

Bridging. Two individuals simultaneously lift up one infant (Fig. 1). When two males sat facing one another, one male pulled up the infant's shoulder, the other male pulled up its hip, and the infant lay on its back, forming a bridge between them. While lifting up the infant, one or both males often sucked or touched the infant's penis or genital area with the expression of teeth-chattering. Males gently handled infants, which rarely showed resistance or gave signs of distress. The infant's mother was quite tolerant of males handling it.

Penis-Showing. A male raised his leg and showed his penis to another male. The latter male sometimes responded to penis-showing by manually touching it or other areas of the presenting male.

Presenting. A male standing in close proximity to another male showed his perineum. The male's posture was the same as female presenting behavior.

Penis-Sucking or Genitalia-Sucking. A male sucked the penis of another male, while they embraced one another with teeth-chattering and vocalizations. In some cases, males sucked one another's penes simultaneously. While holding an infant, males sucked its genitalia, occasionally turning it upside down.

Embracing. Males embraced and touched one another's penes while teeth-chattering and vocalizing.

Holding. A male sat hugging an infant ventrally for 1–20 min, while keeping his arms on the infant's back. While holding an infant, males sometimes carried it ventrally.

Mounting. A male mounted another male while teeth-chattering and vocalizing and simulating the posture of a copulating heterosexual pair.

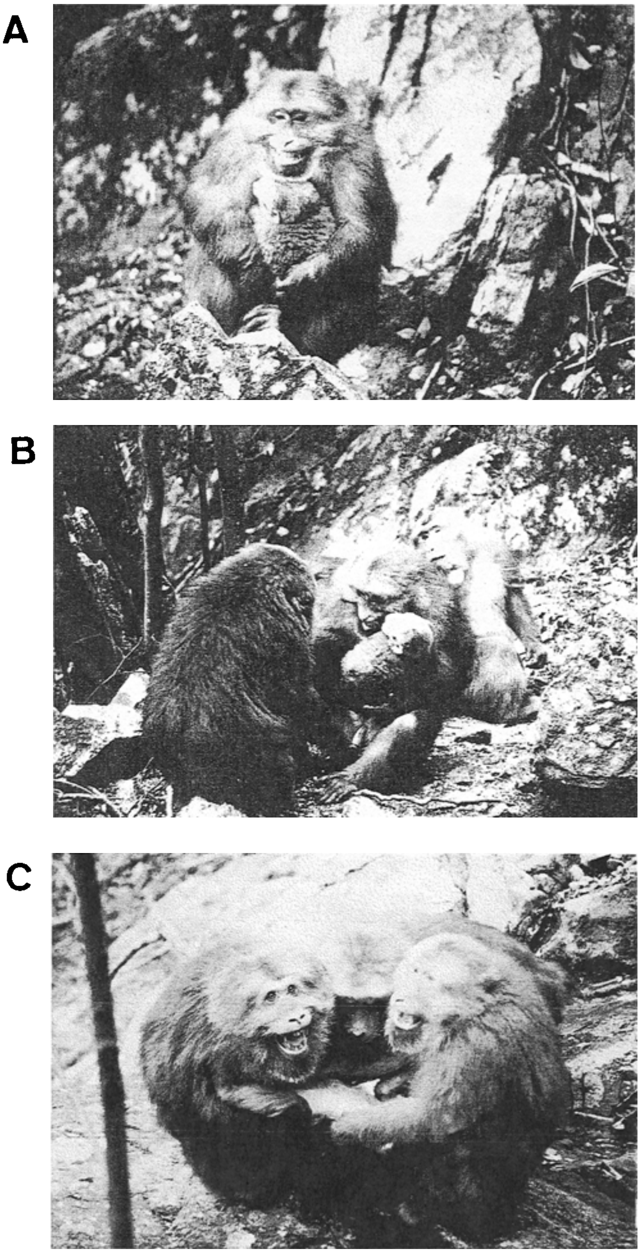

Fig. 1. Bridging between adult male Tibetan macaques. (A). An adult male holds an infant. (B) A male carries and presents an infant to a second male. (C) Two males simultaneously lift up an infant in a nonagonistic context.

RESULTS

Male–Male Interactions and Bridging

Social Contexts of Bridging

In study periods 2 and 3, a total of 333 bridgings was recorded. Thirty-five (10.5%) of them occurred in tense social contexts caused by aggressive interactions in the group. Four (1.2%) occurred after a male that was attacked by another male carried an infant to the attacker. Eighteen (5.4%) occurred after aggression in which one of the two males that performed bridging was involved. Thirteen (3.9%) occurred after aggression in which neither male was involved. The other 298 (89.5%) bridgings occurred in nonagonistic contexts, when group numbers were resting and no conspicuous interaction was observed among any group member before them.

Sequence of Interactions Between Males

I analyzed bridging and other male–male interactions during nonagonistic contexts. Whereas bridging occurred during triadic male–infant interactions, other social behaviors—penis-showing, presenting, embracing, penis-sucking, and mounting—occurred mainly during dyadic male–male encounters (Fig. 2).

A triadic male–infant interaction (TMII) is defined as an interaction in which two males are in close proximity and at least one of them handles an infant. The sequence of TMII is classified into three types. *Type 1*: A male held an infant and carried and presented it to another male in order to initiate bridging behavior with him. *Type 2*: A male approached another male that was holding an infant. In this type, the male holding an infant did not necessarily hold it for bridging. The approaching male initiated the bridging. *Type 3:* Other cases, e.g., when a male approached another male, one of them held a nearby infant and presented it to the other, or both males almost simultaneously handled a nearby infant.

During 316 cases of type 1 TMII, 185 (58.5%) bridgings occurred. During 115 cases of type 2 TMII, 70 (60.9%) bridgings occurred. When a male was holding an infant, other males did not approach with another infant. In 396 cases of male–male encounters in which neither male was holding an infant prior to the encounter, 51 (12.9%) type 3 TMII occurred. During type 3 TMII, 43 (84.3%) bridgings occurred. During the

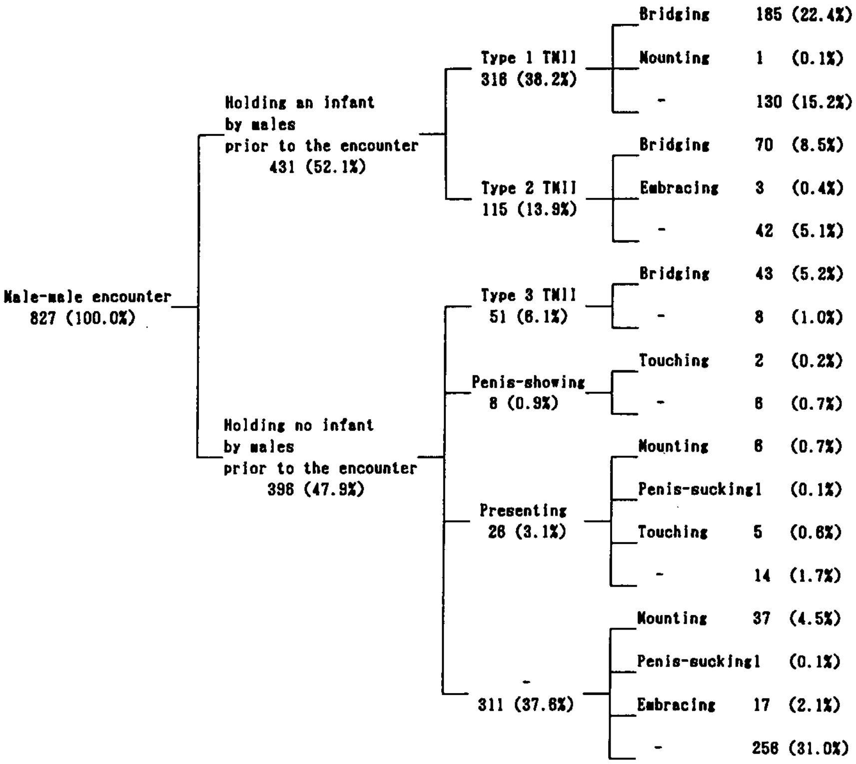

Fig. 2. Sequence of social behavior during male-male encounters. Male-male encounter: A male approached another male in nonagonistic context. Type 1-3 TMII: Each type of triadic male-infant interaction in which two males were in close proximity and at least one of them handled an infant. Right column is the number (and percentage) of social behaviors recorded during male-male encounters.

other 345 dyadic male-male encounters, the approaching male exhibited 26 (7.5%) presentings and 8 (2.3%) penis-showings. All these behaviors, except one instance of presenting, were performed by the subordinate male. During 345 dyadic male-male encounters, 43 (12.5%) mountings, 17 (4.9%) embraces, and 2 (0.6%) penis-suckings occurred, while only 1 (0.2%) mounting and 3 (0.6%) embraces occurred during 482 TMII. In male-male dyads, dominant males did not mount subordinate males more frequently than vice versa (Wilcoxson matched-pairs signed-ranks test, $t = 24$, $n = 21$, n.s.).

Distribution of Bridging Among Males

Table II shows the distribution of bridging recorded during three types of TMII. In each one, an approaching male is the initiator of bridging. In male–male dyads, when one frequently initiated bridging with another, the second male also frequently initiated bridging with him (Spearman's rank correlation, $r_s = 0.56$, $n = 21$, $p < 0.01$).

Natal adolescent male CS, which was the lowest-ranking male, initiated bridging most frequently in each type of TMII. He frequently approached and initiated bridging with adult males, especially three higher-ranking ones: BD, HM, and WS.

Effects of dominance rank on the occurrence of bridging shows that lower-ranking males more frequently initiated bridging than higher-ranking males did, and higher-ranking males were more frequently chosen for a recipient male in bridging than lower-ranking males were (Fig. 3). In type 1 TMII, higher-ranking males were approached by another male that was holding an infant more frequently than lower-ranking males were (Spearman's rank correlation, $r_s = -0.93$, $n = 7$, $p < 0.05$). Lower-ranking males carried an infant to another male more frequently than higher-ranking males did, though the correlation is not significant (Spearman's rank correlation, $r_s = 0.36$, $n = 7$, n.s.). In male–male dyads, subordinate males carried an infant to dominant males more frequently than vice versa (Wilcoxon matched-pairs signed-ranks test, $t = 0$, $n = 21$, $p < 0.01$). Although subordinate males approached dominant males more frequently than vice versa in dyadic male–male encounters (Wilcoxson matched-pairs signed-rank test, $t = 27.5$, $n = 21$, $p < 0.05$), subordinate males were more likely to approach with an infant than vice versa, based on the percentage of approaches in which an infant was carried (Wilcoxon matched-pairs signed-ranks test, $t = 0$, $n = 21$, $p < 0.01$). In type 2 TMII, higher-ranking males that were holding an infant were more likely to be approached by another male than were lower-ranking males that were holding an infant, based on the percentage of holding infants in which there was an approach (Spearman's rank correlation, $r_s = -0.93$, $n = 7$, $p < 0.05$).

Effects of Bridging on Subsequent Interactions

After bridging, close proximity—within reach—was maintained and social grooming occurred more frequently than in cases when bridging did not occur, i.e., when the recipient male refused the infant provided by the other male (Fig. 4). No aggressive interaction occurred after bridging in any type of TMII, while 9 (7.4%) aggressive interactions occurred when

Table II. Distribution of Bridging Behavior Among Adult and Adolescent Males[a]

Approacher			Type of TMII[b]																							
			Type 1, Recipient								Type 2, Recipient								Type 3, Recipient							
Name	Rank	Age	BD	HM	WS	EX	IBB	CY	CS	Total	BD	HM	WS	EX	IBB	CY	CS	Total	BD	HM	WS	EX	IBB	CY	CS	Total
BD	1	8	—				3		1	4	—	7		1			1	9	—	2		1			2	5
HM	2	8+	11	—			1			12	12	—		3			1	16	10	—					1	11
WS	3	8+	5	7	—		4		4	20		4	—		4		2	10	1		—		1			2
EX	4	8+	4	2	1	—	1			8	2			—				2	3			—				3
IBB	5	8+	16	9	8	1	—			34	5	2	3		—			10	2	1			—			3
CY	6	8+						—		0						—		0						—		0
CS	7	5	70	17	16		4		—	107	17	3	2		1		—	23	11	5	3				—	19
Total			106	35	25	1	13	0	5	185	36	16	5	4	5	0	4	70	27	8	3	1	1	0	3	43

[a] Bridging behaviors after aggressive interactions were not included.

[b] TMII (triadic male–infant interactions) are classified into three types (in the text).

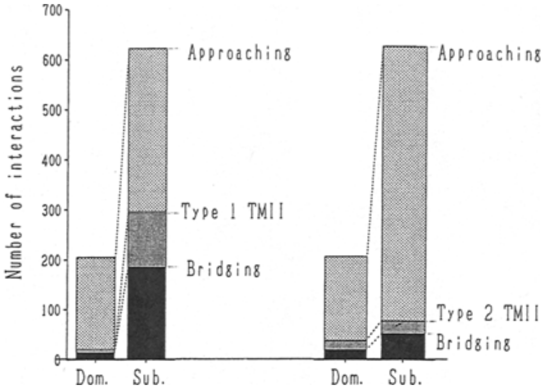

Fig. 3. Direction of approaches in triadic male-infant interactions. Dom.: A dominant male approached a subordinate male. Sub.: A subordinate male approached a dominant male. Approaching: Total number of male approaches to another male. Type 1-2 TMII: Number of each type of triadic male-infant interaction recorded during male-male encounters. Bridging: Number of bridging episodes recorded during male-male encounters.

bridging did not occur in type 1 TMII and 2 (4.4%) occurred in type 2 TMII.

In male-male dyads, males initiated bridging more frequently with males that they groomed more frequently (Spearman's rank correlation, $r_s = 0.45$, $n = 21$, $p < 0.01$). This correlation may be the result of the fact that subordinate males initiated bridging with dominant males more frequently than vice versa, if subordinate males also groomed dominant males more frequently than vice versa. However, during the study period, subordinate males did not groom dominant males more frequently than vice versa (Wilcoxon matched pairs signed rank test, $t = 37$, $n = 21$, n.s.). Males initiated bridging more frequently with a male from which they received grooming more frequently, though the correlation is not significant (Spearman's rank correlation, $r_s = 0.25$, $n = 21$, n.s.). Finally, males more frequently groomed another male from which they received grooming more frequently (Spearman's rank correlation, $r_s = 0.38$, $n = 21$, $p < 0.01$). Thus, males that frequently performed bridging with each other frequently groomed each other after bridging between them.

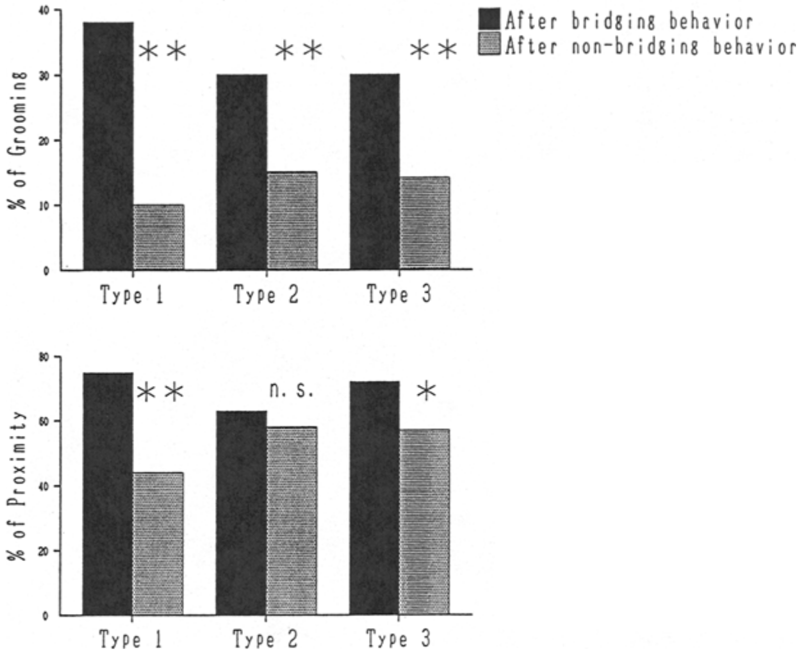

Fig. 4. Percentage of social grooming and close proximity after bridging behavior. Percentage of social grooming between males and close proximity (within hand-reaching distance) for more than 1 min. after bridging and nonbridging behavior. After bridging: Bridging occurred when one of the males handled an infant. After nonbridging: Bridging did not occur because a male did not receive an infant provided by another male when one of them handled it. Types 1–3: Types of triadic male–infant interactions. Chi-square test: (**) $p < 0.01$; (*) $p < 0.05$; (n.s.) not significant. Interactions in which aggression occurred between males were excluded from the analysis.

Male–Infant Interaction

Development of Social Behavior of Immatures with Adult Males

I analyzed social interactions between adult males and immatures during four mating seasons: periods 1, 2, 4, and 5 (Fig. 5). Male and female infants were held, groomed, had their genitalia sucked, and were used in bridging by adult and adolescent males. Males performed bridging 0.35 time/hr on the average, male infants were used in bridging 0.43 time/hr, and female infants were used 0.04 time/hr. Compared to immature females, juvenile and adolescent males had frequent interactions with adult and ado-

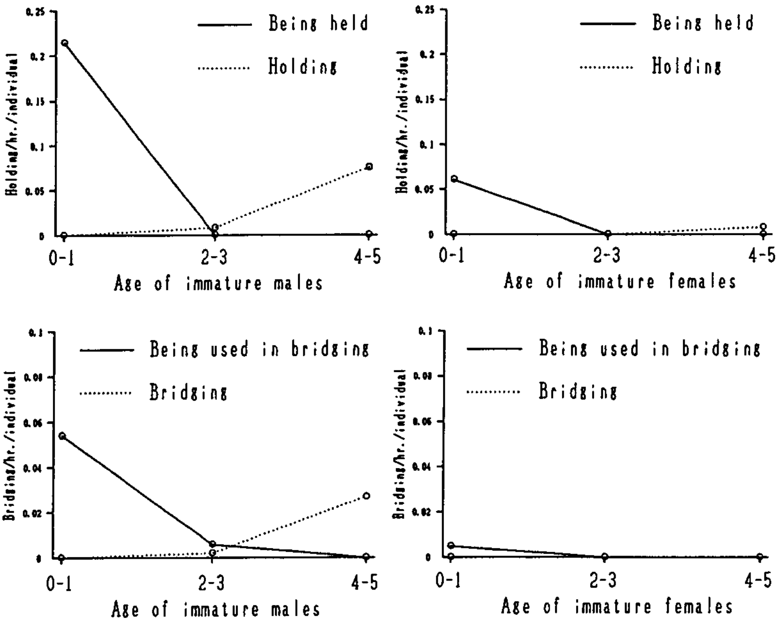

Fig. 5. Development of social behavior of immature individuals with adult males. Holding: An immature male or female held another immature. Being held: An immature male or female was held by adult or adolescent males. Bridging: An immature male or female performed bridging with adult or adolescent males. Being used in bridging: An immature male or female was used in bridging by adult or adolescent males. Holding/hr./individual: Mean number of holdings in which a focal animal was involved per hour per possible recipient individual. Bridging/hr./individual: Mean number of bridgings in which a focal animal was involved per hour per possible recipient individual.

lescent males, in which they were used in bridging, or in turn, they themselves performed bridging with the males. They also showed embracing, mounting, penis-sucking, and bridging with each other. After maturity, adult males maintained their interactions with other adult males. On the contrary, juvenile and adolescent females interacted mostly with their mothers, and rarely showed bridging with males, though they held infants in dyadic interactions. Adolescent females approached, presented their genitalia to, and groomed adult males, which is similar to the interactions between adult males and adult females.

Table III. Number of Instances of Holding an Infant by Adult and Adolescent Males[a]

	Holder male						Infant (sex)					
Study period	Name	Age	Age class	Rank	Natal	Newcomer	ZM(m)	GHH(m)	BX(f)			Total
1	HM	8+	A	1	?	No	c		c			0
	WS	8+	A	2	No	No	3	3				6
	EX	8+	A	3	No	No	5	1	c			6
	YSZ	8+	A	4	No	No	33*	14	1			48
	IBB	8+	A	5	No	Yes	2	12				14
	CY	8+	A	6	No	Yes						0
	BD	5	AD	7	Yes	No	24	36*	1			61
	CS	4	AD	8	Yes	No	48*	30	1			79
	Total						115	96	3			214
							ZCT(m)	ZZ(f)	YM(f)	GHR(f)	ZTZ(f)	
2	HM	8+	A	2	?	No	33*c	1c	8	10c	1	53
	WS	8+	A	3	No	No	29*		25*c	6	4	64
	EX	8+	A	4	No	No	5	17*	3	1		26
	IBB	8+	A	5	No	No	67*	1	3			71
	CY	8+	A	6	No	No	1		1			2
	BD	6	sA	1	Yes	No	54*	1c	1c	2c		58
	CS	5	AD	7	Yes	No	203*					203
	Total						392	20	41	19	5	477
							YTT(f)	GFT(f)	CBX(f)			
4	HM	8+	A	2	?	No	6c	4c				10
	EX	8+	A	3	No	No						0
	IBB	8+	A	4	No	No	11	13*c				24

	CY	8+	A	5	No	No	4					4
	HZ	8+	A	6	No	Yes						0
	BD	7	sA	1	Yes	No	45*c					45
	CS	6	sA	7	Yes	No	10		k			10
	CFE	5	AD	8+	No	Yes						0
	LBU	5	AD	8+	No	Yes						0
	ZY	4	AD	8+	No	Yes						0
	GY	4	AD	8+	No	Yes						0
	LBE	4	AD	8+	No	Yes						0
	ZW	4	AD	8+	Yes	No						0
	Total						76	17	0			93
							GHL(m)	ZTB(m)	ZCS(m)	ZB(m)	YZ(f)	
5	HM	8+	A	3	?	No	1c	3	c	1c	1c	6
	EX	8+	A	7	No	No	3	5	1	1	1	11
	IBB	8+	A	4	No	No	5c	6	9c	2c	c	22
	CY	8+	A	5	No	No		1				1
	HZ	8+	A	6	No	No		3	3	2		8
	XX	8+	A	8+	No	Yes		1		1		2
	GX	8+	A	8+	No	Yes						0
	GS	8+	A	8+	No	Yes	2	36*	3	4	1	46
	BD	8+	A	2	Yes	No	13	25*	12c	1	#	51
	CS	7	sA	1	Yes	No	10	4	14*	4		32
	ZY	5	AD	8+	No	No	c	3	3c			6
	GY	5	AD	8+	No	No						0
	ZW	4	AD	8+	Yes	No	3	1k	3k	9k		16
	AD	4	AD	8+	No	No						0
	YG	4	AD	8+	Yes	No	2		1	1	k	4
1	Total						39	88	49	26	3	205

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[a] Age class: A, adult; sA, subadult; AD, adolescent. Natal: yes, natal; no, nonnatal; ?, unknown. Newcomer: yes, a male that immigrated into the study group during the study period; no, a resident male that had been resident in the study group in the preceding study period. (*)An infant that was held by each male more frequently than expected. Chi-square test, $p < 0.05$. Expected value of each cell = number of infants held by each male/number of young infants. (c) A male whose mother formed a consortship with each male; (k) a male that is of the same matrilineage with each natal male.

Male Preference for Infants

I use the frequency of holding infants by adult and adolescent males as an index of male preference for infants. Males frequently held the same infant that they used in bridging, as indicated by a positive correlation between the frequency of bridging in type 3 TMII and the frequency of holding, excluding cases in which bridging occurred (Kendall rank correlation, $\tau = 0.60$, n.s., in period 1; $\tau = 0.64$, $p < 0.01$, in period 2; $\tau = 0.50$, n.s., in period 4; $\tau = 0.64$, $p < 0.01$, in period 5). Young infants (<1 year) were held by males more frequently than older infants (1–2 years) were (Mann–Whitney U test: $n1 = 24$, $n2 = 24$, $Z = 2.56$, $p < 0.05$, in period 1; $n1 = 35$, $n2 = 21$, $Z = 2.94$, $p < 0.01$, in period 2; $n1 = 39$, $n2 = 65$, $Z = 0.97$, n.s., in period 4; $n1 = 75$, $n2 = 45$, $Z = 5.00$, $p < 0.01$, in period 5). Among young infants, males were held by males more frequently than females were (Mann–Whitney U test: $n1 = 16$, $n2 = 8$, $U = 12.5$, $p < 0.05$, in period 1; $n1 = 7$, $n2 = 28$, $Z = 3.32$, $p < 0.01$, in period 2; all young infants were female in period 4; $n1 = 60$, $n2 = 15$, $Z = 3.42$, $p < 0.01$, in period 5). Males held one or more particular infants more frequently than expected in 15 of 173 male–infant dyads (Table III). Among males that formed consortships, and females that had a young infant during the mating season, males held an infant more frequently than expected in 4 (15.4%) of 26 consort male–female pairs, versus only 11 (7.5%) of 147 nonconsort male–female pairs (Fisher's exact probability test, $P = 1.89$, n.s.). Among natal males and young infants, males held an infant more frequently than expected in 0 (0%) of 6 male–male pairs within the same matrilineage and in 7 (17.9%) of 39 nonrelated male–infant pairs (Fisher's exact probability test, $P = 0.68$, n.s.).

Which males held an infant frequently was affected by multiple factors such as dominance rank, age, natal group, and length of residence in the group. However, Table III shows that young natal males frequently held infants. During periods 1 and 5, natal males more frequently held infants than nonnatal males did (Mann–Whitney U test: $n1 = 6$, $n2 = 15$, $U = 18$, $p < 0.05$, in period 1; $n1 = 20$, $n2 = 50$, $Z = 2.56$, $p < 0.05$, in period 5). Also, the most frequent infant-holder is the natal adolescent male CS in periods 1 and 2, and he is the natal subadult male BD in period 4. These two males became the highest-ranking males after maturity. On the contrary, five adolescent low-ranking males, CFE, LBU, ZY, GY, and LBE, which immigrated into the study group during period 4, did not hold infants. Among them, CFE, LBU, and LBE emigrated from the study group during that period.

DISCUSSION

Testing the Agonistic Buffering Hypothesis

Data obtained from this study generally support the agonistic buffering hypothesis.

Subordinate males, which had more probability of being attacked, initiated bridging more frequently than dominant males did. In addition, compared to dominant males, subordinate males were more likely to approach dominant males when they themselves or the recipient held an infant than when neither male held an infant. When subordinate males without an infant approached dominant males, the former sometimes presented or engaged in penis-showing. Apparently, subordinate males had to reduce social tension by means of these appeasement behaviors. When neither the approaching male nor the recipient male had an infant, males sometimes performed mounting, embracing, and penis-sucking. This might indicate that males performed these greeting behaviors when there was no infant available.

Bridgings rarely occurred in agonistic contexts. This indicates that males did not restrict it to occasions when they needed to avoid imminent aggression from dominant males. Instead, males might perform bridging to avoid potential aggression in the group.

Bridging was never followed by aggressive interactions, though a male that carried an infant to another male was occasionally attacked when bridging did not occur. Bridging was followed by social grooming and close proximity more frequently than when bridging did not occur during a TMII. A positive correlation between the frequency of bridging and that of social grooming indicates that males that frequently performed bridging with each other formed or expected to form affiliative social relationships by frequent social grooming.

Testing the Enforced Baby-sitting Hypothesis

Data obtained from this study do not support the enforced baby-sitting hypothesis. Based on holding an infant by males, natal males did not prefer infants of their own matrilineage to other infants. It is not clear whether males prefer their possible offspring because paternity of infants in unknown in this group. However, adolescent males and newly immigrant males that rarely copulated with adult females in the preceding mating season also had affiliative interactions with infants, which indicates that frequent affiliative interactions between males and particular infants had no close relation with their kinship.

I obtained no evidence to suggest that frequent interactions with males were crucial for infant survival. All infants that did not interact with adult males also survived during the study period. Although female infants had less frequent interactions with adult males than male infants did, population changes from 1985 to 1992 (Wada and Xiong, 1995) show no sex difference in mean survival rate of infants during the first year of life: 82.4% (14/17) for male infants and 81.0% (17/21) for female infants (Fisher's exact probability test, $p = 1.25$, n.s.). If male–infant interactions provide benefits for the infant and reduce the cost of caretaking by the infant's mother, birth intervals after sons should be shorter than those after daughters. However, population parameters (Wada and Xiong, 1995) show no difference in mean birth intervals: 15.3 months after sons and 17.1 months after daughters, among 25 birth intervals from 1985 to 1992 (Mann–Whitney U test, $n1 = 11$, $n2 = 14$, $U = 65$, n.s.).

Comparison Between Bridging of Tibetan Macaques and TMII of Other Species

TMII of baboons are different from the bridging of Tibetan macaques. During TMII of baboons, one of two males carried an infant in agonistic male–male encounters, while in bridging of Tibetan macaques, two males simultaneously lift an infant in nonagonistic contexts.

In summary, bridging among male Tibetan macaques has the following features. Most bridgings occur in nonagonistic contexts. Lower-ranking males and adolescent males initiate bridging frequently. Bridging is often followed by social grooming between the males. Male infants are more frequently used than female infants are. Particular infants are used by each male in bridging. These features are like those of male Barbary macaques (Deag, 1980; Deag and Crook, 1971; Kuester and Paul, 1986; Smith and Peffer-Smith, 1982; Taub, 1980a, 1984). The rate of bridging is also similar: 0.35/hr/male in Tibetan macaques and 0.43/hr/male in Barbary macaques (Smith and Peffer Smith, 1982).

The tolerance of the infant's mother is necessary for males to use it in bridging. In Barbary macaques, estrous females frequently copulate with most of the males in the group, so any male could be the father of an infant (Taub, 1980b). This mating system may reduce the probability of infanticide and may affect the mother's tolerance. In Tibetan macaques, males form consortships with particular females, by frequently following her. However, because the consortships changed within one mating season, and females copulate with nonconsort males as well as their consort males, females copulate with many males in the group throughout a mating season. In addition, females do not show clear sexual swelling during the estrous cycle (Zhao, 1993), and they copulate after conception during the prolonged mating season (Zhao and Deng, 1988b; Wada and Xiong, 1995).

In Barbary macaques, the enforced baby-sitting hypothesis is based on the finding that bridging frequently occurred between males that preferred the same specific infant (Taub, 1980a, 1984). However, males did not prefer infants of their own matrilineage to other infants, and contacts with males did not have a positive influence on infant survival (Kuester and Paul, 1986). Therefore, it is moot which infants were preferred and why males preferred them. Male Tibetan macaques initiated bridging with consorts more frequently than with nonconsort females, in which cases they used an infant offspring of the female (Ogawa, 1995). This results, to some extent, in the male's affiliative interaction with the infant of his consort, though the effect of consortships upon male preference for infants is not significant. Furthermore, bridging males used an infant that a recipient male preferred, probably because it was more appeasing than other infants would be (Ogawa, 1995). The observed preference for a certain infant could be caused by the following processes, without the effect of kinship: One male preferred a specific infant, such as a male or that of his consort; other males used it to bridge with him; and they all preferred it both to bridge with each other and in dyadic male-infant interactions.

There are some differences between bridging in Tibetan macaques versus Barbary macaques. Like females, male Tibetan macaques usually carry an infant ventrally, while male Barbary macaques carried them dorsally (Deag and Crook, 1971). This causes some differences between the two species in the form of bridging. Male Tibetan macaques used infants even after they were >1 year, while male Barbary macaques switched to newborn infants in each birth season (Deag, 1980). Moreover, bridging in Tibetan macaques might be connected with various other affiliative behavior between males.

The Relation Between Bridging and Social Structure of Tibetan Macaques

The socionomic sex ratio (adult male/adult female) of Tibetan macaques is high, compared with those of other nonhuman primates (Caldecott, 1986). The mean sex ratio of the study group from 1985 to 1992 is 0.94 (Wada and Xiong, 1995) and that of groups at Mt. Emei ranges from 0.30 to 0.90 (Zhao, 1994). Barbary macaques (Taub, 1980b) and bonnet macaques (*Macaca radiata*) (Simonds, 1965; Sugiyama, 1971) also have high socionomic sex ratios. This indicates that male–male competition over estrous females should be high in these species. However, male Tibetan macaques (Deng and Zhao, 1987) and male bonnet macaques (Koyama, 1973; Simonds, 1965; Sugiyama, 1971) are tolerant of each other and engage frequently in various affiliative behaviors with body contact. In contrast, in macaques such as *Macaca fuscata* (Mori, 1975, 1977; Takahata, 1982) and *Macaca mulatta* (Drickammer, 1976), males rarely interact with each other, and they have lower socionomic sex ratios than those of Tibetan and bonnet macaques. This indicates that the affiliative behavior of Tibetan and bonnet macaques may reduce social tension among males. The reduction of social tension may enhance male intrasexual tolerance and may result in high socionomic sex ratios.

Male Tibetan macaques more frequently interact with infants than male *Macaca fuscata* (Alexander, 1970; Hiraiwa, 1981) and *Macaca mulatta* (Vessey and Meikle, 1984) do. Male *Macaca fuscata* (Itani, 1959) and *Macaca radiata* (Silk and Samuels, 1984) occasionally use an infant for agonistic buffering. However, male Tibetan macaques not only hold an infant in close proximity with another male but also transform this dyadic behavior into triadic bridging behavior. During penis-showing, embracing, and penis-sucking, males might show, touch, and suck penes to reduce social tension between them. Likewise, bridging seems to enhance affiliation, with males using an infant as a substitute for the penis, probably because it is more effective for appeasement.

Male Tibetan macaques emigrate from their natal group after sexual maturity (Zhao, 1994). Although frequent interaction with adult males is not essential for an infant's survival, they may facilitate affiliative relationships with adult males until maturity, and then they may obtain benefits from the affiliative relationships with the adult males, such as forming alliances in agonistic interactions. In fact, two natal adolescent males in the study group, which had been used in bridging when they were infants, frequently initiated bridging with adult males, stayed in their natal group after maturity, and became the highest-ranking males. However, the phenomenon of natal males staying in their natal group after maturity may be one of the byproducts of provisioning, as reported for *Macaca fuscata* (Sugiyama and Ohsawa, 1982). In contrast, five immigrant adolescent males that had no interaction with infants, rarely interacted with adult males. Three of them did not raise their dominance rank before they emigrated from the study group.

In Tibetan macaques, male use of infants in bridging and frequent male–infant interactions might have a close relation to the high socionomic sex ratio and frequent interactions between adult males, especially between adults and adolescents.

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