学位申請論文

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「Social relationships in bridging behavior among Tibetan macaques.」

(チベットモンキーのブリッジング行動における社会関係)

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学位申請論文要旨

題目：「チベットモンキーのブリッジング行動における社会関係」

本論文は、チベットモンキー(*Macaca thibetana*)のブリッジング行動についての研究報告である。ブリッジング行動は、２頭のオトナ個体がコドモを間にはさんで一緒に抱き上げる行動で、この時オトナ個体はコドモの性器をなめたり触ったりする。類似の行動を行うバーバリーマカク(*Macaca sylvanus*)の研究では、この行動の機能に関して２つの説が提唱されている。コドモを抱くことにより、劣位個体が、優位個体からの攻撃を抑制するとする「アゴニスティック・バファリング」説と、自分の血縁者に対する世話の特殊型だとする「インホース・ベビーシッティング」説である。本研究では、中国安徽省黄山のチベットモンキーの複雄複雌群の調査から、ブリッジング行動を初めて定量的データに基づいて分析し、以下の結果が得られた。

チベットモンキーでは、ブリッジング行動は自分の血縁者に対する世話とは関係がない。この行動は、コドモを社会的道具として利用してオスーオス間の攻撃を抑制するだけにとどまらず、その行動を行った後で親和的交渉を促進し、オスーオス間の親和的社会関係を樹立、維持する機能を果たしている。行動形態及び行動連鎖の類似性からみて、ブリッジング行動は、オスーオス間でペニスをなめたり触ったりしながら抱き合う行動に、コドモ、特にオスのコドモのペニスを代用として使った行動であると考えられる。このため、オスーオス間のブリッジング行動ではメスよりもオスのコドモがよく使われた。一方、利用されるオスのコドモにとっては、ブリッジング行動に使われ、オトナオスとの交渉を反復して持つことには、将来そのオスと安定した社会関係を持つことを容易にするという利益があると思われる。チベットモンキーの群れは、他のマカク属の種と比較してオトナメスに対するオトナオスの割合が高く、オスーオス間には潜在的な緊張が高いと考えられる。オスーオス間では、抱き合い行動などの緊張を緩和するための親和的社会行動が頻繁に行われた。こうしたチベットモンキーの社会の特徴が、オスーオス間、特にワカオスとオトナオス間の社会交渉において、ブリッジング行動が頻繁に行われる事と関係していると考えられる（論文１）。

各オスは群れ内の特定のコドモと親和的関係を形成していた。オスは、相手オスと親和的関係にあるコドモを他のコドモより頻繁にブリッジング行動に使っていた。オスは、相手オスとコドモとの親和的関係を認知し、その知識に基づいてブリッジング行動に使うコドモを選択していたと示唆される（論文２）。

オスーメス間では、オスは相手メスの産んだコドモをそのメスとのブリッジング行動に使っていた。そして、この選択がブリッジング行動の成功率を高めていた。また、オスは、自分とコンソート関係にあるメスと頻繁にブリッジング行動を行っていた。オスーメス間のブリッジング行動は、コンソート関係の維持と関係していると考えられる（論文３）。

論文２、３より、チベットモンキーのオスは、自分を含まない他者と他者の間の社会関係を認知し、相手個体と親密な関係にあるコドモをブリッジングに選択するという巧妙な手段によって、相手個体との社会交渉をより円滑にしていると考えられる。

主論文1

「Bridging behavior and other affiliative interactions among male Tibetan macaques *(Macaca thibetana)*.」

（チベットモンキーのオス間におけるブリッジング行動と他の親和的交渉）

Title: Bridging Behavior and Other Affiliative Interactions among Male Tibetan Macaques (*Macaca thibetana*)

Running title: Bridging Behavior among Tibetan Macaques

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ABSTRACT

Bridging behavior and social relationships between adult males and infants were studied in a free-ranging group of Tibetan macaques (*Macaca thibetana*) at Mt Huangshan, China. Tibetan macaques performed bridging behavior in which two adult males simultaneously lifted up an infant, sucked or touched the infant's genitalia, and then groomed each other in non-agonistic contexts Males also expressed social behaviors with other males, such as mounting, penis-sucking, and embracing while touching each other's penes. Males may perform bridging, in which they use 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 maintain affiliative social relationships with other males, much the same as with other dyadic affiliative social behavior between males. Males had frequent interactions with male infants, such as holding, grooming, penis-sucking, and using them in bridging Although these interactions might not have a positive influence on infant survival, these interactions might facilitate the maintenance of affiliative relationships with adult males until they reach maturity High socionomic sex ratio (adult male / adult female), and frequent interactions between males, especially between adolescent males and adult males, might have a close relation to the development of males' use of infants in bridging behavior which have contributed to frequent male-infant interactions

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 (review in Whitten, 1987). In monogamous species, such as marmosets, tamarins, and titis, adult males carry their own offspring and provide benefits for the infant (Epple 1975; Kleiman, 1977) On the contrary, in multi-male multi-female groups of macaques and baboons, males interact with infants less frequently than males of monogamous species (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 their care-taking in their offspring (Trivers, 1972)

By contrast, frequent affiliative male-infant interactions have been observed in multi-male multi-female groups of Tibetan macaques *(Macaca thibetana)*. Male Tibetan macaques occasionally show social behavior in which two individuals simultaneously lift up one infant (Deng, 1993). This behavior is defined as 'bridging' behavior in this paper Male Barbary macaques *(Macaca sylvanus)* also perform similar bridging, and have frequent interactions with infants (Deag and Crook, 1971, 1980; Kuester and Paul, 1986; Smith and Pepper Smith, 1982; Taub, 1980a) Deag and Crook (1971) proposed the 'agonistic buffering' hypothesis to explain the function of this behavior 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 the 'enforce baby-sitting' hypothesis. Related males such as matrilineal siblings may use a related infant for bridging between them, inform one another which infant is their relative, and developed a special 'care-taking' relationship with the infant. The same form of social behavior has been anecdotally reported in the genus *Macaca*: *Macaca arctoides* (Estrada, 1977, 1984), *M. fascicularis* (de Waal et al , 1976), and *M. assamensis* (Kawamoto, personal communication).

Also, similar triadic male-infant interactions were reported in baboons *(Papio cynocephalus, P anubis, Theropithecus gelada).* Male baboons who carry an infant during agonistic male-male encounters may exploit an infant to reduce the probability of being threatened and to increase their relative dominance rank (Dunbar, 1984; Packer, 1980; Ransom and Ransom, 1971; Smith and Whitten, 1988; Smuts, 1985; Stein, 1984; Strum, 1984), although males may be protecting their possible offspring from aggression by immigrant males (Busse and Hamilton, 1981) During some of these interactions, males may solicit support of the infant's mother and develop a social relationship with the mother (Dunbar, 1984; Smith and Whitten, 1988; Smuts, 1985; Stein, 1984)

In this study, bridging among male Tibetan macaques is examined to understand the functions of this behavior Because bridging in Barbary macaques has been extensively studied on the basis of quantitative data, and seems similar to that in Tibetan macaques, the 'agonistic buffering' and the 'enforce baby-sitting' hypotheses will be tested in Tibetan macaques The

'agonistic buffering' hypothesis predicts that (1) males who 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 'enforce baby-sitting' hypothesis predicts that (1) males interact with their related infants, and (2) infants who interact with males derive benefits from the interactions. Next, bridging in male Tibetan macaques is compared to triadic male-infant interactions of other nonhuman primates. Finally, bridging is discussed, from the point of view of the social structure of Tibetan macaques.

MATERIALS

This study was conducted at 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). Among these groups, the 'Yulingkeng' group (Wada et al , 1987) has been studied extensively since 1985 All individuals of the study group were identified based on physical characteristics This group was provisioned only during the study periods to facilitate observations Monkeys were given corn four times a day at a feeding station. Matrilineal kinships and population changes of the study group caused by birth, death, and male transfer, have been known since 1985 (Wada and Xiong, in preparation) Table I shows the age-sex composition of the study group. Tibetan macaques live in stable multi-male multi-female groups. Males

emigrate from their natal group after sexual maturity, while females remain in their natal group throughout their lives. Females mature at 5 years of age and males at 6-7 Infants are mainly born from early January to early May (Deng and Zhao, 1987; Zhao and Deng, 1988a; 1988b; 1988c).

METHODS

Data was collected during four mating seasons (September to January) and one birth season (March to April) from 1989 to 1992 (see Table I). Total observation time was 70,404 minutes. Observations were conducted both at the feeding station and in the forest

While individuals fed at the feeding station, all occurrence behavior sampling (Altmann, 1974) was used. Based on this sampling, supplanting behavior showed that adult males were ranked in a linear hierarchy

In the forest, data was obtained by focal animal sampling (Altmann, 1974) during study periods 1, 4, and 5. Mean focal sampling time on 12 immatures was 847 (range: 561-1469) minutes During focal sampling, I also recorded all-occurrences of male-infant interactions ad libitum (Altmann, 1974): holding infants by males, males' grooming infants, genital-sucking of infants by males, and males' use of an infant in bridging During periods 2 and 3, when male-male encounters were observed, the entire sequence of the male-male interaction was recorded until one of the males left the other These data were analyzed to examine the proximate effects of social behavior on the subsequent male-

male interactions. During mating seasons, males formed consortships with particular females A consortship is defined as a male-female dyad who maintain prolonged proximity mainly due to the male's frequent following of the female. I recorded these consortships each day

Social behaviors recorded during the observations are described.

1 Bridging behavior: two individuals simultaneously lifted up one infant (Figure 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 Infants were handled gently and rarely showed resistance or gave signs of distress. The infant's mother was quite tolerant of males' handling her infant

2. Penis-showing behavior: a male raised his leg and showed his penis to another male. The latter male sometimes responded to penis-showing by touching the penis or other body parts of the former male with his hand.

3. Presenting behavior: a male standing in close proximity to another male showed his genital region, as is observed among females.

4. Penis-sucking or genitalia-sucking behavior: a male sucked the penis of another male, while they embraced one another with teeth-chattering and vocalizations In some cases, males sucked their penes mutually While holding an infant, males sucked the infant's genitalia, occasionally turning the infant upside down

5. Embracing: males embraced and touched the penes of one another with teeth-chattering and vocalizations.

6. Holding: a male sat and hugged an infant ventrally for about one minute to over twenty minutes, keeping his arms on the infant's back. While holding an infant, males sometimes carried the infant ventrally

7 Mounting: a male mounted another male while teeth-chattering and vocalizations, assuming a similar posture to that of a copulating male-female pair

RESULTS

Male-male interactions and bridging behavior

1. Social contexts of bridging behavior

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

2. Sequence of interactions between males.

Further analysis of bridging and other male-male interactions during non-agonistic contexts was conducted. Bridging occurred during triadic male-infant interactions, while other social behaviors such as penis-showing, presenting, embracing, penis-sucking, and mounting mainly occurred during dyadic male-male encounters (Figure 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 the males handles an infant The sequence of TMII can be classified into three types. Type 1: a male who held an infant, carried and presented the infant to another male. In this type, the approaching male carried an infant to initiate bridging behavior with another male. Type 2: a male approached another male who was holding an infant In this type, a male holding an infant did not necessarily hold the infant for bridging. The approaching male initiated the bridging Type 3: other cases, such as when a male approached another male, one of the male held a nearby infant and presented the infant to the other males, 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 other 345 dyadic male-male encounters, the approaching male showed 26(7.5%) presenting and 8(2.3%) penis-showing behaviors. All these behaviors, except one instance of presenting, were performed by the subordinate male. During 345 dyadic male-male encounters, 43(12.5%) mounting, 17(4.9%) embracing, and 2(0.6%) penis-sucking behaviors occurred, while only 1(0.2%) mounting and 3(0.6%) embracing occurred during 482 TMII In male-male dyads, dominant males did not mount subordinate males more frequently than vice versa (Wilcoxson matched pairs signed rank test, T=24, n=21, n.s.)

3. Distribution of bridging behavior among males.

Table II shows the distribution of bridging recorded during three types of TMII In each type of TMII, an approaching male is defined as the initiator of the bridging In male-male dyads, when a male frequently initiated bridging with another male, the latter male also frequently initiated bridging with the former male (Spearman's rank correlation, r_S=0 56, n=21, p<0.01)

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

Effects of dominance rank on the occurrence of bridging shows that lower-ranking males more frequently initiated bridging than did higher-ranking males, and higher-ranking males were more frequently chosen for a recipient male in bridging than lower-

ranking males were (Figure 3) In type 1 TMII, higher-ranking males were approached by another male who was holding an infant more frequently than were lower-ranking males (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 did higher-ranking males, although the correlation was 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 (Wilcoxson matched pairs signed rank 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 percent of approaching in which an infant was carried (Wilcoxson matched pairs signed rank test, T=0, n=21, $p<0.01$) In type 2 TMII, higher-ranking males who were holding an infant were more likely to be approached by another male than were lower-ranking males who were holding an infant, based on the percent of holding infants in which there was an approach (Spearman's rank correlation, r_S=-0.93, n=7, $p<0.05$)

4. Effects of bridging behavior on the subsequent interactions.

After bridging, close-proximity (within hand-reaching distance) 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

(Figure 4). No aggressive interaction was observed after bridging in any type of TMII, while 9(7 4%) aggressive interactions occurred when 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 whom 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 (Wilcoxson matched pairs signed rank test, T=37, n=21, n.s.). Males initiated bridging behavior more frequently with a male from whom they received grooming more frequently, although the correlation was not significant (Spearman's rank correlation, r_S=0.25, n=21, n.s.) Finally, males more frequently groomed another male from whom they received grooming more frequently (Spearman's rank correlation, r_S=0.38, n=21, p<0.01) Thus, males who frequently performed bridging with each other, frequently groomed each other after bridging between them.

Male-infant interactions.

1. Development of social behavior of immatures with adult males.

Social interactions between adult males and immatures during four mating seasons (periods 1, 2, 4, and 5) were analyzed

(Figure 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 times per hour on the average, male infants were used in bridging 0.43 times per hour, and female infants were used 0 04 times per hour. Compared to immature females, juvenile and adolescent males had frequent interactions with adult and adolescent 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, although they held infants in dyadic interactions. Adolescent females approached, presented their genitalia to, and groomed adult males, which was similar to the interactions between adult males and adult females.

2. Male's preference for infants.

The frequency of holding infants by adult and adolescent males is used as an index of males' preference for infants. Males frequently held the same infant whom 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 the cases in which bridging occurred (Kendall rank correlation, τ=0 60, n s , in period 1; τ=0 64, $p<0.01$, in period 2; τ=0 50, n.s , in period 4; τ=0 64, $p<0.01$, in period 5) Young infants

(<1 year) were held by males more frequently than were old infants (1-2 years) (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, male infants were held by males more frequently than female infants 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 who formed consortships, and females who had a young infant during the mating season, males held an infant more frequently than expected in four(15.4%) of 26 consort male-female pairs, while only in eleven(7 5%) of 147 non-consort male-female pairs (Fisher's exact probability test, P=1 89, n s) Among natal males and young infants, natal males held an infant more frequently than expected in zero(0.0%) of 6 male-male pairs within the same matrilineage, and in seven(17 9%) of 39 non-related 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 did non-natal males (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 was the natal adolescent male CS in periods 1 and 2, and was 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, who 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 supports the 'agonistic buffering' hypothesis. (1) Subordinate males, who had more probability of being attacked, initiated bridging behavior more frequently than did dominant males. In addition, compared to dominant males, subordinate males were more likely to approach dominant males when they themselves or the recipient male held an infant than when neither male held an infant. When subordinate males without holding an infant approached dominant males, the former males sometimes showed presenting or penis-showing. These indicate that potential tension existed between adult males, and that subordinate males had to reduce the tension by means of these appeasement behaviors. (2) Bridgings rarely occurred in agonistic contexts. This indicates that males did not confine this behavior to avoid imminent aggression from dominant males. Rather, males might perform bridging to avoid potential aggression in the group. (3) Bridging was never followed by

aggressive interactions, although a male who 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 who frequently performed bridging with each other, formed or expected to form affiliative social relationships by frequent social grooming When neither the approaching male nor recipient male handled an infant, males sometimes performed mounting, embracing and penis-sucking This might indicate that males performed these greeting behaviors when there was no nearby infant available Thus, males might perform bridging, not only to reduce the probability of aggression, but to promote the subsequent affiliative interactions between males Just as other affiliative behaviors such as mounting, embracing, and penis-sucking, bridging seems a type of affiliative behavior in which males exploit an infant as a social tool

Testing the 'enforce baby-sitting' hypothesis.

Data obtained from this study does not support the 'enforce baby-sitting' hypothesis. (1) Based on holding an infant by males, natal males did not prefer infants of their own matrilineage to other infants. It was not clear if males prefer their possible offspring, because paternity of infants is unknown in this group However, adolescent males and newly immigrant males who rarely copulated with adult females in the preceding

mating season, also had affiliative interactions with infants. These indicate that frequent affiliative interactions between males and particular infants had no close relation with their kinship

(2) No evidence was obtained suggesting that frequent interactions with males were crucial for infants' survival All infants who did not have interactions with any adult males also survived during the study period. Although female infants had less frequent interactions with adult males than did male infants, population changes from 1985 to 1992 (Wada and Xiong, in preparation) show no sex difference in a 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 care-taking by the infant's mother, birth intervals after sons should be shorter than those after daughters. However, population parameters (Wada and Xiong, in preparation) show no difference in mean birth intervals: 15.3 month after sons, and 17 1 month after daughters, among 25 countable 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 were 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 up one infant in non-agonistic contexts.

In summary, bridging among Tibetan macaques has the following features. Most bridgings occurred in non-agonistic contexts. Infants were handled gently and rarely showed resistance. The infant's mother was tolerant of males' handling her infant. Lower-ranking males and adolescent males initiated bridging frequently. Bridging was often followed by social grooming between the males. Male infants were more frequently used than were female infants. Particular infants were used by each male in bridging Natal males did not hold infants of their own matrilineage more frequently than other infants. Contacts with males did not have a positive influence on infant survival These features above are common with those of Barbary macaques (Deag, 1980; Deag and Crook, 1971; Kuester and Paul, 1986; Smith and Pepper Smith, 1982; Taub, 1980a, 1984). The occurrence rate of bridging is also similar: 0 35 /hour / male in Tibetan macaques, and 0 43 /hour /male in Barbary macaques (Smith and Pepper Smith, 1982). The 'agonistic buffering' hypothesis (Deag and Crook, 1971) and the 'enforce baby-sitting' hypothesis (Taub, 1980a, 1984) were proposed to explain the function of bridging among Barbary macaques The 'enforce baby-sitting hypothesis' is based on the finding that frequent affiliative interactions were observed between males and particular infants, and that bridging was frequently observed between males who preferred the same infant (Taub, 1980a) However, natal males did not have frequent affiliative interactions with infants of their own matrilineage than other infants, and frequent interactions with males were not

crucial for infants' survival (Kuester and Paul, 1986). Therefore, it remains in question which infants were preferred by males and why males preferred the particular infants in bridging

Male Tibetan macaques initiated bridging with their consort females more frequently than with other non-consort females, in which cases they used an offspring infant of the female (Ogawa, in preparation) This results, to some extent, in the male's affiliative interaction with the infant of his consort females, although the effect of consortships upon male preference for infants was not significant in this study Furthermore, in bridging between males, males used an infant whom a recipient male preferred, probably because that infant was more effective for appeasement than other infants (Ogawa, in preparation) The observed preference for a certain infant could be caused by the following processes without the effect of kinship 1) one male preferred a certain infant such as a young male infant or the infant of his consort female. 2) other males used that particular infant for bridging with the male. 3) these males preferred that infant both in bridging with each other and in dyadic male-infant interactions. This process should cause a tendency for lower-ranking males to prefer the same infant whom higher-ranking males prefer, if the preference of the higher-ranking males does not change. Kuester and Paul (1986) reported the correspondent tendency that young male Barbary macaques, who were generally lower-ranking, preferred the same infants as old males did

There are some differences between bridging in Tibetan macaques and that in Barbary macaques. Male Tibetan macaques

usually carried an infant ventrally as did female Tibetan macaques, while male Barbary macaques did so dorsally (Deag, 1971) This causes some difference in the form of bridging between the two species Male Tibetan macaques used infants even after infants were over one year of age, while male Barbary macaques changed their use of older infants to new born infants in each birth season (Deag, 1980) In addition, bridging in Tibetan macaques might be connected with other various affiliative behavior between males, as discussed below

The relation between bridging behavior and social relationships among males and infants.

Socionomic sex ratio (adult male / adult female) of Tibetan macaques is high, compared with other nonhuman primates (Caldecott, 1986) The mean sex ratio of the study group from 1985 to 1992 was 0.94 (Wada and Xiong, in preparation) and that of groups at Mt Emei was 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 perform frequent and various affiliative behaviors with body contact. By contrast, in other 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 ratio than did Tibetan and bonnet macaques. This indicates that such social behavior of Tibetan and bonnet macaques may reduce social tension between males. The reduction of social tension may solicit males' tolerance of each other and may result in high socionomic sex ratio, in spite of high potential competition between males. Male Tibetan macaques have frequent interactions with infants, compared to other macaques such as *Macaca fuscata* (Alexander, 1970; Hiraiwa, 1981) and *Macaca mulatta* (Vessey and Meikle, 1984) 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 such dyadic behavior into triadic bridging behavior. Bridging of Tibetan macaques may be closely connected with affiliative behaviors such as embracing and penis-sucking in which males touched or sucked the penis of a recipient male. Males might use an infant, especially the infant's penis, as a substitute for their own penis, probably because it is more effective for appeasement. This may be one of reasons why adult males used male infants more frequently than female infants

The tolerance of the infant's mother is necessary for males to use her infant in bridging In Barbary macaques, estrous females frequently copulate with most of the males in the group, and so each male seems a possible father of each 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 the female. However, because the consortships changed within one mating season, and females copulate with non-consort males as well as their consort males, females copulate with many males in the group throughout one mating season In addition, females do not show clear sexual swelling during their estrous cycle (Zhao, 1993), and copulate even after their conception during the prolonged mating season (Zhao and Deng, 1988b; Wada and Xiong, in preparation). This mating system may also make paternity of infants uncertain, reduce the probability of infanticide, and may affect the mother's tolerance.

Male Tibetan macaques emigrate from their natal group after sexual maturity (Zhao, 1994) Natal adolescent males especially had frequent affiliative interactions with infants. In the study group, two natal males who had frequently initiated bridging with adult males, stayed in their natal group after maturity, and became the highest-ranking males, although the phenomenon that natal males stayed in their natal group after maturity, is one of the byproducts of provisioning as reported in *Macaca fuscata* (Sugiyama and Osawa, 1982) On the contrary, five immigrant adolescent males who had no interaction with infants, rarely interacted with adult males. Three of the five males did not raise their dominance rank before they emigrated from the study group. Although frequent interaction with adult males is not essential for an infant's survival, these interactions 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 Tibetan macaques, high socionomic sex ratio and frequent interactions between adult males, especially between adult and adolescent males, might have a close relation to the development of males' use of infants in bridging behavior which have contributed to frequent male-infant interactions

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REFERENCES

Alexander, B K. (1970) Paternal behavior of adult male Japanese monkeys. *Behaviour* 36: 270-285.

Altmann, J. (1974) Observational study of behaviour: sampling methods. *Behaviour* 49: 227-265.

Busse, C., and Hamilton, W J (1981) Infant carrying by male chacma baboons. *Science* 212: 1281-1283.

Caldecott, J O. (1986). Mating patterns, societies and the ecogeograghy of macaques. *Aim. Behav* 34: 208-220

Deag, J M., and Crook, J H (1971) Social behaviour and "agonistic buffering" in the wild Barbary macaques, *Macaca sylvana L. Folia Primatol* 15: 183-200

Deag, J M. (1980) Interactions between males and unweaned Barbary macaques: testing the agonistic buffering hypothesis. *Behaviour* 75: 54-81

Deng, Z. and Zhao, Q. (1987) Social structure in a wild group of *Macaca thibetana* at Mount Emei, China. *Folia Primatol* 49: 1-10.

Deng, Z. (1993) Social development of infants of *Macaca thibetana* at Mount Emei, China *Folia Primatol* 60: 28-35.

Drickammer, L. C., (1976) Quantitative observation of grooming behaviour in free-ranging *Macaca mulatta. Primates* 17: 323-335.

Dunbar, R. I (1984) Infant-use by male gelada in agonistic contexts: agonistic buffering, progeny protection or soliciting support? *Primates* 25: 28-35.

Epple, G (1975) The behavior of marmoset monkeys

(*Callithricidae*). In Rosenblum (ed.), *Primate behavior: developments in field and laboratory research, Vol 4.*, Academic Press, New York, pp 195-239

Estrada, A. (1977) Social relationships in a free-ranging troop of stumptail macaques *(Macaca arctoides)*: male-care behaviour I *Primates* 18: 793-813.

Estrada, A. (1984). Male-infant interactions among free-raging stumptail macaques. In Taub, D. M. (ed.). *Primate paternalism*, New York, Van Nostrand Reinhold, pp.56-87.

Itani, J. (1959) Paternal care in the wild Japanese monkey, *Macaca fuscata fuscata. Primates* 2: 61-93

Hiraiwa, M. (1981) Maternal and alloparental care in a troop of free-ranging Japanese monkeys. *Primates* 22: 309-329.

Koyama, N (1973) Dominance, grooming and clasped-sleeping relationships among bonnet monkeys in India. *Primates* 14: 225-244.

Kurland, J A , and Gaulin, S. J C. (1984) The evolution of male paternal investment: effects of genetic relatedness and feeding ecology on the allocation of reproductive effort In Taub, D M. (ed.), *Primate paternalism*, New York, Van Nostrand Reinhold, pp 259-308.

Kleiman, D. G. (1977) Monogamy in mammals. *The quarterly review of Biology* 52: 39-69

Kuester, J , and Paul, A. (1986) Male-infant relationships in semifree-ranging Barbary macaques *(Macaca sylvanus)* of Affenberg Salem / FRG: testing the "male care" hypothesis. *Am. J Primatol* 10: 315-327

Mori, A (1975) Signals found in the grooming interactions of

wild Japanese monkeys of Koshima troop. *Primates* 16: 107-140.

Mori, A. (1977). Intra-troop spacing mechanism of the wild Japanese monkeys of Koshima troop. *Primates* 18: 331-357.

Ogawa, H. (in preparation). Recognition of social relationships in bridging behavior among Tibetan macaques (*Macaca thibetana*)

Ogawa, H. (in preparation) Triadic male-female-infant relationships and bridging behavior among Tibetan macaques (*Macaca thibetana*)

Packer, C. (1980) Male care and exploitation of infants in *Papio anubis. Anim. Behav.* 28: 512-520.

Ransom, T. W , and Ransom, B. S (1971) Adult male-infant relations among baboons *(Papio anubis). Folia Primatol* 16: 179-195

Silk, J B , and Samuels, A (1984) Triadic interactions among *Macaca radiata*: passports and Buffers. *Am. J. Primatol.* 6: 373-376.

Simonds, D. E. (1965) The bonnet macaque in south India. In de Vore (ed.) *Primate behavior: field studies of monkeys and apes*, Holt, Rinehart and Winston, New York, pp.175-196.

Smith, E. O , and Pepper Smith, P G. (1982) Triadic interactions in captive Barbary macaques *(Macaca sylvanus, linnaeus*, 1758): "agonistic buffering"? *Am. J. Primatol.* 2: 99-107

Smith, E. O., and Whitten, P L. (1988). Triadic interactions in savanna-dwelling baboons. *Int J. Primatol.* 9: 409-424

Smuts, B B. (1985) *Sex and friendship in baboons*. Hawthorne,

New York, Aldine.

Stein D. N. (1984). *The sociobiology of infant and adult male baboons.* Norwood, New Jersey, Albex.

Strum, S. C. (1984) Why males use infants. In Taub, D. M. (ed.),*Primate paternalism*, New York, Van Nostrand Reinhold, pp 20-55

Sugiyama, Y (1971) Characteristics of the social life of bonnet macaques (*Macaca radiata*) *Primates* 12: 247-266

Sugiyama, Y , and Osawa, H. (1982) Population dynamics of Japanese monkeys with special reference to the artificial feeding. *Folia Primatol.* 39: 238-263.

Takahata, Y (1982) Social relations between adult males and females of Japanese monkeys in the Arashiyama B troop. *Primates* 231: 1-23

Taub, D. M. (1980a) Testing the "agonistic buffering" hypothesis. *Behav. Ecol Sociobiol* 6: 187-197

Taub, D. M. (1980b) Female choice and mating strategies among wild Barbary macaques (*Macaca sylvanus L.*) In Lindburg, D. G. (ed), *The macaques: studies in ecology. behavior, and evolution,* New York, Van Nostrand Reinhold, pp.287-344.

Taub, D. M. (1984) Male caretaking behavior among wild Barbary macaques (*Macaca sylvanus*) In Taub, D M. (ed.), *Primate paternalism*, New York, Van Nostrand Reinhold, pp 20-55

Trivers, R. L. (1972) Paternal investment and sexual selection In B. Campell (ed), *Sexual selection and the descent of man,* Aldine, Chicago, pp136-179.

Vessey, S. H , and Meikle, D B (1984) Free-ranging rhesus monkeys: adult male interactions with infants and juveniles.

In Taub, D. M. (ed.), *Primate paternalism*, New York, Van Nostrand Reinhold, pp 113-126.

de Waal, F B. M., van Hooff, J A. R. A M., and Netto, W J (1976). An ethological analysis of types of agonistic interaction in a captive group of Java monkeys (*Macaca fascicularis*) *Primates* 17: 257-290.

Wada, K., Xiong, C., and Wang, Q. (1987) On the distribution of Tibetan and rhesus monkeys in southern Anhui, China. *Acta Thrologica*. 7: 148-176

Wada, K., and Xiong, C. (in preparation) Population changes of Tibetan monkeys with special regard to birth interval

Whitten, P L. (1987) Infants and adult males In Smuts, B., Cheney, D., Seyfarth, R , Wrangham, R., and Struhsaker, T (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp.343-357

Zhao, Q. (1993). Sexual behavior of Tibetan macaques at Mt Emei, China. *Primates* 34: 431-444.

Zhao, Q. (1994) Mating composition and intergroup transfer of males in Tibetan macaques *Macaca thibetana* at Mt Emei, China. *Primates* 35: 57-68.

Zhao, Q., and Deng, Z. (1988a) *Macaca thibetana* at Mt Emei, China: I A cross-sectional study of growth and development *Am. J. Primatol* 16: 251-260

Zhao, Q., and Deng, Z. (1988b) *Macaca thibetana* at Mt. Emei, China: II Birth seasonality *Am. J Primatol* 16: 261-268

Zhao, Q., and Deng, Z (1988c) *Macaca thibetana* at Mt Emei, China: I Group composition. *Am. J Primatol* 16: 269-273.

CAPTION

Figure 1 Bridging behavior between adult male Tibetan macaques

A: an adult male is holding an infant. B: a male carries and presents an infant to a second male. C: Two males simultaneously lift up an infant in a non-agonistic context

Figure 2. Sequence of social behavior during male-male encounters.

Male-male encounter: a male approached another male in non-agonistic contexts Type 1-3 TMII: each type of triadic male-infant interaction in which two males were in close proximity and at least one of the males handled an infant (see text) Each figure shows the number and percent of social behaviors recorded during male-male encounters.

Figure 3. Direction of approaching 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 (see text) Bridging: number of bridging behaviors recorded during male-male encounters.

Figure 4　Percent of social grooming and close-proximity after bridging behavior

Percent of social grooming between males and close-proximity (within hand reaching distance) for more than one minutes after bridging behavior and non-bridging behavior　After bridging behavior: bridging behavior occurred when one of males handled an infant　After non-bridging behavior: bridging behavior did not occur, because a male did not receive an infant provided by another male when one of males handled an infant.　Type 1-3: types of triadic male-infant interactions (see the text).　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

Figure 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 holding in which a focal animal was involved, per hour per possible recipient individual　Bridging /hr /individual: mean number of bridging in which a focal animal was involved, per hour per possible recipient individual

Table 1. The age-sex composition of the study group for each study period

	Study period	Period 1		Period 2 ##		Period 3 #		Period 4 ###		Period 5	
	Month/Date/Year	12/05/'89-01/21/'90		11/18/'90-01/11/'91		03/30/'91-04/23/'91		12/05/'91-01/15/'92		09/18/'92-11/04/'92	
	Observation time (minutes)	13596		18166		8063		13582		16997	
Age-class	Years of age	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Adult	(Male : ≧ 8 years of age) (Female: ≧ 5 years of age)	6	5	5	7	5	7	5	8	9	9
Subadult	(Male : 6-7 years of age)	0	-	1	-	1	-	2	-	1	-
Adolescent	(Male :4-5 years of age) (Female:4 years of age)	2	2	1	2	1	2	6	1	5	2
Old Juvenile	(3 years of age)	0	2	1	1	1	1	4	2	2	1
Young Juvenile	(2 years of age)	1	1	1	2	1	2	2	1	1	4
Old Infant	(1 year of age)	1	2	2	1	2	1	1	4	0	3
Young Infant	(< 1 year of age)	2	1	1	4	1	4	0	3	4	1
Total		12	13	12	17	12	17	20	19	22	20

Sixteen infants were born from 1989 to 1992.
Fourteen males immigrated into and seven males emigrated from the group from 1989 to 1992.
#: composition in period 3 was same as that in period 2. Although one female infant was born at the last day of period 3, it was not included in the table.
##: one adult female died in period 2.
###: one adult, five adolescent, and three juvenile males immigrated into the group in the period 4.
However, two adolescent and one juvenile males emigrated from the group, and one juvenile male died in period 4.

Table 1

Table 2

Table II. Distribution of bridging behavior among adult and adolescent males

Type of TMII #			Type 1								Type 2								Type 3							
Approacher			Recipient								Recipient								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	6					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

Number of bridging behaviors during type 1-3 TMII.
Bridging behavior after aggressive interactions was not included.
#: TMII (triadic male-infant interactions) are classified into three types (in the text).

Table 3

Table III. Number of holding an infant by adult and adolescent males

Study period	Holder male						Infant (sex)					Total
Period 1	Name	Age	Age-calss	Rank	Natal	New comer	ZM(m)	GHG(m)	BX(f)			
	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 k			61
	CS	4	AD	8	yes	no	48 *	30	1			79
	Total						115	98	3			214
Period 2	Holder male						ZCT(m)	ZZ(f)	YM(f)	GHR(f)	ZTZ(f)	
	HM	8+	A	2	?	no	33 *c	1 c	8	10 c	1	53
	WS	8+	A	3	no	no	29 *		25 *c	8	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 *	1 c	1 c	2 c		58
	CS	5	AD	7	yes	no	203 *					203
	Total						392	20	41	19	5	477
Period 4	Holder male						YTT(f)	GFT(f)	CBX(f)			
	HM	8+	A	2	?	no	6 c	4 c				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
Period 5	Holder male						GHL(m)	ZTB(m)	ZCS(m)	ZB(m)	YZ(f)	
	HM	8+	A	3	?	no	1 c	3	c	1 c	1 c	6
	EX	8+	A	7	no	no	3	5	1	1	1	11
	IBB	8+	A	4	no	no	5 c	6	9 c	2 c	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 *	12 c	1	#	51
	CS	7	sA	1	yes	no	10	4	14 *	4		32
	ZY	5	AD	8+	no	no	c	3	3 c			6
	GY	5	AD	8+	no	no						0
	ZW	4	AD	8+	yes	no	3	1 k	3 k	9 k		16
	AD	4	AD	8+	no	no						0
	YG	4	AD	8+	yes	no	2		1	1	k	4
	Total						39	88	49	28	3	205

Age class: A - adult, sA subadult, AD adolescednt.
Natal: yes natal, no non-natal, ? unknown.
New comer: yes a male who immigrated into the study group during the study period,
no a resident male who had been resident in the study group in the preceding study period.
*: an infant who was held by each male more frequently than expected. Chi-square test, *=p<0.05.
Expected value of each cell = number of holding infants by each male / number of young infants.
c: a male who's mother formed a consortship with each male.
k: a male who is of the same matrilineage with each natal male.

Figure 1

Figure 2

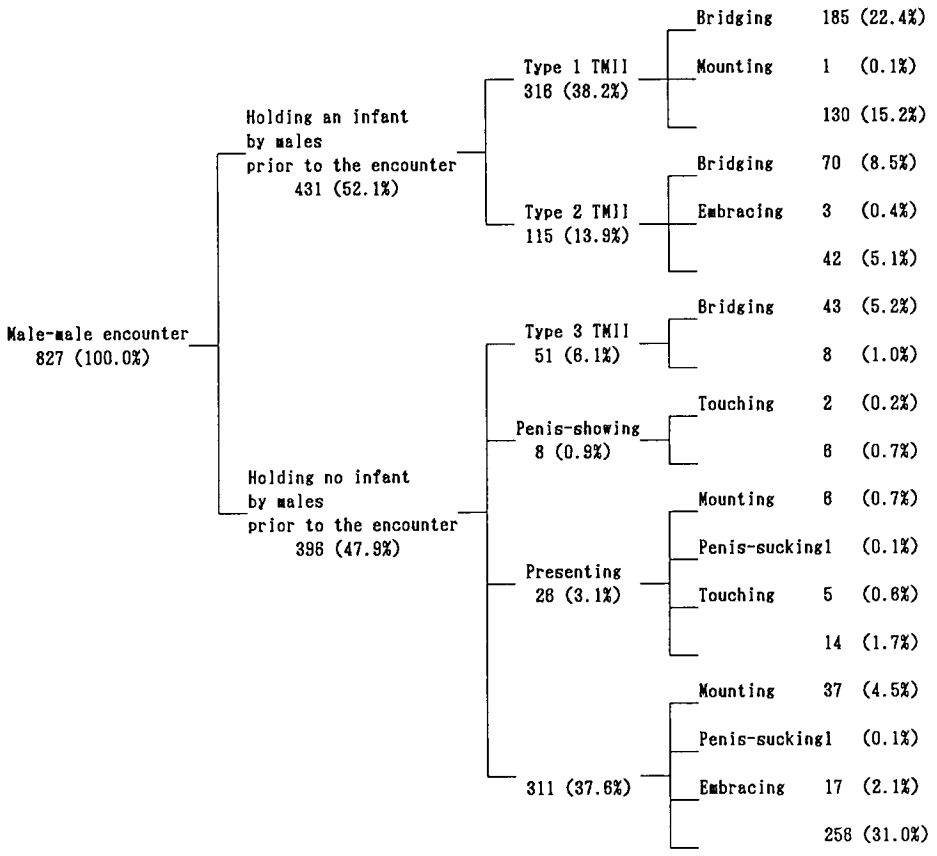

Male-male encounter
827 (100.0%)
Holding an infant
by males
prior to the encounter
431 (52.1%)
Holding no infant
by males
prior to the encounter
396 (47.9%)
Type 1 TMII
316 (38.2%)
Type 2 TMII
115 (13.9%)
Type 3 TMII
51 (6.1%)
Penis-showing
8 (0.9%)
Presenting
26 (3.1%)
311 (37.6%)
Bridging 185 (22.4%)
Mounting 1 (0.1%)
130 (15.2%)
Bridging 70 (8.5%)
Embracing 3 (0.4%)
42 (5.1%)
Bridging 43 (5.2%)
8 (1.0%)
Touching 2 (0.2%)
6 (0.7%)
Mounting 8 (0.7%)
Penis-sucking 1 (0.1%)
Touching 5 (0.6%)
14 (1.7%)
Mounting 37 (4.5%)
Penis-sucking 1 (0.1%)
Embracing 17 (2.1%)
256 (31.0%)

Figure 3

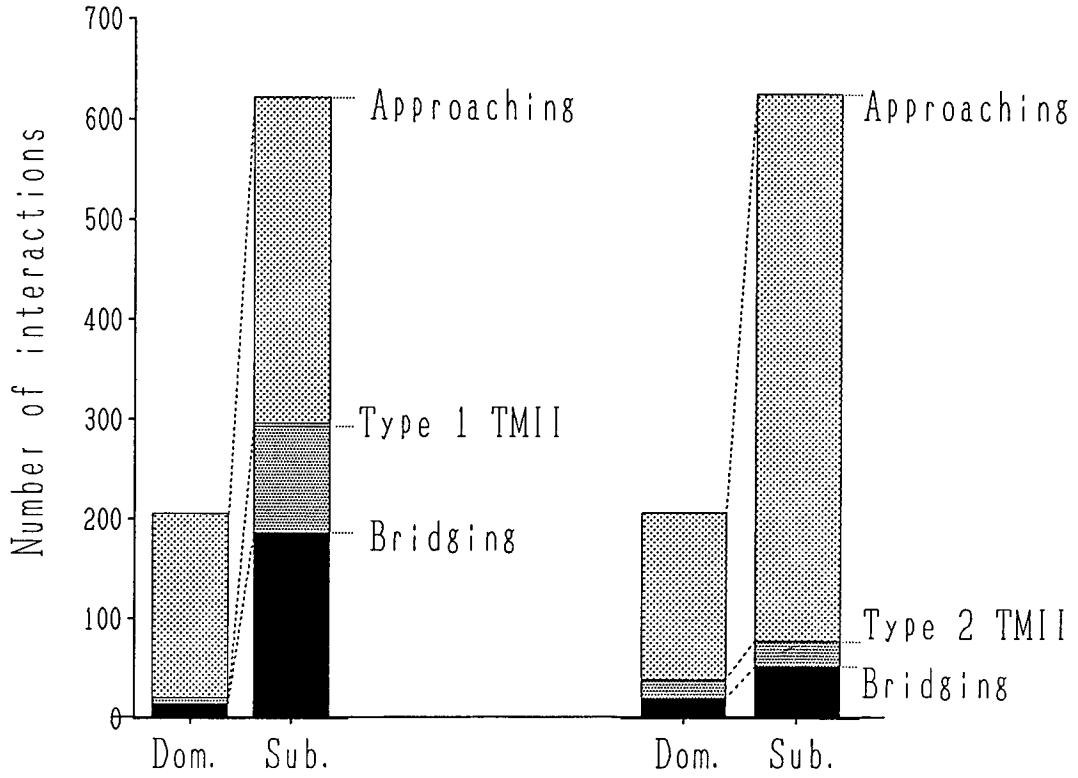

Number of interactions
700
600
500
400
300
200
100
0
Approaching
Type 1 TMII
Bridging
Approaching
Type 2 TMII
Bridging
Dom.
Sub.
Dom.
Sub.

Figure 4

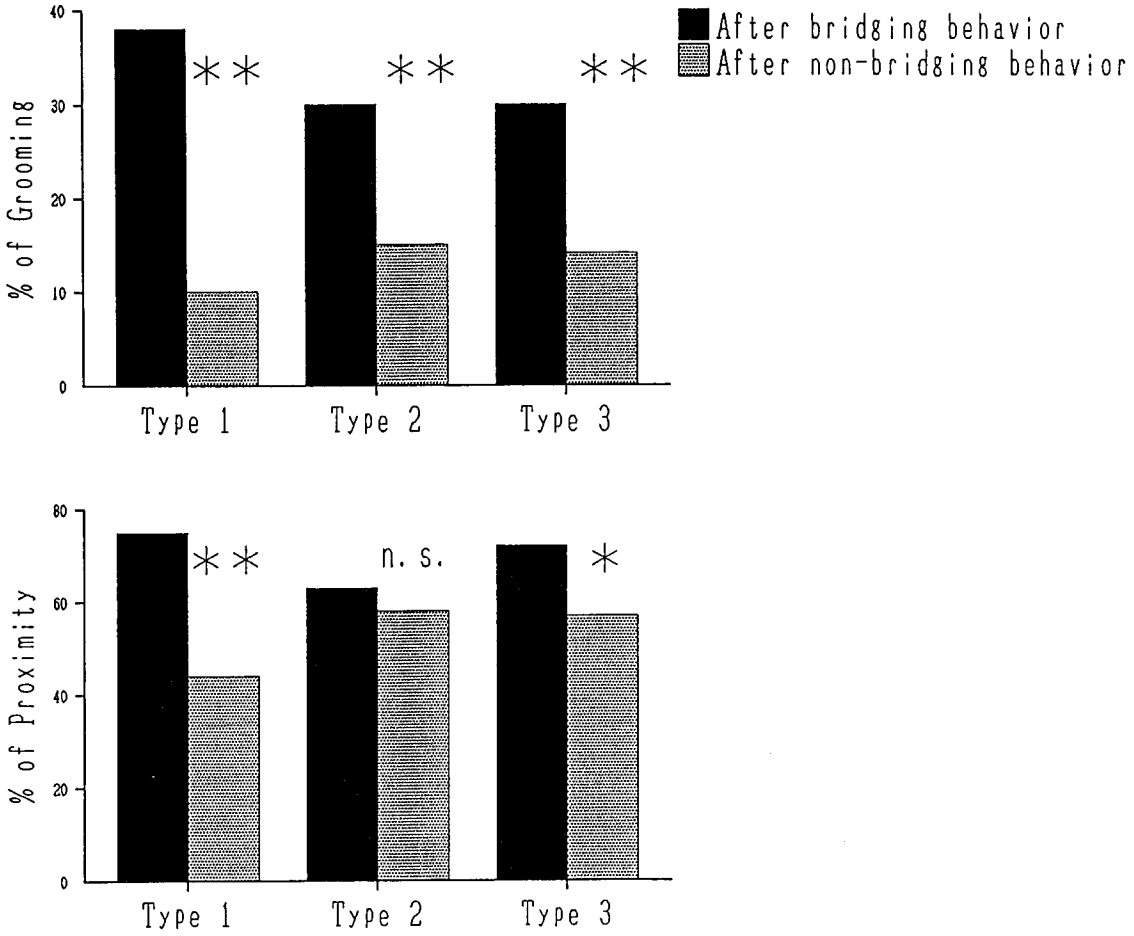
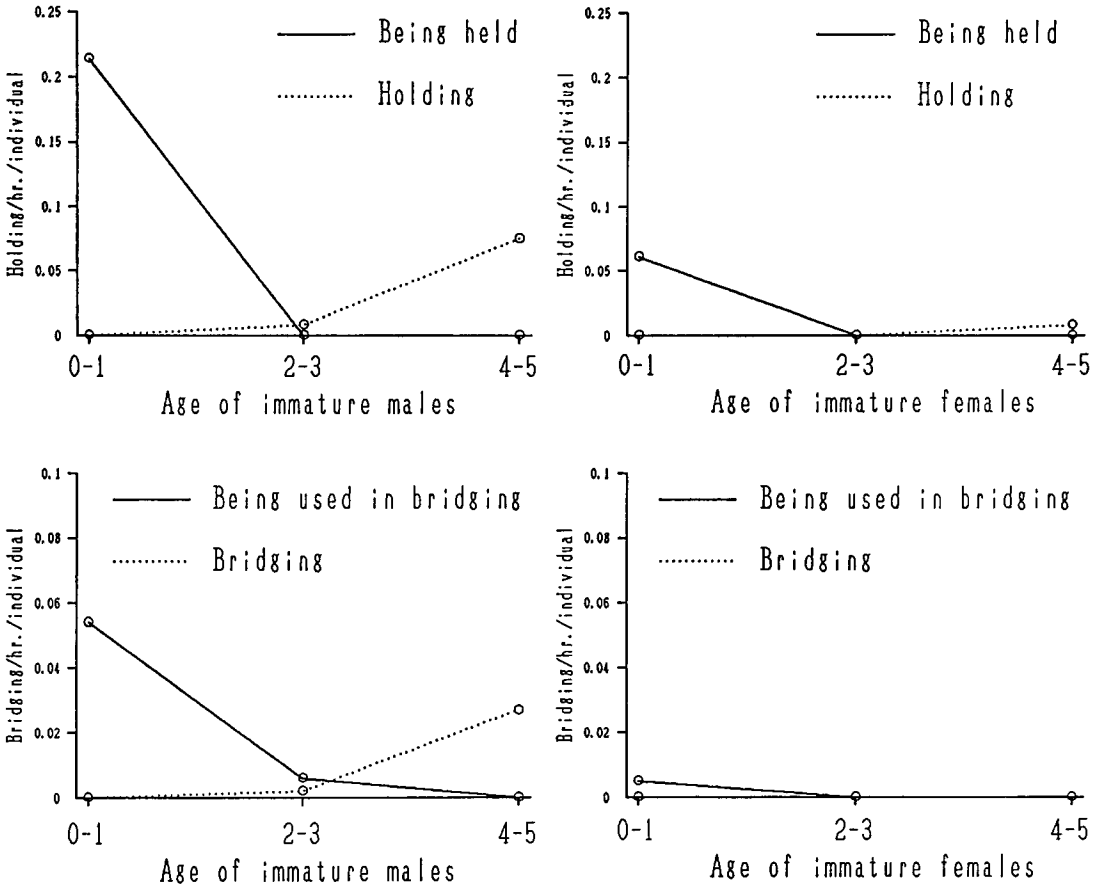

After bridging behavior
After non-bridging behavior
% of Grooming
40
30
20
10
0
**
**
**
Type 1
Type 2
Type 3
% of Proximity
80
60
40
20
0
**
n. s.
*
Type 1
Type 2
Type 3

Figure 5


Being held
Holding
Holdings/hr./individual
0.25
0.2
0.15
0.1
0.05
0
0-1
2-3
4-5
Age of immature males
Being held
Holding
Holdings/hr./individual
0-1
2-3
4-5
Age of immature females
Being used in bridging
Bridging
Bridgings/hr./individual
0.1
0.08
0.06
0.04
0.02
0
0-1
2-3
4-5
Age of immature males
Being used in bridging
Bridging
Bridgings/hr./individual
0-1
2-3
4-5
Age of immature females

主論文2

「Recognition of social relationships in bridging behavior among Tibetan macaques *(Macaca thibetana)*.」

(チベットモンキーのブリッジング行動における社会関係の認知)

Title: Recognition of Social Relationships in Bridging Behavior among Tibetan Macaques (*Macaca thibetana*)

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ABSTRACT

Bridging behavior among male Tibetan macaques (*Macaca thibetana*) was studied in a free-ranging group at Mt. Huangshan, China. This behavior was defined as a type of affiliative behavior in which two individuals simultaneously lifted up one infant. Bridging behavior occurred after an adult male carried an infant to another male or approached another male who was holding an infant Each male frequently held and groomed a particular infant in the group, which was named an 'affiliated' infant of the male. Males were more frequently provided with their affiliated infant by other males than with other non-affiliated infants This finding suggests that male Tibetan macaques recognized the affliative relationship between a male and his affiliated infant, and chose that infant for bridging behavior on the basis of this knowledge. Such choice might be important for effective bridging behavior or other affiliative interactions between males

Key words

bridging behavior, affiliated infant, recognition of relationships, Tibetan macaque, agonistic buffering

INTRODUCTION

Most nonhuman primate societies consist of a variety of social relationships. Under such complex circumstances, individuals should modify their behavior according to social relationships among other individuals, as well as those between themselves and others [Harcourt, 1988] Nonhuman primates identify each other [e.g Hansen, 1976] and recognize the relationships between themselves and others [Gouzoules, 1984; Fredrickson & Sackett, 1984]. Furthermore, a laboratory experiment provided evidence that *Macaca fascicularis* was able to recognize the social relationships between other individuals, such as those of mother-infant pairs in the group [Dasser, 1988]. Indeed, recent studies have suggested that nonhuman primates such as *Cercopithecus aethiops* [Cheney & Seyfarth, 1986, 1989] and *Pan troglodytes* [de Waal, 1989] may use such knowledge to manipulate others during polyadic interactions

In the present study, I analyzed triadic male-infant interactions among Tibetan macaques (*Macaca thibetana*). In this species, males often simultaneously lifted up one infant [Deng, 1993], as observed in Barbary macaques *(Macaca sylvanus)* [Deag & Crook, 1971; Taub, 1980] This behavior is named 'bridging' behavior in this report Bridging behavior has been reported in *Macaca arctoides* [Estrada, 1977; Hendy & Rhine, 1977], *M. fascicularis* [de Waal et al , 1976], and *M. assamensis* [Kawamoto, personal communication] Similar interactions, in which one of two males held an infant during agonistic male-male encounters, have been reported in *Papio cynocephalus* and *P anubis* [Ransom &

Ransom, 1971; Strum, 1984; Stein, 1984; Smuts, 1985] and *Theropithecus gelada* [Dunbar, 1984]. Deag and Crook [1971] proposed the 'agonistic buffering' hypothesis which stated that lower-ranking males carried an infant to reduce the likelihood of an agonistic response from higher-ranking males.

In the above species, males interacted with particular infants during both triadic and dyadic male-infant interactions [Taub, 1980; Packer, 1980; Estrada, 1984; Strum,1984; Stein, 1984; Dunbar, 1984; Smuts, 1985; Whitten, 1987; Smith & Whitten, 1988] Male Tibetan macaques also often hold or groom particular infants, and use the same infants in bridging behavior (see Results) If male Tibetan macaques recognize 1) the affiliative relationships between males and particular infants, and 2) males' preferences for those infants for use in bridging behavior, then they might be expected to choose an infant based on the social relationship between the recipient male and the infant To test this prediction, I examined whether males frequently used such an infant for bridging behavior with another male.

METHODS

Tibetan macaques live in stable multi-male multi-female groups, as reported in studies at Mt Emei, China [Zhao & Deng , 1988a, 1988b, 1988c] Nine groups of wild Tibetan macaques inhabit Mt. Huangshan (30°29'N, 118°11'W) in the Anhui province, China [Wada et al , 1987] Among these groups, the 'Yulingkeng' group [Wada et al , 1987] has been studied extensively since 1985. All individuals were identified by physical

characteristics. Matrilineal kinships and male transfers have been known since 1985. Based on birth records, this group consisted of 25 individuals including 6 adult males (>7 years), 2 natal adolescent males (4-6 years), and 6 infants (<2 years) during the study period. Monkeys were given corn four times a day at a feeding station to facilitate observations.

Adult and adolescent males were ranked in a linear hierarchy on the basis of supplanting behavior, based on all occurrence behavior sampling [Altmann, 1974] while subjects fed at the feeding station.

In the forest, data was obtained by focal animal sampling on a continuous basis [Altmann, 1974] during an 88 day period from December 5, 1989 to January 21, 1990 and from March 12 to April 20, 1990. During focal sampling, I also recorded all-occurrences of male-infant interactions ad libitum [Altmann, 1974] Total observation time was 37,208 minutes, and mean focal observation time was 3,021 (range: 2,725-3,606) minutes on three infants (<1 year). and 1,290 (range: 1,195-1,454) minutes on the other three infants (1-2 years) Frequency of holding an infant by males recorded by ad libitum sampling showed highly significant correlations with data from focal sampling (Kendall rank correlation test, T=0.86, $p<0.01$, in the case of three infants; T=0.64, $p<0.01$, in the case of one infant), or, in the other cases, holding an infant was not observed during either of the observations Therefore, the data from both focal sampling and ad libitum sampling was analyzed in this study Bridging behavior was defined as a behavior in which two individuals simultaneously lifted up one infant Details of this behavior

are described in another report [Ogawa, in preparation].

RESULTS

During the study period, 70 instances of grooming between adult males and infants, 240 bridging behaviors between males, and 713 holding an infant by males, were recorded.

Table I shows the distribution of holding an infant, excluding those cases in which holding was used for bridging behavior. Males held four of six infants in the group. All males, except for one male, held infants non-randomly among those four infants. Here, an infant who was held by a given male most frequently is regarded as the male's 'affiliated' infant. Infants who were held frequently by a male, were also frequently used in bridging behavior by that male (Kendall rank correlation test, τ=0.48, $p<0.01$), and were also frequently groomed by that male (Kendall rank correlation test, τ=0.53, $p<0.01$).

Of the 229 interactions in which a male carried and presented an infant to another male, 142(62.0%) resulted in bridging behavior (Table II) Of the 146 interactions in which a male approached another male who was holding an infant, 98 (67 1%) resulted in bridging behavior During bridging behavior, the two males sat facing one another with teeth-chattering, simultaneously lifted up the infant and sucked or touched the penis or genitalia of the infant. Lower-ranking males more frequently initiated bridging behavior than did higher-ranking males (Wilcoxon signed rank test, T=41, n=28, $p<0.05$) Furthermore, within male-male dyads, each male was more likely to

be provided with his affiliated infant by other males than with other non-affiliated infants (Wilcoxon signed rank test, $Z=3.1$, $n=47$, $p<0.01$). Based on the relationships males and infants, all male-male dyads were classified into two groups When both males had the same affiliated infant, they carried their affiliated infant to each other more frequently than other infants (Fig. 1). When males had different affiliated infants, they also carried the other male's affiliated infant to him more frequently than other infants (Fig 1).

DISCUSSION

While handling an infant, male macaques [Itani, 1959; Deag and Crook, 1971] and male baboons [Ransom & Ransom, 1971; Strum, 1984; Stein, 1984] may use the infant to regulate relationships with another male, especially to reduce the likelihood of an agonistic response from a higher-ranking male (agonistic buffering) In Tibetan macaques, this hypothesis is supported by the present finding that lower-ranking males more frequently initiated bridging behavior than did higher-ranking males.

Each male frequently held and groomed his affiliated infant Male preference for his affiliated infant may be affected by a consortship with the infant's mother [Ogawa, in preparation] Under such circumstances, an affiliated infant of recipient male might be more effective for agonistic buffering than other infants In fact, male Tibetan macaques used the affiliated infant of recipient males for bridging behavior Male Barbary macaques also performed bridging behavior in which males

frequently used an infant with whom they formed affiliative relationships [Taub, 1980, 1984]. Young male Barbary macaques, who were lower-ranking, frequently interacted with the same infants as did old males [Kuester & Paul, 1986] These findings may suggest that males interacted with affiliated infants of higher-ranking males to perform bridging behavior with those males Males could not make this choice depending on the response of the recipient male, because approaching males were rarely attacked by the recipient male even when they carried non-affiliated infants to him. Male Tibetan macaques might recognize the relationship between a male and his affiliated infant, and on the basis of this knowledge, choose that infant for bridging behavior Such choice might be important for effective bridging behavior or other affiliative interactions between males.

CONCLUSIONS

1. Male Tibetan macaques frequently held and groomed a particular infant, which was named the male's affiliated infant.
2. Males more frequently provided recipient males with affiliated infant of the recipient male than with other non-affiliated infants.
3. Males may recognize the affiliative relationship between a male and his affiliated infant, and choose that infant for bridging behavior on the basis of this knowledge.

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REFERENCES

Altmann, J Observational study of behaviour: Sampling method. BEHAVIOUR 49:227-265, 1974.

Cheney, D L ; Seyfarth, R.M. The recognition of social alliances by vervet monkeys. ANIMAL BEHAVIOUR 34:1722-1731, 1986.

Cheney, D L.; Seyfarth, R.M. Reconciliation and redirected aggression in vervet monkeys, *Cercopithecus aethiops.* BEHAVIOUR 110:258-275, 1989.

Dasser, V A Social concept in Java monkey ANIMAL BEHAVIOUR 36:225-230, 1988

Deag, J M ; Crook, J H. Social behavior and "agonistic buffering" in the Barbary macaque, *Macaca sylvana L.* FOLIA PRIMATOLOGICA 15:183-200, 1971.

Deng, Z. Social development of infants of Macaca thibetana at Mount Emei, China. FOLIA PRIMATOLOGICA 60:28-35, 1993.

Dunbar, R.I Infant-use by male gelada in agonistic contexts: agonistic buffering, progeny protection or soliciting support ? PRIMATES 25:28-35, 1984.

Estrada, A. Social relationships in a free-ranging troop of stumptail macaques *(Macaca arctoides)*: Male-care behaviour I PRIMATES 18:793-813, 1977

Estrada, A Male-infant interactions among free-ranging stumptail macaques, pp6-87 in PRIMATE PATERNALISM. Taub, D.M., ed New York, Van Nostrand Reinhold, 1984

Frederickson, W T ; Sackett, G.P Kin preferences in primates (*Macaca nemestrina*): Relatedness or familiarity ? JOURNAL OF COMPARATIVE PSYCHOLOGY 98:29-34, 1984.

Gouzoules, S. Primate mating systems, kin associations, and cooperative behaviour: Evidence for kin recognition ? YEARBOOK OF PHYSICAL ANTHROPOLOGY 27:99-134, 1984

Harcourt, A.H. Alliances in contests and social intelligence, pp132-152 in MACHIAVELLIAN INTELLIGENCE: SOCIAL EXPERTISE AND THE EVOLUTION OF INTELLECT IN MONKEYS, APES, AND HUMANS Byrne, R.W.; Whiten, A., eds. Oxford, Clarendon Press, 1988.

Hansen, E.W. Selective responding by recently separated juvenile rhesus monkeys to the calls of their mothers. DEVELOPMENTAL PSYCHOBIOLOGY 9:83-88, 1976.

Hendy, N H.; Rhine, R.J Social development stumptailed macaques (*Macaca arctoides*): Momentary touching and other interactions with adult males during the infant's first 60 days of life. PRIMATES 19:589-600, 1977

Itani, J Paternal care in the wild Japanese monkey, *Macaca fuscata fuscata*. PRIMATES 2:61-93, 1959

Kuester, J ; Paul, A. Male-infant relationships in semifree-ranging Barbary macaques *(Macaca sylvanus)* of Affenberg Salem/FRG: Testing the "male care" hypothesis. AMERICAN JOURNAL OF PRIMATOLOGY 10:315-327, 1986.

Ogawa, H Bridging behavior and other affiliative interactions among Tibetan macaques *(Macaca thibetana)*. in preparation.

Packer, C. Male care and exploitation of infants in *Papio anubis*. ANIMAL BEHAVIOUR 28:512-520, 1980

Ransom, T W ; Ransom, B.S. Adult male-infant relations among baboons (*Papio anubis*) FOLIA PRIMATOLOGICA 16:179-195, 1971

Strum, S.C. Why males use infants, pp146-185 in PRIMATE PATERNALISM. Taub, D.M. ed New York, Van Nostrand Reinhold,

1984.

Smith, E.O.; Whitten, P.L. Triadic interactions in savanna-dwelling baboons. INTERNATIONAL JOURNAL OF PRIMATOLOGY 9:409-424, 1988.

Smuts, B.B. SEX AND FRIENDSHIP IN BABOONS. Hawthorne, New York, Aldine, 1985.

Stein D.N THE SOCIOBIOLOGY OF INFANT AND ADULT MALE BABOONS. Norwood, New Jersey, Albex, 1984.

Taub, D.M. Testing the "agonistic buffering" hypothesis. BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY 6:187-197, 1980.

Taub, D.M. Male caretaking behavior among wild Barbary macaques (*Macaca sylvanus*), pp20-55 in PRIMATE PATERNALISM. Taub, D.M ed. New York, Van Nostrand Reinhold, 1984.

de Waal, F B.M.; van Hoof, J.A.R.A.M.; Netto, W J An ethological analysis of agonistic interaction in a captive group of Java monkeys (*Macaca fascicularis*). PRIMATES 17:257-290, 1976

de Waal, F B.M. PEACEMAKING AMONG PRIMATES. Cambridge, Massachu setts, Harvard University Press, 1989.

Wada, K.; Xiong C.; Wang, Q. On the distribution of thibetan and rhesus monkeys in southern anhui, China. ACTA TEOLOGICA SINICA 7:148-176, 1987

Whitten, P L. Infants and adult males, pp. 343-357 in PRIMATE SOCIETIES, Smuts, B , Cheney, D , Seyfarth, R., Wrangham, R., and Struhsaker, T eds. Chicago, University of Chicago Press, 1987

Zhao, Q.K.; Deng, Z.Y *Macaca thibetana* at Mt Emei, China: I A cross-sectional study of growth and development AMERICAN JOURNAL OF PRIMATOLOGY 16:251-260, 1988a.

Zhao, Q.K.; Deng, Z.Y *Macaca thibetana* at Mt.Emei, China: II. Birth seasonality. AMERICAN JOURNAL OF PRIMATOLOGY 16:261-268, 1988b.

Zhao, Q.K.; Deng, Z.Y *Macaca thibetana* at Mt.Emei, China: III Group composition. AMERICAN JOURNAL OF PRIMATOLOGY 16:269-273, 1988c.

LEGENDS

Fig. 1 Affiliated and non-affiliated infants used in bridging behavior.

The percent of all cases in which an infant was held, in which either an affiliated or non-affiliated infant was carried to another male Affiliated infant: a male was provided with his affiliated infant. Non-affiliated infant: a male was provided with his non-affiliated infant. Same: an initiator male's affiliated infant was the same infant as that of a recipient male (Wilcoxon signed rank test, n=10, T=0, *=P<0 05) Different: an initiator male's affiliated infant was different from that of a recipient male (Wilcoxon signed rank test, n=37, T=67, *=P<0.05).

Table 1

Table 1. Number of Holding an Infant by Adult and Adlescent Males

Male			Infant (0-1 yr)						Total
Name	Age (yrs)	Rank	Name Age Sex	ZM <1 yr Male	GHG <1 yr Male	BX <1 yr Female	YG 1 yr Male	BS 1 yr Female	ZK 1 yr Female	
HM # *	>8	1		5	5	10	2	0	0	22
WS **	>8	2		15 **##	7	6	2	0	0	30
EX **	>8	3		6	8	28 **	2	0	0	42
YSZ **	>8	4		105 **	13	4	16	0	0	138
IBB **	>8	5		9	20 **	0	2	0	0	31
CY	>8	6		1	0	0	1	0	0	2
BD **	6	7		30	74 **	1	16	0	0	121
CS **	5	8		68 **	36	2	17	0	0	123
Total				239	163	49	58	0	0	509

#: a male who did not hold infants randomly. Chi-square test, *=p<0.05, **=p<0.01
##: an infant who was held by each male more frequently than expected.
Chi-square test, **=p<0.01. Expected value of each cell = total number of infants by each male / 4 (number of infants who were held by males).

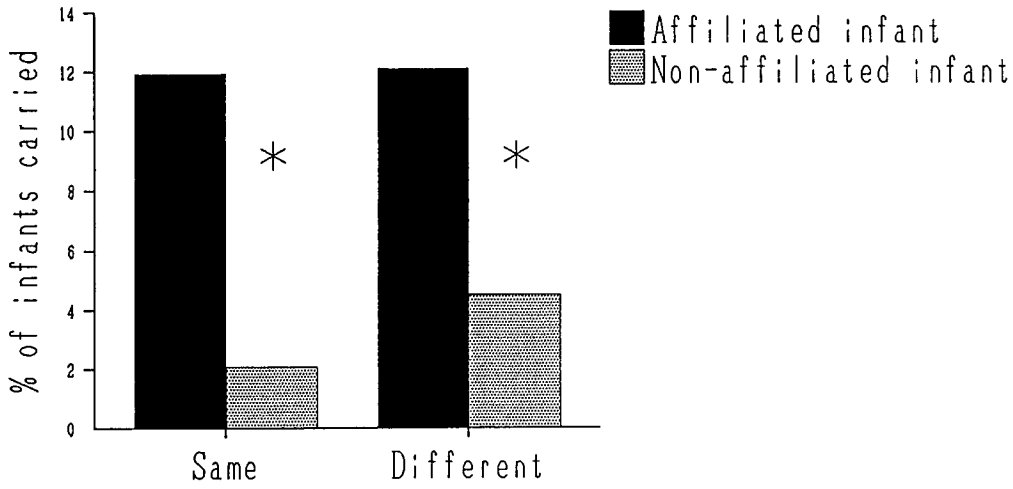
Table 2

Table 11. Distribution of Bridging Behavior among Adult and Adolescent Males

Initiating male #	Recipient male ##								Total
	HM	WS	EX	YSZ	IBB	CY	BD	CS	
HM		1	8	1	0	0	0	0	10
WS	4		8	3	1	0	0	0	16
EX	8	2		2	0	0	0	0	12
YSZ	15	6	5		4	2	0	3	35
IBB	12	1	1	3		0	0	0	17
CY	4	1	2	0	0		0	0	7
BD	13	6	6	7	0	0		6	38
CS	0	0	0	2	0	1	4		7
Total	56	17	30	18	5	3	4	9	142

Number of bridging behaviors among adult and adolescent males is shown.
#: initiating male is a male who carried an infant to another male prior to the bridging behavior.
##: recipient male is a male who was provided with an infant by the initiating male.

Figure 1


% of infants carried
14
12
10
8
6
4
2
0
Same
Different
Affiliated infant
Non-affiliated infant
*
*

主論文３

「Triadic male-female-infant relationships and
bridging behavior among Tibetan macaques *(Macaca thibetana)*.」

(チベットモンキーにおけるオスーメスーコドモ３者の社会関係と
ブリッジング行動)

Title: Triadic male-female-infant relationships and bridging behavior among Tibetan macaques (*Macaca thibetana*)

Short title: Triadic relationships and bridging behavior

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Triadic interaction

Social cognition

Consortship

Agonistic buffering

Infant carrying

Affiliative behavior

Social tool

Abstract

Bridging behavior between males and females was studied in a free-ranging group of Tibetan macaques (*Macaca thibetana*) at Mt. Huanshan, China. Bridging behavior is defined as a behavior in which two individuals simultaneously lift up an infant. Male-female bridging behavior occurred in non-agonistic contexts, and was more frequently followed by social grooming between the partners than when bridging behavior did not occur. This indicates that bridging behavior is an affiliative social behavior in which an infant was used as a social tool. Males initiated bridging behavior more frequently than did females. However, males did not carry an infant to a female for 'agonistic buffering'. Males were most likely to carry an infant to its mother. This indicates that males recognized mother-infant pairs in the group, and that males specifically chose the female's offspring for bridging behavior. The choice of the female's offspring made the occurrence of bridging behavior more likely. During the mating season, higher-ranking males formed consortships with particular females by maintaining prolonged proximity to them. Males performed bridging behavior with their consort females more frequently than with non-consort females, and more frequently than during other non-consort periods. Male-female bridging behavior might contribute to the development and maintenance of consortships.

Introduction

Triadic interactions in which two individuals simultaneously lift up an infant have been reported in the genus *Macaca*: *Macaca sylvanus* [1-8], *M. arctoides* [9-11], *M. fascicularis* [12], *M. assamensis* [personal communication, Kawamoto], and *M. thibetana* [13-15]. In this paper, this behavior is called 'bridging' behavior An individual who is holding an infant sometimes approaches or is approached by another individual, the two individuals then lift up the infant simultaneously, and lick or manipulate the infant's genitalia [1-15].

Male-male bridging behavior has been studied most intensively in *Macaca sylvanus* [1-8] Subordinate males carry an infant to dominant males to reduce the likelihood of an aggressive response from the dominant male (agonistic buffering), although dominant males occasionally carry an infant to subordinate males [3,4] Tibetan macaques also perform similar male-male bridging behavior [13-15] In this species, male-male bridging behavior occurred in non-agonistic contexts and promoted subsequent affiliative social interactions between males [15] Thus, male-male bridging behavior was a type of affiliative behavior in which males used an infant as a social tool to develop and maintain social relationships with other males

Male Tibetan macaques also perform bridging behavior with females as well as with males In this paper, male-female bridging behavior is analyzed on the basis of data obtained during four mating seasons. The function of male-female bridging behavior is analyzed and compared to male-male bridging behavior.

Finally, bridging behavior is discussed in the context of triadic male-female-infant social relationships.

Materials and Methods

This study was conducted on a free-ranging group of Tibetan macaques at Mt Huangshan in Anhui province, China, from 1989 to 1992. Nine groups of wild Tibetan macaques inhabit Mt. Huangshan [16]. Among these groups, the 'Yulingkeng' group [16] has been studied extensively since 1986 All individuals of this group were identified based on physical characteristics, and were provisioned only during the study periods to facilitate observations. The 'Yulingkeng' group is a multi-male multi-female group. the same social structure as the Tibetan macaques in Mt. Emei, China [17,18]. Table 1 shows the age-sex composition of the study group for each study period No births were recorded during each study period. Hence, the birth season was estimated to be similar to that at Mt Emei, where females give birth from mainly early January to early May (mean: March) [19]

The data were obtained during four mating seasons from September to January (table 1) Total observation time was 62,341 minutes. Both focal animal sampling and ad libitum sampling methods [20] were used. During focal animal sampling, I also recorded all bridging behaviors and triadic male-female-infant interactions observed ad libitum. Bridging behavior was defined as a behavior in which two individuals simultaneously lifted up an infant A triadic male-female-infant interaction

was defined as an interaction in which a male and a female were in close proximity and at least one of the pair handled an infant.

Adult and subadult males were ranked in a linear hierarchy based on supplanting behaviors, which were recorded using the all occurrence behavior sampling method [20] while individuals fed at the artificial feeding site. Adult and subadult males were divided into two major dominance rank classes: half of all males were higher-ranking and the others were lower-ranking. All newly immigrant males were lower-ranking in each study period. All higher-ranking males were dominant to all adult and adolescent females.

Consortships, which were characterized by a male frequently following a particular female, were recorded each day Among them, seven consort male-female pairs were analyzed in detail on the basis of 2,774 minutes of focal sampling during their consort periods. Male social relationships with their consort and non-consort females were analyzed on the basis of the Hinde's index ([proportion of male approaches] - [proportion of male leaves])[21], and percent of time spent in 2.5 m proximity (within a distance of 2.5 m) and close-proximity (within hand-reaching distance)

Results

Patterns of triadic male-female-infant interactions and distribution of male-female bridging behavior

Table 2 shows patterns and social contexts of triadic male-

female-infant interactions. A total of fifty-four bridging behaviors were recorded during the study periods. Only four (7.4%) of the bridging behaviors occurred in agonistic or tense social contexts. The other fifty (92.6%) bridging behaviors occurred when no conspicuous interaction was observed among any group members prior to the bridging behavior Twenty (37.0%) bridging behaviors occurred when an individual who was holding an infant carried it to another individual, and nineteen (35.2%) occurred when an individual holding an infant was approached by another. Fifteen (27 8%) bridging behaviors occurred in other contexts, such as when one individual approached another, handled a nearby infant, and then presented the infant to the recipient Prior to triadic male-female-infant interactions, males held the infant more frequently than did females (Chi-square test, X^2=9.34, p< 01) and males approached females more frequently than vice versa (Chi-square test, X^2=9.34, p<.01) During triadic male-female-infant interactions, subsequent social grooming between the male and the female occurred more frequently after bridging behavior was observed (27 of 54: 50 0%) than when bridging behavior did not occur, i e. when the recipient individual refused the infant provided by the other individual (8 of 59: 13.5%) (Fisher's exact probability test, p< 01) One copulation and three genital inspections occurred during these interactions

Table 3 lists the males and females who performed bridging behaviors. Among twenty-nine adult and subadult males, eight (57%) of fourteen higher-ranking males performed bridging behavior with females, while only three (21%) of fourteen lower-

ranking males did so (Fisher's exact probability test, p=.263, n.s.). Higher-ranking males performed bridging behavior more frequently than lower-ranking males (Mann-Whitney U test, N1: number of higher-ranking male=14, N2: number of lower-ranking male=14, U=50.5, p< 05) Only two (14%) of fourteen adolescent males and two (17%) of twelve juvenile males performed bridging behavior None of the seven immigrant males perform bridging behavior during the study period of their initial arrival

All bridging behaviors involved young infants (less than one year of age). Male infants were involved in seventeen (31%) of fifty-four bridging behaviors, and female infants were involved in thirty-seven (69%) (Chi-square test, X^2=3.3, n s.).

Thus, higher-ranking males were most likely to initiate and perform bridging behavior with adult females, in which young infants were used.

Male-female relationship during consort period

During the mating seasons, a total of forty five consort male-female pairs were recorded. Among adult and subadult males, twelve (86%) of fourteen higher-ranking males formed consortships with females, while only two (14%) of fourteen lower-ranking males did so (Fisher's exact probability test, p= 051, n s)

Figure 1 shows that both 2.5 m proximity and close-proximity were higher with consort females than with non-consort females (Wilcoxon signed rank test, n=7, T=0, p<.05). Hinde's index showed that males were more responsible than females for maintaining proximity to both consort and non-consort females (Wilcoxon signed rank test, T=0, n=7, p< 05) Males were more responsible for maintaining 2.5 m proximity with consort females

than they were with non-consort females (Wilcoxon signed rank test, n=7, T=0, p<.05).

Among adult and adolescent males and females, bridging behavior occurred in eleven (24%) of forty-five consort pairs, while it occurred in only six (2%) of 356 non-consort pairs (Fisher's exact probability test, p<.01). In addition, males performed bridging behavior with consort females during consort periods more frequently than during non-consort periods (Wilcoxon signed rank test, n=11, T=7, p<.05; table 3).

Triadic male-infant-female relationship

The offspring of the recipient female was involved in forty-nine (93%) of fifty-four bridging behaviors (table 3) In addition, when a male first held an infant and carried it to a female, he carried the infant to its mother more frequently than expected by chance (Chi-square test, X^2=76.6, p< 01; figure 2) Figure 2 also shows that bridging behavior occurred more frequently when males carried an infant to its mother (15 of 45: 33%) than when males carried an infant to a female other than its mother (0 of 7: 0%) (Fisher's exact probability test, p< 01).

Discussion

In Tibetan macaques, most male-female bridging behavior occurred in non-agonistic contexts. Furthermore, the likelihood of social grooming between the male and the female was greater if the male-female-infant interaction included bridging behavior These findings are similar to those found for male-male bridging behavior in Tibetan macaques [15] These indicate that male-

female bridging behavior is also a type of affiliative social behavior in which an infant is used as a social tool

Males held male infants more frequently than female infants during dyadic male-infant interactions, and they also used male infants more frequently than female infants during male-male bridging behavior [14] On the contrary, in male-female bridging behavior, female infants were frequently used as much as male infants However, infants were used non-randomly. In most cases, the offspring of the recipient female was used in male-female bridging behavior In addition, when a male held one of infants before approaching a female, the male carried an infant to its mother This indicates that males recognized mother-infant pairs in the group, and that males made specific choices of infant when they carried an infant to a female. Also, in male-male bridging behavior, males were more likely to carry an infant to a male who had formed a special affiliative relationship with the infant [14] These results indicate that males choose infants who are most familiar to the recipient individual This choice could make the triadic interaction more successful. In fact, bridging behavior occurred more frequently when a male carried an infant to its mother than when a male carried an infant to a female other than its mother This means that males not only used an infant as a social tool, but also made the most effective choice of an infant in bridging behavior, by recognizing mother-infant pairs in the group

Male-female bridging behavior was different from male-male bridging behavior in the following way In male-male bridging behavior among Tibetan macaques [14,15] and among *Macaca sylvanus*

3,4], subordinate males carried an infant to dominant males more requently than vice versa. Male *Macaca radiata* [22] and male *apio cynocephalus* [23,24] are less frequently threatened by nother male while they are holding an infant. These data ndicate that holding an infant by males had, to some extent, a unction of 'agonistic buffering' among these males. On the ontrary, in male-female bridging behavior among Tibetan acaques, males initiated bridging behavior more frequently than id females, and higher-ranking males were more likely to perform ridging behavior with females than did lower-ranking males. hese data indicate that males did not carry an infant to a emale for 'agonistic buffering' Immigrant males who were ubordinate to adult females may not have been able to reduce the robability of being attacked by females, because females ometimes did not allow immigrant males to hold their offspring. ales performed bridging behavior only with adult and adolescent emales Males were more likely to perform bridging behavior ith their consort females, with whom males maintained prolonged roximity. Thus, males directed bridging behavior not to females ho were dominant to them, but to females with whom they formed onsortships.

In other species, adult males also frequently interacted and ormed affiliative relationships with particular infants whose others were familiar to them [1,2,23-32] During agonistic ale-male encounters, male *Theropithecus gelada* held and carried nfants in order to solicit support of and develop social elationships with their mothers, as well as to reduce the robability of being threatened and to protect the infant

[27,28]. Similarly, in male-female bridging behavior among Tibetan macaques, males used the most effective means by which to ensure the occurrence of bridging behavior more likely by choosing the offspring infant of the recipient female. Male-initiated bridging behavior was not agonistic buffering but may possibly be affiliative behavior which facilitates the development and maintenance of consortships with females

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References

1 Macroberts MH: The social organization of Barbary apes (*Macaca sylvana)* on Gibraltar Am L Phys Anthropol 1970; 33:83-100.

2 Burton FD: The integration of biology and behavior in the socialization of *Macaca sylvana* of Gibraltar; in Poirier FE (ed): Primate Socialization. New York, Random House 1972.

3 Deag JM, Crook JH: Social behaviour and "agonistic buffering" in the wild Barbary macaques, *Macaca sylvana L.* Folia Primatol 1971;15:183-200.

4 Deag JM: Interactions between males and unweaned Barbary macaques: testing the agonistic buffering hypothesis Behaviour 1980;75:54-81

5 Taub DM: Testing the "agonistic buffering" hypothesis. Behav Ecol Sociobiol 1980;6:187-197.

6 Taub DM: Male caretaking behavior among wild Barbary macaques (*Macaca sylvanus*); in Taub DM (ed.): Primate Paternalism. New York, Van Nostrand Reinhold, 1984,pp20-55.

7 Smith EO, Peffer Smith PG: Triadic interactions in captive Barbary macaques (*Macaca sylvanus, Linnaeus*, 1758): "agonistic buffering"? Am J Primatol 1982;2:99-107

8 Kuester J, Paul A: Male-infant relationships in semi-free-ranging Barbary macaques *(Macaca sylvanus)* of Affenberg Salem / FRG: testing the "male care" hypothesis Am J Primatol 1986;10:315-327

9 Estrada A, Sandoval JM: Social relations in a free-ranging troop of stumptail macaques *(Macaca arctoides)*:

male-care behaviour. Primates 1977;18:793-813.

10 Estrada A: Male-infant interactions among free-raging stumptail macaques; in Taub DM (ed.): Primate Paternalism. New York, Van Nostrand Reinhold, 1984,pp56-87

11 Smith EO, Peffer Smith PG: Adult male-immature interactions in captive stumptail macaques (*Macaca arctoides*); in Taub DM. (ed.): Primate Paternalism. New York, Van Nostrand Reinhold, 1984,pp88-111.

12 de Wall FBM, van Hooff JARAM, Netto WJ: An ethological analysis of types of agonistic interaction in a captive group of Java monkeys (*Macaca fascicularis*) Primates 1976;17: 257-290.

13 Deng ZY: Social development of infant of *Macaca thibetana* at Mount Emei, China. Folia Primatol 1993;60:28-35

14 Ogawa H: Recognition of social relationships in bridging behavior among Tibetan macaques (*Macaca thibetana*) in preparation.

15 Ogawa H: Bridging behavior and other affiliative interactions among male Tibetan macaques (*Macaca thibetana*). in preparation.

16 Wada K, Xiong C, Wang Q: On the distribution of Tibetan and rhesus monkeys in Southern Anhui, China. Acta Thrologica 1987;7:148-176

17 Zhao Q, Deng Z: *Macaca thibetana* at Mt. Emei, China: I Group composition Am J Primatol 1988;16:269-273

18 Deng Z, Zhao Q: Social structure in a wild group of *Macaca thibetana* at Mount Emei, China. Folia Primatol 1988;49:1-10

19 Zhao Q, Deng Z: *Macaca thibetana* at Mt. Emei, China:

II. Birth seasonality. Am J Primatol 1988;16:261-268.

20 Altmann J: Observational study of behaviour: sampling methods. Behaviour 1974;49:227-265.

21 Hinde RA, Atokinson S: Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. Anim behav 1970;18:169-176.

22 Silk JB, Samuels A: Triadic interactions among *Macaca radiata*: passports and buffers. Am J Primatol 1984;6:373-376.

23 Packer C: Male care and exploitation of infants in *Papio anubis*. Anim behav 1980;28:512-520.

24 Stein DN: The sociobiology of infant and adult male baboons. Norwood, New Jersey, Albex. 1984.

25 Strum SC: Why males use infants; in Taub DM (ed.): Primate Paternalism. New York, Van Nostrand Reinhold, 1984,pp146-185.

26 Smuts BB: Sex and Friendship in Baboons. Hawthorne, New York, Aldine, 1985.

27 Mori U: Development of sociability and social status; in Kawai M (ed.): Contributions to Primatology, vol 16: Ecological and Sociological Studies of Gelada Baboons, Basel, S. Karger, 1979.

28 Dunbar RI: Infant-use by male gelada in agonistic contexts: agonistic buffering, progeny protection or soliciting support? Primates 1984;25:28-35.

29 Whitten PL: Infants and adult males; in Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds.): Primate Societies. University of Chicago Press, Chicago, 1987,pp343-357

30 Takahata, Y: Social relations between adult males and females of Japanese monkeys in the Arashiyama B troop. Primates 1982;23:1-23.

31 Kaufmann JH: Social relations of adult males in a free-ranging band of rhesus monkeys; in Altmann SAA (ed.): Social Communication among Primates. Chicago, University of Chicago Press, 1967

32 Breuggeman JA: Paternal care in a group of free-ranging rhesus monkeys (*Macaca mulatta*). Folia Primatol 1973;20: 178-210.

Heading:

Table 1 The age-sex composition of the study group for each study period

Table 2 Patterns of triadic male-female-infant interactions

Table 3 The distribution of male-female bridging behavior

Legend:

Fig. 1 Comparison of male social relationships with consort and non-consort females

Hinde's index: (proportion of male approaches) - (proportion of male leaves) Percent of proximity: duration of proximity as a fraction of focal animal observation time. 2.5 m proximity: within a distance of 2.5 m. Close-proximity: within hand-reaching distance. Consort female: the female with whom a male formed a consortship. Non-consort female: the female with whom a male did not form a consortship. Wilcoxon signed rank test, n=7, *=p<.05.

Fig 2 Number of infants used in bridging behavior

Number of interactions: number of times a male carried an infant to a female and number of bridging behaviors. Male carrying an infant: a male carried an infant to a female. Expected: expected number of times a male carries each infant to a female. That is, (total number of times a male carries infants to the female in a given study period) / (number of young infants in the same study period) Bridging behavior: a male performed bridging behavior with a female. Offspring infant: the offspring of the female was involved in the triadic male-female-infant interaction Other infant: infants other than the offspring of the female were involved in the interaction.

Table 1

	Study period	Period 1		Period 2		Period 3		Period 4	
	Month/Date/Year	12/05/'89-01/21/'90		11/18/'90-01/11/'91		12/05/'91-01/15/'92		09/16/'92-11/04/'92	
	Observation time (minutes)	13598		18186		13582		16997	
Age-class	Years of age	Male	Female	Male	Female	Male	Female	Male	Female
Adult	(Male : ≧ 8 years of age) (Female: ≧ 5 years of age)	6	5	5	7	5	8	9	9
Subadult	(Male : 6-7 years of age)	0	-	1	-	2	-	1	-
Adolescent	(Male :4-5 years of age) (Female:4 years of age)	2	2	1	2	6	1	5	2
Old Juvenile	(3 years of age)	0	2	1	1	4	2	2	1
Young Juvenile	(2 years of age)	1	1	1	2	2	1	1	4
Old Infant	(1 year of age)	1	2	2	1	1	4	0	3
Young Infant	(< 1 year of age)	2	1	1	4	0	3	4	1
Total		12	13	12	17	20	19	22	20

Fourteen males immigrated into and seven males emigrated from the study group from 1989 to 1992.
Sixteen infants were born from 1989 to 1992.
One adult female died in period 2, and one juvenile male died in period 3.

Table 2

Social contexts and pattern of triadic male-female-infant interactions	Number of interactions			
	Approacher			
	Male	Female	Both or unknown	Total
Non-agonistic context				
A holder approached another	52 (15) #	5 (5)		57 (20)
A holder was approached by another	15 (11)	21 (7)		36 (18)
Other cases ##	1 (1)	1 (1)	13 (10)	15 (12)
Agonistic context				
A holder approached another	0 (0)	0 (0)		0 (0)
A holder was approached by another	0 (0)	1 1		1 (1)
Other cases ##	3 (2)	0 (0)	1 (1)	4 (3)
Total	71 (29)	28 (14)	14 (11)	113 (54)

#: number of bridging behaviors is shown in ( ).
##: other cases, such as when a male or a female handled a nearby infant, and then used the infant in bridging behavior.

Study period	Individuals who performed bridging behavior								Number of bridging behaviors					
	Male			Female			#### Consortship		##### Consort period		Non-consort period		Female's Offspring was used	Total
	Name	# Age	## Rank	Name	# Age	### Infant's sex		Duration (Days)		######		######		
Period 1	YSZ	A.	L.	FM	AD.	-	+	14	0	(0.00)	1	(0.03)	0	1
	BD	AD.	-	HH	A.	M.	-	0	-	-	-	-	4	4
Period 2	BD	sA.	H.	HH	A.	F.	+	3	0	(0.00)	2	(0.04)	2	2
	BD	sA.	H.	BH	AD.	-	+	18	3	(0.17)	0	(0.00)	0	3
	HM	A.	H.	HH	A.	F.	+	17	13	(0.76)	2	(0.05)	15	15
	WS	A.	H.	YY	A.	F.	+	18	4	(0.22)	2	(0.05)	6	6
	YBB	A.	L.	ZC	A.	M.	-	0	-	-	-	-	3	3
	CS	AD.	-	ZC	A.	M.	-	0	-	-	-	-	1	1
Period 3	BD	sA.	H.	YT	A.	F.	+	39	3	(0.08)	1	(0.04)	4	4
	HM	A.	H.	FM	A.	F.	+	25	1	(0.04)	0	(0.00)	1	1
	HM	A.	H.	YT	A.	F.	+	2	0	(0.00)	1	(0.02)	1	1
	YBB	A.	(M.)	YT	A.	F.	-	0	-	-	-	-	2	2
	CS	sA.	L.	FM	A.	F.	-	0	-	-	-	-	1	1
	GHG	J.	-	FM	A.	F.	-	0	-	-	-	-	3	3
	GHG	J.	-	BH	A.	F.	-	0	-	-	-	-	1	1
Period 4	CS	sA.	H.	ZC	A.	M.	+	5	1	(0.40)	0	(0.00)	1	1
	BD	A.	H.	HH	A.	M.	-	0	-	-	-	-	2	2
	BD	A.	H.	ZC	A.	M.	+	10	1	(0.10)	0	(0.00)	1	1
	HM	A.	H.	HH	A.	M.	+	8	1	(0.17)	0	(0.00)	1	1
	GHG	J.	-	FM	A.	-	-	0	-	-	-	-	0	1
							Total		27	(0.18)*	9	(0.02)*	49	54

Male-female pairs who performed bridging behavior are listed.
Age: A.=adult; sA.=subadult; AD.=adolescent (see table 1).
Rank: rank class among adult and subadult males, H.=higher-ranking; L.=lower-ranking; (M.)=the 4th-ranking among 7 males.
Infant's sex: sex of young infants (<1 year of age) of the female, M.=male, F.=female, - =no infant.
Consortship: + =the male-female pairs formed consortships, - =the male-female pairs did not form consortships.
Consort period: bridging behaviors occurring during consort periods.
######: mean number of bridging behaviors per day, during consort and non-consort periods.
*: Wilcoxon signed rank test, n=11, T=4, *=p<.05.

Table 3

Figure 1

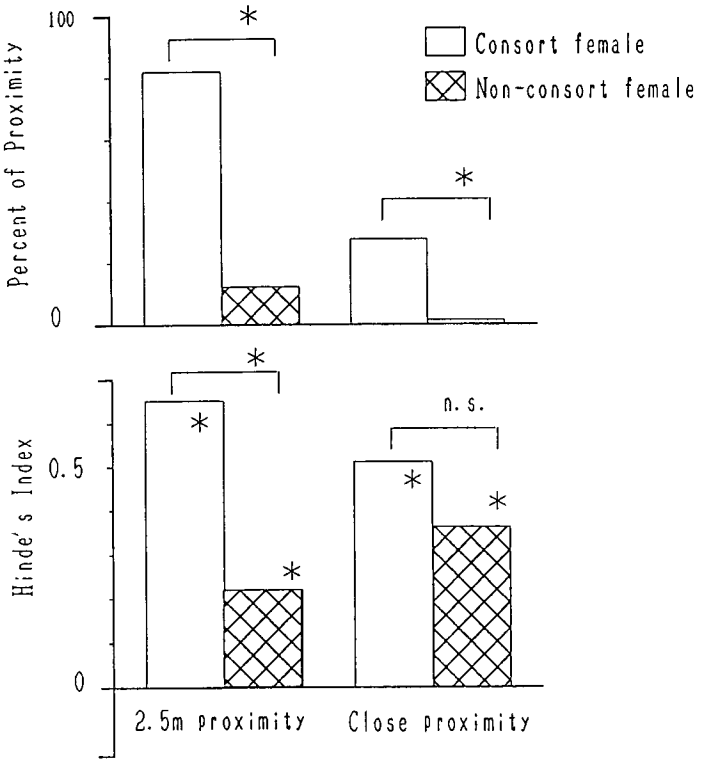
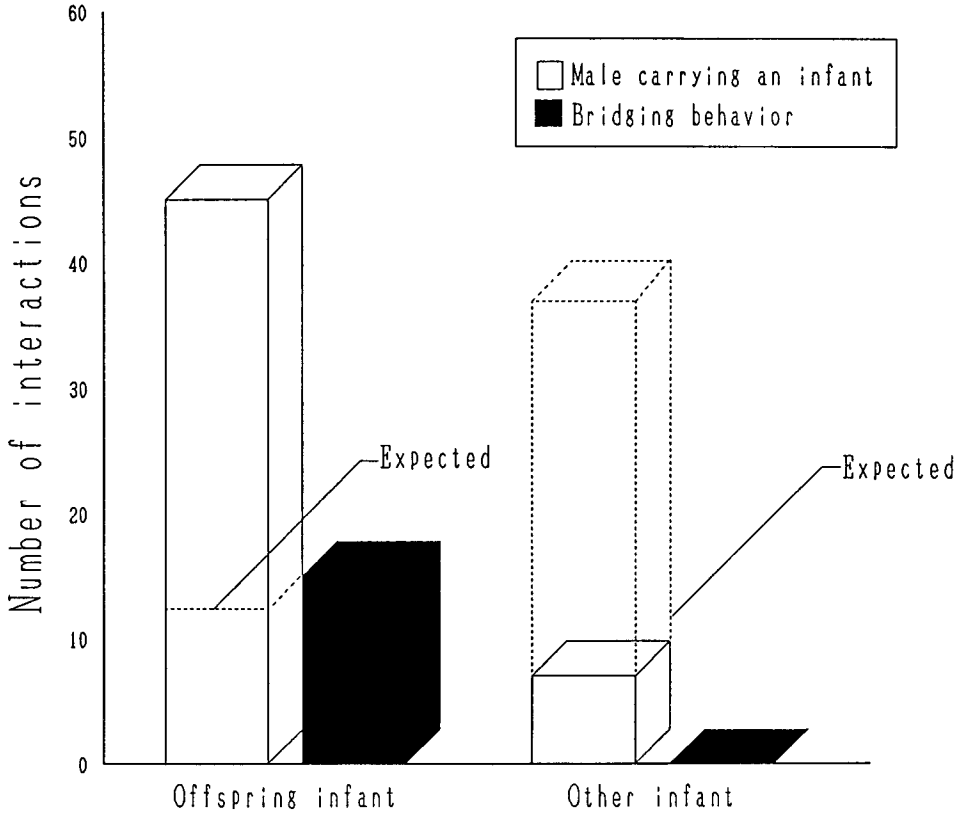

Percent of Proximity
100
0
Consort female
Non-consort female
*
*
Hinde's Index
0.5
0
*
*
*
*
n.s.
2.5m proximity
Close proximity

Figure 2


60
50
40
30
20
10
0
Number of interactions
Male carrying an infant
Bridging behavior
Expected
Expected
Offspring infant
Other infant