Anthropology and Museum Studies   College of the Sciences

2014

Male Tibetan Macaques' (Macaca Thibetana) Choice of Infant Bridging Partners

Briana Bauer
Central Washington University

Lori K. Sheeran
Central Washington University, sheeranl@cwu.edu

Megan D. Matheson
Central Washington University

Jin-Hua Li
Anhui University

R. Steven Wagner
Central Washington University

Follow this and additional works at: http://digitalcommons.cwu.edu/
anthropology_museum_studies

Part of the <u>Anthropology Commons</u>

Recommended Citation

Male Tibetan macaques' (*Macaca thibetana*) choice of infant bridging partners

Briana BAUER[1,*], Lori K. SHEERAN[1,2], Megan D. MATHESON[3], Jin-Hua LI[4,5],
R. Steven WAGNER[1, 6]

1. *Primate Behavior and Ecology Program, Central Washington University, WA 98926,USA*

2. *Department of Anthropology, Central Washington University, WA 98926,USA*

3. *Department of Psychology, Central Washington University, WA 98926,USA*

4. *School of Resources and Environment, Anhui University, Hefei 230026, China*

5. *School of Life Sciences, Anhui Normal University, Wuhu 241000, China*

6. *Department of Biological Sciences, Central Washington University, WA 98926,USA*

Abstract: Adult male Tibetan (*Macaca thibetana*), Barbary (*M. sylvanus*), and stump-tailed macaques (*M. arctoides*) engage in bridging, a ritualized infant-handling behavior. Previous researchers found a bias toward the use of male infants for this behavior, but its function is debated. Explanations include three hypotheses: paternal care, mating effort, and agonistic buffering. We studied a group of habituated, provisioned Tibetan macaques to test whether adult males' affiliative relationships with females predicted their use of an infant for bridging. We also examined biases for sex, age, and individual in males' choice of bridging infant. We collected data via all occurrences, focal animal, and scan methods, from August to September 2011 at the Valley of the Wild Monkeys, China. We found that male infants were significantly preferred over females for bridging, but of three male infants in the group, only one was used by all males, while one male infant was used less often than expected. Adult males had females they were significantly more likely to be proximate to and/or to groom, but these corresponded to the mother of the bridging infant for only one male. Our results are most consistent with the agonistic buffering hypothesis: lower-ranked males used the alpha male's preferred bridging infant in an attempt to regulate their interactions with the alpha.

Tibetan macaques (*Macaca thibetana*) live in stable, multi-male/multi-female groups and are distributed across east and central China (Ogawa, 1995a; Zhao, 1996). The species is female-philopatric and forms linear dominance hierarchies (Thierry & Aureli, 2006). Adult male-infant interactions are generally rare in multi-male/multi-female social groups such as those found in macaques and baboons (Estrada & Sandoval, 1984; Kurland & Gaulin, 1984; Packer, 1980; Ransom & Ransom, 1971; Smith & Whitten, 1988; Smuts, 1985); however, Tibetan, Barbary (*M. sylvanus*), and stump-tailed (*M. arctoides*) macaques exhibit a type of triadic affiliation called bridging (Deag & Crook, 1971; Estrada & Sandoval, 1984; Ogawa, 1995a). Bridging is defined as two individuals simultaneously lifting an infant accompanied

by affiliative behaviors such as teeth chattering (Berman et al, 2004; Ogawa, 1995a). While adult females and juveniles participate in bridging, primatologists have focused on adult males' use of infants (Deag, 1980; Ogawa, 1995a).

Three hypotheses have been proposed to explain bridging and other male-infant interactions: 1) paternal investment/enforced babysitting (Kümmerli & Martin,

2008; Taub, 1980); 2) mating effort (Smuts, 1985; Taub, 1980; Thierry & Aureli, 2006); and 3) agonistic buffering (Deag & Crook, 1971; Ogawa, 1995a; Paul et al, 1996; Kümmerli & Martin, 2008; Zhao, 1996). The paternal investment and enforced babysitting hypotheses make similar predictions: that males preferentially interact in ways that enhance survival of infants related to them (Paul et al, 1996). The enforced babysitting hypothesis proposes that matrilineally-related males use a related infant to bridge and form a caretaking relationship with the infant (Ogawa, 1995a). Neither of these hypotheses have strong support from field observations. Paul et al (1996) found that while males did prefer specific infants for triadic interactions, these were not infants who were related to them. Ogawa (1995a) found that males did not prefer to use infants of their own matriline, and newly immigrated males who lacked biological relatives in the group still bridged.

The mating effort hypothesis suggests that males use interactions with infants to influence female mate choice (Ménard et al, 1992; Paul et al, 1996). In olive baboons (*Papio anubis*), Smuts (1985) found affiliations between particular males and females, which in turn mediated males' interactions with infants. Similar adult male-female relationships have been observed in macaques, but Paul et al (1996) found no support for the mating effort hypothesis in their study of Barbary macaques (*M. sylvanus*).

Deag & Crook (1971) proposed that adult male primates use infants in order to regulate relationships with other males and called such interactions agonistic buffering. This hypothesis predicts that subordinate males use infants to reduce or avoid aggression from more dominant males (Deag, 1980; Thierry & Aureli, 2006). There is support for this hypothesis in Tibetan (Ogawa, 1995a) and Barbary (Paul et al, 1996) macaques. Subordinate male macaques in both species were more likely to approach a dominant male than the reverse and often accompanied the approach with affiliative behaviors; in Tibetan macaques, bridging is followed by proximity and grooming between the adult male bridging partners. Male Barbary and Tibetan macaques prefer the same infant (the male's affiliated or primary infant) for bridging and for male-infant dyadic interactions. The affiliated infant hypothesis predicts that a male is more likely to accept a bridge from a male carrying his affiliated infant. Affiliated infant choice may be based on kinship, infant sex, social rank of the adult male, infant's birth

order, and consortships or friendships with the infant's mother (Deag, 1980; Ogawa, 1995a, b; Taub, 1980; Zhao, 1996). Some baboon species (*Theropithecus gelada*: Dunbar, 1984; *P. cynocephalus*: Smith & Whitten, 1988; *P. anubis*: Smuts, 1985) display triadic male-infant interactions in which a male may look for support from, and develop a social relationship with, the infant's mother. In *P. anubis*, males are more likely to carry the infants of their female friends (Smuts, 1985; Stein, 1984). Deag (1980) proposed that male Barbary macaques choose infants for triadic interactions based on the existence of a friendship with the infant's mother, and Ogawa (1995a, b) and Zhao (1996) both noted that adult male Tibetan macaques showed a preference for the infants of consort partners. Alternatively, Paul et al (1996) found that in Barbary macaques adult male-female friendships did not typically extend to the females' infants, and for Tibetan macaques, the most consistent observation with respect to bridging is that adult males prefer to bridge with male offspring <1 year old (Ogawa, 1995a, b, c; Wang et al, 2008).

We hypothesized that adult male Tibetan macaques would bridge using particular infants. To test the mating effort hypothesis for bridging, we predicted that males would bridge more often using the infants of their preferred adult female grooming and proximity partners.

MATERIALS AND METHODS

Study Site and Species

We conducted this study from 04 August to 28 September 2011 at Mt. Huangshan, Anhui Province, China. Mt. Huangshan is a popular tourist area and UNESCO World Heritage site. The study site is south of the main park and is called the Valley of the Wild Monkeys. The research site is described in further detail by Berman & Li (2002).

The study group, Yulingkeng A1 (YA1), has been observed and monitored by researchers since 1986, resulting in known individual identities and maternal lineages (Berman et al, 2004). During the study period the group consisted of 27 individuals (Table 1), including 4 adult males, 8 adult females, 11 juveniles (1−4 year), and 4 infants. Tibetan macaques mate from July to December, with most births occurring between January and April (Li et al, 2005). Our data collection occurred during part of the mating season, and this likely impacted on adult male-female affiliation.

Observation platforms were built in 1994 (Berman et al, 2007) for tourists and researchers to easily view the monkeys. We collected data from these platforms. Park staff provisioned the monkeys with corn approximately 4 times per day. Data were collected between 0830h to 1700h during provisioning and non-provisioning times.

Data Collection

We collected bridging data and data on adult male-female grooming and proximity. All researchers achieved an inter-observer reliability of >90% on location, individual identification, and target behaviors. We used sections of ethograms published in Ogawa (1995a: bridging and sequence of bridging initiation) and Berman et al (2004: affiliative and aggressive interactions) to collect bridging and other behaviors.

Zhu et al (2013) conducted a study of the dominance hierarchy for this population that overlapped with our study period, so we used his rank results and a separate hierarchy for each sex (Table 1).

Table 1   YA1 Group composition (Jiang Ting and Zhu Lei, personal communication)

Age/Sex class[a]	Name	ID (Rank[b])	Mother	Birth or immigration year
Adult ♂	TouGui	TG (1)	TouTai	b. 2003 (natal male)
	ZiLong	ZL (2)	??	i. 2006
	GaoShan[c]	GS (3)	??	b. 1984 (natal male)
	BaiTou	BT (4)	??	i. 2011
Adult ♀	YeMai	YM (6)	Ye[d]	1990
	TouTai	TT (3)	Tou[d]	1991
	YeZhen	YZ (2)	Ye[d]	1992
	TouHong	TH (7)	TouGou[d]	2003
	YeHong	YH (5)	YeMai	2003
	HuaHong	HH (8)	Hua[d]	2003
	TouRui	TR (1)	TouTai	2004
	HuaHui	HHU (4)	Hua[d]	2005
♂ 3 year	TouRongBing	TRB	TouTai	2008
	YeRongBing	YRB	YeZhen	2008
♀ 3 year	TouXiaXue	TXX	TouHong	2008
♀ 2 year[e]	YeChunYu	YCY	YeMai	2009
	TouRongYu	TRY	TouTai	2009
	TouHuaYu	THY	TouRui	2009
♂ 1 year	HuaXiaMing	HXM	HuaHong	2010
	TouRongGang	TRG	TouTai	2010
	YeRongQiang	YRQ	YeZhen	2010
	YeChungLong	YCL	YeMai	2010
♀ 1 year	YeXiaXue	YXX	YeHong	2010
♂ Infant	Dumbo	DM	HuaHong	04 May 2011
	Scar Face	SF	TouRui	11 June 2011
	Wee-Wee	WE	HuaHui	23 June 2011
♀ Infant	Sissy	SS	TouHong	21 Feb 2011

[a]: In 2006 and 2007, only two male offspring survived to adulthood. Both had emigrated by the time of our study in 2011; [b]: See Zhu et al, 2013 for calculation of YA1 dominance rankings in 2011; [c]: GS was likely born in YA1 (Ogawa, 2006) but has emigrated several times. He returned to YA1 in 2005 and remained there continuously through the time of our study in 2011; [d]: Denotes dead individuals; [e]: In 2009 only females were born.

We conducted 5 minute focal samples, with instantaneous recording at 30 second intervals, on all adult males in a predetermined, random order (Martin & Bateson, 2007). During focal samples, we recorded grooming bouts between adult males and females. Following each focal sample, we conducted location scans, during which we recorded the identity and location of all adults and infants. To facilitate data collection on the

location of individuals, Matheson et al (2006) divided the provisioning area into approximately equal zones based on natural breaks, and we used these designations to indicate monkey location. We considered adult males and females to be proximate if they were touching or within arm's length as recorded during both focal samples and location scans (Sheeran et al, 2010). During location scans, we also noted whether or not mothers were carrying their infants.

We recorded data on adult male bridging behaviors through all occurrences sampling (Martin & Bateson, 2007). When we noted bridging or suspected that it would occur (e.g., an adult male approached or picked up an infant), we suspended focal samples and location scans, and the bridging individuals became the focus of our attention until the bridging behavior ended. We recorded the duration, sequence of initiation, and participants for each bridge. Following Ogawa (1995b), we defined the bridge initiator as the male who held the infant as he approached another male. We determined the observed frequencies of bridges for each male by counting the times a male successfully initiated a bridge with another male. We also recorded failed bridges, defined as cases when one male failed to accept the infant from a male initiator (Ogawa, 1995b).

Data analysis

We used *chi*-square tests to determine if each adult male was proximate to and/or groomed an adult female more often than expected, with the proximity frequency equal to the number of instantaneous records collected during scan samples. We converted the number of instantaneous records of adult male-female grooming into a rate for each focal sample, and then averaged the rates for each dyad. We used *chi*-square tests to determine whether adult males: 1) preferred to use particular infant(s) to initiate bridges; 2) had an affiliated infant and, if so; 3) preferentially received affiliated infants during bridging. We report standardized residuals $\geq |2|$ as indicative of individuals used significantly more or less often than expected. All analyses were conducted in Vassar Stats Website for Statistical Computations (©Richard Lowry 1998−2013), with alpha set to 0.05.

RESULTS

Dominance hierarchy and bridging behavior

During the study period, the bridges an adult male initiated with an infant versus the bridges he received

followed his rank: alpha male TG had the lowest ratio (5 initiated:29 received=0.17), followed by beta ZL (12:17=0.82), gamma GS (11:5=2.20), and recent immigrant BT (29:6=4.80).

Bridging partner preference: Infants versus juveniles

For both successful and failed bridges males used infants (*n*=80) more often than they used juveniles (*n*=5). The majority of bridges with infants (57/80 or 71%) and with juveniles (4/5 or 80%) were accepted.

Infant preference: males versus females

One female and 3 male infants (<1 year) were born in in the group prior to our study. In chi square analyses, we weighted expected values based on the 2011 infant sex ratio. Male offspring were used in 75/80 successful and failed bridges compared to 5/80 for the female infant (Table 2). The female infant was used less than expected for all adult males' successful (*n*=57, χ^2=7.16, *df*=1, *P*=0.0075, standardized residual [SR] ♀=−2.45) and failed (*n*=23, χ^2=6.39, *df*=1, *P*=0.0115, SR ♀=−2.40) bridges. Sufficient data existed to test for significant differences in BT's successful (*n*=29) and total (*n*=44) bridges. BT showed no significant preference for infants by sex (*df*=1; successful bridges: χ^2=0.56, *P*=0.4543; total bridges: χ^2=3.67, *P*=0.0554). In 2011, there was 1 female and 4 male juveniles (b. 2010) in the study group. Two male juveniles were exclusively used in the 5 juvenile bridges we observed.

Thus, for successful and failed bridges, 3 adult males used male infants more often than expected by chance. Juveniles were used infrequently for bridging, but all juvenile bridges were with males.

Infant preference: individual

Males' preferences for infant bridging partners were not evenly distributed across the 4 infants for successful (*n*=57) or failed (*n*=23) bridges (*df*=3; successful bridges: χ^2=49.74, *P*<0.0001, SR ♂DM=+5.76, SR ♂ WE=−3.25, SR ♀SS=−2.45; failed bridges: χ^2=13.35, *P*=0.0039, SR ♀SS=−2.40). Out of BT's successful (*n*=29) and total (*n*=44) bridges, he used ♂WE less than expected in his successful bridges (χ^2=11.14, *df*=3, *P*=0.011, SR ♂WE=−2.32). He selected ♂SF more often and ♂WE less often than expected in his total bridges (χ^2=23.09, *df*=3, *P*<0.0001, SR ♂SF=+3.32, SR ♂WE=−2.71).

We further examined male use of infants by analyzing cases when >1 infant was proximate to a male before

Table 2   Distribution of infants used in bridges by each adult male; male ranks in parentheses

		Infant				Juveniles[a]	
		♂DM	♂SF	♂WE	♀SS	♂Yerongang	♂Tourongang
	Successful	11	12	1	5	0	0
BT (4)	Failed	4	10	1	0	0	0
	Successful	10	0	1	0	0	0
GS (3)	Failed	4	0	1	0	0	0
	Successful	10	2	0	0	0	2
ZL (2)	Failed	2	0	1	0	0	0
	Successful	5	0	0	0	1	1
TG (1)	Failed	0	0	0	0	1	0
	Successful	36	14	2	5	1	3
All males	Failed	10	10	3	0	1	0
	Total	46	24	5	5	2	3

[a]: No bridges were observed using other juvenile males or the female born in 2010.

he initiated a bridge. Such situations were rare and never involved all 4 infants, but there were limited occurrences of >1 infant being proximate to a male when the male picked up an infant for bridging. ♂DM was chosen over ♂SF 7 times, and over ♂WE 4 times. ♂SF was chosen over ♂DM 5 times and over ♂WE 4 times. ♂WE was chosen over ♂SF once. These data indicate that adult males tended to prefer 2 male infants (DM and SF) over ♂WE when choices of >1 infant were available.

An infant's availability for bridging might be related to its age and/or how often it was carried by its mother. We examined how often mothers carried each infant using data from location scans during which the infant in question was visible. All of the infants spent the majority of their time off of their mothers' bodies, though there was variability in the percentage of time each was being carried, which was related to infant age: oldest infant ♀SS was carried in 6.5% ($n=23/356$ scans) of location scans compared to 17.5% ($n=114/651$) for ♂DM, 37.8% ($n=141/373$) for ♂SF, and 45.0% ($n=163/362$) for the youngest infant ♂WE. ♂DM was the infant most often used in bridges and he was off of his mother's body about 80% of the time. ♀SS was the infant most often off of her mother (93% of the time), but she was the infant least frequently used for bridging.

The affiliated infant hypothesis stipulates that adult males will receive bridges more often from an initiator carrying the recipient's affiliated infant. In our dataset, the alpha and beta males did not have an infant with whom they interacted dyadically, but gamma male GS and lowest-ranked male BT did (♂DM for GS, $\chi^2=27.09$,

$df=3$, $P<0.0001$; ♂SF for BT, $\chi^2=15.06$, $df=3$, $P<0.01$). GS was offered ♂DM in 6 bridges, and ♂SF and ♂WE were each offered to him once. GS accepted bridges only with ♂DM ($n=5$), his affiliated infant. BT received all bridges offered to him ($n=6$): 4 using ♂DM and 2 using ♂SF, his affiliated infant.

Adult Female Proximity and Grooming Partners

We observed 305 scans in which adults were proximate to one another (Table 3). Three of the 4 adult males (TG, GS, BT) were significantly proximate to, or out of proximity with, 1 or more adult females. BT was the only male who was proximate to the mother of 1 of the 2 infants he used for bridging. TG was proximate to the mother of his bridging infant less often than expected. We recorded a total of 220 focal samples from adult males (TG 53, ZL 59, GS 56, BT 52), and these were evenly distributed among males ($\chi^2=0.55$, $df=3$, $P=0.9078$). To avoid pseudo-replication in our grooming analysis, we calculated the rate of grooming for each focal sample and then averaged the rates of grooming for each dyad (Table 4). For each of the 4 males, associations with female grooming partners were not evenly distributed (Table 4). TG and ZL groomed the mother of the males' preferred bridging infant *less* often than expected, while GS and BT groomed with her *more* often.

TG and BT each associated with the same female for both proximity and grooming. GS had different partners for proximity and grooming. ZL had no female proximity partner preference, but he groomed 3 females significantly more often than other females. In a comparison

Table 3 Instantaneous records of male-female proximity per dyad; infants in brackets; significant ($\geq |2|$) standardized residuals in parentheses

Males	Females							
	TH [♀SS]	YZ	TT	YM	TR [♂SF]	YH	HHU [♂WE]	HH [♂DM]
TG[a]	7	13	5 (−2.27)	35 (+5.98)	9	24 (+2.95)	9	4 (−2.54)
ZL[b]	5	9	5	8	4	4	5	1
GS[c]	13	0 (−3.14)	5	24 (+4.49)	8	13	5	11
BT[d]	14	1 (−2.83)	5	11	5	4	0 (−3.14)	39 (+9.26)

[a]:χ^2=61.70, *df*=7, *P*<0.0001; [b]:χ^2=8.37, *df*=7, *P*=0.2011; [c]:χ^2=37.35, *df*=7, *P*<0.0001; [d]:χ^2=113.91, *df*=7, *P*<0.0001.

Table 4 Average rates of male-female grooming per dyad per focal sample; infants in brackets; significant ($\geq |2|$) standardized residuals in parentheses

Males	Females							
	TH [♀SS]	YZ	TT	YM	TR [♂SF]	YH	HHU [♂WE]	HH [♂DM]
TG[a]	0 (−6.81)	0.6 (+2.00)	0 (−6.81)	0.8 (+4.64)	1.0 (+7.87)	0.6 (+2.00)	0.6 (+2.00)	0.1 (−4.90)
ZL[b]	0 (−6.20)	0.9 (+8.17)	0.7 (+5.59)	0.5	1.0 (+9.95)	0 (−6.12)	0 (−6.12)	0 (−6.12)
GS[c]	0.1 (−3.32)	0 (−5.23)	0 (−5.23)	0 (−5.23)	0.5 (+3.56)	0.2 (−2.37)	0.6 (+6.43)	0.9 (+11.39)
BT[d]	0 (−3.02)	0 (−3.02)	0 (−3.02)	0 (−3.02)	0 (−3.02)	0 (−3.02)	0 (−3.02)	0.7 (+21.14)

[a]:χ^2=212.35, *df*=7, *P*<0.0001; [b]:χ^2=351.63, *df*=7, *P*<0.0001; [c]:χ^2=282.59, *df*=7, *P*<0.0001; [d]:χ^2=511, *df*=7, *P*<0.0001.

of infant and female affiliation partners, 2 males demonstrated a relationship. One of GS's grooming partners was the mother of his bridging infant. BT was proximate to and frequently groomed the mother of 1 of his bridging infants.

Bridges involving juveniles can be used in a preliminary fashion to explore whether adult males used the juvenile offspring of their female affiliates. The 5 bridges involving juveniles were initiated by alpha TG and beta ZL. They used 2 of the 5 1-year-olds, the male offspring of TT and YZ. TG and ZL both groomed YZ more often than expected, and ZL groomed TT more often than expected.

These results in aggregate suggest that YA1 male Tibetan macaques have particular associations with females for grooming and proximity, but these preferences may be unrelated or coincidental to the identity of the infants used by males for bridging, at least for long term group residents (TG, ZL, GS). Males' competition for reproductive females likely also influenced their affiliation with females.

DISCUSSION

Dominance hierarchy and bridging behavior during the study period

Zhao (*M. thibetana*, 1996) and Ménard et al (*M. sylvanus*, 2001) found that lower-ranked males received fewer bridges but initiated more compared to higher-ranked males. This was true of our data, too: alpha male TG initiated the fewest bridges and received the most (0.17), followed by beta ZL (0.82), gamma GS (2.20), and finally BT (4.80). BT joined the study group approximately 6 months before the study began. He initiated more than half (44/80) of all failed and successful bridges we observed involving infants. His comparatively high bridging rate may have influenced his choice of infants, causing him to be less selective of the infants used than was true of adult males with lower rates of initiating bridges.

Bridging partner preference: infants over juveniles

In their study of YA1 Tibetan macaques, Wang et al (2008) noted that males used infants rather than juveniles for bridging (see also Zhao, 1996). We found a similar result: in successful and failed bridges, adult males used infants 80 times, compared to 5 bridges using juveniles. The bridges using juveniles were rare compared to those using infants, but the majority of bridges using either type of immature were successful. Only the alpha and beta males initiated bridges using juveniles, and alpha male TG's only failed bridge was initiated with a juvenile.

Infant preference: males versus females

Wang et al (2008) found that YA1 Tibetan macaque

males preferred to use male infants in bridging. Zhao (1996) reported that in a Tibetan macaque group with 2 male and 2 female infants, males were used in 78 bridges compared to only 26 for females. Ogawa (1995a) showed that YA1 adult male Tibetan macaques held male infants more often than they held female infants, and that male infants were used in bridging 0.43 times/hour compared to 0.04 times/hour for female infants. We found a similar sex-preference pattern for adult males in aggregate, with male infants preferentially used in both successful and failed bridges. The top 3-ranked adult males never used the female infant when initiating their bridges. Adult male BT, however, did not significantly prefer male infants over the female infant and was the only male to use her in his bridges, perhaps because of his high overall bridging rate. BT's bridges with the female infant were successfully completed, indicating that other adult males would receive her as the bridging medium even though they did not use her themselves in bridges that they initiated.

There were 5 young juveniles (b. 2010) in the group (4 male, 1 female). All 5 bridges we observed using juveniles occurred with 2 of the male juveniles. Since there were more male juveniles present, it is not surprising that they were more often used in bridging; however, our data are consistent with previous researchers' observations that males are used for bridging more often than are females.

Infant Preference: Individual

Previous studies found two preferences in adult males' choice of bridging partners: infants chosen over juveniles, and males chosen over females. However, past researchers did not explore whether a bias existed for a particular male infant (see Zhao, 1996). Uniquely compared to other bridging studies in this species, we individually identified infants in the 80 bridges observed. We found that, while male infants were used more often in bridging than was the female infant in our study group, one of the three male infants was used less often than expected, while one male infant was used more often. In aggregate, all of the adult males used lowest-ranked female HH's infant (♂DM) more often than expected in their bridges. In addition to often using ♂DM in his bridges, low-ranked BT also used ♂SF more often than expected. The general preference for ♂DM persisted in those relatively few cases in which males appeared to have a choice of infants before the bridge was initiated.

♂DM, and to a lesser extent, ♂SF were both preferred over ♂WE when > 1 infant was in close proximity to the male before bridging was initiated. Thus, particular male infants were preferred for bridging, rather than males choosing infants based on proximity. We considered infant availability as another potential factor in a male's choice of bridging partner. ♂WE, the infant least often used for bridging, was also being carried by his mother during 45% of location scans, perhaps making him unlikely to be used in adventitious bridges because he would have to be taken from his mother for that purpose. ♀SS, however, was often available (she was being carried during 6.5% of her location scans), but she was used for bridging less often than expected, while ♂SF was infrequently available (he was being carried during 37.8% of his location scans) but was used for bridging by BT more often than expected. Zhao (1996) found that male Tibetan macaques at Mt. Emei would use for bridging an infant being carried by its mother. Therefore, whether the infant is spending a lot of time off of her or his mother does not seem to influence adult male choice of bridging partner in either population.

Previous researchers studying Tibetan (Ogawa, 1995a, b) and Barbary (Taub, 1980) macaques hypothesized that a male's choice of bridging infant may match his preferred infant for other male-infant dyadic interactions (the male's affiliated or primary infant). They predicted that adult males were more likely to accept a bridge from a male carrying his affiliated infant. In our data set, 2 adult males had affiliated male infants: ♂DM for gamma GS, and ♂SF for lowest-ranked BT. GS only accepted bridges using his affiliated infant ($N = 5$). BT received his affiliated infant 2 times and another infant 4 times. Our data are not, therefore, conclusive with respect to the affiliated infant hypothesis, although it may be that recent immigrants and/or low-ranked individuals such as BT receive any bridges offered to them, regardless of infant being used.

In summary, with respect to males' preferences for particular infants, our data indicate that there was a strong preference for 1 male infant, even though 2 other male infants were in the population. The preferred infant was the son of the lowest-ranked adult female. This preference cannot be explained by the infant's availability in terms of being off of his mother's body or in terms of his affiliation with a particular adult male. Barbary macaques at Gibraltar appeared anecdotally to prefer the youngest male infant in the group and would

approach the infant's mother and take the infant for this purpose (Bauer personal observation). In our study population, the preferred infant was the second born in the 2011 birth cohort, so males were not choosing the youngest male infant in the group. This infant was exclusively used by alpha TG in the 5 bridges he initiated. Other males may have followed suit using his favored infant, even if he was not TG's affiliated infant.

Adult female proximity and grooming partners

Ogawa (1995a, b) reported that YA1 Tibetan macaque males preferred as bridging partners the infants of their female consort partners, which suggested that short-term, adult, male-female relationships might influence infant and juvenile bridging partners. We hypothesized that adult males have regular, preferred female partners for proximity and grooming, and that those patterns might predispose males to use those females' infants in bridging.

In our study population, 3 of the 4 males were proximate to a specific adult female more often than expected. Alpha male TG was proximate to females YM and YH more often than expected. Gamma male GS shared with TG a proximity preference for YM. The lowest-ranked male in the group, BT, was more often in proximity with the lowest ranked female, HH. HH's infant ♂DM was significantly preferred by males for bridging, but only BT was frequently in proximity with her, and he did not exclusively use her infant for his bridges (Table 2). Thus, male-female proximity does not explain the pattern we observed in males' choices of infant or juvenile bridging partners and may be more reflective of mating competition. TG and GS were more often proximate to females who did not have dependent offspring during the study period and were likely fertile.

We predicted that a male's grooming partner would be the mother of the infant he used for bridging. All 4 males groomed at least 1 adult female more often than expected. In the case of low-ranked BT, he was proximate to and more often groomed the same female, HH, and she was the mother of 1 of his 2 bridging infants. However, he neither groomed nor remained proximate to the mother (TR) of his other bridging infant. Gamma male GS had 3 female grooming partners, all of whom were different from his proximity females. Both of these females had infants<1 year, but GS groomed more with the mother of the infant he used for bridging less often than expected. Only in our small juvenile bridge data set

(*n*=5) did the expected pattern emerge: alpha TG and beta ZL both groomed with the mothers of the juveniles they used in bridging. In summary, our results indicate that adult males do not necessarily spend time grooming or affiliating with the mother of the infant most often used for bridging, and this is consistent with the findings of Paul et al (1996), who also failed to find support for the mating effort hypothesis in Barbary macaques.

CONCLUSIONS

Three hypotheses have been proposed to explain male-infant interactions: mating effort, paternal investment, and agonistic buffering. Our data showed that males are biased in the choice of individuals used for bridging: infants were used for bridging more than juveniles were, and males were used more than females. Only 1 male was strongly favored by all 4 males, but he was not the youngest member of his birth cohort. Adult males in our study did not necessarily have a grooming or proximity preference for this infant's mother; in fact, 2 males groomed with her significantly less than expected, and 1 male was proximate to her significantly less than expected. The mother of this infant was the lowest-ranked female in the group, so the males were not biased in favor of dominant females' offspring. In this population, it appears that having a strong male-female affiliation is not a necessary prerequisite for using the female's infant in bridges, at least for long-term male residents. Thus, our data do not support the mating effort hypothesis. We could not fully test the paternal investment hypothesis as we lack paternity data for this population, but the three males who could have fathered any of the infants were biased in favor of a particular infant. Our preliminary results are most consistent with an agonistic buffering framework, in which infant choice of bridging partner may aid in regulating male-male relationships through the use of the infant preferred by the alpha male, a pattern which pertained exclusively to the beta and gamma males.

References

Berman CM, Li JH. 2002. Impact of translocation, provisioning and range restriction on a group of *Macaca thibetana*. *International Journal of Primatology,* **23**(2): 383-397.

Berman CM, Ionica C, Li JH. 2004. Dominance style among *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology,* **25**(6): 1283-1312.

Berman CM, Li JH, Ogawa H, Ionica C, Yin HB. 2007. Primate tourism, range restriction, and infant risk among *Macaca thibetana* at Mt. Huangshan, China. *International Journal of Primatology,* **28**(5): 1123-1141.

Deag JM. 1980. Interactions between males and unweaned Barbary macaques: testing the agonistic buffering hypothesis. *Behaviour,* **75**(1): 54-81.

Deag JM, Crook JH. 1971. Social behavior and 'agonistic buffering' in the wild Barbary macaque *Macaca sylvanus*. *Folia Primatologica,* **15**(3-4): 183-200.

Dunbar RIM. 1984. Infant-use by male gelada in agonistic contexts: agonistic buffering, progeny protection, or soliciting support? *Primates,* **25**(1): 28-35.

Estrada A, Sandoval JM. 1984. Male-infant interactions among free-ranging stumptail macaques. *In*: Taub DM. Primate Paternalism. New York: Van Nostrand Reinhold, 56-87.

Kümmerli R, Martin RD. 2008. Patterns of infant handling and relatedness in Barbary macaques (*Macaca sylvanus*) on Gibraltar. *Primates,* **49**(4): 271-282.

Kurland JA, Gaulin SJC. 1984. The evolution of male paternal investment: effects of genetic relatedness and feeding ecology on the allocation of reproductive effort. *In*: Taub DM. Primate Paternalism. New York: Van Nostrand Reinhold, 259-308.

Li JH, Yin HB, Wang QS. 2005. Seasonality of reproduction and sexual activity in female Tibetan macaques (*Macaca thibetana*) at Huangshan, China. *Acta Zoologica Sinica,* **51**(3): 365-375.

Martin P, Bateson P. 2007. Measuring Behaviour: An Introductory Guide. Cambridge: Cambridge University Press.

Matheson MD, Sheeran LK, Li JH, Wagner RS. 2006. Tourist impact on Tibetan macaques. *Anthrozoös: A Multidisciplinary Journal of the Interactions of People and Animals,* **19**(2): 158-168.

Ménard N, Scheffrahan W, Vallet D, Zidane C, Reber C. 1992. Application of blood protein electrophoresis and DNA fingerprinting to the analysis of paternity and social characteristics in wild Barbary macaques. *In*: Martin RD, Dixson AF, Wickings ED. Paternity in Primates: Genetic Tests and Theories. Basel: Karger, 155-174.

Ménard N, von Segesser F, Scheffrahn W, Pastorini J, Vallet D, Gaci B, Martin RD, Gautier-Hion A. 2001. Is male-infant caretaking related to paternity and/or mating activities in wild Barbary macaques (*Macaca sylvanus*)? *Comptes Rendus de l'Academie des Sciences,* **324**(7): 601-610.

Ogawa H. 1995a. Bridging behavior and other affiliative interactions among male Tibetan macaques. *International Journal of Primatology,* **16**(5): 707-729.

Ogawa H. 1995b. Recognition of social relationships in bridging behavior among Tibetan macaques (*Macaca thibetana*). *American Journal of Primatology,* **35**(4): 305-310.

Ogawa H. 1995c. Triadic male-female-infant relationships and bridging behavior among Tibetan macaques (*Macaca thibetana*). *Folia Primatologica,* **64**(3): 153-157.

Ogawa H. 2006. Wily Monkeys: Social Intelligence of Tibetan Macaques. Melbourne: Trans Pacific Press.

Packer C. 1980. Male care and exploitation of infants in *Papio anubis*. *Animal Behaviour,* **28**(2): 512-520.

Paul A, Kuester J, Arnemann J. 1996. The sociobiology of male-infant interactions in Barbary macaques, *Macaca sylvanus*. *Animal Behaviour,* **51**(1): 155-170.

Ransom TW, Ransom BS. 1971. Adult male-infant relations among baboons (*Papio anubis*). *Folia Primatologica,* **16**(3-4): 179-195.

Sheeran LK, Matheson MD, Li JH, Wagner RS. 2010. A preliminary analysis of aging and potential social partners in Tibetan macaques (*Macaca thibetana*). *In*: Banak SD. Collected Readings in Biological Anthropology in Honor of Professor LS Penrose and Dr. Sahrah B. Holt. Merida: Unas Letras Industria Editorial, 349-358.

Smith EO, Whitten PL. 1988. Triadic interactions in savanna-dw elling baboons. *International Journal of Primatology,* **9**(5): 409-424.

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

Stein DN. 1984. The Sociobiology of Infant and Adult Male Baboons. New York: Aldine.

Taub DM. 1980. Testing the 'agonistic buffering' hypothesis. *Behavioral Ecology and Sociobiology,* **6**(3): 187-197.

Thierry B, Aureli F. 2006. Barbary but not barbarian: social relations in a tolerant macaque. *In*: Hodges JK. Biology and Behavior of Barbary Macaques. Nottingham: Nottingham University Press, 1-18.

Wang GL, Yin HB, Yu GJ, Wu MM. 2008. Bridging behavior in Tibetan macaque. *Chinese Journal of Zoology,* **43**(1): 44-49. (in Chinese)

Zhao QK. 1996. Male-infant-male interactions in Tibetan macaques. *Primates,* **37**(2): 135-143.

Zhu L, Li J, Xia DP, Zhu Y, Wang X, Sun B, Wang S. 2013. Stability of the female dominance hierarchy in free-ranging, provisioned adult Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan, China. *Acta Theriological Sinica,* **33**(3): 238-245.