Homosexual mounting in wild male Tibetan Macaques (Macaca thibetana) at Huangshan, China

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Abstract: Homosexual mounting behavior in non-human primates is very common, but its function may vary across species. We studied male-male mounting behavior in a wild troop of Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan China, from August 2010 to May 2011. We used focal behavior sampling and continuous recording to document mounting related behaviors. We found that this behavior occurs among males of all ages, but its frequency decreases with increasing age (P<0.05). Homosexual and heterosexual mountings differ in that the former ones can have 1 or 2 steps, while the latter ones have 4 distinct behaviors. The contexts of male-male mounting varied across the male lifespan. Mounting behavior exhibited during immaturity is crucial to the development of adult homosexual mounting behaviors.

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1. Introduction

The cause of human homosexual behavior is a controversial topic within the legal, ethical and psychiatric professions. Authors with a tolerant or positive view of homosexuality often begin their discussions by emphasizing the frequency with which nonhuman animals engage in homosexual activities implying that homosexuality is 'natural' and therefore acceptable. From a Darwinian perspective, only those traits that increase reproduction fitness can be selectively favored and become widespread. Theoretically, homosexual behavior appears to reduce one's chances of optimizing reproduction. However, some surveys focused on humans showed that the majority of male and female homosexuals also engage in heterosexual relations(Cameron, 2000).

Forms of homosexual behavior have been documented in more than 450 animal species (Bagemihl, 1995). Vasey (1995) reviewed published literature on nonhuman primate homosexual behavior and found that 33 species exhibited it. However, much of this research has focused on captive animals, and relative few data come from field studies(Vasey, 1995). Some studies showed that homosexual behavior is more frequent among captive than among free-ranging animals (Symons, 1979; Parish, 1993), and for some species, homosexual behavior appears to be exclusive to the captive setting. For example, the Bornean orangutan (Pongo pygmaeus) usually lives a solitary life. In the wild, heterosexual mounting occurred during the mating season and homosexual mounting has not been observed, even when two same-sexed individuals encounter one another in the forest. Conversely, in captivity, homosexual mounting has been observed between two young males (MacKinnon, 1974). From observations such as these, some authors concluded that the presence or absence of homosexual behavior is impacted by the environment. Some view it as a by-product of captivity. Among free-living populations, it appears to be less common in monogamous, polyandrous and polygynous primates, and more common among species living in multimale, multifemale and all-male groups (Carpenter, 1942; Gartlan, 1974; Yamagiwa, 1987).

Homosexual behavior is not limited to adults but also occurs among immature animals . Additionally, some studies of both wild and captive animals show that not all mounting behavior is reproductive in function (Owens, 1976), so mounts may instead serve other functions. For this reason, some mounting behaviors have been termed 'socio-sexual' rather than 'sexual' (Owens, 1976). Some studies suggest that there are essential differences between sexual and nonsexual mounting. For example, in Japanese macaque (Macaca fuscata), sexual mounting usually occurs with behaviors including intromission, thrusting, ejaculation etc., but none of these behaviors occur in nonsexual mounting (Hanby and Brown, 1974). Homosexual mounting usually occurrs before puberty, so it is not influenced by elevated sex hormones (Dagg, 1984). Hence, numerous studied suggested that this behavior is not learned during early life stages, but some other studies suggested that homosexual behavior expressed during immature primates' play may function as practice for adult heterosexual copulation (Hamilton, 1914; Bingham, 1928; Baldwin, 1969). Further,

previous studies show that male-male mounting is a part of a dominance display, and mounting behavior is an expression of one's position in the dominance hierarchy. Although homosexual mounting behavior has been recorded across primate taxa, mounting patterns and their functions vary across species (Vasey, 1995). A few studies focus on the function of homosexual behavior in some species , but currently the research about the development of this behavior is limited, particularly in free-living populations.

Like other macaque species, Tibetan macaques live in a society comprised of multiple males, multiple females, and their offspring (Zhang et al, 2010). A separate linear dominance hierarchy exists for adult males and females (Li, 1999). Males usually transfer from their natal groups before sexual maturation, but females live within the natal group for life. In this study, we investigate the development of male-male mounting behavior to document whether the behavior varies in form across the life span and what its potential function(s) might be.

2. Materials and methods

2.1 Study site and subjects

The study was carried out at Mt. Huangshan National Reserve, Anhui Province, China. Mt. Huangshan is a famous tourist destination in east-central China that is a well-known natural attraction and research site. The climate is temperate and subtropical, and middle and lower elevations support mixed evergreen and deciduous forests (McCarthy et al, 2009). Several groups of Tibetan macaques have been found in the forested areas (Berman and Li, 2002; Xia et al, 2008), and they rely on a variety of plant species (Wada et al, 1987). Tibetan macaques belong to national secondary protection animals in China and have been protected since 1940 in the study area.

Table1. Comoposition of YA2 troop

Age group	Male	Female
Infant	$5(3)^{a}$	$3(1)^{a}$
Juvenile	$5(4)^{b}$	$5(2)^{b}$
Adolescent	$4(3)^{b}$	$6(2)^{b}$
Young Adult	4	$12(4)^{b}$
Old	$5(1)^{c}$	$3(1)^{b}$

a: the birth numbers during our study; b: the migrate numbers during our study; c: the death number during our study

Our focus group is named Yulingkeng 2 (YA2) group, which fissioned from the Yulingkeng 1 (YA1) group in 1996 (Li et al, 1996). The original YA 1 group has been studied since 1986 (Maureen et al, 2009). Our behavioral observations were divided into two periods: the mating season (August 2010 to January 2011), and the birth season (March 2011 to May 2011). At the beginning of out study, there were 72 individuals in this group. Every age and both sex classes are recognizable based on natural markings (hair color and bodily form). During our study, the number of individuals in the group decreased to 49 due to fission, emigration and deaths. Table 1 shows the detailed composition of the YA 2 troop during the study period.

The study population is a free-living Tibetan macaque in that there is no constraint on their ranging pattern. They mainly feed on a variety of plants in the forest. However, park staff provision them with dried corn to attract the monkeys to the feeding site and facilitate our observations. Provisioned food totals about 6kg per day, and they are provisioned daily at 9:00am, 12pm, 2pm and 5:30 pm.

2.2 Data collection

All data of behavioral observations were collected by a single observer (Jiang) across 126 days (mean=14 days/month; range=10—19 days/month). Focal behavior sampling and continuous recording were used for data collection. Our focal animals were all of the males in this group. Before our study began, we divided them into 5 grades according their ages: infant (6 months \sim 1 year), juvenile (2 \sim 3 years), adolescent (4 \sim 6 years), young/middle-aged (7 \sim 15 years) and old (\geq 15 years). We divided adult males into high, middle and low ranks.

Observations were carried out twice daily, from 8:30am to 11:30am and from 2:00pm to 5:00pm. The distance between the observer and the monkeys ranged from 5—10m. During every observation period, we observed all male members in one age group and recorded mount related behaviors, including before and after behaviors of mounter and mountee.

2.3 Data analysis

Normality of data distribution was tested by a one-sample Kolmogorov-Smirnov test. We used One-Way ANOVA to test whether homosexual mounting frequencies varied with males' ages. An Independent T test was used to analyze whether there was a significant difference between the average number of heterosexual and homosexual mounting in males. X^2 tests were used to compare adult males' homosexual mounting. For all tests, p was set at .05 and reported probabilities are two-tailed.

3. Results

3.1 Age differences in males' homosexual and heterosexual mounting

Male's homosexual mounting occurred at a frequency of 1.04times/h during our research. A One-Way ANOVA test of males' homosexual mounting among the 5 age groups yielded significant values (F=19.414, df=4, P<0.01) (figure 1). In addition, we found that there was a significant negative correlation

(R=-0.472, n=257, P<0.01) between mounting frequency and the mounter's age: the frequency of

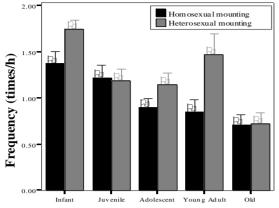


Figure 1. The mounting frequency in every age group

We observed 176 episodes of an adult male receiving a mount. Usually, the high-ranked males were receipients of the mount (44.8%) and middle- or low-ranked males were the mounters. We recorded 191 occurences of adult males initiating mounts. The majority (42.9%) of initiating males were low-ranked. Adult males' rank class differed significantly for both initiating (X^2 =9.686, df=2, P<0.05) and receiving (X^2 =13.648, df=2, P<0.05) mounts (figure 2).

We also recorded cases where a male mounted a female (heterosexual mounting). We found a highly significant between the average number of homosexual and heterosexual mounting in adolescent (t=-3.151, df=110, P<0.05) and young adult (t=-4.799, df=67.553, P<0.01) age classes, but not for infant (t=-0.815, df=111, P>0.05), juvenile(t=0.330, df=97, P>0.05) and old (t=-0.950, df=84, P>0.05) age classes.

homosexual mounting decreases with age.

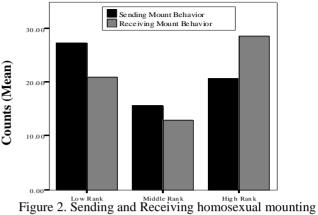
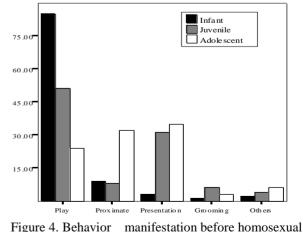


Figure 2. Sending and Receiving homosexual mounting in different ranks in adult males

3.2 Homosexual mounting contexts

Homosexual adult-male (young/middle-aged and old) mounting behavior usually occurred in one of four contexts (figure 3): foraging (N=73, 38.2%), post-conflict (N=57, 29.8%), pre-conflict coalition (N=15, 7.9%) and meetting (N=36, 18.8%). Adult-male mountings were not evenly distributed among these contexts (X^2 =75.990, df=4, P<0.01).

Figure 4 showed the homosexual mounting contexts during immaturity. Nearly all of infants' homosexual mounting occurred in a playing context (N=209, 85.96%). For juveniles, male-male mounting often occurred in play (N=98, 50.78%) and presentation (N=61, 31.61%) contexts. Among adolescents, we found that male-male mounting mainly occurred in contexts of play (N=41, 24.85%), proximity (N=54, 32.73%) and presentation (N=58, 35.15%).



nounting in wild immaturity

usually rests his hands on the female's hindquarters, and clasps her ankles with his feet. Rhythmic pelvic thrusting occurs followed by a short pause during

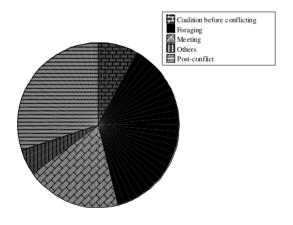


Figure 3. Every condition when homosexual mounting occured in adult males

3.3 Mounting behavioral patterns

During heterosexual mounts, an adult male

ejaculation. Thus, the heterosexual mount usually is comprised of four behaviors: clasp, thrust, intromission, and ejaculation.

We compared the behaviors comprising heterosexual and homosexual mounting using the four behaviors commonly exhibited in homosexual mounts (clasp, thrust, intromission and ejaculation). Occurrences of each behavior were tallied for each male age class (Table 2). Infant and Juvenile males showed clasp and thrust, but not intromission or ejaculation, when mounting others of either sex. Adolescents, Young adult and old males exhibited only clasp during male-male mounting, but all four behaviors occurred in heterosexual mounting.

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	Male to Male				Male to Female					
	Infant (n=246)	Juvenile (n=193)	Adolescent (n=165)	Young Adult (n=109)	Old (n=87)	Infant (n=155)	Juvenile (n=137)	Adolescent (n=153)	Young Adult (n=202)	Old (n=42)
clasping	21.23%	47.5%	79.09%	100%	100%	3.54%	61.36%	93.24%	100%	100%
thrusting	20.32%	11.3%	0	0	0	9.28%	26.58%	53.12%	100%	100%
Intromission	0	0	0	0	0	0	0	69.93%	96.21%	91.73%
Ejaculation	0	0	0	0	0	0	0	47.36%	95.32%	82.56%

4. Discussion 4.1 The development of male-male mounting Socio-sexual patterns of mounting, presenting and mutual embracing have been observed in many primate species (Dixson, 1998). Such behaviors include pelvic thrusting movements and penile erection, and in some cases phallic intromission (Dixson, 1998). Mounting attempts by young male baboons are typically disoriented and incomplete (Vasey, 1995). We observed this lack of orientation, too, when infants first begin boarding their mothers to ride. Soon after infant monkeys can move independently of the mother, they started mounting their peers. In our studies, We found that for both infant and juvenile maturation periods, males mount other male or females with approximately equal frequencies, and a large proportion of these mounts occurring during rough-and-tumble play. For both homosexual and heterosexual mountings, infant and juvenile males exhibited only two (clasp and thrust) of the four behaviors commonly observed in adult heterosexual mounting; they did not exhibit intromission or ejaculation. During the adolescent age, males showed most of the behaviors characteristic of adult male mounting behavior. Adolescent males' frequency of male-female mounting is greater than male-male mounting, and we observed intromission and even ejaculation, though it seems unlikely that adolescent males were fertile before puberty. Vase (1995) argued that achieving intromission stimulates males to mount more often, which may be true of Tibetan macaques, too. The Adolescent male learns that intromission can only be achieved with females. During this stage, homosexual mounting patterns only included clasp, not thrust, intromission, or ejaculation. Like the Adolescent males' mounting behavior, adult males' homosexual and heterosexual mounting were different. Adult male-male

mounting pattern includes only clasp, but adult male-female mounting includes all four mounting behaviors. We conclude that homosexual mounting plays an important role in Tibetan macaques' sociosexual development. Mounting during early stages of life is important in the development of adult mounting behavior. In this species, adult males will need to be able to regulate male-male interactions through the use of homosexual mounts. They also will need to develop the appropriate sequence of behaviors in the heterosexual mount to gain access to fertile females. Both types of mounts have an impact on the male's fitness, albeit a more indirect one in the case of homosexual mounts.

4.2 Social contexts of homosexual mounting

Many authors have argued that male-male mounting is an indication of dominance and latent or expressed power. However, Vasey (1995) notes that this view is an oversimplification of what is probably a more complex process of comunication. For example, in a study of stump-tailed macaques (Macaca arctoides), Bertrand (1969) found four contexts within which homosexual mounting occurred: permission granting, enlistment, excitement and greeting mounts. Hanby and Brown (1974) found that the relation between mounting and rank varied with the social situation in Japanese macaques (Macaca fuscata). Therefore, mounting may have a wide variety of communicatory functions in different primate species, and who mounts whom may vary according to the nature of the communication involved (Vasey, 1995).

During our observations, we found that infants' and juveniles' homosexual mounting behavior mainly occurred during play. This has been found in other primate species (Owens, 1976; Hanby and Brown, 1974; Nadler, 1990). During the adolescent stage, male-male mounting mainly occurs in proximity and presentation contexts, and this mounting pattern tends to persist into adulthood. We found that homosexual mounting behavior in adult males occurs in four contexts. First, when two or more individuals are in close proximity while feeding, male-male mounting was likely to occur, and it seems to signal not tension, but excitement. In the feeding context, lower-ranked individuals tend to mount those of higher rank (N=58, 79.6%). Kuroda (1980:90) also found homosexual behavior occurred under this condition among bonobos (Pan paniscus), but he suggested that this behavior is a mechanism to reduce tension during periods of close proximity in the same food patch. Second, Li (1999) suggested that homosexual mounting among adult male Tibetan macaques is a type of post-conflict reconciliation. Our study supported this conclusion because we also found this behavior occurred after conflicts.

Ren (1990) noted that in Tibetan macaques, the rank of the mounter and the mountee can vary, leading her to conclude that it is reflective of friendly behavior, rather than a dominance display. We found that lower-ranked individuals mounted others more often than they were mounted, but 87% of the mounting behavior we observed was initiated by low-ranked individuals, including mounts where a higher ranked monkey presented to and was mounted by the lower ranked initator. Therefore, homosexual behavior among adult males appears to serve two purposes: it is a method for lower-ranked individuals to maintain social bonds with higher-ranked ones, while reinforcing the relative positions in the dominance hierarchy of the two animals involved in the mount.

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