Non-conceptive sexual behavior and its function in an unusually composed group of Francois langurs (*Trachypithecus francoisi*) in Guangxi, China

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Summary

Heterosexual and homosexual behaviors were observed in a group of Francois langurs (*Trachypithecus francoisi*) at Fusui Nature Reserve, Guangxi, China, from September 2005 to August 2006. The group was unusual in its composition and consisted of one subadult male (SM), one adult female (AF), one subadult female (SF) and a three year old female (JF). Three adults including the resident adult male and the other two offspring had disappeared in early 2005 due to unknown reasons. The observations indicated that AF actively initiated most of the mounting and most of the grooming after mounting. Only SF and SM were involved in mounting events with AF. There are at least four hypotheses to interpret the functions of the nonconceptive sexual behavior of primates; in a group comprising adults of both sexes training is considered the least important function of non-conceptive mountings. Our observations suggest that after the break of the group, the training function of non-conceptive mountings initiated by the only remaining adult individual (AF) might have be increased as a response to the unusual situation.

Những hành vi giới tính không kèm theo giao phối và chức năng của nó đối với quần thể loài Voọc đen má trắng (*Trachypithecus francoisi*) ở Guangxi, Trung Quốc

Tóm tắt

Những hành vi giới tính khác giới và đồng giới đã được quan sát ở một đàn Voọc đen má trắng từ tháng 9 năm 2005 đến tháng 8 2006 tại khu bảo tồn thiên nhiên Fusui, Guangxi, Trung Quốc. Đàn bao gồm một cá thể đực bán trưởng thành, một cá thể cái trưởng thành, một cá thể cái bán trưởng thành và một cá thể cái khoảng 3 tuổi. Trước đó cá thể đực trưởng thành và 2 con non đã mất tích khoảng thời gian đầu năm 2005. Kết quả quan sát cho thấy cá thể cái trưởng thành thường xuyên khởi xướng các hành vi giới tính như chải lông và vuốt ve (không giao phối) với cá thể đực bán trưởng thành và cá thể cái bán trưởng thành. Bốn giả thuyết để giải thích chức năng của các hành vi giới tính không kèm theo giao phối trong quần thể các loài linh trưởng bao gồm: thể hiện sự thống trị, thể hiện sự ham muốn giới tính và khởi động việc giao phối, thể hiện sự trấn tĩnh sau các xung đột bầy

đàn, và thể hiện việc truyền dạy các hành vi giới tính cho thế hệ sau. Với những số liệu thu thập trong nghiên cứu cho thấy hành vi giới tính không kèm giao phối ở đàn có chức năng như một cách truyền dạy các hành vi giới tính cho những cá thể chưa trưởng thành. Đồng thời cũng là hệ quả của việc mất đi của cá thể đực trưởng thành.

Introduction

Sexual behavior between adult and immature individuals is found in many nonhuman primates (e.g. *Gorilla gorilla beringei*, Watts, 1990; *Macaca mulatta*, Perry & Manson, 1995; *Papio cynocephalus*, Rasmussen, 1983; *Pan paniscus* and *Cebus capucinus*, Manson et al., 1997).

Most colobine monkeys live in one-male groups in which the resident male only tolerates smaller or younger males, often his own offspring (Jolly, 1985, Liu et al., 2013). The adult male monopolizes all the fertile females and keeps the females away from other adult males like their grown sons or intruders. This monopolization can be interpreted as an effort of the adult male to maximize breeding success (Cords, 1987). If the male of a group is replaced, the breeding success of the new male will be maximized through the behavior of infanticide (Cheney et al., 1987). All studies on sexual behavior to date are conducted on groups with the typical species-specific composition (Bartlett, 2001; Chapais & Mignault, 1991; Dewsbury, 1972; Edwards & Todd, 1991; Fox, 2001; Kapsalis & Johnson, 1999; Ren et al., 2002a; 2002b; Tyler, 1984; Vasey, 1996; Vasey & Gauthier, 2000; Vasey, 2004a; 2004b). But what happens in respect to sexual behavior if the group has not adult male? Does any sexual behavior occur at all? And if it does, who initiates it? And what is its purpose and meaning?

The group of Francois langurs inhabiting Zuowei village, Fusui County, Guangxi, China (Fig. 1) is such an extreme case.

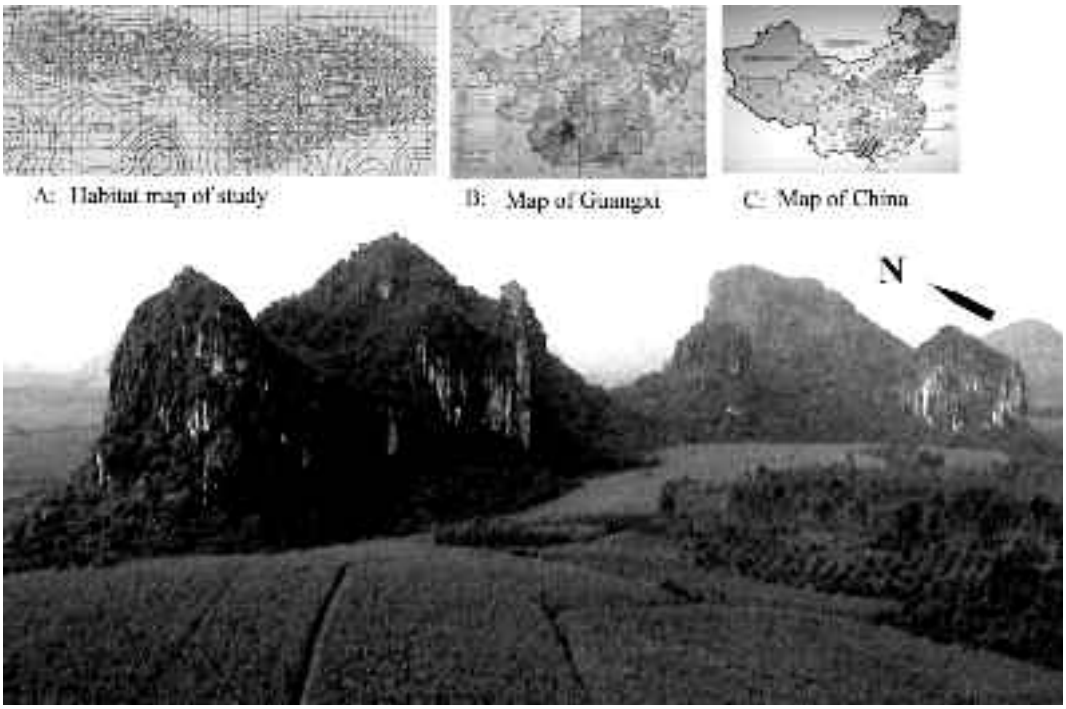

Fig.1. The home range of the Francois langur group, which is isolated by farmland.

Francois langurs are endemic to limestone hill habitats (Nadler, 2006), have special patterns of habitat use and locomotion adaptive to this environment (Zhou et al., 2013) and live typically in one-male/multi-females groups. The species is found in Northern Vietnam and Southern China (Zhang et al., 1992; Canh, 1996; 1997) with an estimated population of approximately 2000 individuals (Zhang & Bleisch, 2006). During the past 30 years, the population suffered a great decline from illegal hunting, human interference, habitat loss and habitat fragmentation. In Guangxi Province, China, the Francois langur population has decreased from 4,000–5,000 in the1980s (Wu, 1983; Wu et al., 1987) to 2,000–2,500 in the mid 1990s (Liu & Wei, 1995). The species continued to decline dramatically and at present only about 300 individuals in 14 isolated populations survive, which represents a 90% decrease in population size since the early 1980s and an 85% decrease since the mid 1990s (Li et al., 2007). A population study in Fusui County provided evidence that the dramatic decline of this langur population is mainly a result of heavy hunting and conversion of their habitat to agricultural farmland (Hu et al., 2004).

This has led to a complete isolation of our study group at Zuowei village. The closest group is 5 km away, being separated from the study group by agricultural land and several villages (Hu et al., 2004; Huang et al., 2006; Li et al., 2007). Since 2001 we studied foraging ecology, ranging behavior and habitat utilization of this group and continuously recorded the group composition. That the group structure suddenly changed to a very unusual composition provided us with an excellent opportunity to study its sexual behaviors, answer the preceding questions and analyze the function of sexual behavior.

Methods

Study Site and Group

The study group inhabits a 42 km^2 karst area in Fusui Nature Reserve, Fusui County, Guangxi, China (22°36'22''-22°41'51''N, 107°23'-107°41'E) (Zhou et al., 2007). They live entirely on the isolated hills, which are about 100 m high and full of rocky cliffs (Fig. 1). Monkeys prefer to utilize the cliffs, as they provide safety against humans and in the past also against other terrestrial predators (Guangxi Forestry Bureau, 1993; Jiang, 1996; Zhou et al., 2007). The flat land surrounding the karst hills is completely cultivated and planted with *Manihot esculeuta*, *Arachis hypogaea*, *Calamus thysanolepis*, *Eucalyptus citriodora* and other crops (Fig. 1). Due to firewood collection by the local villagers, the remaining habitat on the hills lacks large trees (DBH >20cm, Huang et al., 2006). The dominant trees found within the habitat are *Littsea glutinosa*, *Cleistanthus saichikii*, *Albizzia kalacora*, *Sterculia lanceolata*, *Syndilcis montana* and *Pinus massoniana*. The latter species is artificially planted on the lower foothills and their surroundings. The site has a typical north tropical monsoon climate, characterized by an average annual temperature of 21.5°C, an average humidity of 78% and a total precipitation of 1151 mm (Huang, 2002).

At the beginning of 2001 the study group had been observed with four individuals (one adult male and three adult females), the birth of three infants increased the group size to seven by the end of 2002. In 2004 two more infants were born bringing up the group size to nine. Five members of the group disappeared in May 2005 and were never seen since. Four individuals remained in the group - one subadult male (SM) about three years old, one adult female (AF), one subadult female (SF) of similar age as the subadult male, and one juvenile female (JF) about two years old. Most of the observed groups of *T. francoisi* consisted of one male/multi-female groups and this group composition was highly unusual. Without a breeding male no more infants have been born since

2005. Observations in 2010 found there were still four individuals in the group, which confirmed that no infant was born since 2005.

All the research reported here complied with protocols approved by the appropriate wildlife conservation committee of China and adhered to the legal requirements of China.

Data Collection and Analysis

Earlier studies found that this langur group leaves its sleeping cave in the early morning about 6:30am during the raining season and 7:30am in the dry season (Huang et al., 2006). So we started observation around this time and continued until the group returned to the same or another cave to sleep in the evening (Huang et al., 2006). We followed the group when they moved on the farmlands around the isolated hills (Fig. 1). We recorded data on sexual behavior for 10-15 days every month from September 2005 to August 2006. Since we were able to recognize all of the individuals in the group, we chose focal animal sampling (Altmann, 1974) and behavior sampling (Martin & Bateson, 2001). The group was observed from a distance of 30-100 m with binoculars. Mounting behavior was recorded whenever it occurred. The data recorded included the name of the mounter, mountee, and the duration of mounting, time and date as well.

Three mounting patterns were identified during the observation, which are defined as follows:

Pattern A:

Mounter stood with the hind feet on the ground and had its hands on the mountee's hip, while rubbing against the mountee. (cf. *Macaca mulatta*; Akers & Conaway, 1979; *M. fuscata* Wolfe, 1984).

Pattern B:

Mounter applied four limbs on the back of the mountee. (cf. *Macaca mulatta* Akers & Conaway, 1979).

Pattern C:

Two individuals quadrupedally stood on the ground, hip to hip in line, and rubbed each other.

We used the Chi-square tests to test the differences between various variables. All statistical analyses were performed using the SPSS statistical package. Results of the statistical tests were considered significant at the conventional $p \leq 0.05$ (2 tailed).

Results

The total observation time was 2189 hours; 994 hours in 2005 and 1195 hours in 2006. Forty-nine mounting behaviors were recorded in the observation period. The mounting process lasted 4.1 seconds (4.1±2.45, n=49) ranging from 2 seconds to 15 seconds. The three mounting patterns were recorded with the following frequency: 34 times we observed pattern A, 9 times pattern B and 6 times pattern C (χ^2=28.939, df.=2, P<0.001).

The frequency of mounting behaviors in different hours of the day showed a significant variation (χ^2=22.958, df=12, P=0.028). A significant peak in mounting behavior was found between 8:00am and 10:00am. There was a minor mounting peak at 5:00 pm and a lower frequency of mounting behavior was observed during the long siesta time at noon (Fig. 2).

Mounting behavior also occurred significantly more frequently in February and in July (χ^2=46.000, df=11, P<0.001) (Fig 3).

Mounting behavior could either be heterosexual or homosexual. Heterosexual mounting

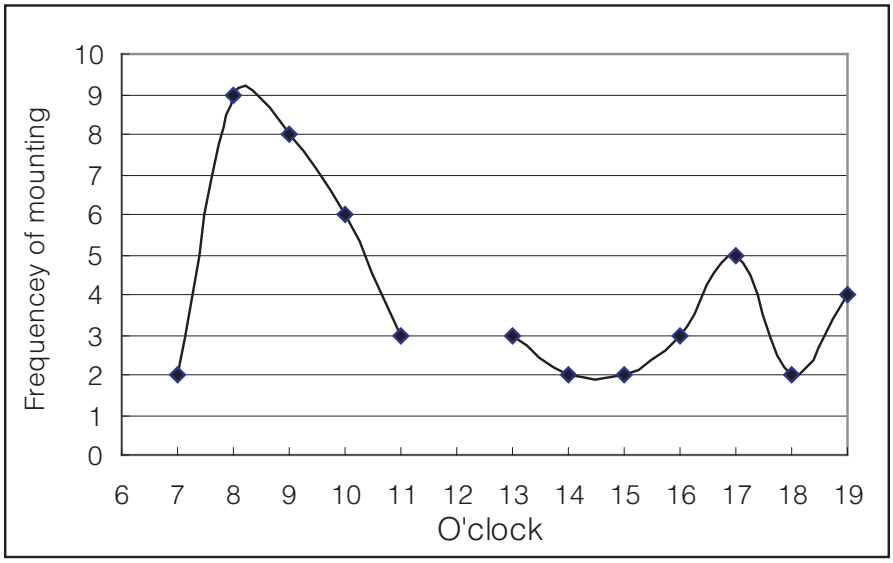

Fig.2. Frequency of mounting behavior of the study group occurred at different times.

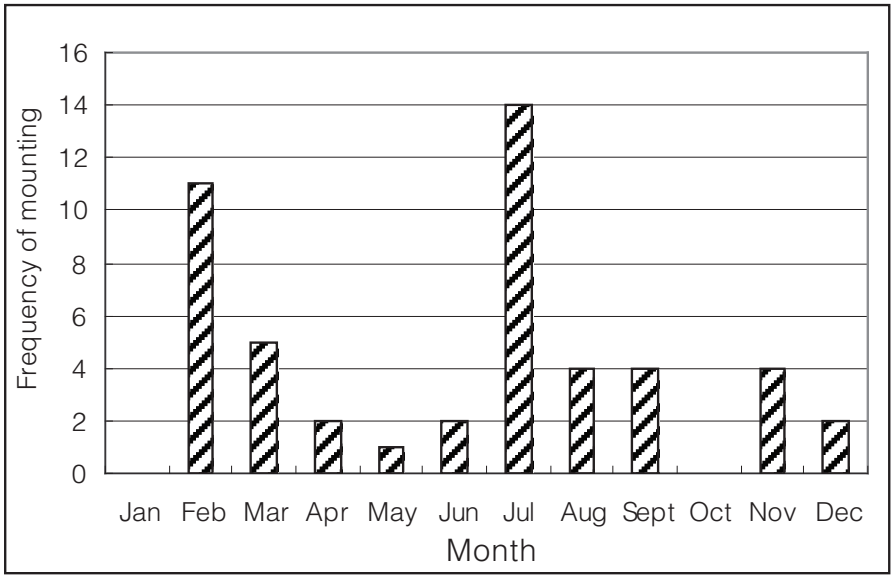

Fig.3. Frequency of mounting behavior of the study group occurred at different months.

accounted for 24.5% of total mounting records. In the heterosexual mounting events, the SM only acted as the mounter (Table 1), and he mounted AF 10 times and SF 2 times. SM was never seen to mount JF. AF often sexually solicited SM first with head shaking and sexual prostration, or grooming the latter. AF often groomed SM after the mounting event. Homosexual mounting contributed to 75.6% out of the 49 mounting events recorded. Between AF and SF, the AF could either be the mounter or the mountee (Table 1), but was the mountee significantly more often than mounter (91.1% to 8.9%). SF and JF were the mounters significantly more than mountee (χ^2=22.224, df=1, P<0.001).

Table 1. Frequency of mounting behavior between different dyads in the study group.

Mounter / Mountee	AF	SF	SM	JF	Total
AF		28	10	3	41
SF	4		2	1	7
SM	0	0		0	0
JF	0	1	0		1
Total	4	29	12	4	49

Grooming behavior often followed the mounting event (32 out of 49 times). Hereby the mountee initiated most of the grooming bouts. For AF, she engaged in mounting 41 times as mountee and 4 times as mounter and she initiated grooming 25 times (78.1%) after being mounted.

JF often sat close to AF during the day, and they often hugged, while SM and SF kept alone during the daily activities.

Discussion

This langur group has been studied for more than six years for its activity and time budget (Huang et al., 2006), diet and feeding strategy (Huang et al., 2008), habitat utilization (Huang et al., 2007) and behavior of cave entering and leaving (Huang et al., 2004). The disappearance of one adult male, two adult females and two other unidentified individuals lead to an unusual group composition and there was no offspring till 2010. However, non-conceptive heterosexual and homosexual mounting behaviors between the adult female and subadult group members were still observed.

Francois langur groups in captivity kept as one-adult male and multi-adult female groups often display mounting behavior. Reports indicate that mounting behavior occurs mostly in the morning and afternoon in February and from July to September (Hu, 2003), similar to the peaks in mounting events we found in our unusual group in the wild. This suggests that the timing of sexual activity (mounting) and seasonal preference are similar both in captivity and wild.

The result of heterosexual copulation is often successful reproduction and the function of the mounting is clear (Hashimoto & Furuichi, 1996).

Homosexual mountings between individuals of the same sex were reported both in captivity and in the wild and may serve different purposes in different primates or in different situations (Akers & Conaway, 1979; Chapais & Mignault 1991; Srivastava et al. 1991; Edwards & Todd, 1991; Kapsalis & Johnson, 1999; Ren et al., 2002a; Vasey, 2004a).

Firstly, homosexual mounting behavior is often interpreted as showing the dominance of the higher ranking mounter over the lower ranking mountee (Srivastava et al., 1991; Akers & Conaway, 1991; Vasey, 2004a). Because mount-giving behavior was linked to the male, while the mount-receiving behavior was linked to the female, the mounter was assumed to play the masculine role and the mountee the feminine role (Srivastava et al., 1991).

Secondly, mounting behavior is related to physical satisfaction. Both mounter and mountee can acquire physical sexual satisfaction through the genital contact (Akers & Conaway, 1991).

Thirdly, homosexual mounting behavior may play an important role in the copulation pattern by raising the interest of the male in the female by mimicking the male copulation act of a potential rival (Parker & Pearson, 1976).

Edwards & Todd (1991) suggested a forth meaning of the mounting behavior in white-handed gibbons (*Hylobates lar*). They concluded the sexual behavior had the function to reassure the mountee after a chase. In *Macaca nigra* the mountee was mounted and comforted after a conflict by the aggressor (Dixon, 1972). Mounting behavior in other primate species, such as baboons (*Papio anubis*), golden snub-nosed monkeys (*Rhinopithecus roxellana*) and chimpanzees (*Pan troglodytes*) serves the same function and is also interpreted as a way of reducing social tension (Ren et al., 2002a; Edwards & Todd, 1991).

Additionally it was also reported that mounting serves a training function for immature individuals in some primates and that adult individuals often invited immature individuals to mount (Edwards & Todd, 1991; Van Lawick-Goodall, 1968).

In this group, there were fecund heterosexual males, and there might have been homosexual mountings already before the group broke apart in 2005. Indeed both the heterosexual and the homosexual mountings in this group might have the same functions as in a normal social group.

But it is also possible that the function of the mountings changed after the group break. After the break AF was the only adult individual and our observations show that she solicited other individuals and initiated most of the mounting behaviors as mountee and received less mounting from other individuals through typical mounting invitations, such as head shaking, presentation of the hindquarters and tail lowering, similar to other primates (Sommer & Rajpurohit, 1989; Srivastava et al., 1991). As a result, she played the main role in both the heterosexual and the homosexual mountings. For her positive behavior, we may suggested she played function of mature female as before to solicit SM to mount her for physical sexual satisfaction and to train SM. She also often solicited SF to mount, which could imply she may act as parent to train SF. She rarely invited JF to mount, possibly because JF was still too young.

SF was mostly involved in mounting behaviors as a mounter especially with AF (Table 1). The mounting behavior between AF and SF does not indicate a demonstration of dominance and subordination, because SF apparently is not a high ranking group member. It does also not serve for reassurance because we rarely observed any conflict between AF and SF. The most likely function of this mounting was training.

SM was the only male and immature. He only was involved in mounting behaviors as mounter, mainly with AF (Table1). Mounting between him and AF does probably not indicate a demonstration of dominance either, as observations of captive Francois langurs have shown that subadults never rank higher than adult individuals (Wang et al., 2006). So in this group mounting served mostly for training and reproduction.

Grooming behavior often occurs before and after mounting encounters in Hanuman langurs (Srivastava et al., 1991). In a one-male Hanuman langur group, the adult male (mounter) often initiated the grooming, while the adult female (mountee) received the grooming and this has been considered to possibly serve as a form of reward (Srivastava et al., 1991; Vasey, 2004a; 2004b). Grooming often occurred also in the study group after mounting similar to observations made in other primates; however as the mountee AF interestingly also was the animal initiating the grooming and not the animal receiving the grooming. So in this case AF was the one giving the reward not the one receiving it. We suggest interpreting the function of the behaviors displayed by AF mostly as training.

In captivity, adult females of Francois langurs were reported to initiate most of the heterosexual mountings (19 out of 24), while the adult male initiated the rest and lower ranking females initiated most the homosexual mountings (28 out of 38) (Wang, 2009). Studies also demonstrated that a high

ranking individual in captivity played as groomer after mounting more than that of reverse (Zhou et al., 2006), which was similar to other primates and different from this unusual group.

Akers & Conaway (1979) argued that captivity could exaggerate behaviors which might be less frequent in wild populations, but it would not change the basic function of mounting. It seemed in the present study that after the group break the dominant AF was unusual likely to solicit others for mounting and grooming, which might imply she was training other individuals in mounting behavior.

In conclusion, the unusually composed group continued to display sexual behaviors after the loss of the adult male. The only adult individual (AF) was positively initiating sexual activity. We suggest that the training function of AF in mounting was exaggerated after the group break.

Acknowledgments

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