

Male homosexual behavior among different age groups in captive stump-tailed macaque (*Macaca arctoides*): socio-sexual or sexually motivated?

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Abstract

The present study aims to determine whether homosexual behavior in stump-tailed macaque males of different age groups were socio-sexual or sexually motivated. Male homosexual encounters were divided into two categories for analysis; manual genital stimulation and actual mounting. Manual genital stimulation in adult males occurred bidirectional, in the context of social affiliations. There was no significant difference between dominant and subordinate partners in terms of genital stimulation performed or received. Mounting was in double foot-clasp position similar to heterosexual encounter. We identified three types of mounts. All types of mounts occurred unidirectional among adult males and mostly occurred in aggressive context. Unique homosexual encounters were observed between α -male and β -male where mounting involved anal intromission terminated by ejaculation and occurred only during the mating season after the heterosexual copulation between β -male and estrous female, which was known to be sexually motivated. We examined several socio-sexual explanations for male homosexual mounting, including (1) dominance-assertion (2) tension-regulation (3) reconciliation and (4) practice for heterosexual copulation. Homosexual encounters between adult males interpreted: a strict relationship between dominant individuals mounting subordinate individuals, reconciliation attempted by the subordinate; and the mechanism employed to regulated aggression and reestablished social bond among adult males. Mounting among immature males occurred bidirectional. Five evidences indicated the homosexual mounting between immature males as socio-sexual behavior. The evidences based on: (a) the mating season (b) the same day heterosexual encounter (c) assistance provided by adult male to immature males (d) occurrence in the context of play (e) immature males in homosexual mounting and learning heterosexual mounting with adult females. The male-male homosexuality adds a new dimension in sexual behavior of stump-tailed macaque.

Keywords: Homosexual behavior, Mounting, Sexually motivated, Socio-sexual, Solicitation, Stump-tailed macaque.

INTRODUCTION

Homosexuality is phylogenetically widespread among the anthropoid but totally absent among prosimians in captive and in the wild primates [1, 2]. Homosexual behavior in terms of forms, context and function has been questioned and criticized for its multifaceted nature of the interaction [3, 4, 5]. It is often thought to be a developmental phase restricted to or common among immature individuals. Nevertheless, it has been observed in all age classes of primates [2]. Berstein, Maslow and Wickler correlated brief mounts contextually with dominant interactions [6, 7, 8]. Chevalier-Skolnikoff considered male homosexual behavior the forms of prolonged genital stimulations, manual or oral, dorsal mountings with pelvic thrust and occasionally intromission without ejaculation between the adult and sub-adult males, and the sub-adult and infant males [9].

Homosexual behavior in animal has traditionally been interpreted as socio-sexual [10] which enacted to facilitate social goal or breeding strategy [11, 12]. The socio-sexual functions are

often seen as their primary purpose [13]. However, Wickler argued that same sex mounting interactions can be sexually motivated or serve some social function [10]. Carpenter suggested homosexual behavior might be a substitute for heterosexual coitus [14]. But Chevalier-Skolnikoff working with captive stump-tailed macaque suggested that homosexuality was not due to the absence of an estrous female. Male-male mounting occurred most frequently in the non-breeding season without pelvic thrust. It did not occur in series or lead to ejaculation like breeding season mounts. He also suggested that adult female homosexual behavior was directly elicited by observing heterosexual interactions [9]. Harlow and Zimmerman studying on rhesus monkeys stressed the significance of peer contact, particularly during play in the development of adult sexual behavior [15]. Homosexual behavior appeared to be less characteristic of monogamous, polyandrous, and polygynous primates, and more common among multi-male multi-female groups [2].

With emergence of sociobiology, homosexuality is no longer viewed as an abnormality. It is viewed as the product of evolutionary processes and explicable in adaptive terms with no supporting evidence [16, 17]. The present study represents the features of male homosexuality in form, context and functions both in adults and immature captive stump-tailed monkeys. The male-male homosexuality observed during the study period adds a new dimension in sexual behavior of stump-tailed macaque.

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METHODS

The study was conducted in captive animals inside the zoological park, Aizawl, India. The study group of 20 animals consisted of 4 adult males (named as Alpha- α , Beta- β , Gamma- γ , and Delta- δ male) of 29, 27, 8, 9 years respectively; 9 adult females of the age ranging from 6-22 years; 4 immature male and 2 immature females of the age group 1.5-2.5 years; and one infant of six months old. All individuals in the study were identified on the basis of morphological features such as face and genital color, nipple shapes, and the pattern of dark patches/scars on face. The monkeys are housed in two indoor rooms and one outdoor enclosure. Individuals of the study group were readily observable regardless of the enclosure they occupied. The α -male died on July, 2010 due to age and the fourth male named δ -male was introduced in the group on December, 2010. The study group does not breed throughout the year unlike reported by Smith [18]. We observed mating during September to February, and birth during February to August. All nine births recorded occur during February to August in the last three years.

Data collection

Focal data and scan sample data [19] were collected for male stump-tailed macaque engaged in homosexual encounters from June 2009 to January 2011. Homosexual behaviors included genital stimulation, ventro-dorsal and ventro-ventral mountings with or without pelvic thrust, anal intromission with or without ejaculation between the same-sex individuals. A simple ventro-dorsal mounting without any pelvic thrust is considered as brief mount. The observations of homosexual encounters involved; sexual solicitations, season of copulation, methods of stimulation (Table 1), mounting position, number of pelvic thrust, duration of copulation and the post-copulation activities. Male dominance ranks were determined by quantifying the number of times males cowered to or avoided one another in dyadic social contexts [20] and a linear dominance hierarchy exists in adult males.

Wilcoxon matched-paired signed-rank test was performed to analyze the pattern of genital stimulation among adult males using SPSS ver. 16.0.

The activities observed are defined as followed:

A. *Homosexual consortship*: When the male engaged in mounts three or more times within 10 min and consortship terminated by a distance of more than 1m and exhibited no mounting for 10 min. Two types of mounting were observed.

- 1) *Double foot-clasp mount*: - when the mounter grasped the mountee's loins with his hands and his feet just above the mountee's ankles.
- 2) *Ventro-ventral mounting*: - when one of the animals holds himself below the other with their heads in opposite direction thereby manually stimulating each other penis.

B. *Solicitations*: An act that leads to prompt mounting [21]. Three types of solicitations were exhibited.

- 1) *Hindquarter presentations*: - When potential mountees stand quadrupedally with their arms and legs flexed and their perineum oriented towards the potential mounter.

- 2) *Back presentation*: - When potential mountees sit with forearms slightly bent and lifting hind-quarter towards the potential mounter. Hindquarter and Back presentations are the signs of invitation to be mounted.

- 3) *Hands-on-hindquarter*: - When potential mounters grasped or placed one or both hands on the hindquarters of the potential mountee. It is a sign to get consent for mount.

C. *Pelvic thrust*: The movement of the mounter's pelvic region toward the mountee's perineum.

D. *Thrusting rate*: The number of thrusts an individual executed during a mount.

RESULTS

Homosexual encounters among adult males

All adult males participated in male homosexual encounters. Initially, there were 3 adult males in the group (α -male, β -male and γ -male). The α -male died on June, 2010 and the δ -male, the fourth one was introduced in the group on November, 2010. The β -male was second in hierarchy in the group till α -male alive. The γ -male dominated over β -male and therefore over the entire group. Male homosexual encounters were recorded under two categories; manual genital stimulation and actual mounting. There were 35 incidents of genital stimulation occurring bidirectionally within the dyads (Table 1), 54.28% were performed by dominant male and 45.71% by the subordinate. Genital stimulation did not reflect dominance-subordinate relation. Wilcoxon test was found to be non-significant ($Z = -1.134$, $p = 0.257$). Only 5.71% of total genital stimulation occurred within 1min. of aggressive interactions between homosexual partners and the majority (94.29%) occurred in the context of social affiliation mainly during grooming. Manual genital stimulation occurred throughout the year.

Three types of mounting were observed in adult males:

1. Mounting without pelvic thrust (brief mounts)
2. Mounting with pelvic thrust without anal intromission and ejaculation.
3. Mounting with anal intromission leading to ejaculation.

Of the 146 mounts observed, 83% were of brief mounts, 10% were without anal intromission and 7% of mounts were with anal intromission and ejaculation. Mounting was unidirectional within the dyads, the dominant male always mounted to subordinate ones. The most dominant male in the group never assumed a female role and the most subordinate male never act as male. Sexual solicitation involved hind-quarter presentation and back presentation as an invitation to mount; and hands-on-hindquarter as seeking permission to mount. Mounting was in double foot-clasp position similar to heterosexual encounters. Agonistic interaction culminated 82% of total mounting where the subordinate male exhibited hind-quarter presentation to dominant male and 18% of mounting occurred in the context of social affiliation like grooming interaction and co-feeding.

Unique encounter between α -male and β -male

Ten unique incidents of homosexual encounters between α -male and β -male occurred in January 2010, on four different days

during the mating season. Details of homosexual encounters are given in table 2. The α -male always mounted over the β -male. Ejaculation was observed in all the episodes. Every episode of homosexual encounter was initiated immediately after the heterosexual encounter between the β -male and estrous females. Pre-copulatory event included the hind-quarter presentation that allows manual genital stimulation and back presentation that solicited to mount. Hands-on-hindquarter led to mounting 7 times of the 10 homosexual encounters. Mounting were in double foot-clasp position. The thrusting rate was 20 (± 3.67)/encounter, ranged from 15 to 25, exhibit by the mounter followed by ejaculation on the back of the mountee. The average duration of pelvic thrust was 12.3(± 4.06) seconds, ranges from 7 to 18 seconds. The average duration of copulation including ejaculatory period was 54.7(± 5.36) seconds, ranges from 45 to 60 seconds. There was no consistency in pelvic thrust rate, duration of pelvic thrust, and the copulation time. The ejaculatory phase was distinguished by a pause followed by stiffening of the body, muscular spasm and rhythmic expiration vocalization. After each ejaculation, both the actors ate the semen which was the main post-copulatory event. Most frequent copulatory event occurred was five times within 40 minutes and shortest intervals between two events was 5 min (Table 2).

Homosexual encounters among immature males

Table 1. Methods of stimulation and number of incidents observed during male homosexual encounters.

Methods of stimulation	Numbers of incidence observed	Among adult males	Among immature males	Types of male participants	Season of occurrence
Genital stimulating of presenting male without mounting.	62	35	27	Adults and immature males	During mating and non-mating seasons
Genitals stimulation followed by mounting.	45	0	45	Only immature males	During mating and non-mating seasons
Mounting without pelvic thrust (brief mount).	181	121	52	Adult and immature males	During mating and non-mating seasons
Mounting with pelvic thrust without anal intromission, stimulating by rubbing penis against the body of mountee.	205	15	198	Adult and immature males	During mating and non-mating seasons
Mounting with anal intromission and ejaculation.	10	10	0	Only between α -male and β -male	Only mating season

Table 2. Homosexual encounters between α -male and β -male on different days in the month of January, 2010.

Date of encounter	No. of Copulation bout	No. of copulatory events.	Time of copulation (am)	Interval between two successive events (min)	No. of pelvic thrust	Duration of pelvic thrust (sec)	Duration of copulation (sec)
7 th	05	1A	7:30	1A&2A=7	20	15	60
		2A	7:37		25	17	60
		3A	7:45	2A&3A=8	22	12	55
		4A	7:50	3A&4A=5	15	8	50
		5A	8:10	4A&5A=20	17	8	52
9 th	02	6B	8:00	6B&7B=10	15	7	45
		7B	8:10		18	9	50
11 th	02	8C	9:00	8C&9C=8	20	14	55
		9C	9:08		25	18	60
15 th	01	10D	8:45		22	15	60
AveraSD					19.9 (± 3.67)	12.3 (± 4.06)	54.7 (± 5.36)

322 homosexual encounters were observed among immature males. All immature males participated in the homosexual encounters, none showed dominance consistently. The homosexual interactions included genital stimulation without mounting (8.38%), mounting with manual stimulation (14%), mounting without pelvic thrust (16.14%) and mounting with pelvic thrust (61.5%). Genital stimulation and mounting was occurred bidirectional within dyads. No prominent sexual solicitation was performed by immature. All types of homosexual encounters between immature males occurred throughout the year (Fig. 1) but homosexual consortship (n=120) occurred only during the mating season. The frequency of mounting with pelvic thrust (67.11% of total mounting) is significantly high during the months of January, November and December (Fig. 1). The forms of mounting differ depending upon the types of mounting. Mounting with and without pelvic thrust was in a double foot-clasp position. Mounting with manual stimulation mainly occurred in ventro-ventral mount and in some occasions, the mounted animal simultaneously bent his head under his own body, thereby reaching the genitals of the mounting animal, manually stimulating them. Mounting occurred mainly during playing (74%) and feeding (24.5%). The adult males provided assistance in 67% of the total mounting with pelvic thrust by holding the mountee's loin.

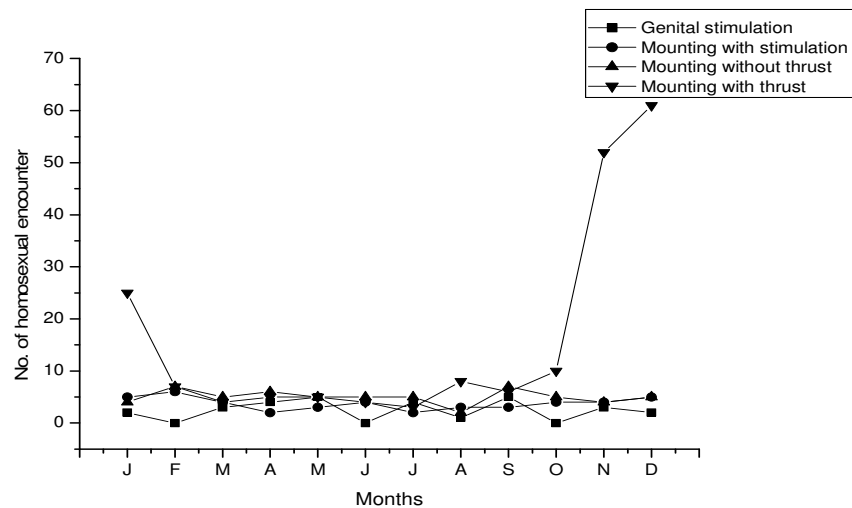


Fig 1. Occurrence of different homosexual interactions among immature male throughout the year.

DISCUSSIONS

Mounting interaction between individuals of same-sex are taxonomically widespread and occurrence is fairly frequent in certain species, but their functional significance, if any, remain obscure [2]. Homosexual behavior has often been considered 'abnormal' or deviant and unadaptive, since it does not obviously serve the reproductive function [9]. Homosexual behavior in non-human primates was due to strong positive emotional ties without a criterion of specific age group and sexes [9]. The most dominant male in our observation never assumed a female role and definite relationship exist between dominance status and sexual role in adult male homosexual mounting. Homosexuality in adult female stump-tailed macaque is known to be sexually motivated where the individuals exhibit copulatory facial expressions and undergo orgasmic uterine contractions [22]. No homosexual behavior has been reported so far among the free-ranging stump-tailed macaque [23, 9, 24]. In the captive environment, stump-tailed macaque showed homosexual encounter occasionally; approximately 6%-24% as frequently as heterosexual behavior [23, 9]. However, in the present study, homosexual encounters for all age classes of males were found to be 5 times more frequent than that of heterosexual interactions. Hanby and Brown reported that infantile homosexual mounts in Japanese macaque (*Macaca fuscata*) occurred in the context of play (70%); proximity or contact (27%), and remaining (3%) occurred in aggressive context [25]. Isosexually reared males of *Macaca arctoides* and *M. mulatta* indicated that a lack of heterosexual experience at immature stage does not necessarily affect the expression of competent heterosexual copulation during adulthood [26, 27]. Nonetheless, among macaques, adequate opportunity to engage in mounting when young is necessary for competent performance of heterosexual copulation in adulthood [28]. In the lights of the above discussion, the following hypotheses are tested.

Mounting between α -male and β -male: Socio-sexual or sexually motivated?

The observations on homosexual encounters between α -male

and β -male, almost same age, indicated that the α -male always assumed a male role and β -male female's role. Both individual showed rigid propensity towards their role. Chevalier-Skolnikoff reported change in role among males during homosexual interactions [9]. Homosexual encounter in this study were observed only during the mating season when the estrous females were also available. The α -male never copulated with any of the estrous female. In several occasions estrous female presented herself to α -male, he rejected the female and copulates with β -male. All the encounters between α -male and β -male occurred after the heterosexual encounter between the β -male and the estrous female. During their heterosexual encounter the α -male chased away the female and approached the β -male. Sexual solicitations by α -male, hands-on-hindquarter, exhibited in 70% of the encounters and back presentation by β -male occurred in 30% of the total homosexual encounters. In every episodes of homosexual encounter the interaction is initiated by manual anal manipulation. However, the extent of anal manipulation was inconsistent during the episode.

The γ -male was introduced from the breeding centre to the study group on 15th, November, 2010. Both α -male and β -male have been living together in the same enclosure since their infant stage. Therefore, most of the group members are the descendants of these two adult males. However, it was unlikely that the α -male and the β -male were behaving in an altruistic way for the reproductive benefit of the γ -male and also, sexual selection would not likely to favored such altruistic behavior. Majority of the primates did not exhibited sexual difference in the frequency with which homosexual behavior is expressed [2]. The sexual differences in frequency of expression of homosexual encounter in some intra-specific group may also be due to factors such as living condition, group composition, and seasonality. However, the study group being living together in the same condition for years, having more female animals in the population, and occurrence of male-male homosexual encounter only during the mating season did not support the concept of intra-specific sexual differences in homosexuality. The unique homosexual behavior between α -male and β -male as sexually motivated behavior was supported by three major evidences as follows. 1. The mounting with ejaculations observed between α -male

and β -male occurred only during the normal mating season and not during other periods/months and also not by other age classes. The similar homosexual interaction did not occurred among other adult males even in the next mating season. 2. This type of homosexual encounter did not serve any of the socio-sexual roles. Grooming pattern between α -male and β -male did not differ during normal days and during homosexual encounters and this behavior did not seemed to reduced aggression nor regulated tension between the participants. 3. The form of homosexual encounters between these two males showed similar activities as seen in normal heterosexual encounters.

Wolfe compared demographic trends and frequency of homosexual behavior between females in two populations of *Macaca fuscata*. She observed that females living with less number of sexually active males were engaged more in homosexual behavior [29, 30]. However, demography seem to have no effects on the expression of homosexual behavior between α -male and β -male since there were more sexually active females in the group. Some studies of group living *Macaca fuscata* and *M. mulatta* indicated that male-male mounting increased significantly when androgen levels are at lower ranges [31, 32]. However, similar studies on *M. arctoides* and *M. mulatta* showed no such correlation [33, 34]. All the encounters in the study result in ejaculation and the form of interaction was same as that of heterosexual coitus, thus this behavior was unlikely to be the product of abnormal excesses or deficiencies in androgen. This kind of homosexual behavior may be a special form of sexual interaction with a definite function of sexual motivation.

Homosexual mounting between adult males: Dominance-Assertion, Reconciliation and Tension-Regulation Hypothesis

Dominance assertion, Reconciliation and Tension-Regulation hypothesis were examined with adult male stump-tailed macaque during homosexual encounters. Mounting of adult male functions as a dominance demonstration. Homosexual encounters between adult males interpreted a strict relationship between dominant individuals mounting subordinates individuals. Majority of the total mounting (82.19%) and every mounting with pelvic thrust without anal intromission occurred within 5min. of an aggressive interaction where the subordinates exhibited hind-quarter presentation that served to reaffirm the dominance and reduced further agonistic interaction. Therefore, homosexual mounting could be interpreted as reconciliation attempted by the subordinates. Homosexual mounting was the main mechanism employed to regulated aggression and re-established social bond among adult males. The thrusting rate (2.66) of mounting without anal intromission seems to provide no sexual pleasure for the partners. Mounting without pelvic thrust in some occasions (9.09%) occurred during feeding time (provisioned food) which work to calmed anxiety and increased tolerance which made food sharing smooth. Hence, brief mount between adult males served to regulate tension within the dyads.

Homosexual interactions between immature males: Practice for Heterosexual Copulation Hypothesis

Four immature males participated in homosexual mounting, and formed six different homosexual dyads. Homosexual behavior between immature males was unlikely to be a form of dominance assertion, because mounting occurred reciprocally. In the present

study, five main evidences indicate the homosexual mounting between immature males as socio-sexual behavior and function as practice for heterosexual copulation. (1) Series of mounting/homosexual consortship (n=120) occurred only during the mating season. Although different modes of mounting between immature male were observed throughout the year, mounting with pelvic thrust commonly (84.73%) occurred in the mating season. (2) Majority of homosexual consortship (91 %) occurred on the same day heterosexual encounter occurred. Homosexual mounting most often follow and appear to be elicited by viewing heterosexual activities. (3) The assistance provided by adults' male to immature males during homosexual encounter. In 67% of the total mounting with pelvic thrust the adult male assist the homosexual encounter by holding the mountee's loin with positive facial expression and teeth chattering. In some incidence, the adult male also manually stimulated mounter's genitals. (4) Homosexual mounting both with and without pelvic thrust was frequently observed during play (74%). Hamilton and Chevalier-Skolnikoff suggested that homosexual behavior expressed during play interaction may function as practice for adult heterosexual copulation [35, 9]. (5) Immature male that participated more in homosexual mounting was found to engage more in heterosexual mounting with sexually mature female. JV2 and JV1 participated in 28.75% and 27.5% of 120 homosexual consortship respectively were observed to engaged in 46.15% and 38.46% of 39 heterosexual encounter between immature males and sexually mature female.

CONCLUSIONS

Our study did not seem to support homosexual behavior as an abnormal behavior. Homosexual behavior among the male stump-tailed macaque was found to be either socio-sexual behavior or sexually motivated depending on the age group and the individual participated. Homosexual interaction among immature males was considered to be training for adult sexual roles. Adult males' mounting interpreted dominant-subordinate relationship and function as the method of reconciliation and tension-regulation employed by the subordinate male. The unique incidents of mounting between α -male and β -male seems to be sexually motivated.

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