Homosexual Behavior in a Laboratory
Group of Stumptail Monkeys (Macaca
arctoides)\(^1\): Forms, Contexts, and Possible
Social Functions\(^2\)

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Observations of stumptail monkeys revealed frequent prolonged, intense genital stimulation between individuals of the same sex, both males and females, adults and infants. These homosexual interactions occurred in positive emotional contexts, were accompanied by positive emotional facial expressions, and often were evidently elicited by the observation of heterosexual behavior. Infants' first copulations were performed with adults of the same or opposite sex who actively aided them. This suggests that homosexual and heterosexual encounters function as training for adult sexual roles, and that homosexual behavior is a basic primate pattern not exclusive to man.

Key Words: homosexual behavior; Macaca arctoides; macaque; socialization; monkey.

INTRODUCTION

It is commonly thought that human sexual behavior is unique in its variability, diversity of sexual objects, and freedom from current physiological

This research was supported in part by the Interdisciplinary Training Program, Langley Porter Neuropsychiatric Institute, University of California, San Francisco, and by United States Public Health Service Training Grant MH-7082, from the National Institutes of Public Health.

\(^1\) The stumptail macaque, Macaca arctoides, was formerly designated Macaca speciosa L. Geoffroy, 1926. For nomenclature, see Fooden (1967a,b) and International Commission on Zoological Nomenclature (1970).

\(^2\) This article was part of the symposium "Biological and Cultural Bases of Sex Role Differentiation," presented at the Meetings of the American Association for the Advancement of Science, December 1971, in Philadelphia.

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state. Actually, sexual behavior in nonhuman primates shares some of these qualities often ascribed exclusively to man. Studies on the nature of human sexual behavior from Ellis in 1896 to Kinsey in the 1940s and 1950s and Masters and Johnson in the 1960s and 1970s have described the prominence of both "normal" and "perverted" sexual behavior in preadolescents and in adults. The data on stumptail monkeys presented here help to place the determinants of human sexual behavior and sexual role into a broader primate perspective. They indicate that these kinds of sexual behaviors occur in infants and adults of primate species other than man, and are probably basic primate behavioral patterns.

In the course of a year-long study, 36 homosexual encounters were recorded in one laboratory group of ten stumptail monkeys (Macaca arctoides) living in a social group. Whether the frequency of homosexual behavior seen in this group is typical of the species is not known. However, my brief observations of a captive colony of M. arctoides at the University of California, Berkeley, and observations by Kling (1972) of two other colony groups at Rutgers Medical School, also revealed frequent homosexual encounters, suggesting that stumptail macaques may have a propensity for such behavior. On the other hand, Bertrand's (1969) descriptions of genital rubbing during "bullying," genital manipulation, and mounting behavior between various sex-age combinations in her groups of stumptail macaques may or may not have involved the prolonged, intensive genital stimulation between like-sexed individuals defined here as homosexual behavior. Female mounting occurred in only one of her groups, suggesting that this behavior might be a cultural tradition, as paternal care of infants evidently is in Japanese macaques (Macaca fuscata) (Itani, 1959).

In a comparative study on captive and free-ranging hamadryas baboons (Papio hamadryas), Kummer and Kurt (1965) found that the behavioral repertoires of the two groups were quite similar, although the frequencies of behavior, including some sexual behavior, were different in the two groups. Rowell (1967) also found such similarities in repertoires and differences in frequencies in wild and caged anubis baboons (P. anubis). Accordingly, it appears that behavior observed in the laboratory does reflect the behavioral range of the species, although the frequencies with which a particular behavior occurs in the wild may be altered by captivity.

The present study offers an opportunity to examine the homosexual potentials of nonhuman primates in terms of the forms of their behavior, to examine the conditions under which this kind of behavior occurs, and to investigate the possible social functions of the behavior.

Homosexual behavior in primates has been reported before, both in the laboratory and in the wild (Beach, 1949, and Ford and Beach, 1952, have reviewed homosexual behavior in mammals), but such reports are rare. Previous investigations have usually focused on brief mounts, or they have considered brief mounts and prolonged homosexual interactions together. Brief mounts
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Generally have been found to correlate contextually with dominance interactions (Bernstein, 1970; Maslow, 1936; Talmage-Riggs and Ansche1, 1973; Wickler, 1973; Zuckerman, 1932). There has been little study of the contexts of these formally different prolonged homosexual interactions.

The most detailed accounts of primate homosexual behavior, evidently incorporating prolonged genital stimulation, were reported by Hamilton (1914) and Kempf (1917). The same animals, 28 monkeys of three species—rhesus (*Macaca mulatta*), irus macaques (*M. fascicularis*), and baboons (unspecified)—were studied. The groups were composed of animals of both sexes, housed in cages about 18 ft high by 4 ft wide by 5 ft deep, although the animals were often released to roam at large. In these groups, male homosexual copulations were frequent and often included anal intromission and ejaculation. Extensive manual genital stimulation was also reported. Hamilton noted that homosexual behavior was particularly prevalent in immatures, and Kempf postulated that a specific homosexual stage ontogenetically precedes the heterosexual phase of life. Kempf also noted that the homosexual behavior he observed appeared to be strongly affected by dominance relationships, and that the subordinate animal gained social protection, while the dominant received sexual rewards.

Carpenter (1942) reported that among free-ranging rhesus monkeys (*Macaca mulatta*) at Cayo Santiago, an island off the coast of Puerto Rico, mountings with pelvic thrusts—which may have involved prolonged genital stimulation—occurred between eight of 150 females. Carpenter (and also Beach, 1949) suggested that homosexual behavior might be a substitute for heterosexual coitus. This has been postulated particularly for females who might be sexually attracted to other females in estrus (the period of sexual receptivity when ovulation generally occurs) or might themselves turn to other females during their early estrus period when they might not yet be of interest to males. Gordon and Bernstein's (1973) experimental study of captive male rhesus monkeys also suggests that male homosexual behavior is a substitute for heterosexual coitus in rhesus monkeys.

Hanby and Brown (1974), in a study on the development of sociosexual behavior in a captive group of approximately 100 Japanese macaques (*Macaca fuscata*) living in a 2-acre corral, present data on male-male and female-female mountings, some of which evidently involved prolonged genital stimulation. They found that in infants up to 1½ years of age male-male mounting, usually accompanied by pelvic thrusts, occurred with approximately the same frequency as male-female mounting. Most of these infantile homosexual mounts (70%) occurred in the context of play; the rest (about 27%) occurred in the context of "proximity" or "contact," while only 3% occurred in aggressive contexts. Among animals over 1½ years of age, male-male mountings occurred most frequently in the nonbreeding season. About half the time, these nonbreeding season mounts occurred without pelvic thrusts and did not occur in series or lead to ejaculation.
as breeding season mounts often did. These relatively brief adult male mountings usually occurred after one male simply approached, or was approached by, another male. Female-female mounting was much less frequent than male-male mounting, and, unlike male-male mounting, occurred mostly during the breeding season, with adult females (over 3½ years) responsible for most of the female-female mounting. Female-female mountings were generally accompanied by pelvic thrusts and occurred in series and must have been of relatively long duration. Female-female mountings characteristically occurred in a context of close proximity, the pair usually walking around together or sitting in contact for long periods of time before and after the mounting.

Bingham (1928) reported an incident in which, after a period of masturbation on the part of one captive female chimpanzee (Pan troglodytes), she and another female chimp engaged in a series of embraces and then turned their faces in opposite directions and, standing on all fours, pushed their buttocks together and pushed and slid about in this manner for a short interval (p. 124). Sade (1968) reported one incident of male homosexual behavior in free-ranging rhesus monkeys (Macaca mulatta) between brothers at Cayo Santiago. This relationship included anal intromission and ejaculation (Sade, 1971). Morris (1970) reported on a long-term homosexual relationship between two young captive male orangutans (Pongo pygmaeus), which included frequent anal intercourse. This incident is of particular interest, for the experience resulted in an evidently irreversible reproductively abnormal behavioral pattern in one of the animals. When this orang was later paired with a female, he would only perform anal intercourse with her.

Similarly, Erwin and Maple (1976) report that a pair of male rhesus monkeys (Macaca mulatta) reared in a laboratory with exclusive social access to each other during their second year of life performed prolonged reciprocal mounting with anal penetration. Erwin and Maple suggest that the relationship between them was primarily based on mutual affection. However, while these males preferred each other to females as mounting partners, both males did perform adequately with both familiar and unfamiliar female partners.

**METHODS**

This study is based on 500 hr of observation of stumptail macaques made from September 1967 to September 1968 at the Primates Laboratory of the Department of Psychiatry, Stanford University School of Medicine. The monkeys were living in a social group housed in an indoor colony cage 18 ft long by 12 ft wide by 7 ft high. The group consisted of ten animals: one adult male, one subadult male, four adult females, one subadult female, and three infants (one male and two female) who were born into the group and were observed during their first 6 months of life (see Table 1). The adults were born in the wild. The group was formed 1 year before the initiation of the observations reported here, and,
Table I. Composition of the Stanford Group of Stump-tail Macaques

<table>
<thead>
<tr>
<th>Identification No.</th>
<th>Age, sex</th>
<th>Parity</th>
<th>Reproductive condition</th>
<th>Dominance status</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Fully mature male</td>
<td></td>
<td>Breeding</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>Adult female</td>
<td>Probably primiparous</td>
<td>Pregnant, lactating</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>Adult female</td>
<td>Primiparous</td>
<td>Cycling, pregnant,</td>
<td>6</td>
</tr>
<tr>
<td>4</td>
<td>Adult female</td>
<td>Primiparous</td>
<td>Cycling, pregnant,</td>
<td>4</td>
</tr>
<tr>
<td>5</td>
<td>Adult female</td>
<td>Multiparous</td>
<td>Lactating</td>
<td>9</td>
</tr>
<tr>
<td>6</td>
<td>Subadult male</td>
<td></td>
<td>Breeding</td>
<td>8</td>
</tr>
<tr>
<td>2-1</td>
<td>Infant female</td>
<td>Nulliparous</td>
<td>Cycling</td>
<td>7</td>
</tr>
<tr>
<td>3-1</td>
<td>Infant male</td>
<td></td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>54-2</td>
<td>Infant female</td>
<td></td>
<td></td>
<td>10</td>
</tr>
</tbody>
</table>

Consequently, these observations reflect the behavior of animals in a well-integrated group.

Two observational methods were employed during the study. About 425 hr of qualitative observations were made on the whole group of animals, with running notes being taken on the animals' various activities. Not all sexual interactions that occurred during these observations were recorded, since it was not possible to simultaneously record all the activities. The sexual encounters were recorded in longhand, and care was taken to consider the total behavior of the particular animal(s) being observed, as well as to note sequential behaviors and interactions between animals.

A total of 75 hr of time-sampled quantitative observations were made, focusing on one animal at a time. All the sexual encounters in which focus animals were involved were recorded. Most of these data were recorded on checklists. Behavior was recorded according to the different body parts involved, including facial behavior, and according to the different sensory modes in which communications occurred. Prolonged interaction between like-sexed animals, involving intensive stimulation of at least one of the participating animals, was considered a homosexual encounter. Mounts and their various components were timed with a stopwatch. (See Chevalier-Skolnikoff, 1975, for a more detailed description of methods.)

FINDINGS

Homosexual Behavior Among Males

Thirteen incidents of male homosexual behavior were recorded during this study. All three males participated in male homosexual encounters. Such encounters occurred between two of the three potential pairs of males: the adult and subadult males, and the subadult and infant males.
Unlike heterosexual copulations, which were relatively stereotyped in form, male homosexual behavior was extremely varied. In the heterosexual encounters observed during this study, either the male or the female approached the potential mate, looking at the other with a direct gaze often accompanied by positive facial expressions, such as the lip-smacking, puckered-lips, or square-mouthed expressions (see Chevalier-Skolnikoff, 1974a, Fig. 1a-c). The female then presented her rear to the male, who, after a brief oral or manual examination of the female's genitals, mounted her from behind. In the mounted position, he grasped her loins with his hands and her legs with his feet (see Chevalier-Skolnikoff, 1974a, Fig. 2b). The copulation lasted an average of 2.8 min and consisted of three phases — a pre-ejaculatory phase, an ejaculatory phase, and a post-ejaculatory phase. During the pre-ejaculatory phase, which lasted about 1 min, the male executed about 60 pelvic thrusts. The ejaculatory phase was distinguished by a pause followed by stiffening of the body and muscular spasms and was accompanied by a characteristic intense frowning round-mouthed facial expression and rhythmic expiration vocalizations (see Chevalier-Skolnikoff, 1974a, Fig. 1d). The post-ejaculatory phase lasted about 2 min, during which the pair remained united. (For further descriptions of the heterosexual copulation pattern in this species, see Bertrand, 1969; Blutron-Jones and Trollope, 1968; Chevalier-Skolnikoff, 1975; Lemmon and Oakes, 1967. See also Kanagawa et al., 1972, on the copulatory behavior of vasectomized males, whose behavior differs from that described in the other studies.)

Male homosexual encounters included prolonged manual genital stimulation, sometimes mutual; oral genital stimulation (fellatio), also sometimes mutual; dorsal mountings with pelvic thrusts and, occasionally, anal intromission. Some encounters consisted of sequences involving several methods of stimulation. No ejaculations, or evidence of orgasm were observed in this study during male homosexual encounters.

Homosexual manual genital stimulation was effected in one of three ways (see Table II): In association with mountings, the animal who was being mounted would reach back and manipulate the genitals of the mounting animal (see Chevalier-Skolnikoff, 1974a, Fig. 3a), holding his partner's penis in one hand and moving his hand back and forth along the shaft, or one monkey presented to a second monkey, who manually stimulated the presenting animal. In the case of mutual stimulation, the partners would present simultaneously, thereby bringing their genitals together and, standing rump to rump, would reach back and simultaneously manipulate each other's genitals (see Chevalier-Skolnikoff, 1974a, Fig. 3b).

Oral genital stimulation also occurred in several fashions (see Table II). One male might present and the second animal would orally stimulate the first, licking the presenting monkey's penis or taking his penis in his mouth and evidently sucking on it as he stood behind him. Or the second monkey might mount the first in a peculiar fashion that permitted him to simultaneously orally stimu-
Table II. Methods of Stimulation Recorded in Male Homosexual Encounters

<table>
<thead>
<tr>
<th>Method of stimulation</th>
<th>Number of incidents recorded</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mounting with pelvic thrusts, the mounter stimulating himself by rubbing his penis against the animal mounted</td>
<td>5</td>
</tr>
<tr>
<td>Mounting with intromission and pelvic thrusts</td>
<td>1</td>
</tr>
<tr>
<td>Mounting with oral stimulation of animal mounted</td>
<td>2</td>
</tr>
<tr>
<td>Mounting with mutual oral stimulation</td>
<td>2</td>
</tr>
<tr>
<td>Mounting with manual stimulation of mounter by animal mounted</td>
<td>4</td>
</tr>
<tr>
<td>Presentation, with the second male orally stimulating the presenting male</td>
<td>2</td>
</tr>
<tr>
<td>Presentation, with the second male manually stimulating the presenting male</td>
<td>1</td>
</tr>
<tr>
<td>Mutual presentations with mutual manual stimulation</td>
<td>2</td>
</tr>
</tbody>
</table>

*a Some encounters involved several methods of stimulation occurring in sequence; consequently, the numbers of incidents add up to more than 13 (the number of encounters recorded).

late his partner (see Chevalier-Skolnikoff, 1974a, Fig. 3c). On some occasions, while being stimulated in the manner just described, the mounted animal simultaneously bent his head under his own body, thereby reaching the genitals of the mounting animal, orally stimulating them (see Chevalier-Skolnikoff, 1974a, Fig. 3d).

The single recorded case* of anal intromission occurred as follows:

Stanford, 8/19/68, 11:45 a.m. (Description from notes.) The subadult male, No. 5, presents to the five-month-old infant male, No. 3-1, reaching back toward the infant with one hand. The infant mounts the subadult. The subadult manipulates the infant's penis with the extended hand while the infant remains awkwardly mounted too low on the subadult. The subadult ceases the genital manipulation and pushes the infant's posterior up toward his anal region and, with his hand, guides the infant's penis into his anus. The infant makes about three pelvic thrusts, and the subadult pulls the infant down from his mounted position. The infant starts to leave. He returns, and the subadult draws him to his ventrum and embraces him. The subadult grooms the infant.

As in the above incident, hugs and embraces, often accompanied by the excited teeth-chattering expression, frequently followed male homosexual encounters.

*Several cases of anal intromission were observed; only one was recorded.
The positive facial expressions generally associated with heterosexual copulations also accompanied various phases of the male homosexual encounters.

In all male homosexual encounters, one member of the pair assumed the sexual role carried out by the opposite sex in heterosexual coitus. In two incidents, both monkeys took on female sexual roles (they simultaneously presented and manipulated each other’s genitals). On the 11 other occasions, only one animal took on a female role. The subordinate animal, who was the subadult male, No. 5, in both male pairings, took the female role ten times and a male role three times. The infant, No. 3-1 (who was dominant over the subadult, probably because of the high dominance status of his adoptive mother), enacted a female role five times and a male role seven times. The adult male, No. 1, the most dominant male in the group, never assumed a female role. There seemed to be a definite relationship between dominance status and sexual role in these male homosexual interactions. The more dominant the animal, the more frequently he adopted a male sexual role.

The settings and contexts of homosexual behavior were examined to gain some understanding of the social determinants and functions of homosexual behavior. The one recorded incident of prolonged oral genital stimulation between the adult male (No. 1) and subadult male (No. 5) took place at the beginning of the study. At that time, the subadult male was still sexually immature, as evidenced by the absence of observed ejaculations during heterosexual copulations.

The two monkeys had a strong affectional tie. The subadult was very submissive toward the adult and frequently addressed subordinate gestures toward him, such as subordinate presentation. The adult was always friendly and protective of the subadult, generally taking his part in aggressive encounters. The two often spent rest and sleep periods huddled together, the subadult with his back up against the ventrum of the adult, who sat with his arms around the younger animal, often holding the subadult’s penis in one hand. Such behavior has also been observed between males in colony groups of stumptail monkeys at Davis (Lindburg, 1969).

During active periods, the adult male often approached the subadult from the rear and briefly examined his genitals. Such behavior is common in stumptail macaques. Males often examine the genitals of other males as part of their dominance behavior, and they also examine females both in dominance and in

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4 The infant’s dominance was manifested by his ability to displace the subadult male or to take food from in front of him.
4 Female No. 4, the infant male No. 3-1’s adoptive mother, was the second most dominant adult female in the group. His biological mother, No. 3, was relatively subordinate. Six days before No. 3-1 was born, female No. 4 gave birth to an infant who was stillborn or died within 12 hr after birth. When No. 3-1 was first seen, within 5 hr after birth, he was being carried by female No. 4, rather than by his biological mother, female No. 3. Evidently female No. 4 had taken him from the more subordinate mother, female No. 3. Female No. 4 cared for No. 3-1 and nursed him throughout the study.
sexual interactions. Adults of both sexes routinely direct such behavior toward infants (Bertrand, 1969; personal observations). However, these incidents between the adult and subadult male were accompanied by the positive facial expressions that generally accompany precopulatory sexual examinations, rather than the threat expressions that often accompany dominance mounts, and they were also accompanied by the intensely excited teeth-chattering expression. Furthermore, these examinations were frequently followed by embraces and affec-
tionate mutual mouth nibbles.

It was in this social setting, on a day in which the patterns of huddling while holding the penis and anogenital examination were particularly evident between the two animals, that after one of the usually brief anogenital examinations, the adult male proceeded to orally stimulate the genitals of the subadult for a prolonged interval. The two animals subsequently embraced and then huddled in their characteristic manner, the adult holding the subadult’s penis in one hand. Approximately 1½ months after the above encounter, the subadult male began showing evidence of sexual maturity: heterosexual copulations were accompanied by ejaculation, his face began to assume the adult red sexual coloration, his browridges became heavier, and his canine teeth perceptibly increased in length. At this point, the relationship between the two males became less intense, and, although they remained amicable until the end of the study, they soon ceased their frequent embraces and mutual mouth nibbles and their character-
istic huddling pattern.

Male homosexual encounters occurred most frequently between the sub-
adult male (No. 5) (who by this time was probably sexually mature) and the infant male (No. 3-1). They, too, occurred in the context of an intensely positive emotional relationship. From the time the infant was approximately 5 weeks of age, the subadult male spent much time with him. By the infant’s ninth week, the subadult male gave the infant routine parental care (which males characteristically do in this species, despite its seeming incongruence with the male sexual role). This parental care consisted of carrying, grooming, and holding the infant. He also played with the infant, which mothers tend not to do. During active periods of the day, the infant often was held and carried by the subadult male as much as by his mother. The first sexual interactions between these two animals were observed during the infant’s fifth week, when the infant performed rudimentary mounts on the subadult male. During the infant’s fourth month, his homosexual behavior with the subadult male became more elaborate. At this point, the two animals began to engage in oral and manual genital stimulation as well as mounting. During his fifth month, the infant was observed to achieve anal intromission (with pelvic thrusts, but without ejaculation or evidence of orgasm) with the aid of his partner (see, for example, the preceding quote from notes). This sexual aspect of the relationship between these two animals continued to be important until the end of the study when the infant was 6 months old.
An examination of the immediate contexts in which male homosexual encounters occurred reveals that only one of the 13 recorded incidents took place during or after an aggressive interaction. Five occurred in friendly contexts, such as after grooming or after embraces between the two monkeys. Eight of the 13 encounters took place on days in which a female in the group was evidently in estrus\(^7\) and much heterosexual sexual activity was occurring (see Table III).

The males, including the infant, often appeared to become sexually aroused by this heterosexual activity prior to the homosexual encounters. On some occasions, the male involved in the heterosexual encounter became one of the principals in the homosexual encounter. This suggests that it was not the absence of an estrous female that led to the male homosexual encounters. Michael (1969) reported evidence that pheromones, or smell stimuli, from the estrous female rhesus monkey (*Macaca mulatta*) are involved in eliciting male sexual behavior. Although it is possible that pheromones are involved in eliciting the homosexual behavior reported here, homosexual relationships between the male stump-tails were always an aspect of more generalized close affectional ties that were evidently rewarding to both the parties involved. In the relationship between the adult and subadult males, the adult gained reassertion of dominance while the subadult gained social protection. In the subadult-infant pair, the more dominant infant received parental care, and both parties gained play partners. All animals benefited at least on occasion in terms of sexual stimulation and general affective rewards.

**Homosexual Behavior Among Females**

Only adult and subadult females manifested homosexual behavior. Unlike male homosexual behavior, female homosexual behavior was rather stereotyped in form. One female mounted another by actually climbing on top of her, grasp-

\(^7\) The term “estrus” refers to the period near the time of ovulation during which a female mammal is sexually receptive. In this study, estrus was inferred behaviorally from observations of females repeatedly initiating or submitting to copulations, since external signs of estrus, such as genital swelling or reddening, rarely occur in this species (Trollope and Britton-Jones, 1970; personal observations). This interpretation of copulatory behavior indicating female estrus was often substantiated by the observation of its occurrence at approximately monthly intervals over several months in particular females. However, it could not be established that all the copulatory behavior of all the females occurred in monthly cycles, and some copulatory sequences may have occurred when females were not in estrus, or at least not ovulating. Bertrand’s (1969) observations of females copulating during menstruation support this latter possibility, as do the experimental studies by Slob *et al.* (1974), who found that intact females copulated throughout their cycles, and that ovariectomized females continued to copulate, although at somewhat lower frequencies than prior to surgery. These data on copulations occurring out of ovulation phase suggest that copulatory behavior is more independent of hormonal cycles in stump-tail monkeys than in most or all other primate species, with the exception of human beings.
ing the mounted female's shoulders with her hands and her hips with her feet. Subsequently, by thrusting, she rubbed her genitals on the rump of her mount (see Chevalier-Skolnikoff, 1974a, Fig. 2a). The mounting female was thereby genitally stimulated but the mounted female was not. Despite this lack of stimulation for the mounted female, she generally appeared to be very excited, and both animals usually made intense, friendly facial expressions before, during, and after the mounting.

Female mountings were of approximately the same duration as heterosexual copulations (around 2 or 3 min), and the phases were parallel. During the first phase, the mounting animal made a great number of pelvic thrusts, about the same number as the male makes in heterosexual copulations. On three recorded occasions, the mounting female (the most dominant female in each case) evidently reached orgasm, for she displayed all the behaviors characteristic of males during orgasm—pausing after the series of thrusts, stiffening, and then displaying muscular body spasms accompanied by the frowning round-mouthed expression and rhythmic expiration vocalizations. Extended postejaculatory phases, as seen in males during heterosexual copulations, were not observed, although the female having the orgasm did remain mounted during the period in which she made the characteristic orgasmic facial expression and vocalization. As in the case of male homosexual encounters, females often embraced after these homosexual mountings.

Evidence of orgasm in nonhuman female mammals has been reported (e.g., Zumpe and Michael, 1968; Burton, 1971; Fox and Fox, 1971), but no studies have described complete and obvious naturally occurring orgasmic patterns such as those observed in this study. Interestingly, all the obvious female orgasms observed here occurred during homosexual interactions. However, there is evidence that orgasms may also occur during heterosexual coitus (Chevalier-Skolnikoff, 1971, 1974a).

Four of the five adult and subadult females participated in female homosexual encounters; the most subordinate female (No. 54) was not involved. However, only two of the females (Nos. 2 and 4) ever took the male roles, and these were the two most dominant females; in every instance, the mounting female was dominant over the one being mounted. Every female in the group had one or two other females with whom she interacted most frequently (e.g., groomed, huddled). Some pairings changed over time, and others remained quite stable. As in the case of male homosexual interactions, females tended to mount other females with whom they had these close affectional ties. The most subordinate female in the group was also the most solitary animal with the weakest affectional bonds with other group members. She did not take part in any prolonged homosexual interactions, although she was frequently briefly mounted by adult females—often after being chased and bitten—in dominance interactions.

Despite the consistently higher dominance position of the mounting females, only two of the 23 female homosexual mountings occurred in aggressive
Table III. Contexts in Which Homosexual Encounters Occurred

<table>
<thead>
<tr>
<th>Context</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(13 encounters)</td>
<td>(23 encounters)</td>
</tr>
<tr>
<td>Aggressive [e.g., immediately (within seconds) after a fight]</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>“Friendly” (e.g., immediately after grooming or after approaches that culminate in embraces)</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Sexual (e.g., during or immediately after or between heterosexual copulations)</td>
<td>8</td>
<td>14</td>
</tr>
<tr>
<td>Context unknown</td>
<td></td>
<td>6</td>
</tr>
</tbody>
</table>

*Numbers of encounters occurring in particular contexts do not necessarily add up to the number of encounters, for some encounters occurred in two simultaneous contexts.

contexts (see Table III). These two cases occurred immediately after fights within the group. Female stumptails customarily embrace each other, briefly mount each other, or make half-mounds after group fights (personal observations), and Bertrand (1969) reported genital rubbing during “bullying” episodes. One might therefore expect to see homosexual behavior in such a context. However, most homosexual behavior observed during this study did not occur in or immediately following aggressive situations. One of the 23 mountings occurred in a generally friendly context, and 14 occurred in sexual contexts. In all the 14 cases occurring in sexual contexts, a female other than the mounting female was evidently in estrus, for she was repeatedly soliciting copulation and being mounted by one of the males prior to the homosexual encounter. In four cases, the female who was mounted homosexually was the female in estrus. In the other ten cases, females not in estrus were mounted. In no case was the mounting female in estrus, nor was she ever observed to come into estrus within 2 days of a homosexual encounter. Furthermore, in every case, the mounting female was lactating. These data indicate that, in most cases, prior heterosexual copulations were the immediate precursor to female homosexual activity. For example, observations were made during a series of eight complete copulations, each culminating in ejaculation, between the adult male and subadult female which were followed by a female-female homosexual encounter. The following are excerpts from the sequence:

Stanford, 4/25/68, 4:40 p.m. The subadult female (No. 6) presents to the adult male (No. 1), turning her head back to look at him over her shoulder with a direct gaze. The male mounts and obtains intromission and begins making pelvic thrusts, with a [friendly] square-mouthed expression on his face. Adult female No. 3 an-
proaches with a square-mouthed expression and dances excitedly about, looking at the copulating couple. After 51 pelvic thrusts and 1 minute 46 seconds, the adult male ejaculates, pauses and then shows muscular spasms accompanied by the frowning round-mouthed look and rhythmic expiration vocalizations. The pair remains united during the 1 minute 47 seconds of the postejaculatory phase. The male dismounts, and the subadult female leaves.

4:57 The subadult female presents to the adult male, turning her head and looking back at him over her shoulder. The adult female (No. 2) approaches and presents to the adult male, looking back at him between her spread legs. The male ignores both females.

5:02 The subadult female and the adult male copulate again. While the couple is thus occupied, an adult female (No. 54) approaches the copulating pair and presents to the adult male; he ignores her.

5:11 The subadult female and the male copulate again. Adult females No. 2, No. 3, and No. 54 and the six-month-old infant female, No. 2-1, all approach excitedly. The infant has a square-mouthed expression. Female No. 2 alternately directs open-mouthed stare expressions [threats] at the copulating subadult female, and lip-smacking [friendly] expressions and teeth-chattering [excited friendly but nervous] expressions and squeaks at the adult male. Shortly after: The female No. 2 approaches female No. 3, mounts her, and rubs her genitals on No. 3's rump. Female No. 2 dismounts from No. 3 and approaches and mounts female No. 4 and rubs her genitals on No. 4's rump. (No orgasm occurred during either of these homosexual encounters.)

The observations of female homosexual behavior support some of the conclusions based on male homosexual behavior. First, homosexual behavior is not exclusive to infants and, in fact, the female infants did not participate at all. Second, it often appears to be directly elicited by observing sexual interactions. Third, it occurs between animals with close affectional ties (although this factor is less salient in females than in males). Fourth, dominance relationships are reflected in the homosexual interactions, although dominance need not be a primary elicitor of the behavior. They also indicate that neither the male nor the female form of sexual behavior is necessarily directly dependent on an estrous hormonal state in a female.⁸

**DISCUSSION: SOME POSSIBLE FUNCTIONS OF HOMOSEXUAL BEHAVIOR**

Homosexual behavior has often been considered "abnormal," or deviant and unadaptive, since it does not obviously serve the reproductive function. However, these observations of male, female, and infantile homosexual behavior in stumptail macaques, as well as reports in the literature of homosexual behavior in free-ranging macaques, suggest that homosexual behavior in nonhuman primates may not be abnormal and may foster general social cohesion.

⁸See Beach (1968) for a summary article on the available evidence on the factors involved in the control of mounting behavior in female mammals. See also Eaton (1973), Dixon et al. (1973), and Saayman (1973) on hormonal determinants of mating behavior in female primates.
In this study, prolonged homosexual encounters occurred between animals with strong affectional bonds, as manifested by their frequent grooming and huddling together, and supporting each other in dominance interactions with other monkeys. The sexual interactions in the homosexual dyads, especially between males, appeared to underscore these animals’ close affectional ties. These data suggest that prolonged homosexual encounters usually differ functionally (represent the assertion of affectional ties) from brief homosexual mountings, which represent an assertion of dominance.

Male and female homosexual behavior in this study often followed prior heterosexual activity in the group. This suggests that copulating animals emit some sort of stimulus to other animals watching them. In females, the correlation was especially high. Since monkeys of this species do copulate when females are out of ovulatory phase, the viewing of heterosexual coitus is a likely elicitor. Furthermore, since the females who initiated homosexual activities apparently were not in the ovulatory phases of their cycles, their homosexual behavior evidently was not elicited directly by estrous hormonal states.

The work of Harlow and his coworkers (e.g., Harlow, 1960, 1961; Harlow and Harlow, 1962; Harlow and Zimmerman, 1959) on rhesus monkeys, *Macaca mulatta*, has stressed the significance of peer contact and, particularly, play in the development of adult sexual behavior. In this study, also, contact with peers was one setting in which rudimentary sexual activity was observed. However, in this mixed-aged social group, early male infantile sexual behavior occurred not only during interactions with other infants of both sexes but with adults as well (see Chevalier-Skolnikoff, 1974b). The assistance provided by adults of both sexes to infants during sexual activity suggests that homosexual and heterosexual encounters with adults as well as with infants function as training for adult sexual roles. However, long-term, exclusively homosexual experience, as cited by Morris (1970) in the case of the male orangutan, may result in a reproductively abnormal adult sexual role.

Several conclusions can be drawn from this study that have general bearing on the whole view of the evolution of sexual behavior:

1. Homosexual behavior is not exclusive to man. Consequently, homosexual behavior is not dependent on exclusively human biology, or on human capacity for culture or learning.
2. Nonhuman primate sexual interactions, like those of man, can be variable in form.
3. Homosexual behavior in nonhuman primates is not limited to any specific age period, and primates probably have the capacity for both male and female sexual roles throughout their lives.

Other conclusions and inferences from this study may or may not be generalizable:

1. Homosexual behavior occurs between individuals who have strong positive emotional ties.
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2. Homosexual interactions most often follow and appear to be elicited by viewing heterosexual activities.

3. Homosexual behavior, like heterosexual copulation, does not appear to be dependent on an estrous hormonal state in stumptail females, although it was observed in adult but not in infant females.

4. Homosexual behavior between animals with strong positive emotional ties, in sexual contexts, with prolonged genital stimulation effected by various means and sometimes culminating in orgasm, subjectively appears to be pleasurable and sexually stimulating to the animals involved, as the term “erotic” implies for formally similar behavior in man.

5. For infants, both heterosexual and homosexual interactions, with peers and with adults, may be training for adult sexual roles.

ACKNOWLEDGMENTS

I wish to express thanks to David Hamburg and R. C. Boelkins, Directors of the Primates Laboratory of the Department of Psychiatry, Stanford University School of Medicine, who kindly provided the animals and laboratory facilities for this study. I thank Frank Beach for his helpful comments on an earlier version of this article. I thank Julie Pesonen, Janice Andersen, and Harriett Lukes for their assistance in the preparation of the manuscript.

REFERENCES


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