

## Skewed Sex Ratios and Female Homosexual Activity in Japanese Macaques: An Experimental Analysis

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**ABSTRACT.** In this paper we present the results of a behavioral experiment conducted to test whether homosexual consortships and sexual solicitations among female Japanese macaques (*Macaca fuscata*) increase in the context of operational sex ratios that are heavily skewed towards females. The study involved a baseline period of observation on an intact social group which had a female-biased sex ratio typical of this species. During the experimental period which followed, we created a sub-group with an operational sex ratio that was heavily skewed towards females. Compared to the baseline period, females solicited significantly more same-sex individuals for sex and formed significantly more homosexual consortships during the experimental period of the study. Females did not appear to engage in homosexual activity during the study's experimental period simply because they lacked heterosexual alternatives. Instead, we suggest that an abundance of certain types of preferred, same-sex sexual partners and/or a scarcity of opposite-sex sexual competitors best account for the increased levels of female homosexual behavior observed at this time.

**Key Words:** Japanese macaques; Homosexual behavior; Sex ratios.

### INTRODUCTION

Homosexual activity in the form of mounting, sexual solicitations, and/or consortships, is taxonomically widespread among primates and occurs quite frequently in certain species (VASEY, 1995; BAGEMIHL, 1999). Understanding the patterns, functions and motivations underlying these behaviors can help elucidate the overall dynamics of social and sexual/reproductive relationships in primate societies. In some primate species, for example, homosexual activity plays an important causal role in structuring affiliative relationships and dominance hierarchies (e.g. FAIRBANKS et al., 1977; DE WAAL, 1987; SMUTS & WATANABE, 1990; PARISH, 1994; WHITE & LANJOUW, 1992; VASEY, 1996). Homosexual interactions can also influence the expression of heterosexual activity whenever inter-sexual competition for sexual/reproductive partners is manifested (AKERS & CONAWAY, 1979; HARCOURT et al., 1981; LINN et al., 1995; VASEY, 1998a, b).

Despite these implications, quantitative research on primate homosexual behavior remains infrequent, spurring charges that primatologists have failed to develop any sort of encompassing theoretical framework for identifying and interpreting such interactions (WOLFE, 1991). WICKLER (1967) attempted to develop one such theoretical framework by arguing that behaviors which were sexual in form could serve some adaptive social function such as dominance demonstration. Following this proposal, other "socio-sexual" functions were suggested for primate homosexual behaviors such as alliance formation (FAIRBANKS et al., 1977), tension reduction (KURODA, 1984), and reconciliation (DE WAAL, 1987). Similarly, it has been suggested that these behaviors represent part of a reproductive strategy aimed at attracting reproductive partners, obtaining alloparental care and/or reducing competitors' receptivity (reviewed in VASEY, 1995; BAGEMIHL, 1999).

WICKLER's (1967) "socio-sexual hypothesis" provides a valuable framework for understanding homosexual activity in primates but, taken alone, it remains theoretically limiting. This is because primate homosexual behavior is not always enacted to mediate adaptive social or reproductive functions (VASEY, 1995, 1998b, in press; BAGEMIHL, 1999). For example, female Japanese macaques frequently engage in homosexual mounting during consortships in captivity (e.g. VASEY, 1996, 1998a; VASEY et al., 1998; CHAPAIS et al., 1997) and under free-ranging conditions (ENOMOTO, 1974; FEDIGAN & GOUZOULES, 1978; TAKAHATA, 1982; GOUZOULES & GOY, 1983; WOLFE, 1984). Despite over 40 years of research on this species, however, there is no evidence that these interactions are adaptive. Instead, several studies show that female Japanese macaques do not engage in homosexual interactions to facilitate adaptive social or reproductive goals (GOUZOULES & GOY, 1983; VASEY, 1995, 1996, 1998a; VASEY et al., 1998). Since female homosexual activity does not appear to interfere with the participants' reproduction in this particular species (FEDIGAN & GOUZOULES, 1978; GOUZOULES & GOY, 1983; WOLFE, 1984; VASEY et al., 1998) it probably represents a neutral trait (see FUTUYMA & RISCH, 1984; VASEY, 1995, 1998b). As this example demonstrates, additional theoretical approaches to primate homosexual behavior are needed beyond WICKLER's (1967) socio-sexual hypothesis.

An individual's behavior is determined, in large part, by the pool of conspecifics with whom it can potentially interact (ALTMANN & ALTMANN, 1979). Not surprisingly then, some of the earliest primatological research on the subject of homosexual behavior held that same-sex sexual interactions increased in groups with unusually skewed sex ratios (e.g. KEMPF, 1917). In terms of Japanese macaques, observational research is somewhat equivocal, however, regarding the relationship between female homosexual activity and skewed sex ratios. Based on their 3-year study of the Arashiyama West (Texas) population of Japanese macaques, FEDIGAN and GOUZOULES (1978) argued that the availability of males did not affect the number of females who formed homosexual consortships. In contrast, WOLFE (1984) demonstrated that a twofold increase in the number of sexually mature males in the Arashiyama West population was associated with a 27% decrease in the frequency of female homosexual behavior over a 4-yr period. In addition, when females in the Arashiyama West population had access to half as many sexually mature males as those in the Arashiyama B (Japan) population, they formed homosexual consortships almost three times as often (WOLFE, 1984).

In this paper, we present the results of a behavioral experiment conducted to test whether homosexual activity between female Japanese macaques increases in groups with operational sex ratios that are heavily skewed towards females. The experiment involved two phases. We began with a period of baseline observation on the intact study group which had a female-biased sex ratio typical of this species. Following this, we created an experimental sub-group with an operational sex ratio that was heavily skewed towards females. We then compared the number of homosexual consortships formed as well as the number of same-sex individuals solicited for sex during the study's two phases. We conclude by examining a number of hypotheses which might account for the expression of homosexual activity in the context of the experimental period's skewed operational sex ratios.

## METHODS

### SUBJECTS AND STUDY SITE

The study group totaled 38 individuals (1 sexually inactive female, age 24 yr; 16 sexually

active females, ages 3.5–24 yr; 5 sexually active males, ages 4–10.5 yr; 16 immature individuals) housed at the Université de Montréal's Laboratory of Behavioral Primatology (230m<sup>2</sup>). The adult sex ratio of the study group fell within the normal range reported for free-ranging populations of Japanese macaques (range=0.1–1.4; YAMAGIWA & HILL, 1998). The group comprised three unrelated matriline named A, B, and C.

Subjects were observed during a baseline and an experimental period. During the baseline period, the monkeys were observed in two indoor rooms and two outdoor enclosures. During the experimental period, the living quarters were divided into two sections occupied, respectively, by an experimental and a non-experimental sub-group. The experimental sub-group had access to two indoor rooms and one adjacent outdoor enclosure. The rooms and enclosures were furnished with swinging and climbing devices. Animals were fed daily with a mixture of grains, monkey chow, fruit, and vegetables. Water was available at will.

#### DATA COLLECTION AND EXPERIMENTAL PROTOCOL

To control, in part, for behavioral variation across the females' 28-day menstrual cycle (ENOMOTO et al., 1979), we conducted baseline and experimental observations on identical days across separate 4-week periods. Thus, data were collected by both authors during December 1994 (baseline period) and January 1995 (experimental period) on identical days (2, 5–24;  $N=21$  days/4-week period). Three hours of observation took place every day between 09:00 and 13:30 during which we recorded all occurrences of consortship formation and sexual solicitations. Observations took place from a raised mezzanine which looked out onto all of the rooms and enclosures occupied by the monkeys. As such, all members of the group were readily observable regardless of the room or enclosure they occupied. A total of 126 hr of data were collected.

In the afternoon of January 1, 1995, we created an experimental sub-group with an operational sex ratio that was heavily skewed towards females by removing four of the group's five sexually active males. Thus, the experimental sub-group contained all of the adult females and all of the immature individuals present during the baseline period, but only one of the sexually active males. To control for the confounding effects of male dominance acquisition over females, the study group's alpha male (*B4*) was chosen as the sole male to remain in the experimental sub-group. Removal of the four other males was accomplished in a few minutes by channeling the monkeys through a network of rooms and sliding doors. The resulting experimental and all-male sub-groups were physically and visually separated from each other.

Outside the peak months of December and January, sexual activity occurred at lower levels and among fewer individuals during the 1994–1995 mating season. This inter-month variation in the expression of sexual activity mitigated against data collection on a sufficient number of proceptive females for a second baseline period (i.e. a third 4-week period) following the experimental period.

#### DEFINITIONS

*Homosexual and heterosexual consortships* occurred when two non-kin females, or a non-kin male and female, engaged in three or more mounts within a 10-min period. Consortships terminated when the two partners were separated by a distance of more than 1 m and exhibited no mounting for 10 min. *Sexual solicitations* prompted mounting and included pushing, grabbing, head bobbing, screaming, presenting the hind-end or inclined back, placing one's hands on another's hindquarters, lip quivering, intense gazing, and body spasms in various combinations (ENOMOTO, 1974; VASEY et al., 1998).

Females were considered *proceptive* if they engaged in mounting and/or performed sexual solicitations on a given day. Females from different matriline were considered to be *non-kin*, as were cousins and aunt-niece dyads. Evidence indicates that female Japanese macaques treat each other as non-kin when their level of relatedness is less than  $r=0.25$  (CHAPAIS et al., 1997). Close female kin ( $r \geq 0.25$ ) never formed homosexual consortships. Males were considered to be *sexually active* if they formed heterosexual consortships and ejaculated.

The *estimated time of conception* was determined by subtracting the gestation period for Japanese macaques ( $173 \pm 6.9$  days) from the date of parturition (NIGI, 1976). *Operational sex ratio* refers to the number of sexually active males to proceptive females at any given moment.

#### DATA ANALYSIS

*Daily homosexual consortship rates* and *daily heterosexual consortship rates* were calculated by dividing the number of homosexual or heterosexual consortships a female formed on any given day by the number of potential homosexual or heterosexual consortships which she could have formed on that day. *Potential homosexual consortships* were calculated based on the number of proceptive, non-kin females with whom a female could have consorted on any given day. *Potential heterosexual consortships* were calculated based on the total number of sexually active males in the study group during any given phase of the study. A female's *average homosexual consortship rate* and *average heterosexual consortship rate* for a given period (baseline vs experimental) were calculated by adding her daily homosexual or heterosexual consortship rates and dividing the sum by the number of days on which she was proceptive.

*Daily homosexual solicitation rates* and *daily heterosexual solicitation rates* were calculated by dividing the number of same-sex or opposite-sex individuals a female solicited by the number of potential same-sex or opposite-sex individuals which she could have solicited on any given day. *Same-sex individuals which could potentially be solicited* included any proceptive, non-kin female. *Opposite-sex individuals which could potentially be solicited* included any sexually active male. A female's *average homosexual solicitation rate* and *average heterosexual solicitation rate* for a given period were calculated by adding her daily homosexual or heterosexual solicitation rates and dividing the sum by the number of days on which she was proceptive.

Females from the B matriline could not form heterosexual consortships with non-kin males during the experimental period of the study because they were all related to the sole male (B4) in the experimental sub-group. Thus, data on average consortship and solicitation rates for B matriline females were not calculated since they were not comparable across the study's two periods or across matriline. Baseline and experimental data for A and C matriline females were compared using the Wilcoxon matched-pairs signed-ranks test (SIEGEL & CASTELLAN, 1988). By comparing behavioral rates we were able to control, in part, for variation in female proceptivity across the baseline and experimental period. Statistical comparisons could not be made for some females which were proceptive during only one phase of the study. All statistical tests were two-tailed.

#### RESULTS

The majority of sexually active females in the study group ( $N=16$ ) engaged in homosexual consortships ( $N=11$ ) and solicited same-sex individuals for sex ( $N=12$ ) during the period of data collection. These females ranged in age from 4.5 to 24 yr and came from all three matriline. Similarly, the majority of sexually active females participated in heterosexual con-

**Table 1.** A and C matriline females' average homosexual consortship rates and average homosexual solicitation rates during both the baseline and experimental periods.

Females	Average consortship rate		Average solicitation rate	
	Baseline	Experiment	Baseline	Experiment
A7	18.3	31.1	18.7	32.3
A32	0	0	0	0
A31	12	24.2	12.7	22.2
A2	14.7	43.3	15.3	45
A22	0	24.2	0	23.8
C	7.7	24.8	9.4	25.8
C32	0	0	3.6	16.7
C31	15.7	49.2	13.6	28.6

Females listed in descending order of rank.

**Table 2.** A and C matriline females' average heterosexual consortship rates and average heterosexual solicitation rates during both the baseline and experimental periods.

Females	Average consortship rate		Average solicitation rate	
	Baseline	Experiment	Baseline	Experiment
A7	0	25	0	25
A32	13.3	100	20	100
A31	5.3	0	7.4	0
A2	1.2	5.3	0	0
A22	0	0	20	0
C	14	0	8	0
C32	5	0	15	100
C31	3.5	20	2.4	0

Females listed in descending order of rank.

sortships ( $N=14$ ) and solicited males for sex ( $N=15$ ) during the data collection period. These females ranged in age from 3.5 to 24 yr and came from all three matrilines.

During the baseline period of the study, the operational sex ratio was 0.31. During the experimental period of the study, the operational sex ratio was skewed to 0.09.

Average consortship and solicitation rates were calculated for eight females from the A and C matrilines which were proceptive during both periods of the study (Tables 1 & 2). Females' average homosexual consortship rates increased significantly in the experimental period of the study ( $\bar{X}=32.8$ ,  $SE=4.9$ , range=24.2–49.2) compared to the baseline period ( $\bar{X}=11.4$ ,  $SE=3$ , range=0–18.3) ( $N=6$ ,  $T=21$ ,  $p<0.05$ ) (Table 1). Females' average homosexual solicitation rates also increased significantly in the experimental period of the study ( $\bar{X}=32.4$ ,  $SE=3.7$ , range=16.7–45) compared to the baseline period ( $\bar{X}=12.2$ ,  $SE=2.7$ , range=0–18.7) ( $N=7$ ,  $T=28$ ,  $p<0.02$ ) (Table 1).

Females' average heterosexual consortship rates showed no significant change from the baseline ( $\bar{X}=6$ ,  $SE=2.2$ , median=2.7, range=0–14) to the experimental ( $\bar{X}=21.5$ ,  $SE=14.8$ , median=4.3, range=0–100) phase of the study ( $N=7$ ,  $T=19$ ,  $p=0.47$ ) (Table 2). Likewise, there was no significant difference in the females' average heterosexual solicitation rates across the baseline ( $\bar{X}=10.4$ ,  $SE=3.3$ , median=0, range=0–20) and the experimental ( $\bar{X}=32.1$ ,  $SE=19.3$ , median=7.7, range=0–100) phases of the study ( $N=7$ ,  $T=18$ ,  $p=0.58$ ) (Table 2).

We tested whether increases in homosexual activity from the baseline to the experimental period reflected changes in the females' reproductive status. The data did not support this interpretation. Following the study period, three of the females (A31, A2, and C31) for which average consortship and average solicitation rates were analyzed gave birth. Based on their

estimated times of conception, it was determined that all three females conceived before the study began, not during the study period.

Following this, we tested whether the increased homosexual activity manifested by A and C matriline females during the study's experimental period reflected a lack of sexual motivation on the part of the sole sexually active male (*B4*) who was present. The data did not support this interpretation. On 71.4% of days during the experimental period ( $N=21$ ), *B4* sexually solicited one or more females, but they chose to participate in homosexual consortships instead. Most of the A and C matriline females which formed homosexual consortships behaved in this manner at some point during the study's experimental period (83.3%;  $N=6$ ).

Next, we tested whether the increased homosexual activity manifested by females during the experimental period reflected an inability on the part of *B4* to attend to every proceptive female simply because he was always occupied in a heterosexual consortship. The data did not support this interpretation. *B4* was actually unable to form any heterosexual consortships on 52.4% of days during the experimental period. Despite his attempts to attract females on these days, they chose instead to engage in homosexual consortships.

Finally, we tested whether females rejected sexual solicitations by *B4* during the experimental phase of the study because they did not consider him to be a potential mate. The data did not support this interpretation. Most females who rejected a sexual solicitation by *B4* at some point during the experimental period in favor of a same-sex sexual partner, also formed heterosexual consortships with *B4* at some other time during the study (83.3%;  $N=6$ ).

## DISCUSSION

Understanding a group's demographic structure is important for understanding the short- and long-term dynamics of primate behavior (ALTMANN & ALTMANN, 1979). In this study, we examined the role that one aspect of demographic structure, operational sex ratio, played in the expression of female homosexual activity in Japanese macaques. Compared to the baseline period, females solicited significantly more same-sex individuals for sex and formed significantly more homosexual consortships while members of an experimental sub-group in which they outnumbered males by 11 to 1. Although the sex ratio created during the experimental period of the study was heavily skewed towards females, highly skewed sex ratios (e.g. 0.1) have also been reported for free-ranging populations of Japanese macaques (YAMAGIWA & HILL, 1998). Increases in female homosexual activity during the experimental period of the study did not reflect a rise in the overall levels of sexual behavior at this time. Instead, there was no significant change in heterosexual solicitations or consortships across the study's two periods. Moreover, increases in female homosexual activity during the experimental period of the study could not be attributed to some change in the reproductive status of subjects between the baseline and experimental periods since none of the A and C matriline subjects conceived during the period of data collection. In sum, the results of this behavioral experiment support and extend WOLFE's (1984) earlier observational research by showing that homosexual consortships and sexual solicitations increase among female Japanese macaques as the number of adult males to adult females in a population decreases.

The expression of homosexual activity in the context of skewed operational sex ratios is most commonly attributed to an absence of opposite-sex mates (hereafter, the "heterosexual deprivation hypothesis") (see BAGEMIHL, 1999). From this perspective, homosexual behavior is characterized as a HOBSON's choice, that is, a choice which is made for want of any opposite-sex alternative (VASEY, 1998a, b, in press). Heterosexual deprivation is not, however, an adequate

explanation to account for the increased level of female homosexual activity observed during this study's experimental phase. Although there was only one sexually active male (*B4*) present during the experimental period with whom females could form consortships, he was frequently available and motivated to engage in heterosexual activity. Nevertheless, many of the females he solicited for sex simply opted to engage in homosexual consortships instead.

It is possible that these females rejected *B4* in favor of same-sex sexual partners simply because they never favor him as a mate under any circumstances. If this were the case, one might conclude that for all intents and purposes such females had no real heterosexual options during the study's experimental period. However, the data do not support this version of the heterosexual deprivation hypothesis either. The majority of females who rejected a sexual solicitation by *B4* in favor of a same-sex sexual partner also formed heterosexual consortships with *B4* at some other point during the study. This suggests that most females which engaged in homosexual activity in *B4*'s presence also identified him as an acceptable male mate.

In place of the heterosexual deprivation hypothesis we suggest two alternative, but complementary hypotheses which better account for the relationship between skewed operational sex ratios and female homosexual activity in Japanese macaques. The first of these hypotheses we refer to as the "bisexual preference hypothesis." It holds that higher levels of female homosexual activity observed in the context of female-skewed operational sex ratios can be primarily attributed to female preference for certain same-sex sexual partners relative to certain opposite-sex mates. The likelihood that these preferences will be expressed simply increases whenever preferred same-sex sexual partners are abundant in the population. From this perspective then, it is not an absence of males, *per se*, which promotes the expression of female homosexual activity, rather, it is a paucity of preferred male mates coupled with an abundance of preferred female sexual partners. In support of this hypothesis, we note that female Japanese macaques are not preferentially heterosexual as is commonly assumed (VASEY, 1998a). Instead, they are best characterized as bisexual. Moreover, previous studies suggest that mutual sexual attraction and gratification provide sufficient motivation, in and of themselves, for female Japanese macaques to engage in homosexual interactions (VASEY, 1996, 1998a; VASEY et al., 1998). As such, the increased level of female homosexual activity observed during this study's experimental period might have been due to the overall abundance of females at this time, many of whom preferred each other as sexual partners in comparison to the experimental sub-group's only sexually active male, *B4*.

WOLFE (1984) adopts one version of the bisexual preference hypothesis by arguing that female Japanese macaques prefer novel female sexual partners over familiar male mates. It is possible that FEDIGAN and GOUZOULES (1978: 494-5) were also arguing for some version of the bisexual preference hypothesis when they stated "...homosexual consortships appeared to be part of a larger pattern of female sexual initiative..." and as such, "...females were not forced to choose other females due to lack of males."

The second hypothesis which might shed light on the relationship between homosexual activity and skewed operational sex ratios is the "opposite-sex sexual competitor hypothesis." It holds that female homosexual activity increases in the context of female-skewed operational sex ratios because male sexual rivals are scarce under these demographic conditions and, as such, females are more able to access and maintain preferred, same-sex sexual partners. In support of this hypothesis, we note that Japanese macaques routinely engage in inter-sexual competition for female sexual partners (VASEY, 1998a). These interactions commonly involve costs for both female participants (i.e. the female sexual competitor, and the focus of competition) which include the risk of injury, rank decreases, and stress-related effects stemming from the need for increased vigilance against male sexual competitors (pers. obs.). In the absence of male sexual

competitors, the costs associated with acquiring and maintaining preferred, same-sex sexual partners would likely be lower and consequently, the frequency of female homosexual interactions would likely be higher. As such, the increased level of female homosexual activity observed during this study's experimental period might have been due to the fact that females were relatively unconstrained to pursue preferred, same-sex sexual partners because only one opposite-sex sexual competitor, *B4*, was present at this time.

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