

BRIEF REPORT

Ovarian Cycle Phase and Same-Sex Mating Behavior in Japanese Macaque Females

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The relationship of the ovarian cycle phase to same-sex mounting activity in adult female Japanese macaques (*Macaca fuscata*) was studied during the 1997/1998 mating season. Fecal samples were collected from eight female subjects two to three times per week and analyzed by enzyme immunoassay for fecal hormone levels. Hormone profiles of estrone (E1) and pregnanediol (PdG) were used to separate ovarian cycles into three phases: follicular, periovulatory, and luteal. Patterns of same-sex and heterosexual mounting behavior in the females were analyzed for phase variation during conceptive cycles. Same-sex mounting among female Japanese macaques occurred most frequently during the follicular and periovulatory phases of the cycle, and not at all during the luteal phase, paralleling the pattern found in heterosexual mounting behavior. These findings suggest a link between hormonal fluctuations and patterns of sexual mounting, regardless of whether the partner is of the same or opposite sex. *Am. J. Primatol.* 63:25–31, 2004. © 2004 Wiley-Liss, Inc.

Key words: Japanese macaque; fecal steroids; nonconceptive behavior; ovarian cycles

INTRODUCTION

Examples of same-sex mating behaviors have been widely reported across anthropoid species, and such behaviors have been observed in every family of primates except prosimians [Vasey, 1995]. However, the issues of whether these behaviors are primarily sexual in motivation (as opposed to ritualized dominance or affiliative interactions), and whether they are affected by the hormone status of the participants are seldom addressed (but see Wallen and Parsons [1997]).

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Female courtship and mounting of other females have been reported in many free-ranging and captive groups of Japanese macaques [Fedigan & Gouzoules, 1978; Takahata, 1982; Vasey, 1996; Wolfe, 1984]. Same-sex mating behavior in monkeys is usually characterized by ventrodorsal mounting accompanied by thrusting [Vasey, 1995]. We consider mounting interactions between two female Japanese macaques to be sexual, for a number of reasons: 1) such behavior is confined to the mating season and occurs when the females are showing other signs of proceptivity; 2) contact between the two females is maintained by courtship signals, mutual following, and allogrooming, in a manner virtually indistinguishable from that of heterosexual pairs; and 3) females avoid mounting interactions with close matrilineal female relatives, just as they avoid male relatives [Chapais & Mignault, 1991; Chapais et al., 1997; Wolfe, 1984]. Some studies have suggested a relationship between proceptivity (or “estrus”) and homosexual activity in female Japanese macaques [e.g., Fedigan & Gouzoules, 1978; Wolfe, 1979]; however, no direct studies of the hormonal status and cycle phase pattern of females during same-sex mating have been published.

The Arashiyama West (Texas) troop of Japanese macaques (*Macaca fuscata*) is known for its high rates of female–female sexual behavior during the mating season [Wolfe, 1979; Gouzoules & Goy, 1983]. Females that engage in such behavior are not exclusively homosexual; typically, they engage in heterosexual activity as well. The proportion of Arashiyama West (AW) females engaging in same-sex mating behavior varies from year to year (61% [Fedigan & Gouzoules, 1978], 78% [Wolfe, 1979], and 51% [Gouzoules & Goy, 1983]). The Arashiyama B troop (Japan) displays a somewhat lower, but also variable, proportion of females engaging in same-sex mating behavior (27% [Wolfe, 1986] and 47% [Takahata, 1982]). Wolfe [1984, 1986] proposed that the higher rates of same-sex mating activity in the AW group are related to a sex ratio that is skewed in favor of adult females (i.e., a “shortage” of adult males). Vasey and Gauthier [2000] documented experimentally that female–female mating behavior in Japanese macaques increases as the number of adult males to females decreases. However, they argued that it is not a shortage of males, but the lowering of constraints imposed by aggressive male competitors, and the relative increase in the availability of preferred female sexual partners compared to preferred male sexual partners that allow female–female mating to flourish under skewed sex-ratio conditions.

The present study examines cyclic phase variation in relation to same-sex mounting behavior in AW Japanese macaque females. We previously documented that heterosexual mounts in these monkeys occur more frequently during the follicular and periovulatory phases of the ovarian cycle, at a time when pregnanediol (PdG) levels drop to baseline [O'Neill, 2000; O'Neill et al., in press]. Wolfe [1979] suggested that homosexual behavior coincides with periods of estrus, near the time of suspected ovulation. This study addresses the question of whether same-sex mating pairs display cyclic patterns of sexual behavior similar to those exhibited by heterosexual pairs. Specifically, we compare rates of same-sex mounting across the ovarian cycle phases and rates of same-sex vs. heterosexual mounting within each phase of the cycle.

MATERIALS AND METHODS

The subjects of this study were eight adult female Japanese macaques living in a 65-acre enclosure at the Arashiyama West Texas Snow Monkey Sanctuary (for details on the group structure and history, see O'Neill [2000] and Fedigan and Asquith [1991]). Behavioral data were collected during the 1997/1998 breeding

season, from October to April. Chi-square goodness-of-fit tests were performed to test the prediction that the frequency of mounting events was directly proportional to the amount of time we observed the subjects in each of the three cycle phases. Descriptive statistics (i.e., comparisons of means and standard deviations) are presented regarding the rates of heterosexual and same-sex mounting events.

Fecal samples were collected two to three times per week from the eight target females between the hours of 8:00 A.M. and 6:00 P.M. Ovarian steroids were extracted according to the procedure described by Strier and Ziegler [1997] and Ziegler et al. [1997]. Fecal samples were analyzed by enzyme immunoassay (see O'Neill [2000] and O'Neill et al. [in press] for detailed descriptions of the assays and validations used).

Given an estrone (E1) excretion delay of approximately 24 hr (as previously described for macaques [Dixon, 1998]), and the temporal pattern of fecal collection, the onset of PdG increase was considered to be the best predictor for estimating the first day of ovulation [Strier & Ziegler, 1997]. Progesterone synthesis from the ovary actually begins to increase prior to ovulation, within hours of the gonadotropin surge [Espey & Lipner, 1994]. Consequently, the sample preceding the first day of the PdG increase was considered to represent the most likely day of ovulation. The periovulatory phase was therefore conservatively defined as the estimated day of ovulation \pm 3 days.

RESULTS

We used the results of the hormone analyses to create hormone profiles for each female (Fig. 1). The cycles were divided into three phases: follicular (when PdG has dropped to baseline levels); periovulatory (when PdG levels begin to slightly rise, and E1 levels reach their peak); and luteal (when PdG levels stay well above baseline for an extended duration, and E1 levels return to baseline). In all, 27 complete cycles in eight females were identified.

Five of the eight females in our sample engaged in same-sex mating behavior. Of these five, three were involved in same-sex activity during cycling ($n = 16$ cycles), and the other two exhibited such behavior during pregnancy. We focused our comparison mainly on the three individuals that engaged in same-sex mating during cycling.

First we compared the occurrence of mounting across the cycle phases for the three target females. They were observed for 47 hr during the follicular phases, 38 hr in the periovulatory phases, and 58 hr in the luteal phases. We found that heterosexual mounts were not distributed across the three cycle phases proportionately to the amount of time observed. In particular, heterosexual mounts during the luteal phase occurred far less frequently than would be expected if this behavior were equally likely to occur during any phase of the cycle (mounts directed to males: $\chi^2 = 111.78$, $df = 2$, $P < 0.001$; mounts received from males: $\chi^2 = 168.28$, $df = 2$, $P < 0.001$). Likewise, same-sex mounting was not distributed across the three cycle phases proportionately to time observed; again, mounts during the luteal phase occurred less frequently than expected (mounts directed to other females: $\chi^2 = 109.22$, $df = 2$, $P < 0.001$; mounts received from other females ($\chi^2 = 40.26$, $df = 2$, $P < 0.001$).

We present the mounting rates (frequency per hour) in Fig. 2a and b. The general pattern observed is that all four types of mounting interaction (heterosexual directed, same-sex directed, heterosexual received, and same-sex received) occur to some extent during the follicular phase, increase by a modest

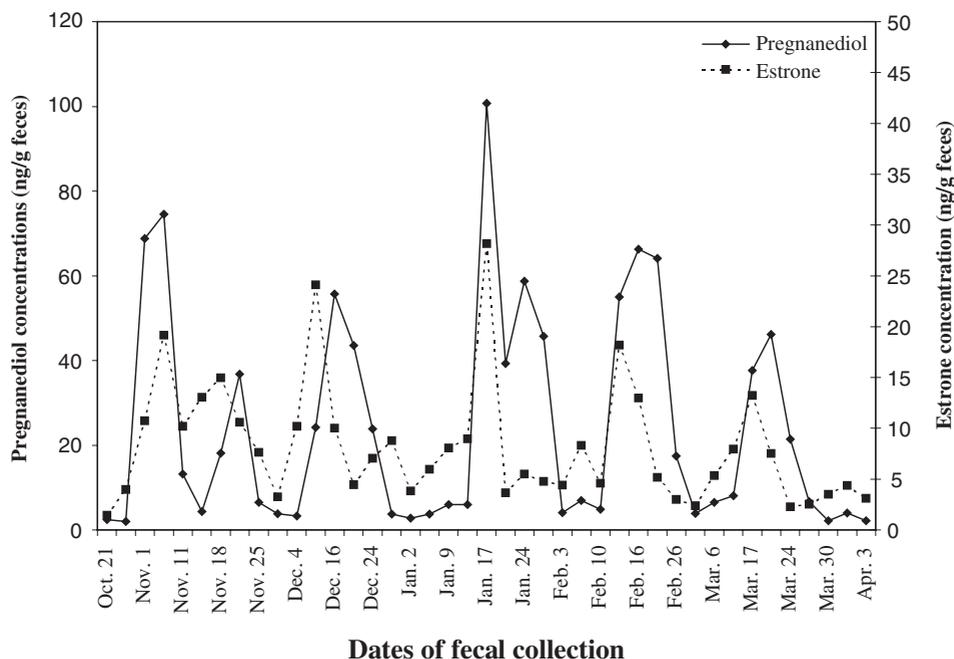


Fig. 1. Representative hormone profile for one female Japanese macaque during the 1997/1998 mating season. Base levels of pregnanediol indicate the follicular phase of the cycle, the day of the estrone surge (or the first day pregnanediol levels begin to rise) \pm 3 days represents the periovulatory phase, and a sustained increase in pregnanediol represents the luteal phase. This figure represents six complete cycles for one female. Individual hormonal profiles are available in O'Neill [2000].

amount in the periovulatory phase, and drop to zero occurrences in the luteal phase.

Next we examined the comparative rates of heterosexual vs. same-sex mounting within each phase of the cycle. During the follicular phase, the three target females directed a mean of 7.92 mounts/hr to other females and 4.42 mounts/hr to males. They received 1.92 mounts/hr from other females and 1.54 mounts from males. During the periovulatory phase, the target females directed 5.45 and 8.86 mounts/hr to males and other females, respectively, and they received 8.18 and 4.65 mounts/hr from males and other females, respectively. Thus, during the two phases of the cycle in which mounting occurred, the rates of same-sex mounts were not very different from the rate of heterosexual mounts. The only time the rate of heterosexual mounting was higher than that of same-sex mounting was during the periovulatory phase, when females received more mounts from males than from other females.

Two of the eight subjects engaged in same-sex mounting after they became pregnant, rather than during cycling. The rate of mounts directed by pregnant females was similar for same-sex and heterosexual mating pairs (5.13/hr and 5.67/hr, respectively) and the rate of mounts received by pregnant females was also similar for same-sex and heterosexual mating pairs (13.17/hr and 16.86/hr). Same-sex mounting, like heterosexual mounting, took place between the 6th and 10th weeks of gestation, and coincided with a marked decrease in PdG levels at that time [O'Neill, 2000; Gouzoules & Goy, 1983].

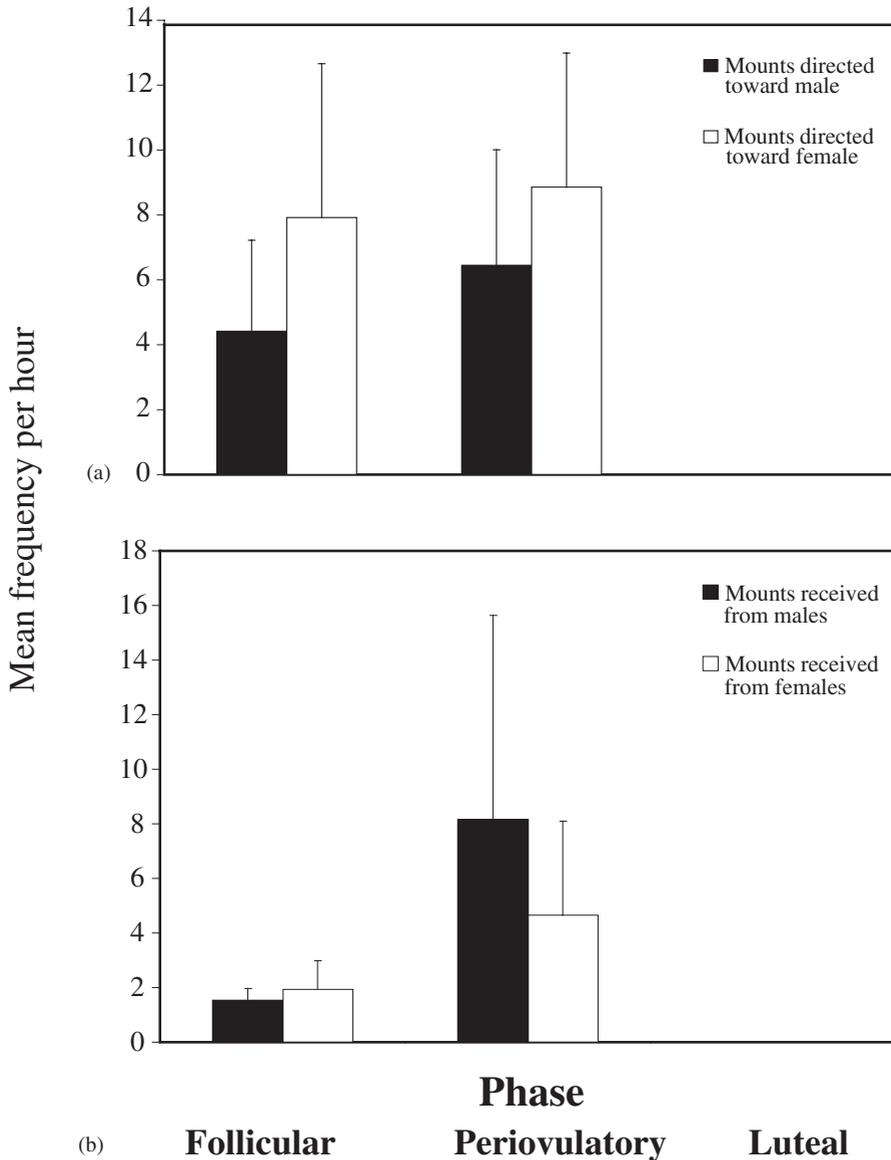


Fig. 2. Heterosexual and same-sex mounting activity in three female Japanese macaques during three phases of the cycle ($X \pm SE$). a: Rates of mounts directed by target females toward male and female partners. b: Rates of mounts received by target females from male and female partners.

DISCUSSION

More than half of the females (63%) in our sample exhibited same-sex mounting behavior either before or after conception, and they both directed and received these behaviors. The females that engaged in same-sex mounting during cycling exhibited it in the follicular and periovolutary phases, and there was a complete absence of such activity during the luteal phase. Same-sex mounts occurred most frequently during the same phases of the cycle (follicular and

perioovulatory) as heterosexual mounts, and rates of same-sex mounting were not conspicuously different from rates of heterosexual mounting. This pattern supports earlier suggestions that homosexual activity is linked to periods of sexual proceptivity [Fedigan & Gouzoules, 1978; Wolfe, 1984]. Furthermore, the same-sex mating observed in this study included most of the behavioral elements that are typical of heterosexual mating in Japanese macaques (e.g., courtship signals, series mounts, pelvic thrusts, formation of consort bonds, etc.). Taken together, these findings suggest a link between hormonal patterns and sexual proceptivity, regardless of partner preferences.

Females may choose same-sex partners to minimize interruptions from unwelcome male solicitors (O'Neill, unpublished data), because there is a higher ratio of preferred female to preferred male partners [Vasey & Gauthier, 2000], for novelty [Wolfe, 1984], for sexual gratification [Vasey, 1995, 2002], or for all of these reasons. By demonstrating a relationship between same-sex mounting and endocrine condition, as well as similar cyclic patterns in homosexual and heterosexual mounting, this study supports the argument that same-sex mounting in Japanese macaque females is primarily sexual in motivation. However, the occurrence of such behavior in nonhuman primates remains insufficiently documented and inadequately understood. Further research is needed to better understand the hormonal correlates of same-sex mating, as well as the underlying factors that influence partner choice.

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