

Female Menstrual Cyclicity and Sexual Behavior in Stumptail Macaques (*Macaca arctoides*)

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*The sexual behavior and female reproductive cycles of a captive group of stumptail macaques (*Macaca arctoides*) were monitored during a 12-month period. The data, consisting of 303 ad libitum mounts and copulations and 125 hr of focal-female testing, were analyzed by their frequency of occurrence during the three hormonal phases of the female menstrual cycle. Regularly cycling females exhibited statistically higher frequencies of all sexual behaviors compared to the amenorrheal controls. Contrary to previous reports which indicate no variation in sexual behavior throughout the reproductive cycle in this species, our data show marked increases in copulations during the periovulatory phase. Male dominance rank is associated with sexual behavior only at midcycle.*

KEY WORDS: *Macaca arctoides*; menstrual cycle; sexual behavior; dominance.

INTRODUCTION

Considerable diversity in patterns of reproductive behavior has been observed within the genus *Macaca*. This behavioral diversity focuses on two central points: (a) the distribution of reproductive behavior on a seasonal basis and (b) the distribution of reproductive behavior throughout the

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female menstrual cycle (Gordon, 1981). First, both seasonally and nonseasonally breeding macaques have been described under natural conditions. For example, free-ranging crab-eating macaques (*M. fascicularis*) have been reported to be nonseasonal breeders (Wheatley, 1981), but clear seasonal mating behavior in free-ranging Japanese macaques (*M. fuscata*) and rhesus macaques (*M. mulatta*) (Carpenter, 1942; Kawai *et al.*, 1967; Southwick, *et al.*, 1965) has been documented. Data from captive, outdoor-living groups are equally diverse, and data from animals housed under laboratory or environmentally controlled conditions often cloud the picture because of reports describing reduced seasonal effects on sexual behavior in some species (Eckstein and Kelly, 1966; Valerio *et al.*, 1969).

Laboratory studies of several macaque species have also demonstrated variations in frequency of sexual behavior throughout the menstrual cycle. Michael and Zumpe (1970), for example, have confirmed the existence of rhythmic changes in sexual activity during all 75 menstrual cycles observed in 32 pairs of rhesus macaques. Enomoto *et al.* (1979) have similarly shown that among Japanese macaques, both the degree of female proceptivity (Beach, 1976) and the male ejaculation rate are significantly higher at midcycle, with the ejaculation rate reaching its peak shortly after the midcycle estradiol surge and, presumably, coinciding with ovulation. The sexual behavior of female pigtail macaques (*M. nemestrina*) is also influenced by ovarian cyclicity, but female proceptivity has been shown to be mediated significantly by the prevailing dominance structure of the group (Bullock *et al.*, 1972; Goldfoot, 1971).

The stump-tail macaque (*M. arctoides*) is of particular interest because it has been reported to lack both types of behavioral cyclicity typically observed in other macaque species and, as such, may be the only nonseasonal, acyclic species. Compound-housed, laboratory-housed, and free-ranging stump-tail macaques have been noted to be nonseasonal breeders (Bertrand, 1969; Dukelow *et al.*, 1979; Hadidian and Bernstein, 1979; MacDonald, 1971; Smith, 1984) and to show no conspicuous swelling of the female's perineum around the time of ovulation (Butler, 1974; Hafez, 1971; Napier and Napier, 1967). Although research on other macaque species has demonstrated a relationship between ovulation and frequency of sexual behavior, studies on the sexual behavior of the stump-tail macaque have not led to such clear results. Previous research on stump-tail macaques using the limited-access and pair-testing paradigms has not demonstrated a correlation between the hormonal status of the female and the frequency of sexual behavior (Linnankoski *et al.*, 1981; Slob *et al.*, 1978a,b; Slob and Nieuwenhuijsen, 1980). Interestingly, Slob *et al.* (1978a) noted an increase in some female solicitory behaviors (i.e., hip present) at midcycle, but they were not able to document a statistically significant increase in copulatory behavior during the periovulatory phase.

Cautionary statements have been provided by many of these investigators concerning the observed lack of mating preference at midcycle in the stumptail macaque. Slob *et al.* (1978a) claim that the separation-reunion paradigm may have a greater stimulatory effect on behavioral interactions in stumptail macaques than in other species. Bertrand (1969) and Linnankoski *et al.* (1981) have noted that the hormonal status of female stumptail macaques may be influenced by environmental conditions. Repeated separations and reunions may exaggerate the use of copulatory behavior as a bonding function. Similarly, Wallen (1982) has demonstrated the influence of environmental variables, such as space, on the sexual behavior of captive rhesus macaques. By comparing frequencies of heterosexual mating during different phases of the female cycle, Wallen (1982) documented the influence of spatial conditions on sexual behavior throughout the menstrual cycle. In contrast to animals confined in a small, pair-test cage, rhesus monkeys maintained in a larger housing area demonstrated a significant decline in ejaculation during the luteal phase. Although both the dominant-male "priority of access" to ovulating female model (Altmann, 1962) and the "female choice" by ovulating female model (Hausfater, 1975) have been demonstrated for matings within a social group, the restricted pair-testing paradigm may provide some males the rare opportunity to mate regardless of the hormonal status of the female.

The purpose of the present study was to determine the effect of the hormonal status of female stumptail macaques on the frequency and nature of heterosexual activity. Three specific questions were asked: (a) Do regularly cycling females differ in frequency of sexual interactions from noncycling and/or irregularly cycling females? (b) Do frequencies of sexual behavior fluctuate throughout the menstrual cycle? and (c) Do males who are assessed as "dominant" by objective, nonsexual criteria exhibit a higher frequency of sexual interactions with females at midcycle?

METHODS

Subjects

The subjects were a captive group of stumptail macaques (*Macaca arctoides*) housed at the Yerkes Regional Primate Research Center Field Station of Emory University, near Lawrenceville, Georgia. The group, consisting of 39 animals, was maintained in a 28.4 × 32.7-m open-air compound with environmentally controlled indoor quarters adjacent to, and accessible via, two metal tunnels. The group was provisioned daily with com-

mercial monkey food and fresh fruit. Observations were conducted from a tower located 4.3-m above one side of the enclosure. All animals were readily visible from the tower.

Procedure

Four types of data were collected during the 12-month study, from May 1982 through May 1983: (a) focal data for all 20 sexually mature females in the group, (b) reproductive cycle data for the same females, (c) *ad libitum* heterosexual mount and copulation data, and (d) dyadic food competition (dominance) data for all group members. During the study, 25 focal-animal samples (Altmann, 1974) were conducted on each of the 20 sexually mature females (minimum age, 5 years), yielding a total of 125 hr of focal observation data. During each 15-min focal session, 11 different solicitory and sexual behaviors were scored between the focal female and all other adults within the group. Table I provides definitions of behaviors used in these analyses. All focal sampling was conducted in a random order

Table I. Operational Definitions of Solicitory and Sexual Behaviors

Behavior	Definition
Hip present	Hips and perineal region of either the focal or the interactant animal are directed toward the other; presenter often looks at presentee; head may be on the ground; hind-leg extension with arms partly or completely flexed or straight; tail often raised.
Hip touch	Touching or grasping the hip of another animal, which usually results in the other animal standing.
Hip raise	Lifting an animal into a quadrupedal position by encircling an arm around its body, by hip grasping or by using a cupped hand at the hips; score in lieu of touch or hip touch.
Attempted hip raise	An unsuccessful attempt to hip raise; score in lieu of touch, hip touch, or genital manipulation.
Genital inspection	Looking at, touching (with face), smelling, or short-duration licking of another's genitals.
Genital manipulation	Touching or manipulating another's genitals using the hands, excluding daps and grooms to the perineal region.
Vaginal dip	Using a finger, inspecting the vagina or rectum of another animal.
Mount	Ventrodorsal heterosexual contact accompanied by hand-grasping of the dorsal hair or skin and ankle-clasping by the male mounter.
Reach back	Mountee reaches back and touches or holds mounter, who is fully mounted.
Ejaculatory pause	Cessation of thrusting during a mount without dismounting; often accompanied by an audible open-mouth pant.
Pair sit	Sitting down behind a female after mounting and still remaining in an approximate mount position, but hip grasp moves further up the body to become a hold to the sides; probably postejaculatory.

without replacement. Observations were recorded exclusively during daylight (0900–1600 hr), 4–6 days per week, typically corresponding to days when sexually mature females were examined for indications of menstrual bleeding (see below).

Data on heterosexual mounts and copulations were collected on an *ad libitum* basis (Altmann, 1974). Mounts were defined as intromission accompanied by pelvic thrusting. Copulations were defined as mounts terminating in ejaculation. All heterosexual mounts and copulations observed, including scheduled and casual observations of the group, were recorded. Since these data were analyzed as a retrospective study and not during separate and independent sampling periods, there should have been no inherent sampling bias (see Murray and Smith, 1983).

Menstrual cycles of sexually mature females were monitored by vaginal swabbing (Brüggemann and Grauwiler, 1972; MacDonald, 1971). The 20 subjects were transferred to a capture unit adjacent to the outdoor section of the animal facility, then passed individually through a series of sequentially smaller chambers until they entered the restraint cage portion of the unit (Smith, 1981). After entering the restraint area, each female hip-presented and was examined for menses with a moistened, cotton-tipped swab; positive reinforcement was provided by a quick release. The entire group passed routinely through the capture unit in less than 20 min with few complications. Although increases in aggressive or sexual behaviors were not apparent at this time, behavioral observations were not recorded for 1 hr preceding and following the examination routine.

Because the mean and modal lengths of menstrual bleeding in stumptail macaques are reported to be 2.8 and 2.0 days, respectively (Brüggemann and Dukelow, 1980), each female was examined four times per week; no more than 48 hr elapsed between successive examinations. The frequency at which the examinations were conducted minimized the probability that menses for a given female could have been overlooked during a non-examination day.

Since dominance was defined as priority of access to a disputed item (Popp and DeVore, 1979), the results of dyadic food competition tests among randomly selected group members served as a measure of dominance. In this portion of the study, a food item of presumed equal value to all subjects was tossed among randomly selected groups of animals. Aggressive and submissive reactions of the participants to the food source and to one another were recorded and used to develop a sociometric matrix (Altmann, 1974). Based on the technique suggested by Bernstein (1968), this matrix was used to determine the dominance ranking of each group member. The predetermined level of significance for all statistical tests was $P \leq 0.05$.

RESULTS

Sixty-five complete menstrual cycles, ranging from 25 to 34 days in length, were detected among 11 of the 20 sexually mature females. The composite mean cycle length [29.2 ± 0.4 (SE) days] was not significantly different from other reported ovarian cycle lengths in stump-tail macaques (Brüggemann and Dukelow, 1980; Harvey, 1983; Slob *et al.*, 1978a; Wilks, 1977).

Based on the hormonal changes outlined by Wilks (1977), the recorded cycles were divided into the follicular, periovulatory, and luteal phases. The 14-day period prior to onset of menstruation, characterized by marked fluctuations in the level of progesterone, was termed the luteal phase. Wilks (1977) distinguished two estradiol peaks in the hormonal cycle of the stump-tail macaque, one on the day preceding ovulation and the other three days postovulation. Because Dukelow and Brüggemann (1979) note a "causative relationship between the preovulatory serum estrogen peak, preovulatory LH peak and the occurrence of ovulation" (p. 82), the 5-day period (containing the LH peak and both estradiol peaks) prior to onset of the luteal phase was termed the periovulatory phase. The remaining portion of each cycle, ranging from 5 to 16 days, was termed the follicular phase.

Cycling vs Noncycling

To determine the degree to which the female reproductive status influences sexual behavior, the 500 focal-animal observation samples were divided into a regularly cycling category (186 tests) and an amenorrheal category (314 tests). The latter was defined as data from irregularly cycling, anestrus, pregnant, and lactating females ($N = 9$). A female was considered irregularly cycling if more than 50% of her menstrual cycles fell outside two standard deviations of the composite mean menstrual cycle length (29.2 ± 0.4 days).

The rate of sexual behaviors (Table I) collected, using focal-animal samples, was pooled for the regularly cycling group and was compared to the rate for the amenorrheal controls (Fig. 1). A test of the equality of variances suggested that they are unequal ($F_{314,186} = 1.33$, $P < 0.05$). Therefore, an approximate t test (Sokol and Rohlf, 1981) was used. The result ($t'_5 = 3.06$, $df = 1$, $P < 0.01$) shows that the mean rate of total sexual interactions for regularly cycling females was significantly higher than the mean rate for the group of amenorrheal controls. The regularly cycling females show a clear pattern of initiating and receiving sexual behaviors more often than the irregularly cycling and noncycling females.

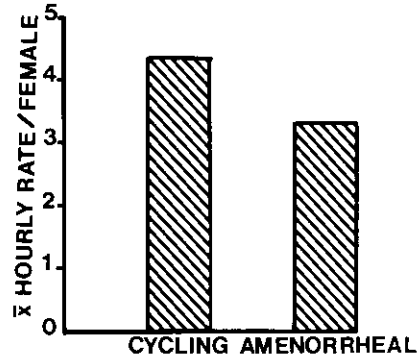


Fig. 1. Comparison of mean hourly rate of total sexual interactions per female for the regularly cycling group and the amenorrheal controls.

Variations Throughout the Cycle

During the present study, 303 *ad libitum* mounts and copulations were analyzed to determine whether their frequency varied throughout the female reproductive cycle. The copulation rate and the mount rate for the three hormonal phases were compared to those expected by chance. Figure 2 shows that although the mount rate varies little during the three phases of the cycle, the copulation rate increases considerably during the

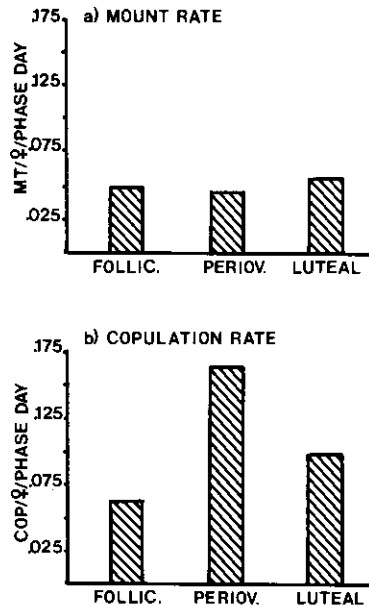


Fig. 2. Mean rate of behavior per female per phase day during the three cycle phases for (a) mount rate and (b) copulations.

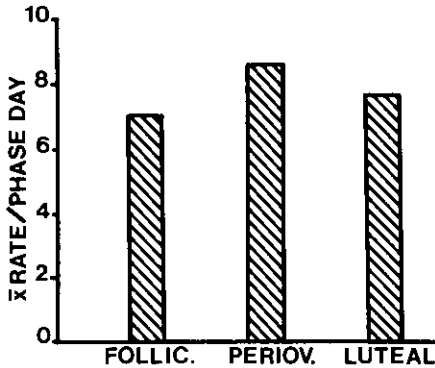


Fig. 3. Mean rate of total sexual interactions per phase day, pooled for all eight males, during the three cycle phases.

periovulatory phase. A chi-square goodness-of-fit test reveals that the periovulatory peak in copulations is significant ($\chi^2 = 14.74$, $df = 2$, $P < 0.001$), but the variation in mount frequency during the cycle is not significant ($\chi^2 = 0.46$, $df = 2$, $P > 0.05$).

To determine further the extent to which sexual behaviors varied throughout the female reproductive cycle, the total frequency of sexual interactions during focal observation (Table 1) was summed for all animals for each of the three cycle phases. The 186 test samples taken from regularly cycling females ($N = 11$) were then divided into three subgroups corresponding to the three phases of the menstrual cycle. The proportion of focal samples that were partitioned retrospectively into the three phase divisions provided an unbiased representation of the cycle, given the variation in length of each cycle phase ($\chi^2 = 2.53$, $df = 2$, $P > 0.05$).

There is little variability in the females' total rate of sexual behavior initiated to and received from all eight males during the three phases of the female reproductive cycle (Fig. 3). Using the chi-square test for goodness of fit, the observed changes in behavioral frequency are not significant ($\chi^2 = 3.31$, $df = 2$, $P > 0.05$). These results indicate that although copulations vary during the female reproductive cycle, both *ad libitum* mounts and total sexual behavior do not. One explanation for the somewhat disparate results may be that many behaviors, including mounts typically regarded as sexual, serve a social rather than a strictly reproductive function. Another possibility, however, is that males of differing social rank have differential access to females during the midcycle phase and, thus, pooling data for all males obscures these differential patterns.

The Effect of Dominance

To examine the effects of male dominance as a variable in the expression of sexual behavior, the eight adult males were divided evenly into either a high-ranking or a low-ranking group, depending on their position in the linear dominance hierarchy. Dominance ranking of the eight males was not associated with animal age, using the Spearman rho rank-order correlation coefficient ($\rho = 0.31$, $N = 8$, $P > 0.05$). Frequencies of total solicitory and sexual behaviors (Table I) were summed separately for the high- and the low-ranking groups.

A G statistic replicated test (log-likelihood ratio test using multiple samples) was used to assess the relationship between the observed and the expected frequencies of sexual behaviors. In this application, the G statistic has an advantage over other nonparametric tests, since G values are additive and can be partitioned or pooled for goodness of fit as well as tested for intergroup heterogeneity using the interaction G test (Sokal and Rohlf, 1981, p. 704). Two parts of the interaction G test were analyzed: (1) the partitioned G test, to determine goodness of fit between the observed and the expected values for the high- and low-ranking male groups; and (2) the heterogeneity test (G_H), to determine the extent of between-group variability for the high- and low-ranking male groups.

The results are shown in Fig. 4. The differences in rate of sexual behavior between the high- and the low-ranking groups are most pro-

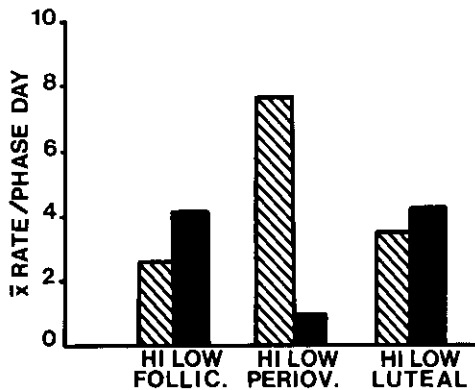


Fig. 4. Mean rate of total sexual interactions per phase day, partitioned by high- and low-ranking males, during the three cycle phases.

nounced at midcycle. During the periovulatory phase, the rate of sexual behavior increases for high-ranking males, but this rate decreases for low-ranking males. Using the partitioned G test for goodness of fit, observed frequencies of sexual behavior vary significantly from expected frequencies during the three phases of the female reproductive cycle for both high-ranking males [$G_{(hr)} = 19.20$, $df = 2$, $P < 0.001$] and low-ranking males [$G_{(lr)} = 14.09$, $df = 2$, $P < 0.001$].

An analysis of heterogeneity was used to determine whether the differences between high- and low-ranking males are sufficient to regard them as being drawn from separate populations. The results ($G_H = 27.30$, $df = 2$, $P < 0.001$) indicate that high- and low-ranking males exhibit two statistically distinct patterns of behavior throughout the female cycle.

A Spearman rho rank-order correlation analysis was used to examine further the relationship between male dominance and rates of total sexual behavior for the three phases of the female reproductive cycle. The results indicate that although male rank is positively correlated with rate of sexual interaction in each cycle phase, there is a statistically significant positive correlation only in the periovulatory phase ($\rho = 0.74$, $N = 8$, $P < 0.05$). When females were, presumably, at the peak of fertility during the midcycle phase, dominant males were engaging in solicitory and sexual behaviors at a significantly higher rate than were subordinate males.

DISCUSSION

These data suggest three conclusions. First, the frequency of sexual interactions in stump-tail macaques is associated with the reproductive state of the female; that is, regularly cycling females engage in sexual interactions significantly more often than irregularly cycling and noncycling females. Second, the frequency of copulations for regularly cycling females varies significantly throughout the phases of the cycle, with the highest frequency occurring during the periovulatory phase. Finally, dominant males exhibit a significantly higher frequency of total sexual behaviors during the periovulatory phase of the female reproductive cycle than during the other phases of the cycle.

An important implication is the extent to which experimental conditions may influence patterns of reproductive activity. Whereas the pair-testing paradigm reveals little or no variation in sexual behavior throughout the female reproductive cycle in stump-tail macaques, behavioral variations become clearly discernible when studied in a larger social unit. The difference in the results of the present study from those of previous investigations may be due to the presence of females in various phases of the

reproductive cycle and/or the presence of several males within the social group, which tends to foster intraspecific competition for mates and to offer many possible dyadic relationships.

Although these results show that male dominance rank is highly correlated with sexual activity during the midcycle phase of the female reproductive cycle, it would be premature to conclude that dominance rank *causes* this activity peak or that it conveys a priority of access to ovulating females. Alternative explanations are possible (Dewsbury, 1982; Kolata, 1976), and one or any combination of behavioral and/or physiological mechanisms associated with dominance rank and sexual solicitations could be involved.

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