INFLUENCE OF DOMINANCE AND PERINEAL TURGESCENCE ON THE SOCIAL AND SEXUAL BEHAVIOR OF FEMALE PIGTAILED MONKEYS (*MACACA NEMESTRINA*)

by

David A. Goldfoot, M.S.

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.........[redacted]..........
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.......[redacted].......
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Chapter I

INTRODUCTION

Endocrine Control of Sexual Behavior in Female Mammals

Ovarian hormones have long been recognized as controlling agents for the expression of sexual behavior in an extremely wide range of animal phyla (Beach, 1961; Young, 1941, 1961). Almost without exception, subprimate mammals demonstrate unique behavioral patterns during the preovulatory phase of the ovarian cycle which are never displayed at any other time. The series of behavioral patterns, collectively defined as behavioral estrus, is characterized by an abrupt onset in the hours or days immediately preceding ovulation, and a species-specific time course. Behaviors which occur during estrus include the display of opisthotonus and/or lordosis in response to the stimulation of a mount, increases in running behavior and other general locomotor activities, and for several species (e.g., guinea pig, cow) the display of mounting behavior by the female (Young, 1941).

Higher primate species do not demonstrate sexual behavioral patterns which fit the definition of estrus, however, since the abrupt onset of sexual behavior and the display of body postures unique to and characteristic of the preovulatory period in lower species are absent in the higher primates. Several studies have revealed, for example, that cattarhine monkeys and apes copulate throughout the menstrual cycle (Hartman, 1928; Eckstein and Zuckerman, 1956; Maslow, 1936; Yerkes, 1939a). As late as 1963, Rowell concluded that sexual behavior in the rhesus monkey was not correlated with any particular phase of the menstrual cycle, and in fact, the highest frequencies of sexual behaviors were seen during infertile phases of the cycle.

Nonetheless, ovarian hormones definitely have been shown to influence the display of sexual behavior in primates. With sophisticated techniques of observation, several investigators have indicated that females accept the male's mounts throughout the follicular phase of the menstrual cycle, but the occurrence of intromissions and ejaculations increases in frequency at midcycle and diminishes shortly after ovulation during the luteal phase of the cycle, in chimpanzee (Yerkes and Elder, 1936; Young and Orbison, 1944), in rhesus monkey (Ball and Hartman, 1935; Michael, Herbert, and Welegalla, 1967; Phoenix, Goy, Resko, and Koering, 1968), and in the pigtailed macaque (Kuehn, unpublished; Bullock, Paris, Resko, and Goy, in press). Michael, Herbert, and Welegalla (1967), Michael, Saayman, and Zumpe (1967a), and Michael and Welegalla (1968) have demonstrated that the probability of mating to ejaculation is greatest at midcycle for the rhesus monkey, that ovariectomy abolishes cyclical changes in mating activity, and that estradiol benzoate can substitute in ovariectomized females for the effect of the secreting ovarian follicle on receptivity. In addition, Trimble and Herbert (1968) and Michael, Saayman, and Zumpe (1967b, 1968) have demonstrated that injections of progesterone, the hormone primarily secreted during the luteal phase of the cycle, inhibit sexual responses in an estrogen-treated, spayed female. Koering, Resko, Phoenix, and Goy (1968) have further refined these observations in rhesus monkey by demonstrating that the probability of a complete mating sequence is correlated with the state of the developing follicle, and that the highest probability of complete mating corresponds with the presence of a preovulatory or early postovulatory follicle. The probability of receiving an ejaculation never falls below .20 in this situation, however, even during the luteal or menstrual phase of the cycle.

Bullock, Paris, Resko, and Goy (in press) have correlated changes of sexual behavior of pigtailed macaque monkeys with the estrogen-controlled cyclical turgescence and deturgescence of perineal sex-skin and plasma progesterone titers seen during the ovarian cycle. These authors found that mating to ejaculation occurred throughout the period of sex-skin turgescence (presumed follicular phase); latencies to ejaculation steadily decreased until the days of peak sex-skin turgescence were attained (preovulatory phase: partially confirmed by laparotomies); inhibition of complete mating series occurred during the period of sex-skin deturgescence (luteal phase); and mating probability and plasma progesterone levels were inversely related.

The consensus, then, is that the copulatory behaviors of heterosexual pairs of infrahuman primates vary cyclically during a menstrual cycle in parallel with cyclical changes of ovarian secretions. The intriguing aspect of these observations is that in the standard laboratory situation in which a male and female are paired together for 10 minutes to 1 - 2 hours on different days of the menstrual cycle, the clearest behavioral indices of female behavioral cyclicity involve behaviors of the <u>male</u> rather than the female. Latency to ejaculation, probability of ejaculation, and probability of intromission are the most accurate measures of female receptivity that have been employed to date. Feminine behaviors such as present-at-distance, present-to-contact, or analyses of time spent in proximity to the male are much less accurate gauges of the female's ovarian condition than the above behaviors, and are so variable from individual to individual that statistical significance is achieved only with very large samples or between extreme cases, such as females at midcycle contrasted with females spayed and left untreated for several weeks (Phoenix and Goy, unpublished). The extreme difficulty of measuring reliable changes of behavior in the female perhaps has led some investigators to conceptualize the problem almost exclusively in terms of peripheral cue systems affecting the male, such as odor or sex-skin condition of the female (Michael and Keverne, 1968).

Observations from field studies suggest, however, that definite changes in the behavior of females as well as differences in the response of males do occur during preovulatory phases of the menstrual cycle, including increased frequencies of presentation, increased time spent by females in proximity to males, and increased aggression by (presumed) preovulatory females towards other females, in rhesus monkey (Carpenter, 1942a,b; Altman, 1962; Conaway and Koford, 1964; Vandenbergh and Vessey, 1968), in baboon (Devore, 1965; Hall, 1965; Hall and Devore, 1965; Kummer, 1968), in Japanese macaque (Tokuda, 1961), and for pigtailed macaque (Bernstein, 1967). Carpenter (1942a), for example, has described striking behavioral changes in female rhesus monkeys during mating seasons on Cayo Santiago Island which involved invasions by the female of the territory of the male, aggression against other females, as well as increased frequencies of copulatory present postures.

> The estrous female, furthermore, is the vortex of stressful relationships in her group. During her receptive period, her social status in the group shifts and she becomes a sexual incentive for the groups' males. She actively approaches males and must overcome their usual resistance to close association, hence she becomes an object of attacks by them. Even other females attack her as a result of her shifted social status. (Carpenter, 1942a, p. 136).

These observations suggest that behaviors of receptivity involve changes in physical location within the troop and aggression towards specific members of the troop, in addition to an increased display of receptive postures. They further suggest that social interactions which contribute to troop structure in the natural, free-ranging situation must shift to accommodate mating, and that a female in preovulatory phases of the menstrual cycle must take an active, if not a causal role in the establishment of the shift. Expressions of receptivity in the rhesus monkey appear to be manifest as complex social interactions among several animals, rather than merely as simple postural changes in response to a single male, and may involve changes in behavioral patterns not usually considered to be primarily sexual in nature.

Endocrine Control of Primate Social Behaviors

Laboratory studies suggest that endocrine states do influence aspects of primate behavior other than sexual responses. Yerkes (1939b) described shifts of social dominance relations between female-female and male-female pairs of chimpanzees in a food competition situation. The dominance shift occurred at peak turgescence for a given female and was apparently independent of the dominance status of that female. If the female was subordinate to the male during days of deturgescence or partial turgescence, she would become dominant during peak turgescence, but if she were normally dominant, then she would become subordinate during days of peak swelling. However, more than half of Yerkes' pairs showed no such dominance shift as the female approached the state of maximum turgescence. Crawford (1940) attempted to quantify these observations further in female-female pairs of chimpanzees, but found dominance changes occurring in only nine of 16 pairs of animals "in which the subordinate obtained more food more often when in genital swelling phases of her cycle ..."

Birch and Clark (1946, 1950) demonstrated that the administration of exogenous estrogen to ovariectomized chimpanzees reliably increased dominance in a food competition situation. Mirsky (1956), however, did not find any correlation between shifts in dominance as a function of the stage of the menstrual cycle for pairs of rhesus monkeys. Clearly the question of endocrine determination of dominance rank remains unresolved.

The obvious similarity between the conclusions and problems drawn from dominance studies and mating studies was that in the pair-test situation, behavioral changes of the female, in contrast to behavioral changes of the <u>pair</u>, were either very difficult to quantify, or were, in fact, nonexistent. In contrast, field studies suggested not only that changes of dominance occurred in preovulatory females, but that these changes possibly contributed to the probability of successful copulation.

The observations of small groups of animals in laboratory situations appeared to offer the advantages of group manipulation and close examination, denied to the field worker, and the opportunity to explore variables of social group factors which were absent in the pair-test situation.

Rowell (1967) and Herbert (1967), to cite two examples, observed certain aspects of sexual behavior in restricted groups of captured animals, and thereby investigated aspects of social influences upon reproductive behavior. Rowell's observations confirmed the impressions of workers in the field that baboons display higher levels of both sexual behavior and agonistic behavior when in phases of maximum perineal turgescence. Herbert (1967) determined that individual differences in a group situation heavily influenced sexual behavior. When two estrogen-treated spayed females were presented simultaneously to a series of males, most males demonstrated decided preferences for one of the females, despite their roughly equivalent endocrine conditions. Herbert was unable to determine qualities which differentiated these females, however.

Laboratory studies such as these have the potential to reveal social as well as endocrine factors which might strongly influence the behavior of primates. If an environment could be engineered in a laboratory situation by restricting the composition of small groups to particular combinations of females in differing stages of the cycle, it would be possible to measure a variety of potential behavioral changes which would be entirely absent in a pair-test situation. At the same time, assessment of ovarian condition and hormonal status could be performed with an accuracy impossible to obtain in the field.

Statement of the Thesis Problem

Maslow (1936) theorized that both ovarian factors and social factors operated together to determine the sexual conduct of primates. The present experiment investigated this hypothesis, as follows:

Groups of pigtailed macaque monkeys (Macaca nemestrina) were observed in order to determine 1) if ovarian factors influenced sexual behavior, 2) if ovarian factors influenced social behaviors not directly related to sexual activity, and 3) if social influences affected sexual behavior. The pigtailed macaque was chosen for this study because this species undergoes cyclical perineal turgescence which can be used as a reliable external indicator of ovarian events (Zuckerman and Eckstein, 1956). It has been shown, for example, that estrogen induces perineal turgescence in the baboon (Gillman, 1938), that progesterone induces deturgescence in baboon (Gillman, 1940, 1942), and that the period of maximal turgescence corresponds with the preovulatory and ovulatory phases of the ovarian cycle (Zuckerman, 1930; Zuckerman and Parkes, 1932; Hendrickx, 1967; Bullock, Paris, Resko, and Goy, in press). The experimental design and detailed procedural descriptions of this study are given in the following chapter.

Chapter II

METHODS

Subjects

Fifteen adult female and six adult, sexually experienced, vasectomized, male, pigtailed macaques (Macaca nemestrina) were used in this study from July, 1968, through January, 1969. All animals were feral and were captured as adults or subadults, and all females were known to have menstruated previously. One year prior to the beginning of this study, the majority of the females had lived together in a large indoor-outdoor run on the Oregon Regional Primate Research Center grounds. In addition, eight of the females had been used previously for a study in which daily measurements of perineal sex-skin turgescence and behavioral interactions with one of the six males were obtained. Hence, each of these eight females had prior experience with one of the six males, and *vice versa*. Five of these eight females were laparotomized two to five times, two to three months prior to the beginning of the present study.

During the present study, all animals were housed in individual cages, in proximity to one another, in a large indoor animal room containing 90 to 100 additional animals. Subjects were under the normal regimen of care for primates at the Oregon Regional Primate Research Center, which included diets of 15 per cent protein content Purina monkey chow and fruits, daily cage-cleaning, daily visual inspection of females and their cages for signs of menstrual bleeding, and bimonthly weighings. Tuberculin skin tests were administered to the females on alternate months, but this procedure was suspended for the males during the course of the study. Veterinary care was required two times during the study: 1) when severe diarrhea lasting four to ten days occurred in many animals; and 2) when a mild epidemic of nose bleeding occurred due to an undetermined virus affecting the upper respiratory system. Behavioral testing was stopped while prescribed antibiotics were given to correct these conditions.

Determination of Sex-Skin Swelling and Menstrual Cycle Length

1. Measurement

The beginning of each menstrual cycle was determined by observing each female daily in its home cage for menstrual bleeding. If blood was seen in the cage but not on the animal, a cotton swab was inserted into the vagina to verify menstruation.

To determine daily changes in perineal sex-skin turgescence, the following procedure was employed: 1) Females were taken from their home cages in small transport carriers to a restraining cage where they were caught by two trained animal caretakers. The men then placed the female in a prone position on a table, with the hind limbs extended and held together just above the knee. Gentle pressure was exerted on the small of the back to maintain the animal's position. 2) Perineal diameters were determined with a pair of large "outside" engineering calipers. A standardized determination was obtained by tattooing all animals prior to the beginning of the study at the lateral extremities of the perineum, directly in line with the superior margin of the ischial callosities. 3) The distance between these points was measured with the calipers on alternate days for the first ten days of the menstrual cycle, and then daily until four to five days after the period of maximal turgescence was passed. Measurements were then continued on alternate days until the next menstruation. All measurements were taken at 1:00 p.m. on weekdays, and between 10:00 a.m. and 12:00 noon on weekends and holidays. The entire procedure of catching, restraining, and measuring averaged less than three minutes for each animal.

The calipers could detect changes of sex-skin diameters to ± 1 mm, and the measuring technique was standardized between three observers. Interobserver reliability was informally determined over a two-week interval to be within ± 1 mm for repeated measurements for the same animals.

In addition to these measurements, blood samples (4 ml) were taken from a femoral vein of each female on day two of the menstrual cycle, and once in the deturgescent period, seven to ten days after maximal turgescence. These samples were taken in order to determine plasma progesterone levels for another study; the results of that study will not be reported in this dissertation.

2. Definition of Sex-Skin Phases

Three conditions of sex-skin swelling were recognized from the daily measurements: early turgescence (T), maximal turgescence (M), and deturgescence (D).

Early turgescence (T) was defined as days two to six of the menstrual cycle, provided that maximal turgescence occurred during that cycle.

Maximal turgescence (M) was defined as the period during which the largest successive sex-skin diameters were attained. The period was of variable length and terminated with 1) a rapid (3 to 7 mm) decrease from maximal size within a 24-hour period, and 2) continued decreases in perineal diameters from the maximum until the next menstruation. The last day of maximal turgescence was called the day of peak. An animal was considered to be in the M condition if she was at least within three days of reaching the day of peak.

Deturgescence (D) was defined as days seven to ten following the day of peak.

Group Compositions

1. General Design

All behavioral observations were made on groups of three females (triads). A triad was observed on a single day under two conditions: 1) Females were tested in the presence of a male for 15-minute tests. Three males were used for each triad, one after another, for three successive 15-minute tests. 2) Females were tested in the absence of a male. Females were observed together for five minutes *before* the first male was brought to them.

2. Types of Triads

Two different types of triads were observed:

a. The Multiphase Triad

Three females, each in a different phase of the sex-skin cycle comprised a multiphase triad: one female was in the T condition of sex-skin turgescence, a second in the M condition, and a third in the D condition. It should be noted from the definitions of these phases that the T and M conditions could only be recognized _ex post facto_. For example, to be in the M condition, an animal had to be within three days of reaching the day of peak. However, the day of peak was recognized only after the process of detumescence was under way. Therefore, data collected for a multiphase triad were accepted only after it was subsequently established that 1) the T female eventually demonstrated a condition of maximal turgescence, and 2) the M female reached the day of peak within three days after the time of testing.

b. The Monophase Triad

Monophase triads were composed of three females all in the same relative phase of the sex-skin cycle. Thus, all females in a monophase triad were in the T condition, or all were in the D condition. No monophase triads composed only of M females were observed.

3. Triad Combinations

The composition of a triad was varied systematically on successive tests.

a. Multiphase Triads

Multiphase triads were formed to allow each of the 15 females to be observed in each of the three conditions of sex-skin turgescence. Rules of triad formation were as follows:

1) Triad compositions were never duplicated. Three females comprising a multiphase triad were never tested together as a group at a later date.

2) Two females were tested together in a maximum of two triads only. This rule attempted to maintain as much independence as possible among triads, and called for females to be tested with two

different partners for each of the three stages of sex-skin turgescence whenever possible.

3) A counter-balanced order of testing was maintained such that one-third of the females were observed in the M condition on their first test, one-third were observed in the M condition on their second test, and one-third were observed in the M condition in their final test.

4) Females were tested in multiphase triads until all fifteen animals had been tested in each of the three conditions of the sex-skin cycle.

5) All three conditions of turgescence did not have to be evaluated within a single menstrual cycle, and this parameter was not experimentally controlled (except for the condition of rule 3).

b. Monophase Triads

All fifteen females were tested at least once in a T-monophase triad and a D-monophase triad. A female was never tested in a monophase triad when she was to be tested in a multiphase triad during the same condition of sex-skin turgescence.

The rules of triad independence (see rule 2 for multiphase triads) were relaxed somewhat for monophase triads, such that whenever three females were in the same phase of the sex-skin cycle, they were tested together, until all fifteen females had been observed in the two monophase conditions. No monophase triad was completely duplicated, however.

Behavioral Testing

1. Apparatus

All behavioral tests were conducted in a large (9-1/2' wide x 5' deep x 7' high) observation room located within a sound-attenuated experimental laboratory directly across the hall from the animals' home cages. The front (9-1/2') wall of the room was constructed of plexiglas, allowing observers to see the entire testing area. Figure 1 illustrates the testing environment.

The observation room was separately illuminated so that the experimenters could sit in semi-darkness opposite the brightly lighted testing area. At the time of a test, animals were individually transported to the room in small carrier cages.

A timer with a minute and quarter-minute display panels was used to measure the length of a test and the latency to certain behavioral events. A tape recorder was used to record behaviors called out by the experimenters and was run continuously throughout a test, thereby serving as a second timing device from which additional latencies and duration measures were obtained.

2. Adaptation

Animals were routinely trained to use the small carrier cage during the course of daily sex-skin measurements. Three to six weeks after sex-skin measuring was begun, animals were individually transported to the room and allowed to explore the area for 15- to 20-minute periods. No behavioral measures were taken; the procedure was intended to familiarize the animals with the testing environment and the conditions of transport into and out of the testing apparatus. The criteria for adaptation were 1) that an animal not vocalize (coo) in the situation, and 2) that no stereotypy (vigorous pacing, hand-biting, etc.) be displayed. Two to four adaptation tests were given to each animal over a two-week period.

Figure 1. The behavioral testing apparatus.

3. Behavioral Testing Procedure

Monophase and multiphase triads were treated identically for all behavioral tests.

a. Determination of Dominance Hierarchies

All tests were conducted by two experimenters, and all tests began at 2:30 p.m. The three females comprising a triad were put into the observation room in a random order. Approximately thirty seconds after the last female entered the room, the timer was activated and the group was observed for five minutes. Dominance orders were judged independently by each observer, based on impressions of body posture, maintenance of central or peripheral areas of the observation room, eye eversion, displacement of one animal by another (animal A approaches, animal B withdraws), and by the display of threats, aggression, and fear grimaces. In addition, all scoreable behaviors of threat, aggression, fear grimacing, approach, withdraw, etc., were recorded. The combination of the impressionistic judgments of the observers and the quantified scores of interaction between animals was used to arrive at a dominance hierarchy for the group. Triads were excluded from consideration of dominance relationships 1) when both observers did not completely agree on dominance order, 2) when objective measurements did not support the agreed-upon dominance hierarchy, or 3) when no clear dominance hierarchy could be discerned by the observers.

b. Social-Sexual Relations

Immediately after this five-minute testing session, a single male, selected at random from the six available males by means of a draw, was brought to the experimental room and was placed in the room with the triad. Social and sexual behavioral interactions were code-named (See Appendix I for Definitions), and were called out by either experimenter as they occurred. Observations were recorded both on the tape recorder and on score sheets kept by one of the experimenters. Immediately after a testing session, the score sheet was checked and corrected on the basis of the tape recording. The scoring procedure provided a record not only of the total frequency of each type of behavioral interaction, but also identified the initiator of the behavior and the receiver of the behavior between females, and between the male and each female.

The male was removed from the observation room after a 15-minute period, and a second male, also randomly selected from the untested five, was immediately placed with the triad. Scoring was then continued for an additional 15-minute period. This procedure was repeated for a third male, after which each animal was returned to its home cage. The entire procedure of being tested for five minutes without the male and being observed with a series of three males is referred to as a "test" in all subsequent chapters of this dissertation.

Chapter III

RESULTS

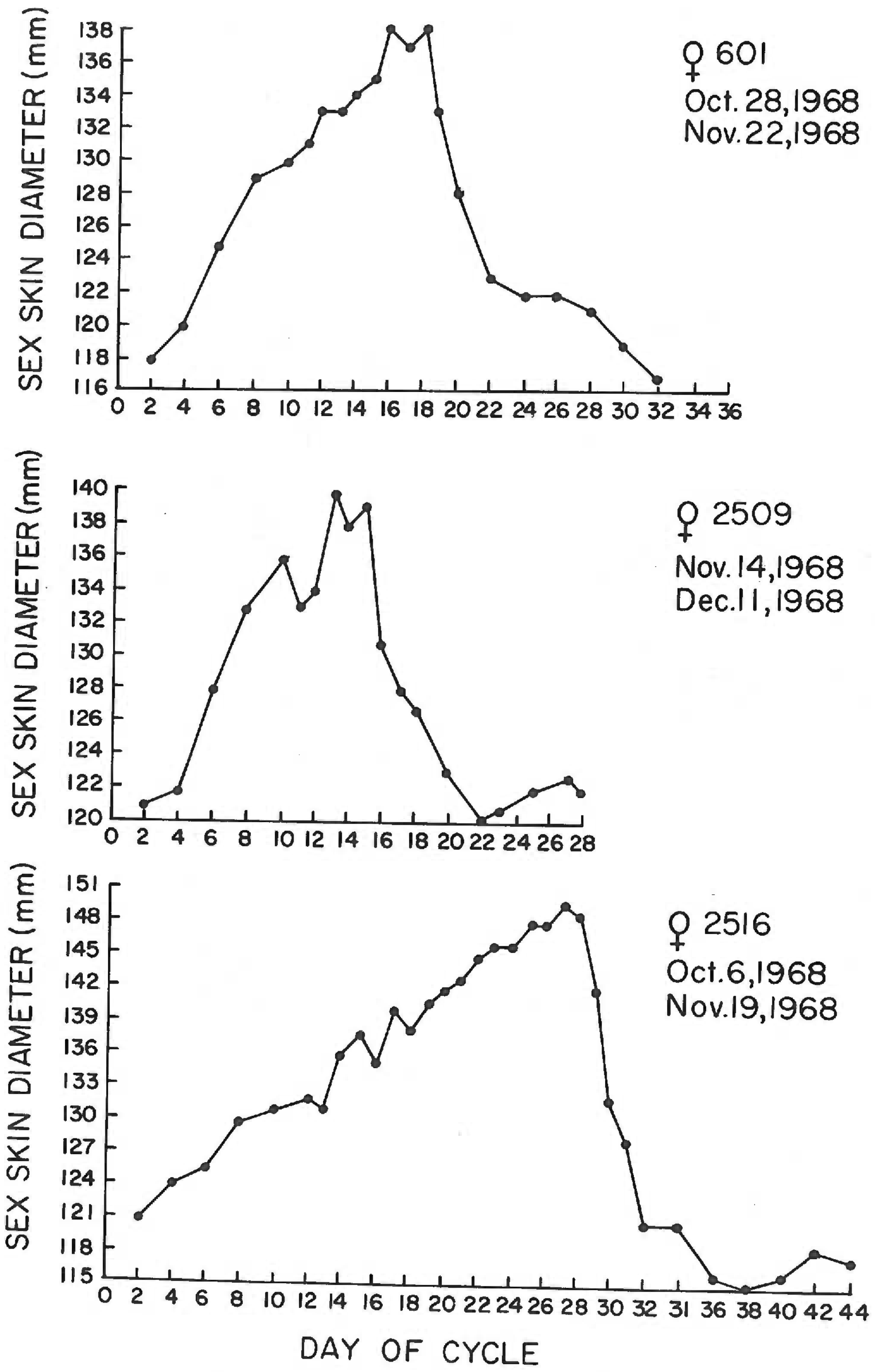
The Determination of Sex-Skin Phases

Daily measurements of sex-skin diameters proved to be a successful means whereby distinct phases of the sex-skin cycle could be detected. Only 5 of 78 observed menstrual cycles (1 - 7 cycles per animal) did not fit the stereotyped pattern of 1) increasing turgescence through slightly more than half the cycle, culminating in 2) a period of maximal turgescence for one to seven days, followed by 3) continued deturgescence for 11 - 18 days. Figures 2, 3, and 4 represent typical variations of sex-skin swelling patterns which were observed, and Appendix II presents summary data for each of the observed cycles. In general, animals exhibited considerable inter-individual variation for length of the menstrual cycle, length of the turgescent phase, and maximum and minimum sizes of perineal diameter attained during a cycle. In contrast, remarkable intra-individual consistency was obtained for these same measures.

1. The character of the early turgescent phase

Animals selected on days 2 through 6 of the menstrual cycle for behavioral testing in the T condition were clearly different from animals in the M and D conditions on the basis of sex-skin status. On these days, animals' sex-skin diameters were 20-40% of the size they would ultimately attain, and thus represented a distinct group, with no overlap in the M condition. The entire phase of turgescence was considered to extend from the first day of menstrual bleeding through the last day of maximal turgescence even though swelling sometimes

Figures 2 - 4. Representative sex-skin cycles for three pigtailed macaques.



SEX SKIN DIAMETER (mm)
138
136
134
132
130
128
126
124
122
120
118
116
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36
♀ 601
Oct. 28, 1968
Nov. 22, 1968
SEX SKIN DIAMETER (mm)
140
138
136
134
132
130
128
126
124
122
120
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28
♀ 2509
Nov. 14, 1968
Dec. 11, 1968
SEX SKIN DIAMETER (mm)
151
148
145
142
139
136
133
130
127
124
121
118
115
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 31 36 38 40 42 44
♀ 2516
Oct. 6, 1968
Nov. 19, 1968
DAY OF CYCLE

commenced before the onset of observed bleeding. Since the length of this phase was extremely variable (Table 1), greater extension of the definition of T would have resulted in poorer separation of the T and M conditions.

2. The character of the maximally turgescent phase

Females reached a maximum diameter of sex-skin swelling (± 2 mm) within 11 to 32 days of menstruation ($\bar{X}$ = 14.91 days) and retained this condition for one to seven days ($\bar{X}$ = 2.87 days). Females tested in the M condition, within three days before the last day of maximal swelling, were 80-100% of the maximum size attained during the cycle. A relationship existed between body weight and the maximum size an animal attained ($r = 0.48$, $p < .05$) and therefore absolute measurements could not be used as a criterion for the attainment of the M condition; instead, each animal was treated as an individual case. Also, since the absolute change in size from minimum to maximum did not correlate with body weight ($r = .03$), no simple rule in terms of a stated millimeter decrease, either in absolute terms or as a fraction of total change, could be used to define the end of the M condition. Again, each animal was treated as an individual case for this decision to be made. Part of this problem was due to individual differences in perineal anatomy. The measuring technique detected changes of diameter from a standard anatomical reference plane for each animal, rather than detecting volume changes of reactive perineal tissue. However, the animals expanded in three dimensions with considerable individual differences, and therefore the measuring system did not reflect the same degree of sensitivity for each animal (e.g., females 2510, 1275, and 2031 expanded considerably more in a plane at right angles to the lateral reference points used). Fortunately, the termination of the M condition was in almost every case clearly recognized by a rather dramatic decrease (4 - 15 mm) within a 24-hr period, with continued decreases for the next several days.

3. The character of the deturgescent phase

The period of deturgescence was easily recognized and presented no problem for the verification of the D condition. The length of the entire phase of deturgescence was highly stable from animal to animal (Table 1), and thus the criterion of D, being 7 - 10 days after the day of peak, allowed animals to be compared with one another under very similar circumstances of sex-skin status. In the D condition, animals were 10-30% of their maximum size for that cycle.

4. Relation of sex-skin phases to ovarian phenomena

Direct inferences concerning ovarian states are not possible from the data collected for sex-skin swelling, since laparotomies or hormonal determinations were not performed. However, indirect evidence was collected which suggests that sex-skin phases reflected ovarian states: Table 1 reveals that the turgescent phase of the cycle was significantly more variable in length than was the deturgescent phase of the cycle. In addition, Figure 5 displays a high correlation between the length of the T phase of the cycle and the length of the menstrual cycle, and a low correlation between the length of the deturgescent phase of the cycle and the length of the menstrual cycle.

Table 1

Length of Sex-Skin Phases and Menstrual Cycles

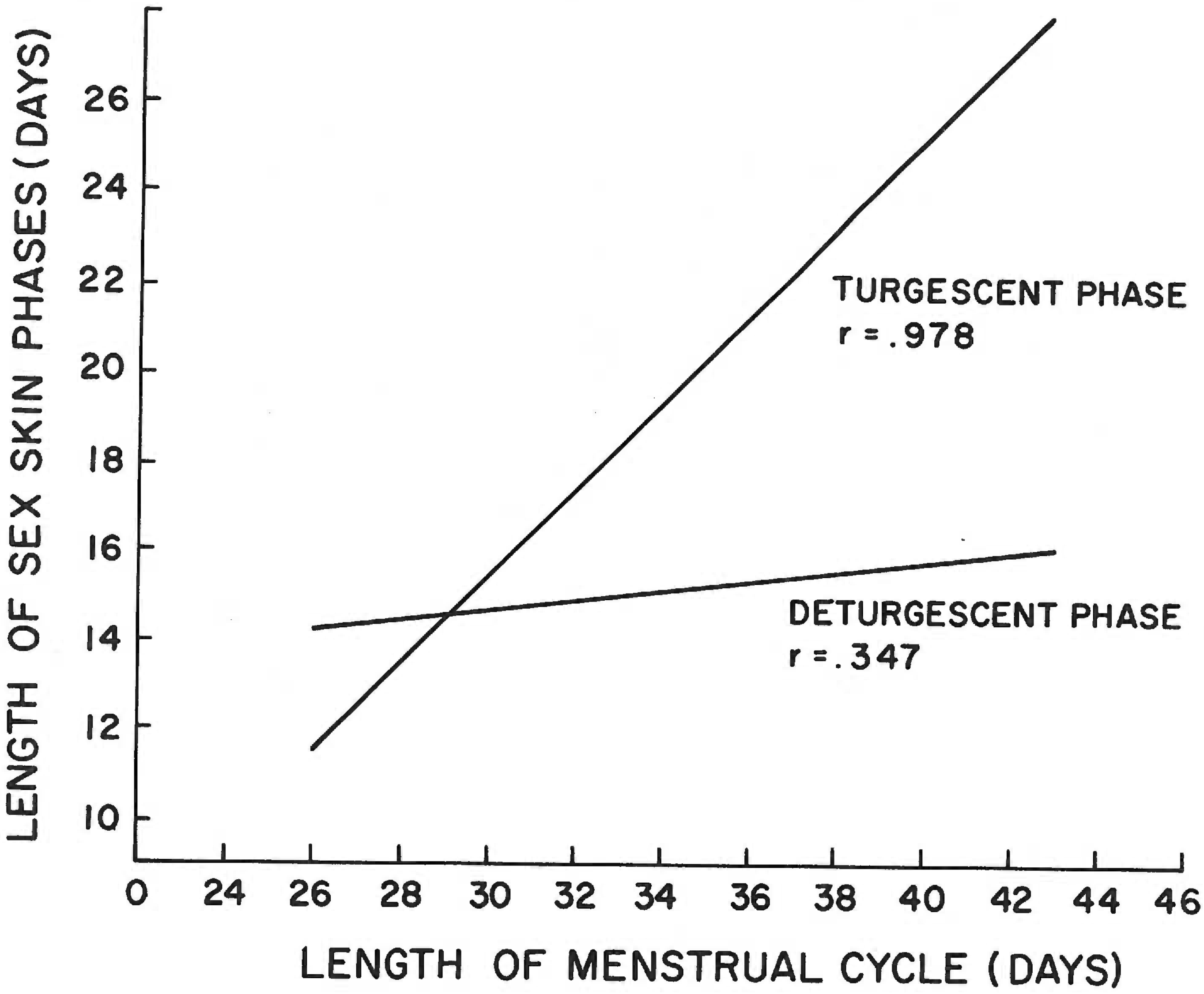
in _Macaca nemestrina_

	Mean (days)	S.D.	Statistical Comparison (F value)
Turgescent Phase	17.78	4.89	8.37^{**}
Deturgescent Phase	14.75	1.69	
Menstrual Cycle Length	32.36	5.14	

Based on 73 cycles for 15 females.

$^{**}p < .01$.

Figure 5. Relation of turgescent and deturgescent sex-skin phases to menstrual cycle length.


LENGTH OF SEX SKIN PHASES (DAYS)
10
12
14
16
18
20
22
24
26
TURGESCENT PHASE
r = .978
DETURGESCENT PHASE
r = .347
0
24
26
28
30
32
34
36
38
40
42
44
46
LENGTH OF MENSTRUAL CYCLE (DAYS)

These results closely resemble the known relationships between certain ovarian actions and menstruation: 1) Folliculogenesis is of variable length; whereas, 2) the life span of the corpus luteum, formed immediately after ovulation, is more nearly constant. Therefore, variation in the length of the follicular stage of the cycle contributes most to the variation in the length of the menstrual cycle. The present measures, therefore, lend support to the suggestion in Chapter I, that external perineal swelling is a useful index of ovarian states.

5. Abnormal cycles

Three cycles shown by 3 different females were clearly deviant from the normal range of data thus far presented. In one female (1275) turgescence did not begin until 23 days after menstruation. For two females (2515, 612), a condition of chronic maximum turgescence extended over several weeks. Daily intramuscular injections of progesterone (0.5 mg/kg) were given to these females in an attempt to establish regular cyclicity. The injections were continued for 30 days in an attempt to recycle the animals at a convenient time for testing. The treatment was successful: both animals responded by becoming deturgescent, and subsequently menstruated 4 and 5 days after the progesterone regimen was discontinued. The subsequent cycle recorded for these animals showed patterns of turgescence and deturgescence which did not deviate from the overall means.

In addition to these anomalies, menstruation was not observed in two other females who showed two distinct cycles of turgescence and deturgescence of normal duration and pattern. It was felt that this observation reflected experimental errors of observation, and that menstrual flow was overlooked, although this could not be substantiated.

Constraints of the Experimental Design

1. Triad compositions

Twenty-six multiphase and 12 monophase triads were formed between October 1, 1968, and February 1, 1969. Five multiphase triads were excluded from all analyses because the animals in those triads originally presumed to be in the M condition did not reach the day of peak within the defined 3-day limit following testing. Table 2 displays the number of times each female was observed under the three phases of the sex-skin cycle in the remaining 21 triads. Eight of the females were tested with two different female partners for each phase of the sex-skin cycle; the remaining 7 females were tested more than once with a female partner from a previous triad.

2. Statistical considerations

Questions which related sex-skin condition to sexual behavior were analyzed for multiphase triads as follows: 1) Three tests for each animal (scores from one triad for each of the three conditions) were included in the data analysis. 2) The first test (series of 3 males) in which an animal was observed in a given phase of the sex-skin cycle was accepted; repeated tests in later triads for that animal in the same phase of the cycle were excluded. 3) Exceptions to rule 2 were made when greater independence could be attained by selecting the second or third test for some animals ($N = 3$). A 15×3 repeated measures analysis of variance was then used to assess significance levels.

Table 2

Frequency of Observations Made on 15 Female Pigtailed Macaques in Three Phases of Sex-Skin Swelling

Animal #	# Times Observed in Multiphase Triads in Each Condition of Sex-Skin Swelling			
	T	M	D	Total
601	3	2	1	6
605	1	1	2	4
609	2	1	2	5
612	1	1	2	4
614	1	2	1	4
1275	2	2	2	6
2031	1	1	1	3
2196	2	1	1	4
2505	2	1	1	4
2509	1	2	1	4
2510	1	2	1	4
2511	1	2	1	4
2514	1	1	1	3
2515	1	1	2	4
2516	1	1	2	4

To determine whether dominance status was related to the display of sexual behavior, a different strategem was required, since only 16 of the 21 multiphase triads were successfully scored for dominance relations, and not all females were represented in each of the three conditions of sex-skin swelling within these 16 triads. In addition, animals were not tested an equal number of times within these triads; therefore, traditional statistical tests were not applied. Table 3 shows the number of times each animal was used in these triads, and indicates the number of times each animal was most dominant (α), second dominant (β), or least dominant (γ). Each test for each female was treated as an independent measure (i.e., as in designs employing random sampling with replacement) in all of the graphs and tables concerning questions of dominance. This procedure was legitimate to the extent that an animal's dominance rating was always relative to the triad conformation in which it was observed. However, the results concerning interactions of dominance and sex behavior must be interpreted with Table 3 in mind, since 7 animals are responsible for 16 scores in the α category, etc.

The Relation of Sex-Skin Condition to Sexual Behavior in the Triad Situation

Females in multiphase triads received and displayed significantly more sexual and social behavior with the male when they were in the M condition of sex-skin swelling than at any other time. The results, summarized in Table 4 and Figure 6, indicate that the behavior of the females changed with the phase of the sex-skin cycle, and, in the M condition, females displayed a variety of relatively unique responses

Table 3

Frequency of Dominance Positions Attained for Females in 16 Multiphase Triads

	Dominance Position			
Female No.	Most Dominant (α)	2nd Dominant (β)	Least Dominant (γ)	# of Triads in which ♀ was a member
601	3	2		5
605	2	1		3
609	2	1		3
612		2	1	3
614		2	2	4
1275		3	2	5
2031	3			3
2196		1	1	2
2505			2	2
2509			4	4
2510		1		1
2511	1	1	2	4
2514	3			3
2515	2	1	1	4
2516		1	1	2

Table 4

Changes in Behavior of Females Observed in Multiphase Triads
During Three Different Phases of the Sex-Skin Cycle
in *Macaca nemestrina*

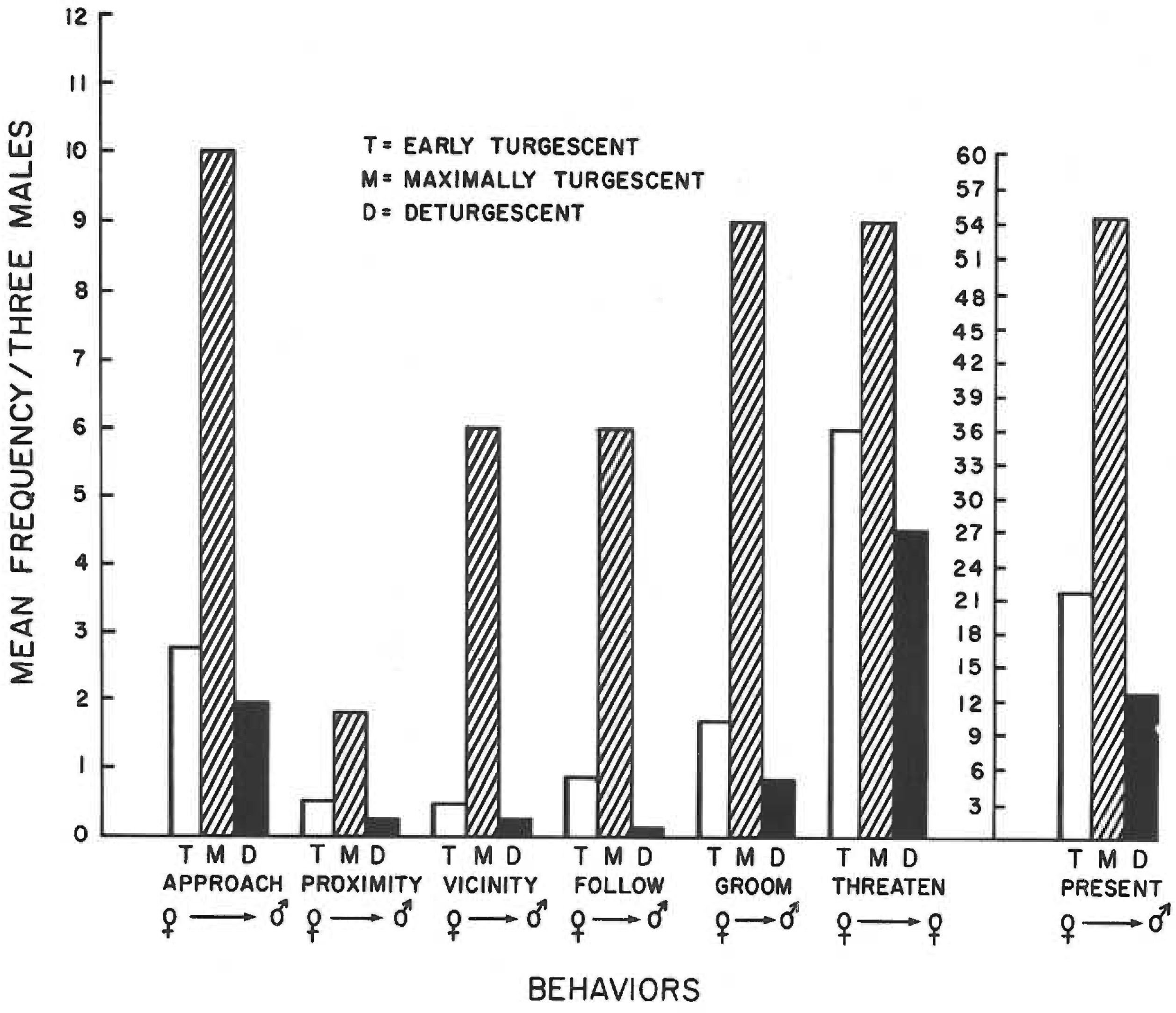
Behavior	Early Turgescent (T)	Maximally Turgescent (M)	Deturgescent (D)	Statistical Comparison (F values)
Sex Pout	0.00	0.87	0.00	4.67*
Present Near	2.07	5.60	0.73	5.92**
Present Far	18.20	36.80	10.40	8.51**
Present to Approach	0.40	5.20	0.67	15.11**
Present to Contact	0.67	6.60	0.53	15.46**
All Presents	21.34	54.20	12.33	15.26**
Approach	2.87	9.93	1.93	10.79**
Proximity	0.40	1.80	0.20	10.06**
Vicinity	1.07	6.07	0.67	10.42**
Follow	0.73	6.07	0.13	10.67**
Closeness	2.20	13.93	1.00	17.10**
Groom	1.67	9.07	0.80	9.17**
Fear Grimace	0.93	0.87	0.80	0.00

Data composed of mean frequencies per 3 males for 15 females tested once in each of the three sex-skin conditions. Females were observed with 3 males successively in each condition.

* $p < .05$.

** $p < .01$.

Figure 6. Changes in behaviors of females tested in three different phases of the sex-skin cycle in <u>Macaca nemestrina</u>.


MEAN FREQUENCY/THREE MALES
0
1
2
3
4
5
6
7
8
9
10
11
12
T= EARLY TURGESCENT
M= MAXIMALLY TURGESCENT
D= DETURGESCENT
T M D
APPROACH
♀ ⟶ ♂
T M D
PROXIMITY
♀ ⟶ ♂
T M D
VICINITY
♀ ⟶ ♂
T M D
FOLLOW
♀ ⟶ ♂
T M D
GROOM
♀ ⟶ ♂
T M D
THREATEN
♀ ⟶ ♀
3
6
9
12
15
18
21
24
27
30
33
36
39
42
45
48
51
54
57
60
T M D
PRESENT
♀ ⟶ ♂
BEHAVIORS

which terminated in successful copulation with the male. When females were tested in the M condition in multiphase triads, they demonstrated significantly more present postures of all forms, more grooming of the male, maintained closer physical distance to the male (Proximity, Vicinity, Follow, Approach) and displayed facial gestures directed towards the male (Sex Pout) which were only rarely displayed at other times of the cycle. Since each female was evaluated in each stage of the cycle in a multiphase triad, these results represent true changes in the behavior of females as they attained the M condition.

In turn, males in the multiphase triad situation clearly responded differentially to the M female on all measures of social and sexual activity. Males ejaculated exclusively with M females, and pouted at them, groomed them, sat near them, approached, contacted and mounted them, all with frequencies of obvious statistical significance (Table 5, Figure 7). Males approached M females on 90% of the occasions that a Present-at-Distance was displayed (PADF), whereas they responded to less than 25% of the Presents-at-Distance displayed by T or D females in multiphase triads. From Table 5, it is clear that the males responded differently to the same female as that female passed from one phase of the sex-skin cycle to the next. It was significantly more probable that a male would interact with a female when she was in the M condition than in either the T or D condition.

Threats by the male were not displayed significantly more often towards females in a particular phase of the cycle, indicating that the M female was as likely to be threatened as a T or D female. The

Table 5

Responses of the Male to Females Observed in Multiphase Triads During Three Different Phases of the Sex-Skin Cycle

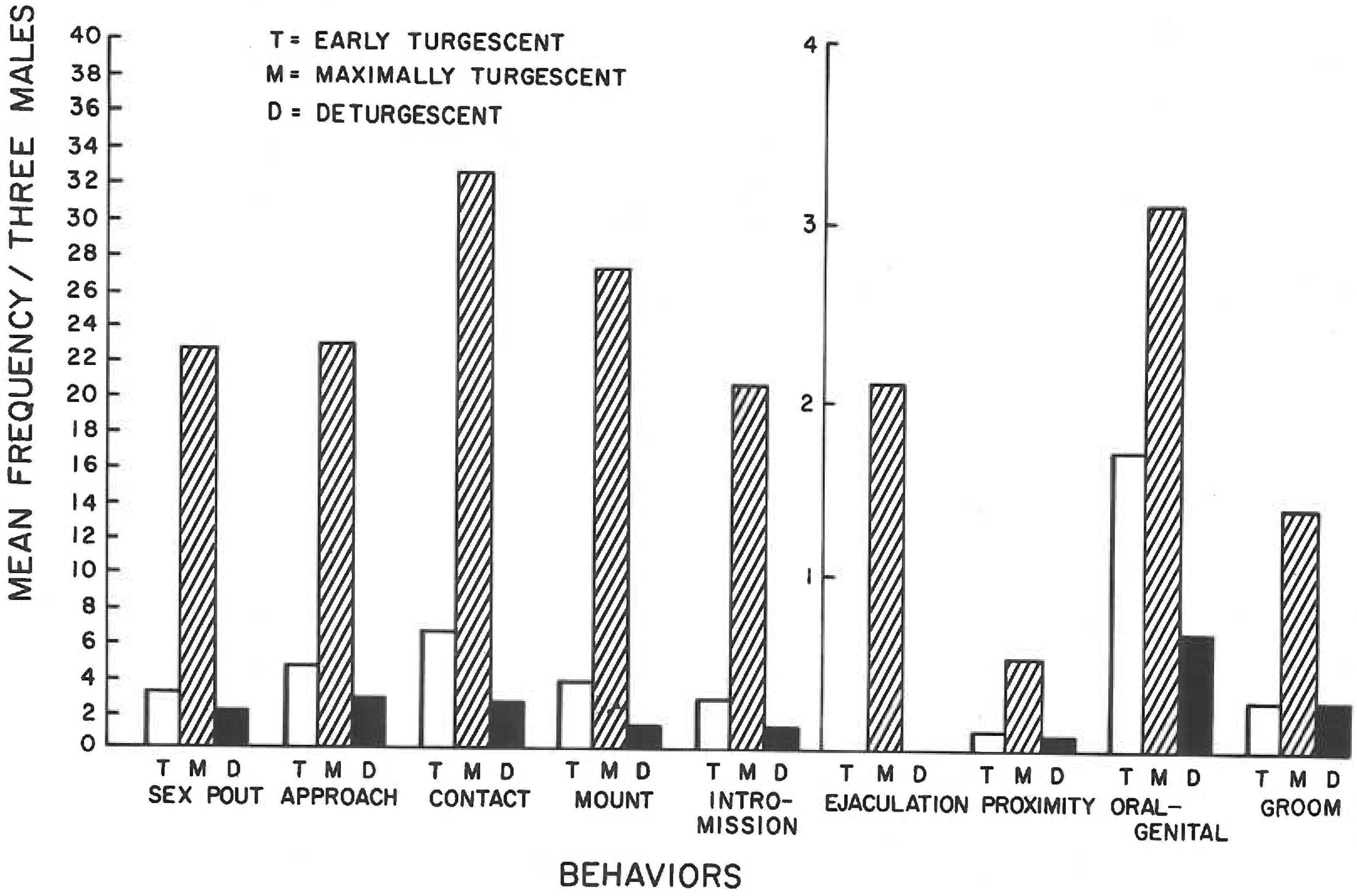
Behavior	Early Turgescent (T)	Maximally Turgescent (M)	Deturgescent (D)	Statistical Comparison (F values)
Sex Pout	3.27	22.47	1.93	61.60**
Approach	4.20	22.60	2.93	35.59**
Contact	6.33	32.67	2.60	87.04**
Mount	4.07	27.47	1.73	67.83**
Intromission	2.47	20.87	0.73	58.79**
Ejaculation	0.00	2.20	0.00	25.42**
Proximity	0.13	0.47	0.13	2.33
Visual Sex X	0.87	1.60	0.67	2.51
Oral Sex X	1.73	3.13	0.67	4.81*
Groom	0.27	1.40	0.33	5.79**
Threat	0.73	0.67	2.60	1.70

Data composed of mean frequencies per 3 males for 15 females tested once in each of the three sex-skin conditions. Females were observed with 3 males in each condition.

* $p < .05$.

** $p < .01$.

Figure 7. Responses of the male to females during three different phases of the sex-skin cycle in _Macaca nemestrina_.


MEAN FREQUENCY / THREE MALES
40
38
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
T = EARLY TURGESCENT
M = MAXIMALLY TURGESCENT
D = DETURGESCENT
4
3
2
1
T M D
SEX POUT
T M D
APPROACH
T M D
CONTACT
T M D
MOUNT
T M D
INTRO-
MISSION
T M D
EJACULATION
T M D
PROXIMITY
T M D
ORAL-
GENITAL
T M D
GROOM
BEHAVIORS

latter finding is important, since it suggests that the male was not overtly responsible for suppressing behaviors of the T and D females.

No statistical differences were found between the T and D conditions for any social or sexual behaviors in multiphase triads, although the females in the T condition displayed and received (nonsignificantly) higher levels of each behavior than did females in the D condition.

The influence of sex-skin status and the presumed endocrine state underlying the condition was emphasized further when the behavior of animals in monophase triads was examined. The behaviors characterizing multiphase triads were found to be uniquely attributable to the presence of a female in the M condition. When males were tested with three females all in the same phase of the cycle (monophase triads) the characteristics of the behavioral interactions differed markedly from those in the multiphase triads. For example, the incidence of ejaculation was only 2 out of 27 possible occurrences in monophase triads compared with 33 out of 45 in multiphase triads. Males responded differentially to individual females comprising the monophase triads, and one female was preferentially treated. Nevertheless, the average frequencies of display were lower with the preferred female in the monophase triad than with the M female of the multiphase triad for 10 of 11 measures studied (Table 6). Correspondingly, M females showed higher average frequencies than the preferentially treated monophase female on all 13 categories of behavior studied (Table 6). Both the preferred female in monophase triads and the M female in multiphase triads displayed greater frequencies of present postures toward the male and both approached the

Table 6

Direction of Differences Between Averages for Maximally Turgescent Females from Multiphase Triads and Preferred Females from Monophase Triads

Behaviors Displayed by Males to Females	Direction of Difference M - Preferred	Behaviors Displayed by Females to Males	Direction of Difference M - Preferred
Sex Pout	+	Sex Pout	+
Approach	+	Present Near	+
Contact	+	Present Far	+
Mount	+	Present to Approach	+
Intromission	+	Present to Contact	+
Ejaculation	+	All Presents	+
Proximity	+	Approach	+
Visual Sex X	-	Proximity	+
Oral Sex X	+	Vicinity	+
Groom	+	Follow	+
Threat	+	Closeness	+
		Groom	+
		Fear Grimace	+

male more than other females in their respective groups. However, only the M female displayed significantly more presents in response to the males' approaches and significantly more presents which were within inches of the male's face (PADN). In addition, only M females showed significantly higher frequencies of behaviors which maintained close physical proximity to the male (Proximity, Vicinity, Follow, and Groom).

The fact that males did behave preferentially toward a particular female in monophase triads raises some very intriguing questions, since females in those triads were specifically equated for sex-skin status, and were not in the M condition. This question is pursued in the next section of this chapter.

Relationship of Dominance to Sexual Performance

The female preferred by males tested with monophase triads was invariably the female rated as most dominant (α) before the introduction of the first male. This relation held true for all 9 of 12 monophase triads in which dominance measures were successfully determined. No significant differences were found between T- and D-monophase triads, and results from these tests were therefore combined. It was the α female in the T-monophase or D-monophase triad who demonstrated the most sex behavior, and in turn received the most contacts, mounts, and intromissions from the males: the β and γ females in the situation displayed only low levels of sex behavior (Tables 7 & 8, Figure 8).

Thus the variable of dominance exerted a marked influence in the group situation in which all females were equated for sex-skin status: The α female maintained her position over the other females in the

Table 7

Behaviors Displayed by Females Towards Males in Monophase Triads

Behavior	Female Dominance Position Alpha	 Beta	 Gamma	Statistical Comparison (F values)
Sex Pout	0.22	0.00	0.00	0.00
Present Near	2.78	0.56	1.11	1.38
Present Far	30.33	12.22	10.89	3.25
Present to Approach	2.56	1.44	2.78	0.65
Present to Contact	4.89	0.78	2.11	5.10**
All Presents	43.89	15.78	15.11	4.30*
Approach	5.67	1.67	1.00	5.27**
Proximity	1.00	1.33	0.33	0.58
Vicinity	5.00	0.67	2.44	2.30
Follow	2.89	0.67	2.00	0.84
Closeness	8.89	2.67	4.78	1.24
Groom	2.89	4.11	2.78	0.24
Fear Grimace	0.11	0.33	0.33	1.09

Data composed of mean frequencies per 3 males for 15 females in 9 triads in which dominance ranking was possible.

* $p < .05$.

** $p < .01$.

Table 8

Behaviors Displayed by Males Towards Females in Monophase Triads

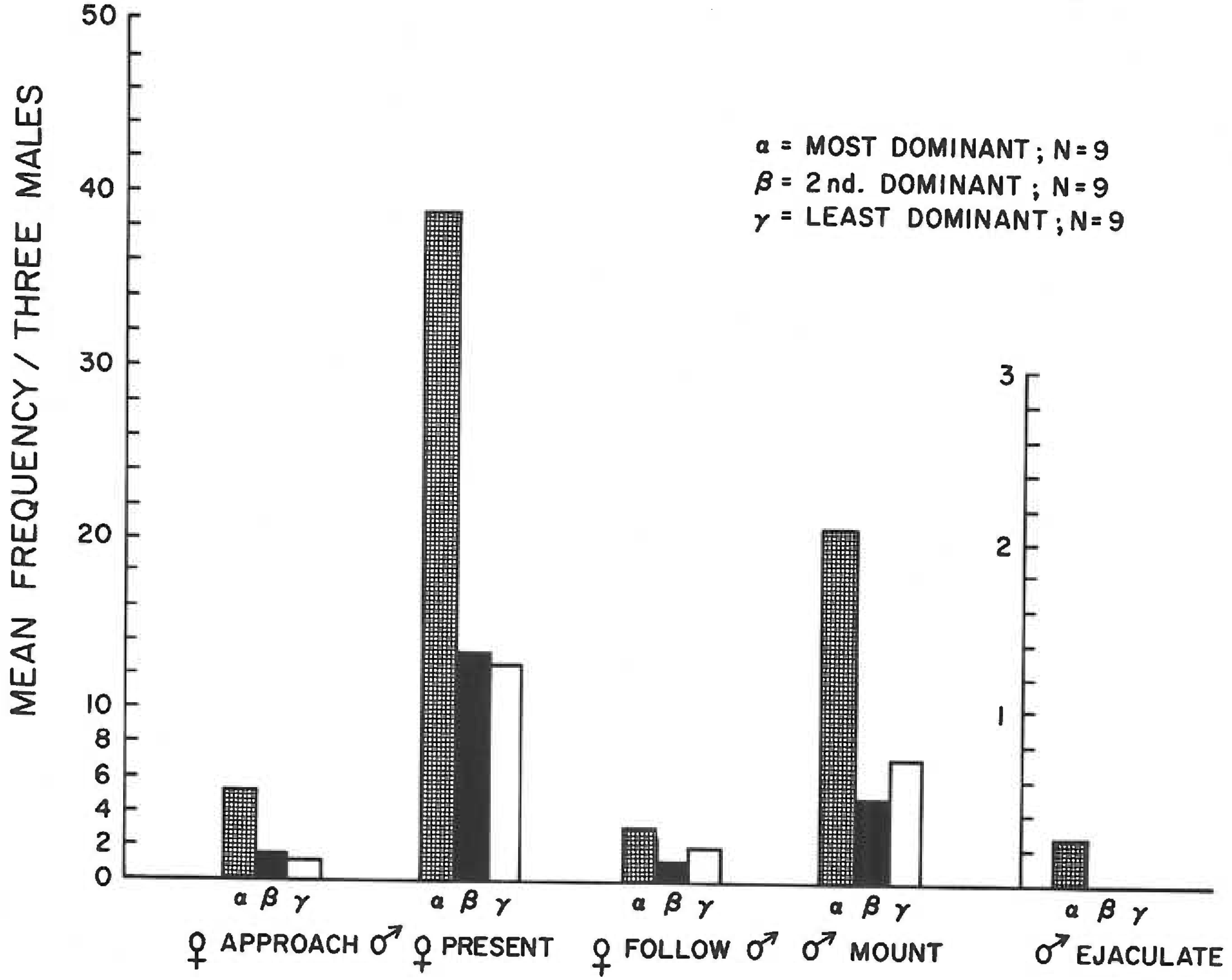
Behavior	Female Dominance Position			Statistical Comparison (F values)
	Alpha	Beta	Gamma	
Sex Pout	5.33	4.78	6.33	0.31
Approach	9.89	6.22	10.00	0.98
Contact	23.56	6.89	11.56	6.12**
Mount	20.44	4.89	7.78	6.29**
Intromission	15.33	3.44	5.44	4.02*
Ejaculation	0.22	0.00	0.00	0.00
Proximity	0.44	0.00	0.56	1.09
Visual Sex X	2.00	1.44	1.11	0.62
Oral Sex X	1.33	0.89	1.22	0.36
Groom	0.89	0.56	0.00	1.29
Threat	1.67	0.44	1.00	0.57

Data composed of mean frequencies per 3 males for 15 females in 9 triads in which dominance ranking was possible.

* $p < .05$.

** $p < .01$.

Figure 8. Relationship of dominance to sexual behavior for females in monophase triads.


MEAN FREQUENCY / THREE MALES
0
2
4
6
8
10
20
30
40
50
1
2
3
α = MOST DOMINANT ; N = 9
β = 2nd. DOMINANT ; N = 9
γ = LEAST DOMINANT ; N = 9
α β γ
♀ APPROACH ♂
α β γ
♀ PRESENT
α β γ
♀ FOLLOW ♂
α β γ
♂ MOUNT
α β γ
♂ EJACULATE

presence of the male and displayed high levels of social and sexual behaviors with him.

If dominance relations among females played a major role in the sexual relations observed in monophase triads, what were its effects, if any, in the multiphase condition? Figure 9 reveals that dominance (measured before the introduction of the males) most definitely was associated with sexual performance in this situation as well (only 4 behaviors are illustrated, although the relation held for all measures studied. By ignoring sex-skin condition, it can be seen that α females received the highest scores for sexual activities, β females were second, and γ females last. Such results would suggest that since sex-skin status was shown to be clearly associated with sexual behavior, and since dominance, measured before the introduction of the male was also associated with sexual behavior, that sex-skin status, and specifically the M condition, must have influenced the dominance hierarchy among females.

This, however, was clearly not the case. Tables 9 and 10 reveal that dominance, always measured prior to the introduction of the males, and therefore independently of the males' influence, was not related to any particular phase of the sex-skin cycle. Dominance relations were successfully determined for 16 of the 21 multiphase triads: relations between animals in the remaining 5 triads were such that 1) differences in dominance could not be discerned by the two observers (three triads), or 2) observers did not agree on the dominance hierarchy (two triads). It can be seen from the tables that the phase of the sex-skin cycle had

Figure 9. Relationship of dominance to sexual behavior for females in multiphase triads.

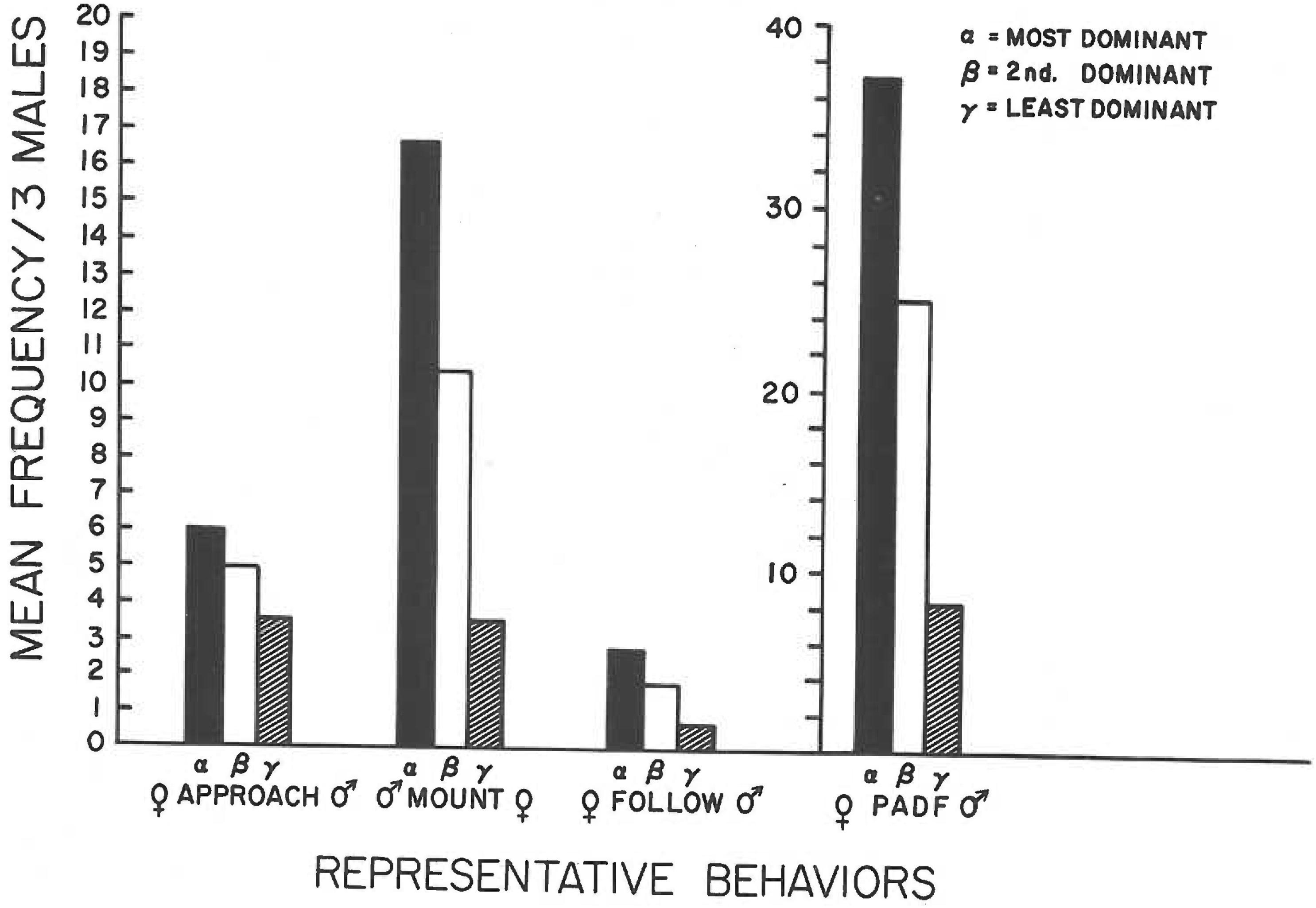

MEAN FREQUENCY/3 MALES
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
10
20
30
40
α = MOST DOMINANT
β = 2nd. DOMINANT
γ = LEAST DOMINANT
α β γ
♀ APPROACH ♂
α β γ
♂ MOUNT ♀
α β γ
♀ FOLLOW ♂
α β γ
♀ PADF ♂
REPRESENTATIVE BEHAVIORS

Table 9

Dominance Rankings Within Multiphase Triads
as a Function of Sex-Skin Swelling

Triad	Sex-Skin Condition		
	T	M	D
1		no rating possible	
3		no rating possible	
5	3	1	2
6	2	1	3
7	1	2	3
8	2	3	1
9	3	1	2
10	3	1	2
11	3	1	2
13	3	2	1
14	3	2	1
15	3	2	1
16	1	3	2
17	1	3	2
19	1	3	2
20	2	1	3
21	1	3	2
22	2	1	3
24		no rating possible	
25		no rating possible	
26		no rating possible	
Sum	34	31	32
Mean	2.13	1.94	2.00

$\alpha = 1$, $\beta = 2$, $\gamma = 3$

Table 10

Distribution of Dominance Ranks Among Three Conditions
of Sex-Skin Swelling (16 Multiphase Triads)

	T	M	D
α	5	7	4
β	4	4	8
γ	7	5	4

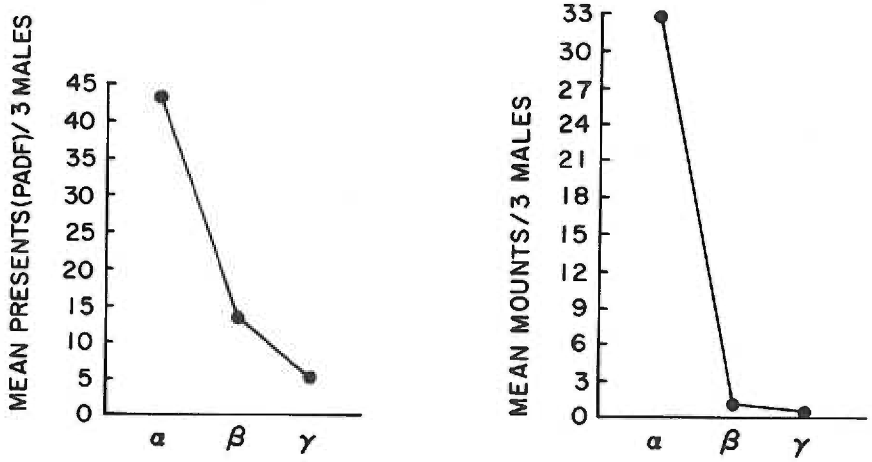
no distinct influence upon dominance relations: 1) the mean dominance ratings for each condition was almost identical; and 2) the number of times animals were α, β, or γ was not associated with particular phases of the sex-skin cycle. It was therefore concluded that sex-skin condition had no pronounced effect upon dominance relations among females in the absence of the male.

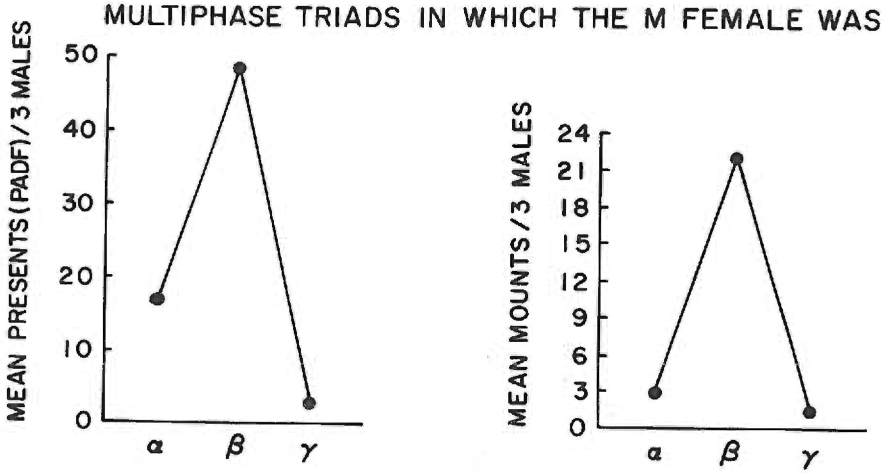
The findings that the dominance hierarchy among females was not related to sex-skin condition, but that sexual behavior was associated with both dominance and sex-skin conditions suggested that an interaction between these two variables existed. Clearly, if sex-skin condition was the only determiner of sexual behavior in the multiphase triad, no relation should have been found between dominance and the display of sexual behavior.

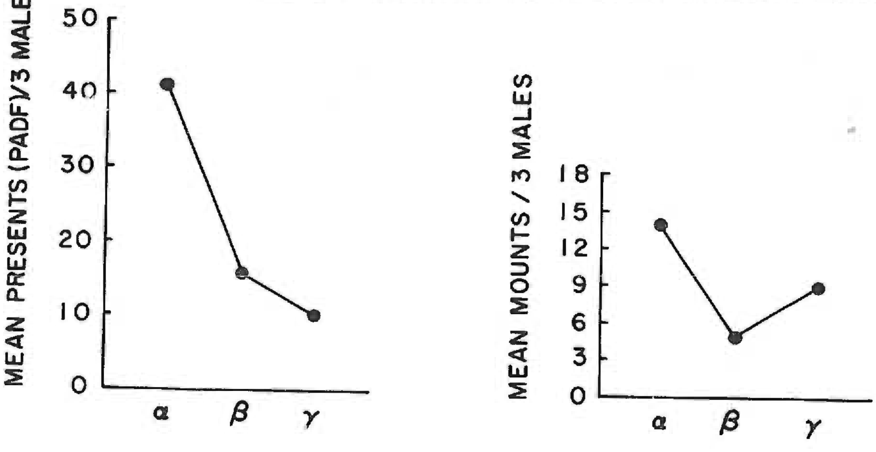
Figures 10 through 15 demonstrate that both dominance and sex-skin condition were operative in determining the sexual relationships of males and females in multiphase triads, and that an interaction between these two factors did indeed exist, since with particular combinations of dominance status and sex-skin condition within an individual, different results occurred. The figures were constructed by classifying multiphase triads in terms of the dominance status of the M female. Only two behaviors were illustrated: male mounts and female presents (PADF). These behaviors were chosen as illustrative of the basic phenomenon which was reflected as well in several other indices of sexual behavior.

When an M female was α in her triad (N= 7 triads), she displayed and received the highest levels of behavior within her group (Fig. 10&11).

Figures 10 — 15. Mounts received and presents displayed by maximally turgescent females of differing positions of dominance in multiphase triads.


MULTIPHASE TRIADS IN WHICH THE M FEMALE WAS α


MULTIPHASE TRIADS IN WHICH THE M FEMALE WAS β


MULTIPHASE TRIADS IN WHICH THE M FEMALE WAS γ

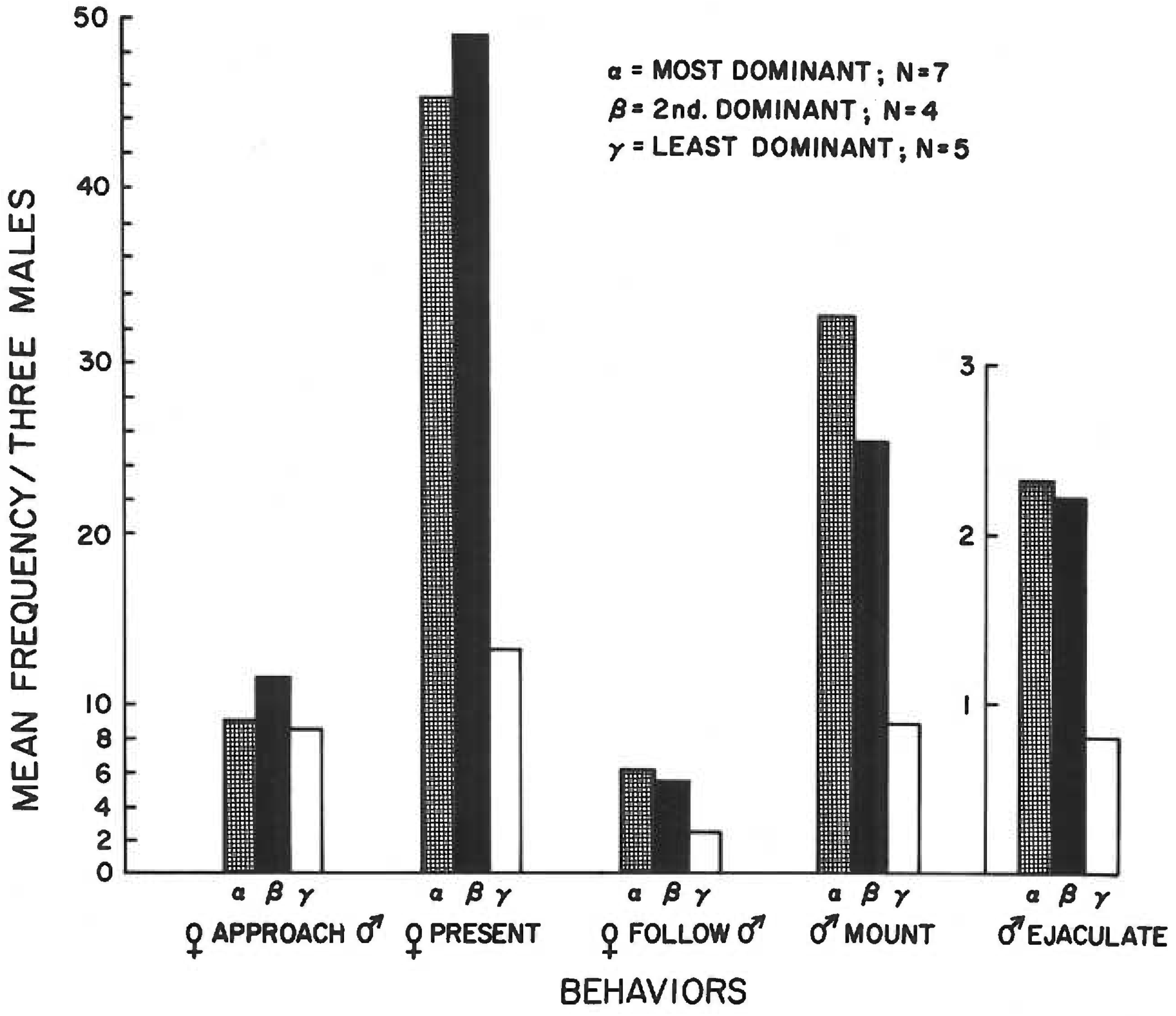
This situation produced the highest overall mounting performance in any triad, and resembled the monophase situation in that both β and γ females were depressed relative to the α female.

In multiphase triads in which the M female was β in the dominance hierarchy (N = 4 triads), the M female also displayed the highest levels of sexual behavior within her group, easily surpassing the performance of her α and γ female partners (Fig. 12 & 13). This was an extremely interesting situation, since it clearly illustrated the fact that an animal in the M condition displayed high levels of sexual behavior even when she was not the most dominant member of the group. β-M females actually displayed higher average frequency of Presents than that for females in any other condition. In monophase triads, it will be remembered, β females <u>never</u> surpassed the performance of the α female for any behavioral measure.

The M condition was not prepotent for females least dominant in their triads, however. As illustrated in Figures 14 and 15, in these triads the α animal displayed the majority of the sexual behavior in spite of the fact that she was not maximally turgescent, and was in the presence of an M female. In these triads, the M female displayed low levels of behavior and was mounted only slightly more than her β partner. The basic difference between γ-M females and M females of higher ranking dominance is further illustrated in Figure 16 for several additional behavioral indices.

Table 11 indicates that part of the explanation for the success of β-M females and the failure of γ-M females might have been due to the intervention by the male. Males actively threatened α females when

Figure 16. Relation between behavior and dominance for the maximally turgescent females in multiphase triads.



MEAN FREQUENCY/ THREE MALES
50
40
30
20
10
8
6
4
2
0
3
2
1
α = MOST DOMINANT; N=7
β = 2nd. DOMINANT; N=4
γ = LEAST DOMINANT; N=5
α β γ
♀ APPROACH ♂
α β γ
♀ PRESENT
α β γ
♀ FOLLOW ♂
α β γ
♂ MOUNT
α β γ
♂ EJACULATE
BEHAVIORS

Table 11

Threats Displayed by Males to Females in Multiphase Triads

	Triads in Which M Female is Most Dominant (α) N = 7			Triads in Which M Female is 2nd Dominant (β) N = 4			Triads in Which M Female is Least Dominant (γ) N = 5		
	α	β	γ	α	β	γ	α	β	γ
Mean Frequency of Male Threats	0	0.44	0	4.5	3.0	0.25	0.20	3.0	0.20

β-M females were present, but did not threaten α females when γ-M females were present.

That social conditions determined this outcome for triads in which the M female was γ is further demonstrated by the following examples: On two occasions, γ-M females were tested individually with a male immediately after their multiphase triad test was over. The same series of three males used in their multiphase tests was used for these pair tests. In the triad, the females did not present to the males, and withdrew from them whenever approached. When removed from the social situation in which they were least dominant, these females were immediately responsive to the males, and the males were highly successful with them. With the other females absent the M female in each case displayed Proximity, Vicinity, Follow, Present, and Approach behaviors to the males, and each male ejaculated with her within 10 minutes.

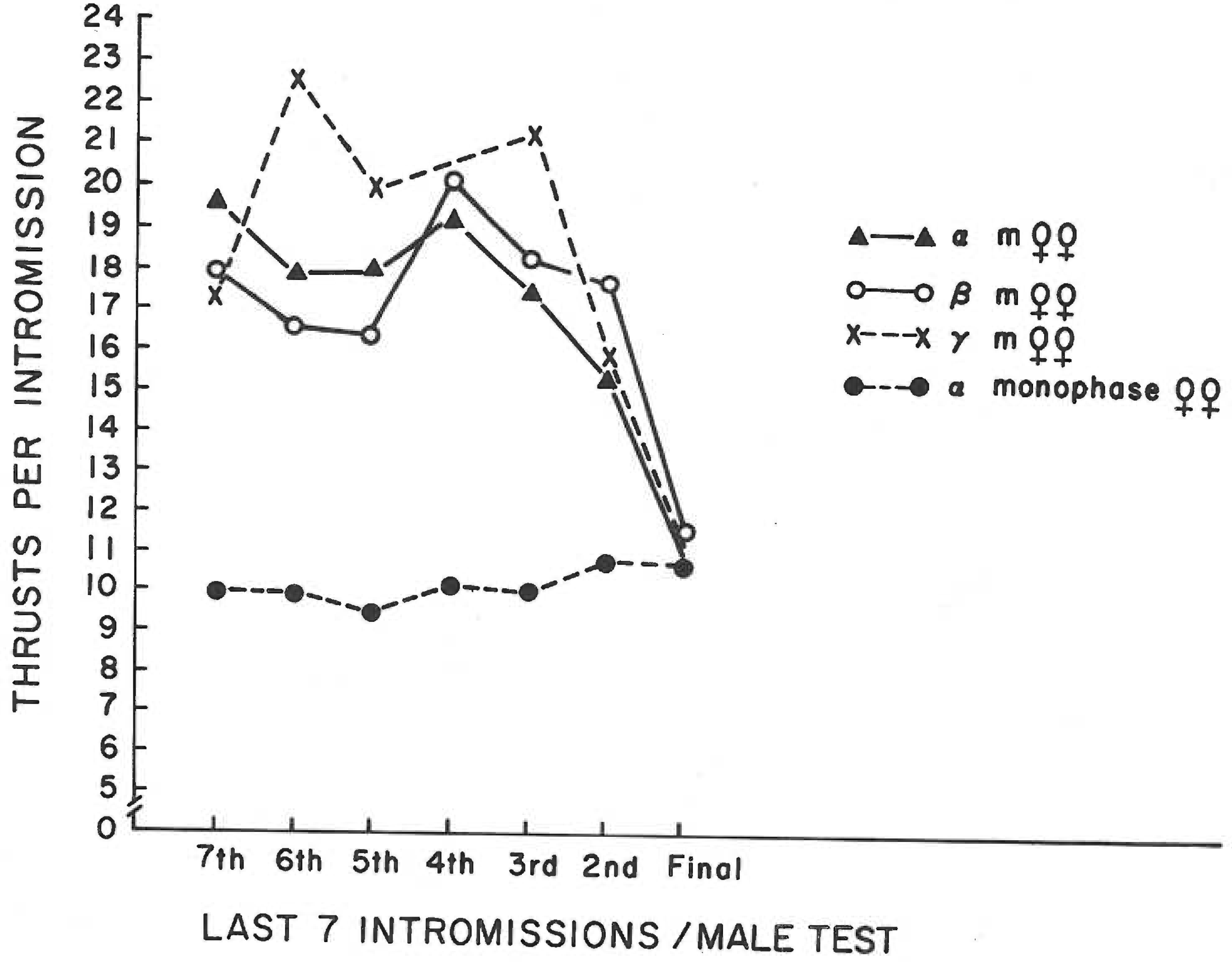
The inverse of this situation was also examined: On a separate occasion an M female was judged to be α in a multiphase triad, and behavioral observations with a series of three males were completed (tests were only 5 minutes long to avoid the occurrence of ejaculations). T and D partners were then replaced with different T and D females, and the M female was rated γ in this new social group. The testing series with the same three males was then repeated. In this new group, the M female no longer displayed presents, etc., that were characteristic of her behavior in the former group situation. Further, the males no longer approached and mounted her, but instead mounted the α female, even though she was in the D condition.

Thus, from these demonstrations and from the data presented in Figures 10 - 15, it is clear that a balance of two critical factors was operative in the multiphase triad, and together determined the amount and kind of sexual relationships which were displayed. Specifically, endocrine conditions operated to increase the probability of insemination of females at a time in the cycle which would maximize the chances for conception. At the same time, however, social factors operated to reduce the probability of insemination of the least dominant female in the group. The endocrine condition associated with the M condition was sufficient to override the dominance hierarchy for females of intermediate dominance status, but was not sufficient to dramatically increase the probability of success for γ females lowest in dominance.

In spite of these social influences, it is interesting to note that the frequency of ejaculations received by γ-M females was substantially higher (4 out of 15) than that received by α monophase females (2 out of 27). Even though α females in monophase triads were mounted more than γ-M females in multiphase triads (means of 20.5 _vs_ 9.0), and had more intromissions with males than γ-M females (means of 15.33 _vs_ 7.80), the γ-M female nonetheless received more ejaculations than the α animals in monophase triads.

From the thrusting data (# thrusts per intromission) presented in Figure 17, it is suggested that the vaginal condition of M females -- even γ-M females -- increased the probability of the occurrence of an ejaculation when an intromission occurred. It can be seen that the male thrusted more than twice as much on each mount with M females than he did with the preferred (α) female in monophase triads. Thus, an

Figure 17. Mean copulatory thrusts per intromission for males tested in multiphase triads with maximally turgescent females of differing dominance status, and of males tested with α females from monophase triads.


THRUSTS PER INTROMISSION
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
0
7th
6th
5th
4th
3rd
2nd
Final
LAST 7 INTROMISSIONS / MALE TEST
▲—▲ α m ♀♀
○—○ β m ♀♀
X- - -X γ m ♀♀
●- - -● α monophase ♀♀

additional mechanism has been found which balances the social conditions tending to decrease mating of low-dominance females with a possible sensory mechanism which increases any M female's chance of being inseminated once intromissions have occurred.

Chapter IV

DISCUSSION

This thesis has dealt with a unique characteristic of primate sexual behavior: mating behavior is seen not only during the preovulatory period, but throughout much of the menstrual cycle. The intent of the experiments presented was to identify both endocrine and social factors which contributed to this phenomenon. Observations of Macaca nemestrina in selected group situations revealed that endocrine conditions exerted significant influences on the display of sexual behavior. Provided that the preovulatory female was not the least dominant female in the group, the behavior of the group was invariably the same: the preovulatory female displayed high levels of sexual behavior while females not in the preovulatory condition displayed comparatively low levels of sexual behavior.

It was not surprising that females displayed the highest frequencies of Presents and received the highest frequencies of Mounts, Intromissions and Ejaculations when in a preovulatory condition, since endocrine factors have been known to influence sexual behavior among mammalian species, including primates, for decades. The thesis did reveal, however, that rather than influencing a restricted number of behaviors, the preovulatory condition determined the increased display of a wide variety of responses which served to augment the probability of copulation with a male.

Secondly, this thesis demonstrated that a variety of ovarian conditions were compatible with the display of sexual behavior. By restricting group composition to females roughly equated for endocrine condition, it was revealed that females in either presumed follicular (T) or luteal (D) conditions displayed relatively high levels of sexual behavior.

The fact that group composition partially determined the behavior of T and D females suggested that social as well as endocrine factors influenced the display of sexual behavior. For most triads observed in which an M female was present, no T or D female displayed high levels of sexual activity. In triads in which no M female was present, one T or D female in each group did display significant amounts of sexual behavior. From results of pair-test studies, almost all T and D females displayed at least moderate to high levels of sexual activity (Bullock, Paris, Resko, and Goy, in press).

The particular social factor found to be of significant predictive value for the display of sexual behavior was social dominance, measured independently of the males' influence. In group situations in which endocrine conditions were equated, the dominant female invariably displayed relatively high frequencies of sexual behavior. In group situations in which one female was in a preovulatory state, social dominance and endocrine factors operated jointly to determine the probability of mating.

Several possible effects of social dominance hierarchies could have been responsible for the relative amounts of sexual behavior displayed by members of triads. It is possible, for example, that the social conditions determining female dominance depressed the sexual behavior of subordinate females in the triad situation.

The results from tests of monophase triads and of multiphase triads in which the M female was α support this hypothesis, in that the most dominant female displayed threat behaviors to subordinate triad members. It is possible that these threat behaviors kept subordinate members from actively competing for the attention of the male. β-M females <u>did not</u> display threat behaviors to the α female in their triads, however, and in fact continued to receive threat behaviors from the α female in the presence of the male. Nonetheless, displays of sexual behavior by T and D females were quite depressed in these triads. In these cases, it was possible that the male intervened in the situation, and actively depressed the α female's behavior with threats of his own. This behavior of the male only occurred when the M female was β, however. A male did not threaten the α female in triads in which the M female was least dominant. It is quite possible that the male did not "defend" γ-M females because they did not display sexual behaviors early in the test which would recruit the assistance of the male. It is recognized, however, that these observations do not establish conclusive evidence that threat behaviors served to depress sexual responses.

Another possibility, suggested by Maslow (1936), is that a dominant female would display aspects of sexual behaviors in order to form an alliance with a male, regardless of her endocrine condition. Such an interpretation, although recognized as being untestable in the present study, could account for the types of sexual behavior displayed by α females in monophase triads. This interpretation would also account for the observation that females in a pair-test situation displayed sexual behavior throughout the majority of the cycle.

A fascinating aspect of primate sexual behavior observed in this study, and most clearly seen in monophase triads, was that social factors were operative throughout the cycle in determining high levels of sex behavior for the dominant member of the group. In the absence of a preovulatory female, members of monophase triads responded to the social conditions of dominance with characteristically high levels of sexual behavior by the most dominant female, and with low levels of behavior by subordinate females.

The apparent influence of social conditions throughout the ovarian cycle on the display of sexual behavior is a unique characteristic of primate behavior. Investigators have realized the importance of social factors affecting sexual responses of other mammalian orders, but these social factors were considered important for determining the quality of sexual behavior only during preovulatory phases; social factors were not known to determine sexual behavior at any other time of the ovarian cycle.

An example of social influences affecting the sexual conduct of dogs demonstrates this contention. Beach and LeBoeuf (1967) have shown that female dogs displayed marked preferences for certain males, and marked aversion for other males throughout the ovarian cycle. When in a preovulatory endocrine condition, the females accepted only males they preferred, and refused the mounts of non-preferred partners. The social aspects which contributed to the preference behavior of females certainly influenced the sexual behavior of this species. However these social influences did not operate outside the preovulatory period to determine sexual behavior. Although preferences were measured throughout the ovarian cycle, the preference relations did not result in sexual activity during periods of physiological diestrus, as they certainly did in Macaca nemestrina.

It is certainly possible that the specific findings of this thesis will not be represented in all primate species, and may be characteristic of only Macaca nemestrina or possibly of promiscuous primate species. It is suspected, for example, that polygynous species such as the hamadryas baboon, will not be sensitive to the specific dominance parameters investigated in this study, since hamadryas baboons are known to form social units of 1 male and 2 - 5 females within baboon troops (Kummer and Kurt, 1963, 1968).. These male units are permanent social structures which do not disband when females are not preovulatory, and thus the relations between the male and the females are much different than that observed for promiscuous species, such as M. mulatta or M. nemestrina. It is indeed possible, however, that social influences determine the formation of these groups and maintain the polygny which is observed in the field.

Several investigators have attempted to explain the sexual behavior of the primate exclusively in terms of gonadal conditions. Zuckerman (1932), faced with the problem of the display of sex behavior during the luteal phase of the cycle in rhesus monkeys, "explained" the phenomenon by suggesting that estrogens must be present during this phase as well as progesterone, since estrogen was the only known causal agent associated with sex behavior. Michael and associates have more recently demonstrated several facilitating and inhibiting effects of gonadal hormones on sex behavior, and have constructed a theory of <u>sexual attractiveness</u> which attempts to encompass the majority of sexual phenomena seen in the primate. Michael and Welegalla (1968), Michael, Saayman, and Zumpe (1968), and Trimble and Herbert (1968) have maintained that three aspects of sexuality must be considered for the female: attractiveness, receptivity (libido), and rejection behavior. Estrogen, these authors maintained, causes the female to be attractive to the male; hence he pursues her and she displays sexual behavior in response to that pursuit. Testosterone, and to a lesser extent, estrogen, elevates female libido in this schema. Trimble and Herbert reported that spayed females displayed elevated frequencies of Presents toward the male when given testosterone propionate. Males did not respond to these females, however, presumably because they were not under estrogenic stimulation, and hence were not "attractive." Finally, when either intact females in the luteal phase of the cycle or spayed females given progesterone simultaneously with estrogen were observed, Michael, Saayman, and Zumpe (1968) reported that males responded to the females (they were still somewhat attractive) but that the females rejected the male's advances. This behavior was of course attributed to progesterone.

Although not disputing the results of these studies, the data obtained in the present study suggest that the concepts of attractiveness, libido, and rejection cannot be rigidly associated with hormonal conditions, since social variables could partially or completely alter these relations. An M female should have been attractive (i.e., mounted often by the male) and should have possessed high libido (i.e., presented often to the male), but if she was least dominant in the group, the male would not respond to her after a few initial attempts which were "refused" by the female. From the operational definitions of Michael's concepts, she demonstrated low attractiveness, low libido, and showed high rejection performance.

It was possible that the ϒ-M females in this study were undergoing anovulatory cycles or were otherwise deficient in hormonal levels characteristic of the preovulatory phase. This was not considered probable, however, since with normal patterns of perineal turgescence, it was unlikely that all ϒ females were anovulatory. Further, if the social situation was modified such that the ϒ-M female was no longer least dominant, then she immediately demonstrated high attractiveness, high libido, and low rejection behavior. Clearly these concepts lose their utility when applied to a group situation.

Michael has suggested in several papers (Michael and Keverne, 1968; Michael and Welegalla, 1968) that attractiveness in the rhesus monkey might well be associated with a pheromone (an odor) secreted during the preovulatory phase of the cycle. Sex-skin swelling in the pigtailed macaque would clearly meet analogous criteria for a visual stimulus which would render the female "attractive." The problem, however, is that an attractive female, by Michael's position, cannot lose her attractiveness if she is not receptive (i.e., she still exudes odor; she remains swollen). Yet, Υ females who were swollen were responded to by the males as unattractive females within only a few minutes of the test in the present study. It is apparent from the responses of Macaca nemestrina that this quality of attractiveness did not <u>determine</u> sexual behavior, but at best was important only during the initial confrontation of the male with the group of females. The male initially responded to the swollen female, but, if her behavior was not suitable, she was quickly abandoned.

To understand the sexual behavior of primates in a social situation, it is obvious that a single-factor hypothesis is inadequate. Gonadal influences are of definite importance, but their actions occur upon a background of individual and group extra-gonadal factors which also must be identified before order can be made of the behavior which is observed. The results of this experiment suggest that three factors, individual differences, social organization and gonadal status, together determine the display of sexual behavior.

As an alternative to Michael's gonadal theory of sexual behavior, the following hypothesis is advanced: The preovulatory condition represents an optimum state of motivation which is expressed in a variety of behaviors which increase the probability of mating. Rather than determining the expression of stereotyped reflex-like behaviors of estrus, the endocrine state of the preovulatory female can be thought to operate on the individual characteristics of a female, against a social background of dominance hierarchy, resulting in the display of varied behaviors which culminate in mating to ejaculation. Increased motivation in a group situation results in that female 1) possibly displaying behaviors which allow her to achieve a more favorable position of dominance (including behaviors which recruit the male's assistance for this), 2) displaying a variety of behaviors which place her in close proximity to the male, 3) displaying high levels of behavior which directly influence the probability of ejaculation. In addition to motivational changes, the M condition supplies the female with sensory attributes such as a distinct appearance, possibly a distinct odor, and possibly a vaginal condition which also increase the probability that ejaculation will occur.

By considering the preovulatory condition to be motivational rather than response-specific for the primate, one can account for the varied individual characteristics which are displayed by M females. Components of individual experience and behavioral flexibility are thus invoked to overcome the social influences which might otherwise decrease the success of a particular preovulatory female in a group situation.

The hypothesis is similar to the situation explored by Nowlis (1941) in which subordinate members of pairs of chimpanzees were severely food-deprived while their dominant partners were satiated or only moderately food-deprived. With high motivation for food, subordinate animals were successful in food competition tests. When equated for food deprivation, the dominant member was always successful.

In parallel, the present hypothesis suggests that subordinate females can obtain the goal object - the male - when in a particular motivational state. Social and motivational forces are both operative, however, and if the female is in a very poor position of dominance, she might be unsuccessful.

Conceptualizing the actions of endocrines in this fashion represents a departure from theories concerned with the sexual behavior of lower orders. Most investigators have inferred that sexual behavior in lower mammalian orders was reflexive in nature, involving relatively few behavioral responses which were controlled almost completely by hormonal variables. It is clear from the results of this study that primate sexual responses are complex and extremely varied in nature, and that they can be predicted not only from specific endocrine considerations, but also from social considerations operative throughout the menstrual cycle. The fascinating individual differences seen between primates in comparable ovarian conditions and the evidence that social relationships influence sexual responses even at times of the cycle when conception is unlikely, suggest that primate sexual behavior can be understood only when considering both endocrine and social variables.

Chapter V

SUMMARY

Fifteen female pigtailed macaques (Macaca nemestrina) were measured for daily fluctuations of perineal sex-skin diameter, which were presumed to reflect ovarian stages of the menstrual cycle. Groups of 3 females (triads) were observed with a series of 3 males for the display of a variety of social and sexual behaviors. Triads were also observed for the display of social behaviors before the first male was introduced. Two types of triads were studied: multiphase triads were composed of 3 females, one in the early turgescent phase of sex-skin swelling, a second at maximal turgescence, and a third in the deturgescent phase of the sex-skin cycle -- multiphase triads were re-formed until each female was seen in all three conditions of sex-skin swelling; monophase triads were composed of 3 females, all in either the early turgescent phase or all in the deturgescent phase of the sex-skin cycle.

Results indicated that both endocrine and social factors interacted in determining the display of sexual behavior. Endocrine factors increased the probability that insemination occurred at an optimum time for conception, while social factors operated to decrease the probability of conception with females who were in positions of very low dominance.

Females received the most sexual behavior from males when in the maximally turgescent phase of the cycle, and displayed behavioral patterns which were relatively unique to the condition of maximal turgescence, provided that they were also the most dominant or second

dominant female in that triad. If the maximally turgescent female was least dominant in the triad, however, she neither displayed nor received significant amounts of sexual behavior. Dominance status among the females, determined before the introduction of the male, was not found to be related to sex-skin condition.

In monophase triads, in which no maximally turgescent female was present and animals were in roughly equivalent endocrine conditions, social factors influenced the display of sexual behavior. The most dominant female of the group always displayed and received the highest amounts of sexual behavior, although several behaviors occurred with lower frequencies than that observed for maximally turgescent females in multiphase triads, including the incidence of proximity behaviors and ejaculations. Both subordinate members of monophase triads displayed very low levels of behavior in contrast to the most dominant female.

It was concluded that endocrine conditions, although not always prepotent, were capable of over-riding social factors which contributed to the display of sexual behavior. Results were discussed in terms of current theories of primate sexual behavior. A suggested motivational framework was outlined which incorporated social as well as endocrine factors for the determination of sexual behavior in higher primate species.

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Appendix I

Behavioral Definitions

All categories of behaviors were scored for males and females with the exception of Vicinity and Follow, which were specifically scored for females.

1. Threat. Includes Distance Threat and Contact Threat:
   a. Distance Threat (DIT). Any of the following behaviors or combination of behaviors which contain obvious and directed orientation towards another animal.
      1) Gape: The head and shoulders are thrust toward the partner while the jaw is abruptly dropped. The mouth is held open but teeth are not fully exposed. Locomotion toward partner is allowed.
      2) Ear Flip: Either rapid ear flipping or sustained ear retraction.
      3) Faint Lunge: Body suddenly directed toward partner, but held in check. Can take the form of cage shaking if eye contact with partner is obvious. Locomotion toward partner allowed, provided no contact is made.
      4) Pout Threat: Jaw jutted forward, lips in a flat pout-like position, ears flattened. Defined contextually; e.g., scored only when accompanied with other distance threat postures.
   b. Contact Threat (CONT): Brief bouts of gentle-moderate biting, shaking, or tugging another animal. Distinguished from Aggression by shorter duration of contact and milder form.

2. Aggression (AGG): Severe biting, often accompanied by chase, and severe forms of shaking and tugging.

3. Approach (APP): Animal A walks in direct line towards Animal B and stops in immediate vicinity of Animal B. Approach not scored if 1) Animal A stops before reaching Animal B, 2) does not stop, but walks farther than 3 feet past Animal B, 3) Animal A does not maintain a uniform and moderate-fast rate of walking.

4. Closeness (APVF): Includes the three following behaviors. Male scored only for Proximity. Females scored for all three categories.

   a. Proximity (PROX)

   Two animals are seated within easy reach of one another. No other activity is performed (e.g., grooming, cage exploration, etc.). The initiator of proximity is credited to the last animal to sit down.

   b. Vicinity (VICN)

   Female stands very close to male (within arm's length or closer). Female may circle male, pace directly in front of him, etc.

   c. Follow (FOLL)

   Female follows male; stops when he stops (allowed to move directly in front of him or to his side). Vicinity or Present often seen after Follow.

5. Sex Pout (POUS): Particular facial expression involving lips pursed into a flat, pouting expression, head extended toward another animal. Defined contextually to occur in situations devoid of threat postures and expressions, and including immediately preceding or subsequent behaviors of sexual nature.
6. Neutral Pout (POUN): Pouts that were displayed in contexts neither sexual nor threatening in nature.
7. Fear Grimace (FG): A facial expression in which lips are retracted to expose teeth with mouth slightly opened: remotely resembling a human smile. Generally occurs with cringing, huddling, or fleeing.
8. Visual Sexual Exploration (Vis Sex X)(VSEX): Obvious visual orientation by Animal A towards ano-genital region of Animal B. Not scored when simultaneously accompanied by Oral Sexual Exploration. Obvious visual orientation is recognized by an intense and prolonged stare, often accompanied by raised or furrowed eyebrows.
9. Oral-Genital Exploration (Oral Sex X)(OSEX): Animal A sniffs or licks genitals of Animal B.
10. Present (ALPS): Stereotyped posture of receptivity, characterized by quadrapedal immobility, orientation of perineum towards partner, moderate extension of fore and hind limbs. Present postures were categorized as follows:

Appendix I - cont'd.

a. Present to Approach (APT)

Present posture assumed by Animal A as Animal B approaches.

b. Present to Contact (CPT)

Present posture assumed after being contacted (see definition #12).

c. Present Far (PADF)

Present posture assumed spontaneously and displayed 1 foot or further from partner.

d. Present Near (PADN)

Present posture assumed spontaneously and displayed within 1 foot of partner.

11. Contact (CON): Animal A lightly touches perineum or hips of Animal B. Forceful contact with lifting (rarely seen) is scored as Positioning.

12. Mount (M): An erect stance in which the hands are placed on partner's hips, perineum, or back, and 1 or both feet are clasping partner's ankles or legs. Thrusting may or may not occur.

13. Intromission (I): Penile insertion, recognized by deep and regular thrusting.

14. Ejaculation (EJC): Recognized by deep thrust which is accompanied by immobility and slight quivering. Anus often dilates and contracts rapidly.

15. Groom (GROO): Stereotyped spreading and picking of hair of partner. May include slaps.

Appendix II

Sex-Skin Turgescence and Menstrual Cycle Length in *Macaca nemestrina*

		Swelling (mm)			Total Range of Fluctuation (maximum-minimum)	Phase Length		Menstrual Cycle Length
Animal	Cycle	Day 2	Peak	Last day of Deturgescence		Turg.	Deturg.	
601	1	123	138	120	20	14	14	28
	2	116	138	119	22	15	13	28
	3	118	138	117	21	18	14	32
	4	117	137	116	21	15	17	32
	5	119	138	118	20	14	15	29
	6	119	138	117	22	14	15	29
605	1	100	116	95	16	13	18	31
	2	101	116	95	21	20	17	37
	3	94	115	90	21	18	16	34
609	1	110	122	104	18	12	14	26
	2	102	121	101	19	15	14	29
	3	102	119	102	17	13	14	27
	4	101	121	101	20	17	14	31
	5	97	121	102	25	17	15	32
	6	100	120	98	22	14	15	29
	7	100	115	98	17	16	12	28
612	1	156	210	154	55	Progesterone		151
	2	151	180	146	30	17	15	32
	3	151	192	150	41	16	15	31
614	1	105	131	103	30	25	14	39
	2	105	131	104	28	25	14	39
	3	102	134	103	34	36	16	52
	4	103	134	105	32	21	16	37
	5	103	128	103	25	17	16	33
1275	1	91	115	91	24	23	15	38
	2	92	115/122	94	30	17/19	15/16	67
2031	1	112	133	105	29	19	13	32
	2	117	134	105	29	16	13	29
	3	109	137	103	34	17	15	32
	4	107	131	102	29	15	13	28
	5	108	135	103	32	19	14	33
	6	111	134	105	27	16	15	31
	7	108	136	104	32	16	13	29

Appendix II - cont'd.

		Swelling (mm)			Total Range of Fluctuation (maximum-minimum)	Phase Length		Menstrual Cycle Length
Animal	Cycle	Day 2	Peak	Last day of Deturgescence		Turg.	Deturg.	
2196	1	104	113	106	9	11	15	26
	2	106	115	105	12	11	18	26
	3	104	117	103	14	17	14	31
	4	105	115	104	11	18	15	33
	5	102	117	102	15	13	15	28
	6	105	119	103	14	12	18	30
	7	105	118	106	13	12	15	27
2505	1	125	151	123	28	23	15	38
	2	124	144/144	122	22	16/15	15/15	61
	3	123	146	122	24	14	15	29
	4	123	147	129	25	17	13	30
	5	128	146	123	25	16	14	30
2509	1	123	143	123	19	13	14	27
	2	124	138	118	20	13	12	25
	3	122	138	120	18	13	13	26
	4	121	139	123	19	15	13	28
	5	123	137	124	19	14	12	26
	6	122	137	118	19	11	13	24
	7	129	138	123	15	14	11	25
2510	1	106	134	106	29	24	15	39
	2	110	131	97	34	12	21	33
	3	98	140	105	42	25	16	41
	4	110	141	106	36	17	15	32
2511	1	123	162	135	39	20	13	33
	2	125	160	129	38	23	14	37
	3	129	165	123	42	19	15	34
	4	124	161	120	42	20	15	35
	5	121	157	129	37	20	14	34
	6	123	152	122	30	14	16	30
2514	1	102	129	100	29	27	17	44
	2	108	124	98	26	16	17	33
	3	96	120	94	26	18	13	31
	4	96	122	96	26	18	15	33
	5	99	123	99	24	25	13	38
	6	105	122	99	23	17	16	33

Appendix II - cont'd.

		Swelling (mm)			Total Range of Fluctuation (maximum-minimum)	Phase Length		Menstrual Cycle Length
Animal	Cycle	Day 2	Peak	Last day of Deturgescence		Turg.	Deturg.	
2515	1	176	181	121	60	Progesterone		95
	2	121	170	141	49	24	12	36
	3	134	174	140	39	31	15	36
2516	1	126	148	121	27	19	16	35
	2	120	148	117	31	20	17	37
	3	121	150	117	33	29	16	45
	4	122	147	118	30	19	16	35
	5	122	150	119	32	23	14	37
	6	122	150	124	28	18	17	35