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ABSTRACT

SEXUAL MATURATION OF FEMALE SAGUINUS OEDIPUS OEDIPUS

by

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The first hypothesis tested was that Saguinus oedipus oedipus females housed with adult males would mature, sexually, at an earlier age than females remaining in their natal groups. The second hypothesis was that certain behavioral interactions involving young females would change in frequency when the females matured.

Seven females were housed with strange unrelated males. Five females remained in their natal groups. Blood samples were taken twice weekly and the plasma was assayed for progesterone. Sexual maturation was defined as that age at which plasma progesterone levels became consistently detectable. Females housed with males did mature at an earlier age than females remaining in their natal groups.

Groups were observed for an average of three, 20-minute periods, each week, during which time the frequency of selected interactions was recorded. It was hypothesized that sexual and affiliative interactions in young female-adult male pairs would increase when the females matured. The frequency of these interactions did not increase with maturation.

It was hypothesized that affiliative interactions between mothers and daughters would decrease while agonistic interactions between them would increase when the daughters matured. The mothers interactions with their daughters were unchanged by the daughters' maturation. No

conclusion could be drawn concerning changes in the daughters' affiliative behavior. Aggression by daughters toward their mothers was infrequent and did not change with the daughters' maturation. The variation between daughters was partially accounted for by the fact that some natal groups contained unrelated males.

It was hypothesized that all females would mark more when mature. Females with unrelated males, either alone or as part of their natal group, displayed an increase in marking. However, mature females in natal groups, alone, showed no increase.

In summary, social environment did affect maturation age. The mother's presence was not related to the daughter's maturation age. However, whether the natal group, as a whole, inhibited maturation, or unrelated males accelerated maturation, or both, remains unknown. Most of the behavioral interactions involving maturing females were unchanged by maturation. There was some indication that certain behaviors were affected by maturation, but only if a strange unrelated male was present.

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INTRODUCTION

One of the pivotal events in the development of a female mammal is sexual maturation. Sexual maturation constitutes numerous changes in a female's physiology, morphology and behavior. Her reproductive system is altered from a state of quiescence to one in which follicular maturation and ovulation occur in a regular, cyclical fashion. The endocrine changes which cause and result from this change in ovarian function also bring about various morphological changes such as vaginal introitus in rodents (Donovan and Van der Werff ten Bosch, 1959; Rogers and Beuchamp, 1974) and perineal swelling in many primates (Rowell, 1977; Wolfe, 1978). In addition to morphological changes, various behavioral changes may also accompany sexual maturation. In some rodent species, the occurrence of certain behaviors, such as lordosis, is very clearly linked to ovarian hormone levels common to a sexually mature, estrous female (Leshner, 1978). However, most behavioral changes associated with sexual maturation in most species are not so clearly linked to specific hormonal changes. The behavioral changes that a female will display at sexual maturation obviously depend upon a number of factors, such as her prior experience and the age, sex, and prior experience of others in her social group.

The age at which a female will begin sexual maturation can be affected by a number of factors. Weight (Wilen and Naftolin, 1977),

nutrition (Zachiarias and Wurtman, 1969), and stress (Christian, 1978) are known to affect maturation rate. The social environment of a young female may also affect her maturation rate. This effect is most amply illustrated in rodents, where the presence of a male, or male urine, may speed up sexual maturation in young females (Kennedy and Brown, 1970; Vandenbergh, 1967, 1969). It has also been found that, in some cases, adult females may inhibit sexual maturation in young females (Cowley and Wise, 1972; Drickamer, 1982; Payman and Swanson, 1980; Rogers and Beauchamp, 1976). There is also some anecdotal evidence indicating that, in certain monogamous mammals, mothers may inhibit sexual maturation in their daughters, through some unknown mechanisms (Kleiman, in press; Seal, et al., 1979).

This study is an examination of the process of female sexual maturation in the cotton-top tamarin, Saguinus oedipus oedipus, a South-American primate of the family, Callitrichidae. Two types of questions are addressed. The first question is whether the type of social grouping in which a young female lives affects the rate of her sexual maturation. Specifically, is there a difference between the maturation rate of a female housed with a strange adult male and a female housed with her natal group (i.e., her parents and various siblings)? Second, the effect of sexual maturation on various social interactions is examined. Specifically are male-female interactions in mated pairs and mother-daughter interactions in natal groups changed by the sexual maturation of the young females?

In captivity, callitrichids are generally housed as nuclear families, that is, as one mated pair with a number of their sets of twin offspring. Generally, the mother is the only female in the group

who reproduces, regardless of the number of adult female offspring present (Epple, 1967,1970a,1975a; Kleiman, in press; Rothe, 1975). This pattern is similar to that seen in other monogamous mammalian species, such as the wolf, the dwarf mongoose, and the gibbon and siamang (Kleiman, 1977; Mech, 1970; Rasa, 1972, 1973; Seal, et al., 1979; Zimen, 1975).

The means by which reproduction is limited to the mother in callitrichid groups is not clear but it is hypothesized that the mother suppresses the sexual maturation of her daughters (Kleiman, in press). Generally, the reproductive state of the daughters in callitrichid groups is unknown, as callitrichid females do not display any reliable external signs of estrus or maturation (Hearn, et al., 1975). Assays of ovarian hormones in blood or urine of daughters in two callitrichid species yield conflicting results. Katz and Epple (1979) report that ovarian hormonal cyclicity is suppressed in young Saguinus fuscicollis females up to two years of age, if they remain in their natal groups. However, Abbott and Hearn (personal communication) each report that young Callithrix jacchus females who are housed in their natal groups do cycle.

Results from studies of various species having a monogamous social structure similar to that of callitrichids indicate that females do mature while with their parents, but at a significantly later age than young in closely related taxonomic groups without a monogamous social structure. For example, female wolves generally mature at around two years of age, compared to ten months for the closely related domesticated dog (Seal, et al., 1979). Similarly, beaver and dwarf mongoose mature significantly later than closely related species

(Kleiman, 1977).

Whether the presence of a strange adult male has an effect on the maturation rate of callitrichid females is unclear. Epple and Katz (1980) and Abbott and Hearn (1978) report earlier ages of first conception in females housed with adult males versus females housed with same-aged males. However, no data are presented on the age of sexual maturation of these females. As stated previously, the faciliatory effect of adult males on female sexual maturation has been amply illustrated in rodents. Based upon the information available on the maturation rate of young females in monogamous family groups, the effect of an adult male upon conception age in callitrichids and the general faciliatory effect of adult males demonstrated in other species, it is hypothesized that young females housed with males will mature significantly earlier than females housed with their natal groups.

Various types of social interactions might be expected to change when a young female begins sexual maturation. Among these, one might expect changes in male-female and mother-daughter interactions. First, probable changes in male-female interactions will be addressed, then those changes likely in mother-daughter relations.

One might reasonably suggest that sexual behavior is likely to be affected by sexual maturation. In many primate species, including some callitrichids, sexual behaviors are displayed by immature individuals, though frequently in an incomplete form (Goldfoot, 1977). Therefore, sexual maturation does not appear to be necessary for the display of sexual behavior. However, in some primates, the frequency of occurrence of certain sexual behavior appears to change as the

female matures (Hanby and Brown, 1974; Wolfe, 1978). It is hypothesized that, in young female-adult male pairs, sexual activity will increase when the female begins sexual maturation.

In monogamous mammals, affiliative behaviors, such as contact and grooming, appear to serve an important role in establishing and maintaining the pair bond. In some monogamous species, sexual activity is reported to be relatively infrequent while affiliative behavior are frequently displayed (Kleiman, 1977; Epple and Katz, 1980). It seems reasonable to assume that this bonding between mates would be dependent upon the sexual maturity of both partners. For this reason, it is hypothesized that affiliative interactions in young female-adult male pairs will increase when the female begins sexual maturation.

There are many questions concerning the relationship between callitrichid mothers and daughters which remain unanswered. As mentioned previously, it has been hypothesized that mothers suppress the sexual maturation of their daughters through some unidentified mechanisms. However, the evidence relative to this hypothesis is conflicting. Similarly, reports of the interactions of adult daughters and their mothers indicate a wide variety of responses. Rothe (1975) reports that, in Callithrix jacchus, daughters are left with their parents for over four years with no increases in agonistic interactions. Rothe (1978) also finds that older daughters tend to have the fewest social contacts with both parents. Other reports on various callitrichids indicate that agonistic interactions between mother and daughter increase as the daughter grows older, frequently becoming quite severe, at ages even younger than four years (Lorenz,

1972; Mallinson, 1975; Snyder, 1972).

Any relationship between these increases in aggression and changes in the daughter's maturation state are unknown, since the daughter's maturation state is generally unknown. However, a link between increases in agonistic interactions between mother and daughter and the daughter's sexual maturation is documented in another monogamous mammal, the wolf (Zimen, 1975), and is suggested in other species, such as the dwarf mongoose (Rasa, 1972,1973) and the siamang (Fox, 1972). Therefore, it is hypothesized that in S. oedipus, a species which also appears to be monogamous, affiliative interactions between mother and daughter will decrease and agonistic interactions will increase when the daughter begins sexual maturation.

Another behavior which might be expected to be affected by sexual maturation is marking frequency. Callitrichids possess highly developed scent glands and marking is a frequent activity of both sexes (Epple, 1967). A number of functions have been attributed to callitrichid scent marking, including sexual signalling (Epple, 1967; French and Snowdon, in press), delineation of territory (Epple, 1967,1970b; French and Snowdon, in press), and expression of frustration or excitement (Epple, 1967; Kleiman and Mack, 1980). Because marking is associated with at least the first two of these functions, its frequency might be expected to vary according to reproductive state. It is then hypothesized that all females will display an increase in marking when they begin sexual maturation.

CHAPTER 1

LITERATURE REVIEW

Introduction

The cotton-top, or crested bare-faced tamarin, Saguinus oedipus oedipus, is a small, squirrel-like primate inhabiting the tropical forests of northwestern Colombia (Hershkovitz, 1977). S.o.oedipus is a member of the family, Callitrichidae. Callitrichids are characterized by small size (100-600 grams), presence of claws on all digits except the hallux, which bears a nail, highly developed sensory vibrissae, highly developed apocrine and holocrine sebaceous scent glands, and generally primitive skeletal features. They are diurnal and omnivorous (Hershkovitz, 1977).

There have been only two general field studies of S. oedipus (Dawson, 1978, S.o. geoffroyi; Neyman, 1978, S.o. oedipus), but these, combined with field studies on related species (Izawa, 1978; Moynihan, 1970; Stevenson, 1978; Thorington, 1968) and numerous studies on various captive callitrichids (Box, 1975; Epple, 1967, 1970, 1975a, 1975b, 1978; Hoage, 1978, in press; Ingram, 1977; Kleiman, 1979; Kleiman and Mack, 1980; Rothe, 1978; Snyder, 1972; Stevenson and Poole, 1976; Vogt, 1978a, 1978b; Welker and Luhrman, 1978; Wolters, 1978), provide some information on the probable social organization of this species. In captivity, callitrichids are generally housed as nuclear families, that is, as one mated pair with a number of their

sets of twin offspring (Epple, 1970a, 1975a; Fitzgerald, 1935; Hiddleston, 1976; Kleiman, in press; Lorenz, 1972; Mallinson, 1975; Rothe, 1975; Snyder, 1972). Attempts have been made to maintain groups with more than one unrelated member of the same sex, but these groups have almost always proven to be unstable, due to fighting between members of the same sex. The aggression is usually most extreme between adult females (Abbott and Hearn, 1978; Epple, 1967; Hampton, et al., 1966; Hiddleston, 1976; Lorenz, 1972; Rothe, 1975).

In general, only one female in a captive callitrichid group reproduces regardless of the number of adult females present (Abbott and Hearn, 1978; Epple, 1967, 1970a, 1975a; Hampton, et al., 1966; Kleiman, in press; Rothe, 1975). Field studies indicate that there is probably also only one reproducing female in wild groups (Dawson, 1978; Neyman, 1977; Stevenson, 1978). Callitrichids generally produce fraternal twins, rarely singletons or triplets (Hershkovitz, 1977). All family members participate in the care of the offspring, which includes continuously carrying them from one to five weeks of age (Epple, 1975b; Hoage, 1978; Ingram, 1977) and either sharing food or allowing them to take food from hand (Epple, 1967; Brown and Mack, 1978). The relative contributions to infant care by the mother, father, and older siblings apparentally vary according to species, age, and social experience (Box, 1975; Brown and Mack, 1978; Epple, 1975b; Hoage, 1978; Ingram, 1977; Vogt, 1978a, 1978b).

The means by which reproduction is limited to only the mother in the family group is not clear. Young females may be physiologically inhibited. Katz and Epple (1979) report that ovarian hormonal cyclicity is suppressed in young Saguinus fuscicollis females within

their family group. However, J.P. Hearn and D.H. Abbott (personal communication) report that young Callithrix jacchus females housed in their family groups do cycle. Also unclear is whether limitation of reproduction to the mother may be the result of behavioral suppression of daughters through agonistic interactions. Parents remain quite tolerant of their offspring, generally, up to around two years of age. Parents are reported to be tolerant of offspring in some groups, while quite aggressive in others, once the offspring are older than two to three years (Kleiman, 1979; Mallinson, 1975; Rothe, 1975; Snyder, 1972). Parent-offspring aggression is also reported in the closely related Callimico (Lorenz, 1972).

The research which will be presented here is an attempt to discover whether the reproductive potential of young female callitrichids is controlled by social influences and how their reproductive state, in turn, affects their social interactions. The literature reviewed deals with the delineation of endocrine and behavioral changes associated with puberty in female mammals, primarily among species which exhibit a monogamous family social structure. The influence of social interactions on maturation will also be addressed.

Sexual Maturation-Endocrine Events

In a post-pubescent female mammal, an endocrine feedback system involving the ovaries, pituitary and hypothalamus controls the events surrounding ovulation and physiological preparation for pregnancy. The general description of these processes, presented here, will be drawn from the literature on rodent and primate reproduction. While the

extensive studies of the reproduction of domesticated animals have been reviewed (Feder, 1981; Legan and Karsch, 1979; Odell, et al., 1970), they will not be considered here.

Gonadotropin releasing hormone (GRH) from the hypothalamus reaches the pituitary via the hypophyseal portal system (Turgeon,1980). The regular, pulsatile release of GRH results in the secretion of follicle-stimluating hormone (FSH) and luteinizing hormone (LH) by the pituitary (Knobil, 1980; Knobil, et al., 1980). FSH acts upon the ovary, resulting in the maturation of follicles (Richards, 1980; Turner and Bagnara, 1971). The maturing follicles produce estrogens, probably through the combined activity of the theca and granulosa cells (Richards, 1980). Increasing estrogen levels act as a negative feedback to the pituitary, resulting in a relatively steady output of FSH and LH (Dierschke, et al., 1974a; Knobil, 1980; Turner and Bagnara, 1971). There is also some evidence that FSH can be independently controlled by factors produced by the dominnant follicle (e.g. inhibin) (Dukelow, personal communication). However, when estrogen reaches a certain critical level and remains at that level for a sufficient time, the estrogen acts as a positive feedback, causing a surge of LH (Turner and Bagnara, 1971) and FSH (Dierschke, et al., 1973) to be released. This gonadotropin surge may be due to increased GRH release from the hypothalamus (Fink, 1979; Turgeon, 1980). It has also been hypothesized that the surge is a result of direct estrogen action on the pituitary (Knobil, et al., 1980). These different mechanisms may reflect a taxonomic difference (Fink, 1979; Knobil, et al., 1980). The surge results in the ovulation of a mature follicle. With ovulation, a corpus luteum is formed in the ovary from

the remaining theca (Mossman and Duke, 1973). Estrogen levels decline and progesterone, produced by the corpus luteum, induces changes in the endometrium in preparation for pregnancy (Turner and Bagnara, 1971; Mossman and Duke, 1973). Increasing levels of progesterone also inhibit LH and FSH release (Dierschke, et al., 1973). If fertilization and implantation do not occur, the corpus luteum regresses resulting in a decrease in progesterone levels.

The process of puberty alters a female from a state in which follicular maturation is not completed and ovulation does not occur to one in which follicular maturation and ovulation occur in a regular, cyclical, fashion. Puberty is a long, complex process involving changes in hypothalamic, pituitary, and ovarian function. At present, there are two hypotheses regarding the pivotal events in the initiation of puberty. One theory contends that, prior to puberty, the estrogen levels required to inhibit gonadotropin secretion are quite low (Donovan and Van der Werff ten Bosch, 1959; Grumbach, 1975; Van der Werff ten Bosch, 1975). With low levels of FSH and LH, due to the low setting of the hypothalamic-pituitary "gonadostat", follicular maturation does not proceed. At puberty, this gonadostat gradually becomes re-set at a higher level, so that much higher levels of estrogens are required to inhibit gonadotropin release. At this stage, FSH and LH levels rise and follicular maturation begins (Grumbach, 1975; Van der Werff ten Bosch, 1975). The second theory contends that low gonadotropin levels in pre-pubescent females are not due to a highly sensitive negative feedback system. This view is supported by the fact that ovariectomy in pre-pubscent female Macaca does not result in immediate gonadotropin increases as it does in

adult females (Dierschke, et al., 1974a). According to this view, changes in the hypothalamus, and possibly other areas of the CNS, which result in a regular, pulsatile release of GRH to the pituitary are the pivotal events in the initiation of maturation. An experimental demonstration of this view is seen in the fact that pre-pubescent female Macaca may be induced to mature, simply by exogenous, regular administration of GRH (Wildt, et al., 1980). These different mechanisms may, again, express taxonomic differences (Dierschke, et al., 1974a). The negative feedback system appears to become effective some time before the positive feedback effects of estrogen are established (Dierschke, et al., 1974a). Therefore, the pubescent female will frequently not ovulate. When the positive feedback effect of high estrogen levels is established, the female will then ovulate and experience the complete estrous cycle, including corpus luteum formation and subsequent rises in progesterone levels (Richards, 1980).

Measuring Sexual Maturation

Clearly, puberty in a female mammal is an extended and complex process which initiates various changes in the female's physiology, morphology and behavior. Measurement of these various changes will provide different levels of information about the female's stage of maturation.

Examination of the ovary, through histology (Dierschke, et al., 1974a; Feder, 1981; Mossman and Duke, 1973) or laparoscopy (Dukelow, et al., 1971; Dukelow, 1975) may reveal ovulation sites or corpora lutea. Examination of the ovary, then provides direct evidence of

ovarian function.

Measurement of the levels of pituitary and ovarian hormones, or their metabolites, in blood or urine may also provide information concerning state of maturation. The use of such endocrine measures has become increasingly common with the development of extremely sensitive assay methods, such as radioimmunoassay (Abraham, et al., 1971; Butcher, et al., 1974; Monroe, et al., 1970; Yalow and Berson, 1971; Yamaji, et al., 1973) and competitive protein binding assay (Butcher, et al., 1974; Preslock, et al., 1973). Increases in LH, FSH and estrogen levels are interpreted as indicating the initiation of puberty, when the hypothalamic-pituitary-gonadal negative feedback system is beginning to operate as it does in a mature female (Dierschke, et al., 1974b; Grumbach, 1974). A surge in the LH level and a subsequent rise in progesterone level are interpreted as indicating the completed maturation of the positive feedback system, with ovulation and subsequent corpus luteum formation (Abbott, 1978a, 1978b; Abbott and Hearn, 1978; Dierschke, et al., 1974b; Grumbach, 1974).

The changes in ovarian hormone levels which are initiated at puberty result in a wide variety of morphological changes. One effect of fluctuating estrogen levels is cyclical changes in the exfoliated cells of the vagina. An increasing estrogen level, such as that occurring during the follicular phase of the estrous cycle, results in growth and cornification of the vaginal epithelium, which can be observed and quantified with properly stained vaginal smears (Naib, 1970; Turner and Bagnara, 1971). Vaginal smears have been used successfully to determine estrous cycle stage (Turner and Bagnara,

1971) and to document sexual maturation (Ramirez and Sawyer, 1965) in rodents, but results of vaginal smears in primates have been highly variable (Hearn and Lunn, 1975; Lang, 1967; Rosenblum and Cooper, 1968; Wan and Balin, 1969).

The development of a variety of morphological characteristics in female mammals may be initiated by the rises in ovarian steroid levels that begin at puberty (Goldman, 1981). These characteristics are frequently used as indicators of sexual maturation. In rodents, vaginal introitus and pelage changes are sometimes used as indicators of puberty (Rogers and Beauchamp, 1974). Mature females of many primate species exhibit swelling and color changes of the perineal skin at estrus (Alvarez, 1973; Rowell, 1970) and the onset of these swellings, combined with onset of menstruation, is used as an indicator of a female's first estrus (Rowell, 1977; Wolfe, 1978). While most studies in which perineal swelling has been used as an indicator of reproductive state have been conducted on Old World primates, at least one New World primate, the howler monkey (Alouatta), also exhibits cyclical perineal swelling (Glander, 1980).

The relationship of these morphological, histological and hormonal measurements to the age at which a female is actually able to reproduce is variable. In any mammalian species, changes which are indicative of rising estrogen titers, only, may indicate that a female had entered puberty but is not ovulating and is still unable to reproduce. The length of time between the point at which a female enters puberty and that at which she is regularly ovulating is variable, both within and between species (Dierschke, et al., 1974b; Rowell, 1977).

Certain measures indicate that a female is ovulating, e.g. those indicating cyclical rises in progesterone levels. However, young ovulating females frequently have insufficient luteal phases and would be incapable of successfully reproducing (Vihko and Apter, 1981). There may also be various behavioral inhibitions to reproduction. These are discussed in a later section.

As a final measure of sexual maturation, age at first parturition or first conception is sometimes used (Drickamer, 1974; Epple and Katz, 1980; Wilson and Gordon, 1980).

Sexual Maturation-Behavioral Events

Along with the various physiological and morphological changes already described, the pubescent female mammal may also experience behavioral changes. The specific behavioral changes that a given female will display obviously vary across different taxonomic groups. The changes will also vary within a species, according to a female's prior experience and the sex, age, and experience of others in her social group. As described previously, callitrichids appear to have a monogamous family social structure. Therefore, this review of the behavioral effects of female sexual maturation will concentrate on some of those interactions which a young female might be expected to experience within a species displaying such a social structure: interactions with a mate and interactions with parents.

Interactions with a Mate. Sexual interactions might reasonably be expected to be affected by the hormonal changes of puberty. The most extensive evidence concerning the effect of ovarian steriods on sexual behavior involve the study of adult sexual behavior. Most female

mammals that have been studied display some qualitative or quantitative cyclicity of sexual behavior, relative to the estrous cycle (Feder, 1981; Leshner, 1978; Luttge, 1971; Nadler, 1975; Rowell, 1972; Scruton and Herbert, 1970). In general, primates display a much less distinct behavioral estrus than other mammals (Leshner, 1978) but there is much variability within primates (Michael and Welegalla, 1968; Nadler, 1975; Rowell, 1972). Within callitrichids, Hearn and Lunn (1975) report no quantitative or qualitative changes in sexual behavior throughout the estrous cycle in Callithrix jacchus while Kleiman (1978) reports cyclicity in the frequency of sexual behavior in Leontopithecus rosalia.

In addition to realizing the correlation between estrous cycle stage and occurrence of sexual behavior, may workers have discovered effects of ovarian steroid manipulations on sexual behavior. Generally, the removal of estrogens, usually through ovariectomy, reduces or eliminates female sexual behavior while the administration of exogenous estrogen re-establishes sexual behavior (Arai and Gorski, 1968; Ball, 1936; Davidson, et al., 1968; Dixson, et al., 1973; Goldfoot, 1977; Luttge, 1971; Luttge, et al., 1975). Again, it has been demonstrated that sexual behavior is less affected by hormonal state in primates than in most other mammals. In some rodent species, the administration of progesterone may facilitate or inhibit sexual response, depending upon the relationship between progesterone and estrogen administration (Powers, 1970; Wallen, et al., 1975). However, in primates, progesterone administration appears to have a general inhibitory effect on sexual response (Michael, 1968; Michael and Zumpe, 1970).

The evidence, then, points to a relationship between the levels of ovarian steroids and female sexual response. Unfortunately, there is very little available in the way of direct evidence of the relationsip between changes in ovarian steroids at puberty and sexual response. In many primate species, adult sexual behaviors, such as presenting and mounting, are displayed by infants and juveniles, though frequently in an incomplete form (Goldfoot, 1977). Therefore, an adult hormonal state does not appear to be necessary for the display of some sexual behaviors. However, the frequency of occurrence of certain sexual behaviors, as well as the form in which they occur, appear to change as the female matures. In studies of macaques, it has been found that young females become both more sexually responsive and more attractive to males as they mature (Hanby and Brown, 1974; Wolfe, 1978). Obviously as a female grows older, many factors may contribute to changes in behavior. As the changes in hormonal state of the females in the studies cited above were neither directly assayed or manipulated, the results do not actually provide direct evidence of a link between the hormonal changes of puberty and sexual response.

Interactions with Parents. In captivity, callitrichids are most successfully housed and reared in a family social structure. This social structure is similar to that which is known to occur naturally in a number of diverse mammalian species, such as wolves, as well as some other canids, beavers, certain mongoose species, gibbons, and siamangs (Kleiman, 1977). This review of the relationship of female maturation to interactions with family members will be taken from the literature on callitrichids and those species with similar social

structure.

Females in monogamous species generally mature at a later age than polygamous females in closely related species (Kleiman, 1977). Up to the age of sexual maturation, relations between young females and parents are generally close and harmonious. When females begin to mature sexually a variety of changes are reported to occur in the various monogamous species, but they all tend to be changes leading to increased aggression toward or exclusion of the young female. In wolves and mongooses, daughters may remain in a social group with their parents well past the age of sexual maturation, but their interactions with one or both parents will be more agonistic, with the parent(s) dominating the daughter. These agonistic interactions will be particularly prevalent during the breeding season (Fox, 1975; Mech, 1970; Rasa, 1972, 1973; Zimen, 1975).

The social organization in wolves has been particularly well studied. In wolves, a sexually mature daughter (as judged by behavior and vaginal bleeding) will be subordinate to her mother, and possibly other female group members (Mech, 1970; Zimen, 1975). Her mother will attempt to keep her from mating by aggressive intervention (Mech, 1970; Zimen, 1975).

Less information is available on the monogamous mongooses. Rasa (1972) reports that in a captive family group of the dwarf mongoose, sexually mature daughters are subordinate to both the mother and the father. During the breeding season, it is the father who aggressively intervenes to prevent mating attempts between the daughter and her brothers (Rasa, 1973). Rood (1980) reports that, in feral groups containing more than one adult female, pregnancies of subordinate

females do occur, but are rarely successful.

While little information is available on hylobatids, Fox (1972) reported that, in a captive group of siamangs, a daughter who was past the age of sexual maturity held a peripheral position in the group. Her invitations to be groomed were always ignored, though she was the most frequent groomer. She was prevented from feeding with the rest of the group by aggression from her father. Her mother also displayed aggression to her on occassion.

While much of this information is anecdotal and very little is known about some of the species, these reports generally indicate increased aggression to and peripheralization of young, sexually mature females, with either the father or the mother displaying aggression toward the daughter. In wolves and mongooses, this aggression seemed to peak when the females of the group were in estrus.

In callitrichids, reports of the interactions of daughters with parents indicate a wide variety of responses. Rothe (1975) reports, that in Callithrix jacchus, daughters are left with their parents well past the age of sexual maturation with no increases in agonistic interactions. Rothe (1978) also finds that older daughters tend to have the fewest social contacts with the parents. Other reports on various species indicate that agonistic interactions between mother and daughter increase as the daughter matures. Snyder (1972) observed the formation of dominance hierarchies between Leontopithecus rosalia mothers and adult daughters with mother being dominant. Removal of young from their parents at around a year of age has been recommended for some species, as keeping them together longer resulted in fighting

between the offspring and the same-sexed parent (Lorenz, 1972, Callimico goeldi; Mallinson, 1975, various Callithrix and Saguinus species). Kleiman (1979) reports infrequent, but quite severe, outbreaks of aggression between L. rosalia mothers and daughters.

The relationship between these increases in aggression and the daughter's sexual maturation is unclear. The daughters in the reports cited were older than the reported age of sexual maturation. However, as the daughters did not reproduce and showed no external signs of estrus, the actual reproductive state of the females in most of these studies is not known. There is some question as to whether they were sexually mature, despite their advanced ages (see Social Influences on Sexual Maturation).

Marking Behavior. Another type of social communication which might be affected by sexual maturation is marking behavior. Callitrichids possess highly developed sebaceous scent glands, which are used in marking objects and occassionally other animals (Epple, 1967; Hershkovitz, 1977). Glands are concentrated in the anogenital and sternal areas. A number of functions are attributed to this marking, including sexual signalling (Epple, 1967; French and Snowdon, in press), delineation of territory (Epple, 1967, 1970b; French and Snowdon, in press) and expression of frustration or excitement (Epple, 1967; Kleiman and Mack, 1980). Expression of at least the first two of these functions might be expected to be affected by reproductive state. As mentioned previously, reports vary regarding whether or not callitrichids display a behavioral estrus. There is also conflicting evidence as to the role of marking in sexual communication. French and Snowdon (in press) found, in Saguinus oedipus, that the females

anogenital marking increases during estrus while Kleiman (1978) reports, in Leontopithecus rosalia marking decreases during estrus. There is no direct information available on the relationship between the hormonal changes of puberty and marking behavior. Both males and females begin to display anogenital marking at a very early age, well before sexual maturation (Epple, 1967, various Callithrix and Saguinus species; Kleiman and Mack, 1980, L. rosalia). However, young females generally mark much less often than their mothers (Epple, 1967; Kleiman and Mack, 1980).

There is more general agreement that sternal marking serves a territorial function (French and Snowdon, in press, S. oedipus). Kleiman and Mack (1980) found that daughters generally did not display sternal marking while still in their family groups, no matter what their age. However, these females would sternal mark when removed from their family groups or if the mother became very ill.

Social Influences on Sexual Maturation

As outlined in the previous section, a female's reproductive state may affect her social interactions. Conversely, the type of social influences to which a young female is exposed may also affect the rate of her sexual maturation.

The fact that social influences may affect a female's reproductive state has been amply illustrated in both natural and laboratory populations of rodents. The observation has been made that, in some rodent species, when densities become very high, reproduction is curtailed (Christian, 1965, 1978; Crowcroft and Rowe, 1957; Louch, 1956; Terman, 1965). This curtailment of reproduction is the result

of both reproductive inhibition of mature females and inhibition of sexual maturation in young females (Christian, 1978). Christian (1965, 1978) has hypothesized that this inhibition is the result of the activiation of the pituitary-adrenocortical axis brought about by exposure to the stressful situation of crowding. Increased levels of corticosteroids have been demonstrated to bring about reproductive inhibition (Jarret, 1965; Hagino, et al., 1969; Smith, et al., 1971), but there have been a number of studies indicating that increased adrenal activity is not necessarily linked with reproductive inhibition in dense populations (Brain and Nowell, 1971; Bronson and Chapman, 1968; Pasley and McKinney, 1973; Sung, et al., 1977).

Reproductive state and maturation rate in female rodents may be altered by certain types of olfactory communication. Exposure to primer pheromones, present in mouse urine, may cause neuroendocrine changes in a female, resulting in changes in reproductive physiology (Leshner, 1978). When adult female mice are exposed to all-female groups or urine from such groups, their estrus is suppressed. This suppression usually takes the form of prolonged anestrus or pseudopregnancy (Rogers and Beauchamp, 1976). Cowley and Wise (1972) found that the effect of exposure to grouped-female urine on prepubertal females was dependent upon the reproductive state of the grouped females. Urine from virgin females delayed first vaginal introitus of young females but urine from pregnant females had either no effect or brought about an earlier vaginal introitus. It is unclear as to whether this phenomenon may play a role in natural populations with high density, in which reproduction is inhibited (Rogers and Beauchamp, 1976).

Exposure to male mouse urine also influences female reproductive state. Prepubertal female mice will display estrous cyclicity at an earlier age when exposed to males or male urine (Kennedy and Brown, 1970; Vandenbergh, 1967, 1969). Early exposure to adult male urine appears to initiate increases in LH levels in the prepubertal female, which, in a matter of days, lead to adult pituitary-ovarian function (Bronson and Desjardins, 1974). Pheromones in male urine also have the effect of synchronizing estrus in groups of adult females exposed to it (Bronson and Whitten, 1978).

Social interactions have been demonstrated to affect reproductive state in female primates, also. Generally, subordinate females are found to be reproductively inhibited. Rowell (1970) found that exposure to frequent aggressive attacks from other females or movement out of an established social group resulted in a longer swelling phase during the menstrual cycle of baboons. Exposure to males did not alter the cycle. Dunbar and Dunbar (1977) found that dominant gelada baboon females more frequently harassed subordinate females when the subordinate females were in estrus and subordinates produced significantly fewer offspring. They hypothesized that harassment during estrus causes an anovulatory cycle or spontaneous abortion. Subordinate talapoin monkeys did not respond to exogenous estradiol implants with an LH surge, as would be expected of normal, reproductive females (Bowman, et al., 1978). When the subordinate females were removed from the group, they would display an LH surge in response to estradiol. As cited previously, it has frequently been reported that in callitrichid groups, only one female reproduces. Abbott and Hearn (1978) and Abbott, et al., (1981) found that, in

Callithrix jacchus, subordinate females never ovulated, had a reduced LH response to LH-RH, and showed no LH surge after administration of exogenous estrogen. These females became fully reproductive when removed from the presence of the dominant female.

Similarly detailed information on the effects of social influences on maturation rates in young female primates is not available. However, Drickamer (1974) does report that daughters of dominant female rhesus monkeys produce their first young at an earlier age than daughters of low-ranking females.

The late maturation of females in monogamous species (Kleiman, 1977) may be the result of social influences. There is anecdotal evidence available from studies of wolves and callitrichids indicating that daughters in these species may in some way be reproductively suppressed by their mothers. Wolves generally reach sexual maturity at around two years of age (Mech, 1970; Seal, et al., 1979). Seal, et al. (1979) report that the dominant of a litter of three female pups came into estrus at a year of age, just before the death of her mother, the alpha-female. The subordinate pups in the group did not mature.

Young female golden-lion tamarins (Leontopithecus rosalia) are reported to be non-reproductive while housed with their parents. They are also known to be inhibited from displaying certain adult behavior patterns, such as sternal marking and arch-walking (Kleiman and Mack, 1980; Rathbun, 1979). However, a ten-month old female, remaining with her natal group after her mother's death, displayed both sternal marking and arch-walking. Unfortunately, no data are available concerning the reproductive state of this female, so that it is

impossible to determine whether this change in behavior was related to sexual maturation.

There have been relatively few studies of callitrichids in which the reproductive state of daughters housed with their parents has been quantified and the available results are conflicting. Katz and Epple (1979) report that young saddle-backed tamarin (Saguinus fuscicollis) females do not display cyclic levels of urinary estrogens when housed with their parents. However, Abbott and Hearn (personal communication) report that young common marmoset (Callithrix jacchus) females housed with their parents do cycle. With so little information available, it is difficult to discern whether these results reflect a true taxonomic difference. Also unknown is the manner in which young callitrichid females might be reproductively inhibited. While pheromones in callitrichid scent marks which would affect female reproductive state have been hypothesized (Abbott, et al., 1981) there is not evidence available to support or dispute this theory.

CHAPTER 2

COMPARISON OF MATURATION AGE OF FEMALES WITH MALES AND FEMALES IN NATAL GROUPS

It is hypothesized that young females housed with males will mature at a significantly earlier age than females housed in their natal groups.

Methods

Subjects. The subjects of this study were twelve, laboratory-born Saguinus oedipus females. The social grouping in which each subject was housed is shown in Table 1.

Two basic social groups were studied. Seven of the females were removed from their natal group and placed with a strange, imported adult male. The other five females remained with their natal groups. Figure 1 provides the ages through which each female was examined. Females who were removed from their natal groups were placed with adult males on the first day they were examined. In the absence of quantitative data on maturation age for S. oedipus, females were paired with males in a relatively wide age range. Based upon the maturation age of 400 days reported by Abbott and Hearn (1978) for Callithrix jacchus and the early results of the present study, the ages chosen for pairing females with males ranged from 294-469 days of

TABLE 1. A description of the social groupings in which the subjects were housed. Infant < 5 months; Juvenile > 5 months but < 24 months; Adult > 24 months.

Subject's Colony ID	Group ID	Individuals housed with Subject: Age/Sex	Relation to Subject
4218	P1	Adult Male	Unrelated
4204	P2	Adult Male	Unrelated
4267	P3	Adult Male	Unrelated
4213	P4	Adult Male	Unrelated
4302	P5	Adult Male	Unrelated
4347	P6	Adult Male	Unrelated
4356	P7	Adult Male	Unrelated
4054	F1	Adult Female	Mother
		Adult Male	Unrelated
		*1, Juvenile-Adult Male	Twin Brother
		1, Infant-Juvenile Male	Younger Brother
		1, Infant-Juvenile Female	Younger Sister
4238	F2	Adult Female	Mother
		Adult Male	Father
		1, Infant-Juvenile Female	Younger Sister
4296	F3	Adult Female	Mother
		**Adult Male	Father
		1, Juvenile Female	Younger Sister
		2, Infant-Juvenile Males	Younger Brothers
4334	F4	Adult Female	Mother
		Adult Male	Unrelated
		1, Juvenile Male	Twin Brother
4349	F5	***Adult Female	Mother
		Adult Male	Father
		1, Juvenile Male	Twin Brother
		2, Infant-Juvenile Males	Younger Brothers

* designates that individual fell into both age categories during course of study
** died when 4296 was 541 days of age
*** died when 4349 was 479 days of age

age.

The mated pairs (P1-P7) were housed in hardware cloth cages, 91x91x122 cm. Females and their natal groups (F1-F5) were housed in cages consisting of two units, of the previously cited dimensions, connected by a doorway. All cages contained a metal nest box and

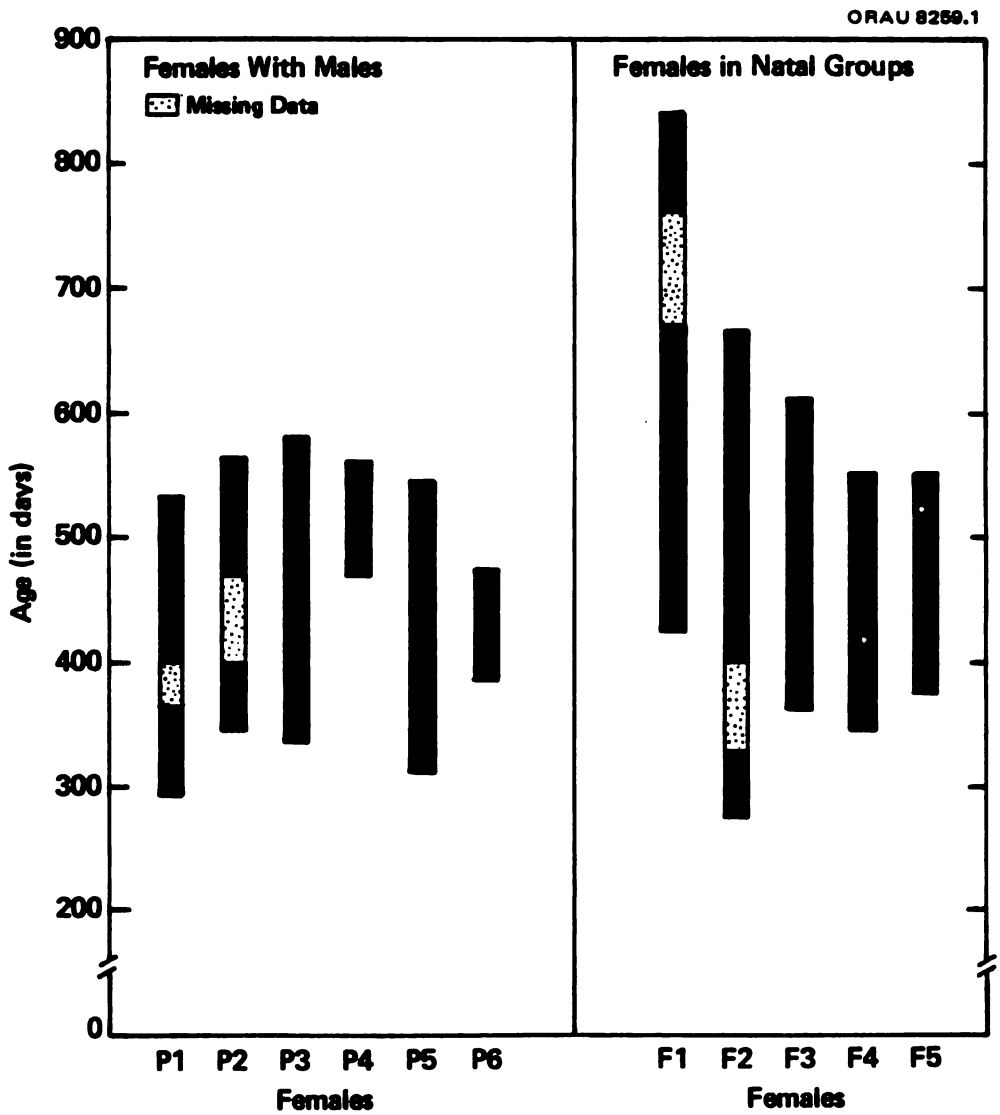


Figure 1. Ages through which each female was examined.

wooden perches. All groups were visually isolated from each other by metal or cardboard partitions. The temperature in the rooms containing the cages was approximately 23^0C and there was a 10:14 light-dark cycle. Each room received some natural lighting through a small window in the door. Each group was fed twice daily. The diet consisted of high protein monkey feed, canned diet, fresh fruit and vegetables, mealworms, live newborn mice, and supplemental vitamins.

Determination of Sexual Maturation. As stated previously, callitrichid females appear to show no reliable external signs of sexual maturation. There is no perineal swelling associated with estrus and no menstruation. In addition, Hearn, et al. (1975) report that there are no reliable, cyclical changes in vaginal cytology in mature C. jacchus females. In the absence of these physiological events that can be used for assessing maturation state, changes in plasma progesterone levels was chosen as the criterion of maturation.

Each of the twelve females was bled twice weekly during the course of the study. In addition, non-pregnant mothers and mothers in the early stages of pregnancy in the five natal groups were also bled. Individuals were caught in a net, in which they were weighed. The animal's legs were then strapped down to a Plexiglass board while the upper part of the body was held by a caretaker. A volume of 1.0 to 1.1ml of blood was taken from the femoral vein in a syringe containing 0.1ml of heparin. After the blood was taken, the animal was given orally 1ml of Incremin, an iron supplement. The tamarins were clearly stressed by the netting and by being held, but they reacted very positively to receiving the Incremin and most grew calmer over time. The blood was placed in a small culture tube and centrifuged at 1800xg

for 15 min. The plasma was removed and stored at -70°C until assayed.

Progesterone Radioimmunoassay. Radioimmunoassay is a procedure in which radioactively labeled antigen (in this case ^{3}H-progesterone) and unlabeled antigen (unlabeled progesterone) compete for a fixed number of antibody sites. The amount of radioactive antigen which binds to the antibody will be dependent upon the amount of competing, unlabeled antigen. When known amounts of unlabeled antigen are used, this relationship may be quantified and applied to determining the amount of unlabeled antigen present in an unknown.

The radioimmunoassay procedure used here followed the methods provided by New England Nuclear Co. (Progesterone [^{3}H] Radioimmunoassay Pak instruction manual). Modifications of the general procedure were taken from Johnston and Mather (1978) and Gibori, et al. (1977). Progesterone [1,2-^{3}H(N)] (280-420 DPM/pg) in benzene and progesterone stock solution (200ng/ml) in phosphate-buffered saline (PBS) were purchased from New England Nuclear Co. Anti-progesterone-11-BSA serum (from sheep #337) was supplied by Dr. Gordon Niswender, Colorado State University.

Prior to assay, the plasma samples were extracted with petroleum ether in order to remove potential cross-reactive corticosteroids. Due to the high specificity of the antiserum no further processing of the plasma was necessary (see Gibori, et al., 1977, for cross-reactivities of the antiserum). A volume of 0.1ml of plasma was placed in a conical glass centrifuge tube along with 0.1ml of ^{3}H-progesterone in PBS (activity: 3000 DPM/0.1 ml). This radioactive progesterone was added to allow for determination of percent progesterone recovered after extraction. All samples were extracted

twice, with an extraction consisting of the addition of 2 ml petroleum ether followed by mixing or shaking for 30-60 sec, centrifuging for 5 min at 1600xg and decanting the ether into a borosilicate culture tube. The ether was then evaporated under a stream of air. After drying, the extract was redissolved in 1ml of PBS. A volume of 0.25ml of this solution was transferred to a scintillation vial containing 10ml of scintillation solution for determination of the percent progesterone recovered after extraction.

All assay procedures were conducted with materials either on ice or refrigerated at 4°C. Two volumes (0.1 and 0.2ml) of the redissolved extracts were assayed. In addition to the extracted samples, a range of known concentrations (2.0ng/0.1ml to 0.0ng/0.1ml) of a standard progesterone solution were assayed. After the addition of the samples and standards to 10x75 mm borosilicate tubes, the volume was adjusted to 0.2ml in all tubes by the addition of the necessary volume of PBS. A volume of 0.1ml of ^{3}H-progesterone (activity: 16700 DPM/0.1 ml) and 0.1 ml of the antiserum (diluted to approximately 35% blank binding) was added to each tube. All samples at both volumes and all standards were assayed in duplicate. In addition to these, a set of duplicate tubes containing 0.1ml ^{3}H-progesterone and 0.3ml PBS (i.e. no antiserum) was prepared for the determination of non-specific binding.

All tubes were vortexed briefly, then allowed to incubate overnight. After incubation, 1ml of a 0.25% Dextran-coated charcoal suspension was added to each tube. Each tube was then vortexed briefly, allowed to incubate for 5 min, then centrifuged at 1800xg for 15 min at 4°C. During the incubation period, the unbound progesterone

is adsorbed onto the charcoal which is spun down to form a discrete pellet. After centrifugation, the supernatant was decanted into 20ml vials containing 10ml of scintillation solution. The vials were shaken then allowed to sit for approximately three hours. These vials and those used to determine percent-recovery were each counted for 5 min under conditions optimal for tritium in a Beckman LS-3100 Series liquid scintillation counting spectrometer.

Results were in the form of counts per minute (cpm). The cpm from each pair of duplicates were averaged and the average cpm of the non-specific binding tubes were subtracted from each sample average to produce a corrected, average cpm (here termed mean cpm) for each sample at each volume and each standard concentration. A standard linear curve was then computed by use of the results from the standard concentrations in the following formulae:

logit Y= a + blogX

where, logit Y= $\log_e[Y/(100-Y)]$

Y= 100(mean cpm at X/mean cpm at 0.0)

X= concentration in ng

The computations were performed using O.R.A.U. computer programs CPM and LOGIT.

Assay Validation. A total of 36 assays were performed, with a total of 692 samples assayed. The mean slope (with standard error) of the standard curves in these assays was -2.61 ± 0.02 and the coefficient of correlation was always greater than 0.99. The lowest detectable level was 0.4ng/0.1ml (4.0ng/1.0ml). Percentage recovery ranged from 52% to 98% with most samples in the 70-80% range. In addition to the plasma samples from the study subjects, each assay

included the extraction and assay of one water sample and two plasma samples from each of two plasma pools, consisting of plasma taken from female S. oedipus outside the study (Pool #1) and female Callithrix jacchus (Pool #2). The mean cpm of the water sample was always greater than 90% of the mean cpm of the Control standard. The pool samples were used to determine the intra- and inter-assay variability. The results are described in Table 2. Coefficients of variation were determined using the methods described by Rodbard (1971). The effect of volume on assay results was analyzed, using the 0.1 and 0.2ml aliquots from the plasma pools. The results, given in Table 2, indicate no substantial effect of volume on assay results.

Table 2. Assay validation.

			Within-assay:		Between-assay:	
Pool#	n	$\bar{x}$(ng/.1ml)	s	c.v.(%)	s	c.v.(%)
1	36	3.7	0.34	9.1	0.57	15.5
2	35	9.4	0.71	7.5	1.50	16.4

Pool#	n	volume assayed	$\bar{x}$(ng/.1ml)	s
1	72	0.1 ml	3.8	0.25
1	72	0.2	3.6	0.23
2	69	0.1	9.6	1.60
2	69	0.2	9.1	1.80

Analyses. The pattern of plasma progesterone changes over time in young females will be fully described in the Results. Young, maturing females displayed a variety of patterns including low, fluctuating levels and clear spikes, indicative of a normal ovulatory cycle. These various patterns of plasma progesterone changes are similar to

those reported for Callithrix jacchus (Abbott, 1978; Abbott and Hearn, 1978) and for young, human females (Apter and Vihko, 1977; Apter, et al., 1978). In the present study, no female less than 357 days ever displayed detectable levels of progesterone.

In consideration of these results, the following operational definitions were employed:

Sexually immature- plasma progesterone levels consistently undetectable (i.e. less than 0.4ng/0.1ml).

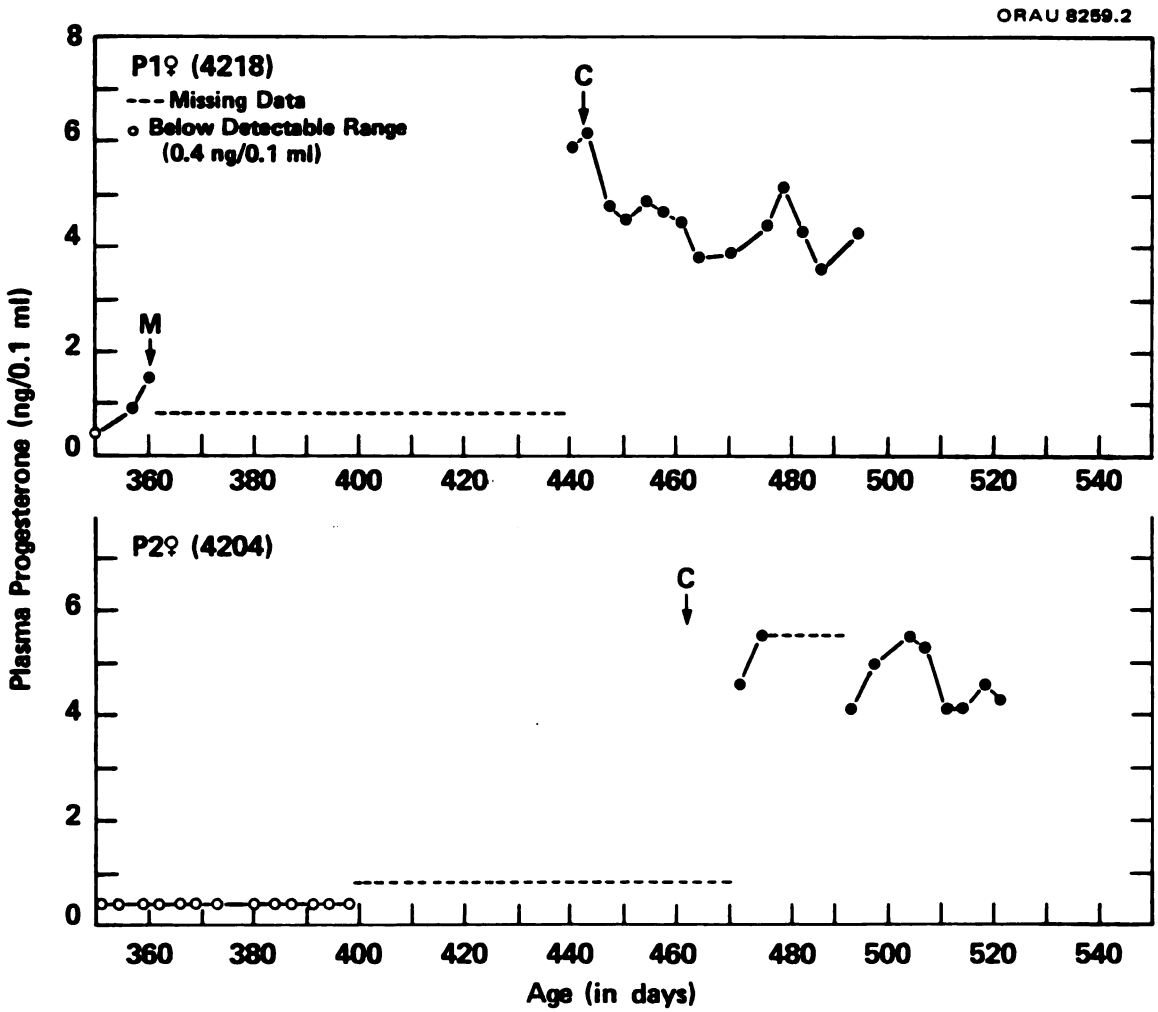
Sexually mature- plasma progesterone levels consistently in the detectable range; this includes low, fluctuating levels as well as clear ovulatory spikes.

The number of females in each maturation state (immature and mature) at 550 days of age in each of the two social groupings (females with males and females in natal groups) were compared, using a Chi-square test. In addition, the mean age at which females were defined as sexually mature was compared between females with males and females in natal groups, using a t-test.

Results

Females Housed with Adult Males. Figure 2 illustrates the changes in plasma progesterone levels across time for the seven females who were each housed with a strange adult male. The graphs indicate progesterone levels for each female from 350 to 550 days of age. Though some were sampled at earlier and later ages, these results are sufficient for illustrating the changes associated with maturation in each female. All females displayed consistently detectable progesterone levels at some point between 360 and 495 days of age.

Figure 2. Plasma progesterone levels of females housed with males.


ORAU 8259.2
P1♀ (4218)
--- Missing Data
o Below Detectable Range
(0.4 ng/0.1 ml)
C
M
P2♀ (4204)
C
Plasma Progesterone (ng/0.1 ml)
0
2
4
6
8
360
380
400
420
440
460
480
500
520
540
Age (in days)

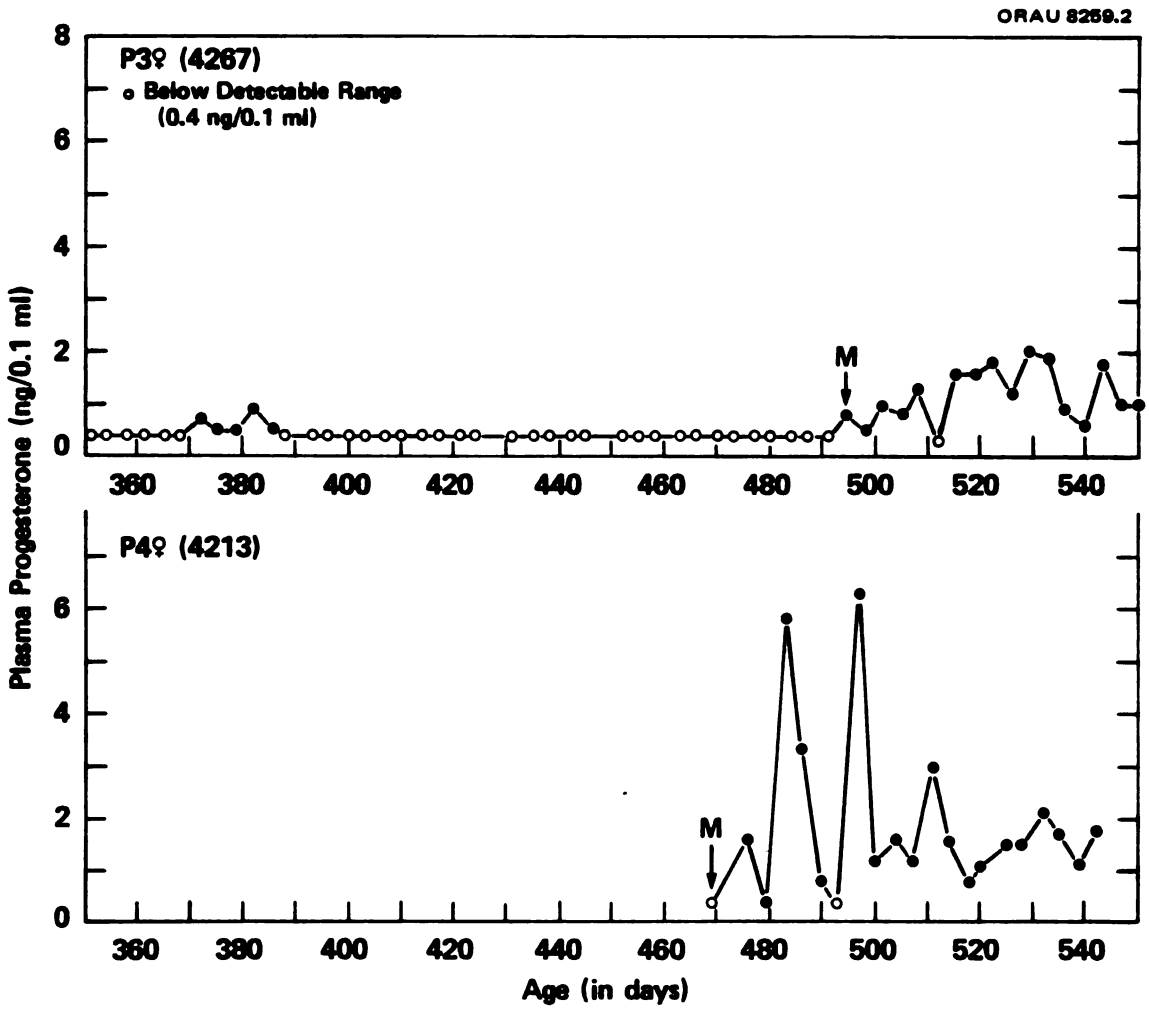


Figure 2. (cont'd.)

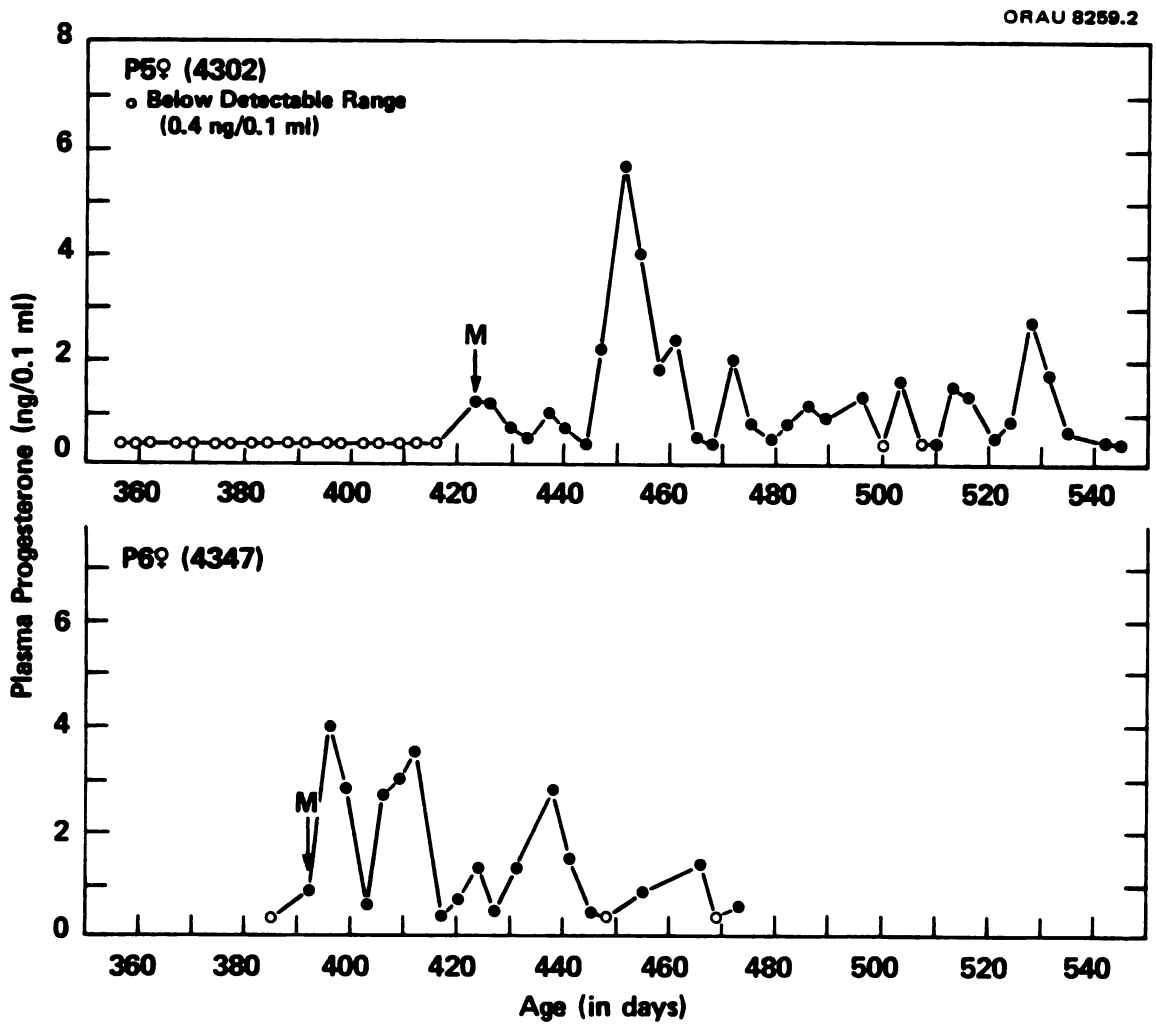


Figure 2. (cont'd.)

There was a great deal of variability between females in the age at which detectable levels were initiated and the pattern of plasma progesterone changes.

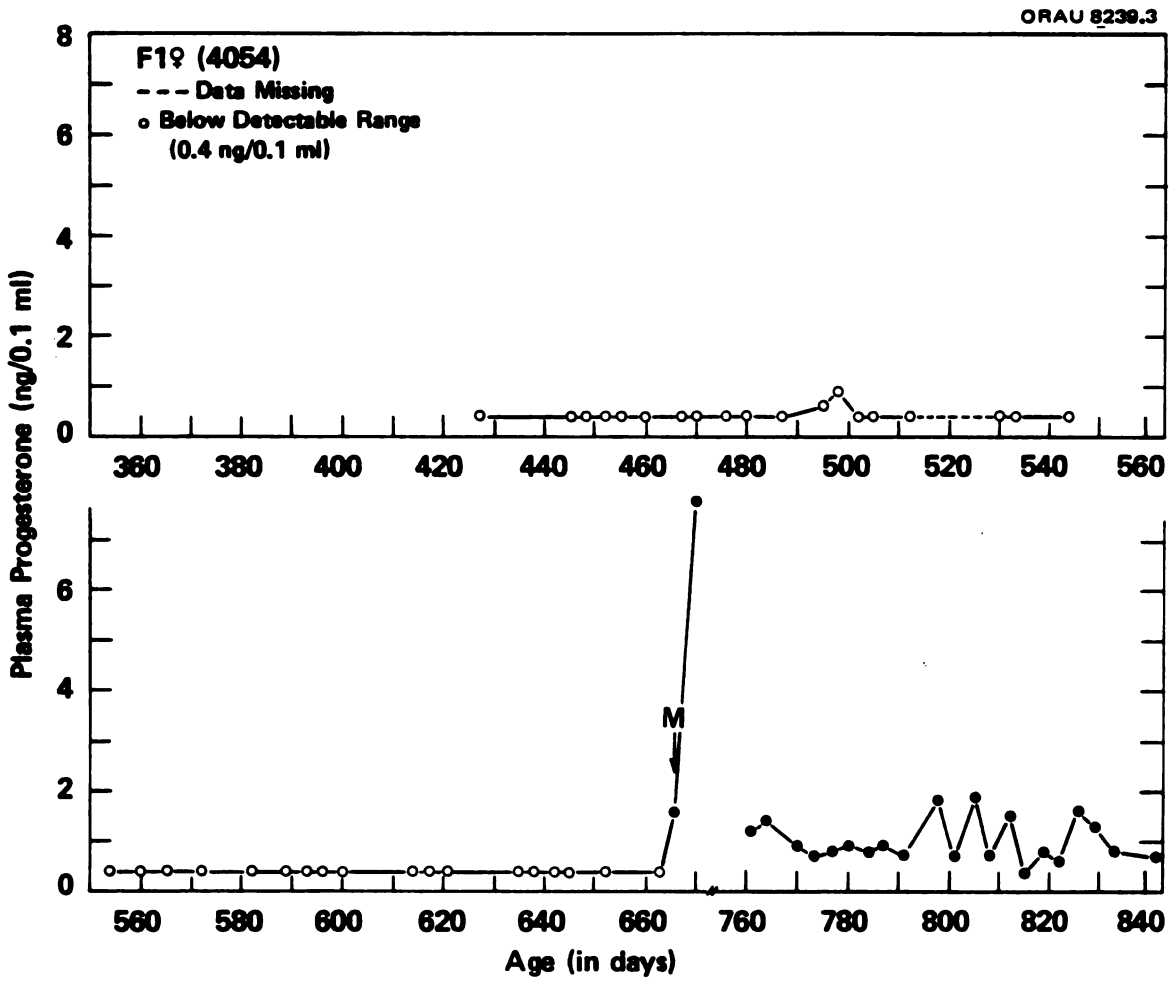
In samples from P1-female, there was a low rise in progesterone at 360 days. Sampling from this female ceased at 364 days and was resumed again at 440 days. After 440 days, P1-female displayed consistently high levels, indicative of pregnancy. Progesterone levels in P2-female were undetectable up to 398 days when sampling ceased. When sampling was resumed at 472 days, P2-female displayed consistently high levels, indicative of pregnancy. P3-female displayed undetectable progesterone levels up to 494 days, when levels rose into the detectable range. The levels then fluctuated below 2.0ng/.1ml until 582 days when sampling ceased. P4-female began displaying high progesterone levels, indicative of ovulation (ovulatory spikes) immediately upon being placed with a strange male at 469 days. Because this female was not paired with a male until well past the earliest maturation ages seen in other females, these results will be omitted from the determination of mean age of maturation of females housed with males. P5-female displayed undetectable progesterone levels up to 423 days, at which point the levels fluctuated below 2.0ng/.1ml. At 451 days, P5-female displayed an ovulatory spike, with a peak progesterone level of 6.0ng/.1ml, after which levels dropped again, fluctuating below 2.0ng/.1ml. P6-female began displaying clear ovulatory spikes, with peak progesterone values of 3.5-4.0ng/.1ml at 392 days. P6-female was paired with a strange adult male sometime between 379-382 days and sampling began at 385 days. It is impossible to determine her

reproductive state from 379-385 days. P7-female was paired with a male at 399 days but sampling could not begin until 421 days. This female displayed consistently undetectable levels to 463 days of age. Levels were low and fluctuating to 491 days at which point levels again dropped into the undetectable range and remained undetectable until sampling ceased at 521 days. Because determination of the age of maturation of this female is impossible from these results, she will be omitted from further consideration.

Females Housed in Natal Groups. Figure 3 illustrates the changes in plasma progesterone levels across time for the five females housed in their natal groups. In some females, the first samples assayed were when the subject was older than 350 days even though samples had been collected at ages beginning well before 350 days. Samples were taken and assayed from all females up to 550 days of age, past the latest maturation age of a female with a male. Four females (F1,F2,F4,F5) displayed consistently undetectable levels of progesterone up to 550 days. One female (F3) displayed an ovulatory spike of 3.0ng/.1ml at 487 days followed by low, fluctuating levels, interspersed with more spikes up to 609 days, when sampling ceased.

Two females (F1,F2) who were still immature at 550 days were sampled past 550 days. F1-female displayed undetectable levels up to 666 days, at which point levels rose to 7.9ng/.1ml by 670 days. Sampling ceased at 670 days and was resumed at 760 days, at which point this female displayed low, fluctuating levels. Sampling again ceased at 840 days. F2-female displayed low, fluctuating levels at 450-475 and 540-550 days, however these detectable levels were not taken as an indication of maturation because they were interspersed

Figure 3. Plasma progesterone levels of females in natal groups.


ORAU 8239.3
F1♀ (4054)
--- Data Missing
o Below Detectable Range
(0.4 ng/0.1 ml)
Plasma Progesterone (ng/0.1 ml)
0
2
4
6
8
360
380
400
420
440
460
480
500
520
540
560
M
560
580
600
620
640
660
760
780
800
820
840
Age (in days)

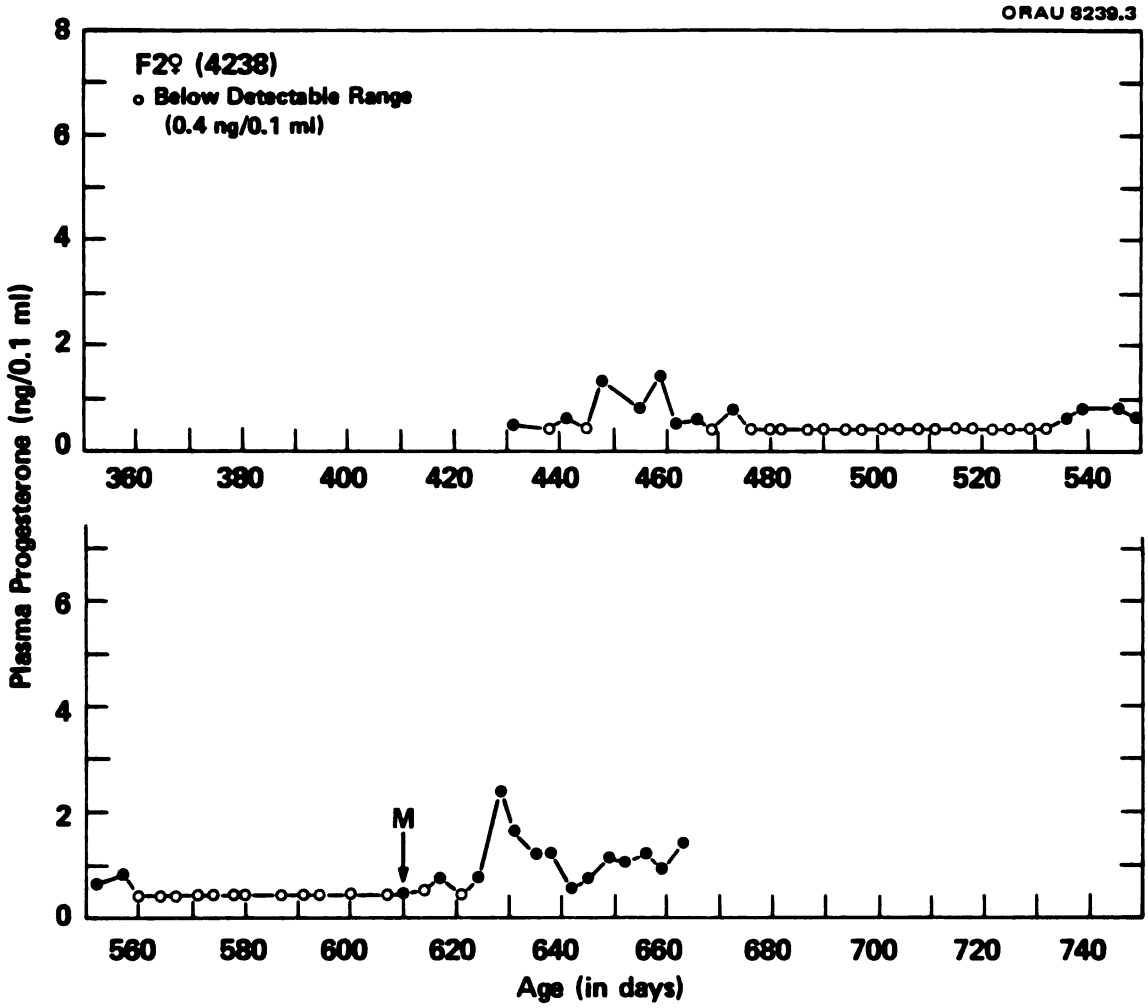


Figure 3. (cont'd.)

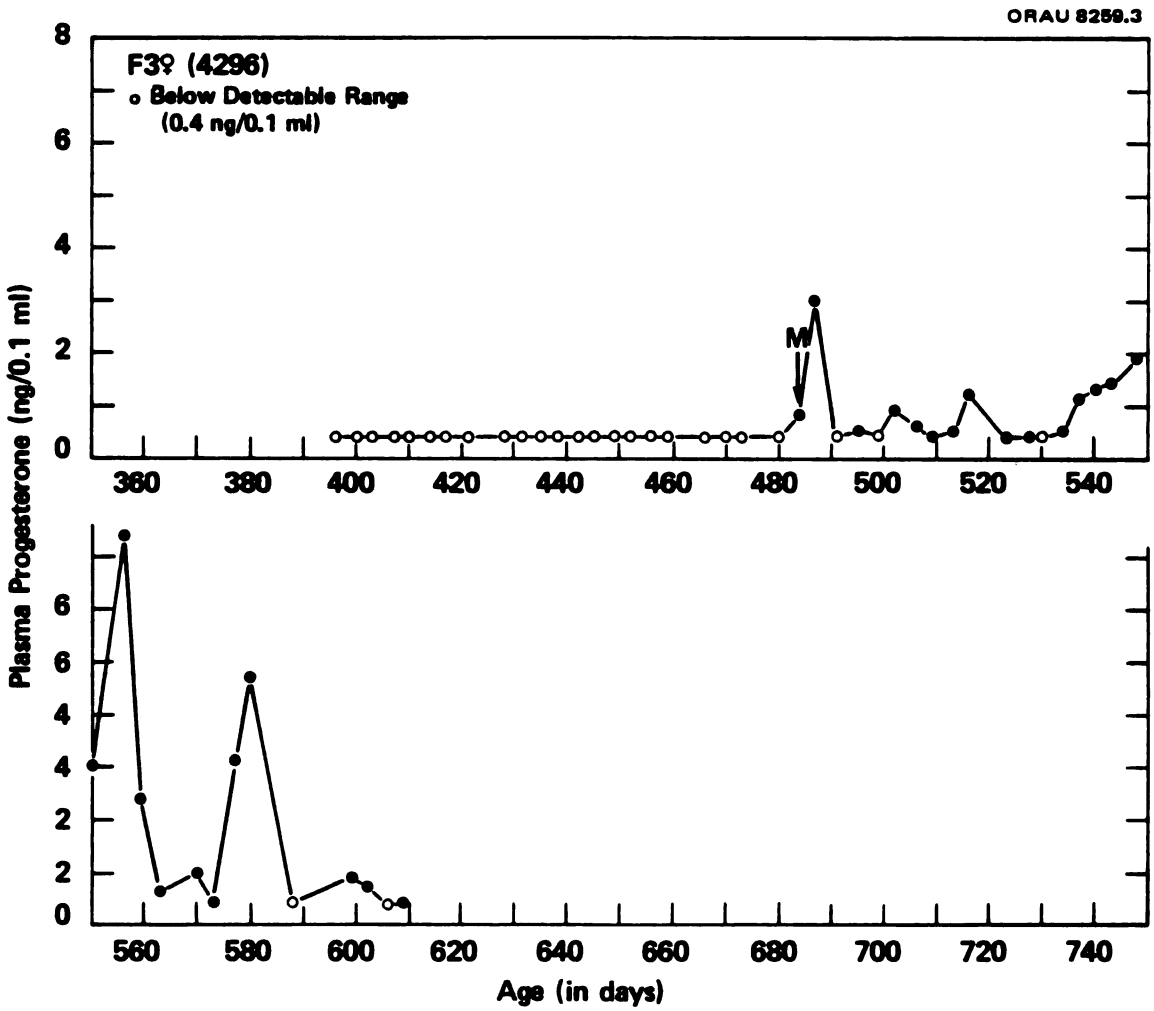


Figure 3 (cont'd.)

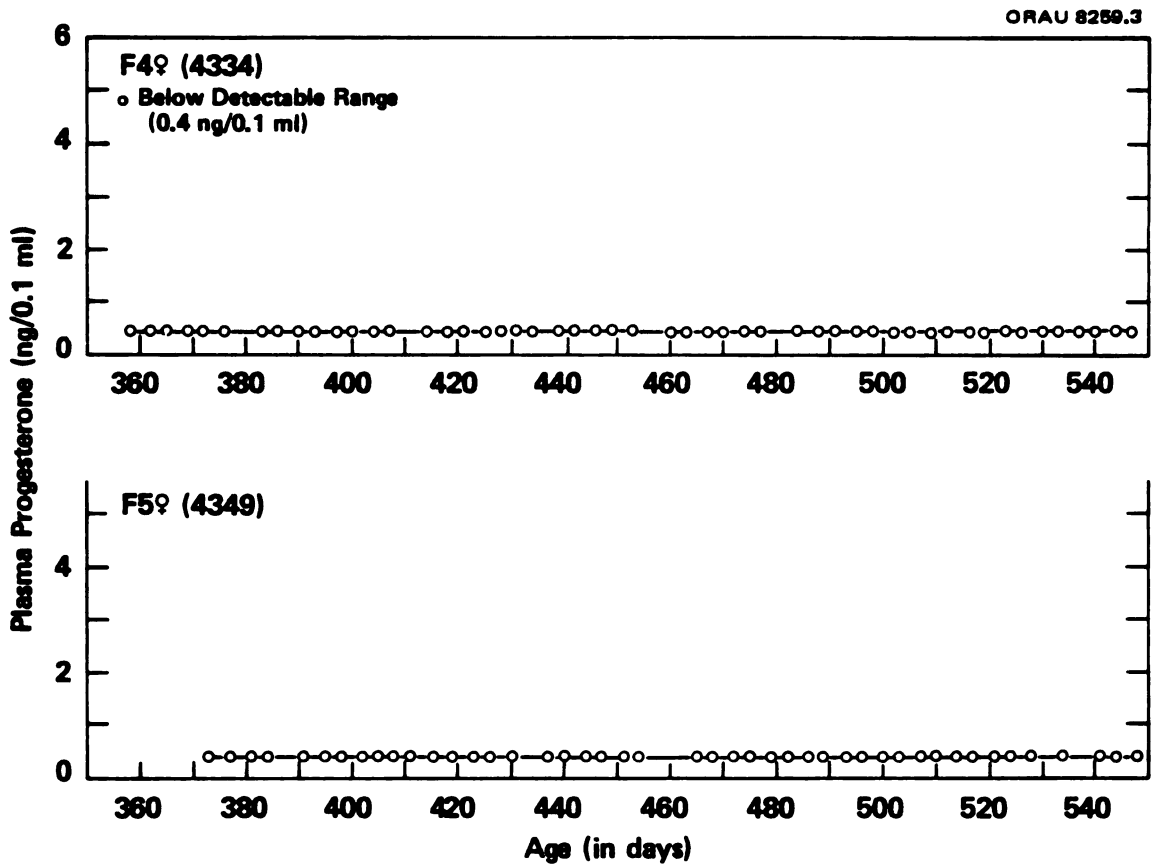


Figure 3. (cont'd.)

with periods of 60-70 days in which levels were undetectable. F2-female did display an ovulatory spike of 2.4ng/.1ml at 620 days and low, fluctuating levels to 663 days. There was no return to consistently undetectable levels after 620 days.

Comparison of Age of Maturation. Table 3 indicates the number of females in each social grouping who were considered mature or immature at 550 days of age. The proportion of mature females with males was significantly larger than the proportion of females in natal groups.

Table 3. Number of females mature at 550 days.

Female housed with:	Female maturation state at 550 days of age: Immature	Mature	Total
Adult Male	0	6	6
Natal Group	4	1	5
Total	4	7	11

$X^2 = 7.54$, $p<.01$

The arrows in Figures 2 and 3 labeled M indicate the age at which each female is defined as sexually mature, according to the operational definition given previously. The arrows labeled C indicate age of first conception in the two females in which pregnancy was followed to parturition (P1,P2). A gestation period of 150 days (Epple, 1967; Hearn, 1978) was used to compute concepton date. With the exclusion of P4-female and P2-female, the mean with standard error of the age of maturation is 417 ± 28.6. If P1-female and P2-female are included by age of first conception, the mean with standard error is 442 ± 17.3. The mean with standard error of the age of maturation

of the three females maturing in their natal groups is 586.7 $\pm$ 53.8. A comparison of the mean ages of maturation indicate that females with males do mature at a significantly earlier age than females in natal groups (417.2 vs. 586.7, $t=-3.01$, $p<.02$; 442.6 vs. 586.7, $t=-3.16$, $p<.02$). This test of means is a conservatively biased test of the hypothesis, because two females in natal groups who were sampled up to 550 days and did not mature by that age were not included in the analysis. They would also obviously mature later than any of the females who were housed with males.

The presence or absence of the mother did not appear to be related to the daughter's maturation rate. F3-female, who matured at 487 days, was housed with her mother continuously. F5-female's mother died when F5-female was 479 days of age, yet she remained immature up to 550 days. In addition, the mother's health and reproductive state apparentally bore no relationship to the daughter's maturation age. The mothers in F2 and F5 were ill and non-reproductive (i.e. displayed consistently undetectable progesterone levels) when their daughter's were 417-663 and 373-478 days, respectively and their daughters were either non- or late-maturing. The mothers in F1, F3 and F4 were all healthy and reproductive and their daughters included early-, late-, and non-maturing females.

Discussion and Conclusions

The difference in maturation age between the two types of social groups is obvious. Females with males mature earlier than females remaining with their natal groups. The average age of maturation of females with males was 417 days, which is quite similar to the age of

first ovulation of 400 days in Callithrix jacchus in peer groups (Abbott, 1978b). Epple and Katz (1980) report much earlier ages of first conception in Saguinus fuscicollis females, the youngest being 211 days. These S. fuscicollis females were paired with males at a much younger age than were the S. oedipus used in the present study (6 months or approximately 180 days vs. 294-469 days). This difference may indicate that female tamarins are physiologically capable of sexual maturation at ages even earlier than those seen in the present study.

While females remaining in their natal groups did mature at later ages than females with males, the fact that they did mature at less than two years of age is of some interest. Results of studies of S. fuscicollis (Katz and Epple, 1979), along with general reports that daughters do not reproduce while in natal groups, have lent credence to the idea that mothers physiologically inhibit their daughters' sexual maturation. One exception to this theory has been reported by Abbott and Hearn (personal communication) who find that C. jacchus daughters mature while in their natal groups. Results of the present study also indicate that S. oedipus daughters prior to two years of age are not completely inhibited from maturing by the presence of their mothers. Possible inhibitions of behavioral maturation and the relationship between behavioral and physiological maturation will be discussed in a later section (see GENERAL DISCUSSION). Because of the limited information available, it is unclear as to whether the results of these various studies represent species differences or variation in husbandry techniques and methodology.

Given that females with males did mature earlier than females in

natal groups, the question remains as to whether this difference reflects male-facilitation of maturation, mother-inhibition of maturation, or both. Much of the circumstantial evidence from the present study weakens the theory of mother-inhibition. As cited previously, daughters did mature in the presence of their mother, with the earliest maturing female (487 days) being housed continuously with her mother. In addition, the reproductive state or state of health of the mother apparentally bore no relationship to the daughter's maturation rate. Finally, one female was examined for 70 days after her mother's death and did not mature, despite the fact that she was well past the earliest ages at which maturation was known to be a physiological possibility.

If the presence of a strange adult male facilitates sexual maturation, this affect appears to require separation of the female from her natal group as well. Two females housed with their mothers were also housed in the presence of an unrelated adult male and these females did not mature at the early ages of those females housed with a male only. The fact that strange adult males in natal groups did not accelerate maturation in young females might be related to a number of factors. It could be that the simple presence of a strange male does not exert a direct neural effect resulting in activation of the pituitary-gonadal axis, as is seen in the accelerated puberty of some rodents (Bronson and Desjardins, 1974). Perhaps certain behavioral interactions between the male and the young female are required for acceleration to occur. Certainly the strange males in natal groups did not have the same types (or the same frequencies) of affiliative or sexual interactions with the daughters as did the males

and young females who were paired. Despite the fact that the mother's presence, alone, does not seem to account for any possible delay in daughter maturation, it might be the case that some factor or combination or factors do serve to make the natal group an inhibiting environment for the young females. It is impossible to determine the validity of any of these possibilities with the information presently available.

CHAPTER 3

BEHAVIORAL CHANGES ASSOCIATED WITH SEXUAL MATURATION

The following *a priori* hypotheses are proposed:

In pairs composed of young females and adult males, sexual interactions will be more frequent when the female is sexually mature than when she is sexually immature.

In pairs composed of young females and adult males, affiliative interactions will be more frequent when the female is sexually mature than when she is sexually immature.

When a young female stays in her natal group, the young female will display less affiliative interactions with her mother when the young female is sexually mature than when she is immature.

When a young female stays in her natal group, the young female will display more agonistic interactions with her mother when the young female is sexually mature than when she is immature.

All young females will mark more frequently when they are sexually mature than when they are immature.

In addition, the following *a posteriori* hypothesis is proposed:

Females housed in natal groups in which the adult male is not their father will differ from females housed in natal groups with their father, in terms of frequency of marking and of affiliative interactions with their mother.

Methods

Behavior Observations. The subjects and their housing conditions have been described previously (Table 1). On an average of three days each week, behavior observations were conducted on all groups. Behavior observations were never conducted during days on which blood was taken. Observations were conducted at all times between 0800 and 1600, with the order in which groups were observed on any given day being random.

A single observation period of a given group lasted 20 min. The observer would sit in visual contact with the animals at a distance of 2.0-2.4 m from the cage. After an habituation period lasting 2-5 min, the observer would record, on a cassette recorder, all occurrences of selected interactions, noting the performer and receiver.

In the young female-adult male pairs, all occurrences of the following interactions were recorded:

A contacts B- A approaches B within an arm's length and both remain at this distance for at least 2 sec.

A grooms B- A, using hands or teeth, examines the coat or skin of B, accompanied by visual inspection.

A sniffs B- A brings his/her face to within 1cm of B's anogenital area.

A nuzzles B- A rubs his/her face on B's back or neck.

A mounts B- A grabs B around his/her torso, from behind, and presses against B's anogenital area.

A thrusts to B- while mounted, A performs thrusting motions with the pelvis.

The first three behaviors (contact, groom, sniff) are considered

affiliative while the last three (nuzzle, mount, thrust) are considered sexual. In addition to these, all instances of either individual marking a cage object or another animal were noted. Marking consisted of rubbing the anogential or sternal area against an object or another animal. Finally, the approximate length (to the nearest half minute) of each contact greater than 1 min was noted.

In the young female-natal groups, the following interactions between mothers and daughters were recorded:

A contacts B- as above.

A grooms B- as above.

A sniffs B- as above.

A grimaces/squeals to B- A, with attention to B, and the corners of her mouth pulled back, exposing the teeth, omits a squealing vocalization.

A cuffs B- A hits or pushes B.

A headshake to B- A, with attention to B, turns her head from side-to-side in a very rapid motion.

A frowns at B- A distinctively lowers the brow, while facing and displaying attention to B.

A stands to B- A, with attention to B, stands, supporting her weight entirely on her hindlimbs.

A chases B- self-explanatory.

A and B fight- A and B grab and bite each other.

The first three behaviors (contact, groom, sniff) are considered affiliative while the remaining behaviors (grimace/squeal, cuff, headshake, grab, frown, stand, chase, fight) are considered agonistic. As with male-female pairs, all instances of either mother or daughter

marking were noted, as were contact times over 1 min.

Analyses- a priori hypotheses. The behavior observations on each female were divided into two groups: those occurring when the female was immature (i.e. when progesterone levels were consistently undetectable) and those occurring once the female had reached the initiation of sexual maturation (i.e. when progesterone levels became consistently detectable). A comparison of the frequency of selected behaviors in the immature state versus the sexually mature state was then made. Because different females were examined across different ages and some matured much later than others, the number of observations of each female in each maturation state vary widely (see Table 4) making any analyses encompassing all females impractical. For this reason, results from each female were analyzed separately.

The method of determining whether the frequency of a behavior varied according to maturation state depended upon the general frequency of occurrence of the given behavior. Two behaviors, mark and contact, occurred frequently and in most observations periods for all groups. In this case, the data were transformed by $\sqrt{x+0.5}$ and the mean frequency/observation period in the immature versus the mature state was compared, using t-tests.

Most of the behaviors, including groom, sniff, cuff, and grimace, were observed in most groups, but were infrequent, seldom occurring more than 1-3 times in an observation period and not occurring at all in many observations. For these behaviors, a Chi-square test was used to determine whether the occurrence of these behaviors was independent of maturation state. Specifically, the number of observation periods in which the behavior occurred or did not occur in each of the two

maturation states was compared. In all statistical analyses, differences were taken to be significant if $p < .05$.

Finally, there were behaviors, including sexual interactions, contacts over 1 min, frown and chase, which did not occur in many groups and were infrequent occurrences in groups in which they were observed. While the occurrence of these behaviors in relation to maturation state will be mentioned, there are too few data for any statistical analyses.

Analyses-a posteriori hypothesis. The comparison within females in natal groups used only the results from immature females, because two of the females did not mature during the course of the study. The type of analysis was again dependent upon the frequency of occurrence of the behavior in question. For infrequent behaviors (groom and sniff), the number of observation periods in which the behavior occurred or did not occur in each of the two social states (natal groups with fathers and natal groups with unrelated males) was compared, using Chi-square tests. For frequently occurring behaviors (contact and mark) all possible pair-wise comparisons of means (transformed by $\sqrt{x+0.5}$) for all females in natal groups were made, using Tukey's test.

Results

Females housed with Adult Males. A total of four females was used to determine whether the frequency of sexual or affiliative interactions varied with the female's maturation state. P4 and P6 were omitted due to insufficient data when these females were immature. Table 4 indicates the number of observation periods for

each pair when the female was immature and mature.

Table 4. Number of observation periods.

Group ID	Number of observation periods when female: Immature	Mature	Total
P1	21	40	61
P2	22	35	57
P3	55	36	91
P4	0	36	36
P5	38	48	86
P6	4	26	30
F1	46	35	81
F2	81	17	98
F3	43	44	87
F4	53	0	53
F5	*47	0	47

Total = 242 hours
Total used in analyses of
a priori hypotheses = 187 hours

* Mother present in 26 periods

Three affiliative behaviors were examined: contact, groom and sniff. Figures 4 and 5 illustrate the frequencies with which males and females contacted each other within each pair. An asterisk indicates a significant difference between the means when immature (I) and mature (M) in a given pair. In male-initiated contacts, two pairs showed a significant decrease when the female matured and two showed no change. Male-initiated contacts did not increase with female maturation. In female-initiated contacts, two pairs showed a significant increase, one a significant decrease and one pair displayed no change. Female-initiated contacts did not change in a

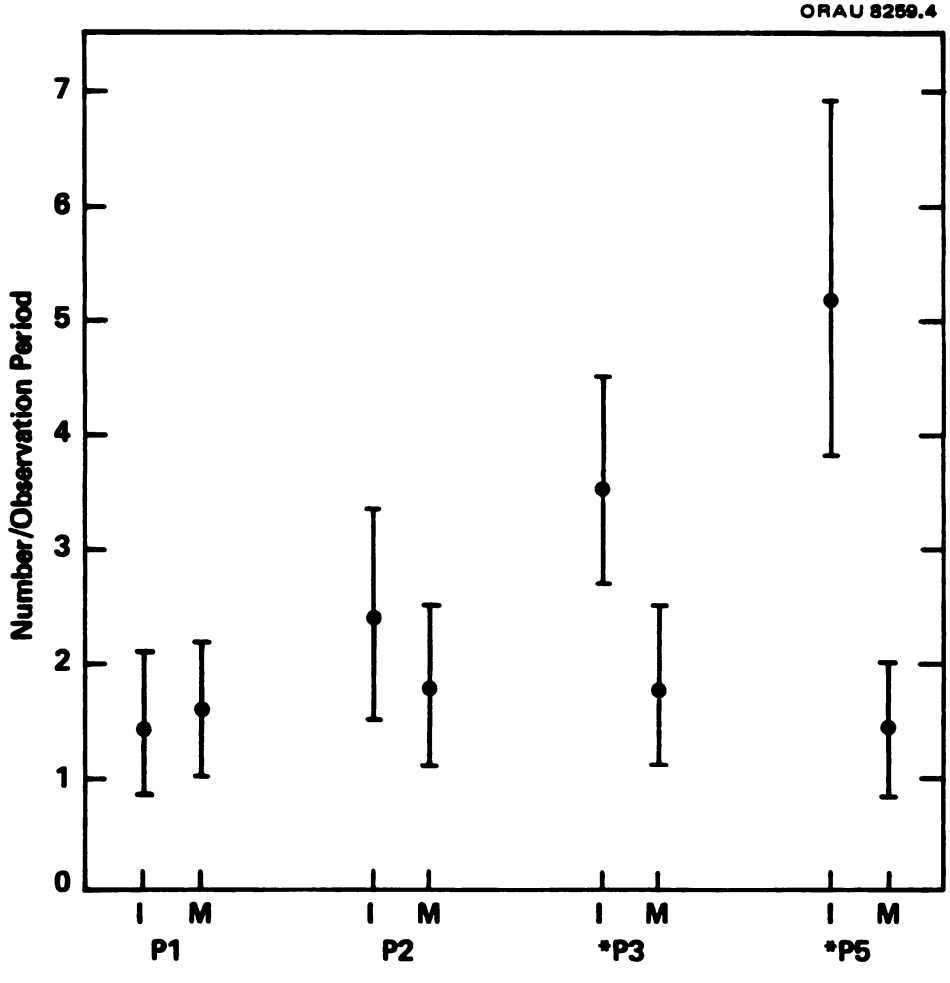


Figure 4. Male-initiated contact frequencies.

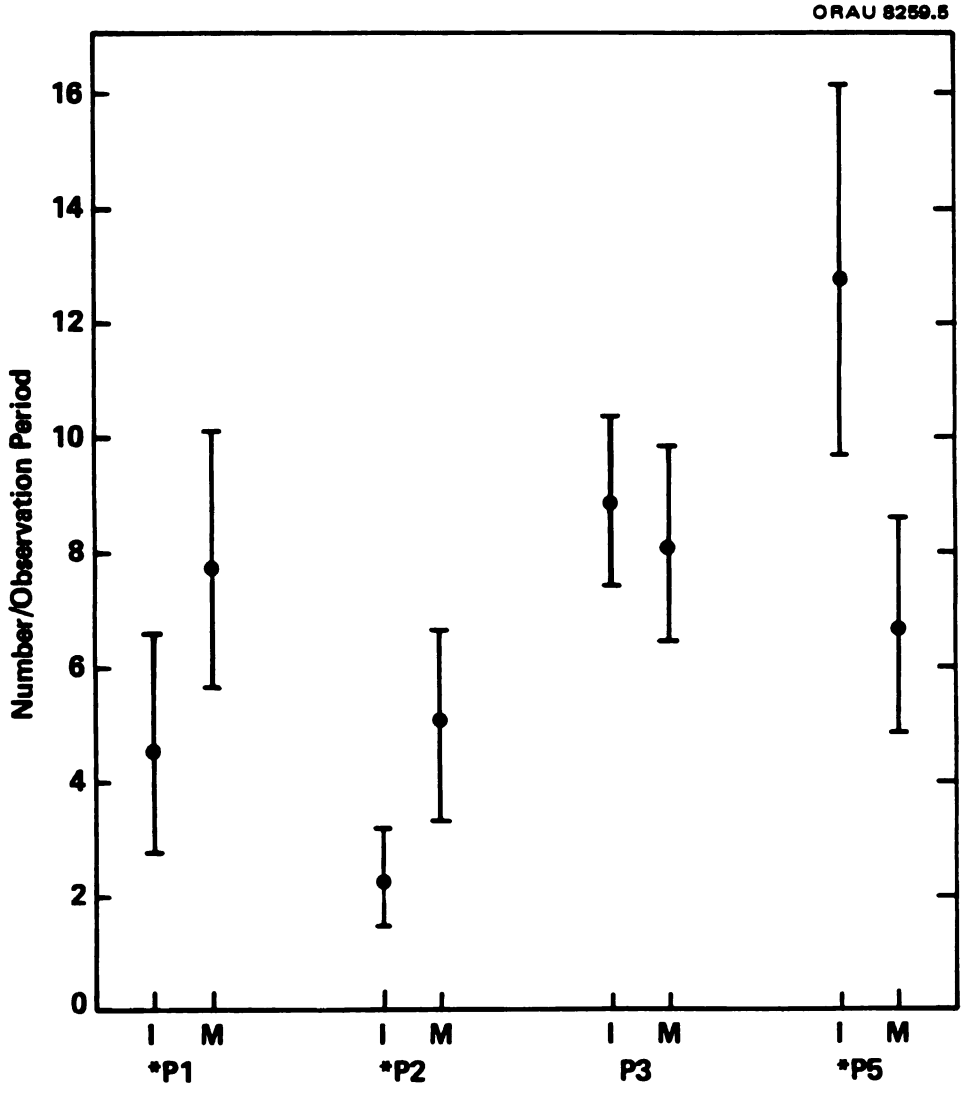


Figure 5. Female-initiated contact frequencies.

predictable direction in relation to female maturation. Grooming was an infrequent interaction. Males groomed females in 7% of the observations periods (2% in P1 to 14% in P5) while females groomed males in 17% of the periods (5% in P1 to 40% in P2). Only two pairs showed any significant relationship between frequency of grooming and female's maturation state. In P5, the males groomed the female less than expected when the female was mature ($X^2 = 5.37$, $p<.025$) and in P2, the female groomed the male less than expected when the female was mature ($X^2 = 5.23$, $p<.025$). Sniffing was also an infrequent interaction. Males sniffed females in 17% of the observation periods (6% in P1 to 28% in P2). Females sniffed males in 16% of the periods (8% in P3 to 38% in P1). No pair showed any significant relationship between frequency of sniffing and females' maturation. In summary, the frequency of the three affiliative behaviors (contact, groom and sniff) in male-female pairs did not increase when the females matured.

Three sexual behaviors were quantified: mount, nuzzle and thrust. Successful mounts accompanied by thrusting were only observed in one pair (P2) on two occassions, during observation periods. Mounts with thrusting were seen in P3 on two occassions, outside of scheduled observation periods. On two occassions in P5, the female was seen at the doorway of the nest box, headshaking and tonguing while the male was also in the box, a probable indication of copulation. Of these six known and probable copulations, five occurred when the female was immature. Unsuccessful mounting by the males occurred most frequently, occuring in 1 observation period in P1, five periods in P3, and 9 periods in P5. Mounting was unrelated to the female's maturation state. In addition to these behaviors, masturbation by the

P3-male was noted on five occassions, two of these being when the female was immature and three when she was mature. These limited observations provide no indication that sexual interactions increase after the females have matured.

Figure 6 illustrates the frequency of female marking in each pair. Mean marking levels were higher in all females once they matured. This difference was significant in 3 females.

Females Housed in Natal groups. A total of three females was used to determine whether the frequency of affiliative or agonistic interactions between mother and daughter varied with the daughter's maturation state. F4 and F5 were omitted because they did not mature during the course of the study. Table 4 indicates the number of observation periods for each group when the daughter was immature and mature.

The same affiliative interactions were examined in mother-daughter pairs as those quantified in male-female pairs: contact, groom and sniff. Figures 7 and 8 illustrate the frequencies with which mothers and daughters contacted each other. The only significant differences in frequency of contacts when immature vs. mature in mother-initiated contacts was in F2, in which contacts decreased when the daughter matured. Two daughters (F2,F3) contacted their mothers significantly less often once they matured. However, one daughter (F1) contacted her mother significantly more often once matured. Grooming was generally an infrequent interaction (see Figure 9) and with one exception, the frequency of observation periods in which it occurred was independent of the daughter's maturation state. The one exception was in F1, in which the daughter groomed the mother more often when

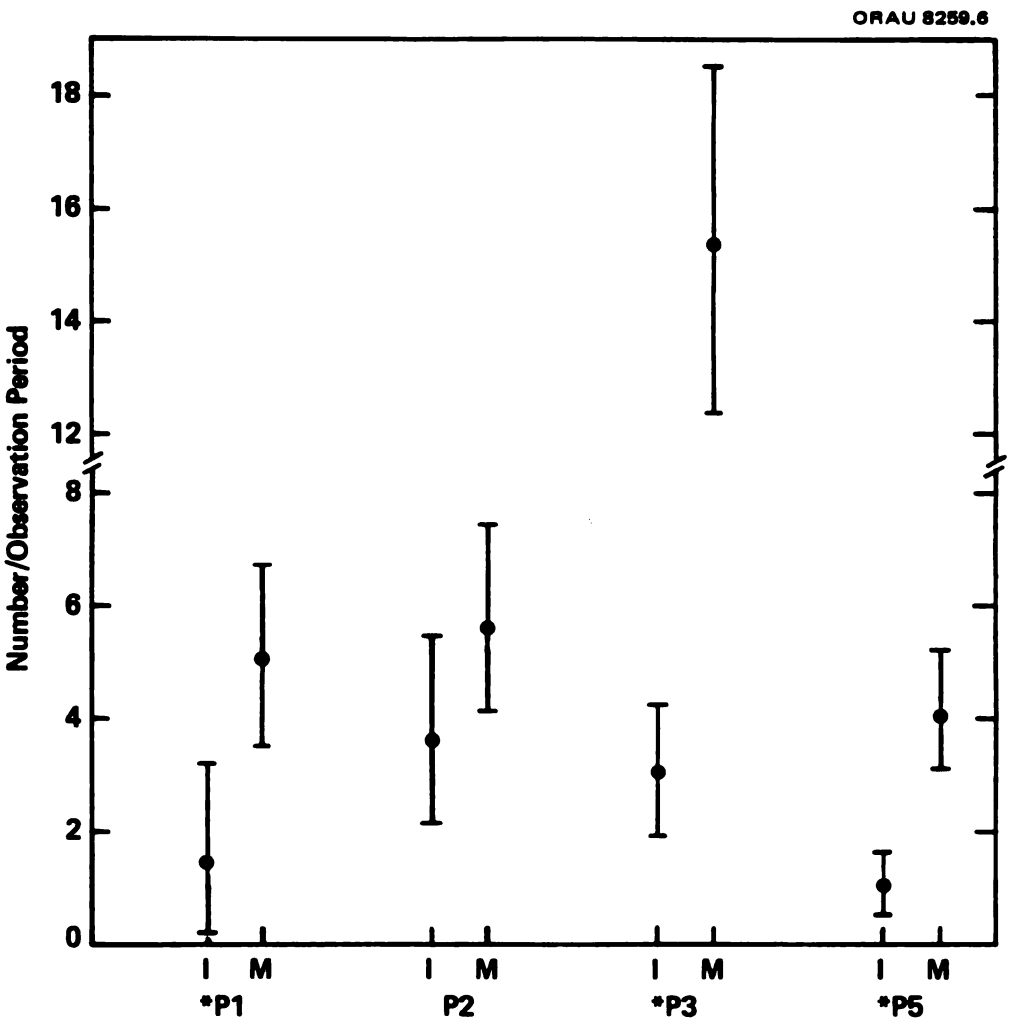


Figure 6. Female marking frequencies.

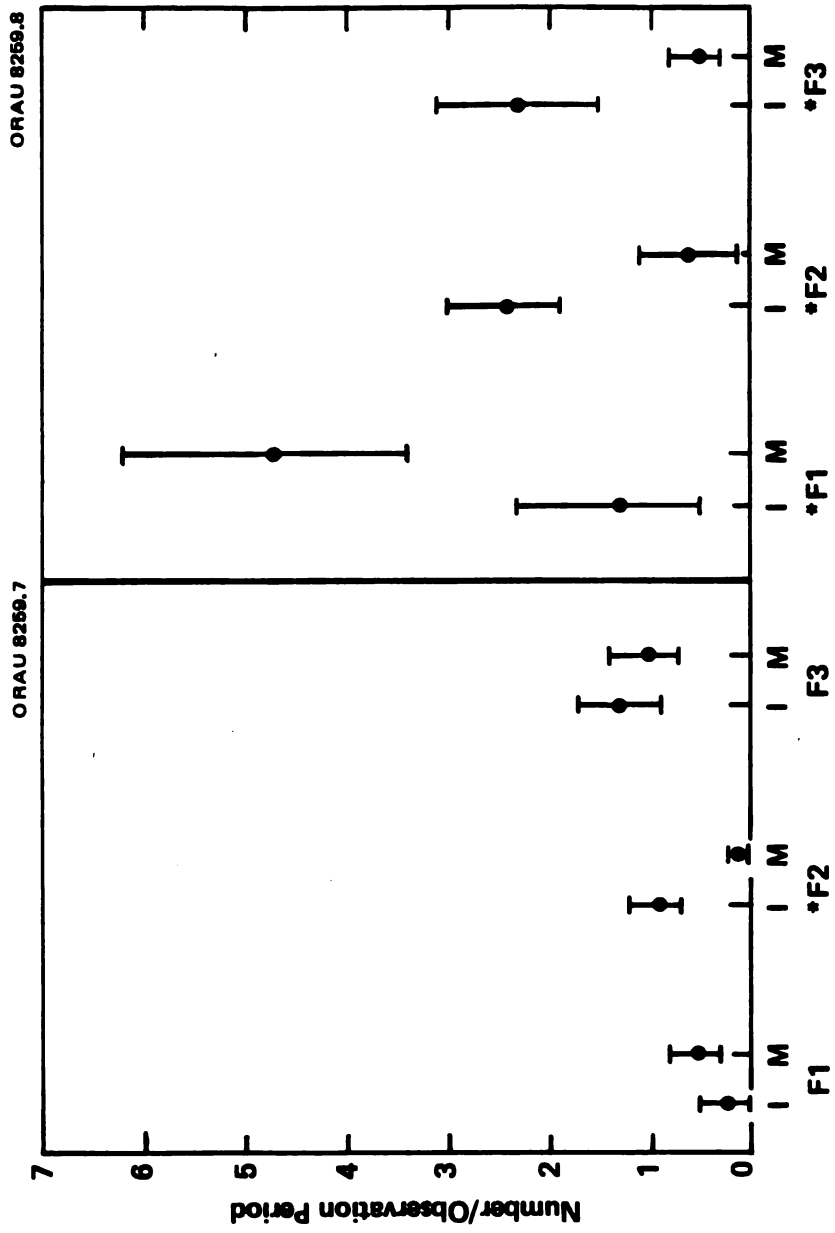


Figure 7. Mother-initiated contact frequencies.

Figure 8. Daughter-initiated contact frequencies.

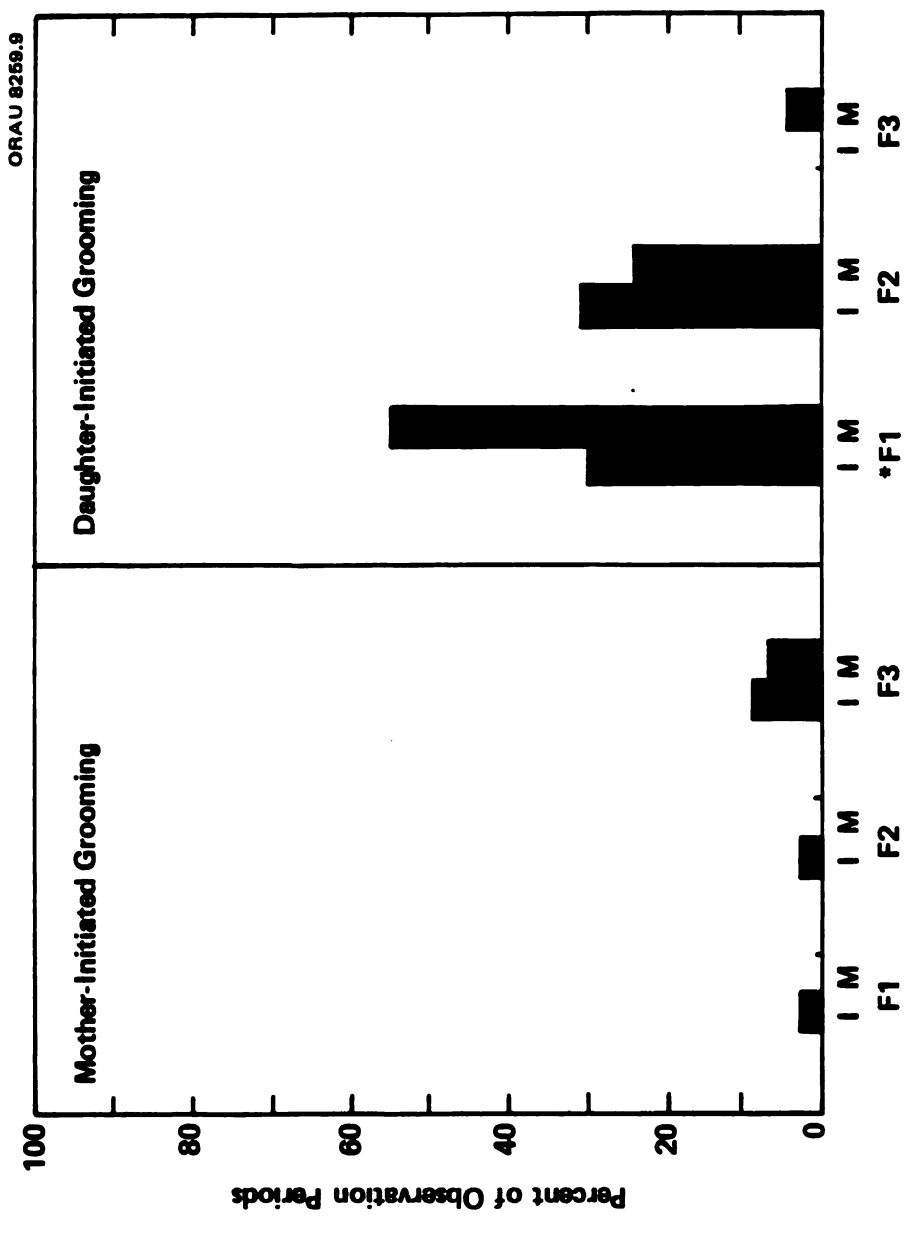


Figure 9. Percent of periods in which grooming occurred.

mature. Sniffing was also a relative infrequent interaction. Mothers sniffed daughters in 4% of the observation periods (1% in F1 to 7% in F3) while daughters sniffed mothers in 33% of the periods (10% in F3 to 65% in F1). Frequency of observation periods in which sniffing occurred was independent of maturation state in all three groups. It is interesting to note that most instances of relatively high frequencies of daughter-initiated affiliative interactions and any increases in those interactions with maturation all occurred in only one group, F1. The other two daughters displayed decreases in contacts and no changes in grooming and sniffing frequencies with maturation.

Two agonistic behaviors were observed across all three groups. These were cuffing, considered aggressive, and grimacing, considering submissive. Figures 10 and 11 illustrate the percentage of observation periods in which these behaviors occurred. Mothers cuffed daughters more than daughters cuffed mothers. However, there was no relationship between the frequency of cuffing and the daughter's maturation state. Mothers were never seen grimacing to daughters. All daughters displayed grimacing only when they were immature. One daughter (F1) displayed grimacing often enough for the difference between the immature and mature state to be statistically significant.

Other aggressive behaviors were observed only in certain groups. Mothers were observed chasing daughters in F2 (8 observation periods) and F3 (2 periods). Of these 10 chases, 7 were when the daughter was immature. Frowning was only displayed by the daughter in F1. She first frowned at her mother nine days after the mother had given birth to the daughter's younger siblings. During this observation period,

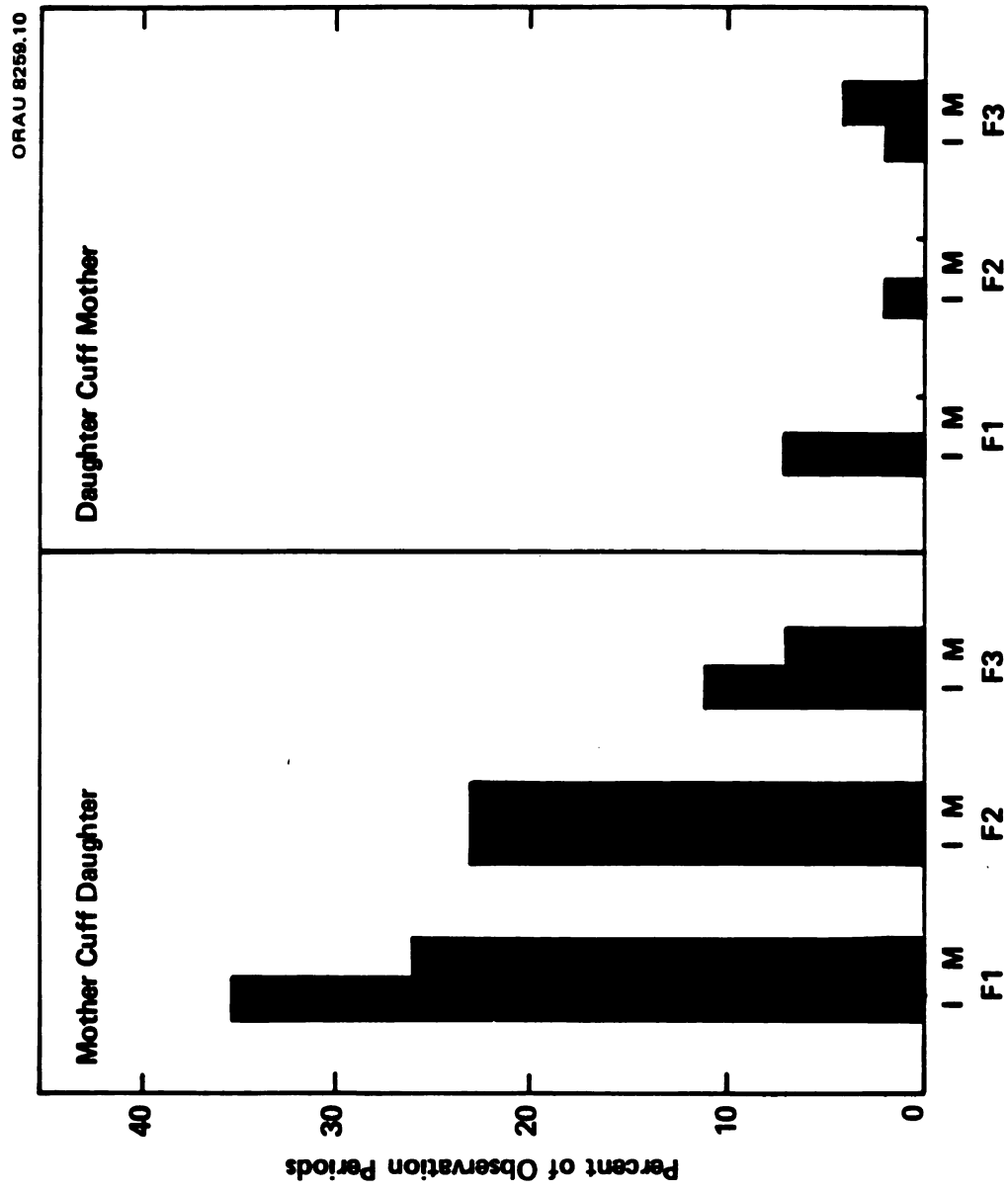


Figure 10. Percent of periods in which cuffing occurred.

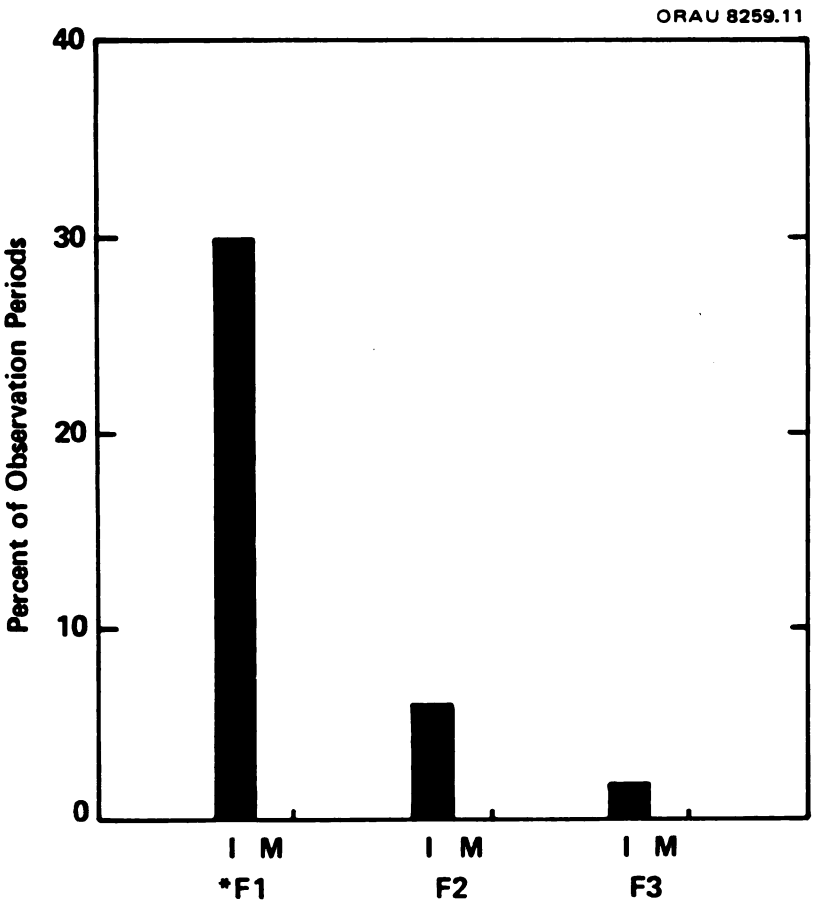


Figure 11. Percent of periods in which the daughter grimaced.

the daughter frequently approached the mother and frowned at her nine times, usually accompanied by standing and headshakes (this is also the only time that standing was seen). The daughter frowned again at the mother during three observation periods, though less frequently within each period. These three periods occurred within two weeks of each other when the mother was about midway through a second pregnancy. No fighting was ever observed in any group.

Figure 12 illustrates the frequency of mother and daughter marking, according to the daughter's maturation state. The only changes in marking behavior occurred in F1, where the mother marked less often and the daughter marked more often when the daughter became mature. A comparison of the daughters' marking frequencies indicate a similar relationship to that seen in affiliative interactions. The daughter in F1 displayed an increase in marking and generally higher marking levels regardless of maturation state than the daughters in F2 and F3 who marked infrequently.

The results reveal no consistent changes in the mothers' interactions with their daughters when their daughters mature. In terms of the daughters' behaviors, the results from F2 and F3 were quite consistent and indicate that daughter-initiated contacts and possibly grimacing decrease when the daughter matures. In contrast, the relatively rare events of grooming, sniffing and marking did not change. The daughter in F1, however, displayed high and increasing levels of most affiliative and marking behaviors throughout her maturation. In an attempt to understand these differences, it was hypothesized that the behavior of F1-daughter could be explained by the fact that she was housed with an unrelated male, in addition to

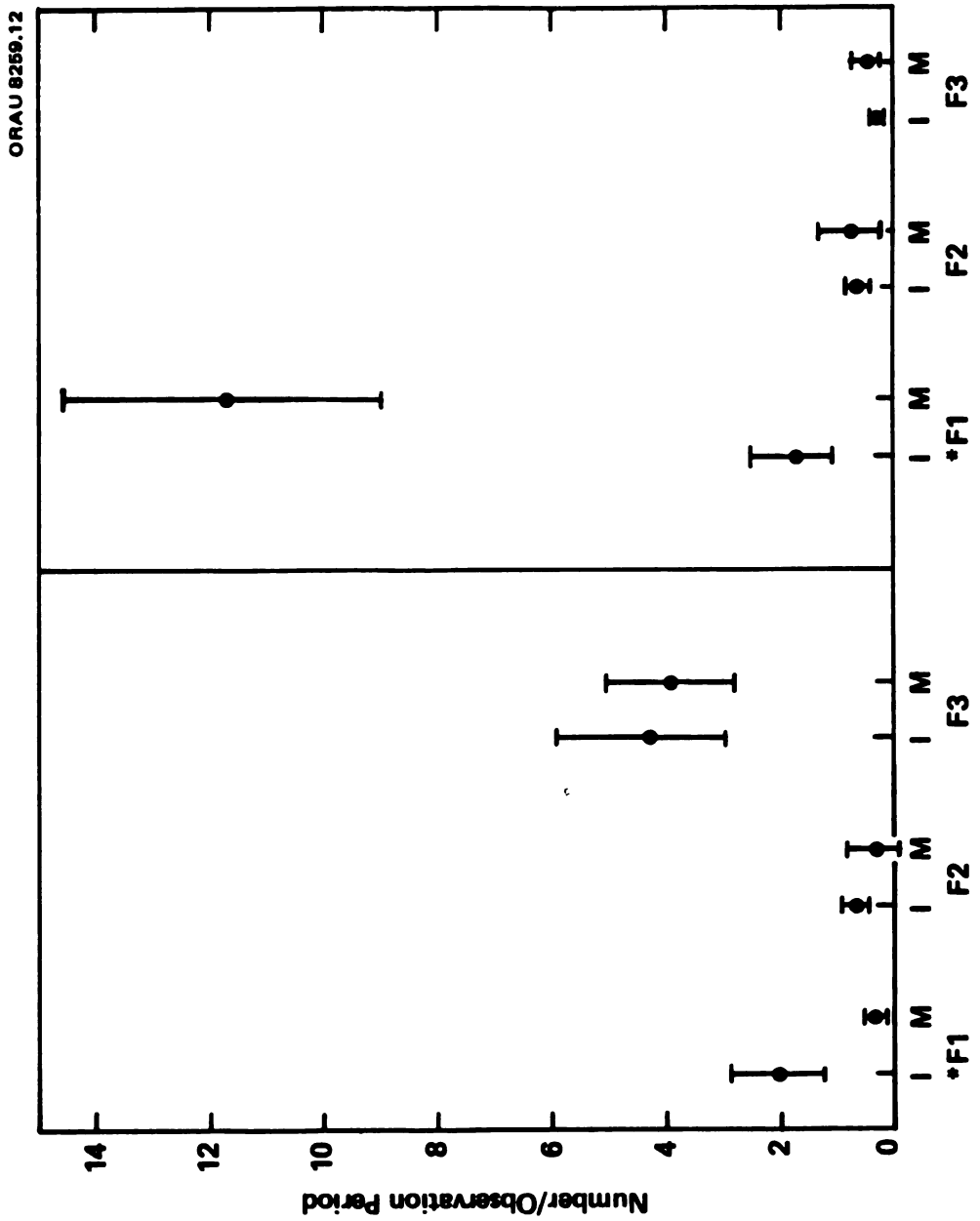


Figure 12. Mother (left) and daughter (right) marking frequencies.

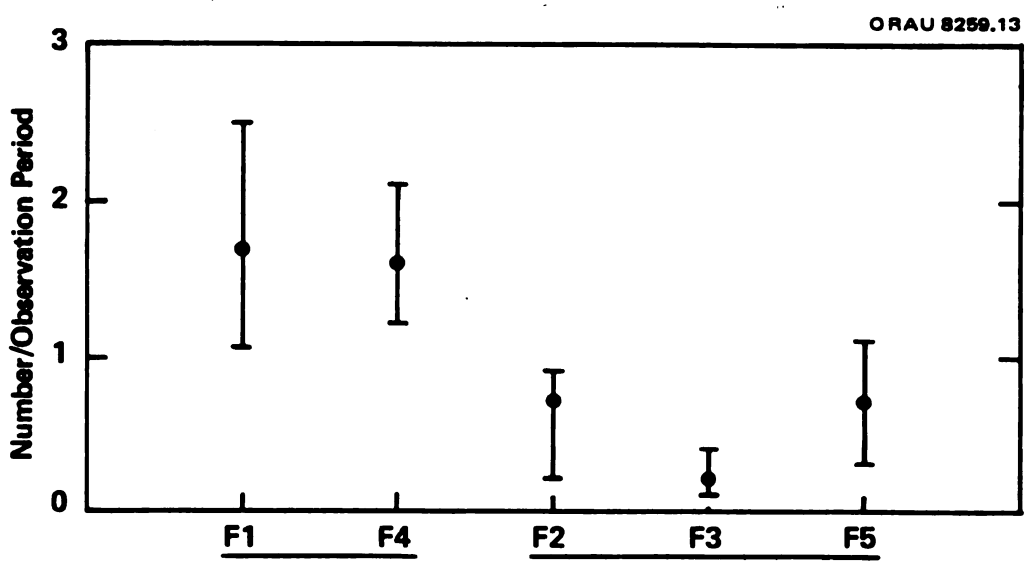


Figure 13. Marking frequencies of immature daughters.

her mother and siblings. Two females (F1,F4) were housed in groups in which the adult male was not their father. These males were placed in the groups when the daughters were approximately 330 and 270 days of age, respectively. Because F4-daughter did not mature during the course of the study, the effect of an unrelated male vs. a father on behavior after maturity could not be examined. However, affiliative and marking behaviors of all immature females in natal groups were compared in order to determine whether F1- and F4-daughters differed from the females housed with their fathers. F1- and F4-female did not differ from the others in mean frequency of contacts of mother or in percentage of observation periods in which grooming occurred. However, they did sniff their mothers in significantly more observation periods (X^2=18.23, df=1,p<.001). F1- and F4-daughters also differed from those females with fathers in terms of marking frequency. Figure 13 illustrates the mean marking frequencies of all daughters when immature (400-620 days of age). F1- and F4-females were very similar and differed significantly from the other three females. It appears then that marking frequency in immature females in natal groups may be affected by the presence of an unrelated adult male.

Discussion and Conclusions

Females Housed with Males. Generally, contact frequencies did not change in a predictable fashion when the females matured. Across pairs, changes in contact frequencies included less contacts once the female matured, more contacts, and no change. Grooming and sniffing, the other affiliative interactions which were quantified, occurred

quite infrequently in all pairs and their frequency of occurrence generally did not vary with the female's maturation state Sexual interactions were also quite infrequent and there was no increase in their frequency with the female's maturation. Sexual and affiliative interactions in young female-adult male pairs have been reported to be infrequent in C. jacchus (Abbott, 1978) and S. fuscicollis (Epple and Katz, 1980). In the present study, these interactions were not only found to be infrequent, but their frequency was found to be independent of the female's maturation state.

The only behavior which does appear to change in frequency with female maturation is marking. Females generally marked more frequently once they matured.

Females Housed in Natal Groups. Mother-initiated affiliative interactions with their daughters generally did not vary with the daughters' maturation state. It is difficult to draw any firm conclusions concerning changes in daughter-initiated affiliative interactions from the results of this study. Two daughters did show a decrease in contacts of their mother once they matured, however one daughter (F1) contacted her mother more frequently when mature. Grooming and sniffing were relatively infrequent behaviors, the occurrence of which was independent of the daughter's maturation state in two groups. However, in one group, F1, the daughter groomed and sniffed her mother frequently and the daughter's grooming frequency increased when she matured.

There is some reason to believe that the behavior of the daughter in F1 can be partially explained by the fact that the adult male in her natal group was not introduced to the group until she was

330 days of age. In a comparison among the five immature females examined in their natal groups, females with unrelated males introduced to the groups when the females were 9-11 months old (F1,F4), were found to sniff their mothers significantly more often than did females with fathers but did not contact or groom their mothers significantly more often than did those with fathers. However, one other observation may have a bearing on explaining the behavior of F1-daughter. In F1, the mother and the adult male frequently remained in extended contact throughout most of an observation period, which was not true of the mother-adult male pair in F4. For this reason, contacts of the mother in F1 usually also brought the daughter into close proximity of the adult male. It is possible that F1-daughter's increased contacts of her mother reflect, to some degree, increased approaches to the adult male.

There are, then, some tenable explanations for the differences between the behavior of the daughter in F1 and the other two maturing daughters. However, the number of females examined is so small (3) as to make any conclusions about the basic <u>a priori</u> hypothesis tenuous.

In terms of agonistic interactions between mothers and daughters, the results are more conclusive. Generally, aggressive behaviors were limited to mothers, while daughters displayed submissive behaviors. However, all agonistic interactions were infrequent. The frequency of aggressive behaviors displayed by the mothers toward daughters did not vary with the daughters' maturation state. Daughters displayed grimacing (a submissive behavior) only when immature. The one exception to this pattern of agonistic interactions was the relatively extreme aggressive displays of the daughter in F1 toward her mother

after her mother's parturition and midway through the mother's subsequent pregnancy. These were periods in which the mother was probably in either post-partum estrus or a false mid-pregnancy estrus (see Kleiman and Mack, 1977). It should be noted that, in F3, the mother displayed cyclical changes in progesterone levels going through a number of periods of low progesterone after her daughter matured, yet the daughter displayed no aggression toward her. There was no adult male present in F3 during this period.

The frequency with which mothers and daughters marked did not vary according to the daughter's maturation state in two groups. In F1, however, the mother marked less frequently and the daughter marked more frequently once the daughter matured. Once again, the behavior of F1-daughter may be related to the fact that she was in the presence of an unrelated adult male. Immature females in natal groups with unrelated males marked more frequently than those with fathers. The marking frequency of these immature females in natal groups with unrelated males was in fact more similar to the marking frequencies of the immature females paired with males than to that of the other females in natal groups.

The *a priori* hypotheses being tested basically proposed a relationship between the frequency of occurence of certain interactions involving young females and the maturation state of those females. Generally, there was no obvious relationship between the interactions observed and the maturation state of the females. The course of behavioral development of females, both in male-female pairs and in natal groups, is probably controlled by a number of physiological and environmental factors. While the endocrine changes

associated with sexual maturation may affect behavior, their occurrence, in and of itself, does not appear to initiate discernable changes in the behaviors examined. The one exception is marking behavior. Sexual maturation was associated with increases in marking behavior in young females housed with males. Yet here is an example of how other environmental factors may interact with the changes of sexual maturation to determine behavior. While two females housed in natal groups matured, they showed no increases in marking behavior. However, one female housed in a natal group containing an unrelated adult male did display increased marking when she matured. Therefore, presence of a strange adult male may be an important factor in determining whether increased marking will be associated with sexual maturation. Though the evidence is much less extensive, the aggression displayed by the daughter in F1 during her mother's probable estrous periods may be another example of a situation in which the presence of a male interacts with maturation state in determining behavior. The evidence for this argument is the difference in the interactions of the mature daughters with their estrous mothers in a group in which an adult male was present (F1) and one in which an adult male was not present (F3).

GENERAL DISCUSSION

Two basic hypotheses were addressed by this study of the cotton-top tamarin, Saguinus oedipus oedipus. The first hypothesis was that the age at which females reached sexual maturity would vary depending upon the social environment in which they were housed. Specifically, it was hypothesized that females housed with adult males would mature earlier than females remaining in their natal groups. The second basic hypothesis was that certain behavioral interactions involving young females would change in frequency when the females matured. The results of this study will be discussed in relation to these hypotheses and the conclusions reached will be related to what is presently known or theorized about the social structure and maturation processes of callitrichid females.

Any discussion of sexual maturation should be prefaced by an exact definition of this term. Sexual maturation, or puberty, is a prolonged process, rather than a distinct event. Any number of histological, physiological, morphological and behavioral changes can be used to describe it and use of different methods will provide different assessments of when an individual is mature. In the present study, the age at which a female's plasma progesterone level remained consistently in the detectable range was used as an operational definition of age of sexual maturation. The fact that progesterone levels consistently rose into the detectable range is an indication

that follicular maturation is proceeding to the point that progesterone is being produced. Most females displayed progesterone spikes that were sufficiently high to be indicative of ovulation during the course of the study. However the relationship between the age of the first ovulatory spike and the age of first detectable levels of progesterone varied between females. There is also probably a variable relationship between the age of maturation, as operationally defined here, and the age at which a female is physiologically capable of maintaining a pregnancy (see Vihko and Apter, 1981).

Effect of Social Organization on Age of Sexual Maturation. In the present study, social organization had a definite effect on sexual maturation rates. Females housed with adult males matured at a much earlier age than females remaining in their natal groups.

The theory that social factors can accelerate or inhibit sexual maturation has been substantiated in a number of taxa. The most extensively understood of these phenomena in mammals is the acceleration of female sexual maturation in rodents by adult males (Bronson and Desjardins, 1974; Kennedy and Brown, 1970; Vandenbergh, 1967, 1969). There is less extensive evidence that adult females may inhibit sexual maturation in young females rodents (Cowley and Wise, 1972; Rogers and Beauchamp, 1976). While social factors are known to affect the reproductive cycle of mature females in non-callitrichid primates (Bowman, et al., 1978; Dunbar and Dunbar, 1977; Rowell, 1970), their effect on sexual maturation appears to be unknown.

Within callitrichids, it has been hypothesized that the presence of the mother inhibits the daughter's reproduction (Epple 1975; Katz

and Epple, 1979; Lorenz, 1972; Kleiman, in press; Kleiman and Mack, 1980). Specifically, it has been hypothesized that this lack of reproduction is due to inhibition of maturation (Kleiman, in press).

In the present study, the presence of the mother, alone, could not account for the relatively late maturation age of the daughters. In previous studies, the possible effect of the mother's presence has usually been confounded with the presence of other members of the natal group, i.e. the father and siblings, while the effect of her absence often is confounded with the presence of an unrelated adult male (Katz and Epple, 1979; Lorenz, 1972). Either of these social factors might have an effect on sexual maturation.

Because the results of the present study, as well as those of others, (Abbott and Hearn, personal communication), indicate that daughters in some callitrichid species may become sexually mature while in their natal groups, the question arises as to why these females generally do not reproduce (Epple, 1967; Kleiman, in press; Rothe, 1975). Two possibilities seem the most tenable. The first is that they are physiologically inhibited at some level other than ovulation. While young females in natal groups may experience the initiation of sexual maturation and ovulation, they may be incapable of supporting a pregnancy. Vihko and Apter (1981) report that, in human females, it is a number of years after the initiation of ovulatory cycles before cycles with normal length luteal phases are a regular occurrence. Fertility, then, may naturally come much later than the initiation of sexual maturation. It may also be that stress reduces fertility in a mature daughter. It has been theorized that inability to reproduce due to spontaneous abortions may be caused by

social stress in some baboon groups (Dunbar and Dunbar, 1977).

The second possibility is that young females are behaviorally inhibited. The occurrence of an incest taboo is reported in some species (Rothe, 1975). The exact role of each group member in maintaining this taboo is unknown. In other monogamous species, active behavioral inhibition of (i.e. intervention in) the sexual activity of offspring by the parents is reported (Mech, 1970; Rasa, 1973). Intervention by parents in their offspring's sexual behavior is not reported to occur in callitrichids. Rather, Rothe (1975) reports that Callithrix jacchus females actively repel the sexual advances of their brothers. It may be that physiological and behavioral inhibition are both in operation. The result might be that daughters within their natal groups seldom become pregnant and, when they do, the pregnancies are generally unsuccessful.

The possibility that unrelated males may facilitate sexual maturation in callitrichid females has been hypothesized (Cebul and Epple, in press). However, as mentioned previously, in most cases the effect of the presence of an unrelated male on maturation is usually confounded with the effect of the removal of the female from her natal group. In the present study, two females were exposed to unrelated males while still in their natal groups and neither of these females matured early. The lack of early maturation of these females could be interpreted in a number of ways. As stated previously (see CHAPTER 3. Discussion and Conclusions) it might be the case that any accelerating effect requires certain sexual or affiliative interactions between the male and the young female. In mature females of many mammalian species, sexual activity can bring about endocrine changes leading to

ovulation (Feder, 1981). It might also be the case that the natal group exerts some inhibitory effect that the unrelated male's presence does not counteract. The lack of early maturation may also simply indicate that unrelated males do not accelerate female sexual maturation in callitrichids, but rather the natal group has an inhibitory effect.

Behavioral Changes associated with Sexual Maturation. The behavioral development of callitrichid females in natal groups has been documented (Cebul and Epple, in press; Epple, 1967; Hoage, in press; Kleiman, in press; Kleiman and Mack, 1980; Rothe, 1978) The behavior of young females with males has also been examined (Abbott, 1978; Epple and Katz, 1980). However, none of these studies attempted to relate behavioral changes to sexual maturation in any form.

One of the basic hypotheses of this study was that certain behavioral interactions involving young females would change when the female matured. The hypothesis was addressed on a very general level. The frequency of occurrence of selected interactions were compared when a given female was immature and mature, with these states defined as previously described. There was no attempt to relate behavioral changes to any of the specific hormonal changes of puberty. Also, the only aspect of behavior which was examined was frequency of occurrence.

It was proposed that affiliative and sexual interactions would increase in young female-adult male pairs when the young females matured. The results, however, indicated no predictable change in the frequency of these interactions relative to the female's maturation state. It is possible that the endocrine events of maturation do have

an effect on male-female interactions, but that the change may be quite gradual. In other primates (Goldfoot, 1977; Hanby and Brown, 1974; Wolfe, 1978) the sexual behavior of mature females does differ from that of immature females but the changes are gradual, stretching over many years.

The specific changes, or lack of change, in affiliative interactions in the various pairs is interesting to note. Male contacts of females generally did not increase when the females matured. The two females which displayed increases in contacts of their mates were the only two known to be pregnant during the course of the study. Wolters (1978) notes, in S.o. oedipus, that male initiations of contact behaviors are quite rare. The high levels of contacts, indicative of mated callitrichid pairs, appear to be primarily initiated by the female. Because female-initiated contacts did increase in the two pregnant females, only, perhaps initiation of pair-bonding affiliations are associated with pregnancy.

Selected interactions of mothers and daughters were also examined. It was proposed that agonistic interactions would increase and affiliative interactions would decrease between mothers and daughters when the daughters matured. The results indicated that the mother's behavior toward her daughter was essentially unchanged by the daughter's sexual maturation. Though it is well-documented that sexually mature females who are unrelated are quite aggressive toward each other (Epple, 1970, 1975; Hampton, et al., 1966; Rothe, 1975), sexual maturation, alone, must not necessarily lead to intra-sexual aggression. Affiliative interactions initiated by the mother were infrequent during the entire study and did not change in frequency

with the daughter's maturation.

In the case of daughter-initiated affiliative interactions, the variation between daughters was so extreme and the sample size so small that any specific conclusions relative to the hypothesis would be tenuous. The results are more consistent in the case of daughter-initiated agonistic interactions and indicate that daughters are generally not aggressive toward their mothers regardless of the daughters' maturation state. The one exception was the occassional and relatively severe aggression displayed by one mature daughter to her mother, which occurred when the mother was probably in estrus. Increases in aggression, both between mothers and daughters and between sisters are reported to occur occassionally in association with the mother's estrus in Leontopithecus rosalia (Kleiman, 1979). However, mature daughters are not necessarily aggressive toward their mothers during the mother's estrus, as another mature daughter in the present study was never seen to display aggression toward her mother, even though her mother was known to experience several low progesterone periods. This difference between the behavior of mature daughters may be related to the fact that, in the group in which aggression occurred, there was a strange unrelated male present, while in the group with no aggression, no adult male was present. The possible interaction between male-presence, hormonal state, and behavior will be discussed later.

Though small sample size hinders efforts to draw conclusions relative to the specific hypotheses, there is one clear conclusion to be drawn. The daughter's sexual maturation, alone, was not related to any consistent change in interactions between mother and daughter. If

the same is true for the daughter's relationship with other family members, sexual maturation of daughters remaining in their natal groups could pass completely unnoticed by an outside observer if no endocrine measures are taken.

Relationship between Social Environment and Behavioral Changes. It was initially proposed that all females would mark more frequently once they matured. Results indicated that females in the presence of a strange unrelated male did mark more when mature, but females in the presence of their natal group, alone, did not. This relationship between increased marking and the presence of a strange unrelated male held true whether the female was with the male, alone, or with the male plus members of her natal group. This relationship, in combination with the anecdotal evidence on daughter aggression during the mother's estrus, points to the presence of a strange unrelated adult male as playing an important role in determining whether sexual maturation of a female brings about changes in her behavior.

In summary, social factors do affect the age of sexual maturation of S.o.oedipus females. Females housed with males mature earlier than females in natal groups. The presence of a reproductive mother in the natal group is not related to the maturation age of the daughter. However, whether the presence of the natal group,as a whole, inhibits maturation or the presence of a strange male accelerates maturation, or both, is still unknown. The frequency of affiliative and sexual interactions in pairs of males and young females does not increase when the females mature, though there is some indication of a possible relationship between increases in female-initiated affiliation and pregnancy. There is also generally little change in frequency of

affiliative and agonstic interactions of mothers and daughters with the daughter's maturation. However, the daughter's behavior may change with maturation if there is an unrelated adult male present in the natal group. Also, only females in the presence of an unrelated adult male displayed any increases in marking when mature. The endocrine changes of sexual maturation may bring about changes in behavior, then, but only under certain environmental circumstances.

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