



Changes in Social Behavior and Their Hormonal Correlates during Pregnancy in Pig-tailed Macaques

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*I conducted a longitudinal study of hormones and social behavior during pregnancy in 8 female pig-tailed macaques (*Macaca nemestrina*) living in a captive social group. Females exhibited reduced grooming activity after the first month of pregnancy and reduced aggressiveness in the last month. Female-male hindquarter presentations and male-female foot-clasp mounts decreased steadily during pregnancy. The week before parturition was associated with lower involvement in all social activities. Monthly changes in plasma concentrations of estradiol and progesterone are correlated with some changes in sexual behavior and grooming performed by pregnant females. Altogether, the findings suggest that pregnancy does not bring about a major disruption of female social relationships with other group members and that the influence of pregnancy hormones on female affiliative and agonistic behavior is less marked than that previously observed for infant-directed behavior.*

KEY WORDS: pregnancy; social behavior; hormones; pig-tailed macaques.

INTRODUCTION

Relative to other mammals of comparable body size, primates have a long gestation ranging from 60 days in mouse lemurs (*Microcebus* spp.) to 266 days in humans (Napier and Napier, 1985). Despite the fact that primate females spend a considerable portion of their adult

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lives pregnant, changes in social behavior in relation to pregnancy have been insufficiently investigated. Some changes in social behavior may be expected because pregnancy is associated with marked fluctuations in concentrations of hormones such as estrogen and progesterone, which affect behavior in primates. For example, changes in steroid hormone levels across the menstrual cycle in macaques are accompanied by changes not only in sexual behavior but also in female-female affiliation and aggression (Wallen and Tannenbaum, 1997).

Some previous studies of nonhuman primates have compared sexual behavior in cycling, pregnant, and lactating females (Chambers and Phoenix, 1982; Nieuwenhuijsen *et al.*, 1986); others have investigated changes in interest in infants during pregnancy (Gibber, 1986; Maestripieri and Wallen, 1995; Maestripieri and Zehr, 1998); and a few have investigated whether aggression done or received by pregnant females differed in relation to the sex of their fetus (Erwin and Anderson, 1975; Sackett, 1981; Silk, 1987; Nieuwenhuijsen *et al.*, 1988). Overall, the picture provided by these studies is that pregnancy is associated with a decreased interest in sex and an increased interest in infants, with the data on aggression and fetal gender being contradictory. We know little about changes in female affiliation and aggression during pregnancy because the only longitudinal studies considering these variables were limited to comparisons between late pregnancy and the early lactation period (Hinde and Proctor, 1977; Martel *et al.*, 1994; Maestripieri, 1994). These studies as well as other anecdotal observations suggest that females become somewhat lethargic and withdrawn from social interactions when they approach the time of parturition.

If longitudinal studies of behavior during pregnancy are few, those attempting to integrate behavioral and endocrine variables are even fewer. Recently, however, Maestripieri and Zehr (1998) investigated longitudinal changes in infant-directed behavior and hormone concentrations during the 24 weeks of pregnancy in pig-tailed macaques. They reported an increase in responsiveness to infants during the last 8 weeks of pregnancy associated with an increase in circulating estradiol and in the estradiol to progesterone ratio.

I have extended the investigation of behavioral changes during pregnancy in pig-tailed macaques to include measures of female affiliative, aggressive, and sexual behavior. I analyzed changes in female behavior during pregnancy in relation to changes in circulating estradiol and progesterone. Furthermore, I verified previous reports of social withdrawal at the end of pregnancy by comparing social activities occurring during the last week of pregnancy with those occurring in the previous weeks.

METHODS

Subjects and Housing

The subjects are 8 pig-tailed macaque females in a social group composed of 3 adult males, 31 adult females and their immature offspring. The group was housed in a 25 × 25-m outdoor compound with attached indoor enclosure at the Field Station of the Yerkes Regional Primate Research Center of Emory University in Lawrenceville, GA. Subjects ranged from 5 to 12 years old and were all multiparous, having delivered at least one offspring before this study. Monkeys were fed twice daily and water was continuously available. I assessed the dominance ranks of all adult females in the group with data on aggression, submission, and displacements collected before the onset of the study. The dominance hierarchy was linear and did not change during the course of the study.

Procedures

I conducted the study from October 1996 to July 1997. I used ultrasonography to detect pregnancy and to estimate gestational stage in females that had been observed mating in previous weeks or looked pregnant. Two females were recruited into the study before conception. The other six females were recruited when pregnancy was verified with ultrasonography. One female was recruited at pregnancy week 3, three at week 5, one at week 8, and one at week 15. I followed all eight subjects until they gave birth or had a miscarriage: two cases, one in the third and one in the fifth month of pregnancy. For the six females that gave birth, the exact gestational stage at the time of recruitment was confirmed retrospectively from the date of parturition, considering an average gestation length of 24 weeks (Ardito, 1976).

On the same day and time each week, I captured all subjects to obtain blood samples. I trained the subjects to run into an indoor capture area, where they were transferred via a transfer box into a standard squeeze cage. I obtained one 3-ml blood sample from the saphenous vein without anesthesia by holding the subject's leg through a hole in the cage. I quickly released her into the group after blood sampling. Blood samples were centrifuged and plasma was frozen at -80°C until assayed for 17- β estradiol and progesterone.

Each week, I focally observed all subjects for one hour from an observation tower which allowed an unrestricted view of the outdoor compound. Observation sessions were randomly distributed between 0800 h and 1900

h. I collected data with a portable computer programmed to record frequencies, durations, and sequences of behavior in real time. Data analyses focused on social interactions between the focal females and all of the other group members except infants (age 0–3 months).

I analyzed the following behaviors: *Grooming* = the number of grooming bouts initiated by the focal females and other animals (frequency), the total duration of grooming done and received by the focal females (duration), and the number of partners that initiated or received grooming from the focal females. A grooming bout ended after a 10-s pause in the behavior. *Aggression* = the number of threats, bites, slaps, or chases initiated or received by the focal females. *Submission* = the number of bared-teeth displays (Maestriperi, 1996) initiated and received by the focal females. *Presentations* = the number of hindquarter presentations initiated by the focal females towards adult and subadult males. *Mounts* = the number of foot-clasp mounts performed by adult and subadult males with the focal females.

I analyzed the behavioral and hormonal data collected during the 24 weeks of pregnancy in six 4-week blocks, which are referred to as pregnancy months. For analytic purposes, I used the mean values of hormonal concentrations or frequency or duration of behavior in each 4-week period. I used both parametric and nonparametric statistics depending on the nature of the data and their distribution. Whenever the data failed to meet the assumptions necessary for the use of parametric tests, e.g., normality of distribution and homogeneity of variance, they were transformed via square-root transformations. Given the small sample size, I set statistical significance at $p \leq 0.1$. All tests were two-tailed.

Hormonal Assays

Hormones were assayed with radioimmunoassay using kits produced by Diagnostic Products Corp. (Los Angeles, CA). The estradiol assay had a sensitivity of 5–7 pg/ml with an intra-assay coefficient of variation (C.V.) of 6% and an interassay C.V. of 11%. The progesterone assay had a sensitivity of 0.20 ng/ml, with an intra-assay C.V. of 4% and an interassay C.V. of 10%. The estradiol assay is a modification of the DPC kit in which the standards are diluted in steroid-free monkey serum, thus eliminating any matrix effects possible with human serum (Wilson *et al.*, 1988). The progesterone assay is also a modification of the DPC kit in which samples are first purified by extraction with anesthesia grade ether (2 × 5 ml) and reconstituted with the kit diluent before assay.

RESULTS

Changes in Social Interactions across Pregnancy

Repeated measures ANOVAs revealed that both the frequency and duration of grooming done by the focal females changed significantly across pregnancy (frequency: $F_{7,35} = 2.17$; $p < 0.08$; duration: $F_{7,35} = 2.03$; $p = 0.09$; Figures 1a, b). Bonferroni-Dunn post hoc tests indicated that the frequency of grooming done was higher in Month 1 than in Months 3, 4, 5, and 6 ($p < 0.1$), while the duration of grooming done was higher in Month 1 than in Months 2, 3, and 4 ($p < 0.1$). The number of partners with which the focal females initiated grooming also changed significantly across pregnancy ($F_{7,35} = 5.44$; $p < 0.001$; Figure 1c). The focal females initiated grooming with a higher number of individuals in Month 1 than in all of the other months (post hoc tests, $p < 0.05$). No measure of grooming received by the focal females changed significantly across pregnancy (frequency: $F_{7,35} = 0.86$; N.S.; duration: $F_{7,35} = 1.23$; N.S.; number of partners: $F_{7,35} = 0.52$; N.S.; Figures 1a,b,c).

Aggression done and submission received by the focal females varied across pregnancy (aggression done: $F_{7,35} = 1.68$; $p = 0.1$; submission received: $F_{7,35} = 2.10$; $p = 0.08$; Figures 2a, b). Post hoc tests indicated that aggression done was higher in Months 2 and 4 than in Month 6 ($p < 0.1$). Submission received was higher in Month 2 than in Months 4 and 6 ($p < 0.1$). No significant change occurred in aggression received ($F_{7,35} = 0.79$; N.S.) or submission done ($F_{7,35} = 1.48$; N.S.) by the focal females. The mean number of episodes of aggression received by focal females during pregnancy is not significantly different in relation to the sex of the fetus (male = 0.20 ± 0.02 ; $N = 4$; female = 0.18 ± 0.03 ; $N = 2$; Mann-Whitney U test: $z = -0.77$, N.S.; the sex of one aborted fetus is unknown).

Mounds varied significantly across pregnancy ($F_{7,35} = 3.55$; $p = 0.01$; Figure 3). Specifically, the number of mounds decreased significantly as pregnancy progressed (Spearman's correlation; $R_s = 0.9$, $p < 0.05$). Interestingly, most mounds observed in the first month of pregnancy were performed by adult males, particularly the alpha male, while the mounds observed in subsequent months were mostly performed by subadult and juvenile males. The number of presentations also decreased in later pregnancy months ($F_{7,35} = 1.78$; $p < 0.1$; Figure 3).

Behavioral Changes prior to Parturition

To assess whether the last week of pregnancy was associated with a significant change in social interactions with other group members, I com-

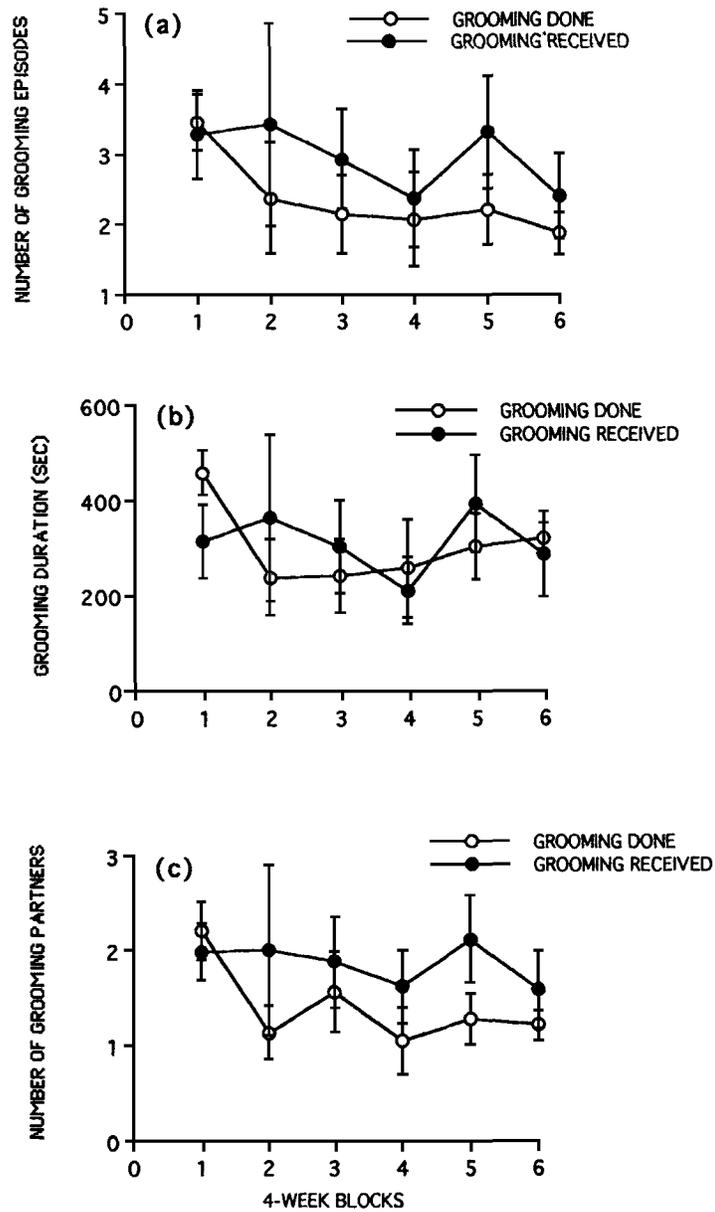


Fig. 1. (a). Number of grooming episodes done and received by pregnant females in their 6 months (4-week blocks) of pregnancy. (b). Total duration of grooming done and received by pregnant females in their 6 months of pregnancy. (c). Number of grooming episodes done and received by pregnant females in their 6 months of pregnancy. In (a), (b) and (c), data are presented in terms of mean values (\pm SEM) per hour per individual.

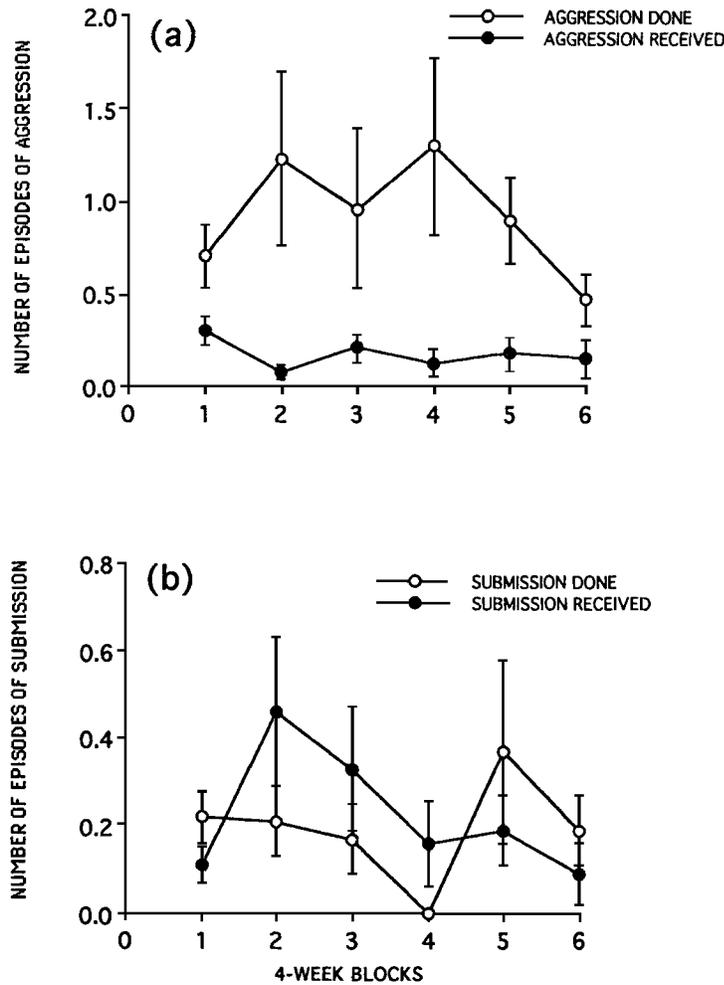


Fig. 2. (a). Number of episodes of aggression initiated and received by pregnant females in their 6 months (4-week blocks) of pregnancy. (b). Number of submissive signals initiated and received by pregnant females in their 6 months of pregnancy. In (a) and (b), data are presented in terms of mean values (\pm SEM) per hour per individual.

pared the behavioral scores recorded during this week with a score averaged across all the previous pregnancy weeks. Table I shows that for all the social interactions considered, the behavioral scores were lower during the week before parturition than in the rest of pregnancy. The Student's *t* tests for paired samples are significant for mounts ($p < 0.05$), aggression performed, and frequency of grooming done and received ($p = 0.1$).

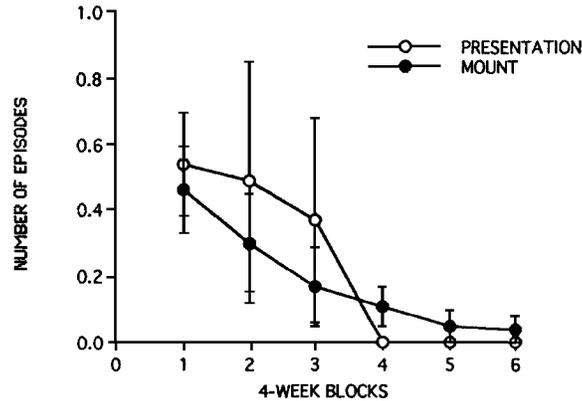


Fig. 3. (a). Number of female-male hindquarter presentations and male-female foot-clasp mounts in the 6 months (4-week blocks) of pregnancy. Data are presented in terms of mean values (\pm SEM) per hour per individual.

Hormonal Changes during Pregnancy and Their Correlations with Behavior

Repeated measures ANOVAs indicated that both plasma estradiol and plasma progesterone levels varied significantly across the 6 pregnancy months (estradiol: $F_{5,47} = 73.27$, $p < 0.0001$; progesterone: $F_{5,47} = 8.08$,

Table I. Comparison between mean values for selected behaviors during the first 23 weeks and the last week of pregnancy^a

	MP (mean \pm SE)	LW (mean \pm SE)	t-test (df = 4)	P
Aggr D	1.18 \pm 0.44	0.20 \pm 0.20	1.96	0.1
Aggr R	0.22 \pm 0.02	0.20 \pm 0.20	0.11	>0.1
Subm D	0.28 \pm 0.13	0.20 \pm 0.20	0.31	>0.1
Subm R	0.29 \pm 0.11	0.20 \pm 0.20	0.43	>0.1
Gr done D	321 \pm 81	152 \pm 126	1.21	>0.1
Gr done F	2.57 \pm 0.69	1.00 \pm 0.55	1.89	0.1
Gr rec D	274 \pm 54	257 \pm 256	0.08	>0.1
Gr rec F	2.87 \pm 0.37	1.40 \pm 1.16	1.53	0.1
Gr partn D	1.33 \pm 0.35	0.80 \pm 0.37	1.21	>0.1
Gr partn R	1.67 \pm 0.11	1.00 \pm 0.77	0.67	>0.1
Mount	0.07 \pm 0.02	0.00 \pm 0.00	2.81	<0.05
Present	0.04 \pm 0.03	0.00 \pm 0.00	1.35	>0.1

^aMP, Mean value for all pregnancy weeks except 24; LW, last week (week 24).

$p < 0.001$). Estradiol levels were significantly higher in Months 5 and 6 than in all previous months ($p < 0.01$; Figure 4a). Progesterone was higher in Month 3 than in Months 1, 4, and 5 ($p < 0.05$), and higher in Month 2 than in Months 1 and 5 ($p < 0.05$; Figure 4b). Monthly changes in the concentrations of estradiol are negatively correlated with monthly changes in the number of mounts (Spearman's correlation, $R_s = 0.94$, $N = 6$; $p < 0.05$), presentations ($R_s = -0.77$, $p = 0.08$), and frequency of grooming done ($R_s = -0.77$, $p = 0.08$). Changes in concentrations of progesterone are negatively correlated with changes in the duration of grooming done ($R_s = -0.66$, $p = 0.1$) and submission done ($R_s = -0.60$, $p = 0.1$). Monthly

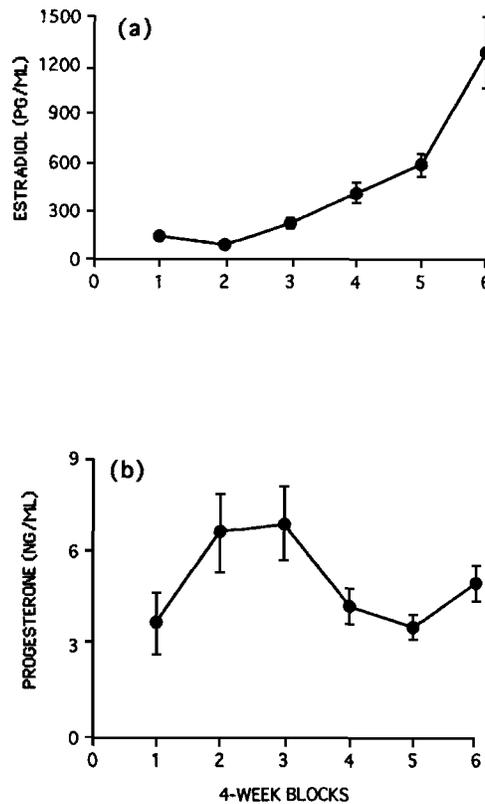


Fig. 4. (a). Mean values (\pm SEM) of plasma concentrations of estradiol (pg/ml) in the 6 months (4-week blocks) of pregnancy per individual. (b). Mean values (\pm SEM) of plasma concentrations of progesterone (ng/ml) in the 6 months (4-week blocks) of pregnancy per individual.

changes in the estradiol to progesterone ratio are correlated with the frequency of grooming done ($R_s = -0.6$, $p = 0.1$), submission received ($R_s = -0.77$, $p = 0.08$), presentations ($R_s = -0.83$; $p = 0.1$), and mounts ($R_s = -0.83$, $p = 0.06$).

DISCUSSION

This longitudinal study of pig-tailed macaque social behavior across pregnancy, although conducted with a relatively small number of subjects, revealed several changes in affiliative, agonistic, and sexual behavior. Adult females groomed a higher number of individuals in the first pregnancy month than in subsequent months. Grooming done in the first month was more frequent and of longer duration as well. In contrast, the grooming received by pregnant females did not vary significantly across gestation. These findings suggest that middle and late pregnancy are associated with a reduction in female grooming activity and its concentration on fewer individuals, probably the closest relatives and friends. The attractiveness of pregnant females as grooming partners to other individuals, however, does not appear to change across pregnancy. A reduction in active grooming after the first month was followed by a reduction in aggressive behavior in the last month of pregnancy. Submissive signals received by pregnant females also decreased in the last month of gestation, probably as a result of reduced aggressiveness. Similar to grooming received, pregnant females continued to be the target of aggression from other individuals at similar rates across gestation, and irrespective of the sex of their fetus (Silk (1987) and Nieuwenhuijsen *et al.* (1988) reported similar findings). The changes in sexual behavior across pregnancy were more marked than those in affiliation and aggression. Sexual mounts and presentations involving adult and immature males decreased steadily across pregnancy, suggesting that as pregnancy progresses, there is a decrease in both female proceptivity and receptivity. In other words, pregnancy is accompanied by a reduction in both female interest in sexual behavior and in their sexual attractiveness to males.

Altogether, these findings, along with those on interest in infants reported elsewhere (Maestripieri and Zehr, 1998), suggest that middle and late pregnancy are accompanied by a reduction in female involvement in affiliative, competitive, and sexual interactions and a concomitant increase in infant caretaking activities, probably in preparation for impending motherhood, when most of her social attention will be directed to her own infant. However, the pregnancy-related changes in social behavior that I observed were relatively minor, a result that may only in part be due to small sample

size. Thus, pregnancy does not appear to be accompanied by a major disruption of social relationships. In particular, with the exception of sexually motivated males, other group members do not appear to treat pregnant females differently as pregnancy progresses. The last week of pregnancy was accompanied by a general reduction in female involvement, as actor or recipient, in social interactions. Reduced social activities may reflect the physical discomfort and lower mobility of pregnant females due to their large body size and weight and allow them to save energy in preparation for the impending delivery.

Pregnancy in pig-tailed macaques was associated with marked changes in the concentrations of plasma estradiol and progesterone. Estradiol increased steadily across the six pregnancy months while progesterone increased in the first three months, decreased in Months 4 and 5, and increased again in Month 6. Monthly fluctuations in estradiol and in the estradiol to progesterone ratio are negatively correlated with changes in mounts and in hindquarter presentations. While these correlations might reflect a direct cause-effect relationship between estradiol, progesterone, and female proceptivity and receptivity (e.g., it is possible that the effects of estradiol on sexual behavior are blocked by rising levels of progesterone), it is also possible that changes in hormonal levels and female sexual behavior are independently correlated with changes in other hormones (e.g., prolactin or oxytocin) or other nonendocrine variables (e.g., body weight). Consistent with the latter hypothesis is the fact that, during the menstrual cycle, presentations and mounts usually increase rather than decrease with increasing estradiol levels (Wallen, 1990).

Estradiol and progesterone are also correlated with some measures of grooming and submissive behavior. Based on previously reported effects of steroid hormones on grooming (Michael *et al.*, 1966), it is possible that pregnancy hormones affect female affiliative behavior in pig-tailed macaques. However, the relationship between hormones and social behavior during pregnancy is less apparent than that between hormones and responsiveness to infants (Maestriperi and Zehr, 1998).

In conclusion, while some of the present findings need to be replicated with a larger sample size in the same or in a different species, my findings suggests that pregnancy is accompanied by some changes in the affiliative and agonistic behavior of female pig-tailed macaques. Such changes are likely to be adaptations to the physical changes brought about by pregnancy as well as to impending motherhood. Since pregnancy occupies a significant fraction of the adult life of female primates, even relatively minor changes in their social behavior need to be taken into account for a comprehensive understanding of their behavioral biology and social dynamics.

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