

Diminished maternal responsiveness during pregnancy in multiparous female common marmosets

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Abstract

Common marmoset monkeys (*Callithrix jacchus*) live in small groups in which, usually, only a single female breeds and all group members provide infant care. When two females breed concurrently, however, they may commonly kill one another's infants, especially during the peripartum period. To investigate the mechanisms underlying infanticide by breeding females, we characterized responses of multiparous females to infants and determined circulating hormone levels in adult females during early pregnancy, late pregnancy, and the early postpartum period. Additionally, we compared the responses of postpartum females to their own infants and infants of other females (unfamiliar infants). Postpartum females were highly maternal toward both their own and unfamiliar infants, and showed no differences in their behavioral or hormonal responses to the two. During both early and late pregnancy, however, these females exhibited longer latencies to initially approach unfamiliar infants and spent less time carrying unfamiliar infants. Moreover, females spent less time carrying unfamiliar infants during late pregnancy than early pregnancy. Most late pregnant females never carried infants, and those that did rejected them quickly. Prolactin concentrations were higher and progesterone concentrations lower postpartum than in early or late pregnancy, while estradiol concentrations, the estradiol-to-progesterone ratio, and cortisol levels were higher during late pregnancy. Within reproductive conditions, however, maternal behaviors were not correlated with hormone levels. These results suggest that maternal responsiveness in marmosets may be attenuated during pregnancy, especially late pregnancy, and this may contribute to infanticide by breeding females.

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Introduction

Common marmosets (*Callithrix jacchus*) are small, New World monkeys that usually exhibit a singular cooperative breeding system: only a single, dominant female breeds in most social groups, and all other group members help to provide care for her offspring (French, 1997; Tardif, 1997). Typically, marmosets of all age–sex classes are attracted to infants and readily engage in parental or alloparental behavior (Yamamoto et al., 1996b). A striking exception may occur, however, in groups containing two breeding

females. Evidence from both field and laboratory studies suggests that in these plurally breeding groups, infanticide may occur surprisingly frequently (reviewed by Saltzman, 2003). In a number of cases, a breeding female has been observed or inferred to kill the infant of another female, and in many of these cases, the infanticidal female was in the late stages of pregnancy (Alonso, 1986; Digby, 1995; Kirkpatrick-Tanner et al., 1996; Lazaro-Perea et al., 2000; Roda and Mendes Pontes, 1998; Saltzman et al., unpublished data; Yamamoto et al., 1996a; reviewed by Saltzman, 2003). Moreover, Digby (1995) found that infants of subordinate breeding females were less likely to survive if they were born synchronously with the infants of the group's dominant breeding female (i.e., ≤ 1 month between births) than if the infants of the two females were born

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asynchronously (i.e., >1 month between births). These findings suggest that in plurally breeding marmoset groups, late pregnant or early postpartum females may routinely attempt to kill other females' infants. In contrast to reports of infanticide in a number of other primate species, in which immigrant males kill unrelated infants (van Schaik, 2000), infanticide in marmosets appears to involve resident females killing the infants of close relatives (Saltzman, 2003).

Although the functional significance of infanticide by female marmosets has been discussed by several authors (Digby, 1995; Digby et al., in press; Roda and Mendes Pontes, 1998; Saltzman, 2003), the proximate mechanisms are unknown. One hypothesis is that breeding females discriminate between their own infants and those of other females (Pryce, 1993), directing maternal behavior only toward their own offspring while behaving aggressively toward other females' infants. Such discrimination could potentially be based on inherent attributes of the infants themselves, or on whether the female first encountered the infants on another female (C.R. Pryce, personal communication). The possibility that female marmosets discriminate between infants has not been tested directly. It is inconsistent, however, with observations of breeding females nursing other females' infants in plurally breeding groups, especially after their own infants have been killed (Digby, 1995; Digby and Ferrari, 1994; Roda and Mendes Pontes, 1998; Saltzman et al., unpublished data).

A second hypothesis to explain infanticide by female marmosets, particularly late pregnant females, is that hormonal changes during late pregnancy promote aggressiveness toward infants. This hypothesis, however, appears to be incompatible with findings from numerous nonprimate species demonstrating that the hormonal milieu of late pregnancy facilitates the rapid onset of maternal behavior (reviewed by González-Mariscal and Poindron, 2002; Numan and Insel, 2003). In primates, the expression of maternal behavior is less critically dependent upon hormones but may be modulated by them nonetheless (Maestripieri, 2001). For example, maternal responsiveness increases across pregnancy in several primate species (Fleming et al., 1997a; Maestripieri and Wallen, 1995; Maestripieri and Zehr, 1998; Rosenblum, 1972), and this effect can be mimicked by treatment of nonpregnant females with exogenous estrogen and progesterone (Maestripieri and Zehr, 1998; Pryce et al., 1993).

Notably, Pryce et al. (1993) have presented evidence that hormonal changes occurring during late pregnancy increase maternal responsiveness in common marmosets. These investigators used an operant conditioning paradigm to train adult female marmosets to press a bar in order to simultaneously (1) gain visual access to a replica of an infant marmoset and (2) turn off an audio tape recording of infant distress vocalizations. Rates of bar pressing by primigravid (first-time pregnant) females were higher during late pregnancy and the early postpartum period than during early to mid-pregnancy. Furthermore, bar pressing by nulliparous, reproductively suppressed females was

increased by an exogenous estradiol and progesterone treatment regimen that mimicked the endocrine milieu of late pregnancy. Multiparous females, however, were not tested because they became highly agitated in response to infant cues and could not be trained on the operant task. In contrast to most other primates, marmosets usually ovulate and conceive within several weeks after parturition (Tardif et al., 2003). Thus, multiparous females are often simultaneously pregnant and lactating, which might modulate their responses to infants during pregnancy.

We conducted the present experiment to investigate possible hormonal influences on maternal responsiveness in multiparous female marmosets and to determine whether marmoset mothers discriminate between their own neonatal infants and those of other females. We compared the responses of multiparous females to unfamiliar infants during early and late pregnancy as well as during the early postpartum period using a longitudinal design. In addition, we compared females' responses to their own infant and to an unfamiliar infant during the early postpartum period, and we compared their responses to unfamiliar infants that were or were not initially encountered on another female. Finally, because estradiol (Fite and French, 2000; Maestripieri and Zehr, 1998; Pryce et al., 1988, 1993), progesterone (Fleming et al., 1997a; Pryce et al., 1993), prolactin (Dixson and George, 1982; Mota and Sousa, 2000; Roberts et al., 2001a,b), and cortisol (Bahr et al., 1998; Bardi et al., 2003, 2004; Fleming et al., 1987, 1997b) have been associated with parental behavior in marmosets and other primates, as well as nonprimate mammals (González-Mariscal and Poindron, 2002; Numan and Insel, 2003), we measured circulating concentrations of these hormones in breeding females and assessed their correlations with maternal responsiveness.

Materials and methods

Animals

Subjects were 12 multiparous female common marmosets (*C. jacchus*) housed at the National Primate Research Center of the University of Wisconsin-Madison. Females were 5.9 ± 0.7 years of age (mean \pm SEM; range: 3.0–10.2 years) at the beginning of testing. Each female had delivered at least one litter prior to this experiment (modal litter size for this species is 2–3 infants; Tardif et al., 2003) and had successfully reared infants (Table 1). Each female was housed with an adult male pairmate and up to 11 offspring (up to 28 months of age), and had visual, olfactory, and auditory access to conspecifics in other cages.

Animals occupied aluminum and welded wire cages measuring $61 \times 91 \times 183$ or $122 \times 61 \times 183$ cm or, for one female and her family, a room measuring $363 \times 212 \times 218$ cm. Lights were on from 0600 to 1800 h, and animals were fed at 1230–1330 h daily. Additional information on

Table 1
Order and timing of tests on individual female marmosets during early pregnancy (EP), late pregnancy (LP), and the early postpartum period (PP)

Test female	Group ^a	Births prior to study ^b	Births during study ^c	Timing of EP test ^{d,e}	Timing of LP test ^{d,e}	Timing of PP test ^{d,e}	Order of reproductive conditions
CJ0268	VIA	2/2, 3/4, 2/2	2/2	UI: -83; DC: -85	UI: -23; DC: -20	UI: 12; OI: 10 DC: 8	LP, PP, EP
CJ0294	VIA	2/2, 2/2, 0/2	2/2	UI: -110; DC: -113	UI: -36; DC: -33	UI: 11; OI: 9 DC: 6	PP, EP, LP
CJ0432	VIA	3/3, 2/3, 1/3	2/3	UI: -76; DC: -80	UI: -55; DC: -51	UI: 14; OI: 9 DC: 11	LP, PP, EP
CJ0428	VIA	1/2, 1/1, 2/2	2/3	UI: -99 ^f ; DC: -102 ^f	N/A	UI: 6; OI: 8 DC: 11	PP, EP
CJ0448	VIA	1/2, 2/2, 1/1	N/A	UI: -101; DC: -99	N/A	N/A	EP
CJ0130	VIP	2/3, 2/3, 2/3	2/3	UI: -109; DC: -107	UI: -29; DC: -31	UI: 5; OI: 9 DC: 11	EP, LP, PP
CJ0224	VIP	1/1, 2/2, 1/1	1/2	UI: -110; DC: -108	UI: -24; DC: -26	UI: 7; OI: 9 DC: 5	EP, LP, PP
CJ0470	VIP	2/2, 1/1	2/3	UI: -106; DC: -108	UI: -46; DC: -44	UI: 6; OI: 10 DC: 8	LP, PP, EP
CJ0476	VIP	1/3	1/2	UI: -114; DC: -112	UI: -24; DC: -22	UI: 10; OI: 5 DC: 7	PP, EP, LP
CJ0492	VIP	2/2, 2/2	2/2	UI: -137; DC: -135	UI: -25; DC: -27	UI: 9; OI: 7 DC: 11	LP, PP, EP
CJ0326	VIP	0/1, 1/2, 1/2	N/A	N/A	UI: -25; DC: -23	N/A	LP
CJ0530	VIP	1/2	2/3	N/A	N/A	UI: 5; OI: 8 DC: 10	PP

^a VIA, View Infant Alone Group; VIP, View Infant with Parent Group.

^b Infant survival for the last three litters born before the experiment (number of infants that survived for ≥ 1 month/number of infants born). Note that some females had delivered only 1–2 litters before this experiment.

^c Infant survival for the litter born immediately prior to postpartum tests (number of infants that survived for ≥ 1 month/number of infants born).

^d Days from parturition.

^e UI, Unfamiliar Infant Test; OI, Own Infant Test; DC, Disturbance Control Test.

^f Female aborted approximately 1 month after EP tests were performed. Timing of EP tests was estimated based on date of the previous parturition, date of postpartum ovulation (from plasma progesterone concentrations), and abdominal palpation.

animal housing and husbandry has been published previously (Saltzman et al., 1998).

Design

The experimental design is summarized in Table 1. Each female underwent a series of infant tests, in which we determined her behavioral and hormonal responses to an unfamiliar or familiar infant introduced into her home cage. We attempted to test each female during early pregnancy, late pregnancy, and the early postpartum period using the date of the previous parturition or ovulation (based on plasma progesterone concentrations; Harlow et al., 1983; Saltzman et al., 1994) and abdominal palpation (Hearn and Lunn, 1975) to estimate stage of pregnancy. The schedule of testing in early and late pregnancy was based on (1) findings by Pryce et al. (1993) that maternal motivation of common marmosets increased dramatically in approximately the final month of pregnancy as compared with early to mid-pregnancy; (2) findings by Digby (1995) that infants of subordinate breeding female marmosets in plurally breeding groups were less likely to survive (possibly due to infanticide) if the two females gave birth within approximately 1 month of each other; (3) previous data indicating that circulating estradiol and progesterone concentrations in pregnant marmosets increase beginning approximately 64 days prepartum (Chambers and Hearn, 1979), and (4) logistical constraints (e.g., restraint of late pregnant females, maximum allowable blood sampling volumes) that prevented us from using females during the final 3 weeks of pregnancy. The schedule of testing during the early postpartum period was based on (1) an attempt to avoid the period of postpartum ovulation and conception (approx-

imately 10–20 days postpartum; Tardif et al., 2003), and (2) preliminary findings that infants older than 2 weeks of age vocally threatened unfamiliar females and resisted their retrieval attempts (Saltzman and Abbott, unpublished data).

In each of the three reproductive conditions, each female underwent one test with an unfamiliar infant (UI) and one with no infant present (disturbance control, DC). In the postpartum condition, females were additionally tested with their own infant (OI). Within each reproductive condition, females underwent the two or three tests at 2- to 4-day intervals. The order of tests within each reproductive condition, as well as the order of reproductive conditions in which individual females were tested, was approximately balanced across animals (Table 1).

To determine whether females respond less maternally to infants that they first encounter with another female (C.R. Pryce, personal communication), we compared responses to infants between females that first viewed unfamiliar infants with their mother and those that first viewed the infants alone. Five females constituted a “View Infant Alone” (VI) group: in each reproductive condition, these animals initially encountered (see below) each familiar or unfamiliar infant alone. The remaining seven animals constituted a “View Infant with Parent” (VIP) group. These animals initially viewed the unfamiliar infant with its mother; in the postpartum condition, they initially viewed the familiar infant with its father (the female’s own pairmate). Three females in the VI group and five in the VIP group underwent infant tests in all three reproductive conditions. Another two females in the VI group and two in the VIP group were tested in only one or two reproductive conditions (Table 1). Between rounds of testing, the females underwent monthly abdominal palpations to confirm and

monitor pregnancies but were otherwise mainly left undisturbed in their home cages.

A total of 28 infants were used. Infants were 5–10 days old during testing and were used in one or two tests each. Unfamiliar infants were not closely related (i.e., not siblings or grandchildren) to test females and, in all but three cases, lived in a different room than the test female. For the remaining three tests, the infant's family was moved out of the room during testing to prevent vocal communication between the infant and its family.

During early pregnancy, 8 of the 10 females had infants (41–74 days of age) living with them, and manual palpation of females' nipples indicated that at least 9 of the 10 females were lactating. During late pregnancy, seven of nine females were producing clear fluid (and, in one case, milk) from their nipples. In the postpartum condition, each female had one or two surviving infants and was lactating at the time of testing.

Infant-test procedure

To prevent injury to infants, during each test (UI, OI, or DC), the test female wore a plastic neck collar (inner diameter: 3.2–3.6 cm; outer diameter: 8.0 cm) with an attached cylindrical "hood" (diameter: 8.0 cm; height: 5.8–6.2 cm) made of polyethylene mesh (diamond-shaped openings: 3 × 3 mm; McMaster-Carr, Chicago, IL). Marmosets could see, hear, and smell but not bite infants through the hood. Females underwent 2–3 habituation trials with the hood within approximately 1 month prior to their first infant test and an additional habituation trial prior to each subsequent round of infant tests. In each habituation trial, the marmoset was fitted with the collar and hood and placed alone in her home cage for approximately 1 h. An observer stood in front of the cage during part of this time to monitor the animal's behavior and to adapt her to the observer's presence.

At 1430–1500 h on the day of each infant test, the female to be tested was captured manually from her home cage and a "pre-test" blood sample was collected within 3 min of initial disturbance to the animal (see below). She was then placed in a stainless steel nestbox (31 × 22 × 18 cm) from her home cage, which also served as a transport box, for approximately 15 min. During this time, all other family members were removed from her home cage and placed in a cage in a separate room. Vinyl shower curtains were suspended across neighboring cages to prevent the female from interacting visually with other marmosets during the infant test. For females that lived in larger home cages, an opaque vertical divider was inserted into the cage to confine the test animal to one half of the cage. For the female that lived in a larger room, testing was conducted inside a standard housing cage (61 × 91 × 183 cm) that had been placed inside the room at least 3 days prior to testing.

Following blood sample collection and preparation of the home cage, the test female was removed from her nestbox and

restrained manually while the collar and hood were placed around her neck and head. She was then returned to her home cage and left undisturbed for a 10-min recovery period. At the end of the recovery period, a small Plexiglas viewing box (25 × 20 × 24 cm), with a perforated floor to allow olfactory investigation, was suspended inside the upper left-hand wall of the female's home cage. In UI tests, the viewing box contained an unfamiliar infant, either alone (VI group) or with its mother (VIP group). In OI tests in the postpartum period, the viewing box contained the test female's own infant alone (VI group) or with its father (VIP group). In DC tests, the viewing box was empty. The viewing box remained in the female's cage for 5 min and was then removed. Approximately 5 min later, the same familiar or unfamiliar infant (or no infant, in DC tests) was manually placed on a 16-cm-wide shelf in the front left corner of the female's home cage, 1 m above the cage floor. For the subsequent 15 min, behavioral data (see Table 2 for behaviors scored) were recorded continuously on a laptop computer by a single, experienced observer sitting quietly in view of the test animal. Tests were terminated immediately if the infant appeared to be in danger from rough handling by the test female. At the end of the test, the female was manually captured and a second blood sample ("post-test") was collected within 3 min of cage entry. The female's collar and hood were then removed, and her nipples were gently palpated manually to determine whether milk could be expressed. Finally, all animals were returned to their home cages.

Blood sample collection and hormone assays

Animals were placed in a marmoset restraint (Hearn, 1977) or restrained manually while blood (0.50–0.75 ml)

Table 2
Behaviors scored

Behavior	Definition
Approach	Females moves to within 10 cm of the infant
Climb on	Infant climbs onto female
Reject	Female forces infant off by rolling, pulling at infant, attempting to bite infant, or rubbing infant against substrate or cage wall
Climb off	Infant climbs off female
Suckling position	Infant's face is in vicinity of female's nipple for >1 s
Inspect	Female performs visual or olfactory investigation of infant with face positioned ≤5 cm from infant
Manipulate hood	Female pulls, scratches, grabs, or bites at the hood over her head
Scratch	Female uses hands or feet to scratch at her own body
Scentmark	Female rubs or drags her anogenital, suprapubic, or sternal region along substrate, object, or infant
Movement ^a	Female is engaged in locomotion or other whole-body movement at 1-min signal

^a Movement was scored instantaneously upon an audible signal from a 1-min timer. All other behaviors were recorded continuously.

was collected from the femoral vein using a heparinized, 1-ml tuberculin syringe and a 27-gauge needle. Samples were immediately placed on ice and subsequently centrifuged at 3400 rpm for 10 min at 4°C. The plasma fraction was aspirated and frozen at –20°C until assayed. All animals had undergone frequent blood sampling several years prior to this experiment. This procedure has been found not to elevate plasma cortisol levels in female marmosets in our colony, following adaptation (Saltzman et al., 1994).

Hormone assays had been fully validated previously for use with marmoset plasma. All plasma samples were assayed in duplicate for cortisol by radioimmunoassay (RIA), as previously described (Saltzman et al., 1994). Assay sensitivity was 0.1 ng/tube (1.0 µg/dl), and intra- and inter-assay coefficients of variation (CVs) of a marmoset plasma pool assayed in quadruplicate in each assay were 4.24% and 12.69%, respectively. All plasma samples were also assayed in duplicate for prolactin by immunoradiometric assay, as previously described (Roberts et al., 2001b). Assay sensitivity was 0.05 ng/tube (1.0 ng/ml), and intra- and inter-assay CVs were 1.04% and 5.10%, respectively.

One of the two plasma samples (pre- or post-test) from each test was assayed for progesterone using enzyme immunoassay as previously described (Saltzman et al., 1994). Assay sensitivity was 3.6 pg/tube (2.7 ng/ml), and intra- and inter-assay CVs were 4.09% and 16.02%, respectively. Due to the large plasma volume required (150 µl), we assayed estradiol in only one plasma aliquot from each female from each reproductive condition in which she was tested, using plasma pooled from several pre- and post-test samples. Estradiol was assayed using RIA following extraction with ethyl ether and celite column chromatography, as previously described (Saltzman et al., 1998). Assay sensitivity was 3.0 pg/tube (10.0 pg/ml), and intra- and inter-assay CVs were 2.25% and 6.72%, respectively.

Data analysis

Hormonal data were subjected to log and exponential transformations as necessary to improve normality and homogeneity of variance (progesterone: 0.2 power; estradiol-to-progesterone ratio: 0.4 power; prolactin: log-transformed; estradiol, cortisol: untransformed) and analyzed by ANOVA and post hoc univariate *F* tests (Systat 5 for the Macintosh). Behavioral data were analyzed by Friedman, Wilcoxon, and Cochran's *Q* tests. For most behavioral analyses, we used two behaviors—latency to initially approach the infant and total time spent carrying the infant—that were most indicative of females' responsiveness to infants. (In most tests, the female approached (72% of tests) and carried [92% of tests] the infant no more than once.) Correlations were calculated using Spearman rank correlation. Results were evaluated using an alpha level of 0.05 (two-tailed).

For analyses of data taken from a single reproductive condition (e.g., comparisons of females' responses to their

own and unfamiliar infants in the postpartum condition, correlations between behaviors and hormone concentrations), we used data from all females that had been tested in that condition (see Table 1). For analyses of behavioral and endocrine responses to infants across reproductive conditions, we used only the eight females that had been tested in all three reproductive conditions. One of these females did not have hormonal data available from the postpartum condition and so was excluded from analyses of hormone levels across reproductive conditions.

Six tests were terminated early (after 2.4–8.6 min) due to rough handling of the infant by the test female (see below). For each of these tests, we terminated the corresponding disturbance control tests after the same length of time to facilitate comparisons of hormonal responses to different test conditions.

Females in the VI and VIP groups showed no significant differences in their behavioral or hormonal responses to unfamiliar infants in any of the reproductive conditions. Therefore, we combined data from the two groups for all subsequent analyses.

Results

Responses to own vs. unfamiliar infant during the early postpartum period

All 10 females tested in the postpartum period approached both their own infant and the unfamiliar infant within 1 s of the infant's introduction into the cage and began to carry each infant within 30 s. Nine of the 10 females then carried the infant for the remainder of the 15-min test. No significant differences were found between females' interactions with their own and unfamiliar infants, including latency to approach the infant, total time spent carrying the infant, number of inspections of the infant, rejection of the infant, and occurrence of the suckling position. Moreover, no differences were found between females' nonsocial behaviors in OI and UI tests, including manipulation of the hood, scratching, scentmarking, and whole-body movement.

Two-way repeated-measures ANOVA comparing plasma prolactin concentrations before and after the OI and UI tests during the postpartum period indicated that prolactin responses to infant tests did not differ between tests with own and unfamiliar infants. Similarly, plasma cortisol levels in the postpartum condition were not affected by the identity of the infant.

Behavioral responses to unfamiliar infants across reproductive conditions

The eight females that were tested in all three reproductive conditions showed marked changes in their behavioral responses to unfamiliar infants. Overall, females were highly

maternal in the postpartum condition, much less so during late pregnancy, and variable in their maternal responsiveness during early pregnancy. Females first approached infants ($P = 0.002$, Friedman) more quickly in the postpartum condition than in either early or late pregnancy (Fig. 1a). Approach latency did not differ significantly between the latter two conditions, but seven of eight females approached the infant more quickly in early pregnancy than in late pregnancy. Total time spent carrying the infant ($P = 0.002$, Friedman; Fig. 1b) was significantly higher postpartum than during either early or late pregnancy, and was significantly higher during early pregnancy than late pregnancy. During early and late pregnancy, infants were frequently carried on the hood, especially while being rejected (proportion of total carrying time on hood: EP $21.6 \pm 13.7\%$, LP $45.4 \pm 19.3\%$, PP $1.1 \pm 1.1\%$, mean \pm SE). When we excluded time on the hood, time spent carrying the infant differed across the three reproductive conditions as before ($P < 0.005$, Friedman; PP vs. EP: $P = 0.025$, PP vs. LP: $P = 0.012$, EP vs. LP: $P = 0.046$). Females also differed across conditions in their likelihood of carrying the infant ($P < 0.05$, Cochran's Q test; Fig. 1c): more females carried infants during the postpartum condition than during late pregnancy ($P < 0.05$, Fisher test), and an intermediate number carried infants during early pregnancy. Moreover, of the females that did carry the unfamiliar infant, only one of eight subsequently rejected it during the postpartum condition, whereas four of six did so in early pregnancy and three of three did so in late pregnancy.

Aggression toward infants

Aggression toward infants occurred infrequently in all three reproductive conditions. In early pregnancy, two females became agitated within 1 min of retrieving the unfamiliar infant and began rolling on their backs, pulling at the infant, and attempting to bite at the infant through the hood. One of these tests was terminated after approximately 5 1/2 min, when the female (CJ0130) persistently attempted to bite at the infant. The other test was terminated after approximately 2 1/2 min when the infant appeared to be in danger of being thrown off the female's (CJ0476) hood. In late pregnancy, all three females that carried the unfamiliar infant became highly agitated within approximately 1 min and, again, vigorously attempted to dislodge the infant by rolling on their backs, pulling at and trying to bite at the infant. In one of these tests, after successfully dislodging the infant, the female (CJ0470) repeatedly threatened the infant vocally and pushed it with her hand, at one point knocking it to the cage floor; the test was terminated at this time (at approximately 5-min duration). Another late pregnant female (CJ0294), after dislodging the infant, held the infant down with her hands and repeatedly attempted to bite at it through the hood; again, we ended the test at this point, about 5 min into the observation. In the postpartum condition, a single female (CJ0130) repeatedly attempted

to bite at both the unfamiliar infant and her own infant, after carrying them for several minutes; this female's two tests were terminated after 8–9 min. Thus, although few females behaved aggressively toward infants in each of the three

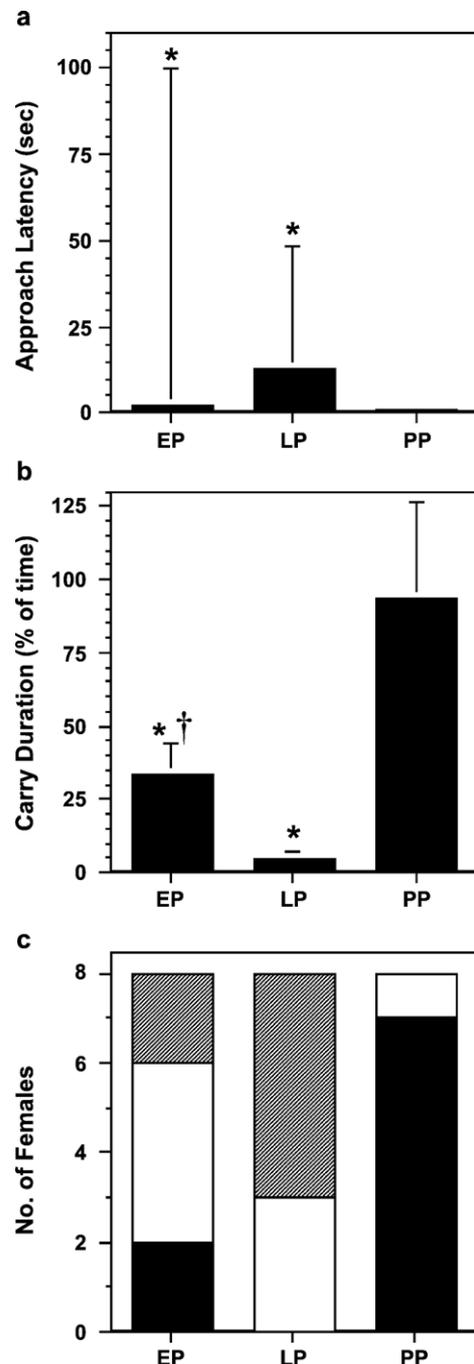


Fig. 1. Behavioral responses of eight female marmosets to unfamiliar infants during early pregnancy (EP), late pregnancy (LP), and the early postpartum period (PP). (a) Latency to initially approach the unfamiliar infant (median + upper 95% confidence interval). (b) Percent of time during 15-min tests (median + upper 95% confidence interval) that females carried the infant. The large confidence interval for PP is due to a single female that rejected the infant. (c) Number of females that did not carry (hatched bars), carried and subsequently rejected (open bars), or carried and did not reject the infant (solid bars). * $P < 0.05$ vs. PP, † $P < 0.05$ vs. LP.

reproductive conditions, aggression was most consistently expressed by those late pregnant females that retrieved the infant.

Hormonal changes across reproductive conditions

As expected, plasma estradiol concentrations changed across reproductive conditions ($F(2,14) = 28.987$, $P < 0.001$; Fig. 2a). Estradiol levels were dramatically higher during late pregnancy than during either early pregnancy or the postpartum period but did not differ between the latter two conditions, presumably due to the occurrence or approach of postpartum ovulation.

Plasma progesterone concentrations, like estradiol, differed across conditions ($F(2,12) = 57.393$, $P < 0.001$; Fig. 2b). Progesterone levels were significantly higher during both early and late pregnancy than postpartum but did not differ reliably between early and late pregnancy. Plasma progesterone concentrations during the postpartum period indicated that four females underwent postpartum ovulation before or during the period of data collection (i.e., progesterone rose above 10 ng/ml; Harlow et al., 1983, Saltzman et al., 1994).

The ratio of estradiol to progesterone concentrations also changed across reproductive conditions ($F(2,12) = 109.857$, $P < 0.001$; Fig. 2c). The E/P ratio was significantly higher during late pregnancy than during early pregnancy or the early postpartum period, and was higher postpartum than in early pregnancy.

Three-way ANOVA [reproductive condition \times infant (UI vs. DC) \times time (pre- vs. post-test)] revealed that plasma prolactin concentrations changed across the three reproductive conditions ($F(2,12) = 13.955$, $P < 0.001$; Fig. 3a) and from before to after each test ($F(1,6) = 7.536$, $P = 0.034$), and that the change over the course of each test differed between reproductive conditions ($F(2,12) = 4.629$, $P = 0.032$); however, these effects did not differ between tests with an unfamiliar infant and those with no infant. Post hoc analyses indicated that plasma prolactin levels overall were higher postpartum than in early ($P = 0.005$) or late pregnancy ($P = 0.003$) but did not differ between the latter two conditions. Moreover, separate analyses within each reproductive condition indicated that prolactin levels did not change across the course of tests during early pregnancy, tended to rise across the course of tests during late pregnancy ($F(1,6) = 5.425$, $P = 0.059$), and declined across the course of each test during the postpartum period ($F(1,6) = 7.873$, $P = 0.031$). Again, however, we found no differences between disturbance control and unfamiliar infant tests.

Three-way ANOVA indicated that plasma cortisol concentrations changed across reproductive conditions ($F(2,10) = 14.935$, $P < 0.001$; Fig. 3b) and across the course of each test ($F(1,5) = 13.021$, $P = 0.015$) but did not differ between tests with an unfamiliar infant and those with no infant and showed no significant interactions among these three factors. Post hoc tests revealed that cortisol

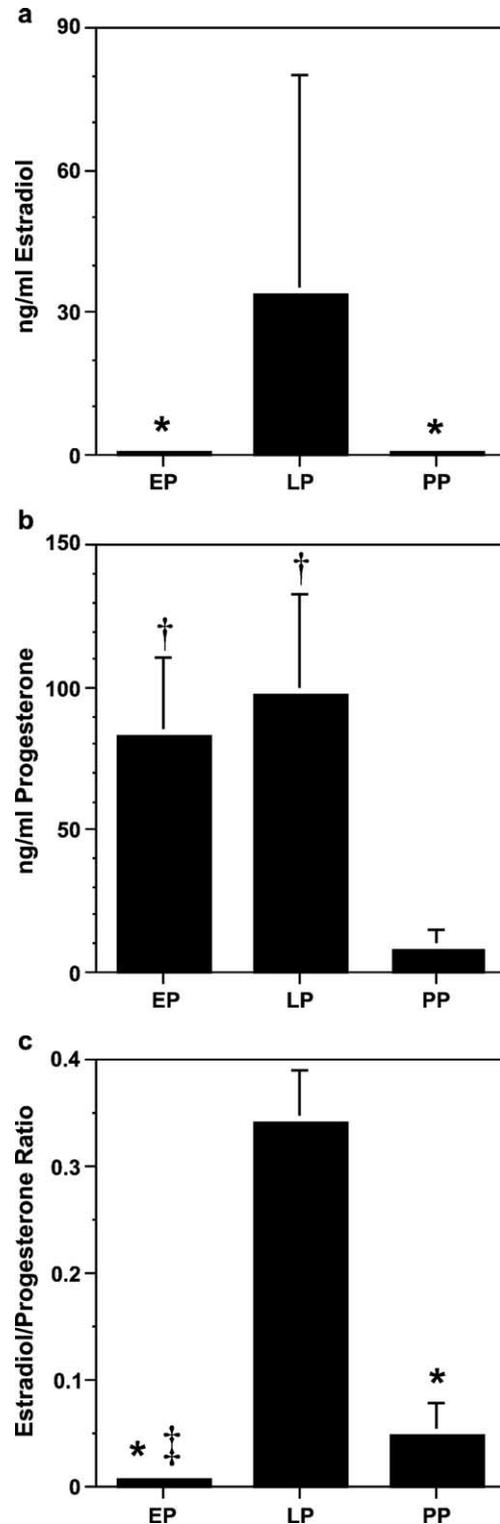


Fig. 2. Plasma estradiol (a) and progesterone (b) concentrations and the estradiol/progesterone ratio (c) (back-transformed mean + upper 95% confidence interval) of eight female marmosets during early pregnancy (EP), late pregnancy (LP), and the early postpartum period (PP). * $P < 0.001$ vs. LP, † $P < 0.001$ vs. PP, ‡ $P < 0.005$ vs. PP.

levels were significantly higher during late pregnancy than during the postpartum period ($P = 0.008$) or early pregnancy ($P = 0.007$) and tended to be higher during

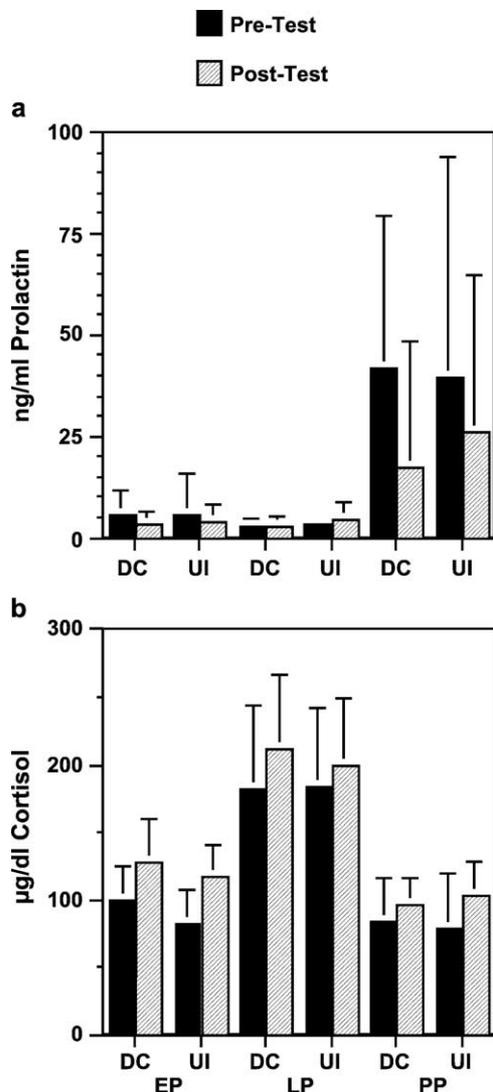


Fig. 3. Plasma prolactin (a) and cortisol (b) concentrations (back-transformed mean + upper 95% confidence interval) of eight female marmosets immediately before and after tests with no infant (DC) or an unfamiliar infant (UI) during early pregnancy (EP), late pregnancy (LP), and the early postpartum period (PP). See text for statistical results.

early pregnancy than postpartum ($P = 0.077$). Cortisol concentrations increased from pre- to post-test in all three reproductive conditions, in both UI and DC tests, presumably due to the stressfulness of some of our experimental procedures (e.g., placement of the hood and collar on the female, separation of the female from her mate and offspring).

Correlations among hormones, behavior, and timing of tests

During early pregnancy, cross-sectional Spearman correlations indicated that females' latencies to initially approach the unfamiliar infant increased as pregnancy progressed ($r_s = -0.648$, $N = 10$, $P = 0.05$), whereas total time spent carrying the infant did not change reliably ($r_s = 0.494$). None of the hormones measured (prolactin [pre-test],

cortisol [pre-test], estradiol, progesterone, or the estradiol-to-progesterone [E/P] ratio) were significantly correlated with number of days prepartum during early pregnancy (Fig. 4).

During late pregnancy, latency to approach the unfamiliar infant ($r_s = -0.370$) and total time spent carrying the infant ($r_s = 0.212$) were not significantly related to the number of days prepartum. Moreover, plasma concentrations of estradiol ($r_s = 0.134$), prolactin (pre-test; $r_s = -0.067$), and cortisol (pre-test; $r_s = -0.504$) were not significantly correlated with days until the subsequent parturition during late pregnancy (see Fig. 4). Progesterone levels, however, tended to correlate positively ($r_s = 0.672$, $N = 9$, $0.1 > P > 0.05$) and the E/P ratio correlated negatively ($r_s = -0.756$, $N = 9$, $P < 0.05$) with the number of days prepartum. In other words, progesterone levels tended to fall and the E/P ratio increased as females approached parturition. We did not perform correlational analyses on data from the postpartum period because animals showed minimal behavioral variability in this condition.

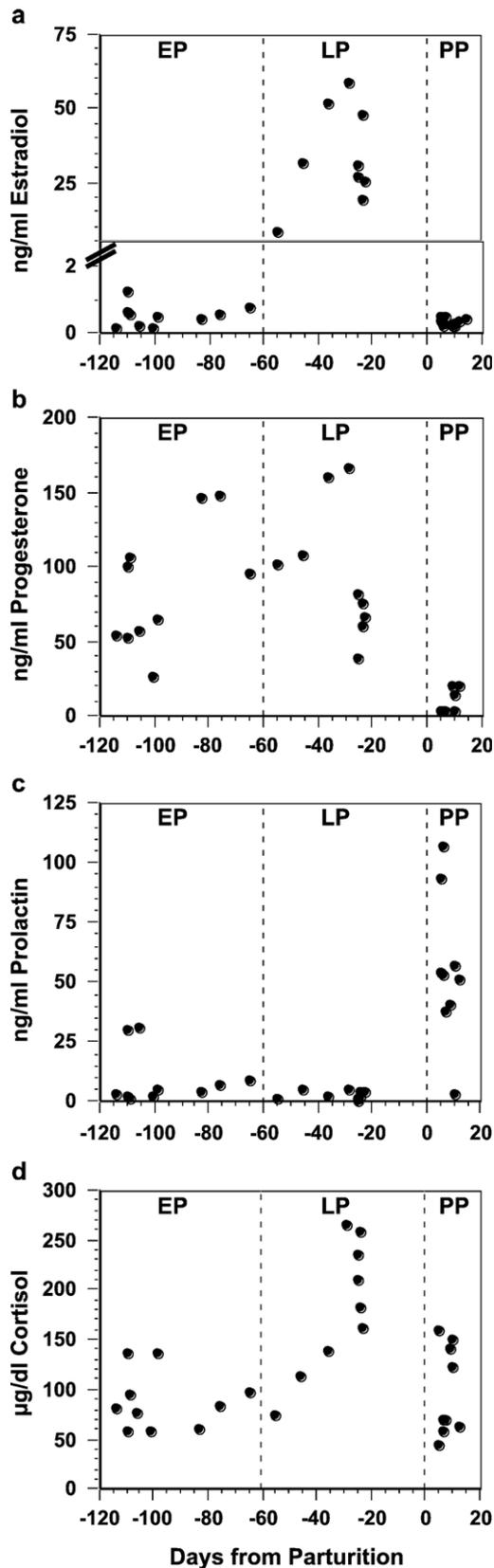
Individual females' latencies to approach the unfamiliar infant and time spent carrying the infant were not significantly correlated with hormone concentrations (pre-test prolactin, pre-test cortisol, estradiol, progesterone, E/P ratio) in either early pregnancy ($r_s = -0.483$ – 0.311) or late pregnancy ($r_s = -0.367$ – 0.233). Similarly, stepwise forward multiple regressions (0.1 to enter, 0.1 to remove) using rank-transformed behavioral and hormonal data indicated that neither of these behaviors was predicted by any of the hormonal variables in either early or late pregnancy.

Discussion

Changes in maternal responsiveness across reproductive conditions

Multiparous female marmosets in this study, like other primates and nonprimate mammals, showed high maternal responsiveness during the early postpartum period (Numan and Insel, 2003). During the first 2 weeks postpartum, marmosets approached both their own and unfamiliar infants immediately, retrieved them very rapidly, and carried them for the entire test period. In contrast to other species, however, marmosets in this experiment showed no evidence of elevated maternal responsiveness during late pregnancy. To the contrary, maternal responsiveness was lowest at this time. Most late pregnant females did not carry unfamiliar infants during the 15-min tests, and those that did rejected them quickly. Females were slower to approach unfamiliar infants during late pregnancy than during the early postpartum period (and, in seven of eight cases, early pregnancy), and spent less time carrying infants during late pregnancy than during either the postpartum period or early pregnancy.

These findings are especially striking because they were obtained with multiparous females that had successfully reared infants previously, indicating that prior experience



with infants—even recent experience—does not permanently maintain high levels of maternal responsiveness (Maestripieri, 1999; but see Pryce, 1993). Furthermore, the common marmoset is a cooperatively breeding species, in which males and nonbreeding females of all ages typically help to rear the infants of the group's dominant, breeding female (Yamamoto et al., 1996b). Marmosets of all age–sex classes will often rapidly retrieve an unfamiliar infant, especially if they have had previous experience with infants (Newman et al., 1993; Pryce, 1993; Roberts et al., 2001b). Thus, our findings suggest not simply that maternal responsiveness increases in the postpartum period, but that it is actively inhibited in pregnancy, even in females with previous maternal experience. It remains to be determined, however, whether this inhibition of maternal responsiveness directly contributes to infanticidal behavior in pregnant females.

Our findings contrast with those of Pryce et al. (1993), who examined the willingness of female marmosets to bar press in order to view a replica of a marmoset infant and to simultaneously turn off an audio tape recording of infant distress vocalizations. Bar pressing rates increased dramatically during late pregnancy as well as during an estrogen and progesterone treatment regimen designed to mimic the endocrine milieu of late pregnancy. Thus, Pryce et al. (1993) concluded that prepartum changes in circulating estradiol and progesterone concentrations increase maternal motivation in marmosets. Several differences between the two studies may account for the disparity in findings. First, while Pryce et al. (1993) compellingly demonstrated that responsiveness to infant-related stimuli increases during late pregnancy, they did not characterize the behavioral responses of pregnant marmosets to live infants. Therefore, the qualitative nature of the females' responsiveness to infants could not be ascertained. It is possible, for example, that the hormones of late pregnancy render female marmosets averse to infant cries. Such an effect could have increased females' motivation to terminate infant vocalizations by bar pressing in the study by Pryce et al. (1993), but might increase their likelihood of avoiding or attacking infants in a setting with more behavioral options available, such as the present experiment. Other stimuli from infants, such as olfactory or tactile cues available to females in our study, but not in the study by Pryce et al. (1993), might similarly have contributed to the differential findings of the two experiments.

Fig. 4. Plasma hormone concentrations of 9–10 female marmosets during early pregnancy (EP), late pregnancy (LP), and the early postpartum period (PP). Estradiol (a) concentrations were determined in pooled blood samples collected from individual marmosets across several days of testing. Progesterone (b) concentrations were determined in individual blood samples collected immediately before or after tests with unfamiliar infants. Prolactin (c) and cortisol (d) concentrations were determined in individual blood samples collected immediately prior to tests with unfamiliar infants. Note that data are cross-sectional and should not be interpreted as longitudinal profiles.

Another difference between the two studies stems from Pryce et al. (1993) testing late pregnant females somewhat closer to parturition than in the current study (25–11 vs. 55–23 days prepartum, respectively). It is possible that maternal responsiveness in our late pregnant females would have been much higher if we had conducted our tests closer to the time of parturition. We did, however, test five of nine females at 23–25 days prepartum, comparable to the timing used by Pryce et al. (1993), and found no significant correlations between number of days prepartum and behavioral responses to infants in late pregnant females. Finally, we used multiparous females, most of which were lactating during early pregnancy, whereas Pryce et al. (1993) used primigravid and nulliparous females. Interestingly, in preliminary tests, Pryce et al. (1993) found that multiparous, nonpregnant females became highly aroused in response to infant stimuli and could not be trained in the operant paradigm, indicating that multiparous and nulliparous females respond differently to distal cues from infants.

It is possible that patterns of maternal responsiveness in pregnant, multiparous female marmosets may differ from those in primigravid females as a result of nipple stimulation or other cues from the females' own infants. Unlike most other primates, marmosets usually ovulate and conceive shortly after parturition, so that lactation coincides with early to mid-pregnancy (Tardif et al., 2003). In rats, nipple stimulation and other tactile cues from pups, especially from young pups, play an important role in the maintenance of maternal behavior, independently of hormones (González-Mariscal and Poindron, 2002; Numan and Insel, 2003; Stern, 1997). Maternal responsiveness in the present experiment was high during the postpartum period, when all females were nursing neonates, low during late pregnancy, when none of the females were housed with young infants, and intermediate during early pregnancy, when most of the females had infants near weaning age (Tardif et al., 2003). Thus, baseline levels of interactions with their own infants may have modulated females' responsiveness to unfamiliar infants in addition to or instead of direct effects of hormones.

Hormonal correlates of maternal responsiveness

It is unclear which hormone(s), if any, influenced the pattern of maternal responsiveness observed in our study. Diminished maternal responsiveness during late pregnancy corresponded with elevations in plasma estradiol levels, cortisol levels, and estradiol-to-progesterone ratios, as compared to early pregnancy and the postpartum period, and with high progesterone and low prolactin levels as compared to the postpartum period. Within reproductive conditions, however, none of these hormones were significantly correlated with individual differences in maternal behavior. Thus, shifts in maternal responsiveness across pregnancy and into the postpartum period may be facilitated by pronounced changes in circulating levels of ovarian

steroids, cortisol, or prolactin, but individual differences in behavior may be more closely linked to nonhormonal factors, such as temperament (Maestripieri, 1999).

Plasma estradiol levels in our animals increased dramatically during late pregnancy, consistent with previous findings in this species (Chambers and Hearn, 1979; Pryce et al., 1993; Torii et al., 1989). Progesterone levels, in contrast, were higher during both early and late pregnancy than postpartum, but did not differ between early and late pregnancy. The absence of a significant difference between early and late pregnancy progesterone levels may reflect the inclusion in our late pregnancy condition of females ranging from 55 to 23 days prepartum. Other investigators have reported that circulating progesterone concentrations remain at luteal-phase levels for the first 10–13 weeks of pregnancy, rise progressively thereafter until peaking 2–5 weeks prepartum, and then decline (Chambers and Hearn, 1979; Pryce et al., 1993; Torii et al., 1989).

Both estradiol levels and the E/P ratio have been implicated in influencing maternal responsiveness in primates, as well as in other mammals (González-Mariscal and Poindron, 2002; Numan and Insel, 2003). In several primate species, prepartum estrogen and progesterone levels predict postpartum patterns of maternal responsiveness or infant survival (Fite and French, 2000; Fleming et al., 1997a; Pryce et al., 1988) or correlate more acutely with concurrent measures of maternal motivation (Maestripieri and Zehr, 1998; Pryce et al., 1993). Furthermore, treatment of nonpregnant female rhesus macaques and common marmosets with estrogen and progesterone increases maternal responsiveness (Maestripieri and Zehr, 1998; Pryce et al., 1993). In nonprimates, estradiol promotes maternal behavior, but only against a backdrop of declining progesterone levels (Numan and Insel, 2003). Progesterone typically plays a biphasic role, first synergizing with estradiol to prime maternal behavior, but later inhibiting maternal behavior. In the present study, therefore, the maintenance of high progesterone levels in late pregnancy may have attenuated female marmosets' maternal responsiveness in spite of their very high estradiol concentrations and E/P ratios.

Prolactin levels in the present study were elevated during the early postpartum period as compared to both early and late pregnancy. This pronounced postpartum elevation of prolactin is consistent with previous findings from common marmosets (Dixon and George, 1982; McNeilly et al., 1981; Moro et al., 1995) and is associated with lactation (McNeilly et al., 1981). Prolactin has been implicated in the activation or priming of maternal behavior in steroid-primed females of several nonprimate species (González-Mariscal and Poindron, 2002) and has been associated with paternal and alloparental behavior in common marmosets (Dixon and George, 1982; Mota and Sousa, 2000; Roberts et al., 2001a,b). However, the role of prolactin in the activation of maternal behavior has not, to our knowledge, been examined previously in marmoset mothers. Our data are

consistent with the possibility that elevated prolactin levels may promote maternal behavior in postpartum, lactating female marmosets. However, because prolactin was low in both early and late pregnancy and did not differ between these two conditions, low prolactin levels cannot, alone, account for the inhibition of maternal responsiveness that we observed most clearly in late pregnancy.

The pattern of cortisol across reproductive conditions was the mirror image of maternal responsiveness: plasma cortisol levels were significantly higher during late pregnancy than during early pregnancy and the early postpartum period (similar to other primate and nonprimate species; Keller-Wood and Wood, 2001) and tended to be higher during early pregnancy than postpartum, whereas the opposite was true of maternal responsiveness. These results, although correlational, suggest that late pregnancy elevations in cortisol may inhibit maternal behavior in marmosets. Mothers' postpartum cortisol levels have been negatively associated with maternal behavior in several nonhuman primates (Bahr et al., 1998; Bardi et al., 2003, 2004), but positively associated with maternal behavior in humans (Fleming et al., 1987, 1997b).

Discrimination between infants

An unexpected finding of this study was that postpartum females did not discriminate between their own infant and an unfamiliar, age-matched infant. Females showed no differences in their behavioral interactions with familiar and unfamiliar infants, in their nonsocial behaviors during infant tests, or in their hormonal (prolactin, cortisol) responses to familiar and unfamiliar infants. Furthermore, we found no differences between females that first encountered unfamiliar infants with their mothers compared to those that first encountered infants that were alone. It is possible that these findings were an artifact of our test procedures. For example, the "hoods" worn by our animals during infant tests to prevent biting might have interfered with the females' ability to investigate infants visually or olfactorily. This seems unlikely. Females were able to position their faces to within ~1 cm of infants and frequently engaged in olfactory and visual investigation at this distance. It may also be relevant that we tested females with unfamiliar infants in the absence of the female's own infant(s). It is possible that females would have been less motivated to interact with unfamiliar infants in the presence of their own infants, or would have shown behavioral discrimination among their own and unfamiliar infants if presented with both infants simultaneously. Nonetheless, similar nondiscriminatory maternal behavior has been reported in titi monkeys (*Callicebus moloch*), in which parents did not discriminate between their own infant and an unfamiliar infant when the two infants were presented either separately or simultaneously in preference tests (Teskey et al., 1993).

Another interpretation of our findings is that female marmosets are unable to discriminate between their own and

unfamiliar infants, at least during the first 2 weeks postpartum. Gubernick (1981) has argued that the primary function of maternal attachment is to enable mothers to provide care selectively to their own offspring and not to other females' infants; therefore, females may not be selected to form specific attachments to their infants under conditions in which there is little risk of misdirecting maternal care. Specifically, mothers may not be expected to discriminate between their own infants and other females' infants in species in which (1) the infants are immobile or semimobile, (2) social units contain only a single breeding female, and (3) groups consist of closely related individuals (Gubernick, 1981), all of which may often apply to marmosets.

Female reproductive competition and infanticide

Inhibited maternal responsiveness during late pregnancy may subserve reproductive competition among female common marmosets. Although many socially subordinate females undergo behavioral or physiological suppression of reproduction (Abbott, 1984; Saltzman, 2003), these females will often begin to breed expeditiously under appropriate social circumstances, such as immigration of an unrelated adult male into the group (Hubrecht, 1989; Kirkpatrick-Tanner et al., 1996; Saltzman et al., 1997, 2004). As a result, although groups of common marmosets typically contain only a single breeding female, two females have been reported to breed concurrently in both wild and captive groups (reviewed by French, 1997; Saltzman, 2003). Breeding females have been observed to kill each other's infants in these plurally breeding groups, and in a number of these cases, the infanticidal female was in the final month of pregnancy (reviewed by Saltzman, 2003). These findings are consistent with both recent theoretical models and empirical results indicating that infanticide may be an effective reproductive strategy in female cooperative breeders (e.g., Clutton-Brock et al., 1998; Digby, 2000; Hager and Johnstone, 2004).

Why should female marmosets kill infants during late pregnancy? If infanticide functions to reduce competition for resources necessary for infant survival, such as alloparents or food (Digby, 1995), then females may have been selected to kill infants that are close in age to their own offspring. Thus, females should be expected to attempt infanticide primarily during late pregnancy or the early postpartum period. To our knowledge, however, infanticide by early postpartum marmosets has not been observed or even strongly inferred (Saltzman, 2003). Results of the present study suggest several possible reasons for this. On a functional level, because females might not be able to discriminate between their own and other females' infants—at least when the infants are very young and close in age—infanticidal postpartum females might risk killing their own infants. On a proximate level, the neuroendocrine mechanisms mediating infanticide may be incompatible with those

promoting maternal behavior during the early postpartum and early pregnancy periods. Additional studies will be needed to characterize these mechanisms and their relationship to changes in maternal responsiveness across pregnancy and lactation.

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