

## 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.,  $\leq 1$  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; Bardí 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  $5.9 \pm 0.7$  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

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