Post-conception reproductive competition in cooperatively breeding common marmosets

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Abstract

Common marmosets are cooperatively breeding monkeys that exhibit high female reproductive skew. Subordinate females usually fail to breed as a consequence of ovulation suppression and inhibition of sexual behavior, and, even when they do breed, typically rear fewer infants than dominants. We evaluated possible mechanisms of post-conception reproductive competition by comparing hormonal profiles across pregnancy, pregnancy outcomes, infant survivorship, and behavior in laboratory-housed families containing one ($N=9$) or two ($N=7$) breeding females. Breeding females in plurally breeding groups did not exhibit well-defined dominance relationships and rarely engaged in escalated aggression with one another. No significant differences were found among singly breeding mothers, plurally breeding mothers, and plurally breeding daughters in urinary chorionic gonadotropin or estradiol sulfate concentrations during pregnancy, fetal biparietal diameter, frequency of spontaneous abortion, frequency of stillbirths, number of live-born infants per litter, or infant mortality rates. When females gave birth while another female in the family was pregnant, however, their infants were highly likely to be killed. The perpetrator was definitively identified in only one family, in which a pregnant female killed her daughter's infant. These results are consistent with observations of free-living common marmosets and suggest that breeding females do not regularly influence one another's pregnancy outcomes, but that they may commonly kill each other's infants, especially during their own pregnancy. Our findings further suggest that infanticide by breeding females may have selected for the evolution of reproductive restraint in subordinate female marmosets.
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Introduction

Cooperative breeders are characterized by extensive alloparental behavior and, frequently, by an asymmetrical distribution of reproductive success, or high reproductive skew, within each social group. In many of these species, behaviorally subordinate females fail to breed altogether; in others, at least some subordinate females may conceive and even produce live offspring, but have low reproductive success as compared to dominant females. The causes of reproductive failure in subordinate females are not always clear. Some authors suggest that reproductive suppression is maladaptive for subordinates but is actively imposed on them by dominant individuals (e.g., Keller and Reeve, 1994; Vehrencamp, 1983). Others, in contrast, argue that reproductive inhibition may be self-imposed by subordinates, allowing them to avoid being harassed or evicted from the group by dominant individuals (Hamilton, 2004; Johnstone and Cant, 1999) or to avoid investing in costly reproductive attempts that are unlikely to succeed (Crespi and Ragsdale, 2000; Hager and Johnstone, 2004; Saltzman, 2003). An understanding of the proximate mechanisms underlying reproductive failure in subordinates may elucidate the evolutionary history and functional significance of female reproductive strategies in these high-skew societies.

Proximate mechanisms of reproductive inhibition have been especially well studied in the common marmoset (*Callithrix*

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jacchus), a small-bodied, cooperatively breeding New World monkey that exhibits high reproductive skew and pronounced female reproductive competition (Abbott et al., in press; Saltzman, 2003). Social groups may contain as many as six adult females, but no more than two of these females breed. Typically, reproduction within each group is monopolized by a single, dominant female, which produces litters of 2–3 infants at roughly 6-month intervals (Digby et al., 2007; Tardif et al., 2003). These infants receive alloparental care from nonbreeding subordinate females as well as all other group members (Tardif, 1997).

Laboratory studies indicate that reproductive skew in marmosets is mediated by suppression of ovulation in many, but not all, subordinate females (Abbott et al., in press). Subordinates in free-ranging groups may also undergo periods of ovulatory suppression, but the prevalence of such anovulation is not yet clear (Albuquerque et al., 2001; Sousa et al., 2005). Reproductive failure in subordinate female marmosets also results, in part, from inhibition of sexual behavior between close relatives. In the field, groups appear to comprise mostly nuclear families with some unrelated immigrants (Faulkes et al., 2003; Ferrari and Digby, 1996; Nievergelt et al., 2000). Closely related males and females do not mate with one another, but field and laboratory studies indicate that immigration of an unrelated male into a group may commonly lead to the onset of plural breeding, with the two breeding females likely to be close relatives (Faulkes et al., 2003; Nievergelt et al., 2000; Saltzman et al., 1997a,b, 2004).

Even when two female marmosets breed concurrently in a group, however, reproductive success is skewed toward the dominant female: subordinate breeding females in free-ranging groups typically produce few or no surviving infants (Arruda et al., 2005; Digby, 1995a; Sousa et al., 2005). The causes of this post-conception reproductive failure in subordinate females are not entirely clear. In several instances, the infants of the subordinate female disappeared within the first few weeks after birth for unknown reasons. In several other cases, infants of subordinate females were killed by the group's dominant female (reviewed by Abbott et al., in press; Saltzman, 2003). It is unknown, however, whether infanticide occurs systematically when two females breed concurrently. Based on the small number of reported infanticides, as well as observations that all subadult and adult callitrichines (marmosets and tamarins) appear to be highly motivated to provide infant care, French (1997, p. 49) concluded that in these species "… infanticide as a common mechanism for reducing subordinate female fertility and maintaining singular breeding within a social group seems unlikely". The high degree of relatedness among most female groupmates (Faulkes et al., 2003; Ferrari and Digby, 1996; Nievergelt et al., 2000) would further suggest that breeding females are unlikely to use infanticide as a common reproductive strategy. Other potential forms of post-conception reproductive competition, such as harassment of subordinates to increase their incidence of spontaneous abortion, reduce their litter sizes, or impair their maternal care, have received little attention in callitrichines. Furthermore, it is unknown whether or how the emergence of a second breeding female compro-

mises reproductive outcomes in the primary or dominant breeding female.

In this study, we investigated whether female common marmosets in laboratory-housed, plurally breeding groups regularly engage in post-conception reproductive competition and whether such competition might maintain reproductive skew. To do so, we generated plurally breeding families by replacing the original breeding male with an unrelated male. We then evaluated urinary concentrations of chorionic gonadotropin (CG) and estrogen metabolites (estradiol sulfate, E_2S) across pregnancy in both singly breeding (mothers) and plurally breeding females (mothers and daughters) to determine whether breeding females impair each other's ability to maintain pregnancy. CG is secreted by the trophoblast and placenta during roughly the first two trimesters of pregnancy in common marmosets and provides a marker of placental differentiation and function, whereas maternal estrogen concentrations provide an index of placental and fetal viability (Tardif et al., 2005; see also Chetty and Elson, 2007). We also characterized fetal biparietal diameter (as an index of fetal growth) during late gestation, pregnancy outcomes, and infant survivorship in singly breeding mothers as well as plurally breeding mothers and daughters. Finally, we compared intrasexual agonism and patterns of maternal and alloparental behavior between singly and plurally breeding females to characterize potential behavioral mechanisms of female reproductive competition. We predicted that breeding females would behave aggressively towards one another, especially during pregnancy, and that such aggression would be associated with altered hormonal profiles across pregnancy, impaired pregnancy outcomes, and reduced infant survival, especially in daughters.

Materials and methods

Animals

We used families of laboratory-born common marmosets housed at the National Primate Research Center at the University of Wisconsin – Madison (WNPRC). At the outset of the study, each family comprised a primary breeding female (mother), 1–3 of her young adult daughters, a breeding male, and, in 11 cases, up to four immature offspring of the breeding female. In five families, the breeding male was the biological father of the adult daughter(s) and immature offspring (control condition). In 11 families, the male was an experienced breeder that was unrelated to the breeding female and her offspring and that had been introduced into the family approximately 5–11 weeks before the beginning of data collection, immediately following removal of the original breeding male as part of a previous experiment (unrelated male condition; Saltzman et al., 2004). Three families were used first in the control condition and subsequently in the unrelated male condition; all others were used in only a single condition. Two mothers were euthanized during the study due to unexpected illness, 28 and 66 days before their daughters gave birth, respectively. A total of eight mothers (five control, three unrelated male) and one daughter whose mother was euthanized (unrelated male) were the only females to conceive in their families (i.e., singly breeding females), while seven mother–daughter pairs (all in the unrelated male condition) bred concurrently (i.e., plurally breeding females). None of the daughters had bred prior to this experiment.

For most families, we collected data on the mother and the eldest daughter or the dominant member of the eldest female–female twin pair. In one family, however, the eldest daughter was behaviorally subordinate to a younger (by 5 months) sister, and the younger sister, but not the elder sister, conceived. Therefore, we collected data on the younger, more dominant daughter. Age at the outset of data collection in singly vs. plurally breeding families did not differ

significantly among mothers (69.0±4.2 vs. 72.6±7.1 months, respectively, mean±SEM; $T=0.45$, $df=13$, $P=0.663$), adult males (77.3±10.0 vs. 79.1± 10.8 months, respectively; $T=0.12$, $df=13$, $P=0.907$), or focal daughters (17.9±1.2 vs. 19.8±0.7 months, respectively; $T=1.27$, $df=13$, $P=0.227$). Female common marmosets can conceive as early as 11 months of age but do not attain full reproductive maturity until approximately 18 months (Abbott and Hearn, 1979). Marmosets were housed and maintained as previously reported (Saltzman et al., 1998), except that lights were on from 0700 h to 1900 h and animals were fed at 1230–1300 h.

All procedures were conducted in accordance with the *Guide for the Care and Use of Laboratory Animals* and were reviewed and approved by the Graduate School Animal Care and Use Committee of UW-Madison. WNPRC is accredited by AAALAC as part of the UW-Madison Graduate School.

Design

We commenced data collection on each family when we determined the mother and/or daughter to be pregnant, on the basis of uterine ultrasonography and plasma progesterone concentrations in twice-weekly blood samples (see below). Throughout the remainder of the pregnancy, we collected urine approximately once per week for analysis of chorionic gonadotropin (CG) and estradiol sulfate (E₂S) concentrations, and performed uterine ultrasonography once per month to confirm maintenance of the pregnancy, to determine the number of fetuses, and to measure biparietal diameters (BPDs). Beginning 2 weeks before each female's anticipated parturition date (determined by the date of ovulation as estimated from plasma progesterone concentrations, and confirmed by uterine ultrasonography), we conducted focal-animal behavioral observations (see below) on each focal female (mother+eldest daughter[s]) four times per week. Behavioral data collection continued on this schedule through the first 4 weeks following parturition or, in several cases, until all of the female's infants had died. Blood samples for analysis of plasma progesterone concentrations were collected twice each week, at 3- to 4-day intervals, from each female until she was determined to be pregnant, or throughout the study for nonbreeding daughters.

Focal-animal observations

We conducted focal-animal observations on mothers and daughters for 15 min per animal per day, 4 times per week: twice at approximately 0900–1200 h and twice at approximately 1400–1630 h. We always observed each mother and her daughter consecutively, with the order of observations balanced across days.

Behavioral data were collected by trained observers to whom the animals had been previously habituated, sitting quietly in full view of the animals. A variety of behaviors, including sexual, agonistic, affiliative, and maternal behaviors, were recorded on a laptop computer each time the focal female performed them to or received them from any cagemate or performed them towards animals in other cages. In addition, at 60-s intervals, upon an audible signal from a timer, we recorded how may infants, if any, each family member was carrying. Inter-observer reliability scores were determined as a composite for all behaviors scored and averaged 89.7±1.5%.

For this paper, we analyzed infant-carrying and female–female agonistic behaviors (vocal submit [ngä], facial submit, vocal threat [erh–erh], fight, attack, cuff, snap bite and ear-tufts flick; see Baker et al., 1999 for definitions); other behavioral data will be presented elsewhere. A marmoset was considered to be subordinate to another individual if she performed submissive behavior to, but did not receive submissive behavior from, the partner (de Waal, 1987; Rowell, 1974; Saltzman et al., 2004).

We colored marmosets' ear tufts (Redken Deco Color, Canoga Park, CA) to facilitate rapid and reliable identification of individuals. This procedure does not appear to alter the animals' behavior or endocrine function (Abbott, 1979). All infants of each breeding female were marked with the same color; thus, we did not differentiate among littermates but could distinguish among infants born to different females within the same family.

Collection of urine and blood samples

We collected urine samples following the procedures described by Saltzman et al. (2004). Briefly, we manually captured animals from their nest boxes at approximately 0645 h, prior to lights-on, and immediately placed each pregnant female in an individual urine-collection chamber, which had been attached to a cage wall inside the family's home cage the previous afternoon. Marmosets were released after at least 1 ml urine had been collected or after 1 h had elapsed, whichever occurred first. Urine was collected from urine-collection chambers by a sterile syringe, transferred to a polypropylene vial, and immediately placed on ice. We centrifuged urine samples at 5000 rpm for 5 min, transferred them to a clean vial, added glycerol (0.52 M; 50 µl per ml urine) to stabilize protein hormones (Livesey et al., 1983), and froze samples at −20 °C until they were assayed.

For collection of blood samples, we manually captured animals and briefly restrained them in a marmoset restraint tube (Hearn, 1977) while 0.1–0.3 ml blood was collected from the femoral vein into a heparinized syringe. This procedure is readily accommodated by marmosets in our colony and has not been found to elevate plasma cortisol levels (Saltzman et al., 1994). Blood samples were immediately placed on ice and centrifuged at 2000 rpm for 10 min, and the plasma fraction was extracted and frozen at −20 °C until assayed for progesterone.

Hormone assays

All hormone assays were fully validated for use with common marmoset plasma (Saltzman et al., 1994) or urine (Saltzman et al., 2004). We assayed plasma progesterone using enzyme immunoassay as previously described (Saltzman et al., 1994). Assay sensitivity was 3.6 pg/tube, and inter- and intra-assay coefficients of variation (CVs) of a marmoset plasma pool assayed in duplicate in each assay were 15.5% and 4.6%, respectively.

Urinary E₂S and CG were assayed in duplicate by radioimmunoassay as previously described (Converse et al., 1995; Saltzman et al., 2004; Ziegler et al., 1993). For E₂S, assay sensitivity was 10 pg/tube, and inter- and intra-assay CVs were 12.1% and 5.2%, respectively. For CG, assay sensitivity was 0.059 ng/ tube, and inter- and intra-assay CVs were 5.7% and 4.2%, respectively. To correct for differences in concentration of urine, urinary E₂S and CG concentrations were divided by creatinine concentrations in the same sample. We assayed creatinine in duplicate as described by Ziegler et al. (1995). Inter- and intra-assay CVs were 13.7% and 3.0%, respectively.

Monitoring of ovarian function and pregnancy

We considered marmosets to have ovulated on the day prior to a sustained (≥2 consecutive blood samples) increase in plasma progesterone concentrations above 10 ng/ml (Harlow et al., 1983). Following ovulation, females were considered to be in the luteal phase of an ovulatory cycle, or pregnant, until plasma progesterone levels fell below 10 ng/ml, and in the follicular phase until progesterone concentrations again rose above 10 ng/ml (Harlow et al., 1983). Marmosets were considered to be anovulatory if progesterone concentrations remained below 10 ng/ml for ≥30 days.

To confirm pregnancies, determine the number of fetuses, and measure BPDs, we performed uterine ultrasonography 20–27 days after each ovulation if plasma progesterone levels remained elevated (>10 ng/ml), and at approximately monthly intervals for the remainder of the pregnancy. Ultrasonography and assessment of pregnancy were performed as described previously (Saltzman et al., 1997b, 2004). The number of fetuses was determined ultrasonographically beginning at approximately day 86 of the 144-day gestation. BPD was determined by one investigator (D.H.A.) with each fetal skull in transverse section and the falx celebri in the field of view. Measurements were made using the ultrasound machine's internal calipers at the time of each female's exam. Ultrasonography performed at 4-week intervals or even more frequently throughout pregnancy does not significantly alter gestation length, inter-birth interval, or litter size in common marmosets (Jaquish et al., 1996; Oerke et al., 1995).

Monitoring of infant births and deaths

Each family was checked at least twice daily, at approximately 0730 and 1230 h, and births, deaths, injuries, and aggression were recorded. Infants were classified as stillborn if they were found dead shortly following birth and the lungs did not float in formalin. Among live-born infants, deaths were attributed

to infanticide if the infant was found dead with wounds on the head and/or body indicative of biting, or if the infant had to be euthanized as a result of such injuries. In most cases, these infants were found partly cannibalized (see Results). It is possible that wounding and cannibalism occurred following spontaneous death of infants; however, the rate of cannibalism in our colony is quite low: during the 3-year period in which this study was conducted, bite wounds and cannibalism were detected in only 20% of the live-born infants that died within 30 days of birth (and in only 5.5% of all live-born infants). Thus, infants that die spontaneously are unlikely to be cannibalized. Three live-born infants in this study were found dead with no sign of injury except that a distal part of the tail was missing. Because cannibalism of a distal portion of a newborn infant's tail is not uncommon in our colony and other captive marmoset colonies, and is not usually fatal (Tardif et al., 2003), and because cannibalism of the distal portion of the tail in these three animals was not associated with other injuries or hemorrhage, we did not attribute these three deaths to infanticide. These deaths, as well as deaths of live-born infants that were found with no external signs of injury, were classified as spontaneous mortality. Such deaths were often associated with poor nutritional status, as indicated by thinness and absence of milk in the stomach, as frequently occurs in at least one infant in triplet or quadruplet litters (see Tardif et al., 2003). Infants were euthanized if they were found wounded or weakened, as commonly performed as routine, humane management practice in marmoset colonies.

Analysis

When data were available from two pregnancies from an individual female within a particular condition (e.g., one mother had two pregnancies in a singly breeding family; two mothers each had two pregnancies in plurally breeding families), we used mean values from the two pregnancies; therefore, each female contributed no more than a single data point to each condition in each analysis. The only exceptions were analyses of fetal BPD, in which each fetus or litter was treated as an independent data point (see below).

For hormonal analyses we determined each female's peak urinary CG/Cr and E_2S/Cr value across pregnancy, as well as her mean value for each hormone for the second (days −96 through −49) and third (days −48 through −1) trimesters of pregnancy; little or no data were available from most pregnancies during the first trimester. We calculated individual females' rates of infant-carrying as the female's actual number of infant-scans carried (i.e., number of 1-minute scans in which infants were carried × number of infants carried per scan) divided by the total possible number of infant-scans (i.e., total number of 1-min scans × total number of infants present). Therefore, an animal that, for example, had two infants but carried an average of one infant on each scan would have a carrying rate of 0.5.

To control for possible effects of parity, we compared infant outcomes of primiparous females (daughters) in the present study with those of all other primiparous females from our marmoset colony during the 3 years in which this experiment was conducted. Data for these additional females were collected from WNPRC's computerized colony records database, and assessments of infanticide were based on necropsy reports using the criteria described above.

For most measures we initially compared singly breeding mothers, plurally breeding mothers, and plurally breeding daughters, using analysis of variance for endocrine data and Kruskal–Wallis tests for behavioral data and reproductive outcomes. Pairwise comparisons following significant Kruskal–Wallis tests were performed using the Nemenyi–Dunn procedure for nonparametric multiple
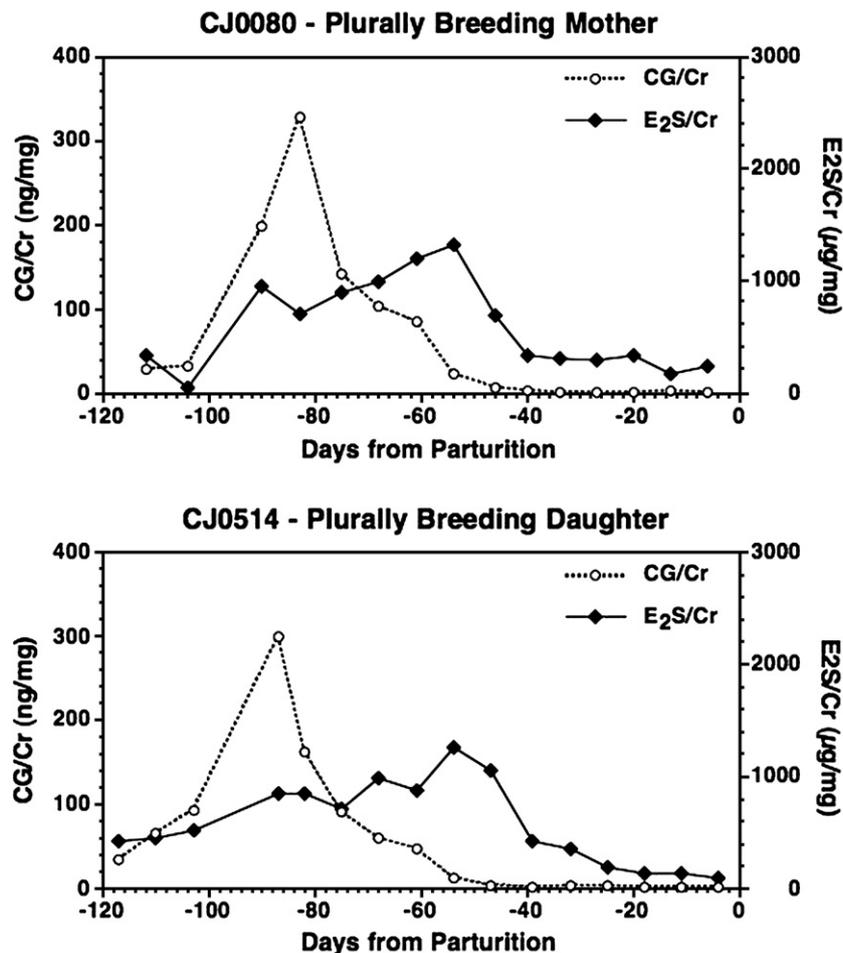

Fig. 1. Profiles of urinary chorionic gonadotropin (CG) and urinary estradiol sulfate (E_2S) concentrations, corrected for creatinine (Cr) concentrations, across pregnancy in two representative female marmosets. No significant differences in hormone concentrations were found among singly breeding mothers, plurally breeding mothers, and plurally breeding daughters.

Table 1
Comparison of urinary chorionic gonadotropin (CG) and estradiol sulfate (E$_2$S) concentrations (mean±SE), corrected for urinary creatinine concentrations, across pregnancy in singly breeding mothers, plurally breeding mothers, and plurally breeding daughters

Group	Peak CG concentration (ng/mg Cr)	Day of peak CG [a]	Mean CG – 2nd trimester (ng/mg Cr)	Mean CG – 3rd trimester (ng/mg Cr)	Peak E$_2$S concentration (μg/mg Cr)	Day of peak E$_2$S [a]	Mean E$_2$S – 2nd trimester (μg/mg Cr)	Mean E$_2$S – 3rd trimester (μg/mg Cr)
Singly breeding mothers (N=6)	155.1±32.3	−90.2±2.1	71.2±11.6	3.6±0.7	1380.2±212.3	−66.8±4.5	941.9±128.7	383.5±65.5
Plurally breeding mothers (N=6)	260.3±21.8	−89.6±2.5	120.3±17.5	3.1±0.2 [b]	1609.4±96.8	−64.2±4.7	1025.4±100.7	319.0±72.9 [b]
Plurally breeding daughters (N=7)	226.1±30.5	−86.7±2.1	112.0±19.3	3.8±0.8	1763.9±289.5 [c]	−59.4±2.9	1150.9±206.9	617.3±147.1
P value (1-way ANOVA)	.064	>0.5	>0.1	>0.7	>0.4	>0.4	>0.6	>0.1

[a] Number of days prepartum.
[b] N=5 due to missing data.
[c] N=6 due to missing data.

comparisons with unequal sample sizes (Zar, 1999). We analyzed fetal BPD by analysis of covariance, using number of days prepartum at the time of ultrasonography as a covariate. Statistical analyses were performed using Systat v. 5.2 for the Macintosh (SPSS, Chicago, IL), and results were evaluated at the 0.05 level (two-tailed).

Results

Endocrine profiles across pregnancy and fetal biparietal diameter

Representative profiles of urinary CG and E$_2$S concentrations across pregnancy are shown in Fig. 1, and hormonal data are summarized in Table 1. None of the endocrine parameters analyzed differed significantly among singly breeding mothers, plurally breeding mothers, and plurally breeding daughters (see Table 1). Peak urinary concentrations of CG, however, tended to differ among the three groups (P=0.064), probably resulting from somewhat lower values in singly breeding mothers compared to plurally breeding mothers and daughters that were without obvious detrimental consequences.

Similar to previous findings in common marmosets, urinary concentrations of CG, which is released by the placenta beginning about day 15–18 of gestation (Webley and Hearn, 1994), peaked approximately 85–95 days prepartum in most females and dropped to very low levels by approximately 45 days prepartum (Chambers and Hearn, 1979; Torii et al., 1989). Urinary concentrations of E$_2$S, reflecting circulating estradiol levels, were more variable but typically rose progressively until peaking at approximately 55–70 days prepartum, and declined progressively thereafter (Eastman et al., 1984; Torii et al., 1989).

Mean BPD of each litter, as determined in the last ultrasound exam performed during each pregnancy (range=1–33 days prepartum), increased across the final month of gestation (F [1,18]=52.512, P<0.0001). When corrected for number of days prepartum, mean BPD tended to differ among the three groups of females (F[2,18]=3.249, P=0.062), with litters of plurally breeding mothers having somewhat lower BPDs than those of both singly breeding mothers and plurally breeding daughters (adjusted least-squares mean±SE at 18.1 days prepartum: 16.2± 0.3 vs. 16.8±0.2 vs. 17.2±0.3 mm, respectively); however, these differences did not reach statistical significance.

Pregnancy outcomes

Pregnancy outcomes and infant mortality are described in detail for each family in Table 2 and are summarized in Table 3. The number of live-born infants per pregnancy did not differ reliably among singly breeding mothers, plurally breeding mothers, and plurally breeding daughters (Kruskal–Walllis H=3.88, df=2, P=0.144; see Table 3). Of the 25 pregnancies detected, 23 were carried to term and resulted in at least one live-born infant. No daughters and only three mothers gave birth to stillborn infants, each of which had two live-born littermates (see Table 2). Two mothers produced litters that were smaller (by one infant) than the litter size determined by ultrasonography during late pregnancy. Because we could not determine whether the missing infants were live-born or identify the cause of mortality, these infants were omitted from all subsequent analyses.

Pregnancy outcomes in common marmosets may be affected by maternal age and/or parity (Rico Hernández and Parás Garcia, 2001; Tardif and Bales, 2004; but see Jaquish et al., 1991; Rothe et al., 1992). Therefore, we compared pregnancy outcomes of plurally breeding, primiparous females (daughters) in this study with those of all singly breeding, primiparous females in our marmoset colony in the 3 years during which this experiment was conducted (N=23). The singly breeding, primiparous females produced 2.0±0.2 live-born infants in their first litter, which did not differ from the primiparous daughters in our experiment (Mann–Whitney U=120.000, df=1, P=0.176; Table 3).

Notes to Table 2:
[a] Infants designated as surviving reached at least 1 year of age.
[b] Ultrasonography (66 and 39 days prepartum) indicated quadruplets.
[c] Breeding male was euthanized 6/4/99 due to chronic illness.
[d] Breeding male was euthanized 7 days prior to birth due to illness.
[e] Ultrasonography (37 days prepartum) indicated triplets.

Table 2
Reproductive outcomes in each family in the Unrelated Male (UM) and Control (C) conditions

Breeding female	Condition	Parturition date/Litter size	Infant outcomes	Other female's reproductive status at parturition
CJ0216 (mother of CJ0466)	UM	Miscarried once during 1/19/99 to 2/15/99, and once during 4/13/99 to 5/13/99	N/A	N/A
CJ0466 (daughter of CJ0216)	UM	3/30/99 $N=3$	2 survived [a] 1 died spontaneously – 3/31/99	Mother pregnant ($\sim$104 days prepartum) or had already miscarried
CJ0310 (mother of CJ0462)	UM	1/7/99 $N=2$	2 survived	Daughter pregnant (136 days prepartum)
CJ0462 (daughter of CJ0310)	UM	5/23/99 $N=3$	3 infanticides – 5/23/99	Mother euthanized 28 days earlier due to illness
CJ0356 (mother of CJ0578)	UM	2/24/00 $N=3$ [b]	2 survived 1 stillborn	Daughter 25 days postpartum (no surviving infants); in luteal phase or early pregnancy (16 days post-ovulation)
CJ0578 (daughter of CJ0356)	UM	1/30/00 $N=2$	1 infanticide – 2/1/00 1 infanticide – 2/17/00	Mother pregnant (25 days prepartum)
CJ0080 (mother of CJ0472)	UM	3/24/99 $N=2$	1 survived 1 infanticide – 3/24/99	Daughter pregnant (41 days prepartum)
CJ0472 (daughter of CJ0080)	UM	5/4/99 $N=3$	1 survived 1 died spontaneously – 5/5/99 1 died spontaneously – 5/8/99	Mother 41 days postpartum (1 surviving infant), pregnant (120 days prepartum)
CJ0386 (mother of CJ0514)	UM	9/5/99 $N=3$	2 survived 1 died spontaneously – 9/6/99	Daughter 6 days postpartum (had 1 surviving infant, which died 3 days later); conceived $\sim$9/11/99.
CJ0514 (daughter of CJ0386)	UM	8/30/99 $N=2$	1 infanticide – 8/30/99 1 infanticide – 9/9/99	Mother pregnant (6 days prepartum)
CJ0388 (mother of CJ0528)	UM	9/28/99 $N=2$	1 infanticide – 9/28/99 1 infanticide – 9/29/99	Daughter pregnant (8 days prepartum)
CJ0528 (daughter of CJ0388)	UM	10/6/99 $N=2$	2 survived	Mother 8 days postpartum (no surviving infants), pregnant (conceived $\sim$10/6/99)
CJ0510 (daughter of CJ0234)	UM	7/26/99 $N=2$	1 survived 1 died spontaneously – 7/27/99	Mother euthanized 66 days earlier due to illness
CJ0270 (mother of CJ0532)	UM	10/2/99 $N=3$	1 infanticide – 10/2/99 1 infanticide – 10/3/99 1 died spontaneously – 10/4/99	Daughter pregnant (118 days prepartum)
CJ0270 (mother of CJ0532)	UM	3/11/00 $N=1$	1 survived	Daughter 43 days postpartum (2 surviving infants), entering an anovulatory period
CJ0532 (daughter of CJ0270)	UM	1/28/00 $N=3$	2 survived 1 infanticide – 1/28/00	Mother pregnant (43 days prepartum)
CJ0306	UM	1/21/00 $N=3$	2 survived 1 infanticide – 1/21/00	Daughter cycling (extended follicular phase)
CJ0300	UM	5/8/99 [c] $N=3$	1 survived 1 stillborn 1 infanticide – 5/8/99	Daughter cycling (follicular phase)
CJ0382	UM	1/28/00 $N=3$	2 survived 1 died spontaneously – 2/6/00	Daughter anovulatory
CJ0216	C	8/1/98 $N=3$	1 survived 1 stillborn 1 died spontaneously. – 8/2/98	Daughter *cycling (luteal phase)*
CJ0356	C	5/4/99 [d] $N=3$	2 survived 1 died spontaneously – 5/6/99	Daughter anovulatory
CJ0392	C	11/22/99 $N=2$	2 survived	Daughter anovulatory
CJ0306	C	5/27/99 $N=2?$ [e]	1 survived 1 infanticide – 5/27/99	Daughter anovulatory
CJ0130	C	11/21/99 $N=3$	2 survived 1 died spontaneously – 11/23/99	Daughter cycling (follicular phase)

Table 3
Summary of reproductive outcomes in mothers and daughters as a function of the reproductive status of the other adult female in the group

Group/Condition	Total # Females	# Live-born infants per pregnancy (mean±SE)	# Surviving infants per pregnancy (mean±SE)[a]	# Infanticides per live-born infant (mean±SE)
Mothers without a breeding daughter (singly breeding, multiparous)	7	2.5±0.2	1.6±0.2	0.1±0.1
Mothers with a breeding daughter (plurally breeding, multiparous)	7	1.9±0.4	1.1±0.4	0.3±0.2
Daughters with a breeding mother (plurally breeding, primiparous)	7	2.6±0.2	1.0±0.4	0.5±0.2
Other singly breeding, primiparous females in colony	23	2.0±0.2[b]	1.3±0.2[b]	0.1±0.1
Mothers and daughters without another pregnant female	10	2.3±0.3	1.6±0.2	0.1±0.1
Mothers and daughters with another pregnant female (<26 days)	5	2.4±0.2	1.8±0.2	0.0
Mothers and daughters with another pregnant female (≥26 days)	6	2.3±0.2	0.5±0.3	0.8±0.1

[a] Survived until ≥30 days of age.
[b] Excludes pregnancies that were spontaneously aborted.

Infant mortality

Of the 55 live infants born during the experiment, 29 (52.7%) survived to at least 1 year of age ("surviving infants"). The remaining infants died by 3 weeks of age as a result of infanticide ($N=16$) or spontaneous mortality ($N=10$). Neither the number of surviving infants per pregnancy (Kruskal–Wallis $H=3.88$, $df=2$, $P=0.394$) nor the proportion of live-born infants that were subject to infanticide in each litter (Kruskal–Wallis $H=0.38$, $df=2$, $P=0.376$) differed reliably among singly breeding mothers, plurally breeding mothers, and plurally breeding daughters (Table 3). Among primiparous females only, the number of infants that survived to at least 30 days of age did not differ among plurally breeding daughters in this study and singly breeding, primiparous females in our colony (Mann–Whitney $U=73.00$, $N=8,23$, $P=0.361$); however, plurally breeding daughters tended to lose more of their infants to infanticide than did singly breeding, primiparous females (Mann–Whitney $U=61.50$, $N=8,23$, $P=0.085$; see Table 3).

To determine whether infants may have been targeted for infanticide as a result of abnormally small body size or poor physical condition, we compared BPD, as determined in the last ultrasound exam performed during each pregnancy, of fetuses whose litters did and did not include at least one infant that was killed. We performed these analyses using BPDs of individual fetuses as well as mean BPD for each litter, with number of days prepartum as a covariate. Both analyses indicated that BPD did not differ between litters that were and were not subject to infanticide (individual BPDs – adjusted least-squares mean±SE at 18.0 days prepartum: $16.5±0.3$ vs. $16.7±0.2$ mm, respectively; $F[1,56]=0.002$, $P=0.964$; mean BPD per litter – adjusted least-squares mean±SE at 17.6 days prepartum: $16.6±0.5$ vs. $16.7±0.3$ mm, respectively; $F[1,20]=0.000$, $P=0.995$).

Inspection of the data indicated that infanticide occurred frequently when either a mother or daughter gave birth while another female in the group was at least 26 days pregnant, but rarely under all other conditions (Mann–Whitney $U=7.00$, $N=14,6$, $P=0.002$). Among litters that were born when no other female in the family was pregnant, $11.3\%±7.4\%$ (mean±SEM per litter) of live-born infants fell victim to infanticide. Infanticide occurred in two families in which only the mother bred (including two litters in one family), as well as in one of the two families in which a daughter gave birth following the death of her mother. Infanticide did not occur in any of the five litters ($N=3$ born to mothers, 2 born to daughters) born while another female in the family was in the initial stages (first 24 days) of pregnancy or shortly ($≤1$ week) before she conceived; in four of these five families, the newly pregnant female was also 6–41 days postpartum.

In contrast, among births that occurred while another female in the group was at least 26 days pregnant, $75.0\%±12.0\%$ of live-born infants in each litter were subject to infanticide. At least one infant was killed in each of these six litters, regardless of whether they were born to mothers ($N=3$ litters) or daughters ($N=3$ litters). The rate of infanticide among litters of daughters with pregnant mothers was markedly higher than among litters of singly breeding, primiparous females in our colony during the same time period (Mann–Whitney $U=5.000$, $N=3,23$, $P=0.004$; Table 3). Among the mothers' offspring, infanticides were not reliably predicted by the occurrence of infanticides in previous litters: of the 5 mothers who had at least one infant killed in this study, only one (which had a pregnant daughter) had had an infant killed previously. Three additional mothers lost offspring to infanticide in previous litters but not in the present study.

Infanticides

Infanticide usually occurred during the first 1–2 days after birth (13 of 16 infants; 81.3%; see Table 2). We were able to definitively identify the perpetrator in only one instance, when a late-pregnant mother (7 days prepartum) attacked the 18-day-old infant of her daughter while the two were alone together in a nestbox. The same pregnant female had been found carrying and eating this infant's newly dead twin 16 days earlier.

We found no evidence that male or female infants were preferentially targeted for infanticide: among the 10 litters in which at least one infanticide occurred, $75.0\%±13.4\%$ of male infants and $50.0\%±18.3\%$ of female infants per litter were killed (Mann–Whitney $U=35.00$, $N=8,6$, $P=0.309$). Similar results were obtained when we analyzed only the six litters in which at least one infanticide occurred in plurally breeding groups ($80.0\%±20.0\%$ of male infants vs. $60.0\%±18.7\%$ of female infants per litter; Mann–Whitney $U=16.50$, $N=5,5$, $P=0.343$). Twelve of the 16 cases of infanticide involved can-
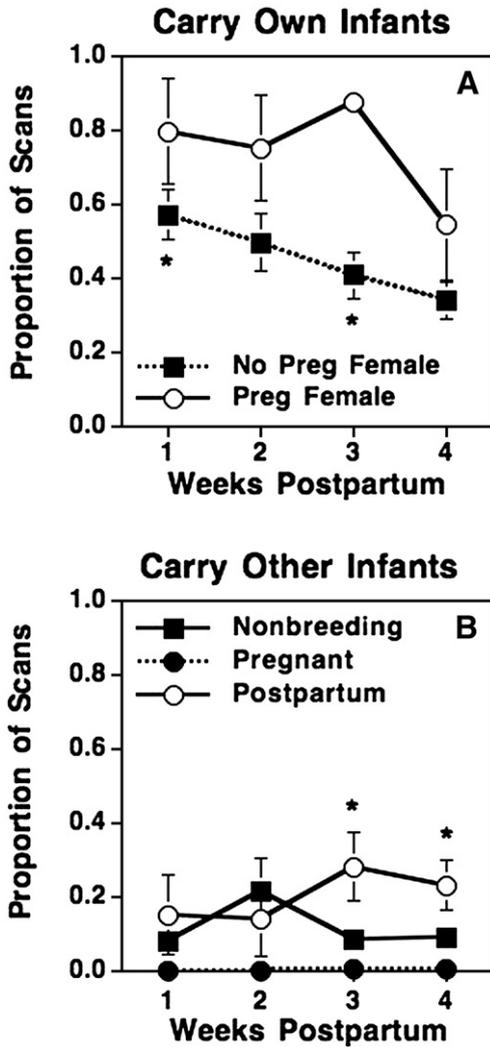
Fig. 2. Proportion of 1-min scans (mean±SEM; corrected for number of infants) in which (A) plurally breeding female marmosets living either with or without a pregnant (≥26 days postconception) female carried their own infants during the first 4 weeks after birth, or (B) pregnant (≥26 days postconception) or postpartum females in plurally breeding families and non-breeding daughters in singly breeding families carried another female's infant(s) during the first 4 weeks after birth. *P<0.05 between groups.

nibalism, which was overwhelmingly focused on the infant's face or head (11 of 12 infants; 91.7%).

Maternal behavior

Females carried their own infants at very high rates during the first week after birth and at progressively lower rates during the subsequent 3 weeks. Singly breeding mothers, plurally breeding mothers, and plurally breeding daughters did not differ in their rates of carrying their own infants in each week (*P* values >0.1). Females that gave birth while a groupmate was pregnant (≥26 days postconception), however, carried their own infants more than did other females; this difference was significant in the first and third weeks postpartum (week 1: Mann–Whitney $U=16.00$, $N=13,6$, $P=0.044$; week 3: Mann–Whitney $U=3.00$, $N=13,3$, $P=.026$; Fig. 2A).

Allomaternal behavior

To determine whether females' allomaternal behavior was influenced by their reproductive status and might be associated with reproductive competition, we compared rates at which pregnant (≥26 days) and postpartum females in plurally breeding families, and nonbreeding daughters in singly breeding families, carried other females' infants during the first 4 weeks of life. In week 1, all three groups carried other females' infants at very low rates. Subsequently, however, all nonbreeding and postpartum females began to carry infants, whereas pregnant females almost never did so (Fig. 2B). Consequently, carrying rates differed among the groups marginally in week 2 (Kruskal–Wallis $H=5.70$, $df=2$, $P=0.058$) and significantly in weeks 3 (Kruskal–Wallis $H=7.91$, $df=2$, $P=0.019$) and 4 (Kruskal–Wallis $H=6.61$, $df=2$, $P=0.037$). Post hoc tests revealed that in both week 3 (*P*<0.02) and week 4 (*P*<0.05), pregnant females carried other females' infants significantly less often than postpartum females, while
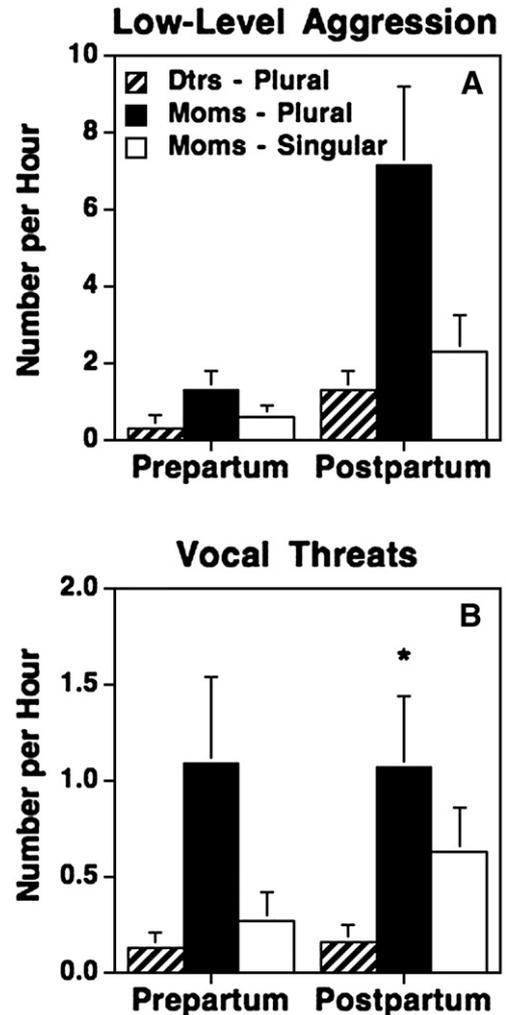

Fig. 3. Hourly rates (mean±SEM) of (A) low-level aggressive behaviors (cuff+ snap bite+ear-tufts flick) and (B) vocal threats performed by mothers and breeding daughters to one another in plurally breeding families, and by mothers to their nonbreeding adult daughters in singly breeding families during the 2 weeks before and 4 weeks after giving birth. *P<0.05 among groups.

nonbreeding daughters carried their mothers' infants at intermediate rates.

Two females produced surviving infants in only two families. In both of these families, each female was observed nursing the other's infant(s) on at least one occasion.

Agonism between adult females

In singly breeding families, agonism between mothers and their oldest daughters during the mother's peripartum period (2 weeks before through 4 weeks after parturition) was mild and infrequent. No fights and only six attacks (including five by one mother) were observed. Nonetheless, each of these seven mothers was clearly dominant to her nonbreeding daughter: each daughter performed submissive behavior (vocal submit, facial submit) toward her mother on multiple occasions, whereas none of the mothers was ever observed submitting to her daughter.

In plurally breeding families, in contrast, dominance could not be determined reliably between mothers and their breeding daughters. Only two of these seven mothers and two of seven daughters submitted to their female groupmate during focal-animal observations. As in the singly breeding families, escalated aggression was rare: in one family, routine monitoring of the animals revealed that the mother and daughter (CJ0388 and CJ0528; see Table 2) fought when they were 56 and 64 days prepartum, respectively, followed by a brief period during which the mother submitted repeatedly to the daughter. In a second family, on the day after the daughter gave birth she attacked her mother (CJ0514 and CJ0386, respectively; see Table 2) and the two fought briefly, again followed by a brief period during which the mother submitted repeatedly to her daughter.

Because all aggressive behaviors except vocal threats (erh–erh) occurred very infrequently, we combined several low-level aggressive behaviors (cuff, ear-tufts flick, and snap bite) for analysis and calculated mean rates for each female's last 2 weeks prepartum and first 4 weeks postpartum. Rates of low-level aggression tended to differ among singly breeding mothers, plurally breeding mothers, and plurally breeding daughters, both prepartum (Kruskal–Wallis $H = 5.55$, $df = 2$, $P = 0.062$) and postpartum (Kruskal–Wallis $H = 5.21$, $df = 2$, $P = 0.074$), with breeding daughters performing fewer aggressive behaviors towards their mothers than either singly or plurally breeding mothers performed toward their daughters; however, these differences did not reach statistical significance (Fig. 3A). Similarly, rates of vocal threats differed reliably among groups after (but not before) parturition (Kruskal–Wallis $H = 7.06$, $df = 2$, $P = 0.029$), as breeding daughters threatened their mothers significantly less often than plurally breeding mothers threatened their daughters ($P < 0.05$; Fig. 3B).

Discussion

Infanticide as a female reproductive strategy

The major finding of this study was that infanticide occurred frequently in common marmoset groups containing two breeding females, particularly when one female gave birth while another was pregnant. In each of the six litters born under these conditions, at least one infant was killed, with a total of 10 out of 14 live-born infants in these litters falling victim to infanticide. These results are surprising in view of the high degree of attraction to infants typically exhibited by both male and female marmosets of all ages, as well as the high relatedness within marmoset groups. Nonetheless, our results are consistent with anecdotal reports from both laboratory (Alonso, 1986; Kirkpatrick-Tanner et al., 1996) and field studies (Bezerra et al., 2007; Digby, 1995a; Lazaro-Perea et al., 2000; Roda and Mendes Pontes, 1998; Sousa et al., 2005) that pregnant marmosets may kill infants born to their groupmates. The present findings thus provide the first clear indication that pregnant marmosets might in fact commit infanticide *routinely* in plurally breeding groups.

Infanticide by breeding females may be relatively common among cooperative breeders. Empirical studies in a wide variety of these species indicate that when two or more females breed concurrently, they often destroy each other's eggs or kill each other's offspring (e.g., social insects: Eggert and Müller, 2000; Keeping, 1992; Ratnieks and Visscher, 1989; birds: Mumme et al., 1983; Vehrencamp, 1977; rodents: Elwood, 1977, 1980, 1981; carnivores: Clutton-Brock et al., 1998; Corbett, 1988; Packer and Pusey, 1984; Rasa, 1987). Although infanticide is likely to be more common among unrelated females, even closely related females may kill one another's offspring (Mumme et al., 1983; Packer and Pusey, 1984; see also Hager and Johnstone, 2004). Moreover, recent theoretical models suggest that infanticide by females can play a key role in generating high reproductive skew in cooperatively breeding species (Hager and Johnstone, 2004) and may be an evolutionarily stable strategy (Tuomi et al., 1997).

Of the 16 inferred infanticides in our study, only one could be attributed unambiguously to a specific perpetrator (the infant's late-pregnant grandmother). Therefore, although infants were killed significantly more often in families containing pregnant females than in other families, we cannot conclude definitively that the infanticides were committed primarily by pregnant females. This possibility is, however, consistent with available evidence. First, as described above, pregnant females have been observed or strongly inferred to kill their groupmates' infants in studies of both captive and free-living common marmosets, most of which have been reported since the completion of our study. In contrast, we are not aware of any observations of male or nonbreeding female common marmosets killing infants in the field. Second, we have found that multiparous female common marmosets exhibit reduced attraction to and tolerance of unfamiliar infants during pregnancy, as compared to the early postpartum period, and that this pattern is especially pronounced during late pregnancy: in a recent study, most females in the third trimester of pregnancy never retrieved an unfamiliar infant that was introduced into their home cage, and those that did so rejected the infant rapidly and aggressively (Saltzman and Abbott, 2005). Third, infanticide in singly breeding families occurs relatively rarely in our colony (5.5% of 202 infants born over a 3-year period) and other laboratory colonies (e.g., 7% of infants in Bardi and Petto, 2002) and may occur primarily under

disturbed or highly stressful conditions, such as during continuous exposure to loud noise (Johnson et al., 1991) or prolonged illness in a parent (Saltzman and Abbott, unpublished observations).

Several authors (e.g., Clutton-Brock et al., 1998; Digby, 2000; Packer and Pusey, 1984) have argued that infanticide by female marmosets and other cooperative breeders is most likely a form of resource competition, by which perpetrators eliminate competition for resources needed by their own infants (e.g., food or alloparents; see Hrdy, 1979). Our finding that marmoset infants are most likely to be killed in groups containing two breeding females, and especially in groups containing a late-pregnant female, is consistent with this possibility. Our results also, however, support the "exploitation hypothesis" of infanticide (Hrdy, 1979), which posits that breeding females kill infants as a source of nutrition. Most of the infanticides in this study involved cannibalism, similar to several (but not all) observations of wild marmosets (Bezerra et al., 2007; Lazaro-Perea et al., 2000, Melo et al., 2003; see also Kirkpatrick-Tanner et al., 1996). Notably, the pattern of cannibalism most commonly observed in our study – focused on the face and head, with the rest of the body left largely intact – is strikingly similar to a case of infanticide and cannibalism that was recently observed (and filmed) in free-living marmosets (Bezerra et al., 2007; see also Kirkpatrick-Tanner et al., 1996; Melo et al., 2003). Cannibalism performed primarily by breeding females would be consistent with the increased energetic requirements of these females (Nievergelt and Martin, 1999). Clearly, additional field studies will be needed in order to clarify the precise role of infanticide by breeding female marmosets in resource competition, resource exploitation, or other functions.

Reproductive competition and pregnancy outcomes

Another unexpected finding of our study, in addition to the high rate of infanticide, was that breeding females did not appear to influence one another's ability to maintain pregnancy or produce live infants. Captive common marmosets may exhibit relatively high rates of miscarriage and prenatal litter reduction during both the embryonic and fetal stages, a pattern that is thought to represent adaptive reproductive flexibility during pregnancy in response to environmental variables (Heger et al., 1988; Jaquish et al., 1996; Tardif et al., 2003; Windle et al., 1999). In the present study, nonetheless, when two females conceived in the same group, we found no evidence that their pregnancies were affected by reproductive competition. Rates of spontaneous abortion, stillbirth, and, apparently, prenatal litter reduction – at least during approximately the last 60 days or so of pregnancy, during which we could reliably count fetuses – were very low under all conditions. Moreover, neither the number of live-born infants per pregnancy nor fetal size (as reflected in biparietal diameter) differed reliably between mothers and daughters or between singly and plurally breeding females. The findings on fetal size should be interpreted cautiously, as the time point at which it was characterized (1–33 days prepartum) differed substantially among litters, and as we used only a single measure of fetal growth. Nonetheless, consistent with these results, we found no significant differences in urinary chorionic gonadotropin or estradiol sulfate concentrations during gestation. Finally, routine monitoring of animals throughout pregnancy, as well as systematic behavioral observations during the last 2 weeks of gestation, indicated that escalated aggression between breeding females occurred relatively infrequently during this time, suggesting that breeding females do not commonly harass or try to evict one another during gestation. In sum, these results indicate that female marmosets in plurally breeding groups do not routinely interfere with one another's pregnancies.

These findings contrast with those from several other cooperatively breeding mammals, in which pregnant subordinates may exhibit altered endocrine function and elevated miscarriage rates. In wild golden lion tamarins (*Leontopithecus rosalia*), for example, fecal estrogen metabolite concentrations have been found to be higher in pregnant subordinates than in pregnant dominants (French et al., 2003). Although the functional significance of this difference, if any, is unknown, elevated prepartum estradiol or estrogen metabolite concentrations may be associated with low neonatal weights (Bales et al., 2002), reduced infant survivorship (Fite and French, 2000), and either diminished or enhanced maternal behavior postpartum (Fite and French, 2000; Pryce et al., 1988) in some callitrichines. In other species, aggression among breeding females appears to increase rates of pregnancy loss in subordinates (e.g., meerkats, *Suricata suricatta*: Young et al., 2006; Alpine marmots, *Marmota marmota*: Hackländer et al., 2003; golden hamsters, *Mesocricetus auratus*: Huck et al., 1983; yellow baboons, *Papio cynocephalus*: Wasser and Starling, 1988). Given such clear effects of female reproductive competition on pregnancy outcomes in other species, it remains unclear why breeding female marmosets fail to systematically direct aggression toward or affect pregnancy in their competitors. One possible explanation is that because dominance relationships between breeding female marmosets may not be well defined, and because common marmosets do not form agonistic alliances, the outcome of such aggression might be unpredictable and therefore highly risky for either breeding female.

Dominance relationships between breeding females

In the present study, as in previous studies of these same families (Saltzman et al., 2004) and other families in our colony (Saltzman et al., 1997b), all non-breeding focal daughters behaved submissively toward their mothers and were therefore considered subordinate by our criterion of unidirectional submissive behavior between two animals (de Waal, 1987; Rowell, 1974). In plurally breeding families, in contrast, dominance relationships between breeding females were not well defined, as previously noted in these same families before and around the time of conception (Saltzman et al., 2004; see also Saltzman et al., 1997b). Mothers consistently performed more low-level aggression and vocal threats to their breeding daughters than vice versa, but these mothers and daughters rarely, if ever, submitted to one another. (In one family, the mother and daughter submitted to one another at different times, with each female doing so primarily when only the other female had live

infants present. In two other families, either the mother or daughter submitted on one or two occasions.) Among free-ranging marmosets, dominance relationships have frequently been identified between breeding female groupmates; however, assessment of these relationships is typically based on the direction and frequency of aggressive, sexual, and even affiliative behavior in addition to submissive behavior (e.g., Arruda et al., 2005; Bezerra et al., 2007; Digby, 1995b; Lazaro-Perea et al., 2000; Sousa et al., 2005). On the basis of aggressive behavior alone, all of the mothers in our plurally (and singly) breeding groups would have been considered dominant to their daughters.

In our study, the presence of another pregnant female in the group, rather than the breeding female's position in the family, was the major determinant of infant survivorship; infants born to daughters and those born to mothers were equally vulnerable to infanticide. Among wild marmosets, in contrast, most observed infanticides have been performed by dominant females (Arruda et al., 2005; Digby, 1995a; Lazaro-Perea et al., 2000; Sousa et al., 2005). Nonetheless, pregnant subordinates have been observed to kill dominant females' infants in at least two wild groups (Bezerra et al., 2007; Roda and Mendes Pontes, 1998). Interestingly, both of these subordinates attained the dominant position in their groups shortly thereafter.

Proximate and ultimate causes of reproductive skew

Results of the present study, together with previous findings in female marmosets, may offer new insight into the evolution of reproductive strategies in high-skew societies. Most subordinate female common marmosets do not breed, as a result of ovulation suppression and inhibition of sexual behavior (Abbott et al., in press; Saltzman, 2003). These pre-conception mechanisms limiting reproduction are not associated with generalized stress or overt aggression, and may be terminated rapidly – even in the presence of a dominant female – when conditions become more favorable for breeding (e.g., an unrelated male joins the group) (Abbott et al., 1997; Saltzman, 2003). Consequently, we and others have argued that pre-conception reproductive inhibition in subordinate female marmosets is not imposed on them by dominant females but instead is mediated by self-restraint (Abbott et al., 1997; Saltzman, 2003; Snowdon, 1996; Yamamoto et al., in press).

Several recent models of reproductive skew suggest that reproductive self-restraint in subordinate cooperative breeders may be adaptive when dominants are able to "punish" subordinates that attempt to breed, either by harassing or evicting them or by making their reproductive attempts costly or risky (Crespi and Ragsdale, 2000; Hager and Johnstone, 2004; Hamilton, 2004; Johnstone and Cant, 1999). Consistent with these models, the present findings suggest that while breeding female marmosets may be unable to prevent conceptions or impair pregnancy outcomes in their groupmates, they may commonly kill other females' infants. Thus, our findings indicate that control by dominant (or breeding) females, in addition to self-restraint by subordinate (or non-breeding) females, may play a key role in maintaining reproductive skew. In addition,

these findings raise the intriguing possibility that infanticide may play a critical role in selecting for reproductive self-restraint in female marmosets living with a breeding female.

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