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RESEARCH ARTICLES

Familial Influences on Ovulatory Function in Common Marmosets (*Callithrix jacchus*)

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Previous studies have indicated that many, but not all, female common marmosets (*Callithrix jacchus*) housed with their natal families undergo social suppression of ovulation. In this study, we further characterized ovulatory activity in common marmoset daughters to determine the prevalence of social suppression of ovulation and to elucidate familial influences on daughters' ovarian activity. Blood samples were collected twice weekly from each of 46 daughters for 5–12 months, usually beginning when the daughters were 12 months of age. Plasma progesterone concentrations indicated that 46.3% of daughters in intact natal families ovulated at least once, with the age at first ovulation averaging 17.2 months; however, none of these daughters became pregnant. Daughters' ovulatory cycles showed several significant differences from those of older females housed with unrelated adults, including longer periods between successive luteal phases, shorter luteal phases, and lower peak and mean luteal-phase progesterone levels. Daughters were significantly more likely to ovulate in families in which the mother was experimentally prevented from sustaining pregnancies, and in families in which the father had been replaced by an unrelated adult male and when the daughter was approximately 10–11 months of age. Daughters in families containing an older sister never ovulated; in contrast, those with a female littermate were not less likely to ovulate than were other daughters, but had more sporadic ovarian cycles and significantly lower mean luteal-phase progesterone levels. These results confirm and extend previous findings that up to half of female common marmosets may ovulate while housed with the natal family but that virtually none sustain pregnancies, suggesting that suppression of ovulation is only one of several components of reproductive failure. Furthermore, these results demonstrate that daughters' likelihood of ovulating, as well as the endocrine profiles of their ovulatory cycles, can be modulated by numerous social influences within the family. Am. J. Primatol. 41:159–177, 1997. © 1997 Wiley-Liss, Inc.

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INTRODUCTION

Marmosets and tamarins (Callitrichidae) exhibit a cooperative breeding system, in which mature offspring remain with the natal family and serve as non-reproductive “helpers at the nest” [Goldizen, 1987; Sussman & Garber, 1987]. Social groups range in size from approximately three to 15 individuals, often including several adults of each sex [reviewed by Ferrari & Lopes Ferrari, 1989]; typically, however, only the most dominant female breeds [reviewed by Abbott et al., 1993; French, 1996]. Several different mechanisms have apparently evolved by which reproduction is inhibited in socially subordinate females. Among golden lion tamarins (*Leontopithecus rosalia*), for example, behavioral inhibition appears to be the primary mechanism of reproductive suppression: adult-aged daughters typically undergo ovulatory cycles while housed with the natal family, but rarely engage in sexual behavior or sustain pregnancies [Hoage, 1982; French & Stribley, 1987; French et al., 1989; Dietz & Baker, 1993]. Among cotton-top tamarins (*Saguinus oedipus*), in contrast, the principal block to reproduction is physiological: adult-aged daughters virtually never ovulate while housed with the natal family [French et al., 1984; Tardif, 1984; Ziegler et al., 1987; Savage et al., 1988; Widowski et al., 1990, 1992; Snowdon et al., 1993]. This suppression of ovulation appears to be mediated by signals from the mother; in several studies, daughters have been found to ovulate following the mother’s death [French et al., 1984; Heistermann et al., 1989; but see Tardif, 1984].

In contrast to both golden lion tamarins and cotton-top tamarins, female common marmosets (*Callithrix jacchus*) housed with their natal families show pronounced variability in ovulatory function. Evans & Hodges [1984] found no evidence of ovulation in six female marmosets housed with their natal families, although two of these females ovulated shortly after removal from their families. Abbott [1984], however, found that a daughter ovulated in eight of 17 families. Finally, Hubrecht [1989] detected ovulatory cycles in two of four females housed in intact natal families and in two of two females living in families in which the father had died. Together, these findings indicate that many, but not all, female common marmosets undergo social suppression of ovulation while housed with the natal family. This conclusion must be considered tentative, however, as a result of the limitations of the three data sets: small sample sizes were used in two of the studies [Evans & Hodges, 1984; Hubrecht, 1989], and in the third, blood samples were collected from each daughter over a relatively short period of time [Abbott, 1984]. Nonetheless, these findings are consistent with recent field studies, in which several groups of common marmosets contained two breeding females [Roda & Roda, 1987; Scanlon et al., 1988; Digby & Ferrari, 1994; Mendes Pontes & Monteiro da Cruz, 1995].

Anovulation in common marmoset daughters appears to be caused by suppressed release of luteinizing hormone (LH) from the pituitary: circulating LH levels in daughters are low and acyclic, compared to those in females undergoing ovulatory cycles, and show a poor response to exogenous gonadotropin-releasing hormone [Abbott, 1993]. The sources of inter-animal variation in the suppression of ovulation and, presumably, of LH release are unknown. Because suppression typically appears to occur in response to cues from the mother, we recently compared daughters that were and were not undergoing ovulatory cycles in their natal families to determine whether they differed in their behavioral interactions with their parents [Saltzman et al., 1997]. However, the two groups of daughters showed no significant differences in their social interactions with the mother and only minor differences in their interactions with the father, suggesting that differences in the quality of daughters' relationships with their parents did not explain differences in ovulatory activity.

Another factor that has been implicated in suppression of ovulation in female callitrichids is dominance relationships among sisters. For example, Heistermann et al. [1989] found that in each of four families of cotton-top tamarins in which the mother had died, only the oldest, most dominant daughter ovulated. Moreover, Snowdon et al. [1993] found that urinary concentrations of LH and estrone glucuronide (E_1G) were lower in cotton-top tamarin daughters living with an older sister than in those with no older sister present in the family.

Ovarian function in daughters may also be influenced by the mother's reproductive state. In free-ranging, polygynous groups of common marmosets, Digby [1995] found that offspring of subordinate females survived only if they were born at least 40 days before or after the birth of the dominant female's offspring; infants born to subordinate females within 30 days of the dominant female's parturition invariably died. Thus, it might be anticipated that subordinate females would be less likely to conceive, and perhaps to ovulate, in the period just before or after the dominant female's post-partum ovulation than at other times. Consistent with this possibility, Snowdon et al. [1993] reported that urinary LH and E_1G levels of anovulatory female cotton-top tamarins housed with the natal family declined significantly in the 3 weeks following the mother's parturition; the authors interpreted this phenomenon as a mechanism preventing reproductive competition between mother and daughter during the mother's post-partum ovulation and conception. In several other cooperatively breeding species, however, subordinate females exhibit ovulatory or birth synchrony with the dominant female [e.g., African wild dog, *Lycaon pictus*: Frame et al., 1979; dwarf mongoose, *Helogale parvula*: Rood, 1980; golden lion tamarin: French & Stribley, 1987], possibly reflecting seasonal constraints on reproduction or benefits associated with communal nursing, joint defense of offspring, or reduced energetic demands on mothers [French, 1994].

Finally, ovarian activity in marmoset daughters seems likely to be influenced by exposure to an unrelated adult male. Female cotton-top tamarins ovulate more quickly, following removal from the natal family, if they are pair-housed with an unrelated male than if housed with familiar males or in isolation [Ziegler et al., 1987; Widowski et al., 1990, 1992]. Moreover, in common marmosets and several other species of callitrichids, daughters appear to be more likely to engage in sexual behavior and to breed in families in which the father has been replaced by an unrelated male than in intact natal families [reviewed by French, 1996]. However, the effect of replacement of the breeding male on ovulatory function in daughters has not been investigated systematically.

The present study was designed to further characterize ovulatory activity in common marmoset daughters and to investigate the proximate sources of variation in social suppression of ovulation. In contrast to previous studies, we used a large number of daughters and collected endocrine data from each one on a systematic basis over a prolonged period of time. This design allowed us to determine the age at first ovulation, to characterize the endocrine parameters of ovarian cycles, and to assess possible familial influences—including the mother's reproductive state, the presence and sex of siblings, and the presence of an unrelated male—on ovulatory function in daughters.

METHODS

Animals and Housing

Subjects were 46 female common marmosets (*C. j. jacchus*) from 16 families. Forty animals were 12.0–12.5 months of age when data collection began, five were 12.5–13.1 months old, and one was 16.6 months old. Most subjects were housed with their natal families, including the mother, father, and up to eight siblings. However, three subjects were housed with the mother, up to three siblings, and an unrelated adult male that had been introduced when the subjects were 10.5–11.2 months old, following the death or removal of the father. Fathers of another two subjects died when the females were 14.5 and 16.4 months old, respectively, and were not replaced by another adult male.

Common marmosets typically give birth to fraternal twins at 5- to 6-month intervals, and we usually remove animals from their natal families at approximately 18–22 months of age. Twenty-three of the subjects had no older sisters present in the family at any time during their lives; the remaining 23 subjects, along with their co-twins, were usually the oldest offspring remaining in their families by 14 months of age (12.2 ± 0.7, mean ± SEM). At the outset of data collection, 17 subjects had a male co-twin living with the family, 14 had a female co-twin, 10 had no littermates, three were a set of female-female-female triplets, and two were from a female-female-male triplet set. No supplemental feeding was instigated following any births.

For colony management purposes, the mothers of 22 subjects were prevented from sustaining pregnancies during at least part of the period of data collection. To accomplish this, we gave each mother an injection of cloprostenol sodium, a prostaglandin F2α analog (Estrumate, Mobay Corp., Shawnee, KS; 0.75 μg, i.m.), at approximately monthly intervals to cause luteolysis and termination of the luteal phase or early pregnancy [Summers et al., 1985]. Mothers of 34 subjects (including 10 mothers that received at least one cloprostenol injection) gave birth at least once during the period of data collection.

In addition to the females housed with their natal families, 14 females that were housed in male-female pairs or that were dominant in mixed-sex groups of unrelated adults were used to provide comparison data. These animals were 23.0–53.1 months of age (36.7 ± 2.2 months) and included six females that had also served as subjects while housed with the natal family; appropriate data from pair- or group-housed animals of the same ages as the daughters were not available. We selected for analysis only those ovarian cycles that ended spontaneously, e.g., without cloprostenol treatment or imposition of subordinate social status.

Marmoset families were housed in stainless steel and wire mesh cages (61 × 91 × 183 cm or 122 × 61 × 183 cm) from which they could see, hear, and smell conspecifics in other cages. For 12 subjects, however, visual access to conspecifics in other cages was minimized for a period of 3–6 months during data collection; this had no discernible effect on the animals' ovarian activity. Cages housing pairs or groups of unrelated adults were identical to those housing families, except that they measured either 61 × 91 × 183 cm or 61 × 61 × 183 cm. Additional information on housing and maintenance of marmosets is provided elsewhere [Saltzman et al., 1997].

Blood Sample Collection, Progesterone Assay, and Pregnancy Detection

Subjects were blood sampled twice each week, at 3- to 4-day intervals, for 4.9–12.4 months (7.7 ± 0.3 months). Animals were manually captured from the home cage and placed in a marmoset restraint tube [Hearn, 1977], and 0.1–0.3 ml blood was collected by femoral puncture into a heparinized syringe. Marmosets received a liquid nutrient treat (Ensure, Abbott Laboratories, Columbus, OH) immediately following blood sample collection and were returned to the home cage approximately 5–10 min following initial capture. This procedures does not elevate plasma cortisol levels and is readily accommodated by marmosets [Saltzman et al., 1994]. Samples were stored on ice and centrifuged at 2,000 rpm, and the plasma fraction was aliquotted and frozen at –20°C.

Plasma progesterone was assayed using a heterologous enzyme immunoassay [Saltzman et al., 1994]. The intra- and inter-assay coefficients of variation of a marmoset plasma pool (38% binding) assayed in duplicate on each plate were 2.79 and 12.12%, respectively ($N = 126$ assays). When a subject's plasma progesterone concentrations remained elevated (> 10 ng/ml) for longer than 30 days, ultrasonography was performed as described previously [Saltzman et al., 1997] to determine whether the animal was pregnant.

Analysis

For calculation of ovarian cycle parameters, plasma progesterone values were graphed and the days on which progesterone concentrations first rose above 10 ng/ml and first fell below this level were extrapolated for each cycle. The day of each ovulation and the duration of each luteal phase, non-luteal period, and inter-luteal period were calculated using the operational definitions in Table I. Luteal phase parameters were calculated only for those ovulatory cycles that were completed while the subject was housed with the natal family.

We estimated the timing of mothers' post-partum ovulations for analyses of maternal influences on daughters' ovulations. To do this, we determined the mean inter-birth interval (IBI) for each of the six mothers whose daughters were included in the analysis, using only conceptions that appeared to have occurred on the first ovulation following parturition (IBI ≤ 183 days; 20 IBIs). We then averaged the six mothers' mean IBIs to yield a grand mean of 157.9 ± 1.6 days. We subtracted 144 days, the average length of gestation [Chambers & Hearn, 1979], from the grand mean IBI to yield a mean latency from parturition to post-partum ovulation of 14 days.

For analyses involving the number of animals or pubertal/adult females present in the family, we calculated the mean number of family members (in-

TABLE I. Ovarian Cycle Parameters Measured and Their Operational Definitions

Parameter	Operational definition
Day of ovulation	The day before a sustained (≥2 consecutive blood samples) elevation of plasma progesterone concentrations above 10 ng/ml [Harlow et al., 1983]
Luteal phase	Any period during which plasma progesterone levels remain above 10 ng/ml in at least two consecutive semi-weekly blood samples [Saltzman et al., 1994]
Non-luteal period	Any period, following the animal's initial ovulation, during which progesterone levels remain below 10 ng/ml; includes anovulatory periods that continue until the end of data collection
Inter-luteal period	Any non-luteal period occurring between two successive ovulations
"Non-conceptive" cycle	Any ovulatory cycle with a luteal phase that ends spontaneously within 30 days of ovulation or in which ultrasonography reveals a single, linear, echogenic interface between adjacent endometrial layers, with no visible uterine lumen [Oerke et al., 1995; Saltzman et al., 1997]

cluding all age classes) or pubertal/adult females (≥ 12 months of age) for each subject on a per-day basis throughout the period of data collection. Endocrine parameters of ovarian cycles, age at first ovulation, and total number of animals or pubertal/adult females in families were analyzed parametrically using analyses of variance and *t*-tests; post hoc comparisons were performed using the Tukey test. The proportion of daughters ovulating under different conditions was analyzed using the Fisher exact probability test or, when sample sizes were large enough, using chi-squared tests. Finally, we determined whether daughters were significantly less likely to ovulate while an older sister was present in the family than when no older sister was present. For each daughter that underwent data collection while housed with an older sister, we generated an individual probability that she did not ovulate while the older sister was present. These individual probabilities were based on the proportion of ovulating animals among daughters that underwent data collection during the same age period without an older sister present. We then calculated the product of the individual probabilities to determine the overall probability that no daughter ever ovulated while housed with an older sister.

RESULTS

A total of 22 of the 46 daughters ovulated at least once, including 19 of 41 daughters (46.3%) living in intact natal families and all three daughters from families in which the father had been replaced by an unrelated male (Table II). Neither of the two daughters ovulated in families in which the father died and was not replaced. Overall, the mean ± SEM age at first ovulation was 16.9 ± 0.5

TABLE II. Summary of Numbers of Daughters, and Proportions That Ovulated, Under Various Social Conditions

Independent variable	Condition	Sample size[a]	Number that ovulated (%)
Presence of father/ unrelated adult male	Father present (intact natal family)	41	19 (46.3)
	Father replaced by unrelated male	3	3 (100.0)
	Father died and not replaced	2	0 (0.0)
Mother's reproductive status (intact natal family; no older sister present; data collection began at 12 months of age)	Mother gave birth[b]	16	4 (25.0)
	Mother did not give birth	10	8 (80.0)
Sex/presence of co-twin (intact natal family)	Female co-twin[c]	12	6 (50.0)
	Male co-twin[c]	15	6 (40.0)
	No littermate	9	4 (44.4)
Sex/presence of co-twin (intact natal family; mother gave birth[b])	Female co-twin	10	4 (40.0)
	Male co-twin	14	5 (35.7)
	No littermate	7	2 (28.6)

[a] Each daughter contributed data to only one condition for each independent variable but may have contributed data to more than one independent variable.

[b] Mother gave birth during, or within one month of, the period of data collection from the daughter.

[c] Excludes daughters in triplet sets.

months (intact natal family: 17.2 ± 0.5 months; father replaced by unrelated male: 15.0 ± 1.0 months, NS). One daughter in an intact family and one in a family containing an unrelated male were already in the luteal phase of an ovarian cycle at the time of their first blood samples, collected at 12.1 and 13.1 months of age, respectively; for calculations of mean age at first ovulation, we used these animals' ages at their first blood samples. The distribution of ages at first ovulation for daughters in intact natal families is shown in Figure 1. One daughter whose father had been replaced by an unrelated male conceived during her first cycle, at 15.8 months of age, and delivered twins, and one daughter housed in an intact natal family had an extended luteal phase that was terminated by cloprostenol after 51 days; however, ultrasonography performed 38 days after ovulation indicated that this female was not pregnant. All other cycles ended spontaneously and therefore were considered non-conceptive by our operational definition.

Ovarian Cycle Parameters

Data were collected on a total of 53 ovarian cycles from daughters housed in intact natal families. Patterns of ovarian activity varied markedly, from a single cycle in each of seven animals to as many as six regular cycles in two animals (Figs. 2, 3). To determine whether cycle profiles changed systematically across successive cycles, we compared inter-luteal period duration (second and third cycles only), luteal phase duration, peak progesterone concentration, and mean luteal-phase progesterone concentration across the first three cycles in the six daughters that underwent at least three complete cycles while housed with the natal family. These analyses revealed that peak progesterone concentration declined significantly across the first

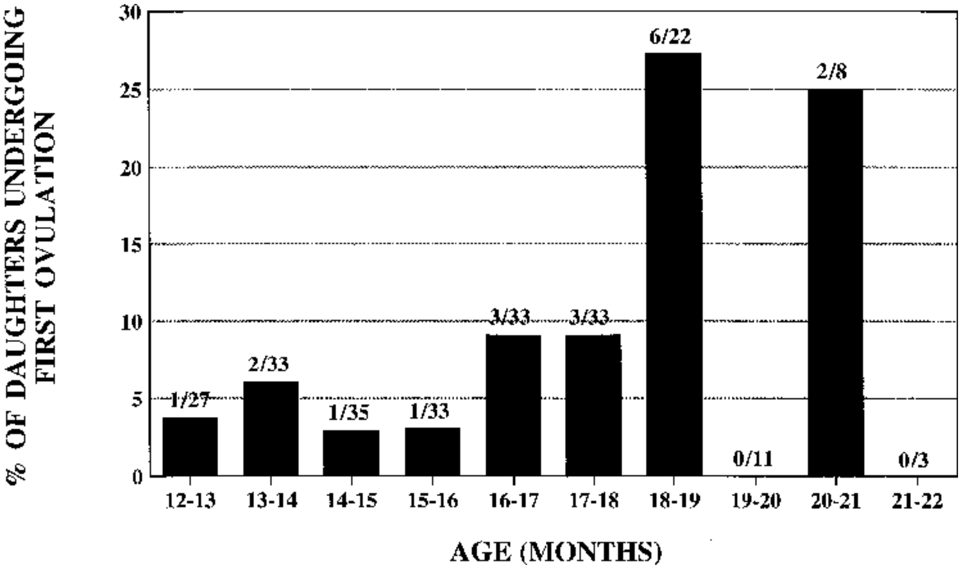

Fig. 1. Percent of daughters undergoing their first ovulation in each month of age during the peri-pubertal period. Numbers above bars indicate number of daughters undergoing their first ovulation during the indicated month (numerator) and total number of daughters that had not yet ovulated prior to that month (denominator). Only daughters living in intact natal families without older sisters present are included. One animal that was in a luteal phase at the beginning of data collection, at 12.1 months of age, is depicted as having undergone her first ovulation at 12–13 months of age.

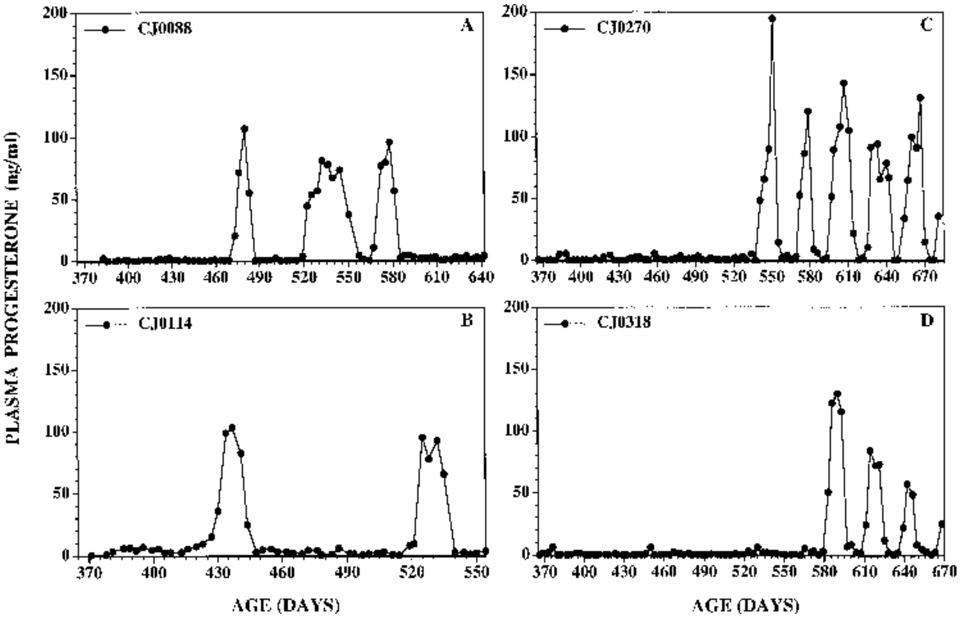

Fig. 2. Plasma progesterone profiles of four daughters, in intact natal families, that had male co-twins (**A**, **B**) or no littermates (**C**, **D**). Marmosets were considered to be in a luteal phase when progesterone levels exceeded 10 ng/ml in two or more consecutive blood samples. X-axis scaling differs slightly between graphs because daughters were removed from their natal families at different ages.

three cycles (F(2,10) = 7.58, $P < 0.01$): peak progesterone values were significantly higher in the first cycle (129.9 ± 15.1 ng/ml) than in the second (100.7 ± 10.3 ng/ml, $P < 0.05$) or third cycle (92.8 ± 14.1 ng/ml, $P < 0.01$). No other significant differences were found across the first three ovarian cycles.

To determine whether daughters' ovarian cycles differed from those of older females (T = 9.30, df = 29, $P < 0.001$, as compared to daughters' ages at first ovulation) that were not housed with their natal families, we performed one-way ANOVAs comparing parameters from (1) cycles of females housed in mixed-sex pairs or groups of unrelated adults, (2) the first cycle of each daughter that ovulated while housed with the natal family, and (3) subsequent (second through sixth) cycles of daughters that ovulated while housed with the natal family (Table III); where data were available for multiple cycles from the same animal, we used the mean value from all relevant cycles. These analyses revealed that luteal phases of daughters' first, but not subsequent, cycles were significantly shorter than those of control females (F(2,41) = 4.36, $P < 0.05$; Tukey test: $P < 0.05$). Daughters also had significantly longer interluteal periods than did control females (T = –2.86, df = 24, $P < 0.01$), although this measure could not be calculated for each animal's first cycle. Consistent with the earlier within-subjects analysis, daughters had significantly lower peak (F(2,41) = 3.20, $P = 0.05$; Tukey test: $P < 0.05$) and mean luteal-phase progesterone concentrations (F(2,40) = 3.89, $P < 0.05$; Tukey test: $P < 0.05$) than control females in their second and subsequent cycles, but not in their first cycles.

Effects of Mother's Reproductive Status

To determine whether daughters' ovarian activity was influenced by their mothers' reproductive status, we first compared the proportion of daughters that

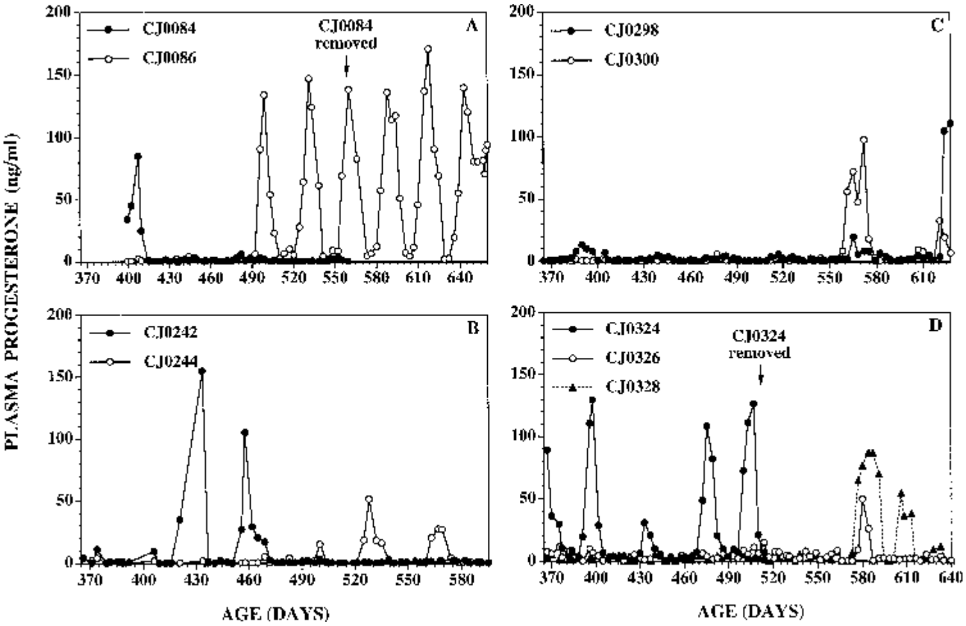

Fig. 3. Plasma progesterone profiles of three female-female twin pairs and one all-female triplet set in which both/all sisters ovulated. A: An unrelated adult male had been introduced into the family when the daughters were 11.3 months of age, following removal of the father due to illness. **B–D:** Daughters were housed in intact natal families. Marmosets were considered to be in a luteal phase when progesterone levels exceeded 10 ng/ml in two or more consecutive blood samples. X-axis scaling differs slightly between graphs because daughters were removed from their natal families at different ages.

did and did not ovulate in intact natal families in which the mother did or did not give birth at least once during, or within 30 days of, the period of data collection. To control for differences in family composition and in duration of data collection, we included in the analysis only those daughters that never lived with an older sister during data collection (see below) and that underwent data collection beginning at 12 months of age. This analysis indicated that daughters' like-

TABLE III. Ovarian Cycle Parameters (Mean ± SEM) of Daughters Living in Intact Natal Families and of Females Housed in Mixed-Sex Pairs or Groups of Unrelated Adults[†]

Ovarian cycle parameter	Daughters		Paired/grouped females	1-way ANOVA (*P* value)
	1st Cycle	2nd–6th Cycle		
Inter-luteal phase length (days)	—	22.4 ± 4.8 (14)	7.5 ± 0.6 (12)	<0.01
Luteal phase length (days)	17.1 ± 1.2* (17)	20.7 ± 2.9 (13)	25.3 ± 2.0 (14)	<0.05
Peak progesterone concentration (ng/ml)	108.9 ± 8.6 (17)	88.9 ± 7.8* (13)	126.7 ± 13.3 (14)	0.05
Mean luteal-phase progesterone concentration (ng/ml)	67.6 ± 5.7 (16)	55.9 ± 4.7* (13)	88.1 ± 12.0 (14)	<0.05

[†] Numbers in parentheses indicate number of animals for which each parameter could be determined.
*$P < 0.05$ vs. paired/grouped females; post hoc Tukey tests.

lihood of ovulating while housed with the natal family was strongly influenced by the mother's reproductive status: eight of 10 daughters (80%) with non-breeding mothers ovulated at least once, compared to four of 16 daughters with breeding mothers (25%; Fisher exact probability test, $P = 0.0091$). As expected, daughters with non-breeding mothers also lived in significantly smaller families than those with breeding mothers (4.7 ± 0.3 vs. 6.2 ± 0.4 family members; $T = -2.90$, df = 24, $P < 0.01$); however, this seems unlikely to account for the difference in the daughters' likelihood of ovulating, because no overall difference in family size was found between all daughters that did and did not ovulate (6.0 ± 0.4 vs. 6.4 ± 0.3 family members, NS).

All three daughters whose fathers were replaced by unrelated males had mothers that gave birth immediately before or during the period of data collection. Therefore, we compared the likelihood of ovulating between these daughters and those in intact natal families with breeding mothers. This analysis revealed that a significantly greater proportion of daughters ovulated in families containing an unrelated male than in intact natal families (Fisher exact probability test, $P = 0.0361$).

A total of 10 daughters ovulated in intact natal families in which the mother gave birth at least once during the period of data collection. To determine whether the timing of daughters' ovulations was influenced by the mother's parturitions or post-partum ovulations, we calculated the average timing of the post-partum ovulation for the mothers ($N = 6$) of these daughters as 14 days following parturition (see Methods). We then performed a chi-square test to determine whether daughters were more or less likely to ovulate within 30 days before or after the predicted day of post-partum ovulation than expected by chance. The results of this test was not significant, suggesting that daughters were neither more nor less likely to ovulate around the time of the mother's post-partum ovulation than at other times. Moreover, when we compared parameters of the first or subsequent cycles between daughters with breeding and non-breeding mothers, we found no significant differences in any measure. Overall, therefore, daughters were more likely to ovulate in families in which the mother never gave birth during the period of data collection than in families in which the mother was breeding, but among those daughters that did ovulate while housed with a breeding mother, no effect of the mother's parturitions on the timing or endocrine parameters of ovarian cycles could be discerned.

Effects of Siblings

We found no evidence that the sex or presence of littermates influenced daughters' likelihood of ovulating in intact natal families. Daughters with a female co-twin, those with a male co-twin, and those with no co-twin did not differ significantly in the proportion of animals that ovulated, whether we analyzed data from all daughters or only from those whose mothers gave birth at least once during, or within 30 days of, the period of data collection (Table II). We also found no evidence that the total number of pubertal/adult females present in the family influenced daughters' likelihood of ovulating: females that did and did not ovulate while housed with the natal family did not differ in the mean number of pubertal/adult females (≥ 12 months of age) present in the family during the period of data collection (2.8 ± 0.2 vs. 2.6 ± 0.1 adult females, respectively; NS). Again, we obtained similar results when we analyzed data only from the 31 daughters whose mothers bred during the period of data collection.

Although daughters that did and did not have female littermates did not differ in their likelihood of ovulating while housed with the natal family, they did show differences in their ovarian cycle profiles (see Figs. 2, 3). Compared to daughters without female littermates, those with female littermates had significantly longer non-luteal periods following the onset of ovarian cyclicity (34.6 ± 6.9 vs. 16.2 ± 4.5 days, respectively; T = 2.29, df = 15, $P < 0.05$), tended to have shorter luteal phases in their first cycles (14.8 ± 1.4 vs. 19.1 ± 1.4 days, respectively; T = –2.05, df = 15, $P = 0.0578$), and had significantly lower mean luteal-phase progesterone concentrations in their subsequent (2nd–6th) cycles (45.3 ± 6.6 vs. 64.9 ± 4.8 ng/ml, respectively; T = –2.46, df = 11, $P < 0.05$). These trends were apparent even in those daughters whose female littermates never ovulated.

Female littermates tended to resemble one another in whether or not they ovulated while housed with the family. In three of eight pairs of female littermates (including one pair of twins whose father had been replaced by an unrelated male), and in the set of female triplets, both or all daughters ovulated. In another two pairs of female littermates, neither daughter ovulated. Thus, in only two of nine sets of female littermates did one but not all sisters ovulate; however, this trend was not statistically significant. In two families, female littermates appeared to “take turns” ovulating, as one twin remained anovulatory for approximately 2–3 months, following an initial 1–2 ovulatory cycles, before the second twin ovulated (Fig. 3A, B). In another two families, however, female littermates ovulated within 3–4 days of one another (Fig. 3C, D).

Older sisters appeared to inhibit ovulatory activity in their younger sisters. Fourteen daughters lived in intact natal families with one or more older sister during part of the period of data collection, yielding a total of 33.3 animal-months of data collection with older sisters present. None of these animals ever ovulated when an older sister was living in the family; however, this effect did not reach statistical significance (see Methods)—whether we included in the analysis all daughters or only those with breeding mothers—because relatively few daughters without older sisters present ovulated during the same age periods. Eight daughters ovulated following removal of the older sister from the family, and a significant negative regression was found between age at removal of the older sister and latency to first ovulation (3.6 ± 1.3 months, range: 0.3–10.9 months; R = 0.83, F(1,6) = 13.00, $P < 0.05$); thus, the older an animal was upon removal of her older sister, the more quickly she began to ovulate.

Differences Between Families

To determine whether daughters were reliably more likely to ovulate in some families than in others, we calculated the proportion of daughters that ovulated at least once in each of the eight intact families (N = 29 daughters) that contributed two or more daughters to the study, using only daughters whose mothers gave birth during, or within 30 days of, the period of data collection. The proportion of daughters that ovulated ranged from none (in three families with 2, 3, and 3 daughters, respectively) to 83% (in one family with 6 daughters) but did not differ significantly between families (Fisher exact probability test).

DISCUSSION

Reproductive failure in subordinate female common marmosets has frequently been attributed to social suppression of ovulation. The results of the present study, however, indicate that anovulation cannot fully account for reproductive failure in daughters. First, in agreement with previous studies [Abbott, 1984;

Hubrecht, 1989], a substantial proportion of daughters in this study did ovulate while housed in intact natal families, but none became pregnant. Second, those daughters that did ovulate might have experienced reduced fertility, compared to other cycling females, as a result of decreased ovulation frequencies and reduced luteal-phase progesterone concentrations. Thus, at least three different components of reproductive suppression—complete suppression of ovulation in some daughters, altered endocrine profiles of ovulatory cycles in others, and inhibition of sexual behavior [Rothe, 1975; Abbott, 1984; Saltzman et al., 1997]—may contribute to reproductive failure in subordinate female marmosets. Furthermore, the expression of each of these components of reproductive failure can apparently be regulated by a variety of social influences within the family [see also Saltzman et al., in press, 1997].

One of the most striking findings of this study was the strong influence of the mother's reproductive status on the daughter's likelihood of ovulating. Daughters whose mothers were prevented from sustaining pregnancies during the daughter's pubertal through early adult period were more than three times as likely to ovulate as daughters whose mothers gave birth at least once during this period. Similar effects of the mother's reproductive activity on her daughters' breeding status have been described in the Mongolian gerbil (*Meriones unguiculatus*), a cooperatively breeding rodent. Gerbil daughters housed with their mother and a sister showed species-typical suppression of reproductive maturation only in groups in which the mother gave birth to a subsequent litter, which was allowed to remain with the group; in contrast, daughters housed with non-pregnant mothers or mothers whose subsequent litters were removed showed no evidence of suppression [Payman & Swanson, 1980]. Moreover, French [1994] found that gerbil mothers had significantly longer inter-birth intervals during periods when their daughters conceived than when daughters did not conceive. In the present study, the mothers that were not allowed to sustain pregnancies were nonetheless likely to be conceiving on a regular basis; thus, some cue(s) associated with mid- to late-pregnancy or with the presence of infants is likely to influence daughters' reproductive function. Chemical signals, probably from the dominant female, have been implicated in mediating suppression of ovulation in subordinate marmosets and tamarins [Epple & Katz, 1984; Savage et al., 1988; Barrett et al., 1990; Abbott et al., 1991] and seem likely to play a role in the intensified suppression seen in daughters with breeding mothers.

The present study also demonstrated that daughters whose fathers had been replaced by an unrelated adult male when the daughters were less than one year of age were significantly more likely to ovulate than those in intact natal families. Incorporation of a novel male into a family has been associated with the onset of sexual behavior and conception in daughters in several callitrichid species [see review by French, 1996], including common marmosets [Abbott, 1984; Rothe & Koenig, 1991; Kirkpatrick-Tanner et al., 1996; Saltzman et al., 1997], buffy-headed marmosets [*C. flaviceps*; Ferrari & Diego, 1992], black-tailed marmosets [*C. argentata melanura*; Carroll, 1986], golden lion tamarins [Dietz & Baker, 1993], and cotton-top tamarins [Price & McGrew, 1991; Savage et al., 1996]. Moreover, preliminary data from our laboratory indicate that replacement of the breeding male can stimulate a rapid onset of ovulatory cyclicity in previously anovulatory, late pubertal to young adult common marmoset daughters [Saltzman et al., in press]. In the current study, the presence of an unrelated male was associated with an increased likelihood that daughters would ovulate—and, in one case, conceive—while housed with the family, even though daughters were in only the pre-pubertal to early pubertal age range at the time of male replacement. It is noteworthy, however, that the age at first ovulation did not differ significantly between these daughters and those in intact natal families. Thus, these findings suggest that incorporation of an unrelated adult male into a family does not accelerate puberty in common marmoset daughters but instead increases the probability that daughters will escape from social suppression of ovulation once puberty has occurred. Although data were available from only two daughters whose fathers died and were not replaced, the finding that neither one ovulated suggests that this effect of male replacement cannot be attributed simply to removal of inhibitory influences from the father but instead requires stimulatory cues, such as behavioral or chemical signals, from the unrelated male.

Our findings on escape from suppression of ovulation in marmosets are consistent with those of Creel & Waser [1991] on failures of reproductive suppression in cooperatively breeding, free-ranging dwarf mongooses. These investigators concluded that pregnancies among subordinate females did not represent "accidental failure(s) of the mechanisms that suppress reproduction" (p. 8) but instead occurred under systematic, predictable circumstances, when the indirect fitness benefits of remaining in a group as a non-reproductive helper no longer exceeded the potential reproductive benefits of emigrating and attempting to breed in a different group. In the present study, and in other research in our laboratory [Saltzman et al., in press, 1997], two factors were most reliably associated with escape from ovulation suppression in female marmosets housed with their natal families: cessation of breeding by the mother, and replacement of the father by an unrelated adult male. As with pregnancies among subordinate mongooses, both of these events are likely to be associated with a decrease in the subordinate's indirect fitness benefits of remaining in the group as a non-reproductive helper. Clearly, daughters whose mothers have stopped producing offspring will have greatly diminished opportunities to increase their inclusive fitness through helping to rear siblings, and daughters whose fathers have been replaced by an unrelated male will have the opportunity to help rear only half-siblings, rather than full-siblings. Thus, whereas daughters in intact natal families will on average be as closely related to their mother's offspring as to their own offspring [coefficient of relatedness (r) = .50], daughters in families containing an unrelated breeding male will be more closely related to their own offspring than to their mother's offspring (r = .25).

In addition to reducing daughters' inclusive fitness benefits, cessation of breeding by the mother and replacement of the breeding male may both directly increase the daughter's likelihood of successfully rearing offspring. Daughters that give birth when the mother is non-reproductive will avoid competition with the mother and her offspring for resources necessary for infant survival, such as alloparents [Digby, 1995]. Furthermore, daughters that breed asynchronously with their mothers might reduce the risk of infanticide to their offspring: all three reported cases, for which the relevant information is provided, in which a dominant female common marmoset was known or suspected to severely injure or kill a subordinate female's infant occurred with a month of the dominant female's parturition [Roda & Roda, 1987; Digby, 1995; Kirkpatrick-Tanner et al., 1996; see also Alonso, 1986]. These possibilities are consistent with the finding that birth synchrony between dominant and subordinate female marmosets in polygynous groups was associated with reduced survival of the subordinate female's offspring [Digby, 1995] and suggest that daughters should be most likely to breed when the mother is least likely to do so. Daughters might also be able to increase their likelihood of producing viable offspring by mating with an unrelated male, if possible, rather than with a close relative: inbreeding has been shown to significantly increase infant mortality in both wild [Dietz & Baker, 1993] and captive [Ralls & Ballou, 1982] callitrichid populations.

Daughters' ovarian activity in the present study was influenced not only by the mother and breeding male but also by older and same-aged sisters. The finding that daughters never ovulated while housed with an older sister, but could ovulate rapidly following removal of the older sister from the family, is consistent with findings in cotton-top tamarins [Heistermann et al., 1989; Snowdon et al., 1993] and Wied's black tufted-ear marmosets [*C. kuhli*; T.E. Smith, C.M. Schaffner and J.A. French, in prep.], and may reflect the low dominance status of daughters housed with older sisters. Intra-sexual dominance relationships within families of common marmosets appear to be age-related, so that parents are typically dominant to their offspring and older offspring are dominant to their younger siblings [Sutcliffe & Poole, 1984]; thus, daughters housed in families containing an older sister are probably no more than third-ranking in the female hierarchy. In "peer groups" consisting of unrelated adult male and female common marmosets, rank 3 subordinate females are subjected to more severe suppression of ovulation than rank 2 subordinates: although both rank 2 and 3 subordinates are typically anovulatory, rank 2 females are significantly more likely to ovulate than are rank 3 females [Abbott & George, 1991]. This difference is probably mediated by differential suppression of gonadotropin release in rank 2 and 3 females, as rank 3 subordinates show significantly lower pituitary responsiveness to exogenous gonadotropin-releasing hormone than do rank 2 subordinates [Abbott et al., 1988]. An analogous rank-dependent mechanism operating in families might account for the reduced occurrence of ovulation in daughters housed with an older sister.

In contrast to daughters living with an older sister, those housed with a female littermate were no less likely to ovulate than other daughters, but showed more sporadic ovulatory cycles and lower luteal-phase progesterone levels. These findings, although unexpected, may also be related to inter-female dominance relationships. Whereas pubertal to young adult daughters living in intact natal families are usually clearly submissive to their mothers and older sisters [Sutcliffe & Poole, 1984] (Saltzman & Vanderloop, unpublished data), extensive, systematic observations of intact families in our colony have indicated that most daughters of this age rarely or never perform submissive behaviors to their littermates in undisturbed conditions [Vanderloop, 1996] (Saltzman & Vanderloop, unpublished data). Thus, dominance relationships among female littermates in intact natal families often do not appear to be highly developed or consistently expressed; even reunion of female co-twins following a 5-hour separation did not consistently elicit dominant-subordinate interactions [Vanderloop, 1996]. The incomplete suppression of ovulatory function that female littermates appear to exert upon one another therefore seems likely to reflect the ambiguity or perhaps temporal instability of these dominance relationships. However, further research will be needed to more fully elucidate the strength, consistency, and stability of dominance relationships between female littermates and their impact on ovulatory function.

The results of this study indicate that even those daughters that do ovulate while housed with the natal family might experience reduced fertility, compared to older females that are pair-housed with males or dominant in social groups, as a result of ovarian cycle abnormalities. Daughters' first, but not subsequent, ovarian cycles had significantly shorter luteal phases than those of older, control females, consistent with the finding in women that short luteal phases "tend to occur more frequently at either end of the reproductive age spectrum" [Lenton et al., 1984, p. 688; Balasch & Vanrell, 1987, p. 557]. Thus, short luteal phases in marmoset daughters' first ovulatory cycles might result from normal reproductive maturation rather than from social suppression. Following their first cycle, however, daughters exhibited significantly longer inter-luteal periods and lower peak and mean luteal-phase plasma progesterone levels than older, pair- or group-housed females. These trends were especially pronounced in daughters with female littermates, suggesting that the differences were caused by social, rather than developmental, factors. Interestingly, shortened luteal phases and extended inter-luteal periods have also been demonstrated recently in Wied's black tufted-ear marmosets housed with their natal families [T.E. Smith, C.M. Schaffner and J.A. French, in prep.].

In women and macaques, luteal phase deficiency may frequently reflect altered release of LH and/or follicle-stimulating hormone (FSH) during the antecedent follicular phase [Sherman & Korenman, 1974; Jones, 1976; DiZerega & Hodgen, 1981; Stouffer, 1990]. Anovulatory subordinate female marmosets housed in their natal families or in groups of unrelated adults exhibit suppressed plasma LH levels and are also likely to experience suppressed FSH levels [Abbott et al., 1988, 1990; Abbott, 1993]. Thus, luteal phase deficiency and oligocyclicity in cycling daughters housed in their natal families, and especially in daughters with female littermates, may result from a partial relaxation of the neuroendocrine mechanisms that more completely suppress gonadotropin release, and thus ovulation, in other subordinate females. The functional significance of this effect is unknown. In women, inadequate luteal phases (characterized by reduced progesterone levels) and oligomenorrhea (the regular occurrence of unusually long ovarian cycles) may be associated with implantation failure and recurring miscarriage [Jones, 1976; Wentz, 1979; Quenby & Farquharson, 1993]. It is therefore possible that marmoset daughters, especially those with female littermates, may be both (1) less likely to conceive than other cycling females, due to their reduced frequency of ovulations, and (2) if conception does occur, less likely to successfully maintain a pregnancy, due to their reduced progesterone concentrations.

In conclusion, this study has demonstrated that escape from social suppression of ovulation in captive common marmoset daughters usually occurs under specific, predictable social conditions. However, it has also confirmed and extended previous findings [Abbott, 1984; Hubrecht, 1989; Saltzman et al., 1997] that the onset of ovulatory function in daughters housed with their natal families is typically not accompanied by the onset of reproduction, presumably due to inhibition of sexual behavior and, possibly, to reduced fertility. This dissociation between ovulation and reproduction raises the question of the functional significance of ovulatory activity in daughters living with their natal families. One possibility is that free-ranging daughters undergoing ovulatory cycles may engage in extra-group copulations, possibly leading to conceptions [L.J. Digby, in prep.]. Another possibility is that ovarian activation increases a daughter's likelihood of behaviorally dominating her sisters or other females, and therefore of attaining a dominant, breeding position in the natal family or in another social group [see Saltzman et al., 1996]. A third possibility is that ovulatory cyclicity in non-breeding daughters primes the animals' future fertility or fecundity [see Creel et al., 1995]. Further research is needed to determine whether such benefits represent important functional consequences of ovulatory activity in non-reproductive daughters.

CONCLUSIONS

1. Almost half (46.3%) of 41 female common marmosets ovulated at least once while housed with their natal families, but their ovulatory cycles had sig-

nificantly longer inter-luteal periods and lower peak and mean luteal-phase plasma progesterone levels than those of older females housed with unrelated adults. No daughters sustained pregnancies while housed in intact natal families.

2. Daughters were significantly more likely to ovulate in families in which the mother was prevented from sustaining pregnancies and in families in which the father had been replaced by an unrelated male.

3. Daughters never ovulated while housed with an older sister. In contrast, daughters that had a female littermate were no less likely to ovulate than those that did not, but showed more sporadic ovulatory cycles and lower mean progesterone levels during the luteal phase.

4. Escape from suppression of ovulation in common marmoset daughters usually occurs under specific, predictable social conditions but frequently is not associated with the onset of reproduction.

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