

## RESEARCH ARTICLES

### Behavioral and Social Correlates of Escape From Suppression of Ovulation in Female Common Marmosets Housed With the Natal Family

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Although female common marmosets typically do not breed while housed with their natal families, up to half ovulate at least once while housed with the intact natal family, and a similar proportion conceive if an unrelated adult male is present in the group. In this study, we investigated the behavioral and social correlates of escape from suppression of ovulation by daughters housed in intact natal families or in families in which the father had been replaced by an unrelated adult male. Focal-animal behavioral data were collected from daughters that were (N = 7) or were not (N = 10) undergoing ovulatory cycles while housed with the natal family and from daughters that were (N = 5) or were not (N = 3) cycling or pregnant in families containing an unrelated male. Additionally, four cyclic and six acyclic females housed in intact natal families underwent simulated "prospecting" tests. Cyclic and acyclic daughters in intact natal families did not engage in sexual interactions with the father and showed few differences from one another in their interactions with the parents. Moreover, cyclic and acyclic daughters did not differ in their willingness to leave the family for short periods or to investigate an unfamiliar family in "prospecting" tests. However, daughters that underwent ovarian cycles in the presence of an unrelated male showed numerous behavioral differences from those in intact natal families, including frequent courtship and sexual behaviors with the male, reduced affiliative interactions with the mother, and elevated frequencies of aggressive display behavior. Moreover, these females were less likely to behave submissively towards the mother or the adult male. These findings suggest that both suppression of ovulation and inhibition of sexual behavior normally contribute to reproductive failure in female marmosets living with their natal families, and that the two components of suppression may become dissociated under specific social conditions. *Am. J. Primatol.* 41:1–21, 1997.

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## INTRODUCTION

Marmosets and tamarins (family Callitrichidae) exhibit a cooperative breeding system, in which individuals remain with their natal groups into adulthood, helping to rear the subsequent offspring of the dominant male and female while failing to reproduce. In several species of callitrichids, reproductive failure in subordinate females has been shown to result from anovulation and inhibition of sexual behavior [Abbott et al., 1981; Abbott, 1984; Epple & Katz, 1984; French et al., 1984; Tardif, 1984; Ziegler et al., 1987; Heistermann et al., 1989; Kuederling et al., 1995]. Both behavioral and physiological suppression are rapidly reversible: when nonreproductive daughters are removed from the natal family and paired with an unfamiliar male, they copulate readily, ovulate within several weeks, and may become pregnant shortly thereafter [Abbott, 1984; Evans & Hodges, 1984; French et al., 1984; Ziegler et al., 1987; Hubrecht, 1989; Widowski et al., 1990].

As with other cooperatively breeding mammals, reproductive failure among subordinate female callitrichids is not always absolute [Creel & Waser, 1996]. In both wild and captive groups of several callitrichid species, two females, often known or suspected to be mother and daughter, have been reported to be pregnant simultaneously or to give birth within a circumscribed period of time [*Callithrix jacchus*: Abbott, 1984; Roda & Roda, 1987; Adler & Jämmrich, 1991; Rothe & Koenig, 1991; Digby & Ferrari, 1994; Mendes Pontes & Monteiro da Cruz, 1995; *C. aurita*: Coutinho & Corrêa, 1995; *Leontopithecus rosalia*: Dietz & Baker, 1993; *Saguinus fuscicollis*: Terborgh & Goldizen, 1985; Calegario-Marques et al., 1995; *S. mystax*: Ramirez, 1984; Garber et al., 1993; *S. oedipus*: Savage et al., 1996; Price & McGrew, 1991; see review by French, 1996]. Several studies of captive common marmosets have also indicated that it may be relatively common for daughters to escape suppression of ovulation while housed with the natal family. In a recent study of 41 daughters, we found that 46% ovulated at least once while housed with the family [Saltzman et al., in press a]. Similarly, Abbott [1984] found that a daughter ovulated in eight of 17 families (47%), and Hubrecht [1989] detected ovulation in four of six daughters (67%) [but see Evans and Hodges, 1984]. Thus, data from field and laboratory studies together suggest that, at least among common marmosets, a substantial proportion of daughters may escape from suppression of ovulation while housed with the natal family and that under certain circumstances, some of these daughters may even give birth in the family.

The source and significance of this variation in the occurrence of reproductive suppression among female callitrichids are unclear. In common marmosets, reproductive suppression within families has frequently been ascribed to rank-related inhibition imposed on daughters by the mother. Daughters are usually subordinate to their mothers [Rothe, 1975; Abbott et al., 1981; Sutcliffe & Poole, 1984], and, at least in laboratory social groups consisting of unrelated adults, subordinate females become anovulatory in response to a dominant female [Abbott, 1984]. One possibility, therefore, is that differences among daughters in the likelihood of ovulating reflect differences in the quality of the relationship with the mother. For example, daughters with highly tolerant, non-aggressive mothers may develop a relatively egalitarian relationship with the mother. Such daughters may therefore be more likely to escape from ovulation suppression than daughters with more aggressive mothers.

### Escape From Suppression of Ovulation / 3

Another factor which is thought to stimulate reproductive activity in callitrichid daughters is the presence of an unrelated adult male. Female cotton-top tamarins undergo their first ovulation more quickly, following removal from the natal family, if pair-housed with an unfamiliar male than if housed with familiar males or in isolation [Ziegler et al., 1987; Widowski et al., 1990, 1992]. In common marmosets, several investigators have reported that mothers and daughters will breed concurrently in families in which the father has been replaced by an unrelated male [Abbott, 1984; Rothe & Koenig, 1991; see review by French, 1996], and preliminary data from our laboratory suggest that replacement of the father by an unrelated male can stimulate the onset of ovulation and sexual behavior in adult-aged daughters [Saltzman et al., in press a, b]. It is unknown whether such stimulation by an unrelated male occurs through alteration of the mother-daughter relationship or through direct stimulatory effects on the daughter which override inhibitory influences from the mother.

The social consequences of escape from ovulation suppression, like the causes, remain unknown. Polygyny in common marmosets and other callitrichids has often been considered an unstable or transitional condition [Terborgh & Goldizen, 1985; Savage, 1990; Price & McGrew, 1991; Dietz & Baker, 1993]. If this is correct, then some mechanism must operate to effect a return to monogyny in previously polygynous groups. One possibility is that the emergence of a second reproductive female causes an escalation of aggression between the two breeding females, leading to alteration or exaggeration of the dominance relationship between them and possibly resulting in imposition (or re-imposition) of reproductive suppression in the subordinate female; this phenomenon has been described in cooperatively breeding rodents, including Mongolian gerbils [Payman & Swanson, 1980] and naked mole-rats [Margulis et al., 1995]. Another possibility is that one breeding female may be expelled from the group, either by peripheralization or by aggression from other group members. Finally, return to monogyny may be brought about by voluntary emigration from the group by one of the breeding females. Therefore, onset of ovarian cyclicity by a daughter may result in increased aggression from the mother or other family members, peripheralization of the daughter or mother within the family, and/or an increased likelihood of the daughter or mother leaving the family.

The present study was designed to investigate the behavior and social dynamics of pubertal to early post-pubertal female marmosets living with their natal families, and particularly to identify the behavioral and social correlates of escape from ovulation suppression in the presence or absence of an unrelated male. We were especially interested in the possibility that ovarian cyclicity in daughters is associated with increased agonism with the mother; such a finding might indicate that the onset of cyclicity in daughters disrupts social cohesion within the family and leads to active competition for exclusive breeding status. Conversely, reduced mother-daughter agonism in families with cycling daughters would be consistent with the hypothesis that relaxation of the dominance relationship between mothers and daughters permits daughters to escape from suppression of ovulation. We also characterized the interactions of cycling and acyclic females with their fathers and unrelated adult males in order to determine whether ovarian cyclicity is associated with sexual interactions with an unrelated male but not with the father. Finally, we performed simulated "prospecting" tests to determine whether occurrence of ovarian cyclicity in daughters is associated with an increased willingness to leave the natal family for short periods of time or to investigate unfamiliar conspecifics.

## METHODS

### Subjects

Subjects were 23 captive-born female common marmosets (*Callithrix jacchus*) between the ages of 15.0 and 23.5 months ( $18.4 \pm 0.5$  months, mean  $\pm$  SEM) at the outset of the study. Previous studies suggest that this age range represents the late pubertal through early adult stages of development [Abbott & Hearn, 1978; Abbott, 1992]; females of this species are capable of ovulating and conceiving as early as 11–12 months of age [Abbott & Hearn, 1978; Saltzman et al., in press a]. Seventeen subjects were housed with their natal families, including the parents and up to six same-aged or younger siblings. Eight subjects were housed with their mother, up to four same-aged or younger siblings, and an unrelated adult male. These unrelated males, or “stepfathers,” had been introduced into the families when the subjects were 10.7–20.7 months of age ( $16.1 \pm 1.5$  months), at least 1.5 months ( $4.0 \pm 0.9$  months) prior to collection of behavioral data, following the death or experimental removal of the father. Two animals were used for behavioral data collection both while housed with the natal family and, 4.2 months later, following replacement of the father by an unrelated male (one of these daughters underwent ovarian cycles under both conditions; the other was acyclic under both conditions); all other subjects were used in only a single condition. Each subject was the eldest daughter or one of the eldest female twins or triplets living with the family during the period of data collection. A total of thirteen natal families and five families with stepfathers were used, and no more than three daughters were used from any one family. Each family was represented only once in each experimental group of subjects (see below), except that two daughters from one family were used in the cyclic/natal condition and two daughters from each of two families were used in the acyclic/natal condition.

Animals were housed in aluminum and wire mesh cages containing an assortment of cage furniture, including perches, nest boxes, and rope ladders. Cages allowed auditory and olfactory contact with marmosets in other cages, but for 12 of the subjects, visual contact with other cages was minimized during the study, as part of a separate experiment. These 12 animals included both cyclic and acyclic daughters, and daughters from both the natal family and stepfather conditions. Cages measured either 61 cm wide  $\times$  91 cm deep  $\times$  183 cm high or 122 cm wide  $\times$  61 cm deep  $\times$  183 cm high. All cages were located indoors, with lights on from 0600–1800 h, ambient temperature maintained at approximately 27°C, and humidity at approximately 50%. Marmosets were fed Zu/Preem Marmoset Diet (Hill’s Pet Products, Topeka, KS) with Provim and Nutra-Plus vitamin/mineral/protein supplements (Nutra-Vet Research Corp., Poughkeepsie, NY), bread, fruit, yogurt, and miniature marshmallows. Monkeys were fed once daily at 1300–1500 h, and water was available ad libitum.

### Behavior in the Home Cage

Thirty-minute focal-animal behavioral observations were performed on each subject two mornings (0900–1200 h) and two afternoons (1400–1700 h) during each of two consecutive weeks, yielding a total of 4 h of focal data per subject. Behavioral data were collected by a trained observer, to whom the animals had been previously habituated, sitting quietly in full view of the animals. Frequencies and, in some cases, durations of specific behaviors either performed by or directed to the focal animal were recorded on a laptop computer (Table I); for social behaviors, the partner’s identity was also recorded. Every 60 s, upon an audible signal

**TABLE I. Behaviors Scored**

Behavior	Definition
<b>Aggression</b>	
Erh-erh	Low-pitched, staccato chattering (“chatters given when angry”: [Epple, 1968] “erh-erh”: [Stevenson & Poole, 1976]; “vocal threat”: [Lipp, 1978; Abbott, 1984])
Ear-tufts flick	Rapid, back-and-forth movement of ear tufts [Stevenson & Poole, 1976; Lipp, 1978]
Frown	Lower eyebrows while staring [Stevenson & Poole, 1976]
Cuff	Swift, superficial blow or scratch performed aggressively [Stevenson & Poole, 1976; Abbott, 1984]
Chase	Pursue partner, with one or both animals exhibiting aggression and/or submission
Fight	Grapple aggressively with partner(s), involving biting, clawing, and wrestling [Lipp, 1978; “attack”: Abbott, 1984]
Attack	Lunge at or pounce on partner aggressively; may or may not result in fight [Abbott, 1984]
Snap bite	Direct a single short, sharp bite at partner [Stevenson & Poole, 1976; Abbott, 1984]
<b>Submission</b>	
Vocal submit (ngä)	Relatively low-pitched, atonal, infantile squeal [Epple, 1968]
Facial submit	Tufts flatten (lower ear tufts against side of head), and/or facial grimace (mouth partially open with corners of mouth retracted, exposing lower and sometimes upper teeth) and/or eyes slit (eyelids half closed) [Stevenson & Poole, 1976; Abbott, 1984]
Continuous submit	Continuous vocal or facial submit lasting $\geq 5$ sec
<b>Avoidance</b>	
Avoid	Starting from a stationary position, move at least one body length away from another animal within 1 sec of the other animal establishing proximity (within 10 cm)
<b>Courtship and Sex</b>	
Sexual solicit	Stare at partner with ear tufts flattened and eyes slit [Abbott, 1984]
Tongue in-out	Rhythmically move tongue in and out of mouth while facing or interacting with partner [Epple, 1967; Stevenson & Poole, 1976]
Mount	Climb on partner’s back from behind and grip partner around waist and legs; may be accompanied by pelvic thrusting [Kendrick & Dixon, 1984]
Attempt mount	Grasp partner and begin to climb onto partner’s back without successfully achieving mount position
<b>Investigative behaviors</b>	
Sniff	Push face against or toward partner, excluding anogenital region
Anogenital inspect	Orient face against or toward anogenital region of partner, or use hands or mouth to investigate anogenital region of partner; includes anogenital groom
<b>Affiliation</b>	
Initiate huddle	Establish passive, torso-torso body contact with partner, with both animals remaining stationary and in passive contact for at least 3 sec [Abbott, 1984]
Groom	Use hands and/or mouth to pick through fur and/or mouth of partner, excluding anogenital region [Rothe, 1971; Abbott, 1984]
<b>Play</b>	
Initiate play	Initiate bout of lunging, grappling, wrestling or chasing with partner for at least 1 sec in absence of aggression or intense submission; play face may or may not be present [Stevenson & Poole, 1976]
Solicit play	Direct play face (open mouth without retraction of lips) toward, pounce on, or initiate grapple with partner, in absence of ongoing play with partner, without resulting in play bout of $\geq 1$ sec
Join play	Join ongoing play bout between two or more partners
<b>Individual behaviors</b>	
Bristle-strut	Arching posture and/or strut locomotion and/or general piloerection (“Katzbucke Imponieren”: [Epple, 1967]; “arch bristle locomotion”: [Stevenson & Poole, 1976])
Scent mark	Rub or drag anogenital, suprapubic, or sternal region along substrate, object, or partner [Epple, 1970; Stevenson & Poole, 1976]
Genital present	Raise tail to expose genitals [Stevenson & Poole, 1976; Lipp, 1978; Abbott, 1984]
<b>1-Minute scan behaviors</b>	
Alone	Not in proximity ( $\leq 10$ cm) to any other animal [Abbott, 1984]
Stationary	Not engaged in locomotion or other whole-body movement

from a timer, the observer additionally recorded whether or not the focal animal was engaged in whole-body activity and whether or not it was in proximity (<10 cm) to any other animal. Monkeys' ear tufts were colored to facilitate rapid and reliable identification of individuals (Redken Deco Color, Canoga Park, CA); this procedure does not appear to alter the animals' behavior or ovarian function [Abbott, 1979]. Interobserver reliability scores for behavioral data collection averaged 89.0%.

### **“Prospecting” Tests**

Ten subjects living with their natal families underwent two “prospecting” tests per week for four successive weeks, beginning one week after the period of focal-animal data collection. “Prospecting” tests were modified from those described by McGrew and McLuckie [1986] and were designed to assess (1) the animals' willingness to leave the family for short periods of time and, once they did so, (2) their willingness to investigate unfamiliar conspecifics. At the outset of each test, the subject was captured manually and placed in a small plexiglass “start cage” (29 × 23 × 41 cm) attached to the front of the home cage, allowing visual, auditory, olfactory, and limited physical contact with family members through the cage mesh. After 5 min, a panel on the start cage was removed, permitting the subject entry into a flexible, translucent plastic tube (7 m long × 17 cm diameter). The tube ended at a plexiglass t-junction (each arm: 38 cm wide × 15 cm deep × 15 cm high), each arm of which was connected to a stainless steel mesh cage (61 × 46 × 61 cm) containing three perches. One of these cages, the “observation cage,” was positioned adjacent to a one-way viewing panel, through which the subject could look into the home cage of an unfamiliar family of conspecifics. The “empty cage” was identical to the observation cage except that the viewing panel was blocked by an opaque partition. For the 30-min duration of each “prospecting” test, the subject could choose to remain in the start cage or to move along the tube and into the t-junction, empty cage, and observation cage.

To facilitate precise identification of the subject's location, the “prospecting” tube was marked off into eight segments of equal length, with segment 1 adjacent to the start cage and segment 8 farthest from the start cage and adjacent to the t-junction. Segments 1–3 of the tube were located in the room housing the animals' families, and ran from the subject's home cage to a doorway opening into an adjacent room; segments 4–8, as well as the t-junction, empty cage, and observation cage, were located in this latter room. Monkeys could not view any conspecifics, except for the natal family and the stimulus family, during “prospecting” tests, and they could not view the stimulus family until they had travelled through the entire tube and entered the t-junction. Thus, willingness to leave the family, at least initially, was independent of attraction to the stimulus family.

Two observers were seated near the “prospecting” tube (one observer in each of the two rooms through which the tube passed) and recorded the subject's behavior—including behaviors directed at the stimulus family, interactions with the natal family, and time of entry into each location (tube segments 1–8, t-junction, empty cage, observation cage)—on laptop computers. At the conclusion of the test, the monkey was manually captured and returned to its home cage. The same stimulus family was used for all “prospecting” tests on any particular subject but not necessarily for different subjects. The positions of the empty cage and observation cage (right or left side of the t-junction) were alternated across successive tests. “Prospecting” tests were conducted between 0900 and 1300 h.

### Blood Sample Collection, Hormone Assays, and Pregnancy Detection

To monitor ovarian activity, we collected blood from all subjects twice per week for at least 5 months, beginning at least 3 months before behavioral data collection began and usually beginning when the animal was 12 months of age. Twice weekly blood sampling has been found to be sufficient to detect the approximately 19- to 20-day elevation of plasma progesterone levels in the luteal phase of the approximately 28-day ovarian cycle of the marmoset [Harlow et al., 1983; Abbott, 1986; Saltzman et al., 1994]. Monkeys were manually captured and briefly restrained in a marmoset restraint tube [Hearn, 1977] while 0.1–0.3 ml blood was collected from the femoral vein into a heparinized syringe. Blood samples were centrifuged at 2,000 rpm for 10 min and the plasma extracted and frozen at  $-20^{\circ}\text{C}$  until assayed for progesterone.

Direct measurements of plasma progesterone concentrations were made, without extraction, using a heterologous enzyme immunoassay [Saltzman et al., 1994]. The sensitivity of the assay at 90% binding was 4.5 pg, and 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).

Marmosets were considered to be pregnant or in the luteal phase of the ovarian cycle when progesterone levels exceeded 10 ng/ml in two or more successive blood samples [Harlow et al., 1983]. When progesterone concentrations remained above this level for >30 days, non-invasive confirmation of pregnancy was obtained from quantitative assessment of ultrasonographic images from transverse abdominal scans of the marmoset's lower abdomen, as previously described [du Boulay & Wilson, 1988; Abbott, 1987, 1992; Oerke et al., 1995]. Animals were manually restrained in a supine position for a maximum of 10 min, without the need for anesthesia or shaving of abdominal hair. Ultrasonography was performed using an Hitachi EUB-410 real-time scanner equipped with an intraoperative (or "fingertip") convex array probe (EUP-F334) operating at a frequency of 7.5 MHz. Using the scanner's calibrated, digitized calipers, measurements were made from transverse sections through the abdomen and uterus. Ultrasonographic images of the uterus of nonpregnant females showed a single, highly echogenic, linear interface between adjacent endometrial layers, whereas those of pregnant females showed two highly echogenic endometrial layers separated by a weakly echogenic, fluid-containing uterine lumen; pregnancy assessment was based on ventrodorsal measurement of lumen diameter [du Boulay & Wilson, 1988; Abbott, 1992; Oerke et al., 1995]. Pregnancy was reliably first detected using ultrasonographic equipment by 18 days following ovulation.

Mothers of 13 subjects were pregnant during the period of behavioral data collection, as determined by abdominal palpation and timing of parturitions, and the mother of one subject was between pregnancies. For colony management purposes, the remaining mothers received injections of a prostaglandin  $\text{F}_{2\alpha}$  analog (Estrumate, Mobay Corp., Shawnee, KS; 0.75  $\mu\text{g}$ , i.m.) at approximately monthly intervals during or around the time of data collection. This treatment causes luteolysis and the demise of the luteal phase or early pregnancy and has been used routinely as a safe and reliable method to regulate fertility of female marmosets in captive colonies [Summers et al., 1985]. Daughters whose mothers were prevented from breeding were distributed across the four experimental groups of subjects (see Analysis).

### Analysis

Seven of 17 daughters living with their natal families and five of eight daughters living with stepfathers showed sustained progesterone elevations (>10 ng/

ml) indicative of a luteal phase or pregnancy during, or within 2 days before or after, behavioral data collection; these animals were categorized as undergoing cyclic ovulatory activity. Three of these daughters, all of which were housed with stepfathers, were found to be in the early to middle stages of pregnancy during behavioral data collection (ventro-dorsal diameters of the uterine lumen in ultrasound scans were 3, 3, and 5 mm, respectively). In contrast to the 12 animals undergoing ovarian cycles or pregnancy (hereafter referred to collectively as “cyclic” animals), the remaining 10 daughters in natal families and three daughters with stepfathers showed no sustained elevations of progesterone within 40 days before and 17 days following behavioral observations; these females were considered to be acyclic. Most acyclic daughters (nine in natal families, one with a stepfather) had never ovulated during the period of blood sampling prior to behavioral data collection. When subjects were categorized by both ovarian activity (cyclic or acyclic) and family composition (natal family or stepfather), the four groups of daughters did not differ reliably in age or body weight at the time of behavioral data collection (acyclic/natal:  $17.3 \pm 0.5$  months, range: 15.1–19.7 months,  $370.8 \pm 13.4$  g; cyclic/natal:  $18.2 \pm 0.5$  months, range: 16.2–20.5 months,  $357.0 \pm 11.2$  g; acyclic/stepfather:  $19.6 \pm 2.0$  months, range: 16.2–23.0 months,  $418.7 \pm 46.0$  g; cyclic/stepfather:  $20.3 \pm 1.3$  months, range: 16.1–23.2 months,  $389.8 \pm 10.6$  g). A more complete description of ovulatory activity among daughters in our colony is provided elsewhere [Saltzman et al., in press a].

Each subject’s behavioral scores were summed across the 4 h of focal-animal observations and are presented as median number of occurrences or median duration of occurrence per hour  $\pm$  95% confidence limits. Scores from “prospecting” tests, including frequencies of specific behaviors and total time spent in each location, were summed across the eight tests. In addition, the latency to the animal’s first entry into each test location was determined, using the cumulative time elapsed across successive tests. All behavioral data were analyzed non-parametrically. Kruskal-Wallis one-way analysis of variance was used for comparisons between females in the acyclic/natal, cyclic/natal, and cyclic/stepfather conditions. Post-hoc comparisons following significant Kruskal-Wallis tests used the Tukey-type test described by Zar [1984], with Dunn’s correction for unequal sample sizes. Because data were collected from only three acyclic females housed with stepfathers (each of which appeared to be the subordinate member of a female-female twin pair, so that ovarian activity and social status were confounded), these animals were excluded from Kruskal-Wallis tests. Instead, their behavioral scores were compared separately to those of cyclic/stepfather females using the Mann-Whitney U-test. For all analyses, significance was assessed at the .05 level.

## RESULTS

### Agonistic Behaviors

Daughters received only  $0.3 \pm 0.4$  bouts per h of aggression from their mothers and  $0.5 \pm 0.4$  bouts per h of aggression from their fathers/stepfathers. Aggression received did not differ reliably as a function of daughters’ ovarian activity or family composition. Daughters almost never directed aggression towards their mothers and fathers/stepfathers and were never observed fighting with their parents, stepfathers, or siblings.

Daughters performed  $0.3 \pm 0.8$  bouts per h of submission (vocal submit + facial submit + continuous submit) to their mothers and  $1.0 \pm 1.5$  bouts per h to their fathers/stepfathers. Frequency of submission performed did not differ as a function of ovulatory activity or family composition; however, cyclic/stepfather daughters were somewhat less likely to submit to either the mother or step-

father/father than the other groups of daughters. Only one of five (20%) cyclic/stepfather daughters ever submitted to her mother, whereas three of three (100%) acyclic/stepfather daughters, six of 10 (60%) acyclic/natal daughters, and four of seven (57%) cyclic/natal daughters did so (NS). Similarly, only one of five (20%) cyclic/stepfather daughters ever submitted to the adult male, compared with two of three (67%) acyclic/stepfather daughters, eight of 10 (80%) acyclic/natal daughters, and seven of seven (100%) cyclic/natal daughters (NS). One cyclic/natal daughter and one acyclic/stepfather daughter each received a single bout of vocal submission from the mother, and fathers/stepfathers never submitted to daughters.

### Avoidance

Frequency of avoiding the father was influenced by daughters' ovarian activity (Kruskal-Wallis,  $H = 11.49$ ,  $N = 22$ ,  $P < 0.005$ ; Fig. 1): cyclic/natal daughters avoided their fathers significantly more often than did acyclic/natal daughters (Tukey-type test,  $P < 0.005$ ). No other significant differences were seen in frequencies of avoiding the father/stepfather or mother ( $0.3 \pm 0.4$  per h), and frequencies of receiving avoidance from the mother or father/stepfather were too low in all groups of daughters to permit statistical analysis.

### Sexual Behaviors

The most striking behavioral differences between daughters housed with the natal family and those whose father had been replaced by an unrelated male involved courtship and sexual behaviors (sexual solicitation + tongue in-out to father/stepfather: Kruskal-Wallis,  $H = 11.20$ ,  $N = 22$ ,  $P < 0.005$ ; mounts + attempted mounts received from father/stepfather: Kruskal-Wallis,  $H = 11.20$ ,  $N = 22$ ,  $P < 0.005$ ). None of the 17 daughters housed with their natal families performed sexual solicitations or tongue in-out to the father or received sexual solicitations, tongue in-out, attempted mounts, or mounts from him (although two cyclic daughters received non-ejaculatory mounts from brothers). The three acyclic/stepfather daughters similarly did not engage in any courtship or sexual behaviors. In contrast, three of the five cyclic/stepfather daughters performed sexual solicits and/or tongue in-out to their stepfathers ( $0.5 \pm 2.3$  bouts per h; Tukey-type test,  $P < 0.01$  compared to acyclic/natal daughters,  $P < 0.05$  compared to cyclic/natal females), and three received mounts and/or attempted mounts from the stepfather ( $0.3 \pm 0.3$  per h; Tukey-type test,  $P < 0.01$  compared to acyclic/natal females,  $P < 0.05$  compared to cyclic/natal females). Overall, four of these five cyclic/stepfather daughters engaged in courtship and/or sexual behaviors with the stepfather. Interestingly, the only daughter in this group that did not engage in these behaviors was also the only one that submitted to the mother or the stepfather, and she submitted to both animals at high frequencies. Mothers were never seen to perform behaviors that disrupted daughters' sexual interactions.

### Investigative Behaviors

Daughters' frequencies of sniffing the mother ( $1.0 \pm 0.4$  per h) and the father/stepfather ( $0.8 \pm 0.7$  per h), as well as of receiving sniffs from the mother ( $0.5 \pm 0.3$  per h), did not differ with ovarian activity or group composition. Sniffs received from the father/stepfather, however, differed significantly between groups

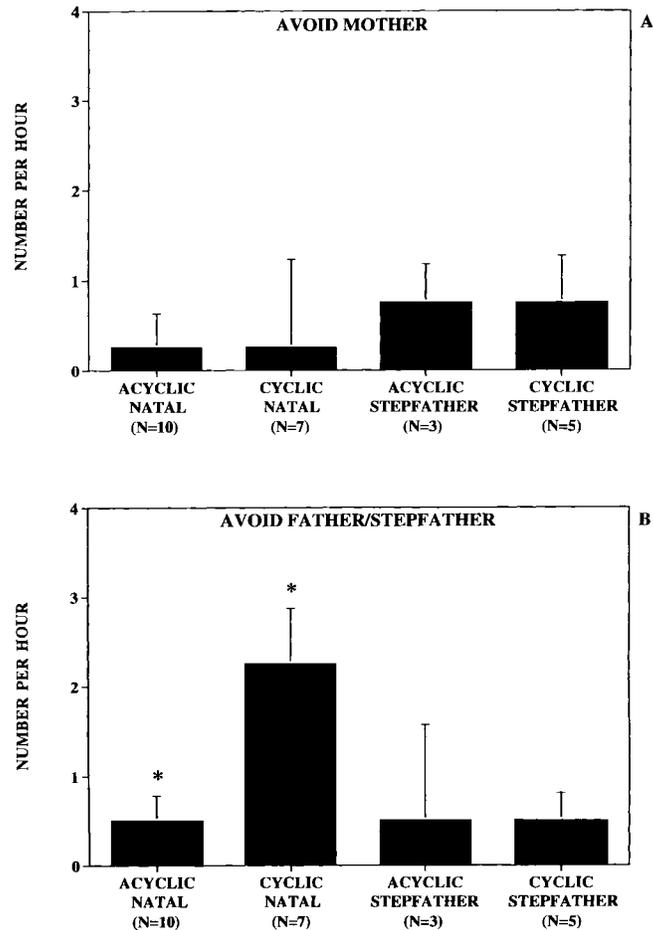


Fig. 1. Number per h (median + 95% confidence limit) of avoidances performed by daughters to (A) the mother or (B) the father or stepfather. Daughters either were ("cyclic") or were not ("acyclic") undergoing ovulatory cycles or pregnancy and were living in either intact natal families ("natal") or families in which the father had been replaced by an unrelated adult male ("stepfather"). Groups marked by \* differ from one another by  $P < 0.005$ .

of daughters (Kruskal-Wallis,  $H = 11.59$ ,  $N = 22$ ,  $P < 0.005$ ). Cyclic/stepfather daughters ( $1.5 \pm 0.8$  per h) received significantly more sniffs than did cyclic/natal ( $0.5 \pm 0.2$  per h; Tukey-type test,  $P < 0.05$ ), acyclic/natal ( $0.3 \pm 0.2$  per h; Tukey-type test,  $P < 0.005$ ) or acyclic/stepfather daughters ( $0.5 \pm 0.2$  per h; Mann-Whitney U-test,  $U = 0.00$ ,  $N = 8$ ,  $P < 0.05$ ). Anogenital inspections to and from the parents and stepfather occurred too infrequently in all groups of daughters to permit statistical analysis.

### Affiliative Behaviors

Frequency of initiating huddles with the mother differed between groups of daughters (Kruskal-Wallis,  $H = 7.21$ ,  $N = 22$ ,  $P < 0.05$ ; Fig. 2): acyclic/natal daughters initiated more huddles with their mothers than did cyclic/stepfather daughters (Tukey-type test,  $P < 0.05$ ). Among daughters housed with a stepfather, cyclic

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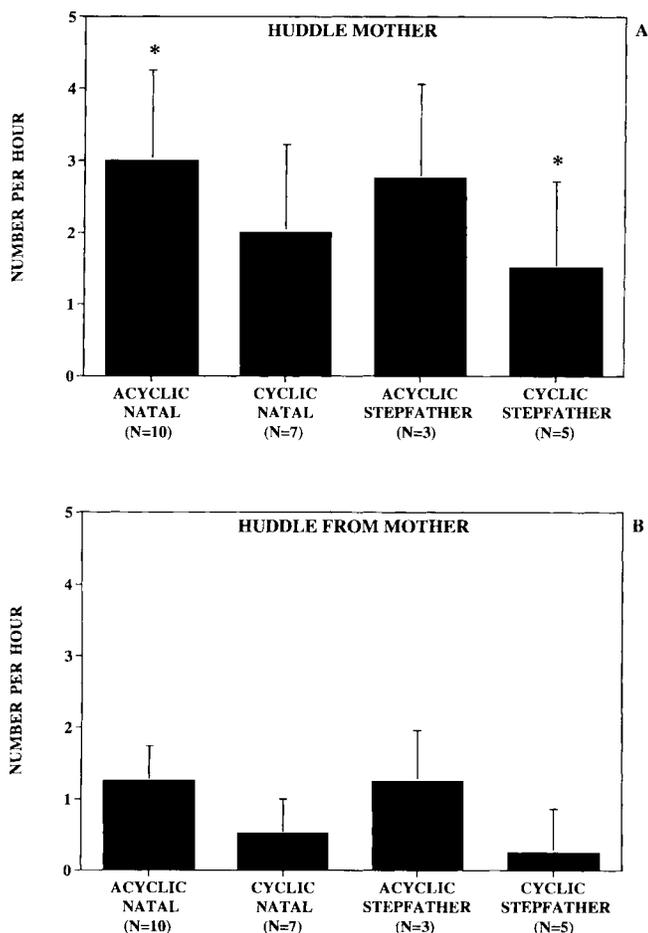


Fig. 2. Number per h (median + 95% confidence limit) of huddles (A) initiated to or (B) received from the mother. Abscissa labels are as described for Figure 1. Groups marked by \* differ from one another by  $P > 0.05$ .

and acyclic animals did not differ reliably. Acyclic daughters also tended to receive more huddles from their mothers than did cyclic daughters, but this trend did not quite reach statistical significance (Kruskal-Wallis,  $H = 5.19$ ,  $N = 22$ ,  $P = 0.0748$ ; Fig. 2). Huddles initiated to ( $2.0 \pm 0.7$  per h) and received from the father/stepfather ( $1.0 \pm 0.4$  per h) were not significantly influenced by daughters' ovarian status or by family composition. Moreover, no differences were found in the amount of time spent huddling with the mother ( $100.5 \pm 62.3$  sec/h) or father/stepfather ( $45.3 \pm 48.9$  sec/h).

Similar to huddles initiated to the mother, grooming performed to the mother differed between groups of daughters (Kruskal-Wallis,  $H = 6.76$ ,  $N = 22$ ,  $P < 0.05$ ; Fig. 3); again, the only significant pairwise difference was that acyclic/natal daughters groomed their mothers significantly more often than did cyclic/stepfather daughters (Tukey-type test,  $P < 0.05$ ). This latter group of animals also tended to receive more bouts of grooming from the stepfather than either acyclic/natal or cyclic/natal daughters did from the father, but this difference was not

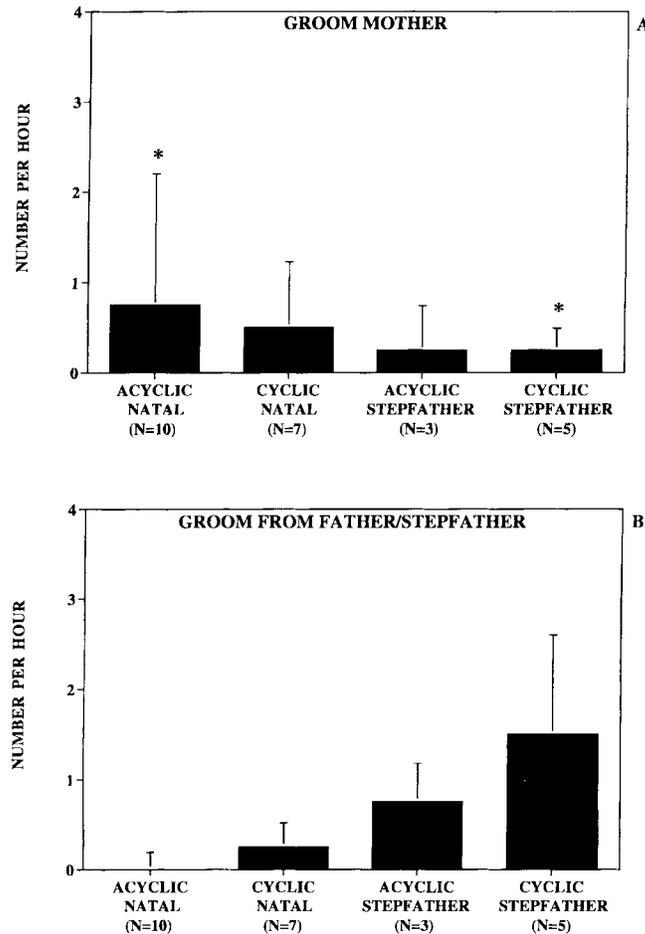


Fig. 3. Number per h (median + 95% confidence limit) of grooming bouts (A) performed to the mother or (B) received from the father/stepfather. Abscissa labels are as described for Figure 1. Groups marked by \* differ from one another by  $P < 0.05$ .

quite significant (Kruskal-Wallis,  $H = 5.42$ ,  $N = 22$ ,  $P = 0.0667$ ; Fig. 3). Grooming performed to the father/stepfather ( $0.3 \pm 0.3$  bouts per h) and received from the mother ( $0.3 \pm 0.5$  bouts per h) did not differ reliably between groups of daughters.

### Play

Because daughters tended to engage in low levels of play behaviors with their parents and stepfathers, frequencies of all three play behaviors (initiate play, solicit play, join play) were summed for analysis. Groups of daughters differed significantly in their frequencies of directing play behaviors toward the father/stepfather (Kruskal-Wallis,  $H = 11.14$ ,  $N = 22$ ,  $P < 0.005$ ). Cyclic/natal daughters ( $0.8 \pm 0.8$  per h) performed significantly more play behaviors toward the father than did either acyclic/natal daughters ( $0.0 \pm 0.1$  per h; Tukey-type test,  $P < 0.05$ ) or cyclic/stepfather daughters (none scored; Tukey-type test,  $P < 0.01$ ). Moreover, a near-significant trend was found in daughters' frequency of receiving play behav-

iors from the mother (Kruskal-Wallis,  $H = 5.61$ ,  $N = 22$ ,  $P = 0.0606$ ), which appeared to reflect a higher frequency among cyclic/natal daughters ( $0.3 \pm 0.4$  per h) than among the other groups of daughters (acyclic/natal:  $0.0 \pm 0.1$  per h; cyclic/stepfather, acyclic/stepfather: none scored). Play behaviors performed to the mother and received from the father/stepfather occurred too infrequently in all groups of daughters to permit statistical analysis. Interestingly, no daughter housed with a stepfather was ever seen to perform play behaviors to, or receive them from, either the mother or the stepfather.

### Individual Behaviors

Daughters were alone in  $62.1 \pm 10.6\%$  of 1-min scans and stationary in  $83.8 \pm 8.7\%$  of scans; these behaviors did not differ in association with ovulatory activity or family composition. Furthermore, no differences were found in the frequency of anogenital scent marking (Fig. 4). However, frequencies of bristle-strutting differed markedly between groups of animals (Kruskal-Wallis,  $H = 13.63$ ,  $N = 22$ ,  $P < 0.005$ ; Fig. 4). This effect seemed to be associated with differential ovarian activity: acyclic/natal daughters bristle-strutted significantly less often than cyclic/stepfather females (Tukey-type test,  $P < 0.005$ ), and tended to bristle-strut less often than cyclic/natal daughters (Tukey-type test,  $0.10 > P > 0.05$ ). Moreover, among daughters housed with a stepfather, acyclic animals bristle-strutted less frequently than cyclic animals (Mann-Whitney,  $U = 0.00$ ,  $N = 8$ ,  $P < 0.05$ ). Genital presentations were performed too infrequently by all groups of daughters to permit statistical analysis.

### “Prospecting” Tests

“Prospecting” tests were conducted on four cyclic and six acyclic daughters living in natal families. The animals showed pronounced variability in their willingness to leave the family and travel through the experimental apparatus. Median latency to move out of visual contact with the family (start cage + tube segment 1) was  $2.9 \pm 14.9$  min and ranged from 0.3–60.3 min. Across the eight tests, daughters spent  $64.3 \pm 11.3\%$  of their time in visual contact with the natal family;  $19.3 \pm 6.1\%$  in the remainder of the tube and t-junction, out of visual contact with the natal family;  $10.3 \pm 5.8\%$  in the observation cage, from which they could view an unfamiliar family; and  $4.8 \pm 5.0\%$  in the empty cage, which did not permit the animals to view conspecifics but which was otherwise identical to the observation cage. Overall, the nine daughters that eventually travelled the entire length of the tube spent significantly more time in the observation cage than in the empty cage (Wilcoxon test,  $Z = 2.55$ ,  $N = 9$ ,  $P = 0.01$ ). Cyclic and acyclic daughters did not differ significantly in the percent of time spent in, or latency to enter, any part of the apparatus. Moreover, cyclic and acyclic daughters showed no significant differences in behaviors performed towards the unfamiliar family, including looking at the family, reaching towards the family, and genital presentations.

## DISCUSSION

Social suppression of ovulation has been well documented in subordinate female common marmosets and has frequently been cited as the primary block to reproduction in these animals. Nonetheless, a substantial proportion of females ovulate at least once while living with their natal families [Abbott, 1984; Hubrecht, 1989; Saltzman et al., in press a]. In the present study, we performed the first systematic investigation of the behavioral and social dynamics associated with escape from ovulation suppression, using female marmosets that were in an

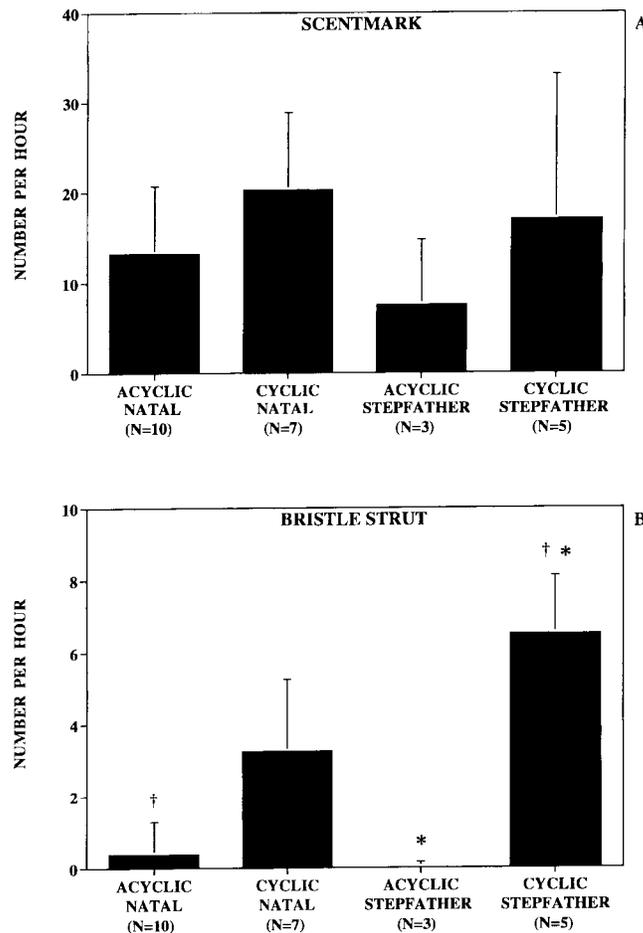


Fig. 4. Number per h (median + 95% confidence limit) of (A) scentmarks and (B) bouts of bristle-strutting performed. Abscissa labels are as described for Figure 1. Groups marked by \* differ from one another by  $P < 0.05$ ; groups marked by † differ from one another by  $P < 0.005$ .

age range in which they should have been generally capable of normal ovulatory function if they had been housed away from their natal families [Abbott, 1992]. Because this study employed a cross-sectional rather than longitudinal design, it did not allow us to distinguish between behavioral causes and consequences of escape from suppression, and necessitated use of multiple daughters from several of the families and use of families that differed in the extent of visual access to conspecifics and in the mother's reproductive condition. In spite of these limitations, however, this study allowed us to evaluate several hypotheses regarding the behavioral and social correlates of escape from suppression of ovulation.

#### Escape From Suppression of Ovulation in Intact Natal Families

Because reproductive suppression in common marmosets appears to depend upon a female's relationship with a dominant female groupmate, we anticipated that the nature of the social relationship with the mother might differ between

daughters which did and did not escape from suppression of ovulation. In agreement with previous studies of common marmosets, aggression in intact family groups in the present study tended to be both infrequent and mild [Rothe, 1975; Stevenson & Poole, 1976; Abbott, 1984; Digby, 1995b]. Daughters engaged in low levels of agonism with their mothers, and no significant differences in agonistic behavior were found between daughters which were and were not undergoing ovulatory cycles. Moreover, cyclic and acyclic daughters housed in intact families did not differ reliably in any other types of social interactions with the mother, including affiliative, investigative, and play behaviors. Our findings do not, therefore, support the hypothesis that escape from ovulation suppression by a daughter results from a particularly harmonious relationship with the mother. Furthermore, they indicate that escape from ovulation suppression can occur even in daughters who are clearly subordinate to their mothers. This conclusion is consistent with findings in wild common marmosets [Digby, 1995b], buffy-tufted-ear marmosets (*C. aurita*); [Coutinho & Corrêa, 1995], and golden lion tamarins [Dietz & Baker, 1993], in which a dominance relationship was apparent between two breeding females in the same social group.

Our findings also fail to support the hypothesis that ovulatory cyclicity in daughters may trigger increased aggression towards or peripheralization of daughters or their mothers, thereby effecting a return to reproductive suppression in, or emigration by, one female, as has been described in cooperatively breeding rodents [Payman & Swanson, 1980; Margulis et al., 1995]. Cyclic and acyclic daughters in intact natal families were similar not only in their agonistic and affiliative interactions with the parents but also in their willingness to leave the family for short periods of time or to investigate an unfamiliar family of conspecifics in simulated "prospecting" tests. Moreover, we found no differences between cyclic and acyclic daughters in the proportion of 1-min scans in which daughters were in proximity to at least one family member. Thus, we found no evidence that escape from ovulation suppression in daughters disrupted social cohesion within the family. A similar conclusion was reached by Hubrecht [1989], who paired four adult female common marmosets, which were housed with their natal families, with unrelated males for 30 min, twice per week. Although two of the daughters in Hubrecht's study were undergoing ovulatory cycles and one became pregnant, no behavioral changes were seen in the daughters or their mothers as a result of the daughters' interactions with an unrelated male; three of these daughters (one cycling, one pregnant, one acyclic) eventually had to be removed from their families, but this was generally due to aggression with siblings rather than with the parents. In the present study, although we did not focus specifically on daughters' interactions with siblings, we observed no fights or other forms of severe aggression with siblings, and daughters never had to be removed from their families.

Within intact families, the absence of social upheaval in association with ovarian cyclicity in daughters may reflect the fact that these daughters are highly unlikely to conceive and therefore pose little threat to the integrity of the monogynous breeding system. In this study, daughters in intact families were never seen to engage in courtship or copulatory behaviors with their fathers and never sustained pregnancies. Although father-daughter incest has been reported in common marmosets, it appears to occur primarily under disturbed and perhaps artificial conditions, such as in groups in which the father has no access to an unrelated female following the death of his mate [König et al., 1988; Adler & Jämmrich, 1991]. In spite of, or perhaps in association with, this "incest taboo," the only significant behavioral differences between cyclic and acyclic daughters in intact natal families in the present study involved social interactions with the father.

Daughters undergoing ovulatory cycles both avoided the father more frequently and directed more play behaviors to him than did daughters that were acyclic. Although the significance of these findings is not clear, one intriguing possibility is that they reflect increased ambivalence or ambiguity in the father-daughter relationship when daughters were undergoing ovarian cycles, with play representing a type of displacement activity.

### **Escape From Suppression of Ovulation in Families Containing an Unrelated Male**

In contrast to escape from ovulation suppression in natal families, ovarian cyclicity in daughters housed with a stepfather was associated with numerous behavioral and social changes. Cycling daughters housed with stepfathers performed higher frequencies of bristle-strutting, an aggressive display behavior [Epple, 1967], than other daughters. They were also the only daughters to engage in sexual and courtship behaviors with the adult male and, compared to other groups of daughters, they received more sniffs from the adult male and were somewhat less likely to submit to him. Compared with acyclic daughters housed in intact natal families, cycling daughters housed with a stepfather also performed fewer affiliative behaviors to the mother, including both huddling and grooming. Moreover, they showed a nonsignificant trend towards being less likely to submit to the mother than daughters in natal families. Together, these findings suggest that daughters which ovulate while housed with a stepfather may assume a more adult-like role in the family, engage in a qualitatively different relationship with the adult male, and undergo a weakening of their affiliative bond with the mother.

Dietz & Baker [1993] have developed a model to account for the association between replacement of the breeding male and mother-daughter polygyny in families of wild golden lion tamarins. According to this model, dominant female tamarins should "permit" their daughters to breed in social groups containing an unrelated male, but not in intact family groups. In the former situation, the fitness cost to the dominant female of sharing her territory with a second breeding female is offset by the dominant female's gain in inclusive fitness, which results from her daughter's production of offspring. In contrast, dominant females that "permit" their daughters to breed in intact natal families will suffer a net loss of fitness: in this situation, the fitness cost of sharing the territory with a second breeding female will not be offset by an increase in inclusive fitness, because the offspring from these incestuous (father-daughter or brother-sister) matings invariably die before weaning [Dietz & Baker, 1993]. Golden lion tamarins differ from common marmosets in that they do not exhibit social suppression of ovulation [French et al., 1989]; however, this model might predict that escape from ovulation suppression in marmoset daughters will lead to increased mother-daughter antagonism, and perhaps peripheralization or expulsion of the daughter by the mother, in intact family groups but not in groups containing an unrelated adult male.

Clearly, these predictions were not borne out in the present study. Daughters that ovulated in intact families and those that ovulated in families containing an unrelated male showed no differences in their aggressive and affiliative interactions with the mother. Moreover, we found no evidence that the mothers' behavior towards their daughters was significantly influenced by family composition or the daughters' ovarian function: all significant differences in mother-daughter interactions involved behaviors directed by the daughter to the mother, rather than vice versa. This pattern probably cannot be attributed to an inability of mothers to detect ovulation in their daughters. Smith [1994] showed that adult male and female marmosets behaviorally discriminated between scent marks from

females in the periovulatory phase of the ovarian cycle and those from anovulatory, subordinate females. Furthermore, in newly formed groups of unrelated adult males and females, dominant females were significantly more likely to direct persistent, severe aggression at subordinate females that had been undergoing ovulatory cycles than at those which were acyclic [Saltzman et al., 1996]. Thus, it seems likely that mothers in the present study were able to detect ovulatory activity in their daughters, but did not respond aggressively. It is also possible, however, that mothers are more likely to terminate their daughters' breeding attempts postnatally, rather than pre-conceptively or prenatally: in both wild and captive polygynous groups of common marmosets, dominant females may kill the offspring of subordinate females [Alonso, 1986; Roda & Roda, 1987; Digby, 1995a; Kirkpatrick-Tanner et al., in press]. In either case, the present findings suggest that ovulation suppression is not actively imposed on daughters by the mother's behavior; instead, suppression of ovulation and escape from suppression may be more appropriately interpreted in terms of daughters inactivating or activating their own reproductive function in response to subtle cues from the social environment. This perspective is consistent with findings that anovulation in subordinate female marmosets is mediated by specific neuroendocrine mechanisms rather than by generalized, harassment-induced stress [Abbott et al., in press].

In conclusion, the results of this study indicate that inhibition of sexual behavior, in addition to suppression of ovulation, makes a significant contribution to reproductive failure in female common marmosets housed with their natal families: although up to half of daughters may ovulate while housed with the family, these daughters do not engage in sexual interactions with the father and show few behavioral changes in general. In contrast, those daughters that ovulate in families in which the father has been replaced by an unrelated male show numerous changes in their interactions with the male and with the mother, and are likely to conceive. Thus, escape from ovulation suppression and escape from inhibition of sexual behavior may become dissociated in female common marmosets, depending upon the social context. Clearly, escape from suppression of ovulation within the family depends upon neither relaxation of a daughter's subordinate relationship to her mother nor stimulation by an unrelated male. However, results of the present study suggest that daughters undergoing ovulatory cycles are likely to undergo concurrent activation of sexual behavior only if an unrelated male is present and if the mother is no longer perceived as dominant. Although the specific mechanisms underlying this reproductive activation are not known, unrelated males seem likely to stimulate sexual behavior in daughters both directly, through their own interactions with the daughter, and indirectly, by facilitating an alteration of the social relationship between mother and daughter.

## **CONCLUSIONS**

1. Escape from suppression of ovulation by female common marmosets housed in intact natal families was associated with few or no changes in social interactions with the parents, in individual behaviors, or in willingness to leave the family and investigate unfamiliar conspecifics.
2. Escape from suppression of ovulation by females whose fathers had been replaced by an unrelated male, in contrast, was associated with numerous behavioral and social changes, including the establishment of a sexual relationship with the unrelated male, a reduction in affiliative behaviors performed to the mother, and an increase in aggressive display behavior.
3. Escape from suppression of ovulation in daughters was not dependent upon stimulation by an unrelated adult male or absence of submissive behavior toward

the mother; however, the onset of ovulatory activity was accompanied by activation of sexual behavior only when both of these factors were present. Thus, avoidance of inbreeding may play a more important role in the maintenance of cooperative breeding in common marmosets than has been previously realized.

4. Both social suppression of ovulation and social inhibition of sexual behavior appear to make significant contributions to reproductive failure in subordinate female marmosets and may become dissociated in specific social contexts.

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