



Wild marmoset (*Callithrix jacchus*) at the EFLEX-IBAMA Field Station in Nísia Floresta, Rio Grande do Norte, Brazil. (Photo by Leslie J. Digby.)



**REPRODUCTIVE COMPETITION AMONG FEMALE
COMMON MARMOSETS (*CALLITHRIX JACCHUS*):
PROXIMATE AND ULTIMATE CAUSES**

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INTRODUCTION

Discussions of reproductive competition have traditionally focused on males. Competition with same-sex rivals for access to females or their gametes is recognized as a critical determinant of male reproductive success, and males of many species possess conspicuous behavioral, physiological, or morphological traits that function in such competition. Among females, in contrast, reproductive success has been thought to be limited less by intrasexual reproductive competition than by access to such resources as nutrients or nest sites [Gowaty, 1997]. In recent years, however, it has become clear that females, too, may engage in intense competition for reproductive ascendancy and that females' reproductive outcomes may be severely constrained by their interactions with other females [Hrdy, 1981; Altmann, 1997; Gowaty, 1997; see Vervaecke et al., this volume]. Agonistic interactions or dominance relationships among females can disrupt numerous reproductive processes, including ovulatory function, sexual behavior, conception, pregnancy maintenance, and infant survival [reviewed by Bronson, 1989; Dixson, 1998]. Consequently, intrasexual competition can result in an asymmetrical distribution of reproduction among females in a group [Keller & Reeve, 1994]; in turn, such reproductive skew can have important implications for the future course of evolution.

Among female primates, reproductive skew and intrasexual influences on reproduction are especially dramatic in the common marmoset (*Callithrix jacchus*) and other callitrichines (marmosets and tamarins). Common marmosets are small-bodied, cooperatively breeding, frugivorous/insectivorous/exudativorous New World monkeys that occupy small home ranges in the Atlantic coastal forests of northeastern Brazil [Sussman, 2000]. Social groups comprise 3-15 individuals, including up to 4-6 adults of each sex and as many as 7 immatures [Hubrecht, 1984; Digby & Ferrari, 1994; Mendes Pontes & Monteiro da Cruz, 1995; Lazaro-Perea et al., 2000]. Few genetic

studies have been performed, but initial results of microsatellite DNA analysis [Nievergelt et al., 2000], as well as findings from behavioral studies [Ferrari & Digby, 1996; Lazaro-Perea et al., 2000], suggest that groups comprise mostly close relatives with some unrelated immigrants. Both males and females apparently may remain with their natal groups into adulthood, but dispersal by both sexes has been reported [Hubrecht, 1984; Scanlon et al., 1988; Mendes Pontes & Monteiro da Cruz, 1995; Lazaro-Perea et al., 2000], as have group fission and fusion [Lazaro-Perea et al., 2000].

Compared to most primates, female marmosets have extremely high potential fecundity: breeding females typically produce dizygotic twins twice per year [Sussman, 2000]. Within each social group, however, reproduction is monopolized by one, or in some cases, two, behaviorally dominant females [Epple, 1967; Rothe, 1975; Abbott, 1984; Digby & Ferrari, 1994; Lazaro-Perea et al., 2000]. Socially subordinate females typically fail to breed and instead, like all other group members, help to rear the offspring of the dominant female [e.g., Epple, 1967; Ingram, 1977; Digby, 1995a]. Thus, in contrast to most other primates, in which subordinate females usually breed but may do so at lower rates than dominant females [Harcourt, 1987], subordinate female marmosets are completely excluded from direct reproduction in a “winner-takes-all” system [Abbott et al., 1993a, 1997; Garber, 1997]. It is unknown whether most female marmosets eventually attain breeding status or whether pronounced skew exists among females in terms of lifetime, as well as short-term, reproductive success.

Callitrichine societies are characterized largely by cooperation and social tolerance [e.g., Caine, 1993; Garber, 1997]. Nonetheless, female marmosets exhibit a number of specialized behavioral and physiological responses to one another – including aggression towards extragroup females, suppression of ovulation, inhibition of sexual behavior and, possibly, infanticide in polygynous groups – that may result ultimately from selection caused by reproductive competition. The possibility that intense reproductive competition may be embedded within a highly cooperative and tolerant social system is consistent with recent models highlighting the potential evolutionary importance of competition even in cooperative, kin-based societies [Griffin & West, 2002; West et al., 2002; see also Garber, 1997].

In this chapter, I will focus on the mechanisms mediating reproductive competition among adult female common marmosets. Specifically, I will review findings from both laboratory and field studies to address the questions of how females may attempt to limit the number of reproductive rivals within their group, what mechanisms are employed to limit reproduction to a single female in each group, and what consequences ensue when a second breeding female emerges. The answers to these questions demonstrate that reproductive competition among female marmosets is manifest both behaviorally and physiologically and that females can severely constrain one another’s reproductive attempts during multiple stages of reproduction. Furthermore, they suggest that, while suppression of reproductive physiology and sexual behavior in subordinate females may be self-imposed rather than aggressively induced by dominant females, aggressive behavior by dominants – especially infanticide – may cause selection for subordinate females to curtail their own reproductive attempts.

Extragroup Aggression

In attempting to secure or maintain a breeding position, a female marmoset might try to limit the number of reproductive rivals in her social group by behaving aggressively toward potential female immigrants. The frequency of immigration is unknown. However, several investigators have observed or suspected females to join new groups [Hubrecht, 1984; Scanlon et al., 1988; Mendes Pontes & Monteiro da Cruz, 1995; Lazaro-Perea et al., 2000]. Immigration by females may be most likely to occur in the absence of resident adult females, presumably due to aggression from resident females or absence of a breeding vacancy [Lazaro-Perea et al., 2000].

Data on the responses of free-ranging marmosets to extragroup conspecifics come mainly from observations of intergroup encounters. In at least some wild populations, *C. jacchus* groups frequently interact with neighboring groups [Hubrecht, 1985; Digby, 1999; Lazaro-Perea, 2001]. Additionally, individual animals occasionally make incursions into other groups' territories, which might facilitate subsequent transfers of individuals between groups [Lazaro-Perea, 2001]. During these encounters with neighboring groups or intruders, females often behave aggressively towards extragroup females. It is possible that this intolerance does not function in reproductive competition but may be related to, for example, feeding competition [see Bicca-Marques, this volume]. However, the sex-specificity of stranger aggression suggests that reproductive competition is at least one determinant.

Lazaro-Perea [2001], for example, observed a total of 251 intergroup interactions among free-ranging groups and found that females were significantly more likely to chase female intruders than male intruders. Breeding females participated in fewer interactions with neighboring groups and intruders than did non-breeding adult females, which may have been a direct consequence of their reproductive status: breeding females reduced their participation in these interactions during late pregnancy and lactation. When they did participate, however, breeding females were significantly more likely to participate in defense against female intruders than against males. Among non-breeding females, the eldest was significantly more likely than younger non-breeders to participate in intergroup or intruder encounters. However, in contrast to breeding females, eldest non-breeding females did not discriminate behaviorally between female and male intruders. Although this last finding is difficult to explain, these results overall are consistent with the hypothesis that females may behave aggressively toward extragroup females to defend either their current breeding status or, for non-breeding females, their position in the reproductive queue [Lazaro-Perea, 2001].

Numerous experimental laboratory studies have further demonstrated that female common marmosets are highly intolerant of extragroup females. Epple [1970] found that females – especially dominant females – living in established mixed-sex groups were highly aggressive towards female intruders released into the group, but were much more tolerant of male intruders. Similarly, when adult female marmosets, either alone or with the pairmate, were allowed to interact across a barrier with a male or female stranger in the familiar home cage or in a neutral test chamber, females usually behaved aggressively toward like-sex strangers, and were significantly more aggressive toward females than toward males [Evans, 1983; Sutcliffe & Poole, 1984a; Harrison & Tardif,

1989; but see Saltzman et al., 1996]. Similar findings have been reported for other callitrichine species, including saddle-back tamarins [*Saguinus fuscicollis*: Epple & Alveario, 1985] and golden lion tamarins [*Leontopithecus rosalia*: French & Inglett, 1989; but see French et al., 1995, on Wied's black tufted-ear marmosets, *C. kuhli* and French & Snowdon, 1981, on cotton-top tamarins, *S. oedipus*].

Intrasexual aggression is also evident when several unfamiliar adults of each sex are simultaneously released into a large cage or observation room to form a new "peer group" [Epple, 1967; Abbott, 1984; Saltzman et al., 1996; see also Rothe, 1975]. Under these conditions, intersexual agonism usually is mild and dissipates rapidly, whereas intrasexual aggression among females is often persistent and severe; typically, one or more females must be removed from the group in order to prevent wounding [Epple, 1967; Rothe, 1975; Abbott & Hearn, 1978; Saltzman et al., 1994].

Saltzman et al. [1996] found evidence that the pattern of intrasexual aggression in new peer groups may be related to females' reproductive status: during the first three days following formation of a new group, subordinate females that had been undergoing regular ovulatory cycles were significantly more likely to receive persistent aggression from the newly dominant female than were subordinates that had been undergoing sporadic, or no, ovulatory cycles. This discrimination may have been mediated by olfactory cues. Scent-transfer studies have demonstrated that female marmosets can distinguish between cyclic (dominant) and acyclic (subordinate) conspecifics or between cycling females in different parts of the ovarian cycle on the basis of olfactory cues alone [Smith & Abbott, 1998]. Thus, females might use olfactory cues to identify those other females that represent the greatest reproductive competition and may specifically target these individuals for aggression.

Aggression toward extragroup females, therefore, may be one line of defense in a female's efforts to maintain her reproductive sovereignty in a group or to defend her position in the reproductive queue. However, the more critical mechanisms of reproductive competition may be those that play out within the social group and result in the curtailment of ovulatory function, sexual behavior, and infant survival in subordinates.

SUPPRESSION OF REPRODUCTIVE PHYSIOLOGY

A particularly striking mechanism of reproductive competition in common marmosets and other callitrichines is the suppression of reproductive physiology in socially subordinate females. For the purposes of this chapter, I define reproductive suppression as partial or complete failure, in response to social stimuli, of the physiological and/or behavioral systems that normally subservise reproduction. As noted by Solomon & French [1997], this term need not imply that suppression is imposed on one individual by another. Reproductive suppression in callitrichines has been discussed extensively elsewhere [e.g., Abbott et al., 1990, 1993a,b, 1997, 1998; French, 1997] and will be reviewed only briefly here.

Abbott & Hearn [1978] first reported that behaviorally subordinate *C. jacchus* females in peer groups comprising approximately three unrelated young adults of each sex typically did not undergo ovulatory cycles, as determined by plasma progesterone levels in blood samples collected at 2- to 3-day intervals. Since then, anovulation, as

determined by measurement of circulating or urinary ovarian hormone levels, has been documented among daughters living with their natal families in captive common marmosets [Abbott, 1984; Evans & Hodges, 1984; Hubrecht, 1989; Saltzman et al., 1997a,b,c], pygmy marmosets [*Cebuella pygmaea*: Carlson et al., 1997], cotton-top tamarins [French et al., 1984; Tardif, 1984; Ziegler et al., 1987; Savage et al., 1988; Heistermann et al., 1989], saddle-back tamarins [Epple & Katz, 1984], and red-bellied tamarins [*S. labiatus*: Kuederling et al., 1995]. Periods of anovulation have also been documented by fecal steroid analysis in some subordinate females in free-ranging groups of common marmosets [Albuquerque et al., 2001], cotton-top tamarins [Savage et al., 1997], and golden lion tamarins [French, 1998; French et al., in press]. In contrast, studies of captive golden lion tamarins [French & Stribley, 1987; French et al., 1989] and Wied's black tufted-ear marmosets [Smith et al., 1997] suggest that all or most adult daughters ovulate while housed with their natal family.

Ovulation suppression in subordinate female common marmosets occurs rapidly, repeatably, and reversibly. When a female marmoset is introduced into a new peer group in which she becomes behaviorally subordinate, plasma levels of luteinizing hormone (LH), a pituitary gonadotropin, drop precipitously in 1-4 days and ovulatory cycles soon cease [Abbott & George, 1991; Abbott et al., 1998]. Conversely, upon removal of a subordinate female from her group, or following removal or death of the dominant female, the subordinate female shows an elevation of plasma LH levels within a few days and typically ovulates in 2-3 weeks [Evans & Hodges, 1984; Abbott et al., 1988; Barrett et al., 1990; Abbott & George, 1991]. Notably, though, not all subordinate females undergo complete suppression of ovulation. Abbott & George [1991] found that 13 of 52 subordinates (25%) in captive peer groups ovulated, although their cycles had short luteal phases compared to those of dominant females. In a study of 41 adolescent or young adult daughters in 14 natal families, Saltzman et al. [1997a] found that 46% ovulated at least once during a period of 5-12 months [see also Abbott, 1984; Hubrecht, 1989]. Compared to older females that were paired with males or dominant in peer groups, daughters' cycles were characterized by extended follicular phases and low luteal phase concentrations of circulating progesterone [Saltzman et al., 1997a]. In both families and peer groups, therefore, most subordinate females are anovulatory, with a smaller number exhibiting impaired ovarian cycles.

Psychosocial Determinants of Ovulation Suppression

What are the psychosocial parameters that lead to suppression of ovulation in subordinate female common marmosets? One possibility is that anovulation results from lack of stimulation by males. Alternatively, it might result from rank-related suppression in response to dominant females. Little evidence supports the former hypothesis. Whereas cotton-top tamarins appear to require stimulation by unfamiliar males in order to initiate ovulatory cyclicality [Widowski et al., 1990, 1992], common marmosets can ovulate even when housed individually [Tardif et al., 1994], in female pairs [Alencar et al., unpublished manuscript], or in the natal family with no direct access to unrelated males [Abbott, 1984; Hubrecht, 1989; Saltzman et al., 1997a,c]. Furthermore, although replacement of the breeding male in families by an unrelated,

unfamiliar male leads to the onset of reproduction in many adult daughters, other daughters remain anovulatory [Saltzman et al., 1997b,c; Saltzman et al., unpublished data]. Finally, anovulation occurs in most subordinate females in peer groups despite the presence of unrelated males [e.g., Abbott & Hearn, 1978; Abbott et al., 1981; Saltzman et al., 1994]. Stimulation by an unrelated male is therefore neither necessary nor sufficient to activate ovulatory function in female common marmosets.

Instead, ovulation suppression appears to result from intrasexual dominance relationships. As described above, previously anovulatory subordinate females typically ovulate shortly after separation from their dominant female groupmate [Abbott & George, 1991]. Moreover, among subordinate females, the intensity of physiological suppression is related to social rank. Although all subordinate females in peer groups typically are anovulatory, rank-3 subordinates are significantly less likely to ovulate than are rank-2 subordinates [Abbott & George, 1991] and show lower pituitary responsiveness to exogenous gonadotropin-releasing hormone (GnRH) [Abbott et al., 1988]. Similarly, the eldest, presumably highest-ranking, daughter ovulates in close to half of captive families, whereas younger, presumably lower-ranking, daughters rarely ovulate, even if they are adult-aged [Abbott, 1984; Saltzman et al., 1997a, unpublished data]. Interesting exceptions to this pattern can occur, however, when a younger sister is behaviorally dominant to an older, anovulatory sister [Saltzman et al., unpublished data].

Recent findings from two laboratories further demonstrate that variation in the occurrence of ovulatory suppression is associated with differences in the quality of the behavioral relationship among females. Alencar et al. [unpublished data; see also Yamamoto et al., 1996] found that in pairs of females in which only one individual ovulated, clear differences in agonism occurred, with the anovulatory female performing submissive behaviors to her cycling cagemate. In contrast, in pairs in which both females (or neither) ovulated, agonistic behavior was more egalitarian and submissive behaviors were not seen. Similarly, in a study by Saltzman and co-workers [unpublished data; see also Saltzman et al., 1997c], adult daughters housed with their natal family were never observed to perform submissive behaviors to their mother, either when undisturbed in the home cage or during reunions following one-hour separations, if they were undergoing ovulatory cycles. In contrast, most anovulatory daughters behaved submissively toward their mother. Interestingly, in both studies, the clearest behavioral differences between female dyads that did and did not contain an ovulatory subordinate were seen in the submissive behaviors exhibited by the presumptive subordinates rather than in aggressive or other behaviors of the presumptive dominants. Thus, the main psychosocial parameter determining ovulation suppression may be a female's perception of herself as subordinate to another female rather than the receipt of specific types or frequencies of agonistic behaviors. Consistent with this possibility, rates of aggression are often very low in established groups of marmosets, especially families [Rothe, 1975; Abbott, 1984; Sutcliffe & Poole, 1984b; Saltzman et al., 1994, 1997c; Digby, 1995b].

This conclusion, however, appears to be at odds with reports that in polygynous groups, one breeding female was subordinate to the other [Alonso, 1986; Digby, 1995b;

Roda & Mendes Pontes, 1998; Lazaro-Perea et al., 2000]. One possible explanation is that dominance relationships among females can be intensified or altered, at least temporarily, by pregnancy, parturition, or the presence of infants [Saltzman et al., unpublished data; see below]. Additionally, this disparity may reflect the use of different criteria for dominance and subordination by different investigators. Whereas some do not consider a female to be subordinate unless she has been observed performing ritualized submissive behaviors to another female [e.g., Saltzman et al., 1994], others infer dominance and subordination from patterns of aggressive behavior or reproduction or do not present explicit criteria [e.g., Roda & Mendes Pontes, 1998; Lazaro-Perea, 2001; Alencar et al., unpublished data]

Sensory Cues Mediating Ovulation Suppression

Ovulation suppression in subordinate female marmosets occurs in response to multiple inputs from the dominant female, including chemical, visual, and behavioral or tactile cues. Marmosets possess well-developed scent glands, distinct scent-marking behaviors, and a functional vomeronasal organ [Hunter et al., 1984; Taniguchi et al., 1992; Epple et al., 1993], and chemical communication has been implicated in both the establishment and maintenance of ovulation suppression. When females were rendered anosmic by ablation of the main olfactory epithelium and the vomeronasal organ prior to their introduction into a new peer group, five of six subordinates continued to ovulate, indicating that olfaction plays a key role in the initiation of ovulation suppression [Abbott et al., 1993b, 1998]. However, the specific role played by olfaction is unclear. One possibility is that newly subordinate females must be able to smell their dominant female groupmate in order to engage the inhibitory neuroendocrine mechanism that terminates ovulatory function. Alternatively, it is possible that newly dominant females must be able to smell their subordinate groupmates in order to appropriately target them for aggression, which may be critical for the initiation of suppression [Saltzman et al., 1996; see also, e.g., Hunter & Dixson, 1983, on owl monkeys, *Aotus trivirgatus*].

Chemical communication also appears to play a role – although not a critical one – in the maintenance of ovulation suppression. Barrett et al. [1990] removed anovulatory subordinate females from their groups and housed them alone, either with or without continued exposure to scent from the familiar dominant female. Although subordinate females eventually ovulated in both conditions, exposure to the dominant female's scent resulted in a significant delay in the onset of ovulation, to 31 days as compared to 10 days in control animals. These findings suggest that scent cues from the familiar dominant female play a role in maintaining ovulation suppression in subordinates but cannot maintain suppression indefinitely in the absence of other cues. Moreover, this effect depends upon recognition of scent from a familiar dominant female. Exposure to scent from an unfamiliar dominant female had no effect on ovulatory function in separated subordinates [Smith, 1994; Smith & Abbott, 1995]. Similar findings have been reported for saddle-back tamarins [Epple & Katz, 1984] and cotton-top tamarins [Savage et al., 1988] removed from their natal families.

When subordinate female common marmosets housed with their social groups were rendered anosmic by ablation of the main olfactory epithelium, the vomeronasal organ, or both, they did not begin to ovulate [Barrett et al., 1993]. In conjunction with the results described above, these findings indicate that olfaction is neither necessary nor sufficient to maintain ovulation suppression in subordinates but may play a redundant role with other types of input. Visual cues from dominant females, as well as either behavioral or tactile cues, have also been implicated in the maintenance of ovulation suppression [Barrett et al., 1993]. Visual exposure of separated subordinate females to the dominant female and other groupmates, like scent transfer, delayed but did not prevent the onset of ovulation [Barrett et al., 1993]. It appears, therefore, that ongoing, direct interactions with a dominant female are necessary for the long-term maintenance of ovulation suppression in subordinates.

One interpretation of these findings is that anovulation represents a classically conditioned response to cues from the dominant female. As conceptualized by Abbott et al. [1997], harassment and intimidation of subordinates by the dominant female (unconditioned stimulus), such as occurs during formation of a new peer group, may initially elicit ovulation suppression (unconditioned response) in subordinates, possibly through a stress-mediated mechanism. Subordinates may learn to associate this harassment and intimidation with olfactory and visual cues from the dominant female so that these cues become classically conditioned stimuli capable of maintaining ovulation suppression (conditioned response) even in the absence of direct behavioral interactions between females. Under some circumstances, for example, following a rank reversal or the death or disappearance of the dominant female, the association between the conditioned and unconditioned stimuli attenuates, leading to extinction of the conditioned response.

The classical conditioning model of ovulation suppression has yet to be tested directly. However, it is consistent with the low levels of intrasexual aggression in most established groups and with the absence of physiological indices of stress among subordinate females in stable groups (see below). In contrast, in some other primate species, in which dominant females actively disrupt subordinate females' reproductive efforts, subordinates are subjected to high rates of aggression and exhibit elevated cortisol levels [e.g., gelada baboons, *Theropithecus gelada*: Dunbar, 1989; McCann, 1996; yellow baboons, *Papio cynocephalus*: Altmann et al., 1988; Rhine et al., 1988; Wasser & Starling, 1988; Sapolsky et al., 1997; reviewed in Abbott et al., 1997].

Physiological Mechanisms of Ovulation Suppression

A series of detailed studies, primarily by Abbott and his coworkers, has greatly advanced our understanding of the mechanisms mediating ovulation suppression in *C. jacchus*. Most of these studies have used captive peer groups comprising unrelated adults, rather than families, to allow for greater experimental control. Although the mechanisms of ovulation suppression have not yet been elucidated fully, findings thus far demonstrate that they are both complex and highly specialized.

Social suppression of ovulation in common marmosets, at least among subordinates in established groups, is not mediated by generalized stress. Several physiologi-

cal parameters that frequently are associated with stress and that can disrupt reproductive function in other taxa do not differ between dominant and subordinate female common marmosets in the expected manner. For example, subordinate females in captive peer groups do not have reduced body weights, elevated circulating concentrations of the anterior pituitary hormone prolactin, or altered levels or disrupted circadian patterning of the pineal hormone melatonin [Abbott et al., 1981, 1997; Webley et al., 1989]. Most strikingly, subordinate female marmosets do not show elevated basal or stress-induced levels of the adrenocortical hormone cortisol, which is often considered the principal indicator of stress and which frequently is thought to be associated with impaired reproductive function in socially subordinate individuals. To the contrary, subordinate female marmosets in captive peer groups show pronounced, persistent reductions in baseline plasma cortisol levels which appear to be mediated, in part, by low levels of reproductive hormones [Saltzman et al., 1994, 1998, 2000, unpublished data; Johnson et al., 1996; Abbott et al., 1997, 1998]. Thus, we have no evidence that subordinate females in established groups experience greater stress than dominants or that stress contributes to suppression of ovulation. However, the possibility that stress may play a role in the initiation of suppression has not been tested.

Social suppression of ovulation in marmosets also does not appear to reflect delayed puberty, as occurs in some rodent species [reviewed by Vandenberg & Coppola, 1986]. Pubertal maturation is a developmental process that can last months to years in primates. This process entails a diminution of inhibitory inputs and increase in facilitatory inputs to the hypothalamic GnRH neurons critical to ovulatory function [Plant, 1994; Terasawa, 1995]. Because adult-aged subordinate females can undergo their first ovulation within the length of a normal follicular phase following separation from the dominant female [Abbott et al., 1988; Barrett et al., 1990; Abbott & George, 1991], the neuroendocrine underpinnings of ovulatory cyclicity appear to be already fully developed. Moreover, even previously reproductive females can become anovulatory if introduced into a group in which they become subordinate [Abbott et al., 1988; Abbott & George, 1991; Saltzman et al., 1994]. Thus, anovulation in subordinate female marmosets represents suppression of reproductive function in fully mature adults, rather than delay of puberty in immature animals, and is mediated not by a generalized stress response but by a specific, possibly unique neuroendocrine mechanism.

Subordinate females show dramatic impairments in ovarian size, content, and function [reviewed by Abbott et al., 1998]. Their ovaries are markedly smaller than those of dominants, and contain smaller and fewer antral follicles. Moreover, ovaries of subordinate females typically contain no corpora lutea or corpora albicantia, indicative of anovulation.

Inhibition of ovarian function, in turn, is mediated by suppressed release of LH from the anterior pituitary. Serial blood sampling of individual animals at 10- to 15-minute intervals for up to 12 hours revealed that whereas plasma LH in dominant females in the mid-follicular phase of the ovarian cycle undergoes approximately hourly pulses, LH levels in subordinate females are low and non-pulsatile [Abbott et al., 1990; P.L. Tannenbaum, N.J. Schultz-Darken & D.H. Abbott, unpublished data]. Three neuroendocrine mechanisms have been identified that contribute to this LH suppression

in subordinates: (1) enhanced sensitivity to negative-feedback effects of estrogen [Abbott, 1988]; (2) failure of positive-feedback effects of estrogen [Abbott et al., 1981]; and (3) enhanced inhibition of LH by endogenous opioid peptides in ovariectomized subordinates as compared to ovariectomized dominants [Abbott et al., 1990]. Preliminary studies of urinary follicle-stimulating hormone (FSH) indicate that this gonadotropin is not suppressed in anovulatory subordinates [Tannenbaum et al., unpublished data].

In many species, pituitary release of LH is thought to reflect the hypothalamic release of GnRH. Because GnRH travels directly from the hypothalamus to the pituitary via the portal circulation and enters the systemic circulation in only minute quantities, GnRH concentrations cannot be determined accurately by peripheral blood sampling. Furthermore, because the pituitary response to GnRH is determined by the dynamic pulsatile patterning of GnRH release over time, GnRH concentrations in individual samples are relatively uninformative [Knobil, 1980]. Because of the technical difficulties in measuring GnRH release, GnRH in subordinate females has often been assumed to show similar suppression as LH, but this assumption was not tested directly until recently. Using push-pull perfusion to directly sample GnRH from the pituitary stalk/median eminence in conscious marmosets over periods of up to 12 hours, Tannenbaum and colleagues [1999, unpublished data; Saltzman et al., 1995; Abbott et al., 1997] have demonstrated that the pulsatile release of GnRH does not differ between dominant females in the follicular phase of the ovarian cycle and anovulatory subordinates, in marked contrast with the differences in plasma LH patterns. These findings suggest that patterns of GnRH and LH release can become dissociated in this species by an as yet unknown mechanism, possibly involving blunted pituitary sensitivity to GnRH.

In summary, suppression of ovulation in socially subordinate females is a common but not universal manifestation of reproductive competition in *C. jacchus* and numerous other callitrichines. Although the specific roles of sensory cues and classical conditioning, as well as the neuroendocrine mechanisms of ovulation suppression, are not yet fully understood, it is clear that these processes permit rapid and reversible reproductive responses to unpredictable changes in the social environment and are highly effective at translating social subordination into infertility.

INHIBITION OF SEXUAL BEHAVIOR

Subordinate female common marmosets typically engage in little or no intragroup sexual behavior [Rothe, 1975; Abbott, 1984; Saltzman et al., 1997c; Digby, 1999]. Two broad hypotheses may be proposed regarding the source of this behavioral inhibition. First, it may result from intrasexual reproductive competition. According to this hypothesis, subordinate females undergo inhibition of sexual behavior, like suppression of ovulation, in response to cues from a dominant female groupmate. Such an effect could be mediated indirectly [i.e., through ovulation suppression, which might decrease a subordinate female's attractivity, receptivity, and/or proceptivity to males; but see Kendrick & Dixson, 1984], or directly (i.e., through harassment of the subordinate female or disruption of her sexual interactions with males). An alternative hypothesis is that failure of subordinate females to engage in sexual behavior results from inbreeding

avoidance. This would be especially applicable to females living with their natal family, in which all males may be close relatives (i.e., father and brothers). Such a mechanism would likely be relevant to free-ranging groups, which may comprise mostly closely related individuals [Ferrari & Digby, 1996; Nievergelt et al., 2000].

Several lines of evidence support a role for intrasexual inhibition of sexual behavior. First, subordinate females typically do not engage in sexual behavior even in groups of unrelated adults, in which inbreeding avoidance should not be a factor [Rothe, 1975; Abbott, 1984]. It can be argued, however, that in this unnatural social context, subordination might activate behavioral and physiological mechanisms that evolved in the context of family groups, so that subordinate females might respond to unrelated male groupmates as though they were close relatives. Second, when subordinate females were removed from these peer groups for brief behavioral tests with unfamiliar males, they solicited and accepted mounts [Abbott et al., 1997]. Third, several investigators have observed females disrupting one another's sexual interactions, in either monogynous [Epple, 1967; Rothe, 1975; Abbott, 1984] or polygynous [Alencar et al., unpublished manuscript] groups. Others, however, have found little or no evidence of mating interference in polygynous groups [Kirkpatrick-Tanner et al., 1996; Lazaro-Perea et al., 2000; Saltzman et al., unpublished data; L.J. Digby, personal communication].

In addition to rank-related inhibition, inbreeding avoidance appears to be a critical determinant of sexual behavior in subordinate females. Marmosets usually avoid sexual interactions with familiar, closely related individuals [Abbott, 1984; König et al., 1988; Saltzman et al., 1997c, unpublished data; Baker et al., 1999], although inbreeding has been reported [Epple, 1970; Anzenberger & Simmen, 1987; Crook, 1988; König et al., 1988; Adler & Jämmrich, 1991]. Daughters housed with their natal family typically do not engage in sexual interactions with their father or brothers, even if they are undergoing ovulatory cycles [Abbott, 1984; Saltzman et al., 1997c, unpublished data]. However, many of these daughters readily solicit and copulate with an unrelated adult male introduced into the family [Kirkpatrick-Tanner et al., 1996; Saltzman et al., 1997b,c, unpublished data; see also Anzenberger, 1985; Hubrecht, 1989]. Notably, Saltzman et al. [unpublished data] found that those daughters that did not engage in sexual behavior with an unrelated male introduced into the family were behaviorally subordinate to the mother and/or a sister, whereas those that did mate with the unrelated male were not. Thus, expression of sexual behavior by female marmosets may be constrained both by the presence of a behaviorally dominant female and by lack of access to an unrelated adult male [Saltzman et al., 1997b,c].

Subordinate females in free-ranging groups may be able to overcome both of these constraints by mating with extragroup males [Hubrecht, 1985; Digby, 1999; Lazaro-Perea, 2001]. Lazaro-Perea [2001], for example, observed 20 extragroup copulations or attempted copulations, all of which involved non-breeding females from monogynous groups. Most of these interactions occurred during encounters between neighboring groups, but several occurred during forays by an individual male or female into another group's territory. Digby [1999] observed a total of 24 extragroup matings, all of which occurred during intergroup encounters. In this study, both breeding and non-breeding adult females in polygynous groups participated in extragroup sexual interactions. The

functional significance of these interactions, however, is not clear. While subordinate females may be more likely than dominant, breeding females to mate with extragroup males [Anzenberger, 1985; Hubrecht, 1985; Lazaro-Perea, 2001], the fact that dominant females occasionally do so as well [Digby, 1999] suggests that other factors, in addition to the intragroup constraints of rank-related inhibition and inbreeding avoidance, may contribute to extragroup sexual behavior. Moreover, extragroup matings may be unlikely to result in conceptions. Many of the females that were observed copulating with extragroup males never bred [Digby, 1999; Lazaro-Perea, 2001], and when breeding females did mate with extragroup males, they did not do so during likely conceptive periods [Digby, 1999]. However, Digby [1999] noted that males often engaged in mate guarding behaviors toward their group's breeding females during intergroup encounters, especially during the female's likely conceptive period. This could indicate that males were responding to the possibility of loss of paternity and, therefore, that these extragroup matings do occasionally result in conceptions.

In summary, then, inhibition of sexual behavior in subordinate female marmosets may be mediated both by the absence of unrelated males in the group and by the presence of a dominant female. Together with suppression of ovulation, this behavioral inhibition minimizes a subordinate's likelihood of breeding and, therefore, maintains high reproductive skew within the group. However, previously non-reproductive females do sometimes escape from both behavioral and physiological inhibition and begin to breed concurrently with another female. Female reproductive competition in these polygynous groups may take on a new, particularly severe form: infanticide, presumably committed by the breeding females on one another's offspring.

INFANTICIDE

Common marmosets and other callitrichines have traditionally been considered monogynous – that is, living in groups containing only a single breeding female [e.g., Epple, 1967; Rothe, 1975; Sussman & Garber, 1987; Ferrari & Lopes Ferrari, 1989]. In monogynous groups, aggression towards extragroup females, suppression of reproductive physiology in subordinate females, and inhibition of sexual behavior as a consequence of social subordination or inbreeding avoidance may be the primary mechanisms of reproductive competition, as described above. Recently, however, a growing number of investigators have described groups of common marmosets in which two females bred concurrently [Alonso, 1986; Scanlon et al., 1988; Adler & Jämrich, 1991; Rothe & Koenig, 1991; Digby & Ferrari, 1994; Mendes Pontes & Monteiro da Cruz, 1995; Kirkpatrick-Tanner et al., 1996; Yamamoto et al., 1996; Saltzman et al., 1997b, unpublished data; Roda & Mendes Pontes, 1998; Lazaro-Perea et al., 2000; Alencar et al., unpublished data]. Polygynous groups have also been described among other callitrichines [reviewed by French, 1997], including black-tailed marmosets [*C. argentata melanura*: Carroll, 1986], buffy-tufted-ear marmosets [*C. aurita*: Coutinho & Corrêa, 1995], Wied's black tufted-ear marmosets [Alonso & Porfírio, 1993], pygmy marmosets [Schröpel, 1998], golden lion tamarins [Dietz & Baker, 1993], golden-headed lion tamarins [*L. chrysomelas*: Chaoui & Hasler-Gallusser, 1999; De Vleeschouwer et al., 2001], cotton-top tamarins [Price & McGrew, 1991], moustached tamarins [*S. mystax*:

Ramirez, 1984; Garber et al., 1993], and saddle-back tamarins [Terborgh & Goldizen, 1985]. It is noteworthy that groups virtually never contain more than two breeding females, despite the common presence of additional adult females [but see Kirkpatrick-Tanner et al., 1996; De Vleeschouwer et al., 2001].

The factors favoring the occurrence of polygyny in natural populations are not known. However, studies of captive marmosets and tamarins suggest that integration of an unrelated adult male into a family may commonly lead to the emergence of a second breeding female [Carroll, 1986; Price & McGrew, 1991; Rothe & Koenig, 1991; Kirkpatrick-Tanner et al., 1996; Saltzman et al., 1997b,c, unpublished data; reviewed by French, 1997]. Results of a recent genetic study of free-living common marmosets are consistent with this pattern. Using microsatellite DNA analysis, Nievergelt et al. [2000] found that in three polygynous groups, the two breeding females were as closely related to each other as mother/offspring or sister pairs but were not closely related to the breeding male. Moreover, almost half of the nonbreeding adults were not closely related to the group's breeding male, suggesting that the male had recently immigrated into the group and began breeding with a mother and daughter or two sisters. Additionally, Dietz & Baker [1993] found that wild golden lion tamarin daughters were more likely to breed polygynously in groups containing an unrelated male than in intact families containing only related males.

Killing of non-descendant conspecific infants by males, especially after takeovers of groups by new males, has been reported in a number of mammalian species, including some primates, carnivores, rodents, ungulates, and cetaceans, and has been interpreted by some investigators as a form of male-male reproductive competition [reviewed in van Schaik & Janson, 2000]. Among common marmosets, however, as in several other mammalian species [reviewed by Digby, 2000; also see Vervaecke et al., this volume], infanticide may be more likely to be performed by females, possibly as a mechanism of female-female reproductive competition. Recent evidence, largely anecdotal, suggests that infanticide may occur regularly in polygynous groups of *C. jacchus*. Infanticide has been observed or inferred at least six times in free-ranging polygynous groups [Digby, 1995a; Yamamoto et al., 1996; Roda & Mendes Pontes, 1998; Lazaro-Perea et al., 2000; Arruda et al., unpublished data] and in at least 12 captive polygynous groups or "potentially polygynous" groups containing two or more adult females and an unrelated adult male [Alonso, 1986; Kirkpatrick-Tanner et al., 1996; Alencar et al., unpublished data; Saltzman et al., unpublished data]. These cases are summarized in Table I. Particularly striking is that many of these cases were known or suspected to involve a female killing the infant(s) of another female that was, or was likely to be, a close relative, a phenomenon that has been reported in several other cooperatively breeding species [e.g., black-tailed prairie dog, *Cynomys ludovicianus*: Hoogland, 1985; dingo, *Canis familiaris dingo*: Corbett, 1988; suricate, *Suricata suricatta*: Clutton-Brock et al., 1998].

Several occurrences of infanticide in free-ranging groups have been described in considerable detail. For example, Digby [1995a] observed the wounding and death of a 24-day-old infant of a subordinate breeding female in a free-ranging group. Although the infanticidal animal could not be identified definitively, circumstantial evidence

Table I. Observed and inferred infanticides in polygynous groups of common marmosets or potentially polygynous groups containing at least two adult females and an unrelated adult male.

Reference	Field/ Lab	# Observed or Inferred ^a	Perpetrator	Comments
Alonso [1986]	Lab	2 presumably observed (same family)	Other (dominant) breeding female (full- or half-sister of infant)	
Digby [1995a]	Field ^b	1 observed	Probably other (dominant) breeding female (possibly not closely related to infant: Nievergelt et al., 2000)	Dominant breeding female gave birth 2 days later.
Yamamoto et al. [1996]; Arruda et al, unpub. data	Field ^b	3 observed	Other (dominant) breeding female (relatedness unknown in 2 cases; grandmother of infant in one case)	
Kirkpatrick- Tanner et al. [1996]	Lab	1 observed	Other breeding female (grandmother of infant)	Unrelated male had been introduced into family following death of original breeding male. Perpetrator gave birth 1 week after infanticide.
Kirkpatrick- Tanner et al. [1996]	Lab	1 inferred (same family as above)	Unknown	Unrelated male had been introduced into family following death of original breeding male. Other breeding female gave birth 4 days after infanticide.
Roda & Mendes Pontes [1998]	Field ^c	1 observed	Other (transiently subordinate) breeding female (relatedness unknown)	Perpetrator gave birth approximately 1 month later.

Table I. (continued)

Reference	Field/ Lab	# Observed or Inferred ^a	Perpetrator	Comments
Lazaro-Perea et al. [2000]	Field ^b	1 observed (same perpetrator and mother of infants as one case observed by Arruda et al., unpub. data)	Other (dominant) breeding female (relatedness unknown)	Two females conceived within approx. 2 months after death of the previous breeding female. Perpetrator gave birth the month after infanticide.
Saltzman et al., unpub. data	Lab	1 observed	Other (transiently subordinate) breeding female (grandmother of infant)	Unrelated male had been introduced into family following death of original breeding male. Perpetrator gave birth 1 week after infanticide.
Saltzman et al., unpub. data	Lab	15 inferred (15 infants in 10 litters in 9 families, including same family as above)	Unknown	Unrelated male had been introduced into each family following death or removal of original breeding male. In 6 families, other breeding female was pregnant at time of infanticide; in 2 families, daughter never bred; in 1 family, matriarch had died prior to death of daughter's infants.
Alencar et al., unpub. data	Lab	1 inferred	Unknown	Female twins housed with unrelated male; only one bred.

^aNumber of litters in which infants were killed.

^bEFLEX-IBAMA field station, Nísia Floresta, Rio Grande do Norte, Brazil.

^cSan Antonio Ranch, Jaboatão, Pernambuco, Brazil.

strongly suggested that it was the group's dominant breeding female, who gave birth two days later. Similarly, Lazaro-Perea et al. [2000] observed a female kill and consume the infant of a female groupmate. The infanticidal female gave birth the following month. Roda and Mendes Pontes [1998] observed a dominant female kill the 2-week-old infant of another female in the same group before giving birth a month later. Arruda and colleagues [unpublished data; Yamamoto et al., 1996] have witnessed four infanticides committed by dominant females in polygynous groups.

Infanticide may also occur frequently in captive polygynous groups. Alonso [1986] reported that a daughter in a captive family began to breed, became dominant over her mother, and committed infanticide on two consecutive sets of her mother's infants. In a large family studied by Kirkpatrick-Tanner et al. [1996], the matriarch and two of her daughters conceived following the death of the original breeding male and subsequent introduction of an unrelated adult male into the group. The matriarch was observed to kill and partially consume the newborn infant of one daughter one week before delivering her own infants. Five months later, when the second daughter gave birth, one newborn infant was found partially cannibalized. The perpetrator could not be identified, but the matriarch gave birth four days later.

Finally, Saltzman et al. [unpublished data] introduced an unrelated, unfamiliar adult male into each of 11 captive families, following the death or removal of the original breeding male, in order to stimulate reproductive activation in daughters. Infanticide – involving the infant(s) of the matriarch (N=4), the infant(s) of her daughter (N=4), or both (N=1) – was inferred in nine of the 11 families containing an unrelated male but in only one of five control families containing the original breeding male. In one family, the matriarch was known to have killed one, and almost certainly both, of her daughter's infants. In the remaining cases, infanticide was inferred from the patterns of wounding on the infants, but the perpetrator could not be identified. In six of the families, one female was pregnant when the other female's infants were apparently killed. These findings provide the first systematic, experimental evidence that infanticide may occur regularly in polygynous groups of common marmosets.

In the study by Saltzman et al. [unpublished data], infanticide appeared to have occurred in two families that contained unrelated males but in which the daughters never bred. In another family, all three of the daughter's newborn triplets were apparently killed, even though the matriarch had been euthanized one month earlier due to illness. In these families, infants might have been killed by their mother, their father, or an older sibling. Thus, families into which an unrelated male has recently become integrated may be prone to infanticide even if only a single breeding female is present. This scenario is superficially similar to the most common situation in which male mammals have been found to commit infanticide: following the takeover of a group by a new male or all-male band, when the new male(s) may kill unweaned infants sired by their predecessors [van Schaik & Janson, 2000; see Crockett and Palombit, this volume]. Infanticide under these circumstances may benefit the perpetrator by terminating the mother's period of lactational infertility, thereby advancing the male's opportunities to inseminate her. In the groups studied by Saltzman et al., however, the infants that were killed were sired by the unrelated males themselves, not by their predecessors. More-

over, adult male marmosets have not been reported to commit infanticide under these circumstances and are usually extremely tolerant of, attracted to, and parental toward both related and unrelated infants [e.g., Ingram, 1977; Newman et al., 1993; Saltzman et al., unpublished data]. Finally, in contrast to many other species, female marmosets do not undergo lactational anovulation. Instead, they typically ovulate and conceive within 2-3 weeks postpartum [McNeilly et al., 1981; Lunn & McNeilly, 1982; Kholkute, 1984], so that infanticide by males would be unlikely to significantly advance the male's mating opportunities. Thus, although male marmosets might occasionally commit infanticide under pathological conditions [e.g., chronic illness: Abbott et al., unpublished data], sexually selected infanticide by males is unlikely to occur in this species.

The prevalence of infanticide in polygynous marmoset groups is unknown. In captivity, infants may be killed within hours after their birth [Kirkpatrick-Tanner et al., 1996; Saltzman et al., unpublished data] and may be consumed by the infanticidal individual and other animals [Kirkpatrick-Tanner et al., 1996; Lazaro-Perea et al., 2000; Saltzman et al., unpublished data]. As a result, it is likely that some occurrences of infanticide are never detected in free-ranging or even captive groups. Moreover, a number of investigators have reported the disappearance of infants in polygynous groups [Adler & Jämmrich, 1991; Digby & Ferrari, 1994; Roda & Mendes Pontes, 1998], which could certainly reflect unobserved cases of infanticide. On the other hand, cases of inferred infanticide [e.g., Kirkpatrick-Tanner et al., 1996; Alencar et al., unpublished data; Saltzman et al., unpublished data] might sometimes reflect post-mortem mutilation or cannibalism of infants that died spontaneously. Finally, it should be noted that all of the reported cases of infanticide in polygynous groups have occurred either in captivity or in disturbed forests or forest fragments containing a high density of marmosets, factors that could conceivably increase the likelihood of infanticide [Mendes Pontes & Monteiro da Cruz, 1995; Roda & Mendes Pontes, 1998].

It is also unclear whether infanticide is significantly associated with polygyny. Infanticide can occur in monogynous groups of stable composition [Rothe, 1977; Poole & Evans, 1982; Johnson et al., 1991; Saltzman et al., unpublished data] but may be less likely to be reported in these circumstances than when it occurs in polygynous groups. Conversely, in both wild and captive groups, two females occasionally have been observed to rear infants successfully during the same time period [Adler & Jämmrich, 1991; Rothe & Koenig, 1991; Digby, 1995a; Kirkpatrick-Tanner et al., 1996; Roda & Mendes Pontes, 1998; Saltzman et al., unpublished data; Figure 1]. However, Digby [1995a] found that subordinate breeding females in polygynous groups were consistently more protective of their infants than were dominant breeding females, resisting attempts by other group members to carry the infants [see also Koenig & Rothe, 1991; Lazaro-Perea et al., 2000]. This pattern could indicate that the threat of infanticide is prevalent enough that female marmosets have evolved behavioral counter-strategies [Digby, 2000].

Although most of the reports of infanticide in polygynous groups of common marmosets have been anecdotal, and several were not fully characterized, it is possible to discern some tentative patterns. First, the most common scenario appears to involve the killing of a subordinate female's infant by a dominant breeding female [Alonso,

Figure 1. A female common marmoset with her 16-week-old twin offspring and her mother's 10-week-old singleton offspring; a third infant of the daughter's was apparently killed shortly after birth. The daughter began to breed concurrently with her mother following the experimental removal of her father and introduction of an unrelated, unfamiliar adult male into the family [Saltzman et al., unpublished data]. (Photo by Jordana Lenon, Wisconsin Regional Primate Research Center.)



1986; Digby, 1995a; Yamamoto et al., 1996; Roda & Mendes Pontes, 1998; Arruda et al., unpublished data]. However as noted above, some authors do not specify their criteria for dominance, and the breeding female that appears to be older or that has been breeding longer may sometimes be considered dominant in the absence of behavioral indicators. In most of the polygynous families studied by Saltzman et al. [unpublished data], the two breeding females were never observed performing submissive vocalizations or submissive facial expressions to one another, in spite of frequent, systematic observations of the families. In several families, however, the original breeding female clearly became behaviorally subordinate to her daughter, at least transiently [see also Alonso, 1986]. Furthermore, dominance relationships between females apparently can be altered by the presence of infants. For example, Saltzman et al. [unpublished data] observed a late-pregnant matriarch repeatedly performing submissive vocalizations to her daughter after, but not before, the birth of the daughter's infants. However, the submissive behavior ceased after the infants were killed [see also Roda & Mendes Pontes, 1998]. Finally, in one of the families studied by Saltzman et al. [unpublished data], infants of both breeding females appeared to have been killed, demonstrating that infants of either female can be vulnerable to infanticide.

Second, infanticide may be most likely to be committed by females who are themselves in the late stages of pregnancy. Based on a total of four pairs of births, Digby [1995a] noted that infants of subordinate breeding females were most likely to survive if they were born at least 40 days before or after the infants of the dominant female, presumably due to reduced competition for resources when birth synchrony was minimized. The increased mortality rate of infants born more synchronously with those of the dominant female might include deaths from causes other than infanticide. However, in a striking number of cases, females have been known or suspected to commit infanticide when they themselves were in the last month of pregnancy [Digby, 1995a; Kirkpatrick-Tanner et al., 1996; Roda & Mendes Pontes, 1998; Lazaro-Perea et al., 2000; Saltzman et al., unpublished data].

These observations of infanticide by pregnant female marmosets contrast with findings in several other species, in which infanticide is committed most often by lactating females [e.g., black-tailed prairie dog: Hoogland, 1985; Columbian ground squirrel, *Spermophilus columbianus*: Stevens, 1998; northern elephant seal, *Mirounga angustirostris*: Le Boeuf et al., 1972; Le Boeuf & Briggs, 1977] but are similar to findings in the suricate, another cooperative breeder, in which pregnant females – especially pregnant dominant females – may frequently kill the infants of female kin [Clutton-Brock et al., 1998]. The pattern of infanticide by pregnant female marmosets is also consistent with results of a recent study in which multiparous female common marmosets' responses to unfamiliar infants, which were introduced briefly into the female's home cage, were assessed during early pregnancy, late pregnancy, and the early postpartum period [W. Saltzman, B. Pape & D.H. Abbott, unpublished data]. In the two weeks after giving birth, females were highly tolerant of and parental toward unfamiliar infants, showing no clear behavioral discrimination between these and their own infants. During pregnancy, however – and especially during late pregnancy – the same females typically ignored unfamiliar infants or behaved aggressively toward them.

Third, although infanticide may occur in the context of heightened agonism between the two breeding females [Roda & Mendes Pontes, 1998], this is frequently not the case [Lazaro-Perea et al., 2000]. To the contrary, the two females may engage in affiliative behaviors with one another shortly after the infanticide has occurred [Digby, 1995a; Saltzman et al., unpublished data] and may even nurse one another's offspring [Digby, 1995a; Roda & Mendes Pontes, 1998; Saltzman et al., unpublished data].

In summary, when other mechanisms of female reproductive competition break down and two females breed concurrently in the same marmoset group, the breeding females might routinely attempt to kill one another's infants. Although we have no clear idea of the frequency of infanticide or its association with polygyny, it appears that infanticide may be quite likely to occur when one female, especially a subordinate, gives birth while another is heavily pregnant. The fact that females may be likely to kill infants that are closely related to themselves hints at the severity of reproductive competition among female marmosets.

EVOLUTIONARY IMPLICATIONS, CONCLUSIONS, and PROSPECTS

The findings reviewed here demonstrate that the pronounced reproductive skew and high potential fecundity of female common marmosets are associated not only with a high degree of cooperation within groups but also with reproductive competition, which is manifest in several phenomena including aggression towards extragroup females, suppression of ovulation and inhibition of sexual behavior in subordinate females, and, possibly, infanticide in polygynous groups. Female marmosets may, therefore, face obstacles to successful reproduction at multiple stages of the reproductive process, from gaining group membership, in some cases, to engaging in fertile matings to successfully rearing offspring. These obstacles may be associated with several different demographic and psychosocial factors. Whereas social subordination appears to play the predominant role in determining ovulatory function and, to a lesser extent, sexual behavior and vulnerability to infanticide, the presence of unrelated males

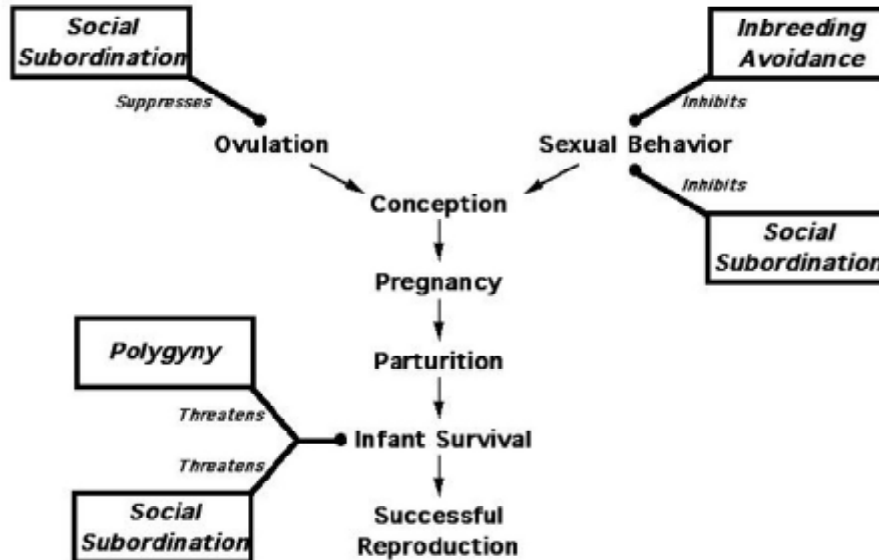


Figure 2. Proposed relationships between stages of reproduction and inhibitory social influences in female common marmosets. Note that social subordination is associated with suppression of ovulation, inhibition of sexual behavior and, in polygynous groups, threatened infant survival (infanticide). Sexual behavior is further constrained by inbreeding avoidance.

in the group and the presence of another breeding female are also key determinants of a female's reproductive success. The hypothesized relationships between these variables and reproductive outcomes are depicted in Figure 2.

The severe constraints on reproduction in female marmosets raise a number of intriguing evolutionary and functional questions. A thorough discussion of these issues is beyond the scope of this chapter [but see reviews by Sussman & Garber, 1987; Goldizen, 1990; Dunbar, 1995; Rylands, 1996; Garber, 1997], however, several especially relevant points are worth mentioning.

First, although several theoretical models of reproductive skew postulate that dominant individuals control the reproductive efforts of subordinates [Vehrencamp, 1983; Reeve et al., 1998; see Hager, this volume], this may not apply to female marmosets in a proximate sense, especially with respect to ovulation suppression. In some species, such as gelada baboons and yellow baboons, reduced reproductive success in subordinate females as compared to dominants is caused by dominant females harassing subordinates. These behaviors appear to disrupt subordinates' reproduction by activating a generalized stress response that potentially can interfere with several aspects of reproductive physiology and behavior, including ovulation, pregnancy maintenance, and maternal care [reviewed by Abbott et al., 1997]. In these species, then, dominant animals actively manipulate subordinates, exploiting the widespread sensitivity of the female reproductive system to inhibition by a variety of

physical and psychological stressors. In contrast, ovulation suppression in subordinate female marmosets is not typically associated with high levels of intrasexual aggression or with physiological indices of generalized stress, such as elevated cortisol levels. Instead, it appears to be mediated by a specialized neuroendocrine mechanism that may have evolved specifically to rapidly switch the reproductive system on or off in response to unpredictable changes in the social environment. In other words, reproductive suppression in female common marmosets may be conceptualized more appropriately as subordinates suppressing their own reproductive physiology in response to cues from a dominant female rather than as dominant females actively imposing suppression on passive subordinates.

Wasser & Barash [1983] have developed a model that postulates the conditions under which female mammals should suppress their own reproduction. Because mammalian reproduction typically involves considerable investment from females and because tradeoffs exist between an individual's current reproductive efforts and her future reproductive prospects, females can sometimes increase their lifetime reproductive success by deferring reproduction until prevailing conditions improve. Specifically, the Reproductive Suppression Model states that "females can optimize their lifetime reproductive success by suppressing reproduction when future conditions for the survival of offspring are likely to be sufficiently better than present ones as to exceed the costs of the suppression itself" [Wasser & Barash, 1983, p 513]. This model generates several important predictions that are especially germane to female marmosets. First, whenever possible, females should base their "decisions" about whether or not to attempt reproduction on cues that are highly predictive of likely reproductive outcomes. Second, to minimize investment in reproductive attempts that are not likely to succeed, they should terminate these attempts as early as possible in the reproductive process, for example, pre- rather than post-conception. Third, because older females have lower expected future reproductive success than younger females, they should be less likely to defer reproduction.

According to this model, the presence of a dominant female groupmate might, for a subordinate female marmoset, provide a reliable indicator that any infants produced by the subordinate are not likely to survive. Consequently, a subordinate might suppress her own ovulatory function (and sexual behavior) in response to cues from the dominant female in order to minimize her investment in unsuccessful reproductive attempts and, presumably, to maximize her chances of reproducing successfully in the future. Although we do not know the likelihood that non-reproductive subordinates will eventually breed [but see Scanlon et al., 1988], Jaquish et al. [1991] found that in a captive population of common marmosets and other callitrichines, females' age at first reproduction was positively related to their survivorship. This relationship is likely to be even more pronounced under natural conditions where increasing parity might increase a female's vulnerability to predation, disease, or food scarcity. By suppressing her own reproductive function, therefore, a subordinate female marmoset might be "making the best of a bad situation" by increasing her likely survivorship and future prospects for direct reproduction in the long term, while possibly increasing her indirect fitness in the short term by helping to rear the offspring of close relatives.

Why should the presence of a dominant female reliably predict that a subordinate's infants will not survive? One possibility is that the dominant female and/or her offspring will be able to outcompete the subordinate female and/or her offspring for access to critical resources, such as food or alloparents. Although we have no direct evidence that such scramble competition contributes to infant mortality in common marmosets, subordinate breeding females may have higher rates of infant mortality than dominants even in the absence of known occurrences of infanticide [Digby, 1995a]. Alternatively, dominant females may pose a more direct threat to the survival of a subordinate's offspring. As reviewed above, the literature on infanticide, although largely anecdotal, indicates that females that breed polygynously, especially if they are subordinate, may face a substantial risk of infanticide, particularly from the other breeding female. If, evolutionarily, the threat of infanticide has been sufficiently large, and the likelihood that a subordinate female will successfully rear offspring sufficiently small, females may have been selected to curtail their own reproductive attempts – through suppression of ovulation and inhibition of sexual behavior – in the presence of a dominant breeding female. Thus, while dominant females may not actively impose reproductive suppression on subordinates in a proximate, mechanistic sense, they may act as an agent of selection, favoring the evolution of reproductive self-suppression in subordinate females [see Creel & Waser, 1997, for a similar argument in carnivores]. In this scenario, then, reproductive suppression in subordinate female marmosets represents primarily a consequence of sexual selection resulting from intrasexual reproductive competition, which may secondarily contribute to cooperative breeding.

A particularly striking characteristic of infanticide in polygynous marmoset groups is that females may be likely to kill infants that are closely related to themselves (e.g., grandchildren or half-siblings) and therefore reduce their own indirect fitness. In so doing, infanticidal females should presumably gain a direct fitness benefit large enough to offset the indirect fitness loss. Digby [1995a, 2000] has argued that infanticide by female common marmosets and other female cooperative breeders is likely to function in resource competition. It is not yet clear for what resources female marmosets may be competing, but food and access to alloparents have been mentioned as possibilities [e.g., Sussman & Garber, 1987; Goldizen, 1990; Digby, 1995a; Rylands, 1996]. Alternatively, infanticide in marmosets might be a pathological behavior engendered by high population densities, poor health or nutritional status, or other organismic or ecological conditions [e.g., Roda & Mendes Pontes, 1998]. Additional research will be needed to determine the fitness consequences of infanticide to perpetrators and how these consequences are achieved.

In spite of the threat of infanticide, previously non-reproductive females may begin to breed in the presence of another breeding female when an unrelated male enters the group. Why should females be willing to invest in risky reproductive attempts under these conditions? Several factors may contribute. First, infanticide notwithstanding, females with access to an unrelated male in the group may be more likely to produce viable offspring than those that mate with close relatives. Studies of both captive [Ralls & Ballou, 1982] and wild [Dietz & Baker, 1993] callitrichines have shown that inbreeding can significantly increase infant mortality. Second, replacement of the

original breeding male by an unrelated male will significantly reduce a daughter's genetic payoffs for serving as a non-reproductive helper. Daughters in intact families with both biological parents can assist in rearing their own full siblings. On average, they will be as closely related to these siblings as they would be to their own offspring [coefficient of relatedness (r) = 0.50]. In contrast, a daughter whose father has been replaced by an unrelated male will have the opportunity to help rear only half siblings ($r = 0.25$), to whom she is less closely related, on average, than she would be to her own offspring [Saltzman et al., 1997a; see also Vehrencamp, 1983]. Although females that breed polygynously might face a distinct risk of infanticide, those that do so following replacement of the father by an unrelated male might have a reasonable likelihood of successfully rearing at least one infant, which would help compensate for the reduction in indirect fitness resulting from the loss of the father.

Furthermore, according to the Reproductive Suppression Model [Wasser & Barash, 1983], females should sometimes attempt to reproduce even under inauspicious conditions, if circumstances are unlikely to improve. Thus, if a female marmoset has little opportunity to join a group with a breeding vacancy and no indication that the tenure of her own group's current breeding female will end soon, she may do better to breed polygynously in the natal group, especially if an unrelated male is present, than to defer reproduction indefinitely and possibly never breed at all. A similar argument may explain why marmosets occasionally mate with close relatives [Epple, 1970; Anzenberger & Simmen, 1987; Crook, 1988; König et al., 1988; Adler & Jämmrich, 1991] despite the relatively high mortality rate of inbred infants [Ralls & Ballou, 1982; see also Dietz & Baker, 1993]. In both cases, older females should be more likely than younger females to engage in risky (i.e., polygynous or incestuous) reproductive attempts. Although age, access to an unrelated male, physical and reproductive status of the current breeding female [Saltzman et al., 1997a, Price, 1998], group size [De Vleeschouwer et al., 2001] and breeding opportunities in other groups are all likely to influence a female's "decision" as to whether or not to attempt reproduction, further research is needed to determine if and how these factors act and interact in determining female reproductive strategies.

Our progress in elucidating the reproductive strategies of female common marmosets and other callitrichines exemplifies an integrative approach utilizing complementary, mutually informed behavioral and physiological studies from the field and captivity. Findings originally made in the laboratory, such as sex-biased extragroup aggression and suppression of ovulation, are now being investigated in wild populations, where their ecological and demographic determinants and functional significance can be evaluated. Conversely, phenomena first reported in wild marmosets, such as polygyny and infanticide, are now being examined in laboratory experiments to identify the behavioral and physiological underpinnings. Often, field and laboratory studies have yielded remarkably concordant results. Although a number of important questions remain unanswered, this integrative approach will doubtless continue to yield many insights, from physiological and even cellular mechanisms through ecological influences, on the ways in which female marmosets constrain one another's, and their own, reproductive efforts.

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