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## Reproductive skew in female common marmosets: contributions of infanticide and subordinate self-restraint

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### Summary

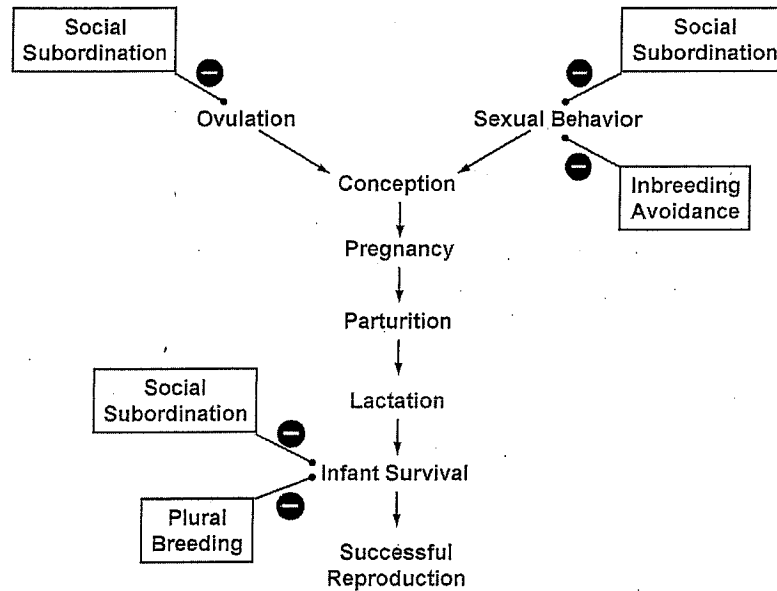
The common marmoset (*Callithrix jacchus*) is a cooperatively breeding monkey that exhibits high reproductive skew among females. At the proximate level, this high skew is maintained, for the most part, by reproductive self-restraint in subordinates, involving specialized behavioral and neuroendocrine responses to the presence of a dominant female. When subordinates terminate this self-restraint, however, dominant females frequently control subordinates' reproductive attempts by killing their infants. Based on data collected over 20 years from both the field and the laboratory, we propose that such infanticide constitutes not only a proximate mechanism limiting subordinate females' reproductive success, but also an ultimate mechanism favoring selection for reproductive self-restraint in subordinate females. Our hypothesis is consistent with both the *commitment model* of reproductive skew (Hamilton 2004), in terms of pre-conception restraint, and the *discriminate infanticide model* (Hager & Johnstone 2004), in terms of infanticide as a mechanism driving subordinate self-restraint. Parallel, long-term field and laboratory studies of common marmosets provide powerful interdisciplinary approaches enabling investigation of mechanisms regulating female reproductive skew at a proximate level, while providing novel insight into potential ultimate causation.

## Introduction

Among primates, moderate female reproductive skew, manifest as high reproductive success among a limited number of adult females in a social group, is associated with social dominance in many species (Abbott *et al.* 2003). Extreme monopoly of reproduction by only one or two females, however, is restricted to most, but not all, members of a single primate subfamily, the Callitrichinae (the marmosets and tamarins). These species, especially the well-studied common marmoset (*Callithrix jacchus*), present an opportunity to integrate both proximate and ultimate explanations of reproductive strategies in order to better understand the evolution and mechanisms of reproductive skew.

Two principal classes of theoretical models have been developed to explain reproductive skew in cooperatively breeding species: *transactional models* (e.g. concession or restraint models) and *compromise models* (e.g. tug-of-war models; reviewed in Hager 2003, Johnstone 2000). One of the variables that distinguishes the different subclasses of these models involves the question of which individuals “control” reproduction. Do dominant females “concede” reproductive control in order to entice subordinates to delay dispersal and instead provide care for the dominant female’s offspring (e.g. Keller & Reeve 1994, Reeve 1998)? Or are dominant females simply unable to completely control subordinates’ reproductive activity, resulting in subordinate females engaging in a “tug-of-war” with dominants and breeding whenever dominant females are unable to prevent them from doing so (e.g. Clutton-Brock 1998, Reeve *et al.* 1998)? Notably, many skew models focus on the dominant breeders and their ability, or lack of ability, to control reproduction in subordinates. Reproductive self-restraint, or self-inhibition, however, may also play a role in determining reproductive skew (Snowdon 1996, Hager & Johnstone 2004). The *commitment model*, for example, proposes that subordinates “commit” to reproductive suppression in exchange for reduced harassment from dominant females (Hamilton 2004).

In recent years, a number of investigators, including ourselves, have argued that not all aspects of diminished reproductive function in subordinate female callitrichines can be attributed to control by dominant individuals, but instead reflect adaptive, self-imposed restraint or commitment to self-inhibition (Snowdon 1996, Abbott *et al.* 1997, Saltzman 2003, Yamamoto *et al.* in press). In this chapter, we will describe patterns of reproductive skew in female common marmosets, and the proximate mechanisms that generate this skew, including both pre-conception mechanisms (e.g. suppression of female reproductive physiology and inhibition of sexual behavior) and post-conception mechanisms (infanticide) (Figure 12.1). Based on these findings, we suggest that while pre-conception reproductive suppression in female common marmosets is



**Figure 12.1** Diagrammatic illustration of proposed relationships between pre- and post-conception stages of female reproduction, and inhibitory social influences operating in common marmoset social groups. Social subordination may determine suppression of ovulation, inhibition of female sexual behavior, and, in plurally breeding groups, vulnerability to infanticide. Female sexual behavior is further constrained by inbreeding avoidance. Modified from Saltzman (2003).

mediated, mechanistically, by self-restraint or self-inhibition in subordinates, it likely evolved in response to a postpartum mechanism of dominant control of reproduction – infanticide – and may be best represented by modified commitment models of reproductive skew. Kin selection, due to the high degree of relatedness among female marmoset group-mates, may have intensified the development of such commitment to reproductive self-restraint.

### Social groups of common marmosets

#### *Free-living groups*

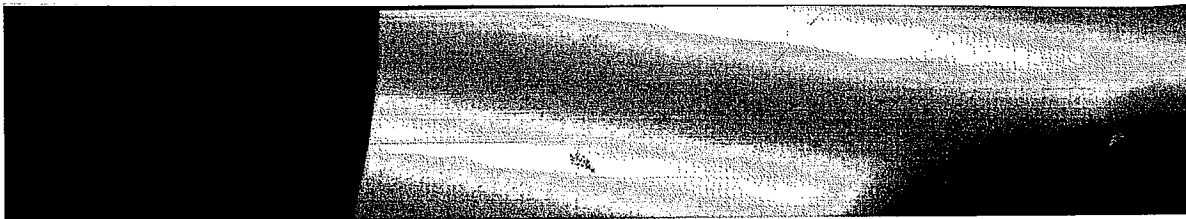
The small body size (< 0.5 kg) of common marmosets reflects an evolutionary process of specialization enabling efficient colonization of marginal and disturbed forest habitats, sometimes at high population densities, in the northern extreme of the Atlantic coastal forest and arid thorn scrub of northeastern Brazil (Ferrari 1993, Rylands & Faria 1993). With limited breeding and dispersal opportunities, it is not surprising to find highly developed forms

of communal living and cooperative breeding (Keller & Reeve 1994, Lacey & Sherman 1997).

In species with high reproductive skew, group size and composition clearly influence the costs and benefits of breeding. The presence of other breeding females, the chances of gaining a reproductive position within a group, and the availability of unrelated males may all play important roles in determining the reproductive strategies of a particular female. Common marmosets tend to live in groups of up to 20 individuals, including multiple adult males and females (reviewed in Digby *et al.* 2007). These groups, like those of most other social primates, are cohesive, with group members remaining within sight of one another over the course of the day and frequently grooming one another (Digby 1995a, Lazaro-Perea *et al.* 2004). Groups typically contain one or two breeding females (which may be close relatives that are unrelated to the breeding male(s)) along with their siblings and/or adult offspring (Nievergelt *et al.* 2000, Faulkes *et al.* 2003); however, population crashes and periods of instability can result in groups containing unrelated females (Lazaro-Perea *et al.* 2000, Faulkes *et al.* 2003). Though polyandry (in which two males share mating access to a breeding female) has been noted in some callitrichines, including common marmosets, the latter tend toward within-group monogamy and polygyny with frequent episodes of extra-group copulations (Digby 1999, Arruda *et al.* 2005; but see also Lazaro-Perea *et al.* 2000). Groups also include non-breeding adult individuals that are not sexually active within the group, but these non-breeders may participate in extra-group copulations (Digby 1999, Lazaro-Perea *et al.* 2000).

Similar to many other species exhibiting high reproductive skew (Reeve & Emlen 2000), common marmosets tend to show low frequencies and intensities of intra-group aggression, although agonism can increase following changes in group composition (Digby 1995a, Lazaro-Perea *et al.* 2000; see also Sussman *et al.* 2005). Attainment of dominance mostly depends on rare instances of aggression when a breeding position has been vacated, while maintenance of dominance requires little intimidation or threat (French 1997, Lazaro-Perea *et al.* 2000). Intrasexual dominance relationships are, nonetheless, apparent. In the field, one breeding female is typically found to be dominant to a second breeding female (in plurally breeding groups), and all breeding individuals are dominant to non-breeders (Digby 1995a, Sousa *et al.* 2005). Under laboratory conditions, breeders are again dominant to non-breeders, but it is often impossible to detect a clear dominance relationship between breeding females (Saltzman *et al.* 1997b, 2004, 2008).

There are several possible explanations for this apparent disparity between field and laboratory observations. First, dominance relationships in wild groups (e.g. Digby 1995a, Arruda *et al.* 2005, Sousa *et al.* 2005, Bezerra *et al.*



2007, Lazaro-Perea *et al.* 2000) are often assessed largely on the basis of the direction and frequency of mildly aggressive behavior (e.g. threats, chases, pilo-erection), sexual behavior, and even affiliative behavior, in addition to submissive behavior (e.g. avoidance/withdrawal, cower), whereas those in laboratory groups have been assessed strictly on the basis of relatively subtle submissive behaviors (e.g. submissive vocalizations, grimaces; e.g. Saltzman *et al.* 2004), which may be difficult to detect in the field. Second, data on agonistic behavior in wild groups are often collapsed across extended time periods, whereas agonistic interactions in laboratory groups may be assessed more acutely. Because dominance relationships between breeding females may be altered transiently by the presence of infants (e.g. Alonso 1986, Roda & Mendes Pontes 1998, Saltzman 2003, Bezerra *et al.* 2007), laboratory studies may be better able to detect short-term changes in the existence or directionality of dominance relationships than has been possible in the field. Nonetheless, for the sake of simplicity, in this chapter we will continue to refer to "dominant" and "subordinate" breeding females, while acknowledging that these dominance relationships between female marmosets may be more complex and transitory than has often been presumed. In plurally breeding laboratory families, we refer to the older breeding female (mother) as the dominant female, in spite of the absence of distinct behavioral indices of dominant or subordinate status (Saltzman *et al.* 2004, 2008).

Common marmoset mothers typically receive extensive help with carrying and feeding infants from all adult and subadult group members (Figure 12.2), beginning on the day of parturition (Digby 1995b, Yamamoto *et al.* 1996). Subordinate breeding females also receive such alloparental assistance, but cooperative care may not begin until the infants are several weeks old (Digby 1995b). Since subordinate breeding females are more protective of their infants, this delay in allo-parental care may result from potential alloparents having limited access to these infants, rather than from group members being unwilling to help.

#### *Laboratory groups*

In captivity, common marmosets can be housed as (1) adult male-female pairs that usually establish families (Layne & Power 2003), (2) families in which the biological mother or father has been replaced by an unrelated adult of the same sex (Saltzman *et al.* 2004), (3) peer groups of adolescents or young adults (Hiddleston 1978, Abbott 1984), and (4) groups of unrelated adults (Saltzman *et al.* 1994). Apart from the case when the breeding male is replaced by an unrelated male (Saltzman *et al.* 2004), most captive groups contain a single breeding female that is usually behaviorally dominant to other female



**Figure 12.2** Common marmosets usually exhibit high levels of infant care, as exemplified by the young infant carried on the back of an older sibling in this photograph. Our studies, however, show that dominant females practice infanticide on infants born to subordinate females when subordinates terminate reproductive self-restraint and produce their own infants. Courtesy of Judith Sparkles.

group members (Abbott 1984, Saltzman *et al.* 2004). Laboratory groups are thus well controlled in terms of size and the degree of relatedness of group members, and provide opportunities for experimental manipulation and elucidation of mechanisms that are not possible with free-living groups.

### **Proximate regulation of reproductive skew**

Reproductive failure in subordinate female common marmosets is potentially mediated at numerous stages of reproduction, occurring either before or after conception (Figure 12.1; French 1997). Possible pre-conception

mechanisms include inhibition of ovarian follicular development and ovulation, as well as inhibition of sexual behavior regardless of whether or not ovarian function is impaired. Post-conception reproductive failure potentially involves impairments in implantation, pregnancy maintenance, lactation, or maternal behavior (Saltzman 2003).

### Inhibition of sexual behavior

Inhibition of sexual behavior, in addition to suppression of ovulation (intermittent or absent ovarian cycles; see below), may contribute to reproductive skew in female common marmosets. Subordinate adult females typically engage in little or no intra-group sexual behavior, both in captivity (Rothe 1975, Abbott 1984, Saltzman *et al.* 1997c) and in the field (Digby 1999). This behavioral inhibition may result, at least in part, from intrasexual reproductive competition and may occur in response to cues from a dominant female group-mate. For instance, in laboratory groups of unrelated adults, dominant females may disrupt sexual interactions involving subordinate females (Abbott 1984) and thus impose a degree of direct reproductive control over unrelated females. Alternatively or additionally, inhibition of sexual behavior may be mediated by avoidance of mating with close relatives. Importantly, both of these mechanisms could contribute to inhibition of sexual behavior in free-ranging groups, since these groups may comprise closely related individuals as well as unrelated immigrants (see above; Ferrari & Digby 1996, Nievergelt *et al.* 2000, Faulkes *et al.* 2003).

Several lines of evidence support a role for intrasexual inhibition of sexual behavior. First, subordinate females engage in little or no sexual behavior even in laboratory groups of unrelated adults (Rothe 1975, Abbott 1984). It can be argued, however, that in this relatively unnatural social context, subordination may activate behavioral and physiological mechanisms that evolved in the context of family groups, so that subordinate females may respond to unrelated male group-mates as though they were close relatives. Second, when subordinate females are removed from these groups of unrelated adults and briefly paired with an unfamiliar male, they solicit and accept mounts (Abbott *et al.* 1997). Third, females may disrupt one another's sexual interactions in both singly (Epple 1967, Rothe 1975, Abbott 1984) and plurally breeding groups (Alencar *et al.* 2006). Several investigators, however, find little or no evidence of mating interference in plurally breeding groups (Kirkpatrick-Tanner *et al.* 1996, Lazaro-Perea *et al.* 2000). Finally, two genetic studies of free-ranging common marmoset groups reveal that some non-breeding adult females are not closely related to the resident breeding male,

suggesting that their reproductive activity may be inhibited by intrasexual competition alone (Nievergelt *et al.* 2000, Faulkes *et al.* 2003), as found in some laboratory groups containing unrelated marmosets (Abbott 1984, Saltzman *et al.* 2004).

Inbreeding avoidance, in addition to rank-related inhibition, has been implicated as a critical determinant of sexual behavior in subordinate females. Common marmosets typically avoid sexual interactions with familiar, closely related individuals (reviewed by Saltzman 2003). In the field, genetic studies indicate that breeding males and females within a group are usually not closely related to one another (Nievergelt *et al.* 2000, Faulkes *et al.* 2003). In captivity, daughters housed with their natal family do not engage in sexual interactions with their father or brothers, even if they are undergoing ovulatory cycles and are not clearly subordinate to their mother or another female group-mate (Abbott 1984, Saltzman *et al.* 1997c, 2004). Many of these daughters, however, will readily solicit and copulate with an unrelated-adult male introduced into the family (Kirkpatrick-Tanner *et al.* 1996, Saltzman *et al.* 1997b, 1997c, 2004; see also Anzenberger 1985, Hubrecht 1989). Notably, we find that when an unrelated male is incorporated into the family, daughters that do not engage in sexual behavior are behaviorally subordinate to their mother and/or a sister, whereas those that mate with the unrelated male are not (Saltzman *et al.* 2004). Thus, expression of sexual behavior by female common 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, 1997c, 2004, Sousa *et al.* 2005).

Subordinate females in free-ranging groups may be able to overcome both of these intra-group behavioral constraints by mating with extra-group males (Hubrecht 1984, Digby 1999, Lazaro-Perea 2001, Arruda *et al.* 2005). Lazaro-Perea (2001), for example, observed 20 extra-group copulations or attempted copulations, all of which involved non-breeding females from singly breeding groups. Digby (1999) observed 24 extra-group matings which involved both breeding and non-breeding adult females in plurally breeding groups. The functional significance of these interactions, however, is not clear. Even when subordinate females become pregnant following extra-group copulations, their infants are unlikely to survive (Arruda *et al.* 2005).

In summary, female reproductive skew in common marmosets is mediated in part by inhibition of sexual behavior in subordinates, which in turn may result from both the absence of unrelated males in the group and the presence of a dominant female. Although subordinate females may potentially use extra-group copulations to circumvent these obstacles, the reproductive consequences of such copulations are not clear.



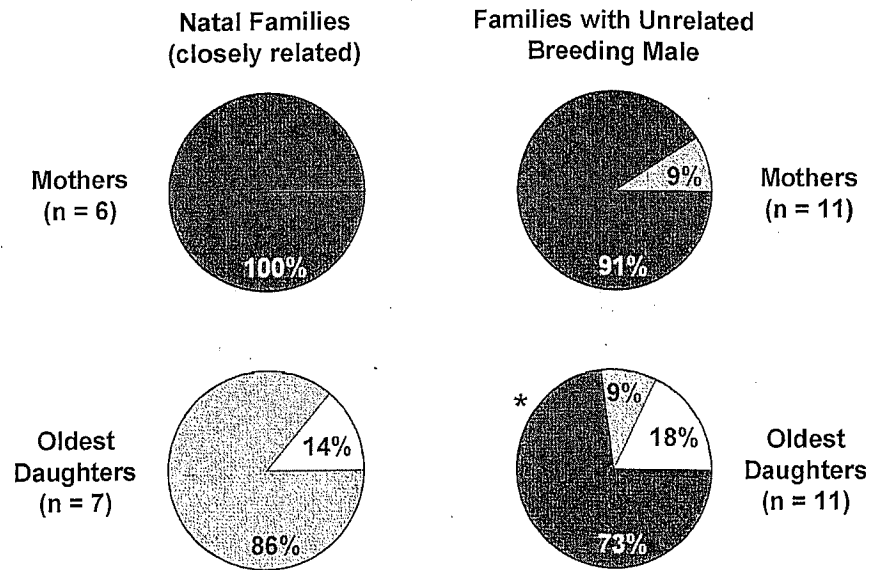
## Suppression of ovulation

### *Free-living groups*

Ovulation suppression in subordinate females appears to be a key mechanism generating reproductive skew in common marmosets. Anovulation, as determined by analysis of circulating progesterone concentrations in frequent (e.g. semi-weekly) blood samples, was first described in subordinate female common marmosets housed in groups of unrelated adults by Abbott & Hearn (1978). Since then, ovulation suppression has also been documented in adult females living with their natal families in captivity (Abbott 1984, Saltzman *et al.* 1997a, 1997b, 2004), and, more recently, in free-ranging groups in Brazil (Albuquerque *et al.* 2001). The prevalence of ovulation suppression in free-living common marmosets is not yet clear. Long-term endocrine monitoring of several wild groups suggests that these groups may commonly contain two cycling or pregnant females (Albuquerque *et al.* 2001, Sousa *et al.* 2005); however, some of these reproductively active subordinates undergo transient periods of anovulation, as determined from patterns of fecal progesterone concentrations (Albuquerque *et al.* 2001). Moreover, because these field studies have simultaneously monitored ovarian activity in only two females per group, it is unknown whether other females (i.e. rank 3 and below) exhibit ovulatory cycles or are likely to undergo suppression of ovulation.

### *Laboratory groups of intact families*

In contrast to field studies, laboratory studies – including studies of both families and groups comprising unrelated adults (discussed below) – have consistently detected ovulatory suppression in subordinate female common marmosets. Many, but not all, adult daughters fail to ovulate while housed with their parents and siblings (Figure 12.3). Several investigators have found that in slightly more than half of the families studied, all daughters were anovulatory (Abbott 1984, Hubrecht 1989, Saltzman *et al.* 1997a, 2004). These daughters typically undergo a rapid onset of ovulatory cycles following their removal from the family, indicating that ovulatory function is inhibited by some aspect of the family environment (Abbott & Hearn 1978, Abbott 1984). Importantly, a sizable minority of families contains at least one daughter undergoing ovulatory cycles (Figure 12.3). These cycles are characterized by low, luteal-phase plasma progesterone concentrations and extended follicular phases, as compared to those of older females not housed within their natal families (Saltzman *et al.* 1997a). Typically, only the oldest daughter (or one of the oldest daughters, in the case of female–female twin pairs) in a family ovulates (Saltzman *et al.* 1997a); however, younger daughters may undergo



**Figure 12.3** Percentage of mature female common marmosets that conceived (dark shading), ovulated but did not conceive (gray shading), or did not ovulate (white areas) in 6 intact families and 11 families in which the biological father was replaced by an unrelated adult male when the eldest daughters were post-pubertal. Modified from Saltzman *et al.* (2004). \*  $P < 0.05$  for percentage of pregnant oldest daughters when comparing natal families and families with an unrelated breeding male.

ovulatory cycles if they are behaviorally dominant to their older sisters (Saltzman *et al.* 2004).

Why does a daughter ovulate in some families, but not in others? One answer appears to be the daughter's relationship with her mother: daughters that exhibit overt submissive behavior toward their mothers are significantly more likely to be anovulatory than daughters that do not behave submissively (Saltzman *et al.* 1997c, 2004). Interestingly, these submissive and non-submissive females do not differ in the behaviors received from their mothers (Saltzman *et al.* 1997c), and aggression between mothers and daughters is typically mild and infrequent (Rothe 1975, Abbott 1984, Saltzman *et al.* 1997c, 2004). Thus, ovulation suppression is closely associated with a daughter's perception of herself as subordinate to another female.

Interactions with males, in contrast, do not reliably influence ovulatory activity in daughters (Figure 12.3). Whereas young adult females in several other species may be stimulated to commence ovulating by exposure to unrelated, unfamiliar males, introduction of a novel male into common

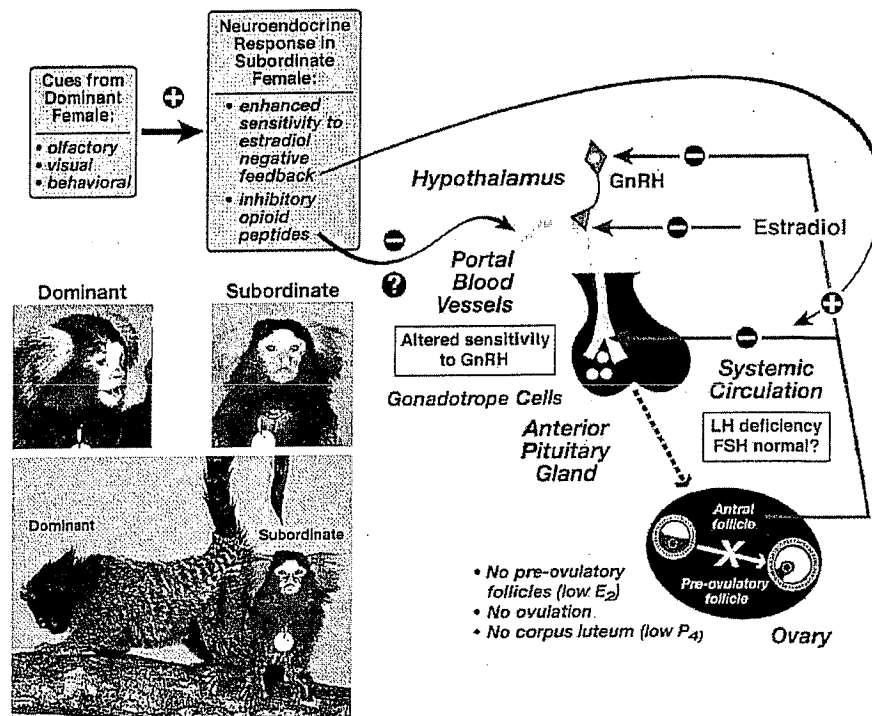
marmoset families does not significantly increase daughters' likelihood of ovulating and does not alter the patterning or hormonal dynamics of their ovarian cycles (Saltzman *et al.* 2004; but see Saltzman *et al.* 1997b). Therefore, suppression of ovulation in young adult female common marmosets housed with their natal families is governed primarily by intrasexual, rather than intersexual, influences.

*Laboratory groups of unrelated adults*

In laboratory groups of unrelated adults, suppression of ovulation is even more striking than in families: while all dominant females (rank 1) undergo ovulatory cycles, about 70% of all subordinate females (ranks 2 and 3) fail to ovulate. This means, however, that about 30% of subordinate females in groups of unrelated adults exhibit one or more ovulatory cycles. Such cycles can include deficient luteal phases (Abbott 1993), suggestive of (1) insufficient gonadotropin secretion from the anterior pituitary gland to support post-ovulatory corpora lutea, (2) deficient pituitary gonadotropin stimulation of pre-ovulatory follicle development (Figure 12.4, Soules *et al.* 1989a, 1989b, Ayabe *et al.* 1994), or (3) a combination of both. Circulating progesterone levels are nevertheless sufficient to support pregnancy in some subordinate females. Social contraception is most effectively maintained in lower-ranking subordinates (e.g. rank 3 and below): while over 40% of rank-2 females undergo one or more ovulatory cycles, only 14% of rank-3 females do so. Thus there appears to be a graded effect of social rank on ovulatory frequency: the lower the social rank, the greater the degree of ovulation suppression.

Such socially determined anovulation in groups of unrelated adults is remarkably reliable, rapidly induced, and readily reversible. The onset of anovulation in subordinate females usually occurs within ~14 days of group formation (Abbott *et al.* 1988, Abbott & George 1991). Subsequently, resumption of ovarian cyclicity following removal of subordinate females from their social groups, or following removal of all higher-ranking females, is equally rapid: the previously subordinate females usually ovulate within about 10 days (Abbott *et al.* 1997), approximately the duration of a normal follicular phase (Saltzman *et al.* 1994).

The ovaries of anovulatory, subordinate female common marmosets have been found to contain no large, pre-ovulatory follicles, in contrast to the large follicles found in the ovaries of dominants (Harlow *et al.* 1986). Taken together, the ovarian and hormonal data from subordinate females suggest that follicular development is inhibited with remarkable precision, so that follicles mature only up to a stage normally achieved at the onset of the follicular phase of the ovarian cycle, but fail to progress when they reach the final stages of



**Figure 12.4** Diagrammatic representation of neural and neuroendocrine mechanisms inhibiting ovulation in subordinate female common marmosets. Examples are shown of dominant females' aggressive and scent-marking displays directed at female subordinates in laboratory groups of unrelated adults. Modified from Abbott *et al.* (1998).

maturation that are dependent on stimulation from pituitary gonadotropins (Figure 12.4). Any diminution in this inhibition, leading to a moderate increase in pituitary gonadotropin release, could well support the final stages of follicle growth, resulting in ovulation indistinguishable from that in dominant females. Such potentially dynamic responses of subordinate females may allow them to rapidly capitalize on acute changes in group composition or social status (Lazaro-Perea *et al.* 2000), typical of a marmoset's opportunistic existence (Rylands & de Faria 1993, Digby *et al.* 2007). While rank-2 subordinate female common marmosets may be best placed in this regard, all adult females retain the capacity to rapidly ovulate and conceive when the social environment permits, such as following the death or disappearance of a breeding female, migration to a nearby group, or fissioning of the original group into smaller groups (Lazaro-Perea *et al.* 2000).

### Neural and neuroendocrine mechanisms implicated in suppression of ovulation

Elucidating the underlying physiological cause of anovulation in non-breeding female common marmosets has been confounded by findings unique to marmosets and probably all other New World primates: common marmosets synthesize and release chorionic gonadotropin (CG) from the anterior pituitary gland (Gromoll *et al.* 2003, Muller *et al.* 2004a), rather than luteinizing hormone (LH), the functionally and structurally similar hormone expressed in the anterior pituitary of Old World primates and other mammals. Correspondingly, common marmosets express altered LH cell membrane receptors that are responsive to CG, but not to LH (Zhang *et al.* 1997, Muller *et al.* 2004b). CG has greater biopotency than LH, circulates for longer, and shows more prolonged release from the pituitary under stimulation from hypothalamic gonadotropin-releasing hormone (GnRH; Tannenbaum *et al.* 2007). Nonetheless, the biological role of pituitary CG remains similar to that of LH in supporting pre-ovulatory development of ovarian follicles, ovulation, and post-ovulatory formation and function of corpora lutea (Muller *et al.* 2004b).

A series of laboratory experiments has suggested that ovulatory suppression in subordinate female common marmosets is mediated by the brain, rather than by primary ovarian or pituitary failure. Circulating levels of pituitary CG are reduced in anovulatory daughters (Abbott 1993) and subordinate females in groups of unrelated adults (Abbott *et al.* 1981), confirming inadequate gonadotropin stimulation of ovarian function (Figure 12.4). Experimentally induced elevations in circulating gonadotrophin levels in subordinate females result in increased circulating levels of estradiol and ovulation (Abbott 1993, Abbott *et al.* 1997), indicative of appropriate ovarian responses to gonadotropin stimulation and an apparent absence of ovarian failure. Repeated injections of subordinate females with supraphysiological doses (1–2  $\mu\text{g}$ ) of exogenous GnRH every 60–90 minutes stimulate pituitary release of CG, resulting in physiologically appropriate circulating levels of this hormone (Abbott 1989). Although such experimental evidence points to the neuroendocrine hypothalamus as playing an overriding role in the mechanism of anovulation in subordinate female common marmosets (Figure 12.4), pulsatile release of GnRH from the hypothalamus is unaltered in subordinate compared to dominant females (Abbott *et al.*, 1998). Instead, pituitary CG responsiveness to GnRH is diminished, since injection of more physiological doses (50 ng) of GnRH fails to elicit CG release in subordinates, in contrast to the CG rise induced in identically treated dominants (Abbott *et al.* 1988). The mechanism responsible for such diminished pituitary

responsiveness to GnRH remains elusive, but may involve other changes in neurosecretion from the hypothalamus.

Such a mechanism, however, does not include typical physiological stress responses (Abbott *et al.* 1997, 1998). For example, while the stress response characteristically involves elevated secretion of glucocorticoids (e.g. cortisol) from the adrenal cortex (Sapolsky *et al.* 2000, Stewart 2003), no such increase is found in non-breeding daughters in laboratory families (Ziegler & Sousa 2002), subordinate females in laboratory groups of unrelated adults (Saltzman *et al.* 1994, 1998), or non-breeding females in free-living groups of common marmosets (Sousa *et al.* 2005). Other manifestations of hypothalamic-related dysfunction commonly associated with ovulation failure in other species, including elevated prolactin secretion by the anterior pituitary (Bowman *et al.* 1978), altered diurnal rhythms and reduced body weight (Yen 2004), are also not found in captive subordinate female common marmosets (Abbott *et al.* 1997). Instead, the anterior pituitary in these subordinates is so highly sensitized to negative feedback by estradiol that even the low levels of estradiol released by anovulatory ovaries suppress CG release (Figure 12.4; Abbott 1988). In addition, a mechanism independent of ovarian hormone feedback, but mediated by endogenous opioid peptides, also suppresses pituitary secretion of CG (Abbott 1993). These mechanisms operate without obvious decrease or alteration in endogenous hypothalamic release of GnRH (Abbott *et al.* 1998).

Associative learning of olfactory, visual, and behavioral cues from the dominant female maintains neuroendocrine suppression of ovulation in subordinate female common marmosets (Abbott *et al.* 1997), indicating a psychological conditioning component to the ovulation-suppression mechanism. Non-breeding females utilize specific cues in their social environment to minimize breeding in the presence of specific dominant females (Figure 12.4). Such specialized mechanisms mean that only a familiar dominant female in a subordinate's own social group carries salience for suppression of ovulation, so that the disappearance of the dominant female or emigration of the subordinate to another social group could readily extinguish this conditioned reproductive inhibition. Such a scenario permits a highly labile response of ovulatory function to changes in a female common marmoset's social status, as illustrated by a variety of systematic manipulations of laboratory groups (Abbott 1984, 1989, Abbott & George 1991).

Taken together, the highly specialized mechanisms maintaining suppression of ovulation in female common marmosets reflect reliable responses to social environments that are not conducive to successful reproduction by more than one female. Such adaptations suggest a high degree of selection for the evolution of multiple mechanisms minimizing a female's

likelihood of breeding under inauspicious social conditions. Not surprisingly, intermittent or absent ovulatory cycles in subordinate females are also observed across a variety of other cooperatively breeding species ranging from primates to rodents (Solomon & French 1997), possibly due to analogous selection pressures.

### **Lack of evidence for post-ovulatory inhibition of female reproductive physiology**

Clearly, intermittent or absent ovulatory cycles and inhibition of sexual behavior in subordinate female common marmosets play a key role in generating reproductive skew. Nonetheless, in both wild and captive groups, numerous subordinate females ultimately terminate their reproductive self-restraint and begin to breed. In the field, these subordinate breeding females produce significantly fewer infants than dominant breeding females and, most strikingly, produce few or no infants that survive beyond the first few weeks of life (Digby 1995b, Arruda *et al.* 2005, Sousa *et al.* 2005). What are the mechanisms that generate post-ovulatory reproductive failure in subordinate breeding females and maintain reproductive skew in plurally breeding groups?

One answer is that young subordinate females undergoing ovulatory cycles may be somewhat less likely to conceive than older dominant females, even when they have access to a suitable mate. When resident breeding males are replaced by an unrelated adult male in laboratory families containing an adult daughter, nulliparous daughters undergoing ovulatory cycles begin to conceive, but at lower rates than their mothers, as determined by endocrine and ultrasonographic monitoring (Saltzman *et al.* 2004). It is unclear whether this fertility difference arises from differences in social status or in age/parity. Following conception, however, gestation, parturition, and lactation proceed unimpaired in these daughters. Primiparous daughters and their mothers produce comparable numbers of infants, at least in the laboratory, with both mothers and daughters exhibiting very low rates of spontaneous abortions and stillbirths (Saltzman *et al.* 2004, 2008). Furthermore, all daughters appear to lactate normally, and mothers and daughters carry their infants at similar frequencies (Saltzman *et al.* in press; but see Digby 1995b). Thus the presence of another breeding female might constrain other females' likelihood of ovulating and conceiving but, following conception, does not appear to further influence pregnancy outcomes or maternal care. Female common marmosets, unlike other female primates, such as baboons (*Papio cynocephalus*: Wasser & Starling 1988), may not be sufficiently aggressive to one another to disrupt each other's pregnancies.

### Infanticide by females

The primary mechanism of post-conception control of reproduction in common marmosets appears to be the killing of other females' infants (e.g. Digby 1995b, Saltzman 2003, Arruda *et al.* 2005, Digby & Saltzman in press). Eight infanticides have been directly observed in wild groups of common marmosets (Table 12.1; note that rates of infanticide are unavailable as total observation time is typically not reported), with seven of these cases occurring in groups containing two breeding females. Multiple infanticides have also been observed or, more commonly, inferred in captive groups containing two breeding females (e.g. Alonso 1986, Kirkpatrick-Tanner *et al.* 1996, Saltzman 2003, Saltzman *et al.* 2008). Observed infanticides in free-ranging and captive groups typically involve dominant breeding females killing infants born to subordinate breeding females, although at least two cases in wild groups were committed by subordinate breeding females (reviewed in Digby & Saltzman in press). In a laboratory study, however, infants of both dominant and subordinate breeding females (mothers and daughters, respectively, in families containing an unrelated adult male) were highly vulnerable to infanticide (Figure 12.5), especially if another female in the group was pregnant at the time of the infant's birth (Figure 12.6; Saltzman *et al.* 2008).

Of the various functional hypotheses put forth to explain infanticide (Hrdy 1979), the one that appears to be most relevant to infanticide by female marmosets is the *resource competition hypothesis*. This hypothesis posits that infanticide enables females to gain either immediate or future access to limited resources (Hrdy 1979; see Sherman 1981, Hoogland 1995 for examples in other mammals). The overall pattern of pregnant female common marmosets committing infanticide is consistent with this scenario: the perpetrator gains increased access to resources (e.g. helpers and food, including allo-nursing by females that have lost their young), decreased future competition, and even a reduced likelihood that its own infants will be killed by the other breeding female (reviewed in Digby 2000). Similar infanticidal patterns are observed across a variety of other cooperatively breeding species (e.g. meerkats, *Suricata suricatta*: Clutton-Brock *et al.* 2001; black-tailed prairie dogs, *Cynomys ludovicianus*: Hoogland 1995; African wild dogs, *Lycaon pictus*: van Lawick 1974).

Reproductive status appears to strongly influence female common marmosets' likelihood of committing infanticide. In both wild and captive populations, infanticidal females are typically in the last 1-2 months of their own pregnancies (Table 12.1; Digby 2000, Saltzman 2003, Saltzman *et al.* 2008); only one postpartum female has been observed to kill another female's infant



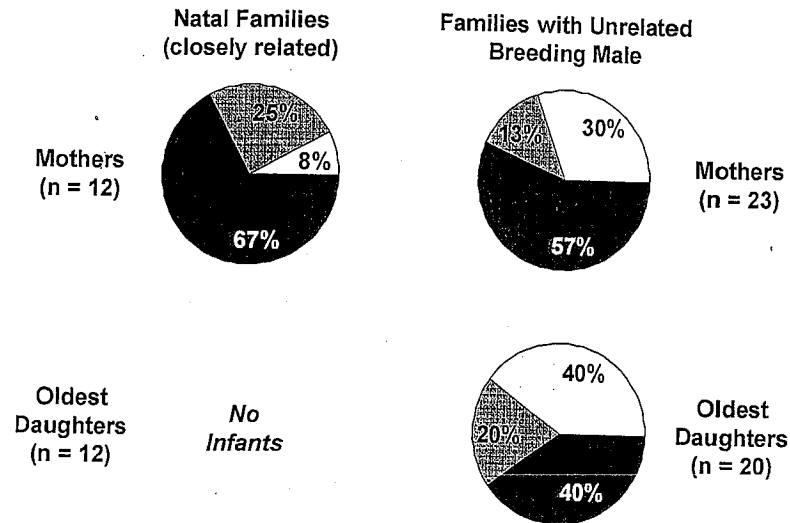
Table 12.1 Cases and contexts of infanticide directly observed in wild and captive groups of common marmosets

Wild/Captive	Victim	Perpetrator	Perpetrator's relationship to the victim	Timing/context of infanticide	Reference
Wild	2-week-old male	Subordinate breeding female	Unknown	Subordinate female, which had been challenging dominant female for several months, attacked infant (on two occasions, the latter being fatal). Perpetrator gave birth one month later and became the dominant female of the group.	Roda & Mendes Pontes 1998
Wild	24-day-old female	Probably the dominant breeding female	Not closely related ( $R < 0.14$ )	Dominant female harassed subordinate female after the subordinate gave birth. One twin disappeared. The infanticide of the second twin was directly observed, but the perpetrator could not be definitively identified, as several animals were in the immediate vicinity of the attack, including the dominant female, the male carrier of the infant, and a young adult male.	Digby 1995a, Nievergelt <i>et al.</i> 2000
Wild	Three infants (one male < 1 month old; details not given for others)	Dominant breeding female	Grandmother in one case, no details for others	In case of male infant killed by grandmother, perpetrator had given birth one month prior to the infanticide.	Yamamoto <i>et al.</i> 1996, Arruda <i>et al.</i> 2005, Alencar <i>et al.</i> 2006

Table 12.1 (cont.)

Wild/Captive	Victim	Perpetrator	Perpetrator's relationship to the victim	Timing/context of infanticide	Reference
Wild	Infant < 1 month old	Dominant breeding female	Unknown	Infanticide occurred approximately one month following group fission. Perpetrator gave birth approximately one month after the infanticide.	Lazaro-Perea et al. 2000
Wild	Infant estimated to be < 1 month old	Dominant female from neighboring group containing no infants	Unknown	Infanticide occurred during incursions by both groups into an unoccupied territory. Infant was cannibalized.	Melo et al. 2003
Wild	1-month-old female	Subordinate breeding female	Unknown	Infant was wounded when first observed. Mother tried to recover infant, but it repeatedly fell. Subordinate female then attacked and consumed part of the infant. The perpetrator gave birth two months later, by which time she had become the dominant female.	Bezerra et al. 2007
Captive	Two infants	Newly dominant female	Sister	The daughter of the group's original dominant breeding female became pregnant and subsequently became the dominant female. The newly dominant female subsequently killed two of her infant sisters.	Alonso 1986

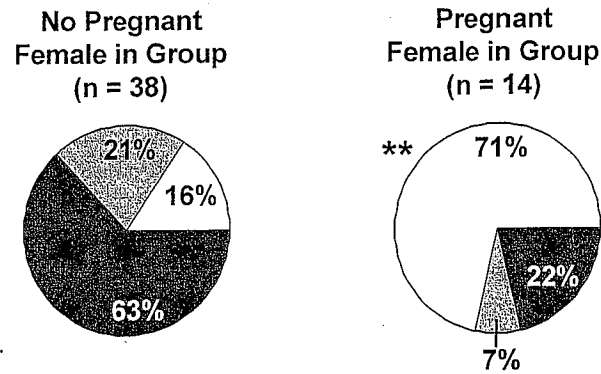
Captive	1-day-old infant	Dominant breeding female	Grandmother	Grandmother grabbed and killed infant on first day after birth and cannibalized the carcass. Perpetrator gave birth one week later.	Kirkpatrick-Tanner <i>et al.</i> 1996
Captive	18-day-old male	Primary breeding female	Grandmother	Perpetrator behaved submissively to the infant's mother the day before the infant's birth. Two days after the birth, the perpetrator carried and ate the carcass of one of the twins, although infanticide was not observed. Perpetrator attacked and severely wounded the second twin at 18 days of age, necessitating euthanasia. Perpetrator gave birth 7 days later, and no further submissive behavior between the two females was observed.	Saltzman 2003, Saltzman <i>et al.</i> 2008



**Figure 12.5** Percentage of infant common marmosets that survived to at least 1 year of age (dark shading), died spontaneously (gray shading), or were killed (white areas) in 6 intact families and 11 families in which the biological father was replaced by an unrelated adult male when the eldest daughters were post-pubertal. Infanticide was more common in groups containing an unrelated breeding male, but this trend was not significant. Modified from Saltzman *et al.* (2008).

(Arruda *et al.* 2005). On a functional level, such precisely timed infanticide reduces competition for helpers to assist with rearing the perpetrator's soon-to-be-born offspring (Digby 2000, Saltzman 2003, Saltzman & Abbott 2005), while eliminating the possibility that an infanticidal female will accidentally kill her own young. On a proximate level, the hormones of late pregnancy are likely to influence females' responses to infants. In a laboratory study, multiparous female common marmosets exhibited minimal attraction to and tolerance of infants during the late stages of pregnancy, especially as compared to early pregnancy or the early postpartum period (Saltzman & Abbott 2005). In addition, early-postpartum females showed identical behavioral responses to their own infants and to unfamiliar, unrelated infants, consistent with the possibility that these females may be unable to discriminate reliably among infants and that infanticidal postpartum females would therefore risk killing their own offspring (Saltzman & Abbott 2005).

As noted above, subordinate breeding females suffer significantly higher rates of infant loss than do dominants (Table 12.1, Figure 12.5), although the relative contributions of infanticide and other causes of mortality are not



**Figure 12.6** Percentage of infant common marmosets that survived to 1 year of age (dark shading), died spontaneously (gray shading), or were killed (white areas) associated with whether or not another female was pregnant in the group when parturition occurred. Data are combined from 6 intact families and 11 families in which the biological father was replaced by an unrelated adult male when the eldest daughters were post-pubertal. Modified from Saltzman *et al.* (2008). \*\*  $P < 0.002$  for percentage of infants killed in families that contained a pregnant female compared to families that did not.

known (Digby 1995b, Arruda *et al.* 2005). As a consequence of the threat of infanticide and the low probability of successfully raising young, females living with a dominant breeding female may well benefit from delaying reproduction and therefore avoiding investment in costly reproductive attempts that are unlikely to succeed (Wasser & Barash 1983).

### Conclusion

Findings from two decades of field observations and three decades of laboratory studies of common marmosets are providing unique insights into the causes of female reproductive skew in this cooperatively breeding primate. Although groups may frequently contain three or more adult females, no more than two females produce offspring per group and, at least in laboratory groups, this is frequently reduced to a single female. Social suppression of ovulation in behaviorally subordinate females is more pronounced in laboratory groups than in free-living groups, while inhibition of intra-group sexual behavior is prevalent among non-breeding females in both captive and free-living populations. Intermittent or absent ovulatory cycles in subordinate females are not mediated by either generalized stress or overt aggression from

the group's dominant female. Instead, non-breeding subordinates exhibit highly specialized physiological responses to a variety of cues from dominant females, which diminish the subordinates' ability to ovulate (Figure 12.4). Inhibition of intra-group sexual behavior by females, on the other hand, is regulated both by intrasexual dominance relationships and by access to unrelated males (Figure 12.1).

With the presence of one or more unrelated males in the group, two females can breed concurrently, resulting in these females killing one another's infants with notable frequency. Infanticide particularly impairs the reproductive success of the subordinate breeding female and is especially costly for marmosets, given their heavy investment in each breeding attempt (e.g. long gestation and high infant-to-maternal body mass ratio: Tardif 1997).

Together, suppression or disruption of ovulatory cycles, inhibition of sexual behavior, and infanticide by breeding females generate high reproductive skew among female common marmosets within each social group. It is not yet known, however, whether such skew results in diminished lifetime reproductive success for subordinate females, or whether it merely reflects temporary postponement of reproduction until a (dominant) breeding position is attained. In addition to seeking out or waiting to obtain a breeding position, subordinate females may become increasingly likely to attempt to breed, even in the presence of a dominant female, with increasing age, as has been reported in cooperatively breeding golden lion tamarins (*Leontopithecus rosalia*: Baker *et al.* 2002), dwarf mongooses (*Helogale parvula*: Creel & Waser 1997), and meerkats (Young *et al.* 2006). Such a scenario would be consistent with laboratory findings of age-related increases in likelihood of ovulation in mature daughters remaining in their natal families, as well as age-related increases in aggressiveness towards unrelated adult females (Saltzman *et al.* 1996, 1997a). According to Wasser and Barash's (1983) *reproductive suppression model*, age-related increases in reproductive attempts, even under suboptimal conditions, should be beneficial to subordinate females because of the diminishing likelihood of obtaining a dominant breeding position in their dwindling lifespan (see also Williams 1966).

The low rates and low intensity of aggression among female group-mates, the absence of stress-related physiological changes in subordinates, and subordinates' use of subtle behavioral and sensory cues from dominant females to trigger suppression of ovulation, all suggest that pre-conception reproductive inhibition in non-breeding female common marmosets is not maintained by a high degree of harassment from dominant females or socially induced stress, and is not actively imposed on subordinates by dominants (at a proximate level). Instead, such inhibition may be maintained by specialized, presumably

adaptive, neuroendocrine responses of subordinate females to infrequent and mild aggression from a dominant female group-mate, resulting in self-imposed inhibition of ovulation and sexual behavior. A key question, however, involves the adaptive significance of such self-restraint in the presence of a dominant female. Why would healthy adult females benefit from curtailing their own reproduction over periods of months or years, even when food resources and potential alloparents may be abundant? The answer may lie, in large part, in infanticide committed by breeding females (e.g. Hager & Johnstone 2004). If this pattern of infanticide evolved before or simultaneously with ovulation suppression, it may well have played a critical role in selecting for the evolution of specialized neuroendocrine and behavioral mechanisms to reduce the likelihood that females would breed in the presence of a dominant, potentially infanticidal, female group-mate (Saltzman 2003). Such specialized responses limiting pre-conception events would minimize subordinates' likelihood of investing in reproductive attempts that are unlikely to succeed, possibly increasing their prospects for survival and successful reproduction in the future (Wasser & Barash 1983, Jaquish *et al.* 1991, Digby 1995b, Saltzman 2003, Gilchrist 2006).

We propose that dominant female common marmosets do not or cannot completely control reproductive attempts by subordinate females at the pre-conception or pre-parturition stages (Figure 12.1). Instead, they use infanticide as a proximate mechanism to limit subordinate females' reproductive success. In so doing, dominant females may also secondarily engage infanticide as an agent of selection favoring commitment to reproductive self-restraint in subordinates. Thus, reproductive skew in this species is generated predominantly, in a proximate sense, by self-restraint in subordinate females but, ultimately, by dominant control over subordinates. This pattern is consistent with both the *commitment model* (Hamilton 2004), in terms of pre-conceptive restraint, and the *discriminate infanticide model* (Hager & Johnstone 2004), in terms of infanticide as a mechanism driving subordinate self-restraint. Since infanticide among common marmosets may commonly involve killing of closely related kin, the stakes would seem to be extremely high for dominant females in maintaining reproductive sovereignty.

#### **Female reproductive skew in common marmosets: comparative aspects and future directions**

Reproductive skew in female common marmosets closely resembles that found in several other mammalian cooperative breeders (Abbott *et al.* 1998), including other callitrichines (French 1997), meerkats (Clutton-Brock

*et al.* 2001), dwarf mongooses (Creel & Waser 1997), African wild dogs (van Lawick 1974), and Damaraland mole-rats (*Cryptomys damarensis*; see Chapter 13). Like marmosets, these mammals live in groups comprising a mixture of close kin and unrelated individuals, and subordinate females occasionally attempt to breed in spite of the existence of behavioral and physiological mechanisms of reproductive self-restraint. Also similar to common marmosets, dominant female meerkats and dwarf mongooses sometimes kill infants born to subordinate females (Creel & Waser 1997, Clutton-Brock *et al.* 2001), especially when pregnant (meerkats: Young & Clutton-Brock 2006). This convergence in mechanisms restricting subordinate female reproduction is striking, given the phylogenetic distances between the mammalian taxa involved. The convergence may therefore reflect adaptation to environmental conditions that make dispersal and independent breeding potentially costly. Comparative biological approaches across mammals, such as those taken by Faulkes & Bennett (2001) with African mole-rats, are needed to elucidate commonalities across different habitats that may select for singular cooperative breeding and high reproductive skew among females.

Further insights into proximate mechanisms regulating reproductive skew in female common marmosets are likely to continue to emerge from integrated research programs focusing on (1) neural and neuroendocrine mechanisms mediating ovulation suppression, (2) neuroendocrine mechanisms underlying infanticide, and (3) organismic and environmental factors influencing individual females' "decisions" to either restrain their own reproduction or attempt to conceive and successfully rear offspring. To clarify ultimate causation of reproductive skew, future research must identify the factors imposing strict limitations on numbers of breeding females in common marmoset groups such that breeding females are driven to kill infants born to female group-mates, regardless of whether the infants are close kin. Our current progress in these areas has come from complementary behavioral and physiological studies from both the field and the laboratory. For example, field observations of plural breeding and infanticide (e.g. Digby 1995b) were reliably reproduced in the controlled setting of the laboratory (Saltzman *et al.* 2004, 2008). Conversely, robust laboratory findings of inhibition of sexual behavior and ovulation in subordinate females (Abbott *et al.* 1997) have led to incorporation of physiological and molecular genetics components in long-term field studies (Faulkes *et al.* 2003, Sousa *et al.* 2005). Such interactive, collaborative, and long-term field and laboratory research approaches have proved highly successful in identifying proximate mechanisms regulating reproduction in female common marmosets, and will continue to refine our understanding of the risks and



choices female marmosets take in attempting to maximize their overall reproductive success.

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