

Review

Reproductive skew in female common marmosets: what can proximate mechanisms tell us about ultimate causes?

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Common marmosets are cooperatively breeding monkeys that exhibit high reproductive skew: most subordinate females fail to reproduce, while others attempt to breed but produce very few surviving infants. An extensive dataset on the mechanisms limiting reproduction in laboratory-housed and free-living subordinate females provides unique insights into the causes of reproductive skew. Non-breeding adult females undergo suppression of ovulation and inhibition of sexual behaviour; however, they receive little or no aggression or mating interference by dominants and do not exhibit behavioural or physiological signs of stress. Breeding subordinate females receive comparable amounts of aggression to non-breeding females but are able to conceive, gestate and lactate normally. In groups containing two breeding females, however, both dominant and subordinate breeders kill one another's infants. These findings suggest that preconception reproductive suppression is not imposed on subordinate females by dominants, at a proximate level, but is instead self-imposed by most subordinates, consistent with restraint models of reproductive skew. In contrast to restraint models, however, this self-suppression probably evolved not in response to the threat of eviction by dominant females but in response to the threat of infanticide. Thus, reproductive skew in this species appears to be generated predominantly by subordinate self-restraint, in a proximate sense, but ultimately by dominant control over subordinates' reproductive attempts.

Keywords: cooperative breeding; reproductive suppression; sexual inhibition; infanticide; dominance; subordination

1. INTRODUCTION

Thirty years ago, [Abbott & Hearn \(1978\)](#) reported that adult female common marmoset monkeys (*Callithrix jacchus*) failed to ovulate when housed with behaviourally dominant females in laboratory groups. This was one of the first demonstrations of socially induced suppression of reproductive physiology in a cooperative breeder (i.e. a species in which individuals routinely provide care for other animals' offspring). Since then, our understanding of reproductive suppression in marmosets has grown tremendously, based on detailed laboratory studies of behavioural, sensory and neuroendocrine mechanisms of suppression, as well as on a growing body of data from free-living marmosets. During the same period, social suppression of reproduction has been documented in several dozen additional cooperative breeders, including mammals (e.g. [Solomon & French 1997](#) and references therein), birds (e.g. [Reyer et al. 1986](#); [Mays et al. 1991](#); [Schoech et al. 1991](#)), fishes (e.g. [Fitzpatrick et al. 2008](#)) and invertebrates (e.g. [Hamilton 2004](#) and references therein). Many of these species have been studied primarily under field conditions, greatly advancing our understanding of the

ecological and demographic determinants of reproductive suppression and, ultimately, reproductive success.

In parallel with the proliferation of empirical studies on reproductive suppression in cooperative breeders, a sizeable and contentious literature has developed over the last 25 years or so addressing the ultimate causes of reproductive skew, or asymmetrical reproductive success within social groups (e.g. [Vehrencamp 1983](#); [Keller & Reeve 1994](#); [Johnstone 2000](#); [Buston et al. 2007](#)). Reproductive skew can have far-reaching implications for the reproductive strategies of individuals. Indeed, theoretical models developed to explain skew have been suggested to 'represent a unified theory of social evolution' ([Buston et al. 2007](#), p. 1644). Cooperatively breeding species are especially informative due to the paradoxical presence of cooperative care of young alongside some of the most extreme manifestations of skew.

Numerous models have been proposed to explain the evolution and maintenance of reproductive skew (reviewed in [Johnstone 2000](#); [Hager 2003](#); [Buston et al. 2007](#)). Most, however, fit into three general categories: concession; restraint; and tug of war. Concession models assume that one individual, the dominant, exerts complete control over reproduction of same-sex individuals within its social group. According to this scenario, dominant

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Table 1. Summary of predictions generated by the major classes of reproductive skew models and empirical findings in common marmosets. (Italics indicate predictions consistent with findings in common marmosets. See text for explanations and additional details.)

	concession models	restraint models	tug-of-war models	findings in common marmosets
do subordinates attempt to breed?	sometimes (when a 'concession' has been made by a dominant)	<i>usually no</i>	yes	<i>usually no</i>
do dominants 'manipulate' (e.g. harass) non-breeding subordinates?	yes	<i>no</i>	yes	<i>no</i>
is reproductive failure associated with stress in non-breeding subordinates?	yes	<i>no</i>	yes	<i>no</i>
do dominants 'manipulate' successfully breeding subordinates or their infants?	no	yes (threatened eviction from group)	yes	<i>yes (infanticide)</i>
do breeding subordinates 'manipulate' dominants or their infants?	no	no	yes	<i>yes (infanticide)</i>

females may allow subordinate females to breed as a 'concession', to ensure that the subordinates will stay in the group and provide care for the dominant female's offspring (reviewed in Emlen 1982; Clutton-Brock 1998; Reeve *et al.* 1998; Reeve & Shen 2006). Restraint models, too, assume that dominants and subordinates engage in transactions, but in this scenario the subordinate restrains its own reproduction in order to avoid eviction from the group (Johnstone & Cant 1999; Buston *et al.* 2007). By contrast, tug-of-war models suggest that control by a single individual is unlikely and that the imbalance in breeding success instead results from a constant struggle among group members, with the dominant monopolizing most, but not all, of the group's reproductive output (e.g. Clutton-Brock 1998; Reeve & Shen 2006). In other words, subordinates are occasionally able to breed not because dominants allow them to, but because dominants cannot prevent them from doing so.

The key distinctions among these skew models relate to which individuals control reproduction within a social group and under what conditions subordinates are able to breed successfully. It is not always clear, however, whether the various theoretical models involve control at a proximate or ultimate level. For example, it is possible that the proximate mechanisms—i.e. the behavioural, sensory and physiological processes—limiting reproduction in subordinates may be self-imposed, but that the ultimate causes of such self-restraint—e.g. selection pressures favouring its evolution—may be imposed by dominant individuals. Thus, it is important to distinguish between *how* animals in high-skew species may limit reproduction and *why* they do so. An understanding of the proximate mechanisms regulating reproductive success in subordinates may be invaluable for assessing the applicability of theoretical models, and may provide crucial insights into the evolution of high-skew societies. Few attempts have been made, however, to integrate proximate and ultimate causes of reproductive skew (but see Snowdon 1996; Creel & Waser 1997; Faulkes & Bennett 2001; Gilchrist 2006).

Common marmosets provide a unique case study for characterizing the proximate determinants of socially induced reproductive suppression and therefore for evaluating the various models of reproductive skew. In

this review, we first describe the predictions that may be derived from each major class of skew models regarding proximate mechanisms generating skew. We then review the physiological, behavioural and sensory processes underlying skew in female common marmosets, integrating findings from field and laboratory studies. Finally, we compare these findings with the predictions from each class of skew model (table 1) and discuss the implications of these findings for our understanding of the evolution of reproductive suppression in subordinate females. The evidence to date suggests that components of both restraint and tug-of-war models are necessary to best understand reproductive constraints in female marmosets.

2. REPRODUCTIVE SUPPRESSION AND REPRODUCTIVE SKEW

How can we distinguish between reproductive self-restraint by subordinates, reproductive control imposed on them by dominants and unrestrained tugs of war for breeding success? We propose that in these various scenarios, different proximate mechanisms limiting reproduction in subordinates and/or different outcomes of these mechanisms are likely to occur. Our major predictions are described in table 1 (see also Snowdon 1996).

Mechanisms controlling reproductive output may be similar under the concession (complete control) and tug-of-war (incomplete control) models. For example, dominant females might monopolize food or other resources necessary for reproduction, interfere with subordinates' sexual interactions, direct aggressive behaviour or harassment at subordinates, or kill subordinates' infants (e.g. Lloyd & Rasa 1989; Faulkes & Bennett 2001; Gilchrist 2006; Young *et al.* 2006). Such manipulation by dominants is likely to provoke a stress response in subordinates (e.g. Abbott *et al.* 2003b; Goymann & Wingfield 2004). A large variety of physical and psychological challenges, or stressors, elicit a common suite of neuroendocrine and physiological changes that collectively serve to mobilize energy and enhance the individual's ability to survive under energetically demanding conditions (McEwen & Wingfield 2003). While the stress response appears to be adaptive under acutely challenging circumstances, it may have pathological consequences if

activated frequently or chronically, especially in response to psychosocial stressors (Sapolsky 2002; Korte *et al.* 2005). In a broad range of taxa, female reproductive physiology and reproductive behaviour are readily inhibited by the stress response, minimizing the likelihood that females will breed under stressful or inauspicious conditions (Wasser & Barash 1983; Ferin 2006). By triggering a stress response in subordinates, dominant females may exploit this sensitivity of the female reproductive system to stress and 'force' subordinates to abandon current reproductive attempts.

Although concession and tug-of-war models may involve similar forms of manipulation by dominants, we can distinguish between the two scenarios based on the consistency and success of these strategies. Concession models predict that dominants will sometimes suspend their manipulative activities and 'allow' subordinates to breed, whereas tug-of-war models make no such prediction. According to concession models, therefore, we would expect to find a negative correlation between manipulation by dominants and reproductive activity in subordinates. In other words, dominants should manipulate non-breeding subordinates but not reproductive subordinates. Under tug-of-war models, by contrast, we should find either no relationship between breeding by subordinates and manipulation by dominants or possibly a positive relationship, as dominant individuals may intensify aggression towards those subordinates that attempt to breed (e.g. Margulis *et al.* 1995; Scheibler *et al.* 2006; Young *et al.* 2006). Thus, manipulation by dominants should lead to reproductive failure in subordinates *consistently* in concession scenarios but *inconsistently* in tug-of-war scenarios. Moreover, whereas concession models describe unidirectional manipulation of subordinates by dominants, tug-of-war models suggest that both dominant and subordinate females will attempt to disrupt each other's breeding attempts.

On the other hand, if subordinate individuals are under selection to curtail their own reproductive attempts in order to avoid such punitive actions by dominants as eviction from the group, as suggested by restraint models, we might expect mechanisms of reproductive suppression to evolve that would minimize costs to subordinates. First, rather than mounting an energetically costly and potentially detrimental stress response, subordinates might be expected to engage specific inhibitory neuroendocrine mechanisms to suppress their own reproductive function in response to the presence of a dominant female in their group. Second, subordinates might be likely to restrain their own reproduction in response to specific behavioural or sensory cues from dominant females, rather than relying on overt, potentially harmful manipulation or aggression by dominants. Third, to minimize or avoid investment in breeding attempts that are unlikely to succeed, subordinates may be expected to inhibit their own breeding early in the reproductive process, such as before conception or during early pregnancy (Wasser & Barash 1983). How do findings in common marmosets fit these various predictions?

3. MARMOSET SOCIAL AND BREEDING SYSTEMS

Common marmosets are small (approx. 300–400 g), frugivorous/insectivorous/exudativorous New World monkeys that occupy small home ranges in the Atlantic coastal

forests of northeastern Brazil (Sussman 2000; Digby *et al.* 2007). They tend to live in cohesive groups of up to 20 individuals, comprising multiple adult males and females and several immatures (reviewed in Digby *et al.* 2007). Groups may contain equal numbers of adult males and females or may be female-biased (Digby 1995b; Lazaro-Perea *et al.* 2000). Typically, only a single dominant male and one or two dominant females breed; the remaining adults and immatures serve as non-reproductive alloparents. Microsatellite and mitochondrial DNA analyses of free-ranging groups indicate that mates are unrelated to one another, while in plurally breeding groups the two breeding females are often closely related to each other and to the remaining group members (Nievergelt *et al.* 2000; Faulkes *et al.* 2003); however, population crashes and periods of instability can result in groups comprising unrelated individuals (Lazaro-Perea *et al.* 2000; Faulkes *et al.* 2003). Marmoset societies are therefore dynamic and unpredictable.

Breeding males and females are dominant to all other group members, as determined on the basis of low-level aggressive or submissive behaviours (e.g. avoidance behaviour, submissive vocalizations, stereotyped submissive facial expressions; Epplé 1967; Rothe 1975; Abbott 1984; Sutcliffe & Poole 1984; Digby 1995b). In addition, an age-related dominance hierarchy is often apparent, either within each sex or in both sexes combined (Sutcliffe & Poole 1984; Digby 1995b). Both males and females may be highly aggressive to unfamiliar or extra-group individuals of the same sex, but within established groups, aggression is usually mild and infrequent (Epplé 1967; Abbott 1984; Saltzman *et al.* 1994, 1997c; Digby 1995b; Sousa *et al.* 2005).

Marmosets exhibit remarkably high annual fecundity for primates (Tardif *et al.* 2003; Digby *et al.* 2007). Females typically give birth to twins, undergo post-partum ovulation and conceive within several weeks after parturition. Gestation lasts approximately 144 days; thus, breeding females regularly produce litters of two or more infants at roughly six-month intervals. Little is known of the average reproductive tenure of breeders in wild populations or the likelihood that a particular subordinate individual will eventually breed. Dominant females, however, have been observed to hold a breeding position for as long as 8 years (maximum lifespan in captivity is approx. 16 years; Abbott *et al.* 2003a), whereas fully mature subordinate females often fail to breed for periods of at least 1–2 years and possibly much longer (Arruda *et al.* 2005; Sousa *et al.* 2005). The effects of age on reproductive inhibition in subordinates, similarly, are not yet clear. Although laboratory data suggest that subordinate females' likelihood of undergoing physiological suppression may decrease with age (Saltzman *et al.* 1996, 1997a), field data indicate that some young subordinate females do attempt to breed, while some older subordinate females remain reproductively inactive for extended periods (Arruda *et al.* 2005).

4. WHAT ARE THE PROXIMATE MECHANISMS INHIBITING SEXUAL BEHAVIOUR IN SUBORDINATE FEMALES?

(a) *Interference by dominant females*

Subordinate female common marmosets engage in little or no intra-group sexual behaviour, both in the laboratory

(Rothe 1975; Abbott 1984; Saltzman *et al.* 1997c) and in the field (Digby 1999; Sousa *et al.* 2005). Several investigators have, on rare occasions, observed dominant females disrupting subordinate females' sexual interactions with males (Epple 1967; Rothe 1975; Abbott 1984). Others, however, have found little or no evidence of mating interference (Kirkpatrick-Tanner *et al.* 1996; Lazaro-Perea *et al.* 2000; L. J. Digby 1992, unpublished data; W. Saltzman & D. H. Abbott 1999, unpublished data) and, in the laboratory groups, most subordinate females are never seen even attempting to mate (Rothe 1975; Abbott 1984). Thus, interference by dominant females is unlikely to be a primary cause of sexual inhibition in subordinates.

(b) *Avoidance of mating with close relatives*

Inbreeding avoidance, instead of or in addition to interference by dominants, may be a key cause of sexual abstinence in subordinate females. Marmosets usually avoid sexual interactions with familiar, closely related individuals (reviewed in Saltzman 2003). Subordinate females in free-ranging groups typically do not mate with their male groupmates but may engage in brief sexual interactions with extra-group males (Digby 1999; Lazaro-Perea 2001; Arruda *et al.* 2005; Sousa *et al.* 2005). It is unclear whether these sexually active subordinates are undergoing ovulatory cycles, however, and extra-group matings do not appear to be conceptive for most females (Digby 1999; but see Arruda *et al.* 2005). Similarly, daughters housed with their natal families in the laboratory do not engage in sexual interactions with their father or brothers (Abbott 1984; Saltzman *et al.* 1997c, 2004), but many of these daughters will readily mate with an unrelated male introduced into the family, even in the presence of the mother (dominant female; Kirkpatrick-Tanner *et al.* 1996; Saltzman *et al.* 1997b,c, 2004; see also Anzenberger 1985; Hubrecht 1989). Notably, daughters that do not engage in sexual behaviour with an unrelated male under these circumstances are clearly subordinate to their mother and/or a sister, whereas those that mate with the unrelated male do not behave submissively towards other females (Saltzman *et al.* 2004). Thus, expression of sexual behaviour by female marmosets may be constrained by both the presence of a socially dominant female and the lack of access to an unrelated adult male (Saltzman *et al.* 1997b,c, 2004). Nonetheless, there is little evidence that dominant females actively and routinely prevent subordinates from mating.

5. WHAT ARE THE PHYSIOLOGICAL MECHANISMS UNDERLYING REPRODUCTIVE SUPPRESSION IN SUBORDINATE FEMALES?

(a) *Suppression of ovulation*

A key mechanism underlying reproductive failure in subordinate female marmosets is socially induced suppression of ovulation. Such anovulation has been documented in subordinate females housed in laboratory groups of unrelated adults (Abbott *et al.* 1981; Saltzman *et al.* 1994), in adult females living with their natal families in captivity (Abbott 1984; Evans & Hodges 1984; Hubrecht 1989; Saltzman *et al.* 1997a, 2004) and, more recently, in subordinates living in free-ranging groups (Albuquerque *et al.* 2001; Sousa *et al.* 2005).

Ovulation suppression is remarkably rapid, reliable and reversible. When a female marmoset is introduced into a new group of unrelated adults in which she becomes subordinate, plasma concentrations of chorionic gonadotrophin (CG; the major luteotrophic hormone secreted by the pituitary in common marmosets; Müller *et al.* 2004) drop precipitously in 1–4 days and ovulatory cycles soon cease (Abbott *et al.* 1988; Abbott & George 1991). Conversely, upon removal of a subordinate from her group, or following removal of the dominant female, the subordinate shows an elevation of plasma CG levels within a few days and ovulates within two to three weeks (Evans & Hodges 1984; Abbott *et al.* 1988; Abbott & George 1991). Ovaries of subordinate females not only fail to ovulate but also are markedly smaller than those of dominants, contain smaller and fewer antral follicles, typically contain no corpora lutea or corpora albicantia, and secrete very little oestrogen or progesterone (reviewed by Abbott *et al.* 1998).

(b) *A role of stress?*

Rank-related reproductive impairments have traditionally been attributed to stress (e.g. Sapolsky 1987; von Holst 1998; Young *et al.* 2006), although this view has been questioned in recent years (Abbott *et al.* 1997; Creel 2001; Sapolsky 2005). In common marmosets, we have found no evidence to support a role of stress in socially induced reproductive suppression. Elevated concentrations of glucocorticoid hormones (e.g. cortisol), for example, are the most commonly used index of stress and may suppress reproductive activity, especially ovulation and ovarian cyclicity, in a number of species (Ferin 2006). In marmosets, however, baseline circulating or excreted cortisol concentrations are not elevated in either non-breeding or breeding subordinate females, as compared with dominant females, in free-living (Sousa *et al.* 2005) or laboratory groups (Abbott *et al.* 1981; Saltzman *et al.* 1994, 1998, 2006a,b; Johnson *et al.* 1996; Ziegler & Sousa 2002; W. Saltzman, R. R. Pick, O. J. Salper, K. J. Liedl & D. H. Abbott 2000, unpublished data). Additional common manifestations of stress that may be associated with anovulation in other species, including elevated circulating prolactin levels (Bowman *et al.* 1978), altered diurnal rhythms and reduced body weight (Yen 2004), are also not found in captive subordinate female marmosets (Abbott *et al.* 1981, 1997).

(c) *Neuroendocrine mechanisms*

If subordinate females are not subject to chronic stress, how is social subordination translated into ovulatory failure? Inhibition of ovarian function is directly mediated by suppression of CG release from the anterior pituitary. Whereas plasma CG in dominant females in the mid-follicular phase of the ovarian cycle undergoes approximately hourly pulses, CG concentrations in subordinate females are low and non-pulsatile (Abbott *et al.* 1990, 1998). Pituitary secretion of LH (or CG) is generally assumed to passively reflect hypothalamic secretion of gonadotrophin-releasing hormone (GnRH); however, the pulsatile release of GnRH does not differ between dominant female marmosets in the follicular phase of the ovarian cycle and anovulatory subordinates (Saltzman *et al.* 1995; Abbott *et al.* 1997; Schultz-Darken *et al.* 2004; Tannenbaum *et al.* 2007; W. Saltzman,

P. L. Tannenbaum, N. J. Schultz-Darken, E. Terasawa & D. H. Abbott 1999, unpublished data). These findings suggest that hypothalamic GnRH and pituitary CG secretion can become dissociated in this species by an unknown mechanism, possibly involving blunted pituitary sensitivity to GnRH and to positive feedback effects of oestradiol (Abbott *et al.* 1981, 1988).

In conclusion, although the precise neuroendocrine mechanism underlying suppression of CG and anovulation has yet to be elucidated, it is clear that this mechanism is not mediated by stress and that it can be activated or inactivated very rapidly in response to salient changes in the social environment, particularly changes involving the presence or absence of a dominant female groupmate. Exposure to an unrelated adult male, by contrast, while playing a key role in the activation of sexual behaviour in females, does not influence the occurrence of ovulatory cycles (Saltzman *et al.* 2004). Moreover, ovulatory cycles in marmosets are not readily suppressed by such non-social challenges as surgery, illness or disruptive experimental procedures (Saltzman *et al.* 1998; Schultz-Darken *et al.* 2004; Tannenbaum *et al.* 2007). Such precise and pronounced social regulation of gonadotrophin secretion and ovulatory function is not found in other anthropoid primates (with the exception of several other species of callitrichids (marmosets and tamarins); French 1997), but occurs in a number of other cooperative breeders (e.g. Faulkes & Abbott 1997; Molteno & Bennett 2000; Solomon *et al.* 2001). Thus, common marmosets and some of their close relatives appear to have evolved a novel mechanism for rapidly switching the female reproductive system on or off in response to cues from a rival female, possibly representing an adaptation for socially dynamic cooperative breeding in an unpredictable environment.

6. WHAT ARE THE SOCIAL CUES THAT TRIGGER REPRODUCTIVE SUPPRESSION IN SUBORDINATE FEMALES?

(a) Aggression

Females of some species disrupt other females' breeding attempts—such as inhibiting ovulation, inducing spontaneous abortion or interfering with maternal care of infants—by directing aggression or harassment at their rivals (e.g. Huck *et al.* 1983; Wasser & Starling 1988; Vick & Pereira 1989; Hackländer *et al.* 2003; Young *et al.* 2006). By contrast, aggression seems to play little role, if any, in limiting reproduction in subordinate female marmosets. Consistent with their absence of elevated cortisol concentrations (Abbott *et al.* 2003b), subordinate females in both captive and free-ranging groups typically receive only mild and infrequent aggression (Rothe 1975; Abbott 1984; Digby 1995b; Saltzman *et al.* 1997c, 2004; Sousa *et al.* 2005). Moreover, whereas dominants of some species intensify their aggression towards subordinates that initiate reproductive attempts (e.g. Wasser & Starling 1988; Margulis *et al.* 1995; Scheibler *et al.* 2006; Young *et al.* 2006), no such pattern is seen in marmosets: subordinate females that ovulate and even conceive receive frequencies and intensities of aggression comparable with subordinates that are anovulatory (Saltzman *et al.* 1997c, 2004, 2008; Alencar *et al.* 2006). Therefore, neither chronic aggression nor acute bouts of targeted aggression appear to play a critical role in preventing

or terminating reproductive attempts in subordinate female marmosets.

Interestingly, however, subordinate females undergoing ovulatory cycles are much less likely to submit to dominant females than are anovulatory subordinates (Saltzman *et al.* 1997c, 2004; Alencar *et al.* 2006). Thus, a female's perception of herself as subordinate to another female, rather than the receipt of specific types or frequencies of agonistic behaviours, may be critical in determining ovulation suppression. Consistent with this possibility, adult female marmosets show pronounced individual differences in aggressiveness and submissiveness, which reliably predict their likelihood of attaining dominant or subordinate status in a new social group and therefore of undergoing ovulation suppression (Saltzman *et al.* 1996; W. Saltzman, N. J. Schultz-Darken, E. Terasawa & D. H. Abbott 1996, unpublished data). These individual tendencies are not necessarily stable across time, however, and appear to be age-related (Saltzman *et al.* 1996; W. Saltzman, N. J. Schultz-Darken, E. Terasawa & D. H. Abbott 1996, unpublished data), suggesting that female marmosets' 'willingness' to accept a subordinate position and consequently to undergo ovulatory restraint may decrease with age, experience and possibly other factors such as relatedness to the dominant female.

(b) Conditioned responses to cues from the dominant female

In contrast to aggression, specific cues from dominant female marmosets appear to play a role in both initiating and maintaining reproductive suppression in subordinates. When females were rendered anosmic by ablation of the main olfactory epithelium and the vomeronasal organ prior to their introduction into a new social group, five of six subordinates continued to ovulate, indicating that olfaction plays a key role in the initiation of ovulation suppression (Abbott *et al.* 1993, 1998). In a separate study, when anovulatory subordinates were removed from their groups and housed alone, continued exposure to scent from the familiar dominant female significantly delayed, but did not prevent, the onset of ovulation (Barrett *et al.* 1990). This effect depended upon recognition of scent from a familiar dominant female; scent from an unfamiliar dominant female had no effect on ovulatory function in separated subordinates (T. E. Smith 1994, unpublished PhD dissertation; Smith & Abbott 1995). Finally, when subordinate females housed with their social groups were rendered anosmic, they did not begin to ovulate (Barrett *et al.* 1993). Together, these findings suggest that olfaction is neither necessary nor sufficient to maintain ovulation suppression in subordinates, but may play a synergistic role with other sensory input. For instance, visual cues from dominant females, as well as behavioural and/or tactile cues, have been implicated in the maintenance of ovulation suppression. Visual exposure of separated subordinates to the dominant female and other groupmates, similar to scent transfer, delayed but did not prevent the onset of ovulation (Barrett *et al.* 1993). Ongoing direct interactions with a dominant female therefore appear to be 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 (Abbott *et al.* 1997). Females that perceive themselves as subordinate learn to associate olfactory, visual or other cues from the dominant with direct behavioural interactions with her, so that these cues become classically conditioned stimuli capable of maintaining ovulation suppression for some length of time, even in the absence of direct interactions between females. In contrast to the long-term maintenance of reproductive inhibition, therefore, the initial onset of suppression, especially in new social groups, might depend upon the receipt of aggression or harassment from the dominant female. Such aggression could then lead to associative learning that subsequently maintains suppression in subordinates. Additional data are needed to evaluate this hypothesis.

7. WHAT ARE THE CAUSES OF REDUCED REPRODUCTIVE SUCCESS IN SUBORDINATE FEMALES THAT ATTEMPT TO BREED?

In spite of the inhibition of sexual behaviour and/or suppression of ovulation in most subordinate females, some subordinates in both wild and captive groups ultimately 'escape' from suppression and begin to breed (e.g. 20–30% of behaviourally subordinate adult females in a wild population were reproductively active at any given time; Digby 1995*b*). These subordinate breeding females have markedly lower reproductive success than dominant females, as few or none of their infants survive beyond the first few weeks of life (field: 33% versus 62% infant survival for subordinates and dominants, respectively, in plurally breeding groups; Digby 1995*a*; 0% versus 71% in groups in which subordinates appear to have conceived during extra-group copulations; Arruda *et al.* 2005; Sousa *et al.* 2005; laboratory: 33% versus 50% in plurally breeding groups; 65% for dominants in singly breeding groups; Saltzman *et al.* 2008). What are the mechanisms generating post-ovulatory reproductive failure in these subordinate breeders?

(a) *Gestation, parturition and lactation*

When mothers and daughters breed concurrently in laboratory families, gestation, parturition and lactation proceed unimpaired (Saltzman *et al.* 2004, 2008; W. Saltzman, K. J. Liedl, O. J. Salper, R. R. Pick & D. H. Abbott 2000, unpublished data). Primiparous daughters and their mothers in these plurally breeding groups, as well as both experienced and first-time mothers in singly breeding families, produce comparable numbers of live infants, with very low rates of spontaneous abortions and stillbirths (Arruda *et al.* 2005; Saltzman *et al.* 2008). Moreover, although pregnant females have been reported to engage in escalated aggression with one another, this does not appear to occur routinely and does not necessarily lead to impaired pregnancy outcomes (Saltzman *et al.* 2008). In captivity, therefore, the presence of a breeding female may constrain other females' likelihood of ovulating and conceiving but, following conception, does not appear to further influence pregnancy, parturition or lactation. A similar pattern may occur in free-living marmosets: numerous subordinate females have been reported to give birth to live infants,

and do not appear to be subjected to increased aggression or eviction (Digby 1995*a*; Lazaro-Perea *et al.* 2000; Arruda *et al.* 2005; Sousa *et al.* 2005).

(b) *Infanticide*

A growing body of evidence suggests that when two female common marmosets breed in the same group, they may regularly kill one another's infants (reviewed by Saltzman 2003; Digby & Saltzman *in press*). Eight infanticides (seven intra-group, one inter-group) have been observed directly in wild groups of common marmosets, all involving breeding females killing other females' offspring (Digby 1995*a*; Roda & Mendes Pontes 1998; Lazaro-Perea *et al.* 2000; Melo *et al.* 2003; Arruda *et al.* 2005; Sousa *et al.* 2005; Bezerra *et al.* 2007). Numerous infanticides have also been observed or inferred in captive groups containing two breeding females (e.g. Alonso 1986; Kirkpatrick-Tanner *et al.* 1996; Saltzman *et al.* 2008).

In wild groups, infanticide typically involves dominant females killing infants born to subordinates; however, at least two infanticides were committed by subordinate breeding females (reviewed by Digby & Saltzman *in press*; see also Arruda *et al.* 2005). In a laboratory study, infants of both dominant and subordinate females (mothers and daughters in families containing an unrelated male) were vulnerable to infanticide (Saltzman *et al.* 2008). Therefore, both dominant and subordinate breeding females may kill infants. Interestingly, subordinates that kill infants born to dominant females have been reported to become dominant after the infanticide (Alonso 1986; Roda & Mendes Pontes 1998; Bezerra *et al.* 2007). On the other hand, free-living subordinate females whose infants are killed or otherwise disappear may subsequently emigrate from their social group (Arruda *et al.* 2005; Sousa *et al.* 2005). This may not occur for several months following the loss of infants, however, and it is unclear what role, if any, infanticide or other forms of aggression may play in precipitating the emigrations.

Reproductive status strongly influences females' likelihood of killing infants. In both wild and captive populations, infanticidal females are typically in the last one to two months of pregnancy (Saltzman 2003). Post-partum females, by contrast, generally do not appear to kill young (Digby 2000; Saltzman *et al.* 2008; but see Arruda *et al.* 2005). The hormonal events of late pregnancy are likely to influence marmosets' responses to infants. In a laboratory study, multiparous females showed minimal attraction to and tolerance of infants during late pregnancy, especially when compared with early pregnancy and the early post-partum period (Saltzman & Abbott 2005). Furthermore, early post-partum females showed identical, highly maternal behavioural responses to their own infants and unfamiliar, unrelated infants, suggesting that these females may be unable to discriminate reliably among neonates. Females that commit infanticide during the post-partum period could therefore be at risk of accidentally killing their own offspring (Saltzman & Abbott 2005), which might select for the avoidance of infanticide during this time.

The effect of kinship on patterns of infanticide is not yet clear. In several laboratory studies, mothers and daughters have been observed or strongly suspected of killing one

another's infants (Alonso 1986; Kirkpatrick-Tanner *et al.* 1996; Saltzman *et al.* 2008). In the field, the genetic relationships between infanticidal females and their victims have not usually been known, although one apparently infanticidal dominant female did not appear to be closely related to the infant's mother (Digby 1995a; Nievergelt *et al.* 2000). Given the high degree of relatedness among most females in free-living marmoset groups, however, the possibility exists that breeding females may commonly kill the infants of their own close relatives.

A pattern of breeding females routinely committing within-group infanticide has not been reported in other primates (Digby 2000; but see Jolly *et al.* 2000; Pusey *et al.* 2008), but is similar to findings in several other cooperative breeders (e.g. Elwood 1977; Vehrencamp 1977; Mumme *et al.* 1983; Packer & Pusey 1984; Rasa 1987; Keeping 1992; Clutton-Brock *et al.* 1998; Eggert & Muller 2000). Thus, this pattern probably represents an adaptation to the intense reproductive competition inherent in cooperative breeding systems. Such infanticide is the only clear evidence for active, dominant-imposed control of reproduction in subordinate female marmosets, in contrast to the overwhelming evidence for subordinate self-restraint.

8. CONCLUSIONS

Findings from three decades of laboratory studies and two decades of field studies on common marmosets provide unique insights into reproductive skew in female cooperative breeders. Many subordinate females do not attempt to breed for periods of months to years, mediated by inhibition of sexual behaviour and/or suppression of ovulation. Other subordinate females do attempt to breed and are able to successfully conceive, maintain pregnancy, give birth and lactate; however, their reproductive success is drastically reduced when compared with dominant females, largely as a consequence of infanticide by pregnant dominants.

What can the proximate mechanisms of reproductive failure in subordinate female marmosets tell us about the ultimate causes of reproductive skew? This question is perhaps best addressed by considering non-breeding and breeding subordinates separately. Findings from non-breeding female marmosets, for the most part, provide little support for the hypothesis that dominant females use overt behavioural tactics to control reproduction in subordinates, in a proximate sense, either in preventing subordinates from breeding or in ceding reproduction to them, as postulated by concession and tug-of-war models (table 1). First, the maintenance, and possibly the initiation, of reproductive suppression does not appear to be associated with either stress in subordinates or manipulation by dominants. Second, we have found no evidence that the occurrence of successful breeding by subordinates results from dominants 'allowing' them to do so, as suggested by concession models. Reproductively suppressed and non-suppressed subordinates receive comparable amounts of aggression from their dominant female groupmates but differ in whether they exhibit submissive behaviour. Thus, preconception reproductive suppression appears more closely tied to social assessments made by subordinate females than to behavioural tactics used by dominants. Furthermore, because

non-reproductive subordinates do not attempt to initiate breeding attempts or to disrupt reproduction in dominant females, tug-of-war models are not applicable.

Restraint models of skew, by contrast, are broadly compatible with the observed proximate causes of reproductive failure in non-breeding subordinate female marmosets. The low rates of aggression among female groupmates, the absence of classic stress-related physiological changes in subordinate females, and subordinates' use of subtle behavioural and sensory cues from familiar dominants to trigger physiological suppression all suggest that preconception reproductive inhibition is self-imposed in subordinates, at a proximate level, via specialized mechanisms that minimize the risk of injury or pathology. Restraint models further postulate that such self-restraint occurs in response to the threat of eviction by dominant females, but this scenario is not well supported by studies of common marmosets. What, then, are the selection pressures favouring the evolution of reproductive self-restraint in subordinate females? This question can be answered by considering the mechanisms of reproductive failure in those subordinate females that terminate their preconception self-restraint and attempt to breed.

Clearly, neither concession nor restraint models can explain the poor reproductive outcomes of breeding subordinates (table 1). Instead, both dominant and subordinate females in plurally breeding groups actively vie for reproductive sovereignty by killing each other's infants, with subordinates in particular losing most or all of their offspring. This scenario is consistent with tug-of-war models, in which subordinate females breed not because dominant females allow them to but because dominant females cannot prevent them from doing so, and in which dominants are able to monopolize most, but not all, of their group's reproductive success.

These findings suggest that infanticide by dominant females might play a critical role in selecting for the evolution of reproductive self-restraint in subordinates (Saltzman 2003; Abbott *et al.* in press). Reproduction is especially expensive for these small primates, given their heavy investment in each breeding attempt (e.g. long gestation and high infant-to-maternal body mass ratio). Therefore, selection should favour females that can detect circumstances highly inauspicious for reproduction—such as the presence of a potentially infanticidal dominant female—and restrain their own reproductive activity under these conditions. By engaging specialized, inhibitory neuroendocrine and behavioural mechanisms in the presence of a dominant female, subordinates minimize their own likelihood of investing in costly 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 1995a; Abbott *et al.* 1997; Saltzman 2003; Gilchrist 2006).

In conclusion, reproductive skew in female marmosets is maintained, at a proximate level, by a combination of self-restraint in non-breeding subordinates and tug of war when subordinates terminate their self-restraint and begin to breed. While manipulation—specifically, infanticide—by dominant females clearly acts as a proximate mechanism limiting reproductive success in breeding subordinates, we suggest that it may be even more critical as an ultimate mechanism, serving as the evolutionary

'stick' by which dominants coerce subordinates into curtailing their own breeding attempts. Many questions remain unanswered concerning the neural, hormonal, sensory and behavioural processes governing reproduction in female marmosets. For example, what determines if or when a particular subordinate female will attempt to breed? What are the specific neural and hormonal pathways that translate social subordination into suppression of pituitary CG release? And does aggression by the dominant female play any role in initiating, even if not in maintaining, reproductive suppression in subordinates? The answers to such questions, from integrated field and laboratory studies, are certain to yield further novel insights into the evolution and functional significance of female reproductive strategies in high-skew societies.

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