

Review

# Adaptations to subordinate status in female marmoset monkeys

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## Abstract

In singular cooperatively breeding mammals, social status is a key determinant of female reproductive success. Usually only one dominant female breeds in a social group. In the common marmoset (*Callithrix jacchus*), a cooperatively breeding primate, adaptations to nonbreeding subordinate status appear to parallel those found in social insect societies which demonstrate similar skew to the marmoset in female reproductive success. Female marmosets exhibit rank-related polyethism in behavior, reproductive neuroendocrinology and non-reproductive physiology, and subordinates participate in alloparental care and territory defense. Olfactory, visual and behavioral cues from dominant female marmosets provide important proximate cues regulating ovarian inhibition in female subordinates. Cooperatively breeding marmosets, therefore, appear to have developed specific neural and neuroendocrine adaptations to subordinate social status analogous to those found in social insects such as the lower wasps, bees and termites. Such parallel developments probably reflect the outcome of repeated convergent evolutionary attempts at adapting to environmental conditions not readily conducive to dispersal and independent breeding. © 1998 Elsevier Science Inc. All rights reserved.

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## 1. Introduction

Food availability, climate and the social environment represent the major ultimate factors regulating reproductive success in female mammals [18]. Proximate cues predictive of favorable food availability and climate serve to activate changes in reproductive physiology, behavior and metabolism, culminating in the optimal timing of courtship, mating, parturition and weaning of offspring [59]. The social environment, however, has a more complex impact on reproductive success and provides a plethora of proximate cues. Social factors regulate the timing of reproductive success in two distinct ways which are not mutually exclusive.

First, social factors can act to modulate the timing of reproduction, when food availability and climate are either approaching or have already reached optimal conditions. For example, olfactory, visual and behavioral cues from rams advance and synchronize estrus in ewes. Increased concentrations of luteinizing hormone (LH) are measurable in the ewes' circulation within minutes of exposure to male cues [62]. However, this stimulatory effect of males occurs only just prior to or at the beginning of the breeding season [23,87].

Second, in addition to modulating the timing of reproduction, social factors can serve as constraints on reproductive success over and above those imposed by food availability and climate. Thus, social factors may effectively 'gate' the relevance of cues related to the physical environment to times when the social environment is suitable for successful reproduction, e.g. when

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high rank or dominant status is attained. In this regard, low social rank or subordinate status has been widely shown to inhibit reproductive function in females in a variety of species [17,62,69] with varying intensity and effectiveness of inhibition [26,34,101].

Many mammalian species are characterized as competitive breeders, in which most or all females in each social group breed. In such species, however, subordinate females may experience lower reproductive success than higher ranking females [61]. Mechanisms by which dominant females may secure their reproductive advantages over subordinate females include: (1) harassment-induced disruption of subordinates' sexual behavior (e.g. stump-tail macaque, *Macaca arctoides* [32]); (2) harassment-induced stress in subordinates, resulting in inhibited ovulation (e.g. cynomolgus monkeys, *Macaca fascicularis* [53]) or failed implantation following conception (e.g. Syrian hamsters, *Mesocricetus auratus* [50]); (3) harassment-related infant loss experienced by subordinates (e.g. yellow baboons, *Papio cynocephalus* [70]); and (4) exclusion of subordinate females from resources essential for successful reproduction, such as food (e.g. red deer, *Cervus elephas* [22]).

In contrast to the graded reproductive suppression found in most competitive breeders, some of the most extreme mammalian examples of dominance-determined female reproductive success are found in cooperatively breeding species. Within social groups of cooperatively breeding species, members other than the genetic parents play crucial roles in successfully rearing offspring. In singular cooperative breeders, reproduction is limited to a single female in each group [29,52]. Reproductive failure in subordinate females in these species may not be dependent upon generalized harassment or resource exclusion [10]. Instead, specialized neuroendocrine and behavioral responses by females to subordinate status may directly inhibit sexual behavior (e.g. golden lion tamarins, *Leontopithecus rosalia*; [40]), ovulation (e.g. common marmosets, *Callithrix jacchus*; [9]) and implantation (e.g. white-footed mice, *Peromyscus leucopus*; [41]). Olfactory, visual and behavioral cues from dominant females have been implicated in the activation or maintenance of specific inhibitory reproductive mechanisms in such subordinate females, indicating a well-developed sensitivity and specialized neuroendocrine response to proximate cues signifying subordinate status [10].

Singular cooperatively breeding species are found throughout the avian and mammalian classes and are characterized by delayed dispersal of offspring from the natal group, reproductive suppression and care for nondescendant offspring [91]. These specialized characteristics resemble those of eusocial insects, in which colonies contain overlapping generations, clear divisions of labor and of reproduction occur, and non-breeding members cooperate in rearing offspring and in protecting and servicing the colony [65,103].

Such similarities in definitional characteristics between cooperative breeders and eusocial insects have prompted Sherman and colleagues [86] to reconsider eusociality as a continuum across which societies of cooperatively breeding vertebrates and invertebrates can be arranged depending upon the degree of skew shown in female reproductive success within social groups (Fig. 1). Such an inclusive concept emphasizes the behavioral similarities between cooperatively breeding vertebrates and invertebrates, encompasses all forms of alloparental care, and removes the traditional distinctions between cooperative breeding and eusociality. Lacey and Sherman [57] have proposed a single integrated hypothesis for the evolution of singular cooperative breeding in both vertebrates and invertebrates. In slightly modified form, their scenario suggests that for cooperative breeding to evolve: (1) ecological constraints on dispersal and on independent breeding became so onerous that coloniality or social grouping was favored; and (2) alterations in the patterns of intra-group relatedness (increased kinship), reproductive biology (development of alloparental care and reproductive suppression among subordinates) and phenotype (somatic and physiological adaptations to social status) further promoted cooperation within such colonies or social groups. In other words, comparable environmental constraints on female reproduction across vertebrate and invertebrate cooperatively breeding species may result in the convergent evolution of similar proximate mechanisms. To date, the concept of a continuum of eusociality has been addressed mainly at the ultimate level of causation. Here, we aim to take the argument to the proximate level and to provide evidence to stimulate further detailed examination.

Our research has focused on proximate mechanisms mediating social regulation of female reproductive success in the common marmoset, a cooperatively breeding anthropoid primate. Our laboratory findings suggest that females have specialized adaptations to subordinate status in terms of behavior, reproductive neuroendocrinology, hypothalamic-pituitary-adrenal function and glucose homeodynamics. In this review, we will discuss how behavioral and physiological consequences of subordinate status in female marmosets appear to reflect a stable alternative to dominant status rather than a state of generalized stress imposed by the dominant female and endured by subordinates to their physiological detriment. We will explore how the social environment provides the predominant cue(s) timing female reproductive effort in marmosets, and we will consider anovulation as just one of many specialized adaptations to subordinate status in this cooperatively breeding species.

Based on the invertebrate literature dealing with cooperative breeding, the adaptations made by female marmosets to subordinate status can be considered as

## Eusociality Continuum

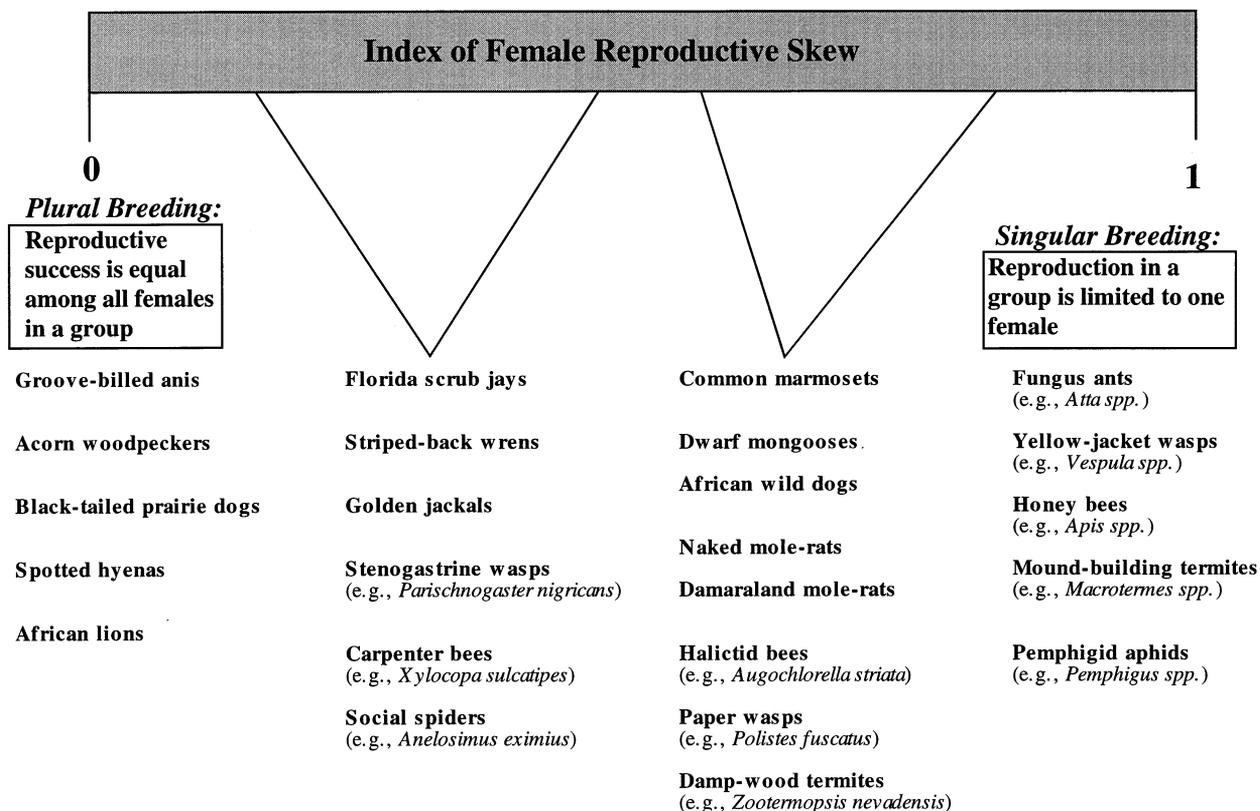


Fig. 1. Diagrammatic representation of predicted locations of selected cooperatively breeding vertebrate and invertebrate species along the eusociality continuum [86], arranged with regard to an index of the skew in estimated lifetime reproductive success of females in a social group [55,86]. Skew equals '0' when female lifetime success is equal among group members and reaches a value of '1' when reproduction is limited to one female in a group. As skew may vary among conspecific groups or populations, species having approximately similar degrees of skew are grouped together. The figure is modified from Lacey and Sherman [57].

examples of polyethism, even if they are reversible with a change in social status [16]. Consequently, we aim to review the degree and nature of polyethism found in female marmosets, as a first step in ascertaining the commonality of proximate mechanisms shaping the specialized adaptations of cooperatively breeding species across vertebrate and invertebrate classes. Such comparative examination of the proximate mechanisms regulating female reproductive success may provide novel insights into the neural mechanisms mediating environmental control of neuroendocrine function.

### 2. Common marmosets

Along with the other members of the family Callitrichidae (marmosets and tamarins), the common marmoset is a small New World primate exhibiting a singular cooperative breeding strategy. In the wild, common marmosets occupy successional forest, forest edge habitat and savanna gallery forest in northeastern Brazil [75]. A characteristic feature of this species is its

exploitation of exudate feeding supplemented by opportunistic feeding on fruits, insects and small vertebrates, which has enabled its habitat expansion despite the extensive deforestation of Atlantic coastal forests.

#### 2.1. Social groups, reproductive division of labor and cooperative behavior

Free-living groups of common marmosets contain 3–15 individuals, usually including 2–4 adults of each sex [28,38]. Groups appear to consist mainly of extended families and possibly unrelated immigrants [39,64]. Offspring remain within their natal group into adulthood, and all group members contribute to infant care, including post-weaning provisioning of infants [40,97].

Both field [49,92] and laboratory [1,30,73,77] studies of common marmosets typically report that only a single, dominant female breeds in each social group but see [28]. Lack of 'helpers' to raise offspring, lack of dispersal opportunities, infanticide by the dominant female, and inbreeding avoidance may contribute to the

ineffective breeding of subordinate females in free-living marmoset groups [12,27,40,71,77]. Subordinate females can sometimes breed successfully in free-living [27,71] and captive [11,74] groups, but these occurrences may depend on the subordinate's parturition occurring more than 1 month before or after the dominant female gives birth, increased food availability, large group numbers (increased numbers of helpers) and high population density (increased need for retention of subordinates for territorial defense) [40].

Callitrichids may migrate into established groups [37,83]. The successful founding of a new group by a single breeding pair appears unlikely because of the relatively high costs of gestation and infant care [40,97] and the minimum quotient of 'helpers' needed to successfully rear the infants of a single breeding female [95]. Thus, cooperation between animals may be required for the successful founding of new marmoset groups, as well as for their maintenance.

## 2.2. Standardized captive social groups

To investigate the proximate behavioral, neuroendocrinological, physiological and sensory regulation of reproductive success in female marmosets, we have established a total of 75 mixed-sex social groups comprising three to seven unrelated adults or postpubertal animals, over a 12-year period, at the Wisconsin Regional Primate Research Center in Madison, WI [79] and at the Institute of Zoology in London, UK [8]. Social groups remain together for 2 months to over 3 years. The social structure of our standardized captive social groups is typical of that for common marmosets. Linear or despotic hierarchies are usually quantifiable within 3 days of group formation, from the directionality of agonism displayed [1,76]. Dominant females are usually the only reproductively active females.

Endocrine monitoring of ovarian activity is accomplished by assessing plasma progesterone concentrations in twice weekly blood samples, which identifies the peri-ovulatory period (day of ovulation  $\pm 1$  day), phases of the ovarian cycle and anovulatory periods [8,45,79]. Stable group composition is achieved by contraceptive management of females with injections of a prostaglandin F<sub>2</sub> $\alpha$  analogue [94]. Routine handling of the animals and blood collection procedures do not result in obvious physiological disturbances or in the disruption of the normal diurnal rhythm of plasma cortisol concentrations [79]. Plasma concentrations of cortisol, dehydroepiandrosterone (DHEA), adrenocorticotrophic hormone (ACTH) and fasting glucose are determined from blood samples taken within 3 min of the investigator entering an animal's cage.

## 3. Behavioral polyethism

Dominant (breeding) and subordinate (non-breeding) females show clear behavioral differences. Within groups in the wild [28,48,92] and in the laboratory [3,13,30,49,73] subordinate females engage in little or no sexual activity. Outside their own group, however, subordinates may readily engage in sexual interactions [3,13,48,49], suggesting that inhibition of intra-group sexual behavior might depend on the presence of a dominant female groupmate and/or a familiarity or incest taboo [3,13,82]. Dominant females also engage in more affiliative interactions with the dominant male than do subordinate females in captive groups [1].

In free-living and captive groups, subordinates participate more in intergroup displays than dominants ([56]; C. Lazaro-Perea and C.T. Snowdon, personal communication). These findings may indicate a significant contribution by subordinates to territorial defense and rank-related divisions of labor.

## 4. Reproductive polyethism

### 4.1. Ovarian and pituitary function

Ovarian size, content and function differ dramatically between dominant and subordinate female marmosets. The average ovarian volume of subordinate females ( $609 \pm 145$  mm<sup>3</sup>; mean  $\pm$  S.E.M.;  $n = 5$ ) is approximately half that found in dominant females in the early to mid-follicular phase of the ovarian cycle ( $1217 \pm 163$  mm<sup>3</sup>;  $n = 8$ ;  $P < 0.01$  vs. subordinate females; Student's *t*-test). The absence of corpora lutea and corpora albicantia in ovaries of subordinate females suggests a lack of recent ovulatory function [9,100]. Ovarian follicle content also differs dramatically between dominant and subordinate females. Ovarian dissection revealed only 80–120 small ( $\leq 1.0$  mm), antral follicles from each subordinate, whereas approximately twice that number of antral follicles were recovered from the ovaries of each dominant [43,44,46,47]. In all, 12% of follicles from the ovaries of dominant females exceeded 1.0 mm in diameter and 3% were preovulatory. Clearly, ovarian function in subordinate female marmosets was severely impaired.

Impaired ovarian function in subordinates was further confirmed by endocrine monitoring. Whereas dominant females ovulate regularly in captive social groups, subordinate females usually exhibit hypogonadotropic anovulation (Fig. 2) [8]. Serial blood sampling every 15 min for 4 h by repeated venipuncture [7] reveals a stark contrast between the low, nonepisodic plasma LH concentrations of subordinates and the higher, episodic plasma LH concentrations of dominant females in the mid-follicular phase of the ovarian cycle (Fig. 3a).

Hypogonadotropism in subordinates is rapidly reversed by a change in social environment. Removal of an anovulatory subordinate from her dominant female results in an elevation of LH levels within 1–4 days [6,8], leading to the induction of ovulatory function almost within the length of a normal follicular phase [15]. Hypogonadotropic anovulation is readily re-engaged when ovulatory female marmosets are returned to subordinate status in their original group or in a new group [8,14].

These findings highlight the remarkably labile pituitary and ovarian responses of female marmosets to changes in social status. This dynamic reproductive neuroendocrine system may be an adaptation to cope with changing environments, varying group composition and an opportunistic existence ([64,75,84]; M.E. Yamamoto and D. Santee, personal communication). Subordinate females also show variability in the degree and duration of hypogonadotropism and ovarian inhibition depending on their subordinate rank, age and group composition [6,77,80]. For example, rank 2 subordinates exhibit less reliable hypogonadotropism and anovulation than rank 3 or 4 subordinates [6], and they may rapidly engage in sexual behavior and commence regular ovulatory cycles following the replacement of the breeding male by an unfamiliar (or unrelated) male

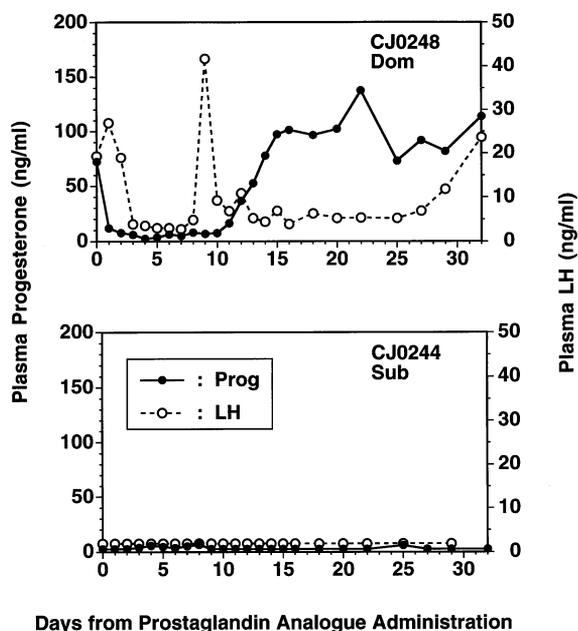


Fig. 2. Plasma concentrations of progesterone (solid circles) and immunoreactive LH (open circles) in (a) a typical dominant female marmoset during an ovarian cycle, and (b) an anovulatory subordinate female following i.m. administration of a prostaglandin  $F_2$  analogue [94]. The elevated LH levels in the dominant female following the prostaglandin analogue treatment and approximately 20 days into the succeeding luteal phase, probably reflect cross-reactivity of the LH assay antibody with circulating levels of chorionic gonadotropin (CG) secreted from the placenta during early pregnancy.

[80,82]. Such a scenario might precipitate the replacement of the original breeding female by a previously subordinate female or the fissioning of the original group into new breeding groups.

#### 4.2. Reproductive neuroendocrine inhibition

There is no evidence of generalized stress in anovulatory subordinate female marmosets. Body weight and diurnal rhythms are unaltered, and there are no elevations in the circulating concentrations of cortisol and prolactin [10,76,79]. Instead, specific inhibitory neuroendocrine mechanisms appear engaged in the maintenance of anovulation in subordinate females. Since pulsatile circulating LH levels usually correspond reliably with pulsatile release of gonadotropin-releasing hormone (GnRH) from the hypothalamus in other mammalian species (e.g. sheep: [58]; rhesus monkey, *M. mulatta*: [99]), the low, non-episodic pattern of circulating LH levels found in anovulatory subordinate female marmosets were initially interpreted as providing indirect evidence for the disruption or inhibition of hypothalamic GnRH release as the cause of the hypogonadotropism. We used two different approaches to test this hypothesis.

Our first approach involved treatment of anovulatory subordinates with exogenous GnRH. Subordinates received approximately hourly subcutaneous infusions of 1 or 2  $\mu$ g GnRH through an indwelling cannula, which was attached to a battery-powered syringe pump housed in a lightweight backpack [5,10]. GnRH treatment induced rapid elevations in circulating LH levels and ovulation within 2 weeks [10]. Two of six GnRH-treated subordinates even became pregnant during the treatment. On termination of GnRH treatment after 1–3 months, the subordinates quickly reverted to their hypogonadotropic state. Rapid induction of ovulatory function in subordinate females by GnRH treatment and the subsequent cessation of ovulatory function when GnRH treatment stopped, are similar to effects on ovulatory function obtained by simply manipulating female social status [8]. These results appeared to implicate pituitary hypogonadotropism in the mechanism of anovulation, and disrupted or inhibited hypothalamic GnRH release in the mechanism of hypogonadotropism.

To directly determine whether disrupted or inhibited release of endogenous hypothalamic GnRH accompanies hypogonadotropism in subordinate females, we measured dynamic GnRH release from the hypothalamus of conscious animals [10,81]. As it is not possible to accurately measure dynamic patterns of hypothalamic GnRH release from peripheral plasma concentrations [21,98], we employed a push-pull perfusion system to measure GnRH concentrations in 10-min perfusate fractions of artificial cerebrospinal fluid collected from

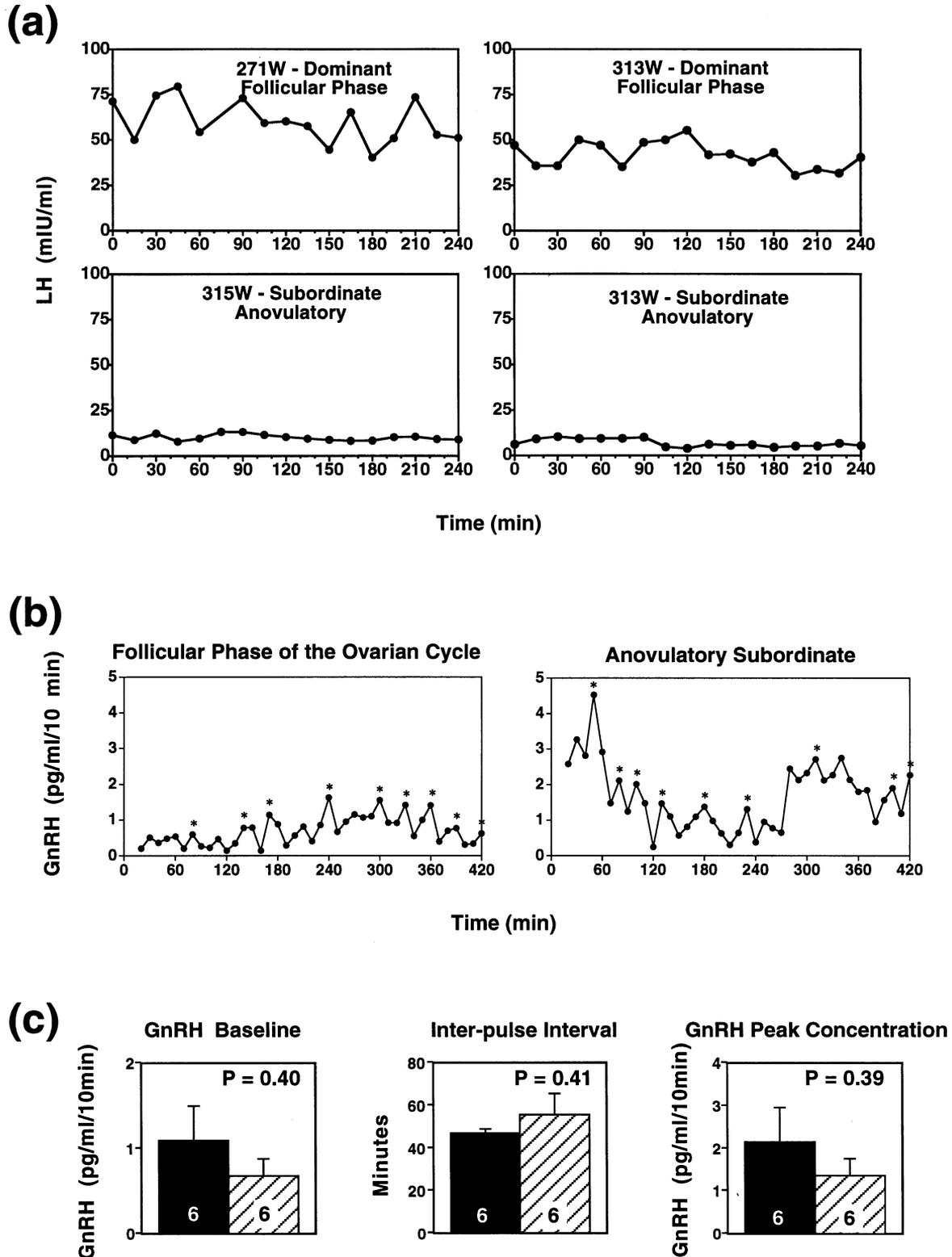


Fig. 3. (Continued)

the pituitary stalk-median eminence (S-ME) of marmosets. Throughout each perfusion, marmosets were restrained in a soft harness opposite their familiar groupmates [10,81].

In contrast to plasma LH concentrations, hypothalamic GnRH concentrations did not differ between dominant and subordinate females. Extra-cellular release of GnRH from the S-ME of anovulatory subordinates

was pulsatile in nature (Fig. 3b), and GnRH was found in similar concentrations to those of dominant females in the mid-follicular phase of the ovarian cycle (Fig. 3b,c) [10,81]. Discrepancies between hypothalamic GnRH release and circulating LH levels have also been recently found in female rats during lactational anestrous [19]. Both of these findings, however, are unconventional. Previously, studies had demonstrated that hypogonadotropism is accompanied by, and is indeed caused by reduced hypothalamic GnRH release, such as in prepubertal female rhesus monkeys [102] and in seasonally anestrous ewes [54]. Certainly in the marmoset, the apparent qualitative differences between hypothalamic GnRH and pituitary LH activity in subordinate females leaves open the possibilities that subtle alterations in hypothalamic GnRH release may be reducing pituitary gonadotropic responsiveness to GnRH or that the primary site for gonadotropic failure may reside at the level of the pituitary. Factors such as reduced pituitary gonadotropic responsiveness to GnRH [8], insufficient endocrine priming of pituitary gonadotrophs [33,104,105], or a combination of factors leading to reduced pituitary sensitivity to GnRH [20], may be responsible for the hypogonadotropic condition of subordinates. Mediation of hypogonadotropism in subordinates by a subtle combination of neuroendocrine and endocrine disruption, rather than by a dramatic change in hypothalamic GnRH release, would be consistent with the extremely rapid changes in LH secretion seen when the social status of female marmosets is systematically manipulated [6,8]. Further elucidation of this possibility must await the outcome of comprehensive quantitative analyses of endogenous GnRH and LH secretion dynamics in dominant and subordinate female marmosets.

Why, then, had exogenous GnRH therapy been so effective in reversing the hypogonadotropism of subordinate females, if pituitary inadequacy plays a major role in its mechanism? The answer may lie in the relatively large doses of exogenous GnRH given during infusion treatments. Each subordinate female marmoset received 1 or 2  $\mu\text{g}$  GnRH intravenously or

subcutaneously, infused at approximately hourly intervals, over a period of several weeks or months [5,10]. These GnRH amounts are well in excess of the 200 ng GnRH given intramuscularly to induce LH release from the pituitary of subordinate females [8] and are similarly in excess of endogenous peak levels of GnRH in hypothalamic push-pull perfusates (Fig. 3b,c). Such supraphysiological episodic GnRH stimulation of pituitary gonadotrophs may have overridden any endogenous pituitary hyporesponsiveness and sufficiently engaged pituitary gonadotropin function to induce ovarian follicular growth, ovulation and normal luteal function [4,10].

Evidence of specific ovarian hormone-dependent and ovarian hormone-independent mechanisms underlying hypogonadotropism has been obtained from manipulation of circulating estradiol levels in female marmosets [2]. As evidence for the former type of mechanism, subordinate females have demonstrated enhanced sensitivity to the inhibitory influences of estradiol feedback on LH secretion. In the case of the latter, experiments employing the opiate  $\mu$ - and  $\epsilon$ -receptor antagonist, naloxone, appear to implicate the inhibitory endogenous opioid peptides in the suppression of LH in ovariectomized, but not intact, subordinate females [5]. Endogenous opioid peptides have also been implicated in estradiol-independent mechanisms of steroid hormone negative feedback regulation of LH secretion in other primates [36]. The inhibitory neuroendocrine mechanisms operating in subordinate female marmosets may, thus, encompass a generalized enhancement of both estradiol-dependent and estradiol-independent negative feedback on LH secretion at hypothalamic and, possibly, pituitary levels. Similar dichotomies in inhibitory neuroendocrine regulation of LH secretion have been found in lactating rats [19,60,88] and in seasonally anestrous ewes [54,66]. Nevertheless, the precise nature of the inhibitory components involved in the neuroendocrine mechanism(s) inducing and maintaining such naturally-occurring hypogonadotropism still await elucidation.

Fig. 3. (a) Typical individual plasma bioactive LH concentrations in two mid-follicular phase dominant female marmosets (271–313W) and two anovulatory subordinate females (315–313W). The plasma samples were obtained without anesthesia from repeated femoral venipuncture every 15 min over four consecutive hours. In contrast to LH values in subordinate females, those in the dominants were higher in value and exhibited an episodic pattern. Note that the LH data from female 313W clearly differentiate when she was dominant in a group (high plasma values and episodic pattern), and then later when she was subordinate (low plasma values and nonepisodic pattern). A quantitative assessment of endogenous LH pulsatility was not performed because of the relatively long inter-sample interval between plasma LH determinations (15 min) relative to the total sample interval (4 h) and a putative pulse frequency of approximately 40–60 min. (b) Typical individual immunoactive GnRH concentrations in 10-min fractions of hypothalamic push-pull perfusate obtained without anesthesia from a female marmoset (CJ0086) while holding (1) dominant status in a social group (during the mid-follicular phase of the ovarian cycle), and later (2) subordinate status in another group (anovulatory). \* Denotes GnRH pulses identified by the computer algorithm PULSAR [98] under both social conditions. Modified from Abbott et al. [10]. (c) Antilog of the transformed mean (+95% confidence limit) of GnRH baseline, interpulse intervals and peak concentration in six females in the midfollicular phase of the ovarian cycle (cycling, solid bars) and in six anovulatory subordinate females (hatched bars). Probability values were derived from Student's *t*-tests.

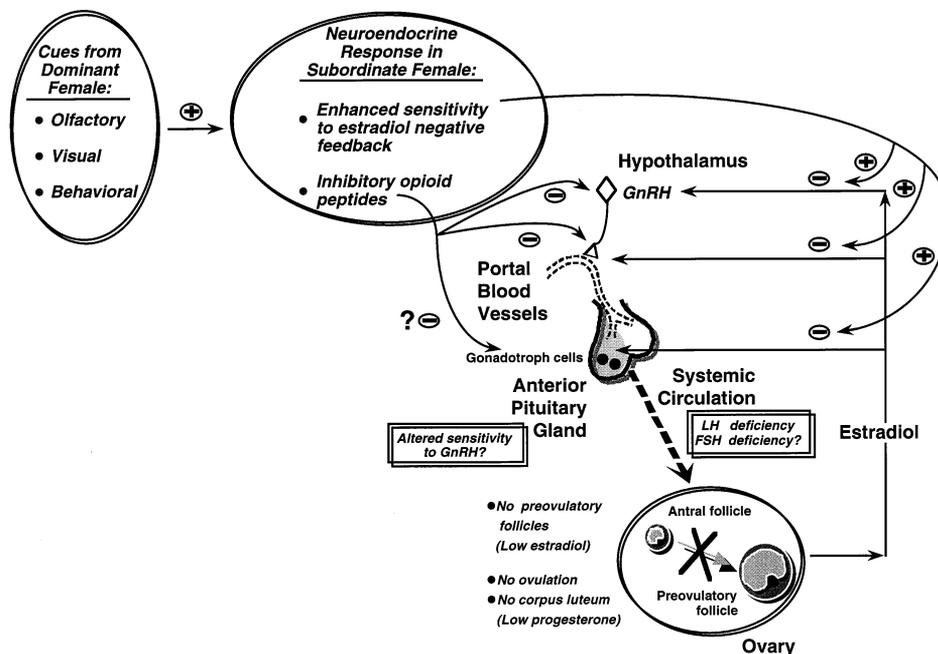


Fig. 4. Diagrammatic representation of the role of olfactory, visual and behavioral cues from dominant female marmosets in maintaining the inhibitory neuroendocrine mechanisms regulating hypogonadotropic anovulation in subordinate females.

### 5. Proximate cues regulating the social inhibition of female reproductive neuroendocrinology

Olfactory, visual and behavioral cues from dominant female marmosets all play a role in maintaining inhibition of ovulation in subordinate females [14]. Marmosets are one of the few primates which possess a fully functional accessory olfactory system and vomeronasal organ in addition to the main olfactory system [51,64,96] and specialized sternal, suprapubic and anogenital scent glands [31]. When subordinate females were removed from their groups and housed singly, but were maintained in scent contact with their dominant females, the onset of first ovulation was delayed to approximately 31 days in comparison to the average of 11 days in controls [15]. Visual cues from dominant females similarly delayed the onset of first ovulation in singly housed subordinate females rendered anosmic [14]. Intriguingly, the effectiveness of olfactory and visual cues to maintain ovarian inhibition lapsed after a few weeks. In addition, odor from a dominant female unfamiliar to the subordinate was ineffective in maintaining ovulatory inhibition in singly housed subordinates [10].

Although both olfactory and visual cues from dominant females may contribute to the maintenance of hypogonadotropism in subordinate female marmosets, behavioral cues from dominant females may provide the predominant inhibitory influence: subordinates rendered anosmic while remaining in their social groups failed to ovulate [14]. Together these findings

suggest that subordinates may learn to associate olfactory and visual cues from an individual female with her dominance status. As a result, the dominant's olfactory and visual cues become conditioned stimuli contributing to hypogonadotropic anovulation in subordinates [10,89]. Associative learning may, therefore, figure prominently in the neural mechanisms translating social subordination into anovulation in female marmosets. This hypothesis, however, remains to be tested.

In addition to maintaining ovarian suppression, olfaction may play a predominant role in its initiation: five out of six female marmosets rendered anosmic prior to their introduction into a newly formed social group failed to demonstrate anovulation on becoming subordinate [5]. The mechanism of this important role of olfaction in the initiation of ovarian suppression is not yet clear. One possibility is that imprinting of olfactory cues from a dominant onto the neural substrate of subordinates might directly activate the neuroendocrine mechanisms inhibiting reproduction. Alternatively, olfactory cues from subordinates undergoing ovarian cycles might elicit aggressive behavior by the dominant, which in turn precipitates rapid inhibition of gonadotropin secretion and of ovulation [76].

A summary of our current understanding of the proximate cues and neuroendocrine mechanism(s) regulating inhibition of ovulation in subordinate female marmosets is shown in Fig. 4.

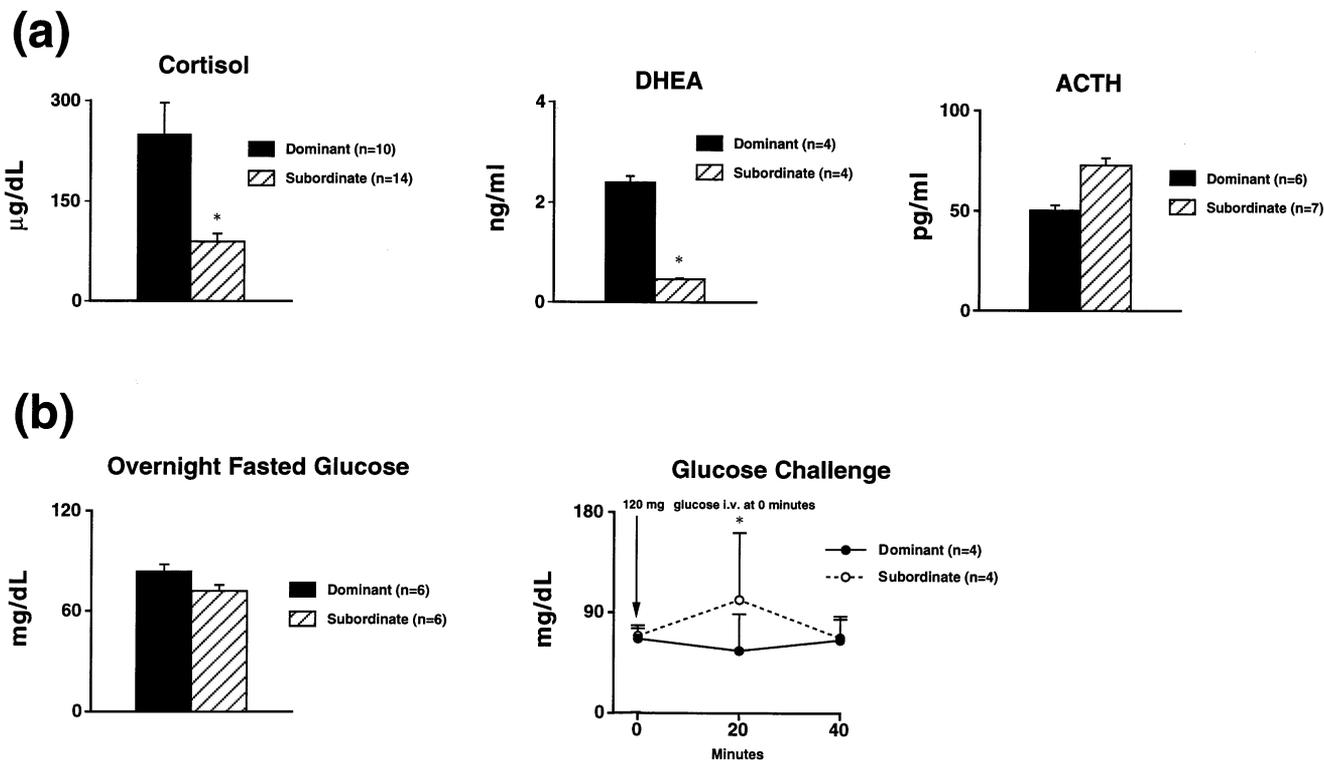


Fig. 5. (a) Antilog of the transformed mean (+95% confidence limit) of plasma concentrations of cortisol, DHEA and ACTH in 4–10 dominant female marmosets in the early to mid-follicular phase of the ovarian cycle and 4–14 anovulatory subordinate females. \*  $P < 0.05$  versus the dominant females, Student's  $t$ -test. (b) Antilog of the transformed mean (+95% confidence limit) of plasma concentrations of glucose following an overnight fast with or without a subsequent intravenous infusion of 120 mg of glucose in 4–6 dominant female marmosets in the early to mid-follicular phase of the ovarian cycle and in 4–6 anovulatory subordinate females. \*  $P < 0.05$  versus dominant females at 20 min and versus subordinate females at 0 min; Post-hoc testing following significant status  $\times$  time interaction ( $P < 0.05$ ) in a two-way ANOVA for repeated measures.

## 6. Adrenocortical and metabolic polyethism

Because subordinate female marmosets exhibited such pronounced reproductive polyethism, we examined two physiological components regulating homeostasis to determine if subordinate females demonstrated any metabolic accommodation of their hypoestrogenic infertile state.

### 6.1. Hypothalamic-pituitary-adrenal (HPA) axis

Within 5–8 weeks of becoming subordinate in a social group, female marmosets exhibit marked decreases in circulating cortisol concentrations (Fig. 5a; [10,76,79]). No such reductions in cortisol are noted in dominant females; thus, subordinate females in well established groups have significantly lower cortisol levels than dominants. This dichotomy in circulating cortisol concentrations was due to subordination per se and was not simply a consequence of decreased plasma estradiol levels secondary to ovulatory suppression in subordinate females: cortisol levels in hypoestrogenic, ovariectomized, pair-housed females did not fall to the same low level as in subordinates [10]. Circulating levels

of DHEA were also decreased in subordinate females (Fig. 5a). Taken together with the cortisol findings, this suggests that social subordination causes an inhibition of the steroidogenic activity of both the zona fasciculata and zona reticularis of the adrenal cortex in female marmosets.

The apparent reduction in steroidogenic output from the adrenal glands cannot be attributed to reduced pituitary secretion of ACTH, as circulating levels of ACTH do not differ between subordinate and dominant females (Fig. 5a; [78]). The reduced cortisol levels, however, may be due to decreased responsiveness of the adrenal cortex to ACTH stimulation, as dexamethasone-treated subordinate females showed poorer cortisol responses to an intravenous injection of ACTH<sub>1–39</sub> than similarly treated dominant females in the early to mid-follicular phase (Saltzman, W.; Schultz-Darken, N.J.; Abbott, D.H.; unpublished data).

Reduced HPA activity in subordinate female marmosets contrasts with findings from many competitively breeding species, in which subordinate individuals show elevated glucocorticoid levels as compared to dominants [10,76,79]. Interestingly, in several other coopera-

tively breeding species, reproductive suppression appears to be associated with either reduced glucocorticoid levels, e.g. African wild dogs, *Lycaon pictus* [24]; dwarf mongoose, *Helogale parvula* [24]; Florida scrub jay, *Aphelocoma c. coerulescens* [85], or with glucocorticoid levels similar to those found in dominants, e.g. cotton-top tamarin, *Saguinus oedipus* [106]; black tufted-ear marmoset, *C. kuhli* [90]; Harris' hawk, *Parabuteo unicinctus* [63]. Thus, heightened HPA activity cannot be invoked as a cause of reproductive suppression in subordinate female marmosets and other cooperative breeders.

## 6.2. Glucose homeodynamics

Adrenal cortisol secretion in primates plays an important homeostatic role in regulating gluconeogenesis from the liver [68]. In human syndromes of chronically lowered adrenal cortisol secretion, such as Addison's disease, there are noticeable deficits in glucose homeodynamics [68]. Hypocortisolemic subordinate female marmosets, however, appear to be able to maintain euglycemia, since plasma glucose concentrations after an overnight fast were comparable to those of dominant females with normal cortisol levels (Fig. 5b). This short-term food deprivation tested the animals' ability to maintain normal circulating levels of glucose in the absence of sustenance. Nevertheless, when the marmosets were given an intravenous bolus of glucose following an overnight fast, to test their ability to take up and clear excess glucose from the circulation, subordinate females were slower in doing so than dominant females (Fig. 5b). The dominant females cleared excess glucose from their circulation within 20 min, whereas, the subordinates took 20–40 min to do so. This apparent difference between dominant and subordinate females in their ability to acutely regulate glucose uptake and clearance during an infusion of glucose suggests that compensatory metabolic processes [25] may not completely ameliorate the detrimental impact of chronic hypocortisolemia on glucose homeodynamics in subordinates.

## 7. Discussion

Subordinate female common marmosets exhibit a constellation of behavioral, neuroendocrinological and physiological differences from dominant females. The characteristics exhibited by subordinate female marmosets are strikingly similar to specializations made to accommodate subordinate status in social insects (Table 1) occupying comparable positions on the eusociality continuum proposed by Sherman and colleagues [86] (Fig. 1). According to the literature on invertebrate cooperative breeding, such adaptations to subordinate

status made by female marmosets should be considered as examples of polyethism, even if they are reversible by changes in social status [16]. In some of the social insects (e.g. paper wasps, Table 1), reversals in female status can occur naturally or can be hormonally induced experimentally. It is intriguing to speculate that specialized inhibitory neuroendocrine mechanisms are responsible for subordination-induced ovarian inhibition in these social insects, similar to our findings in common marmosets [10]. Such environmentally sensitive neuroendocrine mechanisms might be as labile as those found in female marmosets, to enable individuals to readily take advantage of appropriate changes in the social environment, such as the loss of the dominant breeding female, and permit previously subordinate females to effectively engage in competition with conspecifics for the vacant breeding position.

High degrees of intragroup relatedness may contribute significantly [42] to the extreme degrees of polyethism (phenotypically determined differences) and polymorphism (genetically determined differences) shown by some animals in their exquisite evolution of caste-structured eusocial societies (e.g. honey bees, yellow-jacket wasps, naked mole-rat (*Heterocephalus glaber*), Damaraland mole-rat (*Cryptomys damarensis*); Fig. 1). Little is known about intragroup relatedness in free-living groups of common marmosets, but an initial study of matrilineal mitochondrial D-loop DNA from groups at Nisia Floresta in northeastern Brazil suggests an average intragroup relatedness of less than 0.5 (C.G. Faulkes et al., personal communication). These molecular genetic studies of free-living marmosets also suggest that the breeding male in at least two social groups is genetically dissimilar to the other group members [35].

Since cooperatively breeding marmosets and some of the lower social insects appear to exhibit a number of analogous phenotypic and genotypic traits, such shared attributes may well reflect convergent adaptation to environmental conditions inauspicious for dispersal and independent breeding. Future comparative studies of behavioral, neuroendocrinological and physiological attributes of female subordinates in cooperatively breeding species may well reveal characteristics and mechanisms similar to those found in subordinate female marmosets, and would provide further support for considering cooperatively breeding vertebrates and invertebrates in an inclusive eusocial continuum [86]. In this regard, comparative neuroendocrinology provides a powerful tool in furthering our understanding of the proximate regulation of reproductive success in highly social species and may provide unique perspective and insight into both the neural mechanisms mediating environmental control of the hypothalamic-pituitary-gonadal axis and the intrinsic factors shaping the evolution of sociality.

Table 1  
Comparisons of behavioral, reproductive and non-reproductive polyethism characteristics of female common marmosets to those found in females in three groups of social insects exhibiting a similar reproductive skew to marmosets (Fig. 1)

Female characteristic	Marmosets <sup>a</sup>	Halictid bees <sup>b</sup>	Paper wasps <sup>c</sup>	Damp-wood termites <sup>d</sup>
<b>Behavior</b>				
A single, breeding female behaviorally dominates non-breeding (subordinate) females	Yes	Yes	Yes	Yes
Sexual behavior is more frequently exhibited by the dominant female	Yes	Yes <sup>e</sup>	Yes	Yes
Subordinate females preferentially forage in comparison to the dominant female	No	Yes	Yes	Yes
Subordinate females preferentially exhibit territorial defense in comparison to the dominant female	Yes	Yes	Yes	Yes
Subordinate females play important roles in raising and foraging for the dominant female's offspring	Yes	Yes	Yes	Yes
<b>Reproductive function</b>				
Usually only one dominant female breeds	Yes	Yes <sup>e</sup>	Yes	Yes
The dominant female inhibits ovarian function in subordinates	Yes	Some	Yes	Yes
Specific neuroendocrine mechanisms (not stress) regulate ovarian inhibition in subordinates	Yes	? <sup>f</sup>	Possibly <sup>g</sup>	? <sup>f</sup>
Olfactory, visual and/or behavioral cues from the dominant female mediate ovarian inhibition in subordinates	Yes	Yes	Yes	Yes
Subordinate females can replace the dominant female as the breeding female, if the dominant is lost/removed	Yes <sup>h</sup>	Yes	Yes	Some <sup>e</sup>
<b>Non-reproductive polyethism</b>				
Dominant breeding females are larger than subordinate females	No	Yes	No <sup>j</sup>	Yes
Subordinate females form physically differentiated casts	No	No <sup>k</sup>	Slightly	Yes
Subordinate females are physiologically distinct from dominant females	Yes	? <sup>f</sup>	? <sup>f</sup>	? <sup>f</sup>

<sup>a</sup> This paper [40,97]; C. Lazaro-Parea and C.T. Snowdon, personal communication [10].

<sup>b</sup> [16,65].

<sup>c</sup> [16,93].

<sup>d</sup> [16,67].

<sup>e</sup> Except for seasonal production of males [16].

<sup>f</sup> Unknown.

<sup>g</sup> Inhibitory neuroendocrine mechanisms have been demonstrated in subordinate females and are reversed by treatment with juvenile hormone or 20-hydroxyecdysone [72].

<sup>h</sup> Except possibly in natal families which only contain 1<sup>0</sup> relatives [77].

<sup>i</sup> Except for 'soldiers' [16].

<sup>j</sup> Except in newly-established nests [16].

<sup>k</sup> Except in very large colonies [16].

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