## RESEARCH ARTICLE

# Influence of the Mother's Reproductive State on the Hormonal Status of Daughters in Marmosets (*Callithrix kuhlii*)

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Behavioral and endocrine suppression of reproduction in subordinate females produces the high reproductive skew that characterizes callitrichid primate mating systems. Snowdon et al. [American Journal of Primatology 31:11–21, 1993] reported that the eldest daughters in tamarin families exhibit further endocrinological suppression immediately following the birth of siblings, and suggested that dominant females exert greater control over subordinate endocrinology during this energetically challenging phase of reproduction. We monitored the endocrine status of five Wied's black tufted-ear marmoset daughters before and after their mother delivered infants by measuring concentrations of urinary estradiol ($E_2$), pregnanediol glucuronide (PdG), testosterone (T), and cortisol (CORT). Samples were collected from marmoset daughters 4 weeks prior to and 9 weeks following three consecutive sibling-litter births when the daughters were prepubertal (M=6.1 months of age), peripubertal (M=11.9 months), and postpubertal (M=17.6 months). The birth of infants was associated with reduced ovarian steroid excretion only in the prepubertal daughters. In contrast, ovarian steroid levels tended to increase in the postpubertal daughters. Urinary $E_2$ and T levels in the postpubertal daughters were 73.8% and 37.6% higher, respectively, in the 3 weeks following the birth of infants, relative to prepartum levels. In addition, peak urinary PdG concentrations in peri- and postpubertal daughters were equivalent to luteal phase concentrations in nonpregnant, breeding adult females, and all of the peri- and postpubertal daughters showed clear ovulatory cycles. Cortisol excretion did not change in response to the reproductive status of the

mother, nor did the concentrations change across age. Our data suggest that marmoset daughters of potential breeding age are not hormonally suppressed during the mother's peripartum period or her return to fertility. These findings provide an additional example of species diversity in the social regulation of reproduction in callitrichid primates. Am. J. Primatol. 64:29–37, 2004. © 2004 Wiley-Liss, Inc.

## INTRODUCTION

In callitrichid social groups, breeding activity is typically limited to a single adult male and female [French, 1997]. The mechanism underlying this high reproductive skew in males appears to be primarily behavioral in nature, since testosterone levels do not differ dramatically between breeders and nonbreeders, and sons removed from natal family groups readily mate with unrelated female partners [Baker et al., 1999; Ginther et al., 2001]. However, reproductive suppression in subordinate females is mediated by a complex combination of behavioral and endocrine mechanisms that differ by species and social context. Although captive golden lion tamarin (*Leontopithecus rosalia*) daughters show normal ovarian cycles, high levels of aggression from breeding females can prevent reproduction [French et al., 2002]. In contrast, daughters in captive cotton-top tamarin (*Saguinus oedipus*) families do not exhibit ovarian cyclicity while they are in their natal family group [French et al., 1984; Ziegler et al., 1987b]. In marmosets, there is clear evidence of physiological suppression of subordinate females in groups comprised of unrelated males and females [e.g., Abbott, 1993]; however, in family groups, one or more daughters may escape suppression and commence ovulatory cycles [Carlson et al., 1997; Saltzman et al., 1997a, b; Smith et al., 1997; Ziegler & Sousa, 2002]. Regardless of its expression, a prominent functional interpretation of reproductive suppression in family-living callitrichids involves the minimization of intrasexual reproductive competition within the group [Abbott, 1993; French, 1997].

In marmosets and tamarins, breeding females return to fertility and conceive within 2–3 weeks after parturition [French et al., 1996; Ziegler et al., 1987a]. The early return to fertility places the breeding female in direct competition with other potential breeding females, including daughters, for the resources necessary to sustain pregnancy, and for the postpartum resources necessary for care of the subsequent litter, including the alloparental care provided by older offspring [Digby, 1995]. To the extent that breeding females can regulate reproductive function in daughters via olfactory and behavioral cues [French, 1997], mothers might be expected to exert greater control over reproduction in daughters during the postpartum period. The eldest daughters in cotton-top tamarin families do, in fact, show further reproductive suppression following the birth of siblings, with decreased levels of urinary estrone glucuronide ($E_1C$) and luteinizing hormone (LH) during the first 3 weeks postpartum [Snowdon et al., 1993]. Because daughters in this species are already anovulatory, however, they pose little threat to the reproductive hegemony of the breeding female. For callitrichid species in which daughters can and do exhibit ovulatory cycles in their natal groups (e.g., marmosets*)*, suppression of nonbreeder reproduction during

the postpartum period should be particularly pronounced if the phenomenon reflects avoidance of reproductive competition.

In this study, we investigated patterns of urinary hormone excretion in pre-, peri-, and postpubertal female marmosets (*Callithrix kuhlii*) 4 weeks prior to and 9 weeks following the birth of three successive sibling-litters. We measured ovarian steroid activity using patterns of urinary estradiol ($E_2$) and pregnanediol glucuronide (PdG). Urinary cortisol (CORT) excretion was measured to monitor hypothalamic-pituitary-adrenal axis (HPA) activity. Finally, we measured urinary testosterone (T) because there is accumulating evidence that androgens may be important modulators of sexual and aggressive behavior in females [Christiansen, 2001], and evidence that excreted androgens in female marmosets reflect variations in circulating T [Armstrong et al., 2003]. $E_2$, PdG, and T concentrations were expected to increase significantly as the daughters developed through the pubertal stages. Concentrations of cortisol were also expected to increase in correspondence with increases in ovarian activity [Saltzman et al., 1998]. To the extent that breeding females exert control over reproductive potential in their daughters, we also expected to see significant decreases in sex steroid levels in the weeks immediately following the birth of infants, particularly in postpubertal daughters. In contrast, significant increases in cortisol excretion were expected after the birth of a sibling, to the degree that the arrival of new infants and return to fertility in the mother would be potent social stressors for the daughters [Smith&French, 1997b; Ziegler et al., 1995].

## MATERIALS AND METHODS

The subjects of this study were five Wied's black tufted-ear marmoset (*C. kuhlii*) daughters that were housed with their natal family groups at the University of Nebraska at Omaha's Callitrichid Research Center (Table I). (For a description of the housing and husbandry practices used, see French et al. [1996].) The females were sampled for three successive sibling-litters: one in which they were prepubertal (M=6.1 months old), one in which they were peripubertal (M=11.9 months old), and one in which they were postpubertal (M=17.6 months old; categorization based on Smith et al. [1997]).

Urine samples were collected between 0600 and 0800 hr from all subjects one to five times per week, with an average ($\pm$SD) of 1.86 ($\pm$1.18) samples each week, by means of a previously described noninvasive technique [French et al., 1996]. The samples were stored at $-20°C$ until they were assayed. Enzyme immuno-

**TABLE I. Age (in Months) and Litter Composition for Daughters at Pre-, Peri- and Postpubertal Stages of Development**

| Subject ID | Twin sibling | Family rank | Prepubertal | | Peripubertal | | Postpubertal | |
|---|---|---|---|---|---|---|---|---|
| | | | Subject age | Sibling litter | Subject Age | Sibling litter | Subject age | Sibling litter |
| In | Male twin | d1 | 4.9 | MF | 9.9 | FM | 14.9 | M |
| It | Male twin | d1 | 5.0 | FM | 11.9 | FF | 18.6 | MM |
| Xe | Male twin | d2 | 6.9 | FF | 13.5 | MM | 20.0 | FF |
| Vo | Male twin | d1 | 8.8 | FM | 13.8 | F | 18.6 | F |
| De | None | d1 | 4.8 | F | 10.5 | FF | 16.2 | FM |

d1, eldest daughter; d2, second eldest daughter.

assays were utilized to monitor hormone concentrations after enzyme hydrolysis and ether extraction ($E_2$ [Fite&French, 2000] and T [Nunes et al., 2000]) or via direct assay (PdG [French et al., 1996] and CORT [Smith&French, 1997a]). Recovery of $^3$H-labeled steroid after extraction was 57.7% for $E_2$, and 63.1% for T. The intra- and interassay coefficients of variation for all steroid assays were $<7.6\%$ and 15.7%, respectively. Creatinine was measured by a modified Jaffé end-point assay [French et al., 1996], and all hormone concentrations were divided by the creatinine concentrations to control for variable fluid intake and output.

Hormone values for each daughter were averaged for the 4 weeks prior to the birth of siblings to establish a prepartum baseline, and in three 3-week blocks following the birth of siblings, encompassing a majority of the maternal lactation period in *Callithrix* [Missler et al., 1992; Tardif et al., 2001]) and maternal infant-care effort [Nunes et al., 2001]. To assess maturational effects across the three sibling-litter births, we conducted a completely within-subjects, two-way analysis of variance (ANOVA; litter (n=3) × weeks (n=4)) on the urinary excretion profiles for $E_2$, T, PdG, and CORT. Planned within-subjects, one-way ANOVAs were used to assess changes in steroid excretion across the pre- and postpartum phases for each developmental stage. To assess the ovulatory capacity of daughters, we compared the peak PdG concentrations in daughters at each age with luteal-phase peak PdG concentrations in breeding adult females (n=6 females) known to be cycling but not pregnant. We conducted post-hoc analyses using the least-significant difference (LSD) test.

## RESULTS

Although the sample size was limited, we noted significant increases in levels of excreted sex steroids across consecutive sibling-litter births (Fig. 1) that coincided with the developmental stages of the daughters ($E_2$: $F(2,8)=15.74$, $P=0.002$; T: $F(2,8)=10.01$, $P=0.007$; PdG: $F(2,8)=16.14$, $P=0.002$). All three profiles were characterized by extremely low mean levels in prepubertal daughters, and a slight rise in hormone levels in peripubertal daughters (LSD, $E_2$: NS; T: $P=0.017$; PdG: $P=0.021$). The mean levels continued to rise as the daughters became postpubertal (LSD, $E_2$: $P=0.014$; T: NS; PdG: $P=0.017$). All increases in sex steroid concentrations between pre- and postpubertal stage daughters were significant (LSD, $E_2$: $P=0.010$; T: $P=0.024$; PdG: $P=0.015$). There was also clear evidence that peri- and postpubertal daughters displayed one or more ovulatory cycles during the peripartum period of their mother, marked by luteal phase PdG concentrations of $\geq 10$ µg/mg Cr (see Fig. 2). ANOVA and subsequent post-hoc tests revealed no significant differences in peak luteal PdG concentrations among peripubertal daughters, postpubertal daughters, and cycling adult females (13.4 $\pm$ 2.0 µg/mg Cr, 14.1 $\pm$ 1.6 µg/mg Cr, and 12.1 $\pm$ 1.1 µg/mg Cr, respectively). However, prepubertal daughters exhibited significantly lower maximum PdG concentrations compared to all other females (2.1 $\pm$ 0.7 µg/mg Cr; $F(3,17)=15.5$, $P<0.001$). In contrast to sex steroids, concentrations of excreted cortisol did not significantly change across the developmental stages of the daughters ($F(2,8)=2.973$, NS).

The birth of siblings had little influence on hormone excretion across the developmental stages of the daughters. Prepubertal daughters exhibited a nonsignificant pre- to postpartum decrease in $E_2$, T, and CORT levels across all three 3-week blocks ($F(3,12)<1.20$; NS). However, prepubertal daughters exhibited significant changes in pre- to postpartum levels of PdG ($F(3,12)=4.37$,
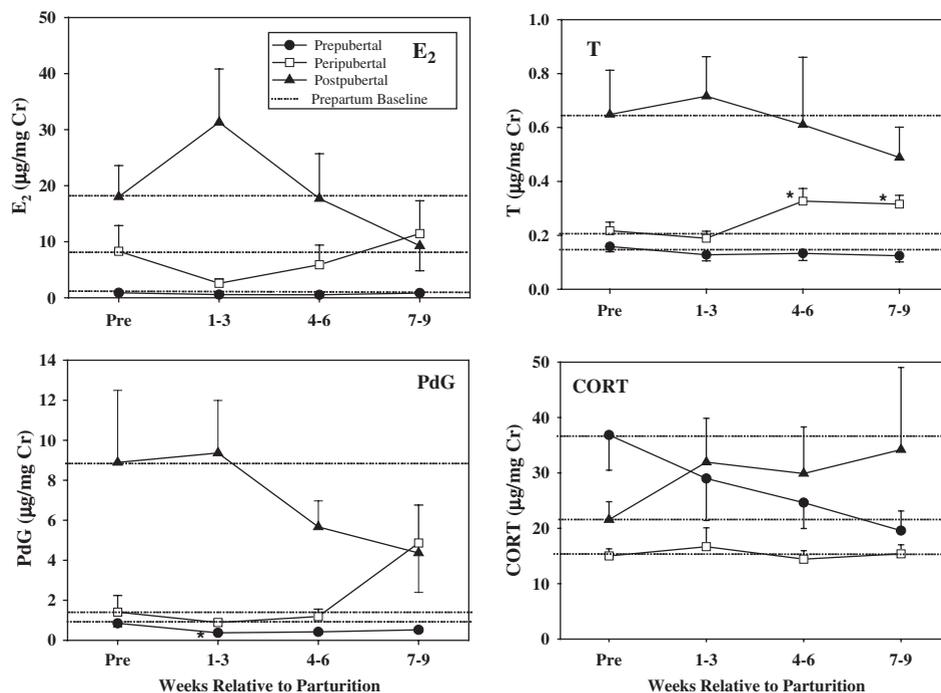
Fig. 1. Mean $\pm$ SEM of urinary estradiol-17$\beta$ ($E_2$), testosterone (T), pregnanediol glucuronide (PdG), and cortisol (CORT) for five Wied's black tufted-ear marmoset daughters over the 4 weeks prior to (pre) and 9 weeks following (1–3, 4–6, 7–9) the birth of three consecutive sibling-litters. *denotes a significant change from prepartum baseline.

$P = 0.027$). A decrease from prepartum levels of PdG was evident for all three postpartum blocks, although only the 55.8% decrease for weeks 1–3 was significant (LSD, $P < 0.05$). Peripubertal daughters did not exhibit significant changes in PdG, $E_2$, and CORT levels ($E_2$: $F(3,12) = 1.19$, (NS); PdG: $F(3,12) = 2.65$, (NS)). In contrast, peripubertal daughters showed significant changes from pre- to postpartum concentrations of urinary T ($F(3,12) = 7.10$, $P = 0.005$). T levels decreased nonsignificantly from prepartum values during weeks 1–3 following a birth (LSD, $P > 0.05$), but significantly increased 50.3% over weeks 4–6 and 45.3% over weeks 7–9 (LSD, $P > 0.05$). Postpubertal daughters exhibited increases of 73.8% $E_2$, 37.6% T, 5.3% PdG, and 48.3% CORT from prepartum levels during weeks 1–3. However, a statistical analysis revealed that these changes, and those of the subsequent weeks, were not significant ($F(3,12) < 1.71$, NS).

## DISCUSSION

Because reproductive suppression in family-living callitrichids involves the minimization of intrasexual reproductive competition within the group, it has been suggested that the breeding female may exert control over her daughters' reproduction during the time of postpartum ovulation, when the breeding position is highly vulnerable [Lazaro-Perea et al., 2000]. Endocrine profiles obtained in a previous study of subordinate tamarins [Snowdon et al., 1993] were consistent with this prediction, but our results from marmosets were not. For the
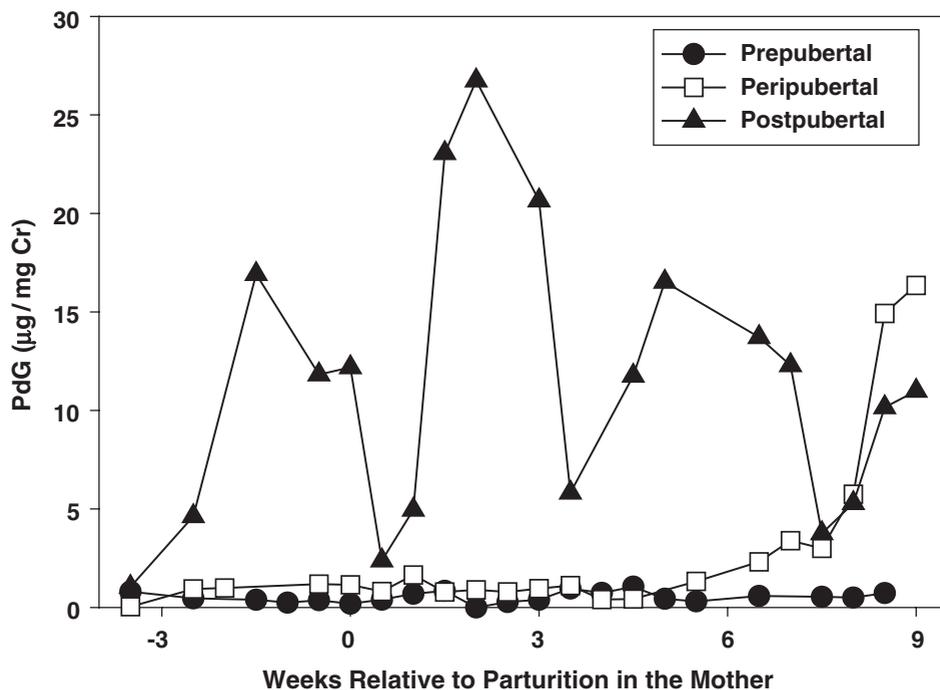
Fig. 2. Representative profile of PdG excretion in a female Wied's black tufted-ear marmoset over the 4 weeks prior to and 9 weeks following the birth of three consecutive sibling-litters, demonstrating luteal phase rises in PdG during the peripubertal (weeks 8–9) and postpubertal (weeks $-2$ to $-1$, $+2$ to $+3$, and $+5$ to $+6$) stages.

marmoset daughters in our study, there were no systematic reductions in ovarian hormone concentrations across the immediate postpartum period in the mother. As predicted, maturational effects on ovarian activity were observed in marmoset daughters as they passed through the developmental stages of puberty [Smith et al., 1997]; however, we failed to detect the expected corresponding increase in hypothalamic-pituitary-adrenal axis activity [Saltzman et al., 1998].

The only finding consistent with the predictions of mother–daughter reproductive competition was the reduction in excreted PdG in the first 3 weeks postpartum in prepubertal daughters. However, the concentrations of PdG are exceedingly low in prepubertal daughters, and even maximum PdG concentrations in these daughters ($2.1 \pm 0.7$ µg/mg Cr) are characteristic of anovulatory adult females [Smith et al., 1997]. It is likely, therefore, that the significant reduction in PdG exhibited by prepubertal daughters does not reflect a functional change in reproductive potential. In contrast to our predictions, we identified significant increases in T in daughters exposed to a second birth of siblings. Although this study did not address the origin of elevated excreted T, previous work on a variety of female mammals (e.g., dogs, baboons, and human females) reveals that ovarian (especially luteal) tissue is a prominent source of androgen [e.g., Castracane et al., 1998]. The functional significance of elevated T may be that it facilitates aggressive and sexual behavior in developing females. Other steroid levels tended to increase (73.8% in $E_2$, 37.6% in T, and 5.3% in PdG) in postpubertal daughters after the birth of siblings; however, these changes in steroid excretion were not significant. Interestingly, both peri- and postpubertal

daughters exhibited peak PdG concentrations during the peripartum period of their mother that were similar to those of nonpregnant, breeding adult females, providing quantitative evidence that the mother's reproductive state has little impact on reproductive function in her older daughters.

Although there were numerous similarities in reproductive parameters between marmosets and tamarins, including suppression of daughters, twin litter births, and a fertile postpartum ovulation, this study also identified important interspecific differences in the timing and intensity of suppression following the birth of siblings. Reproduction may be more costly for tamarins than for marmosets, since tamarins have a longer periods of gestation [French&Fite, 1999] and infant dependence [Snowdon, 1996] than marmosets. Further, observations of free-ranging populations suggest that marmosets have greater mean group sizes than tamarins [Mittermeier et al., 1988], potentially providing breeding female marmosets with more alloparental assistance than may be available to tamarins. These differences may place a greater premium on dominant control of subordinate reproduction in tamarins, and may account for the divergent endocrine responses to maternal reproductive state in daughters. Moreover, this divergence in daughters' endocrine responses may help explain the more frequent observations of plural breeding females in marmosets than in tamarins [French, 1997]. However, further research is necessary to determine the ultimate causes and underlying mechanisms of the observed variation in the timing and intensity of suppression in callitrichid daughters.

There are two possible explanations for the absence of further suppression and a trend toward increased steroid activity following the birth of siblings in marmoset daughters. First, under conditions of abundant resources, the suppression of daughters may be relaxed. Because marmosets are able to give birth to twin litters approximately every 6 months, family groups with sexually mature daughters (12–18 mo) may be saturated with alloparental help. Therefore, a lack of further hormonal suppression at this time may facilitate voluntary emigration of daughters from the natal group, or increase the inclusive fitness of the breeder by allowing a daughter to produce offspring. Second, daughters may increase their resistance to suppression following the birth of infants in preparation for emigration or to take over the breeding position in the natal group. In wild populations of common marmosets, infant birth and conception appear to be socially transitional times, which are marked by the emigration of subordinates and frequent loss of breeders [Lazaro-Perea et al., 2001]. Among captive marmosets, some mature daughters escape from suppression while in their natal groups [Smith et al., 1997; Saltzman et al., 1997a], but most fail to reproduce [Saltzman et al., 1997a]. However, changes in the social environment rapidly induce ovarian activity and sexual behaviors in daughters [Saltzman et al., 1997b; Ziegler&Sousa, 2002]. This swift adaptation to alterations in the daughter's social environment could be extremely beneficial during times of forced or voluntary emigration, or the replacement of resident breeders. Thus, the absence of further suppression and a trend toward increasing steroid levels immediately following the birth of siblings in postpubertal daughters may reflect the priming that allows for this rapid response to social change and successful transition into a breeding role.

Our data present evidence that postpubertal marmoset daughters are not more hormonally suppressed following the birth of siblings, and exhibit a trend of increased steroid production, allowing for greater adaptability to the social change that often follows parturition and the mother's return to fertility. These data provide an example of species diversity in the social regulation of

reproduction in callitrichid primates, and add support to the growing consensus that marmoset mothers have little suppressive influence on reproductive function in their daughters [Saltzman et al., 1997a; Ziegler&Sousa, 2002].

## REFERENCES

Abbott DH. 1993. Social conflict and reproductive suppression in marmoset and tamarin monkeys. In: Mendoza SP, editor. Primate social conflict. Albany: SUNY Press. p 331–372.

Armstrong D, French JA, Puffer AM. 2003. Testosterone administration alters urinary excretion of T and $E_2$ in female marmosets. Am J Primatol 60:110.

Baker JV, Abbott DH, Saltzman W. 1999. Social determinants of reproductive failure in male common marmosets housed with their natal family. Anim Behav 58: 501–513.

Carlson AA, Ziegler TE, Snowdon CT. 1997. Ovarian function of pygmy marmoset daughters (*Cebella pygmaea*) in intact and motherless families. Am J Primatol 43: 347–355.

Castracane VD, Steward DR, Gimpel T, Overstreet, JW, Lasley BL. 1998. Maternal serum androgens in human pregnancy: early increases within the cycle of conception. Hum Reprod 13:460–464.

Christiansen K. 2001. Behavioural effects of androgen in men and women. J Endocrinol 170:39–48.

Digby LJ. 1995. Infant care, infanticide, and female reproductive strategies in polygynous groups of common marmosets (*Callithrix jacchus*). Behav Ecol Sociobiol 37: 51–61.

Fite JE, French JA. 2000. Pre- and postpartum sex steriods in female marmosets (*Callithrix kuhlii*): is there a link with infant survivorship and maternal behavior? Horm Behav 38:1–12.

French JA, Abbot DH, Snowdon CT. 1984. The effect of social environment on estrogen excretion, scent marking and sociosexual behavior in tamarins (*Saguinus oedipus*). Am J Primatol 6:155–167.

French JA, Brewer KJ, Schaffner CM, Schalley J, Hightower-Merritt D, Smith TE, Bell SM. 1996. Urinary steroid and gonadotropin excretion across the reproductive cycle in female Wied's black-tufted-ear marmosets (*Callithrix kuhlii*). Am J Primatol 40:231–246.

French JA. 1997. Proximate regulations of singular breeding in callitrichid primates. In: Solomon NG, French JA, editors. Cooperative breeding in mammals. Cambridge: Cambridge University Press. p 34–75.

French JA, Fite JE. 1999. Reproduction in callitrichid primates. In: Sodoro V, Saunders N, editors. Callitrichid husbandry manual. Brookfield, IL: AZA Neotropical TAG.

French JA, De Vleeschouwer K, Bales K, Heistermann M. 2002. Lion tamarin reproductive biology. In: Santos IB, Santos IB, editors. Biology and conservation of lion tamarins: twenty-five years of research. Washington, DC: Smithsonian Press. p 133–156.

Ginther AJ, Ziegler TE, Snowdon CT. 2001. Reproductive biology of captive male cotton-top tamarin monkeys as a function of social environment. Anim Behav 61:65–78.

Lazaro-Perea C, Castro CSS, Harrison R, Araujo A, Arruda MF, Snowdon CT. 2000. Behavioral and demographic changes following the loss of the breeding female in cooperatively breeding marmosets. Behav Ecol Sociobiol 48:137–146.

Lazaro-Perea C, Castro CSS, Harrison R, Araujo A, Arruda MF, Snowdon CT. 2001. Intergroup interactions in wild common marmosets, *Callthrix jacchus*: territorial defence and assessment of neighbors. Anim Behav 62:11–21.

Missler M, Wolff J, Rothe H, Heger W, Merker H-J, Treiber A, Scheid R, Crook G. 1992.

Developmental biology of the common marmoset: proposal for a ''postnatal staging.'' J Med Primatol 21:285–298.

Mittermeier RA, Rylands AB, Coimbra-Filho AF, Fonseca GAB. 1988. Ecology and behavior of neotropical primates. Washington, DC: World Wildlife Fund. p 610.

Nunes S, Fite JE, French JA. 2000. Variation in steriod hormones associated with infant-care behaviour and experience in male marmosets (*Callithrix kuhlii*). Anim Behav 60:857–865.

Nunes S, Fite JE, Patera KJ, French JA. 2001. Interactions among parental behavior, steriod hormones, and parental experience in male marmosets. Horm Behav 39: 70–82.

Saltzman W, Schultz-Darken NJ, Abbot DH. 1997a. Familial influences on ovulatory function in common marmosets (*Callithrix jacchus*). Am J Primatol 41:159–177.

Saltzman W, Severin JM, Schultz-Darken NJ, Abbott DH. 1997b. Behavioral and social correlates of escape from suppression of ovulation in female common marmosets housed with the natal family. Am J Primatol 41:1–21.

Saltzman W, Schultz-Darken NJ, Wegner FH, Wittwer DJ, Abbott DH. 1998. Suppression of cortisol levels in subordinate female marmosets: reproductive and social contributions. Horm Behav 33:58–74.

Smith TE, French JA. 1997a. Psychosocial stress and urinary cortisol excretion in marmoset monkeys (*Callithrix kuhlii*). Physiol Behav 62:225–2322.

Smith TE, French JA. 1997b. Social and reproductive conditions modulate urinary cortisol excretion in black tufted-ear marmosets (*Callithrix kuhlii*). Am J Primatol 42:253–267.

Smith TE, Schaffner CM, French JA. 1997. Social and developmental influences of reproductive function in female Wied's black tufted-ear marmosets (*Callithrix kuhlii*). Horm Behav 31:159–168.

Snowdon CT, Ziegler TE, Widowski TM. 1993. Further hormonal suppression of eldest daughter cotton-top tamarins following the birth of infants. Am J Primatol 31:11–21.

Snowdon CT. 1996. Parental care in cooperatively breeding species. In: Rosenblatt JS, Snowdon CT, editors. Parental care: evolution, mechanisms and adaptive significance. San Diego: Academic Press. p 643–689.

Tardif SD, Power M, Oftedal OT, Power RA, Layne DG. 2001. Lactation, maternal behavior and infant growth in common marmoset monkeys (*Callithrix jacchus*): effects of maternal size and litter size. Behav Ecol Sociobiol 51:17–25.

Ziegler TE, Bridson WE, Snowdon CT, Eman S. 1987a. Urinary gonadotropin and estrogen excretion during the postpartum estrus, conception and pregnancy in the cotton-top tamarin (*Saguinus oedipus oedipus*). Am J Primatol 12:127–140.

Ziegler TE, Savage A, Scheffler G, Snowdon CT. 1987b. The endocrinology of puberty and reproductive functioning in female cotton-top tamarins (*Saguinus oedipus*) under varying social conditions. Biol Reprod 37:618–627.

Ziegler TE, Scheffler G, Snowdon CT. 1995. The relationship of cortisol levels to social environment and reproductive functioning in female cotton-top tamarins (*S. oedipus*). Horm Behav 29:407–424.

Ziegler TE, Sousa MB. 2002. Parent-daughter relationships and social controls on fertility in female common marmosets, *Callithrix jacchus*. Horm Behav 42:356–367.