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RESEARCH ARTICLE

Social and Developmental Influences on Urinary Androgen Levels in Young Male White-Faced Marmosets (*Callithrix geoffroyi*)

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Callitrichine primates (marmosets and tamarins) often remain in their natal groups beyond the time of sexual maturity. Although studies have characterized the development of female reproductive function in callitrichine offspring, less is known about the male reproductive development. To document reproductive development in male marmosets, we monitored urinary androgen (uA) excretion in males housed in a captive colony of white-faced marmosets (*Callithrix geoffroyi*). Young male marmosets showed relatively low and stable rates of uA excretion early in life, with elevated production at the end of the juvenile period (9–10 months) and again at the onset of adulthood (16 months). uA levels of adult breeding males were also measured to compare to adult-aged sons. Although breeding males did have higher uA levels than their adult-aged sons, these differences did not reach conventional levels of significance. Evidence from some other reports has suggested that androgen levels of males in other species are influenced by social factors, such as the presence of a sexually receptive female or of dependent offspring. In this study, however, uA levels did not vary, based on their mothers' pregnancy status or the presence of younger siblings in the natal group. Patterns of androgen excretion in the white-faced marmoset roughly reflect those of other callitrichine species. Furthermore, unlike callitrichine daughters, gonadal activity in sons does not seem to be sensitive to within-group social cues. Am. J. Primatol. 71:1–8, 2010.

Key words: testosterone; male sexual development; pregnancy status; social status; younger siblings presence

INTRODUCTION

The diversity in morphology, physiology, ecology, and sociality across the primate order has offered an excellent opportunity to study the various factors that influence developmental trajectories. Sexual development in primates is particularly interesting in that it occurs over an extended period of time compared with many other mammalian species [reviewed in Plant, 1994]. In male primates, patterns of steroid production are characterized by relatively high levels of androgen immediately after birth, a subsequent decline, and a period of relative quiescence [cf., Chemes, 2001; Kelnar et al., 2002], followed by a gradual increase that continues until plateauing in adulthood [rhesus macaque (*Macaca mulatta*): Mann et al., 1998; crab-eating macaque (*Macaca fasicularis*): Steiner & Bremner, 1981; chimpanzee (*Pan troglodytes*): Marson et al., 1991; Martin et al., 1977; human (*Homo sapiens sapiens*): Andersson et al., 1998; Forest et al., 1974; Winter et al., 1976; common marmoset (*Callithrix jacchus*): Abbott & Hearn, 1978; Dixson, 1986; cotton-top tamarin (*Saguinus oedipus*): Ginther et al., 2002; also reviewed in Mann & Fraser, 1996]. This time period—from birth to puberty—represents a critical period of development for multiple biological systems [reviewed in Hensch, 2004]. The effects of exposure to androgens and the factors that influence patterns of androgen production during this critical period seem to differ across primate groups [reviewed in Wallen, 2005]. Of particular interest to this study are social factors that might be related to androgen production in developing males.

Because most of the knowledge we have about male developmental androgen production comes from studies on Old World primates, our objective is to expand on the growing base of research on primate species with different social systems by describing the androgen production patterns during

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the development of the male white-faced marmoset (*C. geoffroyi*), a socially monogamous, biparental New World callitrichine primate. Marmoset social structure offers an alternative model for studying sociosexual development in primates, because most Old World primates display polygamous or multimale/multifemale social systems with infant care displayed nearly exclusively by females. Furthermore, male marmosets often remain in their natal groups as sexually mature adults, well beyond the stages of infant and juvenile dependency, and provide alloparental care for their younger siblings [reviewed in French, 1997]. Callitrichines, therefore, possess a unique social system in which sexual development may be studied.

To date, sexual maturation in male callitrichines has primarily been documented in the common marmoset and cotton-top tamarin. In the common marmoset, sexual development is characterized by a relatively high level of circulating testosterone (T) immediately after birth, a subsequent drop in T that reaches a nadir between 3 and 6 months of age, followed by a gradual increase in T production into adulthood [Dixson, 1986]. In common marmosets and cotton-top tamarins, the late juvenile rise in T production precedes testicular growth, typically between 9 and 10 months of age [Abbott & Hearn, 1978; Ginther et al., 2002]. Sexual maturation is completed in the cotton-top tamarin between 22 and 24 months of age, when luteinizing hormone (LH) and T titers reach normal adult levels and, importantly, a rapid switch in the increased production of dihydrotestosterone (DHT) relative to T occurs, possibly signaling the onset of mature testicular endocrine function [Ginther et al., 2002]. Thus, the general patterns and hallmarks of androgen production in callitrichines mirror those of other primate groups. Yet, there is no evidence to suggest that there is active suppression of reproductive endocrine systems in callitrichine sons that remain in their natal group [Baker et al., 1999; Castro & Sousa, 2005; Ginther et al., 2002; Huck et al., 2005], in contrast to the well-documented phenomenon of reproductive suppression in callitrichine daughters [Abbott, 1984; Abbott & Hearne, 1978; Abbott et al., 1988; Albuquerque et al., 2001; Barrett et al., 1990; Bercovitch & Ziegler, 2002; French et al., 1984; Saltzman et al., 1997, 2004; Widowski et al., 1992; Ziegler et al., 1987; reviewed in Abbott et al., 1998; French, 1997; Vandenbergh, 1989].

However, certain group dynamics have been shown to influence androgen secretion in breeding males. The presence of infants, for example, is a prominent social factor that modulates androgen secretion in fathers. Wild mustached tamarins (*S. mystax*) show an increase in fecal T excretion immediately following the birth of infants [Huck et al., 2004]. However, in black-tufted ear marmosets (*C. kuhlii*), T levels decrease during periods in which fathers are more involved in infant rearing [Nunes et al., 2000], and this decrease is more pronounced in fathers with more parental experience and who engage in higher rates of offspring care [Nunes et al., 2001]. Infant-induced declines in androgen production seem to be mediated at least in part by olfactory cues from the infants [*C. jacchus*; Prudom et al., 2008]. Alternatively, androgen levels can become elevated in males across varying phases of the breeding female's reproductive cycle. Androgen levels in male cotton-top tamarins rise throughout periods when their partner is pregnant, peaking just before birth of offspring, compared with when their partner is not pregnant [Ziegler et al., 2004b]. Male cotton-top tamarins also exhibit an increase in urinary androgens (uAs) that coincides with the period immediately before the female's LH peak that commonly occurs shortly after parturition [Ziegler et al., 2004a]. Male common marmosets exposed to olfactory cues collected from females in the periovulatory phase of the ovarian cycle showed significantly higher plasma T 30 min after exposure, relative to exposure to a control scent [Ziegler et al., 2005]. Thus, males seem to be sensitive to the reproductive status of their mates at an endocrine level. The effects of similar social stimuli, such as the reproductive condition of the breeding female and the presence or absence of younger siblings, on hormone profiles of adult-aged sons living in the natal group, however, are largely unknown.

The purpose of this study, therefore, is to characterize patterns of androgen production in developing white-faced marmoset males during the first 2 years of life. Specifically, we examined the developmental androgen levels as a function of three features pertinent to social and sexual development: (1) the individual's age, (2) social status as young adults compared with their fathers, and (3) the time surrounding the birth of infants.

METHODS

Subjects

Subjects were eight white-faced male marmoset (*C. geoffroyi*) offspring living in their natal group, aged 2–24 months at the University of Nebraska at Omaha Callitrichid Research Center. Data were collected from May 2004 to June 2008. All sons lived with their biological mother and father during sampling. Eight adult males, ages 6.6–11.2 years, were used to compare adult male androgen levels to those of young males. Each of the adult males was paired with an unrelated adult female marmoset, and had offspring present during sampling. Table I contains demographic information for all subjects. Animals were socially housed in wire-mesh enclosures no smaller than $1 \times 2 \times 2$ m, with a minimum of 0.8 m^3 per animal. The enclosures included natural

TABLE I. Demographic Information of Young Male White-Faced Marmosets

Name	DOB	Litter size	Mother	Father	Older siblings present (at birth)	Younger siblings present (at 24 months)	Total family size (at 24 months)
Aco	3/24/2004	2	Pop	Ant	0	2	6
Doo	3/31/2004	2	Swe	Ray	0	4	8
Gui	2/3/2005	1	Swe	Ray	2	5	9
Lui	7/8/2005	2	Swe	Ray	3	3	9
Osc	7/12/2005	2	Pop	Ant	1	0	5
Pea	7/12/2005	2	Pop	Ant	1	0	5
Ser	7/21/2006	2	Swe	Ray	4	0	8
Xyl	7/31/2006	2	Lor	Man	0	3	7

branches, a nest box, and various enrichment devices. Colony rooms were maintained at 19.7–22.1°C and on a 12 hr:12 hr light–dark cycle. All animal procedures were approved by the Institutional Animal Care and Use Committee (Protocol ♯: 07-033-FC) and adhered to all legal requirements for research use in nonhuman primates in the United States. Animals were fed once each day at 0800 hr. For a more detailed description of animal housing and husbandry, see Schaffner et al. [1995].

Urine Collection

Urine samples from marmoset sons were collected beginning 1–3 months after birth and ending 24 months after birth. Samples from breeding animals were collected routinely upon entry into the colony. We collected one to three urine samples per week from each male, using noninvasive techniques described by French et al. [1996]. Briefly, we trained subjects to urinate into hand-held pans for food rewards. We collected 0.1–1.0 ml of first void urine samples from each subject between 0600 and 0830 hr. Samples were then transferred to plastic vials, centrifuged at 7,000 rpm for 2 min to remove sediments, and the supernatant portion of each sample was again transferred to a clean vial and stored at −20°C until assayed.

Hormone Assays

uA concentrations were measured using a T enzyme immunoassay previously described and validated for use with marmosets [Nunes et al., 2000]. The T antibody (provided by C.J. Munro, UC Davis; R156/7) used in the assay also cross-reacted with DHT at 57.37%, and thus results are expressed as uA concentrations rather than T concentrations. Cross-reactivities with other steroids were negligible (<1%). Before assay, urine samples (10 μl) were extracted using 5 ml diethyl ether after enzyme hydrolysis with β-glucuronidase (Sigma Chemical, St. Louis, MO). The ether was evaporated in a warm-water bath and samples were reconstituted in 1.0 ml phosphate buffered saline. uA concentrations were adjusted for procedural loss, assessed by the recovery of titrated T after extraction, with a mean recovery of 90.94%. uA concentrations were measured in 85 T assays. The intra-assay coefficient of variation, calculated using duplicate samples of pooled marmoset urine, was 6.92%. The inter-assay coefficient of variation, also calculated using pooled marmoset urine, was 18.31%. To minimize the potential confounding effects of inter-assay variation, all samples collected from an individual male were evaluated in a single assay run when possible. To control for variation in solute concentration of urine samples, we expressed the mass of uA per mass of creatinine (Cr), a product of muscle metabolism excreted at consistent rates. We measured Cr in

urine samples using a modified Jaffe end-point assay [Tietz, 1976], previously described and validated for marmosets [French et al., 1996].

Data Analysis

Excreted uA levels were compared at different time points during the first 2 years of life for each young marmoset. uA concentrations were averaged along four early life stage parameters previously described by Yamamoto [1993], giving a single composite average for each of the following life stages: infant (0–5 months), juvenile (6–10 months), subadult (11–15 months), and young adult (16–24 months). A one-way, repeated measures analysis of variance (ANOVA) was conducted to compare uA levels across these time periods. Post hoc analyses using least significant difference (LSD) comparisons were used to compare uA levels of adjacent life stages only (i.e., infant to juvenile, juvenile to subadult, subadult to young adult).

Analyses were also conducted to analyze the relationship between several different group social factors and uA levels of young male marmosets. An independent samples *t*-test was conducted to compare uA levels of adult-aged sons (16–24 months of age) to their fathers' overall uA levels. Also, uA levels of fathers and sons were compared 30 days before and 30 days following the birth of infants using a 2×2 (fathers vs. sons $\times$ pre- vs. postpartum) repeated measures ANOVA. Ages of all the sons used in this analysis ($N = 5$) ranged from 12.6 to 17.7 months. Each pregnancy was treated as an independent event; therefore, four pregnancies from two different fathers were included in the analysis. Because this analysis is therefore confounded by the use of nonindependent data, we also conducted a one-way repeated measure ANOVA on uA levels 30 days before and 30 days after the birth of infants for sons only.

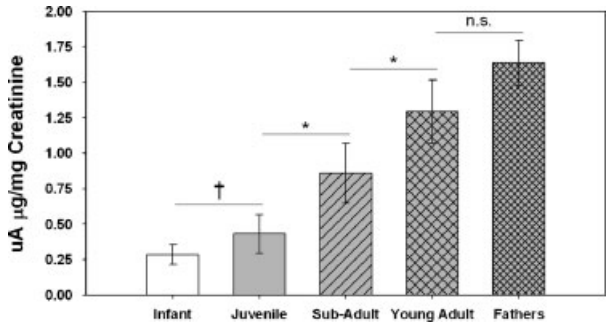

Fig. 1. Patterns of monthly mean urinary androgen (uA) (µg/mg Creatinine) ± SEM across developmental life stages of young white-faced male marmosets with a comparison of average uA levels for breeding males. Mean uA levels for each life stage were significantly higher than the previous life stage, with the exception of juvenile stage uA levels, which were higher than infant uA levels, though not significantly. Fathers showed higher uA levels than young adult males still living in their natal groups, though the difference was not significant. Life stages adapted from Yamamoto [1993]. $^{*}P < 0.05$, $^{\dagger}P = 0.07$; n.s., not significant.

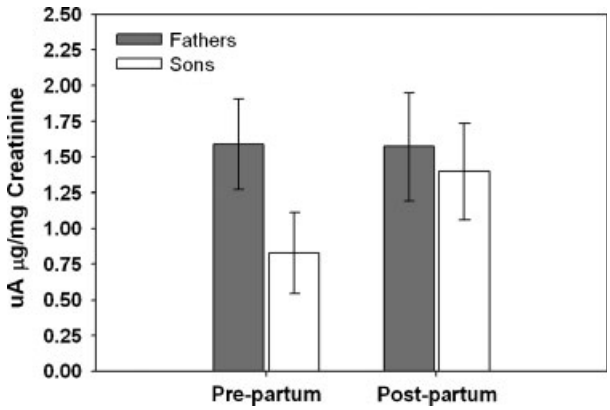

Fig. 2. Urinary androgen (uA) levels of fathers and sons 30 days before parturition and 30 days following parturition. Sons' average uA levels did rise following the birth of infants, though not significantly.

RESULTS

Average uA levels varied significantly across life stages ($F = 13.53$, df = 3, 18, $P < 0.001$; Fig. 1). uA levels in juvenile marmosets were higher than infant levels, but only marginally (LSD = 0.15, $P = 0.07$). All subsequent uA levels for each life stage were significantly higher than the preceding life stage; i.e., subadult levels were higher than juvenile levels (LSD = 0.43, $P < 0.05$) and young adult levels were higher than subadult levels (LSD = 0.45, $P < 0.05$). uA in young male marmosets were excreted at a relatively stable rate, beginning in month 2 and ending in month 8 and 9 where a considerable increase in uA levels occurred. A marked increase in uA levels also occurred at month 16. By 22–24 months of age, young males had reached an average uA excretion levels similar to that of breeding males, though still slightly lower. Mean uA levels during the young adult stage (16–24 months) were consistently the highest of all life stages, ranging from 1.03 to 1.54 µg/mg Cr (Fig. 2).

Mean monthly uA levels of adult-aged sons, ages 16–24 months, did not differ significantly across this time period ($F = 0.63$, df = 8, 56, $P = 0.75$); therefore, overall mean uA concentrations for this life stage were computed and compared with breeding adult uA levels. Although breeding males tended to have higher uA levels (M ± SEM; 1.70 ± 0.22 µg uA/mg Cr) than adult-aged sons (1.25 ± 0.05 µg uA/mg Cr), this difference did not reach conventional levels of statistical significance ($t = 1.12$, df = 14, $P = 0.10$). Next, sons' uA levels did rise somewhat following the birth of infants, though not significantly. No differences were found when average uA levels for fathers and sons 30 days before the birth of infants were compared with uA levels 30 days following the birth

of infants ($F = 2.75$, df = 1, 7, $P = 0.14$). No interaction of age was found between fathers and sons in pre- and postpartum uA levels ($F = 3.06$, df = 1, 7, $P = 0.13$). When only sons were included in the analysis, again no differences were found between uA levels pre- and postpartum ($F = 2.92$, df = 1, 4, $P = 0.16$).

DISCUSSION

The sexual maturation of young white-faced marmosets, as measured by levels of excreted uA, developed over time in a similar trajectory as other reported callitrichine primates [Abbott & Hearn, 1978; Chandolia et al., 2006; Dixson, 1986; Ginther et al., 2002]. Young male white-faced marmosets showed a relatively low and stable rate of uA excretion from ages 2–7 months, followed by an increase in uA at 8 and 9 months of age (late juvenile phase), signaling the onset of puberty and corresponding with the growth in testis size [Abbott & Hearn, 1978; Dixson, 1986]. A marked increase in uA levels occurred at 16 months of age, coinciding with the onset of sexual maturity [as described by Yamamoto, 1993]. By 22–24 months of age, young male marmosets had reached similar but slightly lower average uA excretion levels as compared with breeding males, consistent with previously reported results [Ginther et al., 2001, 2002]. Although a marked drop in early infant androgen levels was not observed in this sample as it has been in the case of other callitrichine species [e.g., common marmoset: Abbott & Hearn, 1978; Dixson, 1986; black tufted-ear marmoset: French & Schaffner, 1995], androgen levels during the 2nd month of life were higher than any of the following 6 months. Because our sample collection for most males began during the second or third postnatal month, it is likely that we did not capture the transiently high androgen levels that characterize 1 month old male marmosets [common marmoset: Abbott & Hearn, 1978; Dixson, 1986; black tufted-ear marmoset: French & Schaffner, 1995]. Although our results are consistent with previous reports, discretion should be used in generalizing the results of this study, owing to the fact that sampling occurred in only three family groups. Genetic influences have been identified that influence the timing of puberty [e.g., mice: Nelson et al., 1990; humans: Townel et al., 2005], and thus such factors should be considered as well.

Sexual maturation in monkeys is marked by an elevation of LH followed shortly thereafter by an elevation in T levels that reflect normal adult range [Abbott & Hearn, 1978; Dixson, 1986; Ginther et al., 2002]. It is also worth noting that cotton-top tamarins exhibit a rapid increase in the production of DHT relative to T levels during the time of pubertal maturation, which may serve as a useful marker for transition to a mature endocrine profile [Ginther et al., 2002]. Such an analysis was not possible in this study, as discrete T and DHT analyses were not conducted. Also, although the patterns of uA levels are consistent between marmosets and tamarins, specific timelines for sexual maturation differ between marmosets and tamarins as marmosets reach sexual maturity faster than tamarins [e.g., about 16 months in common marmosets: Abbott & Hearn, 1978; between 22 and 24 months in cotton-top tamarins: Ginther et al., 2002]. Interspecies life history analyses predict such a difference based on the larger body size of tamarins compared with marmosets (about 0.5 and 0.3 kg, respectively), which is related to ecological differences between species [reviewed in Harvey, 1985].

Circulating T levels of young adult callitrichine sons still living in their natal groups before contact with an unrelated female have been reported to be similar to T levels of the dominant, breeding male [common marmoset: Abbott & Hearn, 1978; Baker et al., 1999; golden lion tamarin (*Leontopithecus rosalia*): French et al., 1989]. In this study, breeding male uA levels were only marginally higher than those of sexually inexperienced adult sons. Thus, adult sons are potentially fertile at the endocrine level while in their natal group, suggesting a lack of reproductive suppression of male offspring by the breeding pair and other within group social cues. However, Ginther et al. [2001] noted that DHT levels in male offspring rise significantly after being removed from their natal group, remaining elevated while singly and pair housed with a novel female until siring offspring. Therefore, DHT seems to be suppressed during periods in which males are exposed to dependent young (younger siblings in the natal group and offspring during pair housing) and are potentially displaying infant care. Similarly, T levels of marmoset fathers have also been reported to be depressed during periods of infant dependency [Nunes et al., 2001]. In this study, uA levels did not vary significantly within young adult males after infant offspring were born into the group. It may, therefore, be that male marmoset offspring are not as sensitive to the presence of infants compared with fathers, though further research is needed to examine whether individual differences in androgen levels are related to individual differences in alloparental care similar to that of paternal care [Nunes et al., 2001]. Moreover, our comparison between fathers and sons around the peripartum period is confounded by the fact that only four pregnancies from two fathers were included. Data from a larger number of fathers and sons is needed to better delineate the differences in changes in androgen levels that may occur during periods of infant dependency.

Despite being potentially fertile at the endocrine level, mature male offspring restrict sexual activity with breeding females. Adult male cotton-top tamarin

sons seem to be unrestricted in the display of sexual behavior as mature males mount others in their natal group (primarily male and female siblings) and have erections at similar rates in their natal groups, compared with when they are paired with unrelated, receptive females [Ginther et al., 2001]. However, they are restricted in displaying sexual behavior toward the breeding females in the natal group compared with being paired with a novel adult female. These observations may be dependent upon certain group dynamics and/or social status. For instance, subordinate immigrant male golden lion tamarins have lower concentrations of fecal T compared with dominant males, whereas adult-aged subordinate sons in their natal groups show only marginally lower fecal T concentrations compared with their dominant father [Bales et al., 2006]. In this study, adult-aged Geoffroy's marmoset sons have similar, though slightly lower, uA concentrations to their fathers while in their natal group. Rather than specific endocrine mediation, it has instead been suggested that behavioral cues from dominant members [Abbott, 1984] and the absence of unrelated breeding females [Baker et al., 1999] are major factors that contribute to the reproductive failure of callitrichine offspring. Young males in the wild are likely to have encountered unrelated females, which may be a critical event in sexual development and androgen production rates. Male callitrichines are opportunistic breeders, often taking advantage of mating opportunities during intergroup encounters in the wild [Digby, 1999; Lazaro-Perea, 2001], even while residing in their natal groups. Experience with an unrelated female may, therefore, be a crucial factor that precludes a sustained elevation of circulating androgens in young males. Such sustained androgen levels may promote a state of reproductive readiness in order for males to take advantage of extra-group sexual encounters that occur in the wild [Baker et al., 1999].

The presence and condition of a breeding female are also important cues for the breeding male and subordinate female members of a social group in callitrichine primates. Breeding male cotton-top tamarins produce elevated uA levels before their mate's postpartum LH peak, possibly promoting optimal functioning in reproduction [Ziegler et al., 2004a]. The T production of daughters varies depending on the pregnancy status of their mother, which is also contingent on the pubertal status of the daughter [Puffer et al., 2004]. Prepubertal daughters produce more T while their mother is pregnant compared with after their mother gives birth, whereas postpubertal daughters produce less T when their mother is pregnant compared with the postpartum period. This study found no significant difference in androgen levels of captive male offspring 1 month before and 1 month following the birth of infants, again suggesting that male offspring are not as sensitive to reproductive cues from the mother as other group members. However, it may be interesting to examine sons' uA levels as a function of the breeding female's ovarian cycle, in light of the fact that breeding males increase sexual behavior (e.g., mounts, ejaculations, solicitations) during the periovulatory phase [Kendrick & Dixson, 1983]. Our current dataset did not provide the temporal resolution necessary to examine this question, however.

In summary, previous findings have suggested that group demographics can affect individual gonadal function in callitrichine species, focusing primarily on daughters. For example, although captive common marmoset daughters engage in sexual behavior with unrelated males present even in their natal group, they do not ovulate if they are behaviorally subordinate to their mothers [Saltzman et al., 2004; but see Ziegler & Sousa, 2002]. Gonadal function in young male callitrichine primates, on the other hand, may be independent of the breeding female's pregnancy status and other social cues in the natal group, as they seem to reach sexual maturity at the endocrine level within this social context [this study]. As reproductive investment is considerably less costly for males than females, subordinate males may be less tolerant of suppression than subordinate females, even while in their natal group. Still, mating behavior with a sexually receptive female may be influenced by group dynamics, such as the presence of an unrelated female [Baker et al., 1999] and possibly behavioral mediation by other group members [Ginther et al., 2001].

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