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Aspects of the Behavioral and Endocrine Ontogeny of Six Moustached Tamarins, *Saguinus mystax* (Callitrichinae)

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Introduction

In order to recognize differences in ontogeny between species and between their life history trajectories, it is necessary to have an understanding of the timing of milestone events in behavior and physiology (Pereira and Leigh, 2003). Assessing when and how individuals become independent from their mother and other caregivers is necessary to evaluate costs of varying parental strategies, which in turn allows broader issues to be addressed, such as the evolution of non-maternal care in anthropoid primates (Ross and Maclarnon, 2000). Patterns of ontogeny may also explain aspects of individual differences in behavior, especially, for example, when same-sexed adults become competitors. Ventura and Buchanan-Smith (2003) have stressed that a good understanding of the species' development and behavior in the wild is essential to assess and ensure the well-being of maturing individuals in captivity. Observations are often anecdotal, but the difficulties and imprecision in obtaining data of this sort under field conditions can be overcome by repeated studies of groups of the same or related species.

The ontogeny of immature primates is tied to endocrinological changes. Typically the gonads are only partially developed at birth. The production of sex hormones such as testosterone increases during puberty until adult levels are reached (Plant, 1988). In adult males, testosterone and other androgens are important in the control of spermatogenesis (Wickings *et al.*, 1986) and seem to play a role in the expression of aggressive behavior and in the achievement of social status, though this latter relationship might be less pronounced in primates (Dixson, 1980; Bouissou, 1983). In three callitrichine species (*Callithrix jacchus*, *Callithrix kuhlii,* and *Saguinus oedipus*), however, newborn males show relatively high testosterone levels that drop after two to six months and rise slowly again thereafter (Abbott, 1984; French and Schaffner, 1995; Ginther *et al.*, 2002). Ginther *et al.* (2002) speculated that this neonatal elevation might be related to the sexual maturation of the gonads, endocrine system, and behavior, but it is not known how representative this pattern may be of other callitrichine species.

During a field study on moustached tamarins (*Saguinus mystax*), we were able to observe some aspects of the development of six immature individuals (five males and one female). For some of them we were able to record, for the first time, the onset and final appearance of a number of behaviors — in particular, the first observations of feeding on solid food, foraging, social play, and marking behavior, and the last days they were carried and successfully begged for food.

We expected that the patterns of testosterone and androgen in the five male immatures would be similar to those of the three callitrichines mentioned above. In addition, the immigration of a new female into one of the groups on 5 December 2001 provided the opportunity to study whether this caused endocrinological changes in the immature males. Given that one subadult male was evicted from the group following the new female's arrival, we also tested whether he and his twin differed in their testosterone levels, and whether their values differed from those of adult males in general. If co-twins differ in their sexual maturation, it might be supposed that the more mature of the two would be forced to leave the group in order to remove a potential competitor. If this is true, it might be expected that the evicted twin had higher testosterone levels than the remaining one. Different testosterone levels due to different aggression levels in the

twins are unlikely, since we were able to show previously that adult moustached tamarins do not differ in their testosterone levels despite different breeding and "dominance" status (Huck *et al.*, 2005b; note: aggression occurs too rarely to establish hierarchical relationships). These results should be considered preliminary owing to our small sample size, but they nevertheless present the first data on the behavioral ontogeny of *Saguinus mystax* and the first endocrine data for immature males of any callitrichine in the wild.

Methods

The study took place in 2001 (January to December) at the Estación Biológica Quebrada Blanco, in northeastern Amazonian Peru (for further details of the study site, see Heymann, 1995). We collected fecal samples and behavioral data from two habituated groups of *S. mystax*, each with two sets of offspring, one born in 2000 and the other in 2001. Group W contained one adult female, three adult males, male twins born in February 2000 (WM4 and WM5), and a single male offspring born in February 2001 (WM6). Group E consisted of three adult females and three adult males, a single male born in May 2000 (EM4), and twins — one male (EM6) and one female (EF4) — born in January 2001. Based on physical characteristics, Soini and Soini (1990) classified moustached tamarins as infants from birth until about three months of age, as juveniles between 4–12 months, as subadults between 13–18 months, and as adults thereafter. Following these criteria, three of the immature males (WM4, WM5, EM4) reached adulthood at the end of the study in December 2001. Two males (WM6, EM6) and one female (EF4) were born near the beginning of the investigation, developing from newborns to relatively independent juveniles over the course of the year (see Table 1). In Group W the breeding female WF1, mother of WM6 and (probably) aunt of WM4 and WM5 (relationships were evaluated by microsatellite analysis as described by Huck *et al.*, 2005a), died near the end of the study (3 December, 2001). Two days later an unrelated female (WF3) immigrated to Group W, and one of the male subadults (WM4) was evicted on 5 December 2001. The composition of the groups and major demographic events are described in more detail by Löttker *et al.* (2004).

We followed each group daily from the time they left their sleeping site (about 05:45) until they entered their sleeping site in the afternoon (about 15:45 h). From January to December 2001 we accumulated a total of 3004 and 3257 contact hours over 330 and 351 days for groups W and E, respectively. The average visibility of individuals — measured as the percentage of hourly scans in which each individual could be seen — was 18.0 and 18.6% for adults and immatures in group W, respectively, and 11.3 and 10.9% for adults and immatures in group E. Following the protocols for behavior sampling of Martin and Bateson (1993), we recorded the first observation of an infant independent of a carrier (being "off"), eating solid food (without distinguishing between prey or fruit), engaging in social play, and foraging for prey. We also noted the last observations of an infant being carried and of successfully begging for food. Except for the data on food-begging, the records were taken from the younger litter in the two groups (i.e., WM6 in group W, and EM6 and EF4 in group E). We were unable to distinguish the Group E twins, EM6 and EF4, until they were 81 days old; until then, data of the first occurrences of either one of the two infants are used. Data on food-begging were recorded from the older immatures (WM4 and WM5 in group W, EM4 in group E).

For hormonal analyses, we collected a total of 151 fecal samples from immature males between January and December 2001 (see Table 1 for the number of samples per individual). Immediately after an animal was seen defecating, the feces were collected and immersed in 96% ethanol. (The protocols for treatment and storage of the samples are given in Huck *et al.* [2005b], as are techniques for hormone extraction and measurement of immunoreactive testosterone by enzyme immunoassay.) Hormone concentrations are given in ng/g fecal dry weight and were log-10-transformed for parametric statistics.

In order to examine changes in testosterone excretion over time, we calculated Pearson's correlation coefficient (r) between age and mean monthly testosterone values. As in *Callithrix jacchus*, *Callithrix kuhlii* and *Saguinus oedipus*, testosterone levels in newborns drop only after two to six months and rise slowly again thereafter (cf. Abbott, 1984;

Table 1. Immatures of *Saguinus mystax* study groups W and E, with mean testosterone values of the males and number of fecal samples analyzed (N).

Individual	Sex	Demographic notes	Mean testosterone ±S.D.	N
Group W				
WM4	M	Born 22 February, 2000; Emigrated 5 December, 2001	2720.0 ± 3274.9 (before 18 mo: 3219.3 ±4046.6)	35
WM5	M	Born 22 February, 2000	1918.6 ±3185.1 (before 18 mo: 1435.6.3 ±1160.7)	40
WM6	M	Born 24 February, 2001	470.8 ±549.4	28
Group E				
EM4	M	Born May, 2000	990.3 ±1057.1	34
EM6	M	Born 21 January, 2001	814.1 ±915.0	14
EF4	F	Born 21 January, 2001	-	-
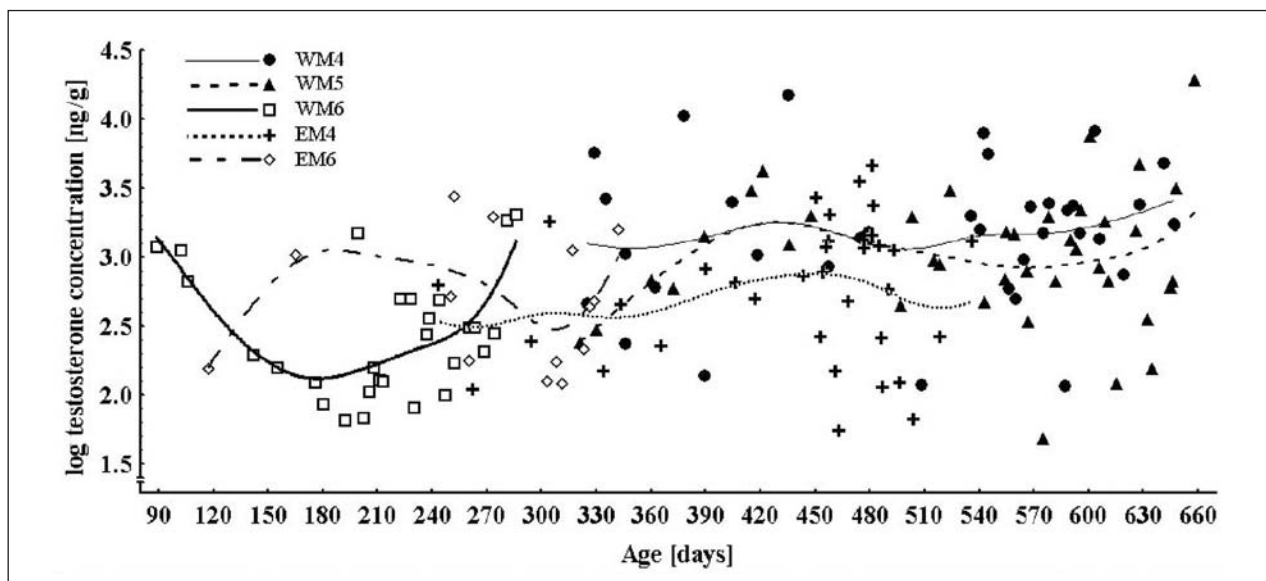
Figure 1. Log-10-transformed fecal hormone concentrations for all individuals related to relative age (in days). Curves give the distance-weighted least-squares fit for each male. Only the month, not the exact date of birth was known for EM4, so it was taken to be 15 May.

French and Schaffner, 1995; Ginther *et al.*, 2002). The data depicted in Figure 1 appear to show a drop in testosterone levels between months 4 and 5 (around day 140). Therefore we also calculated the coefficient r for the younger males WM6 and EM6, excluding the potentially high values before their 140th day of life, which seems to correspond to the turning point in testosterone production described for *Callithrix jacchus, Callithrix kuhlii,* and *Saguinus oedipus* at similar ages (Abbott, 1984; French and Schaffner, 1995; Ginther *et al.*, 2002). Three samples were collected from WM6 before he was 140 days old and one for EM6.

Unfortunately we could not obtain enough samples for statistical analysis after WF1's death (3 December 2001) and the subsequent emigration of WM4 (5 December 2001); we collected only one sample each for WM4 and WM6. Instead, we evaluated whether the mean hormone concentration of these samples collected after the new female had immigrated lay above the 95% upper boundary of the group average when WF1 was still alive. In addition, we compared testosterone levels between the twin brothers in group W and in relation to mean testosterone levels of the adult males in the two study groups W and E (values for adult males appear in Huck *et al.*, 2005b).

Results

Our first and last observations of milestone events in behavior are listed in Table 2. Nursing was observed only rarely and was not included. Apart from "last time seen successfully begging", the data report on the second litters only (WM6 in group W, and EM6 and EF4 in group E). Table 1 shows the testosterone concentrations of all samples by individual and the distance-weighted least-squares fit for each. No immature showed a significant increase in testosterone levels during the year, and none of the correlations between age and mean monthly testosterone values were significant (WM4: r =

0.06, p = 0.86; WM5: r = 0.37, p = 0.23; WM6: r = -0.03, p = 0.94; EM4: r = 0.21, p = 0.50; EM6: r = 0.11, p = 0.83).

When we calculated the regressions for WM6 and EM6 after their 140th day of life, only WM6 showed a significant increase in testosterone values over the following six months until December 2001 (r = 0.50, p = 0.012, see Fig. 1); we did not find such a correlation for EM6 for the seven months after his 140th day of life until December 2001 (r = –0.27, p = 0.37; see Fig. 1).

We had no samples from WM4 after the death of the breeding female WF1. The samples of WM5 and WM6, collected after immigration of the new female, both fell above the 95% boundary (Table 3). WM5 had significantly lower testosterone values than the adult males of group W, but the values of WM4 did not differ significantly from adult levels

Table 2. First and last occurrence of behavioral milestone events in two study groups of *S. mystax.*

	Group W	Group E
First day "off" carrier[a,b]	Day 17	Day 21
First day seen eating solid food[a,b]	Day 30	Day 33
First day seen socially playing[a]	Day 57	Both: Day 37
First day seen foraging[a,b]	Day 103	Day 61
Last day carried[a]	Day 106	EM6: Day 104–105 EF4: Day 114
First time seen marking[a]	Day 154	WM6: Day 99 WF4: Day 114
Last day of successful begging[c]	WM4: Day 325 WM5: 1year 8 days	EM4: 1 year 1 month

[a] N = One individual in group W (WM6) and two in group E (EM6 and EF4)

[b] Infants in group E (EM6 and EF4) were too small to be distinguished

[c] N = Two individuals in group W (WM4 & WM5) and one in group E (EM4)

Table 3. Mean (untransformed) testosterone values and the upper 95% boundary of juveniles of Group W during the tenure of WF1, and the value of a sample collected after the immigration of a new female.

Individual	Mean (with WF1)	95% boundary	Mean of last 3 samples with WF1	Sample with new female (N = 1)
WM4	2720.0	10615.6	3017.9	
WM5	1471.3	4740.2	1487.7	19361.4
WM6	413.4	1488.9	782.3	2022.1

(mean and SD for adults: 2782.1 ± 3233.3; for WM4 and WM5: see Table 1. Scheffé *post hoc* tests: adults vs. WM4: p = 0.72; adults vs. WM5: p = 0.014). The testosterone levels of the twin brothers (WM4 and WM5) did not differ significantly but tended to be lower in WM5 (Scheffé *post-hoc* test: p = 0.30; compare fit curve in Fig. 1).

Discussion

In general, the two study groups showed consistent results but differed in two ways. First, WM6 began foraging and showing social play later than his peers from group E. This might have been due to his having been raised as a singleton; his sibling was killed by a raptor at the age of 28 days (Oversluijs Vásquez and Heymann, 2001). Other studies have shown that infants prefer to play with same-aged playmates and that singletons play significantly less than twins (e.g., Cleveland and Snowdon, 1984). This holds true even when older siblings are available as potential playmates (Cleveland and Snowdon, 1984). Without further study we cannot say whether our results are representative and, if they are, whether the reduced play retarded the development of motor skills vital to foraging or whether — with only a single infant to care for — caregivers are more indulgent, resulting in less need for an infant to forage for itself.

The only slight (non-significant) increase of testosterone levels with increasing age in all subjects was unexpected. WM6 showed a testosterone excretion pattern similar to those described for other callitrichines (Abbott, 1984; French and Schaffner, 1995), with high levels very early in life that drop after three months and then rise again after the seventh month. The similar-aged EM6 did not show this pattern, but this might be due to the fact that only one fecal sample was analyzed before his 140th day of life. There was a strong increase in testosterone concentrations in the samples of WM5 and the considerably younger WM6 collected after the death of the related WF1 and the subsequent immigration of the unrelated female WF3.

With only one fecal sample in each case, this finding must be regarded with caution, but we suspect that the elevated levels might be related to the fact that incest avoidance no longer had a role to play (see also Baker *et al.*, 1999, for *Callithrix jacchus*). In addition, WM4, who was later evicted, seems to have been more precocious than his brother. Although the twins in group W showed no differences in time budgets (G-test with William's correction, G_6 = 11.6, p = n.s.; unpubl. data), their endocrine levels were different

(although non-significantly), and WM4 may have posed more of a threat to the adult males after the arrival of the unrelated female WF3. The testosterone values of WM5 were significantly lower than adult levels, while those of his brother were not. WM4 had apparently reached adult levels before the onset of the study when he was 10.5 months old. In contrast, his twin WM5 reached adult levels only at the end of the study at nearly 23 months old (cf. Ginther *et al.*, 2002, for similar ranges). Age and morphology alone are thus insufficient predictors of sexual maturity, since testosterone levels, which are likely to be related to sperm production and fertility, differ widely during maturation even between twins.

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Introduction

The social group of the brown howler monkey, *Alouatta guariba clamitans* Cabrera, 1940 is typically small (2–12 individuals), with one or two adult males, and more females than males (Silva Jr., 1981; Neville *et al.*, 1988; Mendes, 1989; Steinmetz, 2000, 2001; Treves, 2001; Miranda and Passos, 2005). In primates where males outnumber females, males compete for both females and food, which normally results in groups with dominant males (Clutton-Brock and Harvey, 1977; Dunbar, 1988; Mittermeier *et al.*, 1999). As in all howler monkeys, *A. g. clamitans* is sexually dimorphic; adult males are larger than females and are dominant to them (von Ihering, 1914; Altmann, 1959; Neville *et al.*, 1988; Bonvicino, 1989; Mendes, 1989; Chiarello, 1995; Mittermeier *et al.*, 1999; Treves, 2001). Although howler monkeys are the most studied of the Neotropical primates, most of the research has been concentrated on a few species, in particular *A. palliata* and *A. seniculus*, and only more recently *A. caraya*, *A. pigra* and *A. guariba* (Neville *et al.*, 1988; Bicca-Marques, 2003). Field studies on the composition, social structure and hierarchy of *A. g. clamitans* are rare (Miranda, 2004; Jardim, 2005; Miranda and Passos, 2005), and long-term investigation will be necessary to obtain more detailed information on their social patterns. Here we describe a particular case of an *A. g. clamitans* group in which the dominant animal was an adult female — in effect, a matriarchal group.

Methods

Study area
The study area is a forest fragment of approximately 700 ha in the Chácara Payquerê, a component of the Área de Proteção Ambiental da Escarpa Devoniana, in the municipality of Balsa Nova, Paraná, Brazil (25°29'52"S, 49°39'24"W). This remnant forest is within the Floresta Ombrófila Mista (*Araucaria* Pine Forest biome) and consists mainly of disturbed primary forest, broken by patches of secondary forest.

Methods
Observations of the behavior and ecology of brown howler monkeys in the study area have been continuous since February 2002 (Miranda, 2004; Miranda and Passos, 2004, 2005; Miranda *et al.*, 2005; Miranda *et al.*, in press). The study group, the Forninho Group, was the best known in the area while its members remained together. Our observations here were recorded *ad libitum* (Altmann, 1974). We used the system of age-sex classification proposed by Mendes (1989) and used by Miranda and Passos (2005).