

Testicular Volume and Reproductive Status of Wild *Callithrix jacchus*

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Abstract The social relationship dynamic among callitrichid females is well known. Breeding exclusivity by dominant females involves female-female competition, usually resulting in the inhibition of subordinate reproduction. However, the strategies to maintain the male breeding position are still unclear. Researchers have observed no overt aggression between males, and differences in testosterone levels between dominant and subordinate individuals do not correlate with differences in reproductive success. In *Callithrix* monogamy is the predominant mating system, and testicular size is compatible with the absence of sperm competition. We analyzed testicular volume during development in 95 individuals at different ages (infant $n=12$, juvenile $n=9$, subadult $n=15$, and adult $n=59$). We also investigated if the ratio between testicular volume and body mass correlates with breeding position in the social group. The ratio was significantly higher in breeding males and a positive correlation between body mass and testicular volume is significant only for nonbreeding males. The findings suggest that testicular size varies with male reproductive status in the social group and that the enlargement of testicular volume in breeding common marmoset males seems to be a result of proximate causes and to depend on social and reproductive contexts acting together or separately.

Keywords male reproductive strategies · testis/body mass ratio · wild common marmoset

Introduction

Studies on female sexual strategies have yielded important data on the flexibility of common marmoset mating systems but, for males, few data are available on the mechanisms by which they reach reproductive status and impair the reproduction of

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subordinates. Some researchers have noted the exclusivity of reproduction by adult male *Callithrix jacchus* (Abbott 1984, 1993; Anzenberger 1985; Araújo 1996; Araújo and Arruda 1995; Digby 1999), but Goldizen (1987, 1989, 1990) suggested that for *Saguinus*, polyandry is the main mating system. Comparison of behavioral and endocrine profiles of male *Callithrix khulii* in artificial polyandrous (2 related or familiar males and 1 female) and monogamous groups suggests a nonmonopolizing facultative strategy because males show low overt agonism and differences in behavior and no change in urinary testosterone or cortisol (Schaffner and French 2004). The data suggest low competition between callitrichid males, and according to Huck *et al.* (2005), who tested the prediction of the challenging hypothesis, no change in testosterone occurs between reproductive and nonreproductive free-ranging male *Saguinus mystax*. They suggested that reproductive competition in the tamarins involves no hormonal mechanism but seems to entail a combination of behavioral mechanisms and sperm competition.

Studies on the relationships between wild (Araújo 1996; Lazaro-Perea *et al.* 2000) and captive (Araújo and Yamamoto 1994; Baker *et al.* 1999) common marmoset males also show low agonistic interactions between males. Baker *et al.* (1999), studying fathers and sons in family groups, investigated if reproductive failure in subordinate males was a consequence of competition, avoidance of mating with relatives, or both. They found no significant difference in plasma testosterone between fathers and sons and when tested together they showed significantly less sexual behavior than when tested alone with an unrelated female. The authors suggest that both competition and incestuous avoidance seem to be involved in the reproductive suppression of sons living in family groups. Abbott (1984) also found no difference between plasma testosterone levels of unrelated dominant and subordinate males. Castro and Sousa (2005) described a significant increase in the basal levels of fecal androgen excretion in adult sons vs. their fathers when mothers were pregnant. Baker *et al.* (1999) and Castro and Sousa (2005), respectively, suggested that the similar and higher testosterone levels in adult sons might be an adaptation to being aroused by the presence of a probable mate during intergroup encounters in wild conditions, increasing the opportunity for subordinates to copulate. Long-term data from field studies (Arruda *et al.* 2005; Castro and Araújo 2004; Lazaro-Perea *et al.* 2000; Lazaro-Perea 2001) have reinforced this theory, because free-ranging nonbreeding common marmosets copulate with females from neighboring groups during or immediately after encounters along home-range borders.

Evidence from our field studies shows that common marmoset groups always have a multimale/multifemale social structure, and in some cases it is difficult to identify the reproductive male. Even so, in general, affiliative and sexual interactions (Albuquerque *et al.* 2001; Araújo 1996; Digby 1995, 1999; Lazaro-Perea 2001) characterize breeding pairs in free-ranging groups. Thus, because males living within the same social group show low-intensity agonistic interactions, they might use other tactics to maintain reproductive exclusivity with breeding females. Some authors have described mate guarding and sperm competition as part of male callitrichid strategy (Digby 1995, 1999; Huck *et al.* 2005). For free-ranging common marmosets, mate-guarding behavior is frequently reported around the postpartum period (Albuquerque *et al.* 2001; Arruda *et al.* 2005; Digby 1995; Lazaro-Perea

2001), but according to Harcourt *et al.* (1981) and Dixson and Anderson (2004), common testicular size in marmosets does not suggest sperm competition, as expected for a primarily monogamous species. Though reproductive males performed different roles within the group, mainly during intergroup encounters (Araújo 1996; Lazaro-Perea 2001; Lazaro-Perea *et al.* 2000), no information is available on testicular size associated to social rank. Therefore, we aimed to correlate the stages of development and testicular volume in free-ranging common marmosets and to determine if the ratio between testicular volume and mass depends on the reproductive status of males in the social group.

Methods

Subjects

We collected data from marked, habituated males living in 15 free-ranging groups at the Floresta Nacional de Nísia Floresta field station (FLONA, of the Instituto Chico Mendes de Biodiversidade) 40 km from Natal, NE-Brazil. The station covers 170 ha, 70 ha of which is secondary Atlantic forest, 50 ha Tabuleiro vegetation, and 50 ha exotic trees, mainly *Eucalyptus*.

We captured 12 infants, 9 juveniles, 15 subadults, and 59 adult common marmoset males in manually operated cage-traps, to which we habituated them for 3 d before the actual trapping. On the day of capture, one of us stalked the subjects until they entered the trap. At that moment, we released the door and caught them. We covered the cage with a black cloth to calm them during transfer to a field station laboratory. Once in the laboratory we anesthetized them with 0.03 mg/kg of ketamine hydrochloride and weighed and measured them. After anesthesia recovery, never >1.5 h, we released them at the same location where we trapped them (Araújo *et al.* 2000). After release, we waited until the subjects rejoined the group, which we followed until they retired to the sleeping site. The next day we followed the group from the moment they left the sleeping site. We trapped all infants and juveniles only when we jointly captured another adult and always released them with an adult from their own group.

A tricolored collar and a tattoo on the inner surface of the forelimb identified individuals weighing >200 g. We identified individuals weighing <200 g via tail trichotomy and dyeing different parts of the body with picric acid. We assigned the individuals to 1 of 4 age classes: infants (0–5 mo), juveniles (5–10 mo), subadults (10–15 mo), and adults (>15 mo) per Yamamoto (1993). We used broad age classes to allow for errors in age estimation.

Body Mass and Testicular Volume Measurement

We weighed each male immediately after anesthesia. We then placed him in a prone position to measure the length and width of the testis through the scrotum via digital calipers. The observer pressed the scrotal skin taut to reveal the testis. We did not measure scrotal skinfolds. We performed all the measurements identically to ensure consistency. All the males were wild and we released them into their home range.

We measured both testes in 96% of the individuals. In 4% we measured only the right testis; thus, we used only right testicular measures in the testicular volume analyses. Moreover, there was no difference between the volumes of the 2 testes. (Wilcoxon's matched pairs test: $p=0.21$). We calculated testicular volume via the formula $0.523 \times L \times W^2$ (Abbott and Hearn 1978), wherein L = length and W = width.

We followed 7 of 15 trapped groups once a week to collect behavioral data for other studies for ≥ 1 yr and ≤ 5 yr. The behavioral data allowed us to identify the dominant breeding males ($n=14$), i.e., individuals that copulated or attempted copulation with reproductive females from their social groups for ≥ 1 yr (ca. 2 conceptions from the reproductive female). We considered the other adult males in the groups to be nonbreeding ($n=28$). Some nonbreeding males attempted copulation with females from a neighboring group during intergroup encounters (Arruda *et al.* 2005). We studied the remaining 8 groups for a short period on a more irregular basis and included them only in the analysis of testicular development and aging.

We captured 20 males more than once. In this case, except for the infantile stage, we considered only the measures obtained for the first age class in which the individuals were captured. For those captured twice or more within the same development class, we considered the mean of all measurements. As a result, we had only 1 value for each individual in each age class.

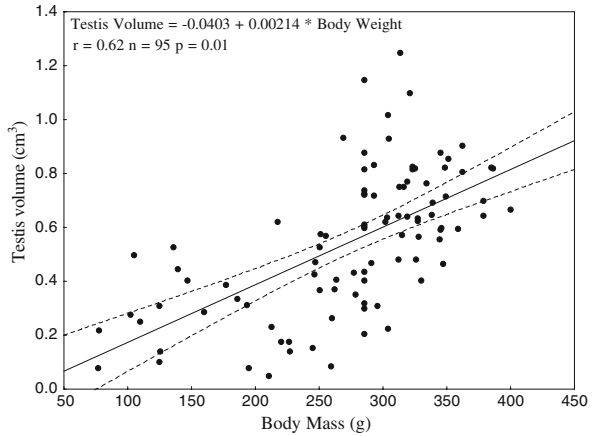
Statistical Analysis

We calculated the ratio between testicular volume and body mass (V_v/B_m) for the 4 age stages. To compare testicular volume and body mass among the age classes and seasons in which we captured the males, we used Kruskal-Wallis ANOVA by ranks (H) and Mann-Whitney U test. We compared testicular volume between breeding and nonbreeding males via the Mann-Whitney U test. We calculated the Spearman correlation coefficient (r_s) via testicular volume and body mass measures (Howell 1998). In all analyses, we established $p \leq 0.05$ as significant.

Results

Testicular volume ($H_{1, 95}=0.26$, $p=0.61$) and body mass ($H_{1, 95}=2.86$, $p=0.09$) do not differ according to capture season (rainy season: March to August; and dry season: September to February). Figure 1 contains a significant positive correlation between testicular volume and body mass ($r_s=0.66$, $p=0.001$), indicating both an increase in testicular volume ($H_{3, 95}=40.48$; $p=0.001$) and body mass with advancing age ($H_{3, 95}=58.47$, $p=0.001$, U test, for all comparisons $p \leq 0.04$). Infants, juveniles, and subadults show similar testicular volumes (U test, $p > 0.05$) and adults show significantly different testicular volume vs. all age classes (U test, $p=0.01$). However, our analysis of relative testicular volumes (ratio between testicular volume/body mass) in the 4 age classes shows that the ratio in the infantile and adult stages is higher than that of juveniles and subadults ($H_{3, 95}=9.72$, $p=0.02$, U test infant \times juvenile and subadult $p=0.05$, adult \times juvenile and subadult $p=0.01$; Fig. 2).

Fig. 1 Correlation between testicular volume (cm³) and body mass (g) in wild common marmosets.



There is a significant difference ($U=85.0, p=0.003$) in testicular volume between breeding and nonbreeding adult males (Fig. 3), but no difference for body mass ($U=190.0, p=0.87$; Table I). There is a significant positive correlation between testicular volume and body mass for nonbreeding males ($r_s=0.59, p=0.009$) but not for breeding males ($r_s=0.47, p=0.09$), as shown in Fig. 4.

Discussion

Body and testicular development in wild common marmosets appears to occur over different age ranges. Using body mass to monitor the physical development of wild common marmosets (Araújo *et al.* 2000) results in the same profile as that described for captive marmosets (Abbott and Hearn 1978). The body and testicular development curves that we obtained are in accordance with the typical pattern for anthropoid primates, with rapid neonatal growth, a slow juvenile phase, and a second peak of rapid development during adolescence (Plant 1988). Body mass values in the adult subjects were similar to those previously described (captive: Abbott and Hearn 1978; wild: Araújo *et al.* 2000) and to those of captives observed for testicular volume (Abbott and Hearn 1978; Dixson 1986). Testicular volume in infants and juveniles is similar but a rapid increase occurred between the juvenile

Fig. 2 Relative testicular volume (cm³) (mean ± SE) at different ages in wild common marmosets. Bars not sharing a same letter are statistically different from each other.

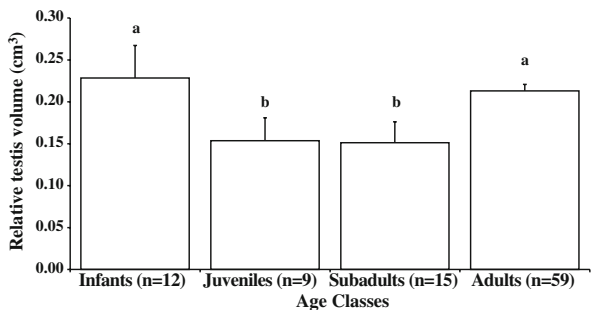
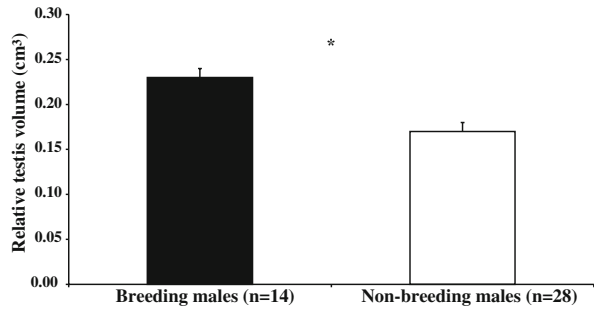


Fig. 3 Testicular volume/body mass ratio (mean \pm SE) in breeding and nonbreeding adult wild common marmosets (* $p=0.01$).



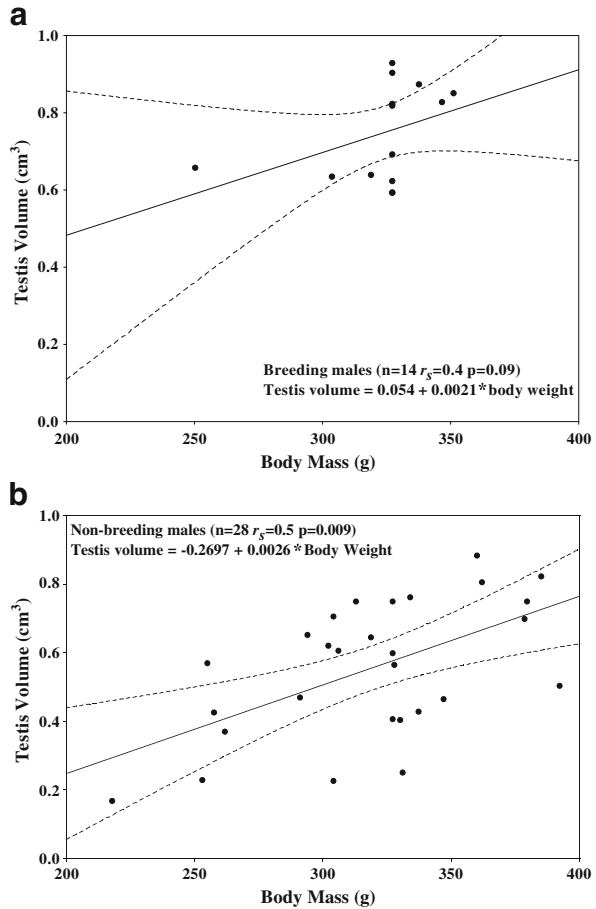
and subadult ages, reaching, as expected, the highest values in adulthood. However, relative testicular volume, i.e., testicular volume/body mass ratio, is comparable in the infantile and adult stages, indicating relatively large testicular volume during infancy. According to Luetjens *et al.* (2005) and Li *et al.* (2005), in common marmosets, after birth the number of testicular germ cells starts to increase from 5–6 wk until 5 mo. The number of both Leydig and Sertoli cells associated with testosterone production and spermatogenetic process, respectively, also increases during the infantile stage, decreasing from the 6th to 8th mo (Li *et al.* 2005). Therefore, the increase in testicular volume in the infantile stage is associated with testicular cell proliferation. Increased testicular volume in adults is related to increased spermatogenetic activity, testosterone production, and spermatozoid maturation (Li *et al.* 2005). The relatively high testicular volume in the infantile stage is also coincident with the peak of testosterone production from birth until the 110th day in male common marmosets (Dixson 1986). It is important to note that we measured the testis when the individuals were 3–5 mo old because the fully descended testes in callitrichids occurs around then (*Saguinus oedipus oedipus*: 8 wk, Ginther *et al.* 2002; *Callithrix jacchus*: 50–70 d, Abbott and Hearn 1978). Indeed, Abbott and Hearn (1978) found a rapid increase in testicular growth from 9 to 24 mo of age. Ginther *et al.* (2002) recorded the same increase for *Saguinus oedipus oedipus*. Though we did not detect the same growth pattern as that of captives in the subadult stage, we noted large variability of volume, which might be due to more regular data collection under captive conditions.

We also found that testicular volume in adult common marmosets varies significantly according to their social status within the group. Our laboratory records and those of other researchers showing that callitrichids do not exhibit linear hierarchy (Araújo 1996; Rylands 1996; Stevenson and Rylands 1988; Sussman and

Table 1 Testicular volume and body mass according to the reproductive status of wild common marmoset (*Callithrix jacchus*) males at FLONA Nisia Floresta, Brazil

Male status	Testicular volume (cm ³)			Body mass (g)		
	Mean	Standard error	Range	Mean	Standard error	Range
Breeding (n=14)	0.75	0.03	0.59–0.93	323.20	6.36	250.30–351.00
Nonbreeding (n=28)	0.56	0.04	0.17–0.88	318.72	8.16	218.00–392.30

Fig. 4 Testicular volume (cm³) and body mass (g) correlation in breeding (a) and nonbreeding (b) wild common marmosets.



Garber 1987; cf. Röthe 1975; Röthe and Darms 1993), suggest that the increase might be related to the role of reproductive males in the social group. Dominant males assume a leadership position during intergroup encounters and, consequently, are more exposed to conflict and aggressive interactions with other individuals. According to Ross *et al.* (2004), testosterone increase in *Callithrix kuhlii* is proportional to the intensity of aggression during male-male conflicts, and males that are more aggressive produce significantly more testosterone than nonaggressive individuals do. Testosterone changes are also related to parental activities (*Callithrix jacchus*: Dixson and George 1982; *Callithrix kuhlii* Nunes *et al.* 2000) and postpartum estrus (Barbosa 2003). Testosterone concentration in *Callithrix kuhlii* also changes with parental care experience. Nunes *et al.* (2000) showed that, even in fathers that spend the same amount of effort in caring for infants, testosterone is higher when they are caring for the first litter than when caring for the second.

We demonstrate that testicular volume in adult common marmosets does not depend on body mass but instead on reproductive status. In all free-ranging groups researchers have studied to date (Araújo 1996; Arruda *et al.* 2005; Digby 1995; Lazaro-Perea *et al.* 2000), the researchers recorded no copulation between

subordinate males and breeding females. However, Arruda *et al.* (2005) noted that subordinate females copulated with extragroup males. The 4 groups Arruda *et al.* (2005) observed are included in our study, as are the neighboring groups containing the extragroup males. The extragroup copulations occurred infrequently in comparison to reproducing pair copulations.

Nievergelt *et al.* (2000) and Faulkes *et al.* (2003, *in press*) used microsatellite genotyping to investigate 5 social groups (also included in our study). The results of the studies suggest that genetic structure may often be more heterogeneous and the relatedness between adult males from the same group is significantly lower. However, given that most of our focal males do not belong to the sample of the aforementioned genetic studies, we cannot use the finding as an argument for the lower testicular volume of nonbreeding males. The breeding males and females are from different lineages resulting from migratory movements between the groups (Faulkes *et al.* 2003, *in press*; Nievergelt *et al.* 2000; Sousa *et al.* 2005, *in press*), which causes reproducing males to mate more regularly, whereas the nonreproducing males mate whenever possible with females from neighboring groups or when they assume a reproductive role (Arruda *et al.* 2005; Yamamoto *et al.* *in press*).

Thus, the increased testicular volume of breeding males seems to be related to challenging situations that dominant males face under natural conditions, such as resource defense (territory, mate, infants) and reproduction itself (mating, sperm production). Therefore, the reproductive strategies of common marmoset breeding males might be a combination of behavioral (mate guarding) and physiological (frequent copulation) mechanisms influencing their reproductive output.

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