Sociality in *Callithrix penicillata*: I. Intragroup Male Profile

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Abstract We analyzed the social interactions and behavior of adult males from a group of black-tufted-ear marmosets (*Callithrix penicillata*) to determine their roles and hierarchy in the group and how their behavior fits within the predictions of monogamic or polyandric mating systems in callitrichines. We monitored 1 group of marmosets from February to October 2005 in central Brazil. We conducted focal subject samples with 20 predetermined behaviors for adult and subadult males and registered all occurrences of agonistic behavior, affiliative behavior, copulations, and alarm vocalizations. Moreover, we recorded the height in the vegetation and proximity to other individuals by the focal subject. Males exhibited no clear dominance hierarchy based on either behavioral data or patterns of scent marking. Copulation and grooming patterns showed a social bond between 1 of the males and the dominant female, suggesting him as the group's putative breeding male, with no apparent competition for the position. There was no difference regarding other behaviors— alarm vocalization, infant carrying, and play—or the use of different vegetation strata among the males, and no indication of a specific role by the putative breeding male or any other male in the group. The presence of multiple males in marmoset groups and the behavioral profile generated in the current study suggest a mating system compatible with monogamy with helpers-at-the-nest structure.

Keywords callitrichinae · dominance hierarchy · intragroup · male behavior · primate

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Introduction

The definition of a mating system takes into account the number of breeding males and females in a social unit. Primate groups exhibit a variety of mating systems including monogamy, polygyny, polyandry, and polygynandry (multiple breeding males and females). Nevertheless, current knowledge about social organization and mating systems suggests that the number of reproductive males and females in a group is not a species-specific characteristic, but may vary among same-specific groups according to differences in habitat and demographic conditions (Strier 2000).

In general, classical studies of primates have emphasized the more conspicuous adult male behaviors such as aggression and dominance disputes, placing them in a central position in their social groups. However, more recently researchers have shown that in many species, the females constitute the real social nucleus and the relationships among males are more complex than had been expected (Hill and van Hoof 1994).

The Callitrichinae, comprising marmosets, tamarins, pygmy marmosets, and Goeldi's monkeys (Rylands *et al.* 2000), presents some striking characteristics associated with male behavior and sociality. The marmosets exhibit very flexible mating systems, with instances of polygyny, polyandry, and monogamy in the same species (Schaffner and French 2004). The presence of potentially reproductive adult males in wild marmoset groups raises questions about their relationships with the dominant females and their social role within the group.

The determination of dominance hierarchies is an important tool to decipher the social structure of groups and may serve as a predictive criterion for the study of behavioral phenomena involving social activities, foraging, and reproduction. In primates, dominance may be associated with a series of benefits, such as priority in feeding, health benefits, reproductive success, and infant survival (Walters and Seyfarth 1987). However, the connection between benefits and dominance rank is not always direct or even real (Qvarnström and Forsgren 1998; Walters and Seyfarth 1987). Research has shown that both dominants and subordinates, may experience physiological costs related to their social status (Creel 2001; Sapolsky 2005).

The presence of multiple adult males in a group appears related either to the failure of the dominant male to expel rivals or to the benefits associated with having male helpers (van Hooff 2000). However, an adult's decision to stay in the group as a helper may be related to ecological restrictions and benefits to future survival, reproduction, and inclusive fitness gains (Heinsohn and Legge 1999; Jennions and Macdonald 1994). The costs of rearing infants may be a key factor in the acceptance of >1 male in a group (van Hooff and van Schaik 1994).

Multimale groups of marmosets may present monogamous reproduction or facultative polyandry, and the degree of relatedness among the males may play an important role in their disputes for reproduction (Baker *et al.* 1999; Schaffner and French 2004). We expect that in groups with multiple members, wherein a queue exists to inherit the dominant breeder position, differences in the degree of help individuals provide will vary according to individual rank (Cant and Field 2005).

Though we now know that the mating system in the Callitrichinae is flexible, even intraspecifically in the subfamily, genetic data are scarce. As a result, behaviors performed by males, such as copulation and competition for females, become

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important diagnostic tools to indicate which mating systems better explain observed reproductive patterns (Baker *et al.* 1993; Heymann 2000; Wang and Milton 2003).

An additional approach to the study of mating systems involves the analysis of costly behaviors conducted by the males. Cooperative breeding subjects may present a pattern wherein dominant individuals are more stressed than subordinates, a cost related to social dominance (Creel 2001). The execution of costly behaviors by adult male marmosets may reflect possible social costs. However, we do not know whether the costs of such behaviors are incurred primarily by dominant males or are distributed evenly among all the adult males.

In Brazil, *Callithrix* is represented by 6 species (Rylands *et al.* 2000) characterized by social groups ranging from *ca.* 3 to 15 individuals and usually comprising family members and nonrelated migrants (Abbott *et al.* 1998; Stevenson and Rylands 1988). *Callithrix* spp. are classified as cooperative breeders because groups contain nonreproductive members that assist in rearing infants (Abbott *et al.* 1998). In wild groups of *Callithrix*, the dominant female may behaviorally and physiologically inhibit the reproduction of subordinate females, though another female commonly ovulates in a group (Sousa *et al.* 2005; Stevenson and Rylands 1988; Yamamoto *et al.* in press). In males, reproductive inhibition appears to be mainly behavioral, and evidence for physiological inhibition is ambiguous (Baker *et al.* 1999).

Black-tufted-ear marmosets (*Callithrix penicillata*), of central Brazil, have particular appeal for studies of sociality because they live in large groups, have adult helpers, and birth infants twice yearly (Miranda and Faria 2001; Vilela and Faria 2004). Despite their status as an endemic species of the rapidly disappearing savanna biome (cerrado) of Brazil, the accumulated knowledge about the species in the wild consists of few studies (Faria 1984; Miranda and Faria 2001; Vilela and Faria 2002, 2004), which lags far behind what is known for their congener, *Callithrix jacchus* (common marmoset).

We studied the social relationships and behavior of adult males in a wild group of *Callithrix penicillata* to determine their roles in the group. Based on the existing models for marmoset mating systems, we addressed the following questions: 1) Do consistent hierarchical interactions occur and reliably reflect relations between breeders and nonbreeders? 2) Do agonistic and marking behaviors reflect the presumed hierarchical structure among males (implying a reproductive dominance)? 3) Do partner preferences occur, and if so, are they signaled by affiliative and sexual behaviors among individuals? 4) What are the potential costs associated with the roles of males in the group?

Methods

Study Site

We conducted the study at Jardim Botânico de Brasília, Brazil (S 15°51′42″ W 47° 49′41″) and surroundings, an area that encompasses both mesophytic forest and dense savanna (cerrado) in which ca. 50% of the trees are 4–10 m high (Miranda 1997). Paved and dirt roads cross the local vegetation, facilitating visualization and

monitoring the group. The regional climate is marked by a distinct rainy season (October–April) and a dry season (May–September).

Study Subjects

We monitored the marmosets from February to October 2005. The initial group comprised 11 individuals (Table 1). In addition, 2 infants were born in February (from RPRD) and 3 in October (2 from RPRD and 1 from CT). We captured 6 marmosets from the group via a multiple-entrance trap and anesthetized them with ketamine (0.12 ml/kg) while they were in the trap. We removed them when unconscious and marked them with picric acid. We individually identified marmosets not captured via distinct body characteristics. We estimated the age of the individuals via body size and state of development of sexual organs, in addition to fur characteristics (development of ear tufts and white frontal blaze). Adults had fully developed ear tufts and sexual organs, whereas subadults had incomplete development of them. We released individuals where captured, and no individual was injured in the process. The group has been a study subject of the Neuroethology Laboratory from Universidade de Brasília for *ca.* 4 yr, and they are habituated to the observers.

Data Collection

Decanini and a field assistant followed the group during the mornings (between 0600 h or when the subjects awoke and 1200 h) or afternoons (between 1200 and 1800 h or until the subjects went to sleep), and usually monitored them at least once a week for each of the periods. We conducted 10-min focal subject samples (Altmann 1974) with 10-min intervals between samplings for adult and subadult males. We determined the order for observations of focal subjects randomly before the beginning of the observations, and if we did not find the subject of choice, we chose the next subject on the list.

For each observation period, we performed a maximum of 3 focal samplings per individual, and samples from the same individual were ≥1 h apart. During the focal sampling, we registered the occurrence and duration of 20 predetermined behaviors

Table 1 Summary characteristics of black-tufted-ear marmoset group at Jardim Botânico, Brazil

Individual	Sex	Age	Focal samples
TST	Male	Adult	74
CMN	Male	Adult	70
CMRC	Male	Adult	66
PTRS	Male	Subadult	65
BC	Male	Adult	63
PM	Male	Adult	62
RPRD	Female	Adult	–
CT	Female	Adult	–
RB	Female	Adult	–
CCL	Male	Infant	–
CESC	Female	Infant	–

on a palmtop (Appendix). We considered only focal observations of >5 min with a visible subject in the analysis. Concerning carrying behavior, we used only data from February 24 to May 24 and from September 22 to October 27 because they corresponded to the periods that the group members carried infants.

Before beginning each focal sample, we recorded the height of the subject in the arboreal stratum (<2 m, 2–5 m, >5 m). The height of the marmoset in the vegetation may be an indicator of vigilance behavior (Steenbeek *et al.* 1999). In addition, we conducted instantaneous scan samples at the beginning and end of each focal sample (Altmann 1974) to register the proximity (≤2 m) of group individuals relative to the focal male.

We registered the following behaviors for all subjects visible during the observation period via an all-occurrences method (Altmann 1974): agonistic behavior, affiliative behavior, copulations, and alarm vocalizations. Agonistic behavior includes contact aggression (biting, fur pulling), *ehr ehr* vocalizations, and chases/lunges followed by submissive behavior from the opponent, such as hiding, aversion, and *nga nga* vocalizations (Lazaro-Perea *et al.* 2004). We determined affiliation via grooming and playful behavior (Stevenson and Rylands 1988).

Data Analyses

We performed the hierarchical structure analyses via the dominance-directed tree method (Izar *et al.* 2006) that applies a technique capable of dealing with complex and nonlinear hierarchies. The method generates a graphic representation of dominance relationships, allowing visual analysis and detection of partial hierarchies.

We used only clearly dyadic agonistic interactions in the hierarchy analyses. By requirement of the method and following the definition of dominance by Drews (1993), which demands a consistent result in favor of 1 dyad member, we established dominance in the dominance matrix only when 1 member of the dyad conducted at least 2 more acts of agonism relative to the number to which it was subjected. Moreover, because it seems improbable that observation can show all hierarchical relationships between dominants and subordinates, to uncover the real hierarchical structure, the method also applies the assumption of transitivity (if A dominates B and B dominates C, then A dominates C) in the dominance matrix. The assumption may lead to the determination of new dominance relationships, distorting the original dominance matrix. It is necessary to evaluate such new information and the severity of distortions, e.g., number of new relationships established.

Because the data did not fulfill the normality requirement for parametric tests, we performed only nonparametric tests. We analyzed the behaviors registered in the all-occurrences (affiliative and copulation) and instantaneous scan sampling (proximity among individuals and height in vegetation) methods via the χ^2 test. We analyzed the differences between the males relative to the behaviors registered during the focal samples via the Kruskal-Wallis test and a nonparametric test *post hoc* (Zar 1999) when necessary.

We report the means of several parameters together with their standard deviations and medians. The significance level is $p \leq 0.05$, and all tests are 2-tailed. We performed the tests via the Excel 2002 and SPSS 12.0.

Results

Agonistic Interactions and Dominance Hierarchies

The data collection comprises *ca.* 327 h of field work. From the 110 possible dyadic interactions among the group's subjects, we observed 41 (38 unidirectional and 3 bidirectional; Table 2). The methods requirement of implying transitivity did not result in great distortions regarding the original dominance matrix and introduced only 1 extra dominance relationship (Table 2, signed [+]).

The dominance hierarchy established (Fig. 1) showed 2 marmosets as partial dominants: male BC and adult female RPRD. Though not subordinate to any of the other individuals in the group, BC was dominant to only 2 females (CT and RB), whereas RPRD dominated all individuals of both sexes, with the exception of BC. There was 1 event of agonistic behavior directed by RPRD toward BC (Table 2), although according to the method applied such information is not enough to establish a dominance relationship between them.Three dominance lineages of adult males (TST, CMRC, and CMN) were subordinate to RPRD. Four adult males (TST, CMRC, PM, and BC) dominated the other 2 females of the group (CT and RB).

The frequency of agonistic behaviors by the males was very low, with only 16 aggressive interactions occurring during focal samples. They basically consisted of lunges and chases without contact aggression, and no injury occurred during the interactions. The mean frequency of agonistic interactions per focal individual equaled 1.886 ± 21.553 s of agonism/h (median, 0.000 s of agonism/h). When we analyzed all occurrences of agonistic interactions of the males (Table 2), it became clear that they were almost never aggressive toward each other or toward the female RPRD. Aggression occurred essentially against infant CCL and females CT and RB.

Table 2 Agonistic behavior matrix for the black-tufted-ear marmoset group

	TST	CMN	CMRC	PM	BC	PTRS	RB	RPRD	CT	CCL	CESC
TST ♂		0 (0)	0 (0)	2 (1)	0 (0)	0 (0)	1 (+1)	0 (0)	5 (1)	1 (0)	0 (0)
CMN ♂	0 (0)		0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	2 (1)	2 (1)
CMRC ♂	1 (0)	0 (0)		2 (1)	0 (0)	2 (1)	6 (1)	0 (0)	8 (1)	2 (1)	0 (0)
PM ♂	0 (0)	0 (0)	0 (0)		0 (0)	0 (0)	5 (1)	0 (0)	5 (1)	1 (0)	0 (0)
BC ♂	0 (0)	0 (0)	0 (0)	0 (0)		0 (0)	4 (1)	0 (0)	4 (1)	0 (0)	0 (0)
PTRS ♂	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)		0 (0)	0 (0)	0 (0)	5 (1)	0 (0)
RB ♀	0 (0)	0 (0)	1 (0)	0 (0)	0 (0)	1 (0)		0 (0)	1 (0)	0 (0)	1 (0)
RPRD ♀	10 (1)	4 (1)	2 (1)	5 (1)	1 (0)	10 (1)	4 (1)		5 (1)	6 (1)	12 (1)
CT ♀	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	1 (0)	0 (0)	0 (0)		0 (0)	2 (0)
CCL ♂	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	1 (0)		0 (0)
CESC ♀	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	1 (0)	

The signaled (+) numbers indicate dominance relationships obtained when transitivity is applied.
Values outside the parentheses refer to empirical observations of agonistic behavior and the values within parentheses refer to assigned dominance status.
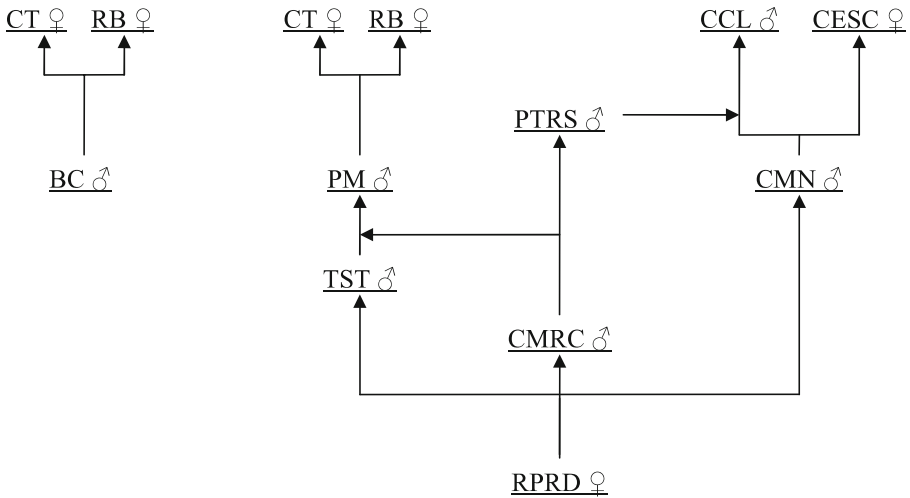
Fig. 1 Dominance hierarchy in black-tufted-ear marmosets.

Social Relationships: Analysis of Behavioral Patterns

Individuals spent *ca.* 11.5 ± 70.052 s/h grooming (median, 0.000 s/h). In the all-occurrences record of grooming, the dominant female RPRD was the main recipient in the group. Males varied in how much time they spent grooming other group members ($\chi^2=31.98$; df=5; $p<0.001$, Kruskal-Wallis test). The test *post hoc* indicated that TST was the main groomer ($Q_{0.05, 6}$; $p<0.05$). He directed grooming mostly toward RPRD, which accounted for 25 (55.5%) of the 45 events in which RPRD was groomed (Table 3).

Table 3 Frequencies of grooming (as initiator and recipient) and playing behaviors for black-tufted-ear marmosets

Individual	Grooming				Playing	χ^2
	Agent	χ^2	Recipient	χ^2		
TST	35	47.648	11	0.026	7	12.347
CMN	0	11.545	9	0.561	1	22.374
CMRC	17	2.577	6	2.664	16	2.854
PTRS	12	0.018	16	1.719	67	74.813
BC	17	2.577	20	6.191	26	0.114
PM	9	0.561	7	1.790	29	0.895
RPRD	2	7.892	45	96.939	–	–
CT	2	7.892	4	4.931	–	–
RB	24	13.435	3	6.325	–	–
CCL	3	6.325	2	7.892	–	–
CESC	6	2.664	4	4.931	–	–
Total	127	103.134[a]	127	133.969[a]	146	113.397[a]

χ^2 tests for grooming used expected values of 11.5 and df=10. Playing expected values were 24.3 and df=5.
[a] $p<0.001$.

Participation in play behavior was mostly by subadult PTRS (Table 3) together with infants CCL and CESC (36 of the 67 events of playing). The proportion of time spent playing also varied among the focal males (χ^2=15.60; df=5; p=0.008, Kruskal-Wallis test), and PTRS was the most active individual for the behavior in comparison with CMN and TST. ($Q_{0.05,\ 6}$; p<0.05, test *post hoc*).

The mean time spent scent-marking was equivalent to 31.6±68.544 s/h per individual (median=0.000 s/h). Males did not differ in the time spent scent-marking (χ^2=4.43; df=5; p=0.49, Kruskal-Wallis test). All scent marks that focal males executed were circumgenital, and we observed sternal markings only in subjects from other groups.

Alarm vocalizations were rare, occurring only 25 times, with a mean individual frequency equivalent to 7.01±88.603 s/h (median, 0.000 s/h). The alarms happened especially when birds flew overhead and also at sightings of small mammals, dogs, and strange people. Males did not differ in their frequency of alarm-calling (χ^2=6.93; df=5; p=0.23, Kruskal-Wallis test). No adult male showed preference for high, medium, or low strata (df=2; p>0.05, χ^2 test). However, subadult PTRS tended to use the low stratum and avoid the high one: expected value (24.7, χ^2 test), observed low value (40; χ^2=9.53), observed medium value (21; χ^2=0.55), and observed high value (13; χ^2=5.52; χ^2_{total} = 15.60; df=2; p<0.001).

All focal males in the group carried infants. After the first birth, RPRD's twins were carried for 3 mo (February 24 to May 24). On September 22, RPRD produced 2 more infants, after which we monitored the group until October 27, at which point, the subjects were still carrying infants. As to CT's offspring, born *ca.* October 26, only CT carried the newborn. There is no significant difference in the proportion of time each of the males carried infants (χ^2=7.44; df=5; p=0.19, Kruskal-Wallis test; Fig. 2).

In most scans, focal males were ≥2 m apart from the rest of the group (we did not include infants in the analysis).TST was alone in 51.7% of the scans, CMN in 69.2%, CMRC in 79.5%, PTRS in 63.3%, BC in 84.6%, and PM in 84.7%. The proximity data show that TST, PTRS, CMRC, and PM had a preference for certain individuals and that TST was the only male that preferentially maintained proximity to RPRD (Table 4).

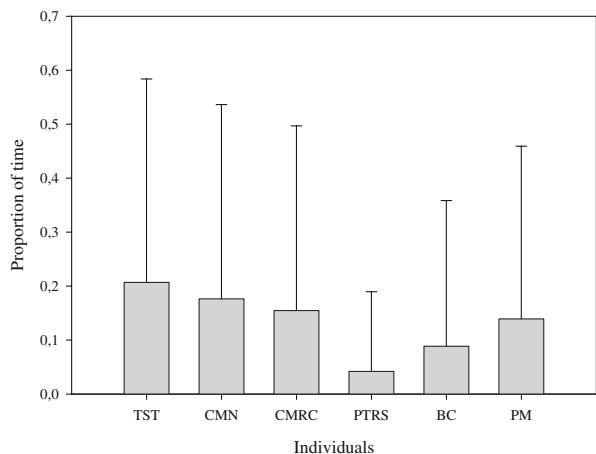Fig. 2 Proportion of time focal males spent carrying infants (mean ± SD).

Table 4 Proximity between focal male and the other individuals

Dyad	Proximity		χ^2	Dyad	Proximity		χ^2
	Observed	Expected			Observed	Expected	
TST-CMN	3	10.6	5.449	PTRS-TST	8	7	0.143
TST-CMRC	4	10.6	4.109	PTRS-CMN	1	7	5.143
TST-PTRS	5	10.6	2.958	PTRS-CMRC	5	7	0.571
TST-BC	3	10.6	5.449	PTRS-BC	5	7	0.571
TST-PM	2	10.6	6.977	PTRS-PM	2	7	3.571
TST-RPRD	46	10.6	118.223	PTRS-RPRD	10	7	1.286
TST-CT	5	10.6	2.958	PTRS-CT	4	7	1.286
TST-RB	11	10.6	0.015	PTRS-RB	3	7	2.286
TST-CCL	13	10.6	0.543	PTRS-CCL	14	7	7.000
TST-CESC	14	10.6	1.091	PTRS-CESC	18	7	17.286
Total	106		147.774[a,b]	Total	70		39.143[a,b]
CMN-TST	6	4.9	0.247	BC-TST	2	2.7	0.181
CMN-CMRC	7	4.9	0.900	BC-CMN	4	2.7	0.626
CMN-PTRS	2	4.9	1.716	BC-CMRC	1	2.7	1.070
CMN-BC	2	4.9	1.716	BC-PTRS	3	2.7	0.033
CMN-PM	2	4.9	1.716	BC-PM	2	2.7	0.181
CMN-RPRD	9	4.9	3.431	BC-RPRD	0	2.7	2.700
CMN-CT	3	4.9	0.737	BC-CT	0	2.7	2.700
CMN-RB	3	4.9	0.737	BC-RB	3	2.7	0.033
CMN-CCL	10	4.9	5.308	BC-CCL	5	2.7	1.959
CMN-CESC	5	4.9	0.002	BC-CESC	7	2.7	6.848
Total	49		16.510[a,c]	Total	27		16.333[a,c]
CMRC-TST	2	4.1	1.076	PM-TST	0	2.4	2.400
CMRC-CMN	2	4.1	1.076	PM-CMN	1	2.4	0.817
CMRC-PTRS	8	4.1	3.710	PM-CMRC	5	2.4	2.817
CMRC-BC	1	4.1	2.344	PM-PTRS	3	2.4	0.150
CMRC-PM	6	4.1	0.880	PM-BC	1	2.4	0.817
CMRC-RPRD	3	4.1	0.295	PM-RPRD	2	2.4	0.067
CMRC-CT	0	4.1	4.100	PM-CT	0	2.4	2.400
CMRC-RB	4	4.1	0.002	PM-RB	7	2.4	8.817
CMRC-CCL	8	4.1	3.710	PM-CCL	2	2.4	0.067
CMRC-CESC	7	4.1	2.051	PM-CESC	3	2.4	0.150
Total	41		19.244[a,b]	Total	24		18.500[a,b]

[a] df=9.
[b] $p < 0.05$.
[c] $p > 0.05$.

We observed copulation between only 2 individuals: TST copulated with RPRD on March 18, and attempted copulations occurred on February 11 and March 17. Olfactory inspection of genitalia also occurred only between TST and RPRD, on March 18 and 25, April 6, and September 29. The regression of the birth date (*ca.* September 21) of RPRD's second set of twins, using a gestation period of 5 mo (Stevenson and Rylands 1988), indicates a probable conception date *ca.* mid-April. Though the probable conception date does not coincide with the observed copulation, the copulation registered between TST and RPRD occurred in the period of postpartum estrus 2–4 wk after the birth of the first set of twins (*ca.* February 24). This suggests that TST is the most likely male breeder of the group.

Discussion

Hierarchical Interactions and Relations between Breeders and Nonbreeders

The low rate of agonistic behavior in the black-tufted-ear marmoset group makes dominance relationships difficult to measure. Nevertheless, we were able to establish a hierarchy structure using the dominance-directed tree method. The obtained structure does not fit a linear pattern. However, the lack of linear hierarchy does not mean the absence of hierarchy (Izar *et al.* 2006). The social structure suggests that the breeding female was dominant in the group. However, the findings show no clear dominance among males, not even of the putative breeder TST.

Our results concerning the hierarchical structure of *Callithrix penicillata* coincides and differs, in several aspects, from those of better known species of Callitrichinae. For instance, in common marmosets, Stevenson and Rylands (1988) report a couple as dominant over the remainder of the group, with the female dominant over the male. Yet, they report that marmoset groups do not form an ordered and linear hierarchy. Baker *et al.* (1993) reported dominance among male golden-lion tamarins (*Leontopithecus rosalia*), with the breeding male retaining the uppermost rank.

Association of Agonistic and Marking Behaviors with Hierarchy among Males

Aggression can be a direct outcome of contests over resources, such as food and sleeping sites, and for males, over access to reproductive females. Males may assume high risks in the disputes because a breeding female may represent greater direct fitness than other resources (Smuts 1987; Walters and Seyfarth 1987).

However, adult male *Callithrix penicillata* did not exhibit high levels of aggressive behaviors among themselves in possible disputes for the breeding position. The dispute for females conceivably takes place through more discrete behaviors, e.g., sperm competition (Schaffner and French 2004; Strier 2000). Alternatively, subordinate males may not compete for the position of breeding male to avoid incest because of a possible high degree of relatedness within the group (Baker *et al.* 1999). As an additional possibility, the low aggressiveness may have been due to a well-established dominance and the fact that, with the exception of new members added through births, a stable group composition was maintained throughout the study period.

Olfactory communication through scent-marking may function in intra- and intergroup contexts among neotropical primates. One possibility is that scent marking is used to transmit intragroup dominance. Such behavior may help to determine and to maintain dominance among group members by suppressing subordinate male aggressive behavior (Snowdon 2004; Walraven and Elsacker 1992). If scent-marking communicates social status within the group, one may expect that dominant individuals should mark more than subordinates do. Such differences in scent-marking by males occur among both golden-lion tamarins and common marmosets (Epple 1973; Miller *et al.* 2003). However, we noted no difference in the males' frequencies of scent-marking, further indicating the absence of clear dominance among them.

Partner Preferences Signaled by Affiliative and Sexual Behaviors

Allogrooming may be a good measure of social relationship among New World primates, generating benefits such as removal of ectoparasites or enhancement of psychological and physiological well-being for the individual groomed (Lazaro-Perea *et al.* 2004). However, because the available time for grooming is restricted in the daily budget, researchers usually analyze grooming relationships in the context of kin selection, reciprocity, and breeding competition (Schino 2001; Silk 1987). Grooming asymmetries between individuals may reflect exchanges in services between partners, e.g., support in disputes, access to food, and help in rearing infants (Lazaro-Perea *et al*. 2004).

The grooming pattern found for the black-tufted-ear marmoset group indicates that the reproductive female RPRD was the main target of grooming executed by TST, suggesting a strong social bond between them. The closer proximity maintained between the 2 individuals and the observed copulation and attempted copulation also support the deduction that the 2 individuals constitute the main reproductive pair in the group. The findings share similarities to what is described for common marmosets, among which the breeding pair remains closer to each other compared to other adults in the group and an asymmetric relationship also exists between the pair, with the male grooming the female more actively (Lazaro-Perea 2000; Stevenson and Rylands 1988).

Potential Costs Associated with Male Roles

The connection between social status and stress-related costs among marmosets points to dominant individuals experiencing a higher cost than subordinates do (Abbott *et al.* 2003; Creel 2001). Infant-carrying behavior is a potentially costly activity because infant size and weight reduces foraging time and ability to move efficiently (Schradin and Anzenberger 2001; Tardif and Bales 1997). Breeding males are expected to be more involved with carrying infants (Schradin and Anzenberger 2001).

However, our results do not indicate that carrying infants was a predominant responsibility of any particular male, and costs were apparently distributed fairly evenly among all males. Therefore, TST in the position of putative breeder appeared to experience no obvious cost. Our results contrast with the findings of a study with captive common marmosets, in which the reproductive males spent more time carrying infants than each of the helpers individually did, a difference that was larger in smaller groups (Mills *et al.* 2004). Though it remains uncertain whether there is a direct causal relationship between the number of helpers and offspring survival in wild groups of callitrichines, the presence of helpers appears to distribute the costs of infant carrying and may result in a greater success of the newborns (Bales *et al.* 2000; Santos *et al.* 1997).

Another probable cost could be the time a subject spends as a social facilitator during situations involving play activities, which lead to infant learning (Strier 2000). Though play behavior also was performed by adults in the focal group, playing occurred predominantly among the youngest individuals, as typically

described by Stevenson and Rylands (1988). None of the adults appeared to experience any cost in this regard.

Predation is a serious threat to callitrichines (Goldizen 1987), and adult males presumably may experience some restrictions in their foraging time to participate in vigilance (Bicca-Marques 2003). Our results for the black-tufted-ear marmoset do not suggest that specific males or the breeding male takes on vigilant roles or emits a higher frequency of alarm calls associated with predator detection. For a few primate species, some evidence favors the proposition. For example, Bicca-Marques (2003) suggests that the dominant male among the emperor tamarins (*Saguinus imperator*) has a special role in vigilance. Also, among langurs (*Presbytis thomasi*), the subjects carry out vigilance in risky positions, such as exposed areas on the ground and in branches in the canopy, especially while females forage on the ground (Steenbeek *et al.* 1999).

Our results do not support the hypothesis positing a relationship between dominance status and the execution of costly behaviors in which dominant individuals experience the highest costs. The findings show no clear cost associated with any male, in aggression, carrying of infants, playing, or vigilance. Allogrooming was the only behavior that clearly differed among the males.

Callitrichine Mating System and Male Roles

More than 1 adult male in cooperative groups of callitrichines warrants an explanation concerning their reproductive role. Monogamy and cooperative polyandry are 2 alternative systems that researchers can apply to describe such systems. Authors who propose cooperative polyandry instead of monogamy as the typical breeding system among callitrichines suggest the following as supporting evidence: large number of groups with several males, low levels of aggression among males within groups, male participation in rearing infants, and sexual activity of >1 male with the same female. However, the mating system of monogamy with helpers at the nest also may be applied to callitrichines (Baker *et al.* 1993). In common marmosets, the high productivity, with 2 births of twins per yr, ensures a good number of related helpers (Ferrari and Digby 1996; Heymann 2000).

We also found this profile in our study of wild black-tufted-ear marmosets. The behavioral data pointed to a monogamous system, with TST as the breeder and the remainder of the adult males as helpers, possibly related. However, one seldom observes wild marmosets copulating, and we could not discard more furtive strategies of extrapair copulation by the main reproductive female, RPRD.

In conclusion, though observations of callitrichines suggest a monogamous mating system, we consider it important to take into account the high level of inter- and intraspecific flexibility (Heymann 2000). Further studies involving genetic data would help to elucidate questions about their mating systems.

Appendix

Table 5 Behavioral repertoire of black-tufted-ear marmosets

Category	Behavior of focal individual
Alarm	Alarm vocalization
Allogrooming	Picking through the fur of another individual
Autogrooming	Picking through one's own fur
Vocalization	Executing vocalization (except alarm, submissive, and aggressive)
Gummivory	Gouging, eating, or licking plant exudates
Foraging	Looking for food or manipulating substrate
Moving	Moving, alternating the position of anterior and posterior members
Resting	Standing still, with members relaxed or the body extended
Stop	Standing still, but members are not relaxed
Avert	Moving >20 cm away from another animal
Nonaggressive approach	Moving toward another animal without displaying signs of aggression
Agonism	Performing *ehr ehr* vocalizations, displaying genitals, chasing, lunging, biting, grabbing other individual
Submissive	Performing *nga-nga* vocalizations
Scent-marking	Rubbing genital or sternal area on a substrate
Play	Rolling on the ground, grabbing and biting another individual in a contained way
Carrying	Carrying 1 or 2 infants
Scratching	Rubbing anterior or posterior members rapidly against the fur
Eating (animal)	Eating animal prey
Eating (plant)	Eating fruits or other plant parts (except exudates)
Copulation or attempted copulation	Mounting or being mounted by a partner, placing genitals in close proximity. Pelvic movements may occur
Other	Behavior that does not fit any of preceding categories

Based on Stevenson and Rylands (1988) and Lazaro-Perea (2000).

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