# Sociality in *Callithrix penicillata*: II. Individual Strategies During Intergroup Encounters

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Abstract In social animals, intergroup interactions, whether through agonistic and competitive behaviors or affiliative ones, can influence important parameters such as home range, territory sizes, and access to resources, which may directly affect both female and male fitness. We studied the intergroup interaction patterns of a wild group of black-tufted-ear marmosets (Callithrix penicillata) in central Brazil. Agonistic interactions occurred at low frequencies during intergroup encounters. The marmosets directed agonistic interactions without physical aggression primarily against same-sex individuals, suggesting that male and female aggression patterns are shaped by their sexual interests. However, females of the focal group also directed agonistic behavior toward extragroup males that attempted copulation. The marmosets appeared to use intergroup encounters to gather information about possible partners and extragroup reproductive opportunities. Intergroup sexual interactions occurred mainly in the form of copulations or attempted copulations by all adults, with the exception of the dominant female. Our results suggest that a possible reproductive strategy used by males is to attempt fertilization of extragroup females. Adult males copulated with the same extragroup female during several opportunities, which suggests sperm competition or the establishment of social bonds with neighboring females.

 $\textbf{Keywords} \ \ \text{affiliative interactions} \cdot \text{agonistic interactions} \cdot \text{Callitrichinae} \cdot \text{intergroup} \cdot \text{primate}$ 

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#### Introduction

The study of intergroup interactions can clarify the complex relationships among neighboring animals (Cant *et al.* 2002; Cheney 1987). In most group-living species, intergroup interactions are agonistic, but the level of hostility between groups may vary, from mutual avoidance to lethal aggression, including chases, aggressive displays, and fights and is, to a great extent, related to territory demarcation and defense (Cheney 1987; Cooper *et al.* 2004). Territorial defense against rival groups occurs in several cooperative breeding species. The relationship between territory quality and reproductive success makes territorial defense one of the groups' most important activities (Cant *et al.* 2002). For primates, success in intergroup competitions can affect home range size and quality, which can have consequences in terms of female reproductive success and probably also male fitness (Cords 2000; Nunn and Deaner 2004).

Moreover, the occurrence of aggressive interactions among individuals within the same group may be influenced by contact with individuals from other groups, frequently of the opposite sex, which suggests that conflicts over access to reproduction also occur (Cant *et al.* 2002; Schaffner and French 1997). The interactions could also function to defend or to secure reproductive resources within the individual's own group. Nonetheless, during the encounters, affiliative interactions can also occur, and include play behavior, grooming, and copulation between individuals of different groups (Cheney 1987). The affiliative component of encounters suggests that, besides territorial defense, encounters may allow access to possible migration and reproductive opportunities (Goldizen 1987).

Cooperative breeding systems are characterized by the involvement of individuals other than the parents in rearing the offspring (Jennions and Macdonald 1994). Cooperative breeding mammals exhibit a variety of mating systems, but reproductive opportunities within the group may be limited to a primary couple (high reproductive skew), and helpers may have little or no direct reproductive success while they remain in the group as subordinates (Abbott *et al.* 1998). Ecological restrictions to migration and benefits of philopatry are among the reasons for helpers to stay in their natal groups (Emlen 1982a, b; Jennions and Macdonald 1994).

Usually, there are 2 possibilities for helpers to reproduce: they may either attain a breeding position in their natal group, or they may migrate to neighboring groups where there may be reproductive opportunities. In the latter context, intergroup encounters allow helpers to obtain information about neighbors, even during aggressive interactions and territorial defense and, in general, the participation of helpers in nonaggressive interactions with extragroup individuals suggests that the contact and knowledge about neighbors may be important functions of the encounters (Lazaro-Perea 2001).

Another possibility for reproduction for helpers is that of extragroup copulation without migration. Males secure clear benefits in terms of direct reproductive success by performing such behavior. For females, in general, the advantages are less clear, but the fact that they sometimes actively search for extragroup copulations suggests that they may also gain benefits, possibly via the increase in genetic diversity of their offspring or by inbreeding avoidance (Cant *et al.* 2002).



Marmosets exhibit cooperative breeding in conjunction with a variety of mating systems, ranging from monogamy to polygyny and polyandry (Rylands *et al.* 2000; Yamamoto *et al.* in press). *Callithrix* comprises 6 species in Brazil, which occur in habitats that include Atlantic and tropical rain forests and savannas with shrubs (Rylands *et al.* 2000; Stevenson and Rylands 1988). Adults range in mass from 300 to 450 g and exhibit characteristic ear tufts. Groups are highly territorial; during intergroup encounters individuals exhibit behavior that includes both agonistic and affiliative components (Stevenson and Rylands 1988). Genetic data from wild callitrichines indicate the possibility of migration for both sexes (Faulkes *et al.* 2003; Nievergelt *et al.* 2000).

Groups are usually structured around a dominant breeding couple with low levels of aggression among members. The dominant female can behaviorally and physiologically inhibit the reproduction of the subordinate females (Stevenson and Rylands 1988). Researchers have shown, especially with common marmosets (*Callithrix jacchus*), that subordinate female reproductive suppression is not complete, and usually ≥1 other female in the group can ovulate (Sousa *et al.* 2005; Ziegler and Sousa 2002). A few studies with captive male callitrichines suggested a degree of endocrine suppression of the sexual behavior of male helpers (Bales *et al.* 2006). However, other studies in captivity and in the wild showed no hormonal suppression of males (Baker *et al.* 1999; Ginther *et al.* 2001; Huck *et al.* 2005). One can perceive the existence of intragroup behavioral incest avoidance (Baker *et al.* 1999; Ginther *et al.* 2001).

Black-tufted-ear marmosets (*Callithrix penicillata*) inhabit forest and savanna formations in the Cerrado biome of central Brazil. In general, they form groups of 2–13 individuals that produce 2 pairs of twin infants per year. Along with common marmosets, they are the most ecologically successful marmosets in the genus (Miranda and Faria 2001). However, there are very few ecological and behavioral studies of wild black-tufted-ear marmosets (Miranda and Faria 2001; Vilela and Faria 2002, 2004). Data from intergroup interactions in the species are also scarce, but Miranda (1997) recorded the occurrence of encounters with agonistic events.

We describe intergroup encounter patterns for black-tufted-ear marmosets to test 2 conjectures: 1) that involvement of breeding and nonbreeding individuals in encounters is substantially different and 2) that individuals may use encounters to gather information about reproductive opportunities.

## Methods

## Study Area

We conducted the study in central Brazil, at the Brasilia Botanical Garden (15°51′ 42″ S, 47°49′41″W) and surroundings. The study site encompasses mesophitic forest and dense cerrado (savanna with shrubs), with about 50% of trees between 4 and 10 m tall (Miranda 1997). Though the area is open to public visitation, there is a low level of human disturbance. There are paved and dirt roads between natural vegetation quadrants, which made tracking the subjects much easier. The regional



climate has distinct rainy (October-April) and dry (May-September) seasons (Miranda 1997).

# Study Subjects and Data Collection

From February to October 2005, we monitored 1 group of black-tufted-ear marmosets, initially comprising 11 individuals (Table 1). We captured 6 marmosets from the group with a multiple entrance trap and anesthetized them with ketamine (0.12 ml/kg). While the individuals were still unconscious, we removed them from the trap and marked them with picric acid. We individually identified other group individuals that we did not capture via distinct body characteristics. We estimated individual ages via body size and state of development of sexual organs, in addition to fur characteristics that include the 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 at the site of capture, and injured none in the process. Staff of the Neuroethology Laboratory from University of Brasilia has studied the group for *ca.* 4 yr, and the individuals are well habituated and allow close proximity of observers for long periods.

The group had a nonlinear hierarchical structure with a dominant female (RPRD) and no clear dominance among males, but data from proximity, grooming, and copulations suggested that individual TST was the putative breeding male (Decanini and Macedo 2008). In February, RPRD produced 2 offspring, and in October 3 more infants were born: 2 from RPRD and 1 from CT.

Observations occurred during morning or afternoon periods, between 0600 h and 1800 h, and generally Decanini and a field assistant followed the group during each period once a week. We determined the beginning of an intergroup encounter when  $\geq 1$  individual from another group was in the proximity of the study group, and it ended when we perceived no individual from another group in the surroundings.

We considered an individual a participant in the encounter when it performed any of the behaviors in Table 2 directed toward an individual from another group. We recorded the time of each interaction and, when possible, the identity or sex of the interacting individuals. During intergroup encounters, we collected data according to the all-occurrences method (Altmann 1974). We defined 2 encounters as independent of each other when they occurred ≥30 min apart.

## Data Analyses

Because the data do not have a normal distribution even when transformed, we used only nonparametric tests. For the data concerning participation in intergroup encounters we used a  $\chi^2$  test (Excel package). In the comparison concerning the frequency of behavior between individuals (agonism and nonaggressive approach), we applied the Kruskal-Wallis test with the SPSS statistics package, and the nonparametric test *post hoc* per Zar (1999) with the Excel package. Our significance level is  $p \le 0.05$  and all the tests are 2-tailed.



Table 1 Individual and intergroup encounter data for the focal group of black-tufted-ear marmosets at the Brasilia Botanical Garden, Brazil

Individual	Sex Age	Age	Status	Participation $(\chi^2)$ Target of agonism	Target o	of agonism		Target o	Target of approach	l u	Copulations or attempts
					Male	Female	Male Female Unknown	Male	Female	Male Female Unknown	
TST	M		Subordinate/putative breeder	9 (1.68)	3	2	7	0	1	0	1
CMN	$\boxtimes$		Subordinate	13 (0.05)	6	0	S	0	5	0	10
CMRC	$\boxtimes$		Subordinate		20	0	∞	0	12	1	6
PTRS	$\boxtimes$		Subordinate	18 (1.27)	56	4	∞	11	3	5	0
BC	$\boxtimes$			18 (1.27)	19	_	∞	0	4	2	9
PM	$\boxtimes$		Subordinate	20 (2.77)	16	7	6	7	9	33	5
RPRD	щ	Adult	Dominant/breeder	5 (5.63)	5	7	2	0	0	0	0
$_{\rm CL}$	ч		Subordinate/breeder	12 (0.24)	7	9	2	0	-	0	2
RB	Щ		Subordinate	18 (1.27)	12	12	7	3	4	1	3
CCL	$\boxtimes$		Subordinate	11(0.58)	11	-	4	4	7	0	0
CESC	щ		Subordinate	8 (2.45)	6	ю	2	-	7	0	0
Total $\chi^2$				(19.95) p < 0.03							

 $\chi^2$  test of participation on encounters: expected value=13.8; df=10 M = male, F = female. We estimated age based on the individual's physical characteristics. The status of individuals is based on Decanini and Macedo (2008). Participation refers to the frequency each individual was involved in intergroup encounters. Agonistic behavior data do not include contact aggression



#### Results

## Patterns in Intergroup Encounters

We recorded 35 intergroup encounters, resulting in 51 h 23 min of observation time. The encounters lasted from 7 min to 3 h 49 min (median=1 h 19 min). Because we conducted observations in half-day periods and some of the morning encounters occurred late in the morning and were therefore interrupted at noon, the maximum duration time may be underestimated. Most of the encounters were between 2 groups (86%) and only 5 were between 3 groups. The number of individuals from the focal group involved in the encounters varied from 1 to 11 (median=4), and in 4 encounters the groups were close together, but no individual presented any of the behaviors in Table 2.

In 74% of the encounters, we observed nonaggressive approaches between individuals from different groups. The proportions of occurrence of other behaviors were: agonism in 63% of the encounters, sexual behavior in 54%, submission in 40%, and affilliative in only 9%. Individuals differed in the degree of their involvement in the encounters (Table 1;  $\chi^2$ =19.95, df=10, p<0.03). RPRD had a lower participation than expected (Table 1;  $\chi^2$ =5.63).

## Agonistic Behavior During Encounters

Intergroup agonistic behaviors by individuals occurred with a mean frequency of  $3.9\pm5.4$  per h (median=2.0), and individuals exhibited significantly different rates of agonistic interactions (Kruskal-Wallis test,  $\chi^2$ =20.14; df=10, p=0.028; Fig. 1). However, the nonparametric test *post hoc* could not define which individuals showed different rates within the comparison (Zar 1999).

Most of the intergroup agonistic interactions occurred without aggressive contact. Genital displays, chases, and lunges corresponded to 85.6% of the events, whereas

Table 2 Behavior during intergroup encounters for black-tufted-ear marmosets at Brasilia Botanical Garden, Brazil

Behavior	Definition
Submissive	Nga-nga vocalizations
Copulation or attempted copulation	Mount or be mounted by a partner, place genitals in close proximity. Pelvic movements may occur.
Affiliative	• •
Grooming	Pick through the fur of another individual.
Play	Roll on the ground, grab and bite another individual in a contained way.
Nonaggressive approach	Move toward another individual without displaying signs of aggression.
Agonism	
Genital display	Raise tail and expose genitals to another individual.
Lunges	Move the body quickly toward another individual or pursue the individual aggressively, without contact aggression.
Contact aggression	Grab, bite, hit, push another individual.

Based on Lazaro-Perea (2000)



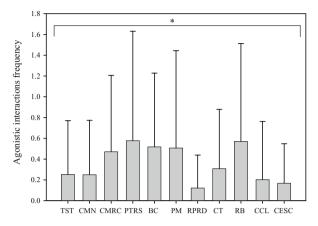


Fig. 1 Agonistic behavior events per hour (mean ± SD) during intergroup encounters for black-tufted-ear marmosets at Brasilia Botanical Garden, Brazil.

contact aggression itself accounted for only 14.4%. Aggressions took place mainly during 6 generalized fights between groups, involving 4–7 focal group individuals, wherein we observed 89.5% of the aggression events. During these fights, it was impossible to record either the identity or the sex of the aggression victims in the focal group or the other groups involved. During one of the fights, several individuals from the focal group were on the ground, biting 1 individual from the other group. However, after the aggression event we saw no individual bleeding or with other injuries.

The data from agonistic behavior without aggressive contact allow a better identification of the target sex for the behaviors (Table 1). In general, males, with the exception of TST, directed agonistic behavior toward other males. The agonistic behaviors of adult females were directed against both strange females and males, with the latter occurring mainly in the form of lunges when the males tried to copulate with them and were repelled. We recorded only 2 events of intragroup aggression during intergroup encounters, and neither of them appeared to be clearly related to the encounters

## Nonaggressive Approach

The mean frequency of nonaggressive approach is  $1.5\pm1.8$  per h (median=0.9), and it differs significantly among individuals in the group (Kruskal-Wallis test,  $\chi^2$ =39.08, df=10, p<0.001). The subadult male PTRS approached extragroup individuals at a significantly higher frequency than CESC, TST, CT, and RPRD did (test *post hoc*,  $Q_{0.05, 11}$ ; p<0.05). PM and CMRC also presented significantly higher frequencies of approach than RPRD did. RPRD approached (nonaggressively) no individual from another group; CT and TST approached extragroup individuals nonaggressively only once, and CESC did so 3 times. Relative to the target sex for nonaggressive approach, it is clear that adult males in general approached females more frequently (Table 1). However, subadult PTRS did not demonstrate this preference.



### Sexual Events

The mean frequency of sexual events during intergroup encounters is  $0.9\pm1.3$  per h (median=0.4). All the group's adults, except RPRD, engaged in sexual contact with individuals from another group (Table 1). However, there is a striking difference between TST (possibly the focal group's breeder) and the rest of the adult males, which sought extragroup copulations more frequently (Table 1). Copulation events and attempted copulations happened even in encounters with aggression. We observed that 36.1% of sexual contact events were followed by agonistic behavior from other individuals against the intruder, whereas in 63.9% of the events a clear reaction to the contacts did not occur. Individuals in the group directed agonistic behavior toward female RB after an extragroup male attempted copulation with her.

In 4 different encounters, 2 males —TST and CMRC; BC and CMN; BC and CMRC; CMN and CMRC— from the focal group copulated with the same female from another group. In another encounter, 3 males —BC, CMN, and CMRC—copulated with the same extragroup female.

We used CT's offspring birth date (*ca.* October 26) to infer probable conception time by considering a 5-mo gestation period (Stevenson and Rylands 1988), which suggested the birth date at *ca.* the end of May. However, the date does not match the observed attempted copulation of CT with an extragroup male (June 30). RB copulated with extragroup males in April and September; however, she showed no sign of pregnancy during the study period.

#### Submissive and Affiliative Behaviors

Only 5 individuals from the focal group (PTRS, PM, CT, RB, and CCL) directed *nga-nga* vocalizations (sign of submissive behavior) toward individuals from other groups. PM showed the most submissive behaviors, and we observed the vocalizations particularly when he left the group and approached another group, where he copulated with a female 3 times in the same day.

Affiliative events were also rare, totaling only 5 observations. On 1 occasion, female RB crossed a telephone wire between 2 forest fragments to another group's territory, where she sniffed the genitalia of 1 male and 1 female, and also groomed a male that had crossed the wire earlier. Three other occurrences consisted of play behavior between 2 infants (CESC and CCL) with another group's infants during an encounter. PM groomed an individual from another group during the same period wherein he remained alone.

#### Discussion

Our main findings on black-tufted-ear marmoset intergroup encounters are that although most of them featured some aggression, rates of aggression during encounters are relatively low. Also, during intergroup interactions, the individuals frequently engaged in activities unrelated to the encounters, such as resting and foraging. Nevertheless, even in calm encounters, they maintained vocal exchanges and visual contact with the other groups, a pattern also described for *Saguinus* 



(Goldizen 1987). Our observations on intergroup interactions in *Callithrix pencillata* are also generally consistent with patterns described for *C. jacchus*, *C. kuhli*, and *Mico intermedius* (Rylands *et al.* 2000; Stevenson and Rylands 1988).

The major difference in intergroup encounters in *Callithrix pencillata* concerns the level of aggression, which appears to be lower versus that in their sister species, *C. jacchus*. Reported encounters in common marmosets range from 1 min and 4 h 17 min (median=17 min), with 90% of encounters including aggressive behavior (Lazaro-Perea 2001). An indication of the calmer nature of the *Callithrix pencillata* is that encounters were of longer duration (median=1 h 19 min), with a lower occurrence of encounters with aggression (63%). Despite the relatively high proportion of encounters with aggressive events, the frequency was not high, and most of the agonistic behavior did not involve contact aggression. Nevertheless, in the few generalized fights we observed, the contact aggression level was high and the possibility of lethal aggression cannot be discarded. A joint attack against an intruder may lead to death, as occurred in *Cebus capucinus* (Gros-Louis *et al.* 2003).

Participation in the encounters was primarily by adults, with the exception of the breeding pair. The breeders' participation pattern differs from findings for common marmosets. Female RPRD and male TST participated less than the minimum for breeders in common marmosets (21% for breeding females and 50% for breeding males; Lazaro-Perea 2001). However, in both studies the subordinate females participated more than the breeding females did.

The costs of territorial defense may be unequally distributed among group members, and male and female behavior may vary according to the importance of different resources for each sex (Cant *et al.* 2002; Cheney 1987). We found that in intergroup encounters, agonism without contact aggression was generally directed toward individuals of the same sex by males and not by females. However, female agonism without contact aggression against males appeared to occur in a specific context of failed copulatory attempts, whereas against strange females they occurred without a clear context. Also, we did not observe males chasing females in their own groups during the encounters.

Females may direct their aggression toward other females, with which they compete for limited feeding resources, because they avoid competing with males, which might help them to dominate other groups (Cheney 1987). It is also possible that females defend their chances of occupying a breeding position within their own groups. Males may participate in aggression primarily against other males, in an attempt to monopolize breeding partners, which they can achieve by chasing away intruder males. Males may also chase females of their own groups, to keep extragroup males away from them (Cooper *et al.* 2004). Lazaro-Perea *et al.* (2000) reported the pattern in common marmosets, but we did not observe it.

Because we observed intragroup sexual behavior only for the breeding couple (TST and RPRD), the only male that could possibly defend a breeding partner was TST, and he directed no clear agonistic behavior against extragroup males. In fact, the breeding couple stayed away from intergroup interactions, contrary to what Baker and Dietz (1996) reported for groups of golden-lion tamarins (*Leontopithecus rosalia*), in which the male and female of the breeding couple were the primary individuals involved in intergroup aggressions. Consequently, the hypothesis of males directing aggression against neighboring males to defend partners does not



seem adequate to explain the apparently monogamous breeding pattern of the black-tufted-ear marmoset group, because nonbreeding males of the focal group were the ones that engaged in same-sex agonistic interactions.

There are several possible explanations for the pattern of nonbreeding male aggression against extragroup males. The aggression may prevent intruder male immigration, which could result in interference in the hierarchy succession queue. Another explanation is that aggression could prevent insemination of subordinate females by extragroup males, which would result in infant rearing costs for the group's individuals. The pregnancy of the group's subordinate females could also interfere in the care of offspring of the dominant pair, in addition to reducing the average relatedness among individuals of the group. Finally, such aggressive behavior could serve as a display, to exhibit male abilities as group defenders to extragroup individuals, possibly leading to better acceptance in future emigrations (Lazaro-Perea 2001). The hypotheses are not mutually exclusive and would require new approaches to distinguish among them.

It is important to observe that most of the female agonistic behavior against intruder males occurred after the females refused to copulate, while most of the aggression against extragroup females was not preceded by any action from them. One can also apply the hypothesis explaining male aggressions against same-sex extragroup individuals to the females.

Participation of different individuals in encounters should reflect a balance between cooperation for territorial defense and individual advantages related to potential breeding partners in nearby groups (Lazaro-Perea 2001). The breeding couple (TST and RPRD) and female CT presented low levels of nonaggressive approach to intruders, whereas the rest of the focal group marmosets exhibited a higher degree of such interactions with neighbors. Similarly, subordinate common marmoset males and females had a higher probability than the breeders of nonaggressively approaching individuals from other groups (Lazaro-Perea 2001).

A pattern of preference emerges when analyzing the sex of the individuals approached by individuals of the focal group. Nonbreeding males in the group (CMN, CMRC, BC, and PM) approached females almost exclusively. Subadult male PTRS, despite being the individual that most nonaggressively approached extragroup individuals, did not present a clear preference for possible female partners, which may indicate his sexual immaturity. There was no indication of opposite-sex preference for focal group nonbreeding females. One possible explanation is that the role for approaching is mostly a male one. Though several possible strategies may ensure reproductive opportunities for nonbreeding subordinate callitrichine females (Albuquerque *et al.* 2001; Arruda *et al.* 2005; Sousa *et al.* 2005; Yamamoto *et al.* in press; Ziegler and Sousa 2002), our observations indicate copulation with extragroup males while remaining in the natal group as the most usual one, adopted particularly by CT and RB.

CT's pregnancy, the subordinate females' copulations with intruders, and the low intragroup aggressiveness during intergroup interactions suggest that among black-tufted-ear marmosets there is a large degree of tolerance for sexual behavior by subordinate females. Ziegler and Sousa (2002) found that captive common marmoset subordinate females presented a fertile estrus and were able to leave and return to their group without aggressive behavior from the breeding couple. However, there



are records of infanticide of subordinate females' offspring among wild callitrichines, and the viability of offspring produced by subordinate females and extragroup males may be very low (Lazaro-Perea *et al.* 2000; Yamamoto *et al.* in press). The fact that CT became pregnant only once during the study period and that we later observed only 1 offspring with her may reflect such a probability.

Repeated interactions and sexual behavior may reduce aggression during migration attempts by subordinate females, despite the possible low direct reproductive value of the behaviors (Lazaro-Perea 2001). In groups with only 1 reproductive female, extragroup copulation may be an effective alternative tactic of subordinate females to contact nonrelated males and gather information about neighboring groups and reproductive vacancies (Arruda *et al.* 2005; Yamamoto *et al.* in press).

The issue of whether callitrichine dominant females remain sexually isolated from extragroup males is not clear cut. In our study, the dominant female engaged in no extragroup sexual contact, which is consistent with observations in some studies of wild groups of common marmosets (Arruda *et al.* 2005; Lazaro-Perea 2001; Sousa *et al.* 2005). However, Nievergelt *et al.* (2000) reported the occurrence of such contacts in the same common marmoset population, and in a captive study of common marmosets, females showed no fidelity to the breeding male and solicited copulation to introduced males (Saltzman *et al.* 2004).

The sexual behavior the nonreproductive adult males exhibited was exclusively extragroup and relatively common during the encounters. Except for a possible cost of aggression injuries during the intergroup encounters, their contacts with neighboring females may lead to a greater reproductive success with no cost of parental care and allow bonding with possible future partners. Lazaro-Perea *et al.* (2000) recorded such an occurrence for common marmosets, wherein males that copulated with extragroup females joined them to form a new group after the breakup of the females' older groups with the deaths of the breeding females.

The copulation of the breeding male (TST) with an extragroup female occurred only once, but it is a behavior that may produce extragroup offspring that do not require parental care. Moreover, the fact that breeding males copulate with extragroup females may be related with the evaluation of future partners and the health and fertility conditions of their own group's dominant females (Lazaro-Perea 2001).

The observations of >1 male copulating with the same female during intergroup interactions indicate a possible polyandrous breeding system with either sperm competition or competition for bonding with future partners. Baker *et al.* (1999) observed in captive common marmosets that parent-offspring pairs copulated with extragroup females with no interference, suggesting a high tolerance among related males. Lazaro-Perea *et al.* (2000) also observed multiple wild common marmoset males copulating with the same female during the phase of new group formation. In our study the event did not occur during group reorganization events, but it is also possible that sperm competition takes place in attempts to produce extragroup offspring.

The observation of affiliative behavior such as grooming may indicate pairbonding between interacting individuals. However, the observed frequency of such behaviors was too low to allow more concise analysis. In both occurrences of



intergroup grooming the focal group's individuals were far from their own groups and were following opposite-sex individuals from another group. Finally, play behavior was restricted to the young, with no clear indication of relationship or possible migration.

Many questions remain for future research on marmoset social systems. Long-term studies of intergroup interactions could help to explain patterns of group dissolution and formation. Moreover, the access to physiological and genetic data of wild groups could improve our understanding concerning individual attitudes relative to extragroup individuals and also the effectiveness of alternative mating strategies. Finally, researchers should address the scarcity of ecological and behavioral data relative to all species in the genus, with the exception of common marmosets, so future comparative studies could help us to understand possible distinctions and similarities between species.

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