# Social Organization in a Wild Population of *Callithrix jacchus*: II. Intragroup Social Behavior

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ABSTRACT. The social behavior of the common marmoset has been well studied in captivity, but little is known about the social dynamics of this species in its natural habitat. Social relationships were studied in three polygynous groups of common marmosets, *Callithrix jacchus*, in northeastern Brazil. Breeding adults appeared to be the center of social life and were the most frequent grooming partners or nearest neighbors for most adult group members. The observations of unidirectional agonistic interactions suggest that breeding adults were also dominant over all other group members, but that neither sex was dominant over the other. The dynamics of within-group social relationships are likely to be important determinants in the reproductive strategies employed by marmoset females.

Key Words: *Callithrix jacchus*; Callitrichidae; Marmoset; Grooming; Dominance.

## INTRODUCTION

The uncommon behavioral and physiological traits of the common marmoset, *Callithrix jacchus*, have made this species the frequent subject of studies of reproductive patterns and behavior. Physiological suppression of ovulation in subordinates, a lack of a post-partum anovulatory period, and twinning all lead to a restricted, yet cooperative, reproductive strategy (HEARN, 1978, 1983; ABBOTT, 1984). Typically, only a single female in the group reproduces, and the burden of raising offspring is shared between group members in a system of cooperative or communal infant care (BOX, 1977; INGRAM, 1977, 1978; TARDIF et al., 1986). With such a restrictive pattern of reproduction, the dynamics of social relationships within a group can clearly have a profound effect on the reproductive success of each group member.

Though the social behavior of marmosets has been the subject of several laboratory studies, their behavior under naturalistic conditions is less well known. Captive studies of *Callithrix jacchus* have typically focused on intragroup social interactions of monogamous family groups (e.g. BOX, 1975; EPPLE, 1975; EVANS & POOLE, 1984; ROTHE, 1974, 1975, 1978; SUTCLIFFE & POOLE, 1984). But, results from recent field studies have indicated that marmosets (genus *Callithrix*) and tamarins (genus *Saguinus*) are not necessarily monogamous under natural conditions (e.g. BAKER et al., 1993; GARBER, ENCARNACION, MOYA, & PRUETZ, 1993; RYLANDS, 1986; TERBORGH & GOLDIZEN, 1985; this study). The possibility that polyandrous, polygynous, and monogamous mating patterns all occur, makes the analysis of intragroup relationships of paramount importance in deciphering the reproductive strategies of these species.

Due to difficulties with visibility and individual identification, only a handful of field studies have addressed intragroup social relationships in the wild (*C. jacchus*: ALONSO & LANGGUTH, 1989; STEVENSON & RYLANDS, 1988; *Saguinus fuscicollis*: GOLDIZEN, 1987; *S. geoffroyi*: LINDSAY, 1979; *S. mystax*: HEYMAN, 1990; *S. nigricollis*: IZAWA, 1978;

*Leontopithecus rosalia:* BAKER et al., 1993; DIETZ & BAKER, 1993), and only a few have done so quantitatively. This paper presents data on intragroup social relationships and dominance hierarchies for three free-ranging groups of *Callithrix jacchus* in northeastern Brazil. This population is particularly interesting because there were two breeding females in each of the three study groups (DIGBY & FERRARI, 1994).

## METHODS

### STUDY SITE AND GROUPS

The study was conducted at EFLEX-IBAMA, an experimental forestry station run by the Brazilian Institute for the Environment in the municipality of Nísia Floresta in the northeastern Brazilian state of Rio Grande do Norte (06°05′S, 35°12′W). The station encompasses 154 ha, of which approximately 70 ha is a reserve of semi-deciduous Atlantic forest. Surrounding plantations consist primarily of coconut (*Cocos*) and eucalyptus (Myrtaceae species).

Three main study groups were monitored in detail. One group (A) inhabited a plantation area, and the other two resided in adjacent ranges in the forest reserve. One of these forest groups (B) was known to cross occasionally into a neighboring plantation area; the other (C) was never seen to leave the forest. During the course of the study, group compositions changed due to births, emigrations, or disappearances. No immigrations were observed. Groups B and C contained more than one adult male and all three groups included multiple adult females and young (DIGBY & BARRETO, 1993). There were two reproductively active females in each of three study groups (DIGBY & FERRARI, 1994).

Beginning in July and August 1991, following a period of habituation and general monitoring, individuals from the three groups were captured and marked for identification. All animals above 200 g were fitted with ball-chain collars strung with color-coded plastic beads that identified the group and the individual. Smaller animals were identified by clipping the tail fur in unique patterns.

### OBSERVATION SCHEDULE

Systematic behavioral observations began in August and September 1991. During periods when there were no infants less than 2 months old in a group, focal animal sampling of adult group members (see below) was conducted on three to five complete days (sleep-tree to sleep-tree) per month. Those periods for each group are as follows: Group A: August – September 1991, December 1991 – January 1992, May – June 1992; Group B: September – December 1991, March – May 1992; Group C: September – October 1991, January – February 1992, April – June 1992.

### BEHAVIORAL OBSERVATIONS

Behavioral observations roughly follow those used by GOLDIZEN (1987). Only animals that were adults at the beginning of the study were used as focal animals (Group A: $n=3$ to 4; Group B: $n=6$ to 8; Group C: $n=6$ to 8). The order of focal animals was changed each day, and care was taken to insure that focal samples for each individual were spread

out over the day and the month. Intervals of at least 90 min separated repeated observation of a focal individual. A total of 452 focal samples were completed for Group A, 364 samples for Group B, and 425 samples for Group C.

Focal animals were followed for 30 min during which their activity, nearest neighbor, and the number of group members within a 2-m radius were recorded on the instant at 2-min intervals. Each 30 min focal contained up to 15 records in each category (activity, neighbor, and number in proximity) depending on visibility. Observations of dominant and submissive behaviors were collected ad lib throughout the study from August 1991 through June 1992, including periods during which young infants were present.

Five sets of data are examined: dominant/subordinate interactions, activity budget, number of group members in proximity to the focal animal, nearest neighbors, and allogrooming.

## Dominant/subordinate Interactions

All observations of interactions that indicated possible dominance or subordination of an individual relative to another group member were recorded. Behaviors classified as indicating dominance included open-mouth threat, nip, cuff, lunge, grab, chase, bite, and "erh-erh" vocalizations. Submissive behaviors included facial grimace, avoidance, cower, and squeal vocalizations (Table 1). Only interactions in which both participants could be clearly identified were included. Interations involving infants begging for food or being refused suckling or transport were not included. Note that because interactions recorded during focal animal sampling (conducted on adult animals only) are used in addition to opportunistic observations, records of dominant/subordinate interactions may be biased such that adults have a higher relative frequency of these behaviors. This bias should not affect the interpretation of the directionality of these interactions.

**Table 1.** Definitions of behaviors.

| Behavior | Description |
| --- | --- |
| Dominant | |
| Open mouth threat | Open mouth stare, bared teeth, often accompanied by a lunge. |
| Nip | A quick chastising bite, similar to a "snap-bite" (STEVENSON & POOLE, 1976). |
| Bite | A severe bite, teeth clenched on the victim. |
| Cuff | A quick, superficial hit. |
| Grab | Gripping the fur of another individual. |
| Lunge | Throwing or jerking the body toward another individual, but stopping short of contact. |
| Chase | Aggressively running after a retreating individual. |
| Subordinate | |
| Facial grimace | Squinting and grimacing, usually accompanied by a cower. |
| Avoidance | Quick movement around or under a branch or trunk in response to another animal's approach. |
| Cower | Sinking down to the substrate and moving the body away from another individual, similar to "withdrawal gesture" and "cringe" (STEVENSON & POOLE, 1976). |
| Squeal vocalization | Infantile squeal given during retreat. |
| General | |
| Grooming | Parting of the fur, inspection and removal of particles. |
| Solicit groom | Presentation of part of the body for grooming. |
| Play | Play-wrestle, play-chase (see STEVENSON & POOLE, 1976 for more details). |
| Scent marking | Any sort of rubbing involving the scent glands, primarily those in the anogenital region. |

*Activity Budget*

Instantaneous records taken during focal animal samples were classified into one of four general categories: rest, travel (locomotion), forage/feed, or social behavior. The proportions of each category for each individual and mean proportions for each group were calculated. Social behaviors included allogrooming, soliciting grooming, play, arch back walk, dominant/subordinate behaviors, and scent marking (Table 1). To test for significant differences in the proportion of time spent in social activities, five subgroup comparisons were made using the Mann-Whitney $U$-test (two-tailed, alpha $<.05$): (1) male vs femals; (2) dominant vs subordinate (as determined above); (3) breeder vs nonbreeder (breeders included females that had given birth and males that were sexually active within the group); (4) breeder females vs nonbreeder females; and (5) emigrants and individuals that disappeared vs individuals resident throughout the study.

*Number of Group Members in Proximity*

The number of group members within a 2-m radius for all instantaneous samples was summed and divided by the total number of records in which the focal animal was in sight to obtain the mean number in proximity per record for each focal animal. The same five subgroup comparisons were made, again using the Mann-Whitney $U$-test.

*Nearest Neighbors*

The nearest neighbor (NN) within a 2-m radius was also recorded on the instant. For each focal animal, the total number of records in which a particular group member was the NN was calculated and divided by the total number of NN records for that focal animal. Only individuals which were present in the group throughout the study are included in this total. Proportions for group members that were born during the course of the study or that emigrated or disappeared during the study were calculated using only the number of NN records collected for the focal animal during that individual's tenure in the group.

*Allogrooming*

The direction of allogrooming and the identity of grooming partners were also recorded on the instant. Proportions of "groom" and "receive grooming" were calculated in the same manner as nearest neighbors, and totals include only records of those animals present in the group throughout the observation period. To test for significant differences in the amount of grooming given versus received, an index was calculated using the total number of "groom" records divided by the sum of all "groom" and "receive grooming" records for that focal animal. These proportions were then used to make the same five subgroup comparisons again using the Mann-Whitney $U$-test. Note that nearest neighbor and grooming partner records are not necessarily independent.

## RESULTS

### DOMINANT/SUBORDINATE INTERACTIONS

Summaries of the dominance interactions in each of the three groups are given in Tables 2, 3, and 4. Such interactions were not frequent and were most commonly seen while

**Table 2.** Dominant/subordinate interactions in Group A.

| | Subordinate | | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | BM<br>*Stv* | BF<br>*Ss* | BF<br>*Sz* | AF<br>*ST\** | JM<br>*Sn* | JF<br>*Si* | IM<br>*Sk\** | IM<br>*Sp\** | IF<br>*Sc\** |
| Dominant | | | | | | | | | |
| *Stv* | — | 3 | 3 | 0 | 3 | 1 | 5 | 0 | 0 |
| *Ss* | 1 | — | 8 | 0 | 2 | 11 | 1 | 1 | 1 |
| *Sz* | | | — | 1 | 3 | 3 | 3 | 0 | 0 |
| *ST\** | | | | — | 0 | 0 | 0 | 0 | 0 |
| *Sn* | | | | | — | 1 | 0 | 0 | 0 |
| *Si* | | | | | 1 | — | 1 | 0 | 0 |
| *Sk\** | | | | | | | — | 0 | 0 |
| *Sp\** | | | | | | | | — | 0 |
| *Sc\** | | | | | | | | | — |

Age classes are those in which the individual was classified at the beginning of the study and are meant to indicate relative ages only. B: Breeding; A: adult; J: juvenile/adolescent; I: infant arranged in order of its birth; M: male; F: female. *Individual was present in group for only a portion of the observation period due to either disappearance/ emigration or birth after the beginning of the study.

**Table 3.** Dominant/subordinate interactions in Group B.

| | Subordinate | | | | | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | BF<br>*Bi* | BM<br>*Bn* | BF<br>*Be\** | AM<br>*Ba* | AF<br>*Bc\** | AF<br>*Bd* | AF<br>*Br* | AF<br>*Bb* | JM<br>*Bk* | JM<br>*Bg* | JM<br>*Bt* | IF<br>*Bl\** |
| Dominant | | | | | | | | | | | | |
| *Bi* | — | 0 | 5 | 0 | 3 | 2 | 3 | 1 | 1 | 1 | 0 | 1 |
| *Bn* | | — | 4 | 0 | 0 | 4 | 4 | 1 | 4 | 1 | 1 | 3 |
| *Be\** | 1 | 4 | — | 0 | 0 | 0 | 3 | 2 | 3 | 0 | 1 | 0 |
| *Ba* | | | | — | 1 | 2 | 2 | 3 | 0 | 0 | 0 | 1 |
| *Bc\** | | | | | — | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Bd* | | | | | | — | 1 | 2 | 2 | 1 | 0 | 1 |
| *Br* | | | | | | | — | 0 | 0 | 0 | 1 | 0 |
| *Bb* | | | | | | | | — | 0 | 0 | 0 | 2 |
| *Bk* | | | | | | | | | — | 0 | 0 | 1 |
| *Bg* | | | | | | | | | | — | 0 | 0 |
| *Bt* | | | | | | | | | | | — | 1 |
| *Bl\** | | | | | | | | | | 1 | | — |

See Table 2 legend for explanation of symbols.

**Table 4.** Dominant/subordinate interactions in Group C.

| | Subordinate | | | | | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | BF<br>*Cl* | BF<br>*Ct* | BM<br>*Cr* | AM<br>*Ch\** | AF<br>*Cd\** | AM<br>*CJ* | AM<br>*Co* | AF<br>*Cb* | JM<br>*Cz* | JF<br>*Cm* | IM<br>*Cal\** | IF<br>*Cx\** |
| Dominant | | | | | | | | | | | | |
| *Cl* | — | 18 | 2 | 0 | 0 | 5 | 4 | 12 | 4 | 5 | 1 | 2 |
| *Ct* | 1 | — | 3 | 1 | 1 | 2 | 1 | 1 | 6 | 1 | 2 | 1 |
| *Cr* | | 1 | — | 0 | 1 | 2 | 0 | 8 | 2 | 0 | 4 | 0 |
| *Ch\** | | | | — | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cd\** | | | | | — | 0 | 0 | 1 | 3 | 0 | 0 | 0 |
| *CJ* | | | | | | — | 0 | 3 | 2 | 3 | 2 | 0 |
| *Co* | | | | | | | — | 5 | 2 | 0 | 5 | 0 |
| *Cb* | | | | | | | | — | 4 | 1 | 1 | 0 |
| *Cz* | | | | | | | | | — | 0 | 3 | 1 |
| *Cm* | | | | | | | | | | — | 0 | 0 |
| *Cal\** | | | | | | | | | | | — | 1 |
| *Cx\** | | | | | | | | | | | | — |

See Table 2 legend for explanation of symbols.

animals were feeding in gum-producing trees. Another common context was when an individual holding young infants would cuff or avoid an animal that had solicited grooming or a transfer of the infants.

Breeding animals were dominant over all others. In each of the three groups there was a dominant/subordinate relationship between the two breeding females, but there was no clear pattern that would indicate whether breeding males were typically dominant over breeding females or vice versa. In Group A, the breeding male *Stv* was dominant over both breeding females while in Group C, the female *Cl* was dominant over both the breeding male and the subordinate breeding female. In Group B, the breeding male, *Bn*, and the dominant breeding female, *Bi*, were never observed to interact in a way that would indicate dominance of one over the other.

Dominant/subordinate interactions were typically unidirectional. The only exceptions among adults were invariably in the context of an individual holding very young infants and cuffing or lunging at another group member getting too close or trying to solicit transfer of the infants. The four instances in which the breeding female *Be* (Group B) was the dominant actor in an interaction with the breeding male *Bn*, all occurred on the same day while *Be* was carrying he 3- to 4-day-old infant.

The dominance hierarchy of nonbreeding individuals appeared to be age related with older animals dominant over younger ones. Dominant/subordinate interactions occurred both within and between sexes, and there did not appear to be separate male and female hierarchies. Only breeding females were observed behaving dominantly toward adult males, and males were more frequently the dominant actors in interactions with females than vice versa. Unfortunately, the small number of nonbreeding adult males makes it difficult to determine if this indicates some degree of male dominance over females.

ACTIVITY BUDGET

On average, 14% (range 5 to 25%) of the focal animals' activities were some form of

**Table 5.** Proportion of activity budget spent in social behavior and mean number of individuals in proximity.

| Group | ID | Status | Social behavior (%) | Mean number in proximity |
|-------|------|--------|---------------------|--------------------------|
| A | *Stv* | BM | .15 | .73 |
|   | *Ss* | DBF | .15 | .89 |
|   | *Sz* | SDB | .24 | .90 |
|   | *ST\** | AF | .08 | .41 |
| B | *Bn* | BM | .19 | .60 |
|   | *Bi* | DBF | .09 | .68 |
|   | *Be\** | SBF | .07 | .38 |
|   | *Ba* | AM | .12 | .70 |
|   | *Bc\** | AF | .19 | .60 |
|   | *Bd* | AF | .19 | .60 |
|   | *Br* | AF | .13 | .47 |
|   | *Bb* | AF | .13 | .45 |
| C | *Cr* | BM | .16 | .77 |
|   | *Cl* | DBF | .25 | .90 |
|   | *Ct* | SBF | .15 | .57 |
|   | *CJ* | AM | .19 | .58 |
|   | *Ch\** | AM | .05 | .25 |
|   | *Co* | AM | .08 | .38 |
|   | *Cd\** | AF | .09 | .30 |
|   | *Cb* | AF | .07 | .35 |

D: Dominant; S: subordinate. See Table 2 legend for explanation of other symbols.

social behavior, typically grooming or being groomed (Table 5). There was no significant difference between the groups in the proportion of social behavior, nor between plantation and forest groups (Mann-Whitney $U$ test). There were also no significant differences in comparisons of male vs female, dominant vs subordinate, breeder vs nonbreeder, breeder female vs nonbreeder female.

## NUMBER OF GROUP MEMBERS IN PROXIMITY

The average number of group members within a 2-m radius per record was calculated for each focal animal. Focal animal means ranged from .25 to .90 individuals/record and averaged .58 individuals/record (Table 5). There was no significant difference between groups or between the plantation group (A) and forest groups (B and C), despite the smaller number of possible neighbors in the plantation group. In the number in proximity for males and females, there was also no significant difference (Fig. 1a). Focal animals that remained in the group throughout the study had a significantly higher number of individuals in proximity than those that disappeared or emigrated ($p < .05$) (Fig. 1b), possibly indicating
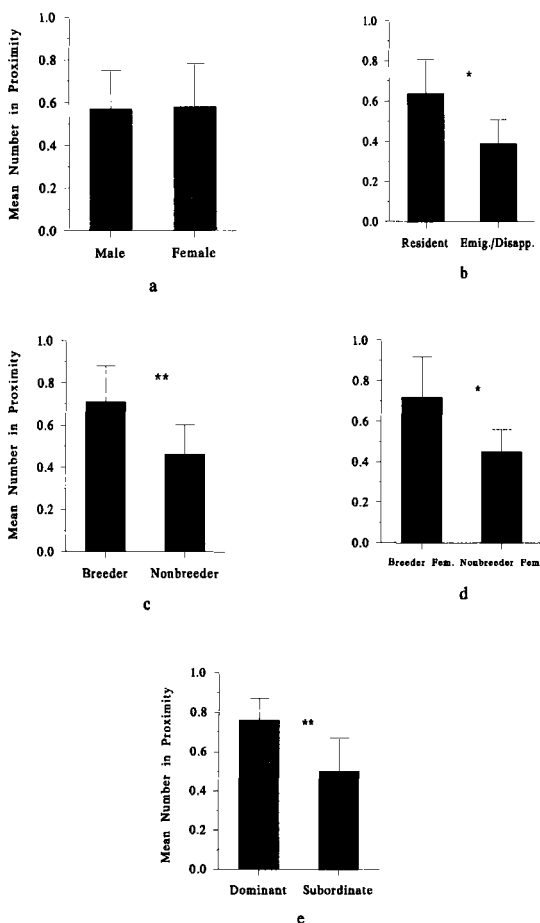


Fig. 1. Sub-group comparisons for the mean number of individuals within a 2-m radius to the focal animal per record. $*p < .05$; $**p < .01$.

that the emigrants were isolated before leaving the group or disappearing. There was also a significant difference between breeders and nonbreeders ($p < .01$), breeder females and nonbreeder females ($p < .05$), and dominant and subordinate focal animals ($p < .01$), with breeding and dominant individuals having a higher mean number of individuals in proximity (Figs. 1c, d, & e). This suggests that breeders and, in particular, dominant animals are central in group social activities.

## Nearest Neighbors

For each focal animal, the proportion of nearest neighbor records recorded for each group member was calculated. The most frequent nearest neighbors were breeding individuals for 18 out of 20 focal animals and were dominant males or females for 14 out of 20 focal animals (Fig. 2). This pattern was especially strong in Group B in which one member of the dominant breeding pair was the most frequent nearest neighbor for all focal animals.

In all three groups, the dominant male was the most frequent nearest neighbor for both breeding females. Interestingly, for the breeding males in Groups A and C, the subordinate breeding female was the nearest neighbor more frequently than the dominant breeding female. The subordinate breeding female in Group B emigrated in March 1992 and had a low proportion of nearest neighbor records for all focal animals in her group.

Infants and juveniles were frequent nearest neighbors (the proportion calculated using only the number of NN records for that focal animal during the individual's tenure in the group) but the frequencies tended to drop as they got older. In both Groups A and C, breeding females were in close proximity to their own offspring more frequently than to the offspring of the other breeding female.
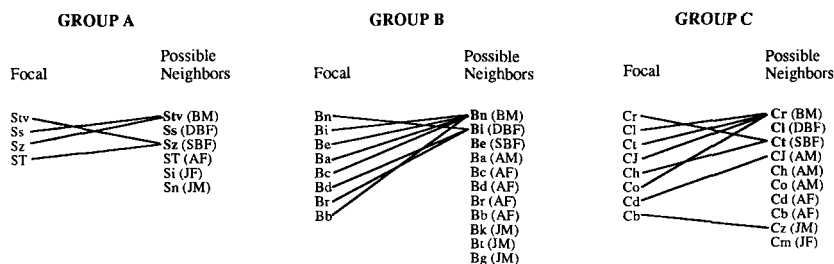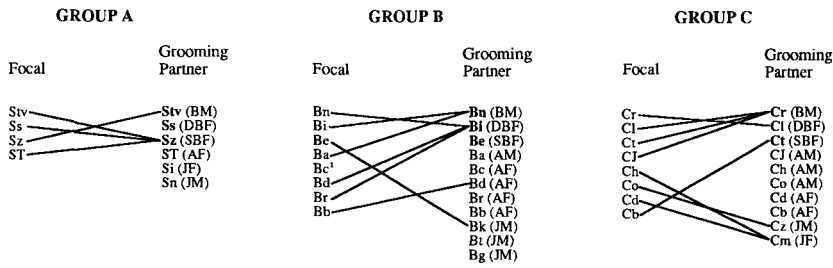


**Fig. 2.** Nearest neighbors. Lines indicate the most frequent nearest neighbor for each focal animal. Note that young born after the start of systematic data collection are not included.

## Allogrooming

Allogrooming commonly occurred during resting periods when the group split into several smaller subgroups. Individuals would solicit grooming by lying in front of another group member and extending or exposing an area to be groomed. Grooming in these groups was consistent with the descriptions given by Woodcock (1978), and Stevenson and Rylands (1988).

Breeding individuals were the most frequent grooming partners in all three groups (Fig. 3). There was no significant difference in who gave versus received grooming in the five sub-groups (male vs female, resident vs emigrant/disappeared, breeder vs nonbreeder, breeder female vs nonbreeder female, and dominant vs subordinate).
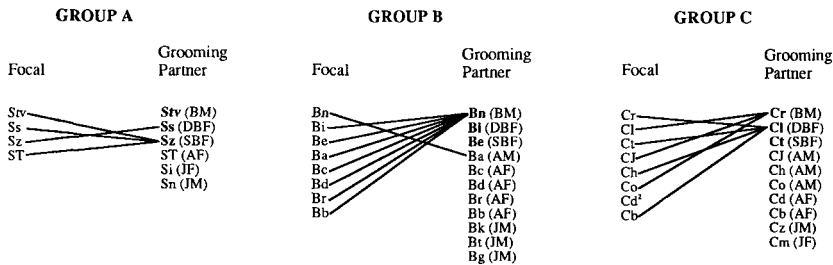
a: groom



b: receive grooming



**Fig. 3.** Grooming partners. Lines indicate the most frequent grooming partner for each focal animal. a: Individuals groomed by the focal animal; b: individuals from whom the focal animal received grooming. Note that young born after the start of systematic data collection are not included. 1: *Bc* groomed *Bi*, *Bn*, *Bd*, and *Bb* in equal portions; 2: *Cd* was groomed equally by *Ct* and *CJ*.

In Group A, the subordinate breeding female, *Sz*, was the most frequent grooming partner (both grooming and being groomed) for each of the other three focal animals. *Sz* groomed the dominant male, *Stv*, most frequently and received grooming most frequently from the dominant female, *Ss*. In Group B, the alpha female, *Bi*, both groomed and received grooming most frequently from the dominant male, *Bn*. *Bn* groomed *Bi* most frequently, but received grooming most often from the group's only other adult male, *Ba*. There are few grooming records for the subordinate breeding female, *Be*, due in part to her emigration in March 1992. A young subadult/juvenile, *Bk*, was her favored grooming recipient, and she received grooming most often from the dominant male, *Bn*. In Group C, the dominant male, *Cr*, and female, *Cl*, were each other's favored grooming partner. As in Group A, the subordinate breeding female in Group C, *Ct*, groomed the dominant male most often, but received grooming most frequently from the dominant female.

In four out of five cases where favored grooming partners were not breeding individuals, the favored partner was a young subadult or juvenile. Three of these five cases also involved focal animals that disappeared or emigrated before the end of the study.

In all three groups, focal animals were groomed most frequently by one of the three breeding adults. Another clear pattern to emerge was that young group members (less than 6 months old) were almost never observed grooming other group members. There was also a tendency for mothers to groom their infants more often than the infants of the other breeding female.

SUMMARY

Overall, dominant and/or breeding individuals appear to be the center of group social life. They were favored nearest neighbors or grooming partners, and had significantly more group members in close proximity to them than other group members. Dominance interactions were typically unidirectional, and the hierarchy appears to be age-related with breeding individuals dominant over all others. While there was a dominant/subordinate relationship between the two breeding females, there was no clear pattern of male/female dominance, nor indication of separate male and female hierarchies.

## DISCUSSION

Most studies of intragroup social relationships focus on how large groups with multiple adult males and females sort themselves out in such a way as to set up priority of access to food or mates and to decrease overall aggression. Such social relationships can be equally important in smaller nuclear or extended family groups, especially when these relationships may determine the length of tenure in the group and who does or does not reproduce. Excellent examples of this are the social relations within groups of callitrichids (*Callithrix, Cebuella, Leontopithecus,* and *Saguinus*).

Laboratory studies of marmoset and tamarin family groups have shown that, typically, only the single most dominant male and female in a group reproduce (*Callithrix*: ABBOTT, 1984; HEARN, 1978, 1983; *Saguinus*: EPPLE & KATZ, 1984; FRENCH et al., 1984). These studies and others documenting high levels of intrasexual aggression (e.g. EPPLE, 1975, 1978; EVANS, 1983) have interpreted these patterns as indicative of a monogamous pair bond. The social dynamic in these groups becomes more complicated if these extended families contain more than one sexually active adult of each sex. Thus the analysis of the social relationships among members of marmoset and tamarin groups has become increasingly important as field studies reveal the variety and flexibility of callitrichid mating patterns under natural conditions (e.g. BAKER et al., 1993; GARBER, PRUETZ, & ISAACSON, 1993; GOLDIZEN, 1987; RYLANDS, 1986).

### DOMINANT/SUBORDINATE INTERACTIONS

Laboratory studies of *Callithrix jacchus* have focused on two types of groups: small nuclear family groups consisting of a mated pair and their offspring or "peer groups" of unrelated adult males and females (e.g. ABBOTT, 1984; EPPLE, 1975; ROTHE, 1974, 1975, 1978; SUTCLIFFE & POOLE, 1984). Agonistic behavior is infrequent in established family groups, but there does appear to be an age-related hierarchy with the breeding pair dominant over their young and older offspring dominant over younger offspring (ABBOTT, 1984; EVANS & POOLE, 1984; SUTCLIFFE & POOLE, 1984). Both ROTHE (1975, 1978) and EPPLE (1975) have reported that males and females form separate hierarchies, but there is still no clear evidence that one sex is dominant over the other (EVANS & POOLE, 1984; SUTCLIFFE & POOLE, 1984). Laboratory studies of *Saguinus* species have produced similar results (BOX & MORRIS, 1980; SNOWDON & SOINI, 1988).

Agonistic behaviors are more common in peer groups, especially in the first few days following group formation (ABBOTT, 1984, 1987; ABBOTT et al., 1988; EPPLE, 1975). In each group the dominant male and female become the breeding pair, and subordinate

females, if still in the group, become reproductively suppressed, i.e. their reproductive hormones fall to levels that prevent ovulation (ABBOTT, 1984, 1987; ABBOTT et al., 1988). In ABBOTT's (1984) study, the breeding pair was co-dominant in 88% of the peer groups, and either the alpha male or female was dominant in the remaining groups, again demonstrating that one sex is not consistently dominant over the other.

Only a handful of field studies of marmosets and tamarins have addressed dominance interactions. None of the past field studies of *Callithrix* have dealt with agonistic interactions quantitatively, but STEVENSON and RYLANDS (1988) do state that the breeding pairs in their study groups of *C. jacchus* and *C. humeralifer intermedius* were dominant to other group members.

The results of this study are consistent with both field and laboratory studies of family groups in that agonistic behaviors were rare. Nevertheless, there were sufficient interactions to indicate that breeding individuals were dominant over all other group members and that older animals were dominant over younger ones. As in captive marmoset groups, and typical of other sexually monomorphic species (KLEIMAN, 1977), there was no clear pattern of dominance between the sexes. Neither did there appear to be separate male and female hierarchies, contrary to ROTHE's (1974, 1975) findings with captive *C. jacchus*.

GROOMING AND PROXIMITY

The results of this study also appear to be consistent with laboratory and other field studies which report grooming and proximity preferences. Several studies have shown that the majority of allogrooming is performed by the adult pair in family groups of *C. jacchus* (ALONSO & LANGGUTH, 1989; BOX, 1975; ROTHE, 1974; STEVENSON & RYLANDS, 1988; WOODCOCK, 1978). Nevertheless, SUTCLIFFE and POOLE (1984) found that individual rank did not correlate with grooming preference. This may be due, in part, to the direction of grooming, with the breeding pair giving more than they received from younger group members (BOX, 1975).

Breeding individuals in this study were also the most frequent nearest neighbors for the majority of focal animals and had a significantly higher average number of group members in close proximity to them. While proximity is not easily studied in captivity due to restricted living space, both EPPLE (1975, *C. jacchus*), and BOX and MORRIS (1980, *Saguinus mystax*), found that members of the breeding pair spent more time in close proximity or contact with each other than with other group members.

That breeding adults were the most frequent grooming partners and nearest neighbors for the majority of adult group members can be interpreted in two ways. First, nonbreeding group members may be strengthening their affiliative ties to the breeding (and more dominant) adults in order to remain in the group. Alternatively, breeding adults may be strengthening their affiliative ties with nonbreeding group members in order to retain their help in caring for offspring. That there is a stronger trend for nonbreeding adults to receive grooming from breeding adults, and in particular dominant breeding adults, may offer some support for the latter alternative. Nevertheless, data from research specifically designed to test these alternatives is needed.

There is currently very little information on the process and timing of dispersal in callitrichids. The finding that individuals that were known to emigrate or had disappeared from a group during the study had significantly lower proximity scores than those that remained in the group may indicate that they had become "socially isolated" before their departure. The three known emigrants both came from groups at the upper limits of

group size described for this genus (15 and 14 individuals for Groups B and C respectively), and their departures occurred when there were young infants in the group. In addition, following their departure emigrants were chased and threatened when they re-encountered their old groups (DIGBY & BARRETO, 1993). Captive studies have shown that as offspring grow older they decrease social contact, even in the absence of parental aggression (cf. ALTMANN, 1980; SUTCLIFFE, 1980 and INGRAM, 1975 cited in SUTCLIFFE & POOLE, 1984). In addition, FERRARI and LOPES FERRARI (1989) observed several group members splitting off from a free-ranging group of *C. flaviceps* after an intergroup encounter and forming a new group in an overlapping home range (see also GARBER, PRUETZ, & ISAACSON, 1993). This suggests that at least some emigrations are voluntary. The results of this study suggest that emigration may also be related to social isolation followed by rejection once the animal has drifted from the group. The relationship between social isolation and dominance status is unclear, in part due to the reproductive and age-dependent nature of the hierarchy. All three known emigrants were full adults, and one was a primiparous subordinate breeding female (DIGBY & BARRETO, 1993). Unfortunately, it is still unknown why these adults left and not others. Indeed, it may be necessary to know the exact ages and genetic relationships (e.g. whether an individual is the offspring of a dominant or a subordinate female) of all group members before a clear pattern will emerge.

POLYGYNOUS AND POLYANDROUS MATING PATTERNS

Based on the assumption that callitrichids are monogamous, several researchers characterized the close relationship among breeding adults as a monogamous "pair-bond" (EPPLE, 1981; EVANS, 1983; EVANS & POOLE, 1983, 1984). But the last decade of callitrichid field research has established that wild groups may have flexible mating patterns with multiple breeding males or females (*Callithrix*: DIGBY & FERRARI, 1994; RYLANDS, 1986; *Leontopithecus*: BAKER et al., 1993; DIETZ & BAKER, 1993; *Saguinus*: GARBER et al., 1984; GARBER, PRUETZ, & ISAACSON, 1993; GOLDIZEN, 1987; TERBORGH & GOLDIZEN, 1987).

Because of the costs involved in infant care, one would expect to see a monogamous mating pattern (and thus some confidence in paternity) in a species where there is cooperative care of offspring, especially if there is a high degree of paternal care (e.g. KLEIMAN, 1977). TERBORGH and GOLDIZEN (1985) explained the presence of "cooperative polyandry" in their population of *Saguinus fuscicollis* as a strategy to gain adult helpers, not by increasing the certainty of paternity, but rather by confusing it. Such a strategy would only be necessary, indeed only tolerated by the males, in small or newly formed groups where there are no older offspring to help care for infants. Polyandry is possible, in part, due to cooperative and affiliative relationships between males. GOLDIZEN (1987) reported that aggression was rare among polyandrous males and that there was no evidence of a dominant/subordinate relationship between them. The social relationships among the reproductive trio were apparently similar to what has been described for monogamous "bonded" pairs.

BAKER et al. (1993) describe the relationships between the two sexually active males in groups of lion tamarins (*Leontopithecus rosalia*) quite differently. In seven out of eight multimale groups, one male was clearly dominant over the other at feeding sites. These dominant males were also responsible for 12 of the 13 copulations observed during the fertile periods of the breeding females. This suggests that, although more than one sexually active male may be present in a group, the dominant male may still be able to monopolize

reproduction. Similarly, groups with two breeding females also exhibited a clear hierarchy (DIETZ & BAKER, 1993). While both females produced offspring, the reproductive success of the dominant was greater than that of the subordinate female. Thus, in both polygynous and polyandrous groups of lion tamarins, status and affiliative relationships have an important effect on an individual's fitness.

The results of this study resemble the findings of DIETZ and BAKER (1993) more closely than those of GOLDIZEN (1987). There was a single dominant male and a clear dominant-subordinate relationship between the two breeding females in each of three groups. As in the lion tamarins, subordinate females had a lower reproductive success than dominant females. In addition, subordinate breeding females were much more protective of their infants than were dominant females, and were the sole caretakers of their infants for the first week of life (DIGBY, 1994). The infants of subordinate females may also face the threat of infanticide at the hand of fellow group members (DIGBY, 1994). Thus, there appears to be a delicate balance in the social relationships between breeding females. Again, the dynamics of social relationships within a group appear to have a profound effect on an individual's reproductive success.

Questions to be addressed by future studies include whether or not the close relationship between breeding individuals, especially between the dominant and subordinate breeding females, precedes their breeding status or is a result of it. Also, are subordinate breeding females simply the eldest daughters of the dominant females, or are they the ones that have the closest affiliative ties? Are the offspring of subordinate females more likely to emigrate, and are their dominant counterparts more likely to inherit breeding positions? These and many other questions can only be answered by further long-term studies.

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