

Passos, FC & Miranda, JMD (Eds.)
A Primatologia no Brasil. Vol. 13
Curitiba: SBPr, 2014
ISBN: 978-85-61048-05-1

CAPÍTULO 15

Social tolerance and affiliation do not associate to success during cooperative problem solving in *Callithrix jacchus* (Linnaeus, 1758)

Rafaela C. Cerqueira^{1*}; Eloysi C.N. Barros¹; Suedja R. Nunes¹; Bruno S.B. Gonçalves^{1,2} & Renata G. Ferreira¹

¹ Universidade Federal do Rio Grande do Norte, Natal, RN, Brasil.

² Instituto Federal Sudeste de Minas Gerais, *campus* Barbacena, Barbacena, MG, Brasil.

*Autor correspondente: falela182@hotmail.com

ABSTRACT. Several studies on nonhuman primates show that the relationships between individuals strongly influence the occurrence of cooperative behavior, both in natural environment and in captivity settings. Recent studies suggest that cooperative breeders present outstanding performance in tasks involving social cognition, such as cooperative tasks with experimental apparatuses. The present study assessed in *Callithrix jacchus*, a cooperative breeder species, if social relationships between subjects are important factors during performance in cooperative tasks. During the experimental procedure the animals participated in three different cooperative tasks: *cooperation task*, *prosocial task* and *control task*. Matrix correlation tests revealed no significant relationship between grooming or proximity and the success during tasks. This lack of association between social tolerance/affinity and success in cooperation tasks stands against this Cooperative Breeding hypothesis. We discuss these findings in light of the contradictory results found in the literature.

Key-words: cooperation, prosocial, social grooming, proximity, marmoset.

RESUMO. Tolerância e afiliação sociais não estão associadas ao sucesso durante tarefas cooperativas em *Callithrix jacchus* (Linnaeus, 1758). Diversos estudos com primatas não humanos mostram que as relações entre os indivíduos têm forte influência sobre a expressão de comportamentos cooperativos tanto em ambiente natural como em cativeiro. Trabalhos recentes sugerem que espécies com cuidado cooperativo de infantes têm desempenho destacado em testes que envolvem cognição social, como testes cooperativos que utilizam aparatos experimentais. O presente trabalho avaliou em *Callithrix jacchus*, uma espécie com cuidado cooperativo da prole, se as relações sociais entre os indivíduos são importantes elementos durante a realização de tarefas cooperativas. No procedimento experimental, os animais participaram de três tarefas cooperativas diferentes: *teste*

de cooperação, teste de prosocialidade e controle. Os testes de correlação de matrizes não revelaram correlação significativa entre relações afiliativas de catação e proximidade e o sucesso em tarefas cooperativas. Essa falta de associação entre tolerância social / afinidade e sucesso em tarefas de cooperação não oferece apoio à hipótese do cuidado cooperativo. Nós discutimos esses resultados à luz dos dados contraditórios encontrados na literatura.

Palavras-chave: cooperação, prossocial, catação, proximidade, sagui.

Introduction

Empirical evidence (naturalistic observations and laboratory results) confirming theoretical models for the evolution of cooperation¹ makes cooperative behavior no longer a paradox to Natural Selection Theory (DUGATKIN 1997). However, at a proximate level, cooperative behavior remains playing a central role to the models for evolution of cognition and the adaptations required for the occurrence of this behavior (HEYES 1998). There is a growing number of studies on the cognition underlying the resolution of cooperative tasks by different species, on the level / complexity of cooperation achieved, and on the environmental challenges faced by those species that present cooperative behaviors (SHETTLEWORTH 2010).

In the experimental analysis of cooperative behavior in primates, once the understanding of the apparatus' physical functioning and of the cooperative challenge is ensured, one

seeks to determine the type of social cognition or social factors involved on the success of the task (CHALMEAU & GALLO 1996). In a first level of analysis it has been observed that social tolerance is an important factor involved in the occurrence of these behaviors (see ANDERSON 2007 for a review) and individuals tend to form cooperative pairs with those animals with whom they have more social affinity (CROFOOT *et al.* 2011). For example, two species of the genus *Macaca* were studied in a comparative study: *Macaca tonkeana* (Meyer, 1899), a highly tolerant species and *Macaca mulatta* (Zimmerman, 1780), who lives in despotic relationships (PETIT *et al.* 1992). The authors used heavy stones on top of food items to test the ability of the animals to cooperate, since a single individual was unable to remove the stone alone and needed the help of a conspecific. The removal of the stone by two individuals was more common in the more tolerant species.

In a work with chimpanzees, MELIS *et al.* (2006) showed that individuals who ate in spatial proximity and in a peaceful manner were more likely to cooperate on a task that required simultaneous actions of two animals for rewards, concluding that tolerance acts as an important limiting factor when

¹ Studies differ in the definition of the term "cooperation" (NOE 2006) and terms widely used in literature such as cooperation, mutualism, reciprocity, reciprocal altruism and symbiosis are sometimes used interchangeably and sometimes used as different categories of the cooperative behavior. The definitions used in this work are presented in the Methodology.

performing these tasks in this species. In another study (HARE *et al.* 2007), the tendency to cooperate was compared between bonobos and chimpanzees, the former much more tolerant living in more peaceful social relations than the latter. It was identified that bonobos were more likely to feed together in a peaceful way than their closest relatives and were more likely to cooperate when the reward was easily monopolizable (HARE *et al.* 2007). However, this difference between species did not exist when the rewards could be shared. The authors concluded that, in chimpanzees, even when two individuals were able to understand the role of his partner to solve the task, cooperation might not have occurred as a result of low social tolerance (HARE *et al.* 2007).

Another way to measure social affinity is observing social grooming (hereafter grooming). The cleaning of other individuals' fur with mouth or hands is a widespread behavior among primates and it has been suggested to have two main functions: the removal of ectoparasites and the maintenance of social relationships. According to DUNBAR (1991) the latter is restricted to Old World species, but contrary to this view, there is a growing number of studies showing that grooming is also related to social relationships in some New World species: *Ateles geoffroyi* Kuhl, 1820 (AHUMADA 1992); *Sapajus nigrinus* (Goldfuss, 1809) (DI BITETTI 1997); *Alouatta seniculus* (Linnaeus, 1766) (SANCHEZ-VILLAGRA *et al.* 1998) e *Callithrix jacchus* (Linnaeus, 1758) (LAZARO-PEREA *et al.* 2004).

Several naturalistic studies show an association between the amount of grooming in dyads and cooperative behavior in conflicts as coalition, cooperative hunting, food sharing and territory defense (for a review, SCHINO & AURELI 2008). Analysis controlling for the effects of the proximity pointed to a pattern of "exchange of exchange of favors" between members of a dyad, either of grooming by grooming, in which case there was a symmetric relationship (HENZI & BARRETT 1999); either of grooming by other behaviors, in which case there was a transposed relationship incorporated, i.e. the individuals cooperated more to those who groomed them more (NEWTON-FISHER & LEE 2011, TIDDI *et al.* 2012). However, studies on chacma baboons did not find such a direct exchange of favors (SILK 2003), but females that formed long term affiliative bonds (as inferred by proximity and grooming) presented increased fitness (SILK *et al.* 2010).

Among New World primates, callitrichid monkeys are receiving increased attention in studies of cooperation (WERDENICH & HUBER 2002, HAUSER *et al.* 2003, CRONIN *et al.* 2005). They are cooperative breeders (STEVENSON & RYLANDS 1988), they share food (FERRARI 1987), including active sharing (ARRUDA 2012, personal communication; for a review, MENEZES 2010, unpublished data), are highly tolerant to each other (FERRARI 1987, KASPER *et al.* 2008) and maintain spatial and behavioral cohesion with its social partners (DIGBY & BARRETO 1993). Grooming does has a social role in *Callithrix jacchus* as observed by

LAZARO-PEREA *et al.* (2004). These authors found that breeding females groomed subordinate females more often than the contrary and they argue that grooming is an important behavior to maintain the social structure of the group, regulating interactions between dominant and subordinate females. Studies with the tamarin - *Saguinus oedipus* (É. Geoffroy in Humboldt, 1812) also indicate a relationship between grooming and infant care by adult sons (GINTHER & SNOWDON 2009).

A link between cooperative breeding and cooperation in contexts other than infant care have already been suggested (SNOWDON & CRONIN 2007, for callitrichidae, CLUTTON-BROCK 2006, for carnivora). Emphasizing such link, BURKART & VAN SCHAIK (2010) suggest that there is a causal relation between cooperative breeding and social cognition. According to the authors, the motivational and cognitive processes necessary for the execution and coordination of helping behavior may also promote cognitive performance in cooperative contexts not directly related to the care of offspring. The high social tolerance, the attention bias toward other group members and the behavioral coordination characteristic of cooperative breeders could enhance their performance in socio-cognitive tasks like cooperative problem solving in captivity (SNOWDON & CRONIN 2007, BURKART & VAN SCHAIK 2010). To CRONIN & SNOWDON (2008), the detached performance of callitrichidae in experimental cooperative tasks may derive from the cooperative breeding system differentiating them from other

most competitive primate species or species that do not form strong social relationships.

In a study of the factors that influence the cooperative behavior of *Callithrix jacchus* (Linnaeus 1758) in an instrumental task, WERDENICH & HUBER (2002) investigated the social conditions which could determine the occurrence of this behavior, with emphasis on the analysis of tolerance and inter-individual distribution of roles to cooperate. The pairs that were successful in the cooperation task were those who, in a previous training phase, the subordinate animal pulled a string on the apparatus so that the dominant could get a reward. The dominant animals shared the reward with their partners, highlighting the importance of tolerance of the former in relation to the latter for the occurrence of cooperation.

BURKART & VAN SCHAIK (2012) used experiments with apparatuses to test social tolerance and motivation to provide food for a partner group in three different species: the common marmoset (*Callithrix jacchus*), a cooperative breeder; the Japanese monkey - *Macaca fuscata* (Linnaeus, 1758), an independent breeder and *Cebus apella* (Linnaeus 1758) – now *Sapajus apella* (LYNCH *et al.* 2012), with an intermediate breeding system. Based on an index of food monopolization (in which low values indicate higher monopolization of food) the authors found that marmosets presented the highest values; *S. apella* had intermediate values and *M. fuscata* had the lowest values, with most food monopolized by alpha individuals. It

was also observed that only marmosets acted prosocially. The cooperative breeding system and the high tolerance of this species were identified as those responsible for this result. However, there are contradictory data. For example, CRONIN *et al.* 2009 did not find a prosocial tendency in *Saguinus oedipus* whereas, in a later work CRONIN *et al.* (2010) found that prosociality could emerge regardless of reciprocity. STEVENS (2010) indicate that, for some callitrichid species, the animals cannot discriminate mates, kin and non-kin during cooperative problem solving. An analysis of the work of BURKART *et al.* (2007) identified, in addition, that the prosocial behavior found in the group did not exist among females.

The present study aimed to study the cooperative behavior of common marmosets (*Callithrix jacchus*) in captivity during the manipulation of apparatuses in cooperative tasks. We tested the null hypothesis that tolerance and social affiliation (measured by means of proximity and grooming behavior) do not influence the execution of cooperative tasks. The alternative hypothesis that tolerance and affiliation do relate with cooperative tasks has two predictions: i. dyads of animals that spend more time in proximity in a non-experimental situation will be more successful in the cooperative tasks; ii. More affiliated dyads (i.e. those that groom more) will also have greater success in cooperative tasks.

Material and Methods

Definitions

In this paper we use the term *cooperation* in reference to behaviors where animals work together to achieve a common goal (MENDRES & DE WALL 2000, WERDENICH & HUBER 2002). The definition of *prosocial behavior* used here is that of BURKART *et al.* (2009), who define them as those behaviors that produce some benefit to a partner (BURKART *et al.* 2009). Finally, the terms cooperative task will be used to make reference to both kinds of behaviors (cooperation and prosocial behaviors).

Animals and housing

We studied two captive family groups of *Callithrix jacchus* from Laboratório de Estudos Avançados em Primatas (LEAP, previously known as Núcleo de Primatologia) at Universidade Federal do Rio Grande do Norte. Each family lived in a masonry enclosure with iron gates and cement floor, measuring 2x1x2m, equipped with platforms and wooden trunks, a feeder, a drinker and a nest box. Each enclosure was partially covered with ceramic tiles allowing the animals to be exposed to natural temperature and light cycle. The animals had visual, auditory and olfactory contact with other family groups. In each family individuals were all related (except for the breeding pair, see Table 1) and by the beginning of the study they had been living together for at least one year (considering only the adults; the other animals had been living together since their birth). All but one

Table 1. Composition and age of the two families studied*.

F09: Animal	1° Set	2° Set	F05/06: Animal	1° Set	2° Set
#Hilderi ♂ breeder	Adult	Adult	Olganita ♀ breeder	Adult	Adult
Frida ♀ breeder	Adult	Adult	Opus ♂	Adult	Adult
Frank ♂	Adult	Adult	Ofélia ♀	Adult	Adult
Fiel ♂	Subadult	---	Onésio ♂	Adult	Adult
Fada ♀	Subadult	Subadult	Otelo ♂	Juvenile	Subadult
Fifi ♀	---	Infant	Osmar ♂	Juvenile	Subadult

* These data refer to the first day of each set of experimental task (see below) and show that the composition of the family F09 varied during the tests. One animal moved out (Fiel) after the first set and it occurred the birth of another one (Fifi), who began to participate in the experiments from the second set on. The composition of the family F05/06 did not changed during the tests and from the second set on the family F09 remained the same until the end of the experiments. # Born in wild.

animal were born in captivity. Table 1 presents the composition of the two family groups that were studied (F09 e F05/06), as well as the sex and age of the animals according to YAMAMOTO (1993).

The animals were identified by the marking of their periauricular tufts, back, front legs and / or hind legs with a solution of picric acid to 5%. This substance causes the body parts to acquire yellowish tones.

Materials

Two identical experimental apparatuses were used for the experiments. Each one (Figures 1 and 2) consisting of a wooden platform with two levers separated by about 40cm. The two levers were stuck on aluminum rails, which allowed them to move as they were drawers. At one end of each lever there was a tray and strings to allow the animals to pull the levers and gain access to the trays with the rewards.

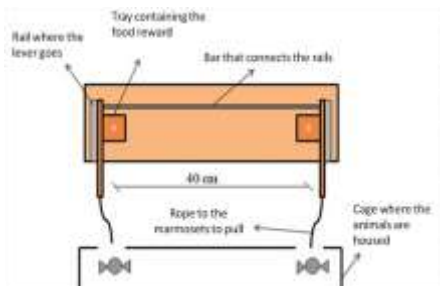


Figure 1. Schematic design of experimental apparatus used in Cooperation Task. In this task, both trays contained food rewards.

The food rewards used were sliced banana with approximately 0,5cm². All experiments were recorded by video cameras that were placed on tripods in front of the cages during the experiments (Figure 3). Computers were used for subsequent analysis of video and data.

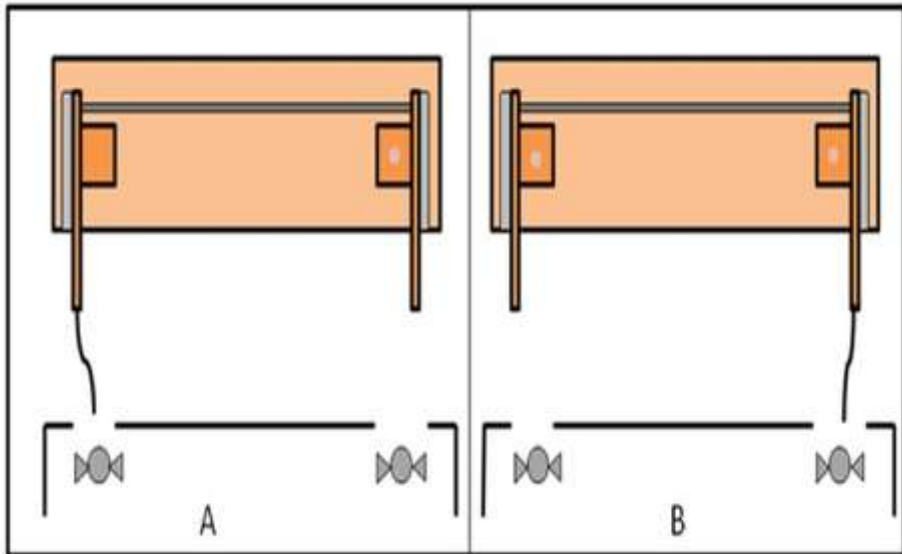


Figure 2: Schematic design of the apparatuses used in Prosocial Task (A) and Control Task (B).

Experimental procedure and cooperative tasks

After a training phase, we performed three different cooperative tasks: *Cooperation task* (Figure 1), *Prosocial task* (Figure 2a); and *Control task* (Figure 2b). The training was made so that individual actions of pulling resulted in obtaining individual food, *i.e.*, the marmosets were trained to pull the strings when the bar that connected them had been removed. Thus, it was not required the simultaneous action of pulling two levers to obtain food rewards, and when an animal pulled a lever, it received a reward.

Two apparatuses were placed in front of each cage so that the ends of the levers containing the strings were inside the cage and the trays containing the bananas were out of reach of the

animals, outside the cages (Figure 3). To bring the tray at reach, each individual must pull the string, which allowed the lever on the trail to move. The animals had visual and olfactory access to the rewards, and to ensure that they would be motivated they were deprived of food for two hours before the training and also before the experimental sessions. All experiments were performed in the afternoon, between 13h and 14h, and the training as well as the experimental sessions was conducted with all individuals of each family inside the cages.

The animals were trained for two weeks in sessions of approximately ten minutes. No individual was manipulated to avoid unnecessary stress, so the training of each marmoset occurred randomly, as the animals were in contact with the apparatus. A success

Social relationships and cooperative tasks in marmosets.

rate was calculated by dividing the number of pulls that resulted in food rewards by the total number of pulls at the lever. We considered it successful when 90% of their pulls resulted in rewards for three consecutive days.



Figure 3. Arrangement of experimental apparatuses and video cameras in front of the cages where the animals lived.

Cooperation Task

After training, we started the Cooperation task. Two identical apparatuses (Figure 1) were positioned at the same time in front of the cages in a similar way to training, which allowed two dyads to be formed in each family, reducing the chances of only a few animals monopolize the apparatus. However, unlike the conditions in the training phase, the levers of the apparatus were connected by a bar, what made necessary two animals to pull the two levers simultaneously so that the trays could approach at their reach. If only one animal pulled a lever, or if two of them pulled without coordinating their actions in time and space, the trays did not slip and it was not possible for them to obtain the rewards.

Prosocial Task

This test evaluated the occurrence of prosocial behavior in marmosets, ie, if the animals were able to perform a task on behalf of a partner. As in the Cooperation task, two apparatuses (Figure 2a) were available for the animals during the sessions. By pulling a lever, the two trays came within reach of each animal in the apparatus, but only the tray of the animal that did not pull contained the reward. The animal that pulled never got the banana but could see that his partner was benefited by his action.

Control Task

A third test was performed to compare to the results obtained in the first two tasks. Only one animal could pull the string, but here, the two animals at the apparatus received the fruit.

In all three tasks, as well as in training, pairs of individuals of each apparatus (an animal in front of each tray) were settled spontaneously, since the animals were not manipulated and were all together in their family cages.

For each test there was a session of ten minutes per day for five consecutive days and the experiments followed the order: Cooperation, Prosocial and Control Tasks. Three sets with the three tasks were performed on each family. As there was a camera for each dyad, it was possible to obtain good quality videos for the analysis of behavioral parameters of interest. With two cameras in each cage (one for each apparatus), the sessions in each family

Social relationships and cooperative tasks in marmosets.

were recorded in two videos, which resulted in four videos for ten minutes each day (two for each family), five days a week during three weeks, resulting in sixty videos by experimental task.

Social Relationships

Data collection

The pattern of social relationship of each individual was recorded by means of affiliative behaviors of grooming and proximity. The records were obtained through the focal instantaneous sampling method (ALTMANN 1974), for ten minutes, at intervals of 30 seconds between records.

Social grooming was defined as the manipulation of fur performed with the hands or mouth, which could occur between two or more animals. It included receiving grooming, when the focal animal received grooming from some other group member, and offering grooming, when the focal animal directed this behavior to other animal. We considered proximity when the focal animal was as far as 15 cm of (an) other animal (LOPES 2002, unpublished data). These data of social relationships were collected in two ways:

- ten days before the onset of the first cooperative testing set, and for other ten days before the onset of the cooperative task of the second set. This occurred because the composition of the family F09 varied between the first and second sets (see Table 1) and because there was an interval in the experiments between

first and second sets (due to a reform in LEAP).

- daily, on the day of each experiment during the second and third sets, one hour prior to each experimental session. During the first set, social data were not recorded in this condition.

In the cooperative tasks, data collection through the videotaping allowed to register the variable “pulls”. These defined the success in cooperative tasks, and in motor terms, it was defined as an animal holding the rope to slide the tray bringing the reward at reach. In the Cooperation task they always occurred in pairs, while in the Prosocial and Control tasks they were performed by one animal only, the active animal.

Data Analysis

The data of social relationships collected for ten days before the start of the first set were analyzed separately from those of the second and third sets, which were analyzed together. The data collected daily before each experimental session during the second and third sets were also analyzed together.

To analyse the importance of social relationships among animals for cooperation and prosociality, matrix correlation tests were performed. As the dyads were randomly formed in the apparatus, there were many possibilities for the formation of pairs, and during data analysis this leads to statistical dependence. We then used the Tau Kr test, since this test takes the dependence of data into account (HEMELRIJK 1990a, b).

Social relationships and cooperative tasks in marmosets.

For each family, we created the following matrices:

- Cooperation Task: a square symmetric matrix, where each cell contained the number of times the animals pulled the string simultaneously.
- Prosocial Task: a square asymmetric matrix of pulls, where the lines represented the number of the pulls of an active animal (the one that pulled the string) to its receptor partner in each dyad formed.
- A square symmetric matrix with proximity data measured by the Jaccard index.
- A symmetric square matrix with grooming data for correlation with the symmetric matrix of pulls of the Cooperation task. This matrix was made by summing the values obtained for each dyad.
- An asymmetric square matrix with grooming data for correlation with the asymmetric matrix of pulls of the Prosocial task, where the lines contained the number of pulls a groomer groomed a gromee.
- We also tested whether grooming occurs in an exchange system, and thus, it was expected that animals would receive more rewards in the Prosocial task from those partners that they groomed more. So, the asymmetric square matrix of pulls of Prosocial task was transposed to be correlated with the grooming matrix.

As animals participated in the experimental tasks in unequal amount of times, all matrixes were normalized to remove the possible effect of a bias in the number of pulls that could exist if different individuals have different participation in the tasks. The Jaccard index was used as a method to normalize the symmetric matrices. For the asymmetric matrices the normalization was made by dividing the number of pulls/ grooming bouts of an animal A directed to a receiver B by the number pulls / grooming bouts of the animal A directed to all animals with which it formed a dyad (normalized cell value = $I_{ab} / \sum I_{ai}$). The correlation tests were performed using normalized matrices, which means that it has been verified if the animals that groom / stay in close proximity above the mean group also cooperate / act prosocial above the average of the group.

Results

The use of the apparatus to obtain food was used successfully by 73% of the animals on the first day of training. Therefore, all animals achieved success in the third day of experiment, but one, who took four days.

Proximity, Cooperation and Prosociality

For the first set, in the Cooperation task, there was no significant correlation between proximity and pulls (F05/06: Tau Kr = 0,21, $p_r = 0,16$; F09: Tau Kr = - 0,11, $p_l = 0,42$). In the Prosocial task, no significant correlation was found (F05/06 Tau Kr = - 0,07, $p_r = 0,35$; F09 Tau Kr = 0,24, $p_r = 0,51$).

Social relationships and cooperative tasks in marmosets.

There was no significant correlation between proximity, success in the cooperation task or success in the prosocial task in the data analysis of the second and third sets (Cooperation: F05/06: Tau Kr = 0,15, $p_r = 0,18$; F09: Tau Kr = 0,2, $p_r = 0,33$; Prosocial: F05/06: Tau Kr = 0,06, $p_r = 0,44$; F09: Tau Kr = 0,31, $p_r = 0,23$).

Grooming, Cooperation and Prosociality

In the first set we did not find a significant correlation between grooming and pulls in any of the families (Cooperation task: F05/06: Tau Kr = - 0,12, $p_1 = 0,32$; F09: Tau Kr = - 0,55, $p_1 = 0,1$; Prosocial task: F05/06: Tau Kr: - 0,27, $p_1 = 0,13$; F09: Tau Kr could not be calculated, because of the great number of cells containing “zero” values). The results showed that there was no exchange of grooming for pulls in F05/06 (Tau Kr = - 0,19, $p_1 = 0,23$) and in F09, Tau Kr could not be calculated.

There was no significant correlation between grooming and pulls in the second and third sets in the analysis of Cooperation data (F05/06: Tau Kr = - 0,15, $p_1 = 0,27$; F09: Tau Kr = 0,2, $p_r = 0,22$). To the Prosocial task, we found significant correlation in F09 (F05/06: Tau Kr = - 0,2, $p_1 = 0,20$; F09: Tau Kr = 0,85, $p_r = 0,01$). Neither in F09 (Tau Kr = - 0,22, $p_1 = 0,23$) nor in F05/06 (Tau Kr = 0,05, $p_r = 0,39$) we found significant correlation between the transposed matrix of pulls in the Prosocial task and the grooming matrix.

Daily data

The correlations analysis using data collected daily, before the start of each experimental session also followed the same pattern. Correlation between pulls and proximity did not show statistical significance in Cooperation task (F05/06: Tau Kr = - 0,07, $p_1 = 0,42$; F09: Tau Kr = 0,14, $p_r = 0,37$). In Prosocial task, there was no significance in F09 (Tau Kr = 0,18, $p_r = 0,37$) but there was in F05/06; however, with a negative correlation, ie, the animals that stayed more frequently in proximity just before the task, cooperated less during the tasks (Tau Kr = - 0,42, $p_1 = 0,02$). The correlation between pulls and grooming was not significant in the Cooperation task in any of the families (F05/06: Tau Kr = - 0,25, $p_1 = 0,09$; F09: Tau Kr = 0,15, $p_r = 0,36$); neither it was in the Prosocial task (F05/06: Tau Kr = - 0,15, $p_1 = 0,19$; F09: Tau Kr = - 0,55, $p_1 = 0,09$). Also, there was no significant correlation between the transposed matrix of pulls and the grooming matrix (F09: Tau Kr = 0,51, $p_r = 0,15$; F05/06: Tau Kr = - 0,07, $p_1 = 0,38$).

Discussion

CRONIN *et al.* (2005), BURKART *et al.* (2009) and BURKART & VAN SCHAIK (2010), argue for the existence of a link between cooperative breeding and cognitive performance, especially in the social field. According to the authors, differential attention during monitoring of conspecifics, the ability to coordinate actions in time and space, the high social tolerance and high sensitivity to signals of others are among the cognitive and motivational processes that underlie the behaviors during the

Social relationships and cooperative tasks in marmosets.

cooperative care of offspring. These processes would facilitate the performance at other social situation, for example, during cooperative tasks. The present study directly tested if the tolerance in spatial proximity and affiliative behavior of grooming influence the occurrence of cooperative behavior in common marmosets (*Callithrix jacchus*), and the results were negative. There was no correlation between the execution of cooperative tasks with grooming or proximity, neither using social data collected for ten days before the experiments, neither using data collected daily, immediately before each task. This lack of association between social tolerance/affinity and success in cooperation tasks stands against this Cooperative Breeding hypothesis, but aligns to the results obtained by STEVENS (2010) that could not find any evidence of the Cooperative Breeding Hypothesis in tamarins. Indeed, CRONIN *et al.* (2009) reported that some animals were less likely to deliver rewards to the partners when the latter displayed signs of interest in them.

The relation between tolerance, affinity and cooperative behaviors may occur in subtle ways, however. We can infer that social relation played a role in these tasks by the behavior of one adult male, Onesio (F05/06). Although not statistically detectable, his singular behavior is noteworthy: during Prosocial tasks he pulled the lever then run to the other tray to get the reward chasing away any animal, and monopolized the tray containing the banana. This occurred for all subjects except for his older brother, Opus. Opus

was allowed to take the reward and unlike what happened with the other animals, which were removed with biting, pushing and other aggressions, few agonistic behaviors were directed to him.

Multi-factorial analyses (*e.g.* taking into account proximity, affinity, hierarchy, sex-age, availability of preferential partners all together) are difficult to conduct due to small sample sizes. Nevertheless, the pattern observed between these brothers is in accordance with the results of BURKART *et al.* (2007) in that female-female dyads did not act prosocially even when prosocial behavior was found at group level. This occurred because a “preferential prosociality” among males and “preferential competitiveness” among females is expected in this species, since pairs of brothers copulate with a single dominant females that hormonally suppress subordinate females (ABBOTT 1984, SOUSA *et al.* 2005, ARRUDA 2012, personal communication).

Also, it is possible that, similar to female chacma baboons (SILK *et al.* 2010), grooming may not be directly exchanged, but would serve a broader social function. This suggestion finds support on the work of LAZARO-PEREA *et al.* (2004), who could not find that grooming was exchanged for a specific service. The authors suggest that dominant females of *Callithrix jacchus* use grooming as an incentive for subordinate females to remain in the group (LAZARO-PEREA *et al.* 2004).

Another possible explanation for the lack of correlation between the variables

measured is the experimental condition, with all the animals together in the same cage. According to BURKART & VAN SCHAİK (2012) the presence of many animals around an experimental apparatus makes it unlikely that animals will choose partners for the accomplishment of tasks, and pulling the string may occur without the control of who is in the other tray. However, this argument goes both ways. If, on the one hand, the analysis of family experimental conditions can make it difficult the choice of a partner, on the other hand the analyses using single caged animals could exacerbate the social stimulus during the experiment, making the observed association between affinity and success in cooperation tasks a by-product result of the experimental conditions. Indeed, HALSEY *et al.* (2006) showed that common marmosets had lower performance in solving the parallel string test in natural environment, and attributed this to the diversity of stimulus in this condition (specially vigilance to predators). Therefore, by testing in group condition the whole social dynamic takes place.

It is worth noting that albeit sharing food (FERRARI 1987) and being highly tolerant to each other (KASPER *et al.* 2008), callitrichid monkeys can sometimes be extremely competitive and aggressive, especially with regards to food and reproduction (MICHELS 1998, LOPES 2002, SOUSA *et al.* 2005, YAMAMOTO 2005, SALTZMAN *et al.* 2009). Other contexts might also trigger severe aggression including threats, biting and slapping, that can be observed both in natural and captive

conditions (SNOWDON & PICKHARD 1999, DE FILIPPIS *et al.* 2009, ARRUDA 2012, personal communication). A long-term survey on captive tamarins found that fights were more common among siblings than parent-offspring conflicts and among same-sex individuals, and that males engaged in more harsh fightings than females (SNOWDON & PICKHARD 1999). In a more recent study on *Callithrix jacchus* the results showed that both males and females behaved as aggressors at the same rate, and that while females attacked only same-sex animals, males attacked both males and females. As well as in the tamarins study, most aggressions involved siblings (DE FILIPPIS *et al.* 2009).

Therefore, in the discussion on the relation between cooperative breeding and cooperative capabilities in common marmosets, not only the cooperative characteristics should be taken into account but also the competitive ones, since they also contribute to shaping the behavioral repertoire of the species. Despite its importance, the competitive aspect of the social dynamics is somehow underscored in most studies on cooperative problem solving on callitrichids due to the experimental setting (BURKART *et al.* 2007, SNOWDON & CRONIN 2007, CRONIN *et al.* 2005, 2009, 2010, CRONIN & SNOWDON 2008, BURKART & VAN SCHAİK 2012).

Inspired by the elegance of the Cooperative Breeding Hypothesis current studies are still presenting contradictory data (as observed from the results obtained on the series of studies conducted by CRONIN, K.A. e

Social relationships and cooperative tasks in marmosets.

SNOWDON, C.T. (CRONIN *et al.* 2009 X CRONIN *et al.* 2005, 2010 e CRONIN & SNOWDON 2008). Although our results indicate that social tolerance and affiliation do not associate to success during cooperative problem solving in *Callithrix jacchus* in group test condition, as well recognized by BURKART & VAN SCHAİK (2012) different results from different experimental conditions can be considered complementary to a more accurate conclusion on this subject.

Acknowledgments

We thank to CNPq for the financial support: a Master of Science grant to R. C. C.; Under graduation grants to E. C. N. B. and S. R. N.; a PhD grant to B. S. B. G.

References

- ABBOTT, D.H. 1984. Behavioural and physiological suppression of fertility in subordinate marmoset monkeys. **American Journal of Primatology** **6**: 169-186.
- AHUMADA, J.A. 1992. Grooming behavior of spider monkeys (*Ateles geoffroyi*) on Barro Colorado Island, Panama. **International Journal of Primatology** **13**: 33-49.
- ALTMANN, J. 1974. Observational study of behavior: sampling methods. **Behaviour** **49**: 227-267.
- ANDERSON, J.R. 2007. Animal behavior: tolerant primates cooperate best. **Current Biology** **17**(7): 242-244.
- BURKART, J.M., FEHR, E., EFFERSON, C. & VAN SCHAİK, C.P. 2007. Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. **PNAS** **50**: 19762-19766.
- BURKART, J.M., HRDY, S.B. & VAN SCHAİK, C.P. 2009. Cooperative breeding and human cognitive evolution. **Evolutionary Anthropology** **18**: 175-186.
- BURKART, J.M. & VAN SCHAİK, C.P. 2010. Cognitive consequences of cooperative breeding in primates? **Animal Cognition** **13**: 1-19.
- BURKART, J.M. & VAN SCHAİK, C.P. 2012. Group service in macaques (*Macaca fuscata*), capuchins (*Cebus apella*) and marmosets (*Callithrix jacchus*): a comparative approach to identifying proactive prosocial motivations. **Journal of Comparative Psychology** **26**: 1-14.
- CHALMEAU, R. & GALLO, A. 1996. Cooperation in primates: critical analysis of behavioural criteria. **Behavioural Processes** **35**: 101-111.
- CLUTTON-BROCK, T. 2006. Cooperative breeding in mammals, p. 173-190. *In*: KAPPELER, P.M. & VAN SCHAİK, C.P. (Eds.). **Cooperation in Primates and Humans: mechanisms and evolution**. Berlin, Springer.
- CROFOOT, M.C., RUBENSTEIN, D.I., MAIYA, A.S. & BERGER-WOLF, T. 2011. Aggression, grooming and group-level cooperation in white-faced capuchins (*Cebus capucinus*): insights from social networks. **American Journal of Primatology** **73**: 821-833.
- CRONIN, K.A. & SNOWDON, C.T. 2008. The effects of unequal reward distributions on cooperative problem solving by cottontop tamarins, *Saguinus oedipus*. **Animal behavior** **75**: 245-257.
- CRONIN, K.A., KURIAN, A.V. & SNOWDON, C.T. 2005. Cooperative problem solving in a cooperatively breeding primate (*Saguinus oedipus*). **Animal Behaviour** **69**: 133-142.
- CRONIN, K.A., SCHROEDER, K.K.E., SILK, J.B. & ROTHWELL, E.S. 2009. Cooperatively Breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their long-term mates. **Journal of Comparative Psychology** **123**: 231-241.
- CRONIN, K.A., SCHROEDER, K.K.E. & SNOWDON, C.T. 2010. Prosocial behavior emerges independent of reciprocity in cottontop tamarins.

Social relationships and cooperative tasks in marmosets.

- Proceedings of the Royal Society B: Biological Sciences** **277**: 3845-3851.
- DE FILIPPIS, B., CHIAROTTI, F. & VITALE, A. 2009. Severe intragroup aggressions in captive common marmosets (*Callithrix jacchus*). **Journal of Applied Animal Welfare Science** **12**(3): 214-222.
- DI BITETTI, M.S. 1997. Evidence for an important social role of allogrooming in a Platyrrhine primate. **Animal Behavior** **54**: 199-211.
- DIGBY, L.J. & BARRETO, C.E. 1993. Social organisation in a wild population of *Callithrix jacchus*. **Folia Primatologica** **61**: 123-134.
- DUGATKIN, L.A. 1997. **Cooperation among animals**. New York, Oxford University Press.
- DUNBAR, R.I.M. 1991. Functional significance of social grooming in primates. **Folia Primatologica** **57**: 121-131.
- FERRARI, S.F. 1987. Food transfer in a wild marmoset group. **Folia Primatologica** **48**: 203-206.
- GINTHER, A.J. & SNOWDON, C.T. 2009. Expectant parents groom adult sons according to previous alloparenting. **Animal Behaviour** **78**: 287-297.
- HALSEY, L.G., BEZERRA, B.M. & SOUTO, A.S. 2006. Can wild common marmosets (*Callithrix jacchus*) solve the parallel strings task? **Animal Cognition** **9**: 229-233.
- HARE, B., MELIS, A.P., WOODS, V., HASTINGS, S. & WRAGHAM R. 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. **Current Biology** **17**: 1-5.
- HAUSER, M.D., CHEN, M.K., CHEN, F. & CHUAN, E. 2003. Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. **Proceedings of the Royal Society B** **279**: 2363-2370.
- HEMELRIJK, C. 1990a. Models of, and test for, reciprocity, unidirectionality and other social interaction patterns at group level. **Animal Behaviour** **39**: 1013-1029.
- HEMELRIJK, C. 1990b. A Matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. **Journal of Theoretical Biology** **143**: 405-420.
- HENZI, S.P. & BARRETT, L. 1999. The value of grooming to female primates. **Primates** **40**(1): 47-59.
- HEYES, C.M. 1998. Theory of mind in nonhuman primates. **Behavioral and Brain Sciences** **21**: 101-114.
- KASPER, C., VOELKL, B. & HUBER, L. 2008. Tolerated mouth-to-mouth food transfers in common marmosets. **Primates** **49**: 153-156.
- LAZARO-PEREA C., ARRUDA, M. F. & SNOWDON C. T. 2004. Grooming as a reward? Social function of grooming between females in cooperatively breeding marmosets. **Animal Behavior** **67**(4): 627-636.
- LYNCH, A.J.W, BOUBLI, J.P., OLSON, L.E., DI FIORI, A., WILSON, B., GUTIERREZ-ESPELETA, G.A., CHIOU, K.L., SCHULTE, M., NEITZEL, S., ROSS, V., SCHWOCHOW, D., NGUYEN, M.T.T., FARIAS, I., JANSON, C., ALFARO, M.E. 2012. Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. **Journal of Biogeography** **39**: 272-288.
- MELIS, A.P., HARE, B. & TOMASELLO, M. 2006. Chimpanzees recruit the best collaborators. **Science** **311**(5765): 1297-1300.
- MENDRES, K.A. & DE WAAL, F.B.M. 2000. Capuchins do cooperate: the advantage of an intuitive task. **Animal Behaviour** **60**: 523-529.
- MICHELS, A.M. 1998. Sex differences in food acquisition and aggression in captive common marmosets (*Callithrix jacchus*). **Primates** **39**(4): 549-556.
- NEWTON-FISHER, N.E. & LEE, P.C. 2011. Grooming reciprocity in wild male chimpanzees. **Animal Behaviour** **81**: 439-445.

Social relationships and cooperative tasks in marmosets.

- NOE, R. 2006. Cooperation experiments: coordination through communication versus acting apart together. **Animal Behaviour** **71**: 1-18.
- PETIT, O., DESPORTES, C., & THIERRY, B. 1992. Differential probability of coproduction in two species of macaque (*Macaca tonkeana*, *M. mulatta*). **Ethology** **90**: 107-120.
- SALTZMAN W., DIGBY, L.J. & ABBOTT, D.H. 2009. Reproductive skew in female marmosets: what can proximate mechanisms tell us about ultimate causes? **Proceedings of the Royal Society B** **276**: 389-399.
- SANCHEZ-VILLAGRA, M.R., POPE, T.R. & SALAS, V. 1998. Relation of intergroup variation in allogrooming to group social structure and ectoparasite loads in red howlers (*Alouatta seniculus*). **International Journal of Primatology** **19**: 473-491.
- SCHINO, G. & AURELI, F. 2008. Trade-offs in primate grooming reciprocation: testing behavioural flexibility and correlated evolution. **Biological Journal of the Linnean Society** **95**: 439-446.
- SHETTLEWORTH, S.J. 2010. **Cognition, evolution and behavior**. New York, Oxford University Press.
- SILK, J.B. 2003. Cooperation without counting. The puzzle of friendship, p. 37-54. *In*: HAMMERSTEIN, P. (Ed.). **Genetic and Cultural Evolution of Cooperation**. Los Angeles, The MIT Press.
- SILK, J.B., BEEHNER, J.C., BERGMAN, T.J., CROCKFORD, C., ENGH, A.L., MOSCOVICE, L.R., WITTING, R.M., SEYFARTH, R.M. & CHENEY, D.L. 2010. Female chacma baboons form strong, equitable, and enduring social bonds. **Behavioral Ecology and Sociobiology** **64**: 1733-1747.
- SNOWDON, C.T. & CRONIN, K.A. 2007. Cooperative breeders do cooperate. **Behavioural Processes** **76**: 138-141.
- SNOWDON, C.T. & PICKHARD, J.J. 1999. Family feuds: Severe aggression among cooperatively breeding cotton-top tamarins. **International Journal of Primatology** **20**(5): 651-663.
- SOUSA, M.B.C., ALBUQUERQUE, A.C.S.R., ALBUQUERQUE, F.S., ARAÚJO, A., YAMAMOTO, M.E. & ARRUDA, M.F. 2005. Behavioral strategies and hormonal profiles of dominant and subordinate common marmoset (*Callithrix jacchus*) Females in wild monogamous groups. **American Journal of Primatology** **67**: 37-50.
- STEVENS, J.R. 2010. Donor payoffs and other-regarding preferences in cotton-top tamarins (*Saguinus oedipus*). **Animal Cognition** **13**: 663-670.
- STEVENSON, M.F. & RYLANDS, A.B. 1988. The marmosets, genus *Callithrix*, p. 131-222. *In*: Mittermeier, R.A., Rylands, A.B., Coimbra-Filho, A.F. & Fonseca, G.A.B. (Eds.). **Ecology and behavior of neotropical primates. Vol. 2.**, p. Washington, World Wildlife Fund.
- TIDDI, B., AURELI, F. & SCHINO, G. 2012. Grooming Up the Hierarchy: The Exchange of Grooming and Rank-Related Benefits in a New World Primate. **PLOS ONE** **7**(5): 1-6.
- WERDENICH, D. & HUBER, L. 2002. Social factors determine cooperation in marmosets. **Animal Behaviour** **64**: 771-781.
- YAMAMOTO, M.E. 1993. From dependence to sexual maturity: the behavioural ontogeny of Callitrichidae, p. 235-254. *In*: RYLANDS, A.B. (Ed.). **Marmosets and tamarins: systematic, behaviour and ecology**. Oxford, Oxford University Press.
- YAMAMOTO, M.E. 2005. Infant care in callitrichids: cooperation and competition. **Annual Review of Biomedical Sciences** **7**: 149-160.