



Male and female breeding strategies in a cooperative primate

Maria Emilia Yamamoto^{a,*}, Arrilton Araujo^a, Maria de Fatima Arruda^a,
Ana Karinne Moreira Lima^a, Jose de Oliveira Siqueira^b, Wallisen Tadashi Hattori^a

^a Graduate Program in Psychobiology, Department of Physiology, Federal University of Rio Grande do Norte, Av. Sen. Salgado Filho, 3000, Caixa Postal 1511, Campus Universitário, Lagoa Nova, 50978-970 Natal, RN, Brazil

^b Department of Experimental Psychology, Institute of Psychology, University of São Paulo, Av. Prof. Mello Moraes 1721, Bloco A, Sala E3, Cidade Universitária, 05508-030 São Paulo, SP, Brazil

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ABSTRACT

Marmosets are cooperative breeders organized as extended family groups, but breeding is generally restricted to a single pair. Breeding competition is fierce in female marmosets; males, on the other hand, show low levels of intragroup aggression. We investigated male and female breeding strategies and the resulting reproductive output in 9 wild groups. Reproductive output, tenure of breeding animals, identification of the breeding system, breeding position replacements, migration and infanticide were recorded; also, we recorded grooming and aggression. Replacement of the breeding male or female was observed on nine occasions. On four occasions, the son of the breeding male inherited the breeding post, but we never observed inheritance of a breeding post by a daughter. Mostly, females attained a breeding post by immigrating to a group that had a breeding vacancy. Our results showed that *Callithrix jacchus* males and females use different strategies to attain a breeding position and maintain it for as long as possible. These strategies prolong the tenure of the breeding position, which is the best way to produce a large number of offspring.

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1. Introduction

Common marmosets (*Callithrix jacchus*) are cooperative breeders that occupy a diversity of different habitats in Brazil. These small primates live in groups that vary in size from 5 to 17 individuals and include adult males and females, as well as immature animals (Araujo, 1996). Studies of captive and wild marmosets suggest that marmoset groups live as extended families or, alternatively, as multimale and multifemale groups, not necessarily close genetic relatives (Faulkes et al., 2003, 2009; Ferrari and Lopes-Ferrari, 1989).

Most studies suggest that breeding in these groups is restricted to just a single pair, which is typical of a monogamous mating system (Araujo, 1996; Arruda et al., 2005; Rothe and Darms, 1993; Yamamoto et al., 2009), although groups containing two breeding females have also been reported in the wild (Arruda et al., 2005;

Digby and Ferrari, 1994; Scanlon et al., 1988; Yamamoto et al., 2009, 2010).

Clutton-Brock et al. (2006) suggest that competition between females is likely to be particularly intense in cooperative breeders where a single female monopolizes reproduction. In fact, breeding competition is fierce among female marmosets and does not seem to be attenuated by kinship. Dominant breeding females frequently harass their own daughters when they are unable to suppress them hormonally, sometimes leading to expulsion from the group (Arruda et al., 2005), and may show similar levels of aggression to both related and unrelated females (Alencar et al., 1995). Moreover, there have been reports of infanticide perpetrated by dominant females (Arruda et al., 2005; Bezerra et al., 2007; Lazaro-Perea et al., 2000; Melo et al., 2003).

On the other hand, males show low levels of intragroup aggression, in both wild (Araujo, 1996) and captive marmoset groups (Araujo and Yamamoto, 1993; Galvão-Coelho et al., 2008). A core group, including the breeding pair and some non-breeding individuals, usually another male, has been described in wild marmoset groups (Araujo, 1996; Koenig and Rothe, 1991). In *Saguinus*, a genus belonging to the same clade, a second male may indicate a polyandrous mating system (Diaz-Muñoz, 2011). For *C. jacchus* there are very few genetic studies and these did not indicate the occurrence

* Corresponding author. Tel.: +55 84 3215 3409.

E-mail addresses: emiliayamamoto@gmail.com (M.E. Yamamoto), arrilton@gmail.com (A. Araujo), mariadefarruda@gmail.com (M.d.F. Arruda), anakarinnelima@gmail.com (A.K.M. Lima), siqueira@usp.br (J.d.O. Siqueira), wallhattori@gmail.com (W.T. Hattori).

of polyandry (Faulkes et al., 2003, 2009; Nievergelt et al., 2000), which is in line with behavioural data.

Yamamoto et al. (2010) suggest that the highly successful *C. jacchus* reproductive system is based on a balance between competition and cooperation. The former enforces reproductive monopolization by females by avoiding the substantial costs of raising more than one set of offspring simultaneously and the latter by providing better breeding opportunities for males through three of the five kinds of cooperation indicated by Diaz-Muñoz et al. (2014), more specifically, competitive coalitions, cooperative polyandry and cooperative parental care.

Hauber and Lacey (2005) suggest that in cooperatively breeding mammals there may be a greater suppression of reproduction in females, leading to greater competition among females than males. This conclusion is very much in line with behavioural and hormonal data on *C. jacchus* (Arruda et al., 2005; Faulkes et al., 2009; Yamamoto et al., 2010). Although breeding is restricted to a breeding pair or trio (Yamamoto et al., 2009), all adult males retain the physiological ability to reproduce, and usually all but one non-breeding female are physiologically suppressed (Sousa et al., 2009). Nevertheless, ovulating subordinate females either breed as a secondary breeder in a polygynous breeding arrangement or present failed attempts to breed/raise infants that usually end in the death of infants and migration from the group (Arruda et al., 2005). Non-ovulating subordinate females may start to ovulate very quickly given favourable social conditions (Saltzman et al., 2005). Therefore, different strategies for the sexes should be expected and breeding positions could be achieved by different means (Sousa et al., 2009; Yamamoto et al., 2009).

In the current study, we investigated the behavioural differences between male and female *C. jacchus* and the patterns of social organization of breeding and non-breeding animals. These data allowed us to characterize different strategies used by males and females to attain breeding status. We also compared the reproductive output of males and females, considering the duration of their tenures. In relation to social relationships, we predicted more affiliative interactions among males, demonstrating the adoption of cooperative strategies, and more agonistic interactions among females, showing the adoption of competitive strategies (Sousa et al., 2009; Yamamoto et al., 2010). We also predicted that males and females would show similar reproductive outputs despite the adoption of distinct strategies, as most reproductive sets are monogamous.

2. Materials and methods

2.1. Study sites

The present study was conducted at two sites, both managed by the Chico Mendes Institute for Biodiversity (ICMbio) and located in the state of Rio Grande do Norte, north-eastern region of Brazil:

- A Caatinga conservation unit (Assu National Forest), located in the municipality of Assu, RN (5°35' S, 36°56' W). This area includes 518 hectares of arboreal shrub vegetation, which is typical of the Caatinga biome, with an average temperature of 28 °C and average rainfall of 70 mm.
- An area of secondary Atlantic Forest (Nisia Floresta National Forest), located in the municipality of Nisia Floresta (06°05' S, 35°12' W), 250 km distant from the other study site. This area includes 175 hectares of mixed semideciduous Atlantic Forest, coconut palms and eucalyptus plantations, with an average temperature of 26.6 °C and average rainfall of 208.5 mm/month.

Common marmosets (*C. jacchus*) were the only nonhuman primate species observed within the study sites and surrounding areas.

All of the individuals from each of the study groups were trapped and fitted with colour bead collars for individual identification. An anaesthetic (ketamine, 10 mg/kg) was injected in the animals for easier handling during collection of biometric data and placement of the identification collars, and to minimize the animal's stress levels. Identification collars were only placed on adults and sub-adults. Animals weighing less than 250 g were individually marked by painting a specific part(s) of the body and/or by shaving a part of the tail, although infants were only marked using body paint.

2.2. Groups

This study focuses on data from long term monitoring of groups until their disappearance or reorganization, representing about twenty years of information on groups' social dynamics in both marmoset study sites. Animals' immigration and emigration, new reproductive pair formation, births, identification of mothers and presumptive fathers were the measures used to obtain the data. Additionally, adults in three of those groups had their affiliative and aggressive interactions recorded in order to describe social relations, more specifically, the dominance relations associated with the reproductive system in those groups.

In the area of Caatinga, one group of marmosets was monitored for 120 months. In the secondary Atlantic Forest, eight groups were monitored for periods varying from 20 to 79 months. During the monitoring period, we recorded more than one reproductive unit (or breeding unit, consisting of males and females that bred regularly and repeatedly in the group, Arruda et al., 2005) occurring successively in Groups 1, 2, 3 and 7. Two mating systems were identified in the groups, monogamy and polygyny, respectively, when the reproductive unit consisted of a single pair, or when systematically, there were two females alternating pregnancy inside the group; also, copulating and being mate guarded by the same male. Mating systems not only varied among the groups, but also within the same group in two cases (Groups 3 and 7), both of which were first characterized as being polygynous, but after a new female assumed the reproductive vacancy, they became monogamous (Table 1). Copulations were recorded opportunistically. Identification of the breeding position of females was based on their pregnancies and birth of infants. The breeding positions of males were identified based on opportunistically recorded copulations and other behaviours that are indicative of mate guarding, such as following the female, grooming and resting together. Migration, disappearance or the death of one or all previously breeding individuals in a particular group resulted in the formation of a new reproductive unit that sometimes included the previously breeding individual(s) and sometimes not (Lazaro-Perea et al., 2000).

2.3. Data recording

We monitored 14 males and 16 females to determine the following variables (Table 1): reproductive output (infants that survived up to 5 months); tenure of breeding animals for both males and females, represented by the total number of months an individual spent as a systematically breeding member of the group; identification of the breeding system(s) of each group as being monogamous, polygynous or both; breeding position replacements, and the identification of which individuals composed the new reproductive sets; migration of both males and females that entered or left the observed groups; and the occurrence of infanticide.

In the three groups mentioned above, we also recorded grooming and aggression. Grooming was recorded through instantaneous animal sampling and aggression through continuous animal

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