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SHORT COMMUNICATION

Matrilineal genetic structure within and among populations of the cooperatively breeding common marmoset, *Callithrix jacchus*

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Abstract

Common marmosets are members of the family Callitrichidae, South American primates characterized by highly social group living and cooperative breeding. In this study we analysed 1112 base pairs (bp) of the mitochondrial control region in 59 *Callithrix jacchus* individuals, sampled mainly from two geographically distinct field sites in N.E. Brazil. Analysis of molecular variation revealed a highly significant genetic structuring of haplotypes between social groups and between populations. Examination of matrilineal genetic structure within social groups revealed that seven of nine recorded breeding pairs were from different maternal lineages, indicating assortative mating and outbreeding. In addition to the breeders, at least six of 10 groups contained adult individuals from different matrilines, with five haplotypes present in one social group of nine animals. Groups of mixed lineages raise questions about potential reproductive conflicts of interest, and the extent of kin-selected altruism in the evolution and maintenance of cooperative breeding in this species.

Keywords: *Callithrix jacchus*, Callitrichidae, cooperative breeding, kin structure, mitochondrial DNA, phylogeography

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Introduction

Marmosets and tamarins of the Family Callitrichidae are small arboreal primates endemic to the northern half of South America. The four genera of 40 or so species are distributed widely in a variety of primary and secondary forest types. Within the family, cooperative breeding strategies are widespread and virtually all species are characterized by small territorial groups of approximately 4–15 individuals, where reproduction is monopolized by one or a small number of dominant individuals of each sex (high reproductive skew; for review see French 1997; Tardif 1997).

The social and reproductive system of common marmosets, *Callithrix jacchus*, is typical of the Callitrichidae. Groups contain 3–15 individuals, and typically a single dominant female breeds, normally producing dizygotic twins. However, plural breeding among females can occur (Digby & Ferrari 1994; Nievergelt *et al*. 2000), and mating systems can be variable both within and between callitrichid species. Polyandry, polygyny and monogamy have all been reported from behavioural observations (Ferrari & Digby 1996). Nievergelt *et al*. (2000) used microsatellite genotyping to investigate three social groups of common marmosets in Nisia Floresta, Brazil, and found two breeding females per group mating with mainly a single dominant male (polygynmonandry). However, the presence of more than one breeding female per group may be atypical (M. F. Arruda *et al*. unpublished; Rothe & Darms 1993). Irrespective of mating system, twin offspring are usually produced in callitrichids, and the main role of nonreproductive helpers in the group is to assist in the care of the breeding female's offspring. This is principally by sharing the burden of carrying the relatively bulky twin infants around their arboreal habitat, although food provisioning may also occur (Tardif *et al*. 1993). Determining the genetic structure and patterns

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of relatedness within social groups is thus crucial in understanding the role of kin selection in the alloparental behaviour observed in marmosets, where these nonbreeding helpers forego their own reproduction and incur energetic costs in altruistic behaviour (Tardif 1997; Sánchez *et al*. 1999; Bales *et al*. 2000). To date, only one study has quantified relatedness and has supported behavioural observations suggesting that most group members are close relatives (Nievergelt *et al*. 2000).

Little is known of the intraspecific population genetics of any of the Callitrichidae, and understanding the broader population genetic structure and phylogeography of species will further our understanding of their social behaviour and have implications for their conservation. Molecular phylogenetic analysis of the genus *Callithrix (*marmosets) by Tagliaro *et al*. (1997) provides strong support for a division into Amazonian and Atlantic forest clades, the latter including the common marmoset. The common marmoset and its sister species the black-eared marmoset (*Callithrix penicillata*) are perhaps two of the most adaptable of the Atlantic forest callitrichid primates, and also exploit more hostile, seasonal habitats such as the caatinga (semi-arid thorn scrub). Although feeding on the exudate of tree bark (gum) supplements a diet of fruit and insects in all species of the genus, the trait of tree gouging and gum feeding is most highly developed in *C. jacchus* and *C. penicillata*. This increased specialization undoubtedly enables them to survive in habitats where fruit may be scarce for long periods of time (Rylands 1984; Ferrari 1993), and may therefore also influence patterns of dispersal, gene flow and genetic structuring of populations. We report here the first extensive intraspecific genetic study of a callitrichid primate using mitochondrial control region sequence variation to investigate micro- and macrogeographical genetic structuring of populations. Specifically we aim to (i) quantify the matrilineal structure of social groups to unambiguously examine kin structure, and (ii) determine the relationships of mitochondrial sequences in the context of population structuring and phylogeographical history.

Materials and methods

Study sites and samples

Wild common marmosets in two areas of N.E. Brazil (Tapacura and Nisia Floresta) which have been the subject of ongoing long-term behavioural studies were examined in detail. Nisia Floresta experimental EFLEX-IBAMA forestry station is located 45 km south of Natal, the state capital of Rio Grande do Norte. Of a total area of 180 ha, 80 ha are secondary Atlantic coastal forest, while 40 ha are composed of experimental plantations of pine, eucalyptus, coconut and commercial species (Santee & Arruda 1994). Study groups occur in both areas of the forest and two of the four social groups investigated here (Belém and Chui) were observed continuously from 1991 to 1996. Tapacura Ecological Field Station lies within an isolated 390 ha block of secondary Atlantic Coastal Forest, surrounded by sugar cane plantations. The vegetation is tropical semideciduous with areas of dense undergrowth, but in places the forest is broken up with smallholdings, grassland and some nonindigenous trees and shrubs. Five main social groups were studied in detail, together with two peripheral animals.

Individuals were chosen for analysis from a large sample set to reflect social structure during a particular time period, as the composition of groups can be dynamic. For Nisia, samples were taken from the period 1995–97, and for Tapacura 1995–96. Further samples were obtained from one colony from the Botanical Gardens in Recifé, approx. 40 km east of Tapacura, and two published sequences obtained from animals collected at Extremos, 15 km north of Natal and approximately 45 km distant from Nisia (Tagliaro *et al*. 1997). The locations of these sites in Brazil are shown in Fig. 1.

Skin biopsies of approximately 2 mm diameter were taken from the ear during routine capture of animals. These were placed in alcohol and stored at –20 °C. Alternatively, or in addition to the biopsies, 30–40 hairs were plucked, sealed into bags and stored at –20 °C.

Mitochondrial DNA analysis

DNA was extracted from hair samples using the procedure described for buccal cells with the GFX™ Genomic Blood DNA Purification Kit (Amersham Pharmacia Biotech), and from the tissue samples using a standard phenol:chloroform methodology. Polymerase chain reaction (PCR) amplification of the control region of the mitochondrial DNA was achieved using combinations of five 'universal' primers (A, B, C, D and G) and a standard PCR protocol, as described for African mole-rats (Faulkes *et al*. 1997).

Initially, sequencing of double-stranded DNA products was performed manually using a Sequenase kit (United States Biochemical), and products were separated using a 6% polyacrylamide gel. Sequencing was carried out in both directions using combinations of all the above primers to obtain complimentary partially overlapping strands. For some samples, and to replicate some manual sequencing, an Amersham MegaBace 1000 automated sequencer was used to separate fragments produced using the Dynamic ET Terminator Sequencing kit (Amersham). Sequences have been deposited in NCBI with Accession nos AY196755–AY196775.

Analysis of mitochondrial DNA sequences

Sequences were compiled for analysis and aligned manually using MacClade version 3 (Madison & Madison 1992). Maximum parsimony was performed using both the

Fig. 1 Sampling map showing the species range for *C. jacchus* (shaded area on main map), and the relative locations of the four sampling sites in N.E. Brazil (inset).

branch and bound and heuristic search options in PAUP* version 4.0b10 (Swofford 2001), with all characters having an equal weighting and gaps treated as a 'fifth base'. Prior to maximum likelihood analysis, MODELTEST 3.06 (Posada & Crandall 1998) was used to establish the evolutionary model most appropriate for the data, and these parameters then used in PAUP*. MODELTEST was also used to perform a likelihood ratio test on trees generated with and without a molecular clock enforced. Bayesian analysis of the sequence data was performed using MrBayes (Huelsenbeck & Ronquist 2001), with starting trees generated both randomly and by prior neighbour-joining analysis with PAUP*, which was also used to construct a consensus tree from the resulting data output. The published sequence for *C. penicillata* (Tagliaro *et al*. 1997) was used for outgroup comparison in all phylogenetic analyses.

The frequency of haplotypes and proportion of sequence variation (calculated from pairwise distances) among social groups within regions and among regions was investigated using analysis of molecular variance (AMOVA; Excoffier *et al*. 1992). AMOVA produces estimates of variance components and *F*-statistic analogues Φ_{ST}, Φ_{SC} and Φ_{CT}, which describe variation at the following levels, respectively: within colonies, among colonies within populations and among populations.

Results

Haplotype diversity

Contiguous mitochondrial control region sequences, 1112 base pairs (bp), were obtained from 57 individuals. Inclusion of two published sequences from Tagliaro *et al*. (1997) gave a total of 59 sequences from which 23 distinct haplotypes were identified as follows (no. individuals/no. social groups in parentheses): Nisia Floresta, 11 haplotypes (27/4); Extremos, two haplotypes (2/–) (Tagliaro *et al*. 1997); Botanical Gardens, Recifé, two haplotypes (2/1) and at Tapacura, eight haplotypes (28/6).

While haplotype diversity was relatively high, considering parents and offspring were included in the data set (23 haplotypes in 59 animals sampled), rates of divergence between them were low, with uncorrected genetic distances ranging from 0.09 to 1.99%. HKY85 corrected values ranged from 0.09 to 2.03%. as follows: within Nisia, 0.72 ± 0.06%, n = 55 pairwise comparisons; within Tapacura, 0.84 ± 0.08%, n = 28; between Nisia and Tapacura, 1.43 ± 0.02%, n = 88. Comparing *C. jacchus* with the outgroup species *C. penicillata*, the average HKY85 corrected genetic distance was 6.36 ± 0.06% (6.02 ± 0.05% uncorrected; n = 23).

Matrilineal structure of social groups

The distribution of haplotypes within and among groups at Nisia and Tapacura is shown in Table 1.

It was not possible to obtain samples from every animal in all groups, but some missing data were inferred from known relationships between individuals and the established pattern of mitochondrial DNA inheritance: mothers and offspring should have the same mitochondrial haplotype, assuming no mutation or paternal leakage. In all 13 cases of samples from known mothers (n = 8) and offspring and siblings/twins that were sequenced, haplotypes were identical.

In seven of the 10 groups the data were sufficiently complete to compare the haplotypes of breeding individuals. Within these seven groups, of nine recorded breeding pairs seven were found to be from different maternal lineages. Table 1 shows clearly that in addition to the breeding male, at least six of the 10 groups also contain individuals from different matrilines, up to a maximum of five in the case of Group 4 in Nisia. Although sample size was relatively small, our results suggest no apparent sex differences in animals of differing haplotypes, indicating that dispersal of both sexes occurs in common marmosets.

Table 1 Distribution of control region haplotypes and social group structure of common marmoset populations at (a) Nisia and (b) Tapacura

Social group (sampling period)	Animal	Status	Haplotype
(a)			
Belém	Brejeiro	Breeding male	17
(May 1996)	Brat	Adult male	17
	Bhaskara	Immigrant male (joined April 1996)	17
	Bonita	Breeding female	18
	Bia	Juvenile of Bonita	18
	Babi	**Juvenile of Bonita**	**18**
	Breno	**Juvenile of Bonita**	**18**
	Beta	**Juvenile of Bonita**	**18**
	Beto	**Juvenile of Bonita**	**18**
	Bethoven	**Juvenile of Bonita**	**18**
Chui	Chris	Adult male (ex breeding male)	17
(September 1995)	Cazuza	Adult male (breeder with Betty)	13
	Colega	Adult female (Catrina†)	13
	Cacá	Adult female (Catrina†)	13
	Chiquita	Adult female (Clara†)	13
	Calua	**Adult female (Clara†)**	**13**
	Betty	**Immigrant female**	**17**
	Cézar	Juvenile (Betty)	17
	Carla	**Juvenile (Betty)**	**17**
Espanha	Enrique	Breeding male	22
(April 1997)	Eric	Adult male	23
	Eduado	Juvenile male (Estela); Expelled by Enrique	24
	Elvira	Adult female; Expelled by Goeth	22
	Adriana	Breeding female	25
	Elaine	*Juvenile female (Adriana)*	*25*
	Elaina	*Juvenile female (Adriana)*	25
	Eda	*Juvenile female (Adriana)*	25
Group Four	Gandhi	Adult male (ex breeder)	16
(September 1995)	Grecia	Breeding female	21
	Goeth	Breeding male (August 96)	21
	Gioconda	Adult female	14
	Gabriela	Adult female	23
	Gustavo	Adult male	15
	Graca	Adult female	
	Gilda	Juvenile female (Grecia)	21
	Gardelia	Juvenile female (Grecia)	21
(b)			
Esparancins	Ursula	Breeding female	10
(1995)	Tiana	Adult female (Ursula)	10
	Sebastian	Adult male (Ursula)	10
	Pamela	**Adult female (Ursula)**	**10**
	Xorona	Juvenile female (Ursula)	10
	Zapata	**Juvenile female (Ursula)**	**10**
	Fatima	**Juvenile female (Ursula)**	**10**
	Edinilza	**Juvenile female (Ursula)**	**10**
	Leticia	**Juvenile female (Ursula)**	**10**
	Clovis	**Juvenile male (Ursula)**	**10**
	Sao Paulo	**Breeding male?**	**10**
	Li	**Juvenile male (Ursula)**	**10**
Estovadins (Est)	Querida	Breeding female	7
(1995)	Zorro	Breeding male? Emigrated	6
	Marcelo	Breeding male?	6
	Xuxa	Juvenile female (Querida)	7
	Irineu	**Juvenile male (Querida)**	**7**
	Elaine	Peripheral female	10
	Iku	**Juvenile male (Querida)**	**7**

Table 1 *Continued*

Social group (sampling period)	Animal	Status	Haplotype
Esmirradins (Esm)	Ilka Maria	Breeding female	9
(1996)	Marciana	Breeding female	9
	Kerida	Ex breeding female	6
	Professor Roberto	Breeding male?	10
	Oquéi	Breeding male?	6
	Linneau	Adult male (Kerida)	6
	Fernanda	**Adult female (Kerida)**	**6**
	Nelson	Juvenile male (Ilka/Marciana?)	8
	Vexame	Juvenile male (Ilka/Marciana)	9
	Wilma	Juvenile female (Ilka/Marciana)	9
Escomprimidins (Esc)	William	Dominant male	10
(1995)	Tonheta	Juvenile male (Ute)	5
	Valente	**Juvenile male (Ute)**	**5**
	Waldemar	**Juvenile male (Wanda)**	**?**
	Wanda	Breeding female	No sample
Espivitadins (Esv)	Claudinha	Breeding female	10
(1996)	Quide	Juvenile male (Claudinha)	10
	LúcioMauro	Breeding male?	10
	Ypsilone	Breeding male?	4
	Isabel Joaquina	**Juvenile female (Claudinha)**	**10**
	Bárbara	**Adult female (Claudinha)**	**10**
	Fernando	**Adult male (Claudinha?)**	**?**
	Hugo	**Juvenile male (Claudinha?)**	**?**
Alagadins (Ala)	616	Peripheral male	10
(1995)	620	Peripheral female	11

†Animal dead or missing. Data from three individuals in italics were sampled 'outside' of the temporal scheme and not included in the analysis. Bold type indicates that the sample was not sequenced, and the haplotype inferred from known mother–offspring or sibling relationship. Known twins are joined by parentheses.

In one group from Tapacura (Esparancins), all group members were from the same matriline.

Population genetic structuring and phylogeographical trends

We used AMOVA to contrast the molecular variance for control region haplotypes (including the inferred haplotype data in Table 1), both within and among social groups and among geographical locations (Nisia Floresta, Extremos, Recifé, Tapacura). Using a null distribution generated by 1000 permutations of the data set, there was a highly significant genetic structuring both between social groups within populations ($\Phi_{SC} = 0.36$; $P < 0.001$) and between populations ($\Phi_{CT} = 0.48$; $P < 0.001$). Of the total variance, 48% was explicable among the geographical locations, 19% among social groups within locations and 33% within social groups. At the geographical level, all the haplotypes identified in the study were restricted in their distribution to their respective regions, with none shared between the four different geographical locations. This suggests that dispersal over long distances is not occurring.

Following hierarchical likelihood ratio tests of different models of evolution, the one found to best fit the data corresponded to the HKY85 + *G* + I model of sequence evolution ($P < 0.0001$). An additional ratio test using the log-likelihood scores of the trees obtained using this model with and without a molecular clock enforced was not significant ($2\delta = 34.36$; d.f. = 23; $P = 0.052$). The phylogram obtained is shown in Fig. 2.

A similar model of evolution to that used for maximum likelihood was also used in the Bayesian analysis. A total of 1 000 000 generations were run in MrBayes, with likelihood scores stabilizing after 30 000 generations. Trees were saved every 100 generations to give a total of 10 000, of which the first 300 were rejected (corresponding to those obtained before the likelihood scores had stabilized).

Of the 1112 characters used, 1019 were constant and 93 were variable. Of the latter, 38 were parsimony informative, while 55 characters were uninformative. Nine equally parsimonious trees were produced that differed only in the branching order of the Recifé and Extremos clades and haplotype '25' relative to each other and the main Tapacura and Nisia clades. Support for each internal

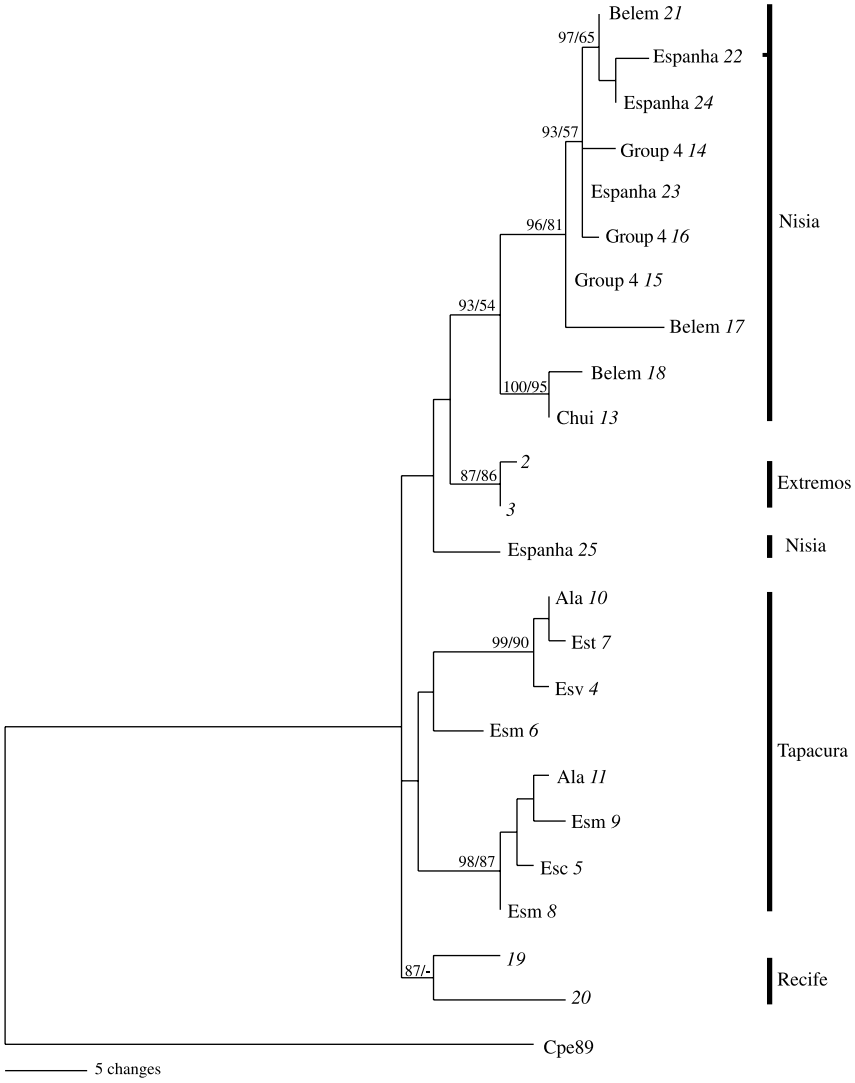

Fig. 2 Phylogenetic relationships of 23 *C. jacchus* control region haplotypes and one outgroup species *C. penicillata* (Cpe). Terminal nodes are labelled with the colony name followed by the haplotype, designated by a number in italics. Geographical locations are labelled and grouped with vertical bars. The phylogram was generated by the maximum likelihood option in PAUP* using a HKY85 + *G* + I model of sequence evolution (see text) with molecular clock enforced, tree score = 2259.5. Numbers on nodes are the bootstrap support values for clades, from the Bayesian/parsimony analysis, respectively. Colony abbreviations for Tapacura as in Table 1.

node was estimated using bootstrap analysis in PAUP* with 100 replicates, and most of the basal nodes in the phylogeny had low (less than 50%) bootstrap support in the parsimony analysis. Despite this, maximum parsimony and Bayesian trees were broadly congruent with the maximum likelihood tree shown in Fig. 2. All resolved (i) a monophyletic clade containing all but one Nisia haplotype (Espanha 25); (ii) a monophyletic Extremos clade; (iii) a monophyletic (Fig. 2) or unresolved Recifé clade; and either (iv) a monophyletic Tapacura clade (Fig. 2) or a polytomous grouping containing two consistently resolved Tapacura subclades and a separate lineage containing haplotype 6.

Discussion

The high haplotype diversity with low genetic divergence is consistent with the hypothesis that *C. jacchus* is a recent radiation. Low levels of sequence divergence among callitrichid primates have also been reported following analysis of nuclear β_2-microglobin sequences (Canavez *et al*. 1999). Despite the small genetic distances observed, a consistent geographical trend in the spatial distribution of mitochondrial control region haplotypes was apparent (with AMOVA revealing significant genetic structuring at the population and colony level).

At the subpopulation level, the haplotype data we have obtained give a fascinating insight into the dynamics of group structure, and its potential consequences for the proximate control of the cooperative breeding system of the marmoset. Of the seven groups where samples were obtained from both breeders, the reproductive males and females were found to have different haplotypes, with two exceptions, indicating that outbreeding for different matrilines was generally occurring. One exception was found in Group 4 at Nisia, where the reproductive female (Grecia)

had originally been breeding with the male Gandhi, from a different matriline. However, Gandhi was expelled by Goeth, another original group member of the same haplotype as Grecia, and Goeth then became the new breeding male. Although sharing the same matriline, Goeth and Grecia may not necessarily have been close relatives risking inbreeding depression; they went on to produce over 20 offspring. The second case was found at Tapacura, in the group Esparancins, where all individuals were haplotype 10. Again, some of these may have been more distant relatives.

Of the nine social groups studied in detail, five contained more than two haplotypes, indicating that in addition to the unrelated breeding pair, individuals from different matrilines were also present. One group containing two haplotypes (Escomprimidins) may have had a third as the breeding female was not sampled. In the extreme, one group of nine individuals had five haplotypes present at the time of sampling (Group 4 at Nisia). These results suggest that at both locations, the genetic structure of *C. jacchus* groups may often be more heterogeneous than the extended family model that has been suggested previously (e.g. Digby & Barreto 1993; Nievergelt *et al*. 2000).

Our data also support the idea that dispersal of both sexes can occur and that individuals immigrate into groups containing other maternal relatives. For example, in the Belém group at Nisia, Bhaskara, the immigrant male was from the same matriline as the two adult males already in the group (including the breeding male). Bhaskara, although an immigrant, was a frequent helper in the group, behaviour which could now possibly be explained by kin-selected altruism (M. F. Arruda, unpublished data). In the neighbouring group Chui, the haplotype of the original breeding male, Chris, suggests that he was an immigrant from Belém. When Betty later joined Chui from Belém (when the previous breeding females in Chui died), Chris was replaced as a breeder by Cazuza, possibly to avoid consanguinous mating: Betty and Cazuza have different haplotypes. Finally, both documented cases of group expulsions at Nisia (one where Enrique expelled Eduado (Espanha group) and another where Goeth expelled Gandi from Group 4), involved animals from different matrilines, suggesting that relatedness may be an important factor in group dynamics.

The common occurrence of nonbreeding adults from different maternal lineages in these social groups suggests that in order to maintain a reproductive advantage within groups, the breeding female may need to exert a controlling influence over the adult nonbreeding helpers. In simple family groups (parents and their offspring), avoidance of incest alone among the helpers results in their nonbreeding status. However, when unrelated adults are present there is the potential for outbreeding among the subordinate helpers. In captivity, reproductive skew in peer groups of unrelated individuals is achieved by a combination of behavioural and pheromonal cues from the dominant female (Barrett *et al*. 1993; Abbott *et al*. 1998). In captive family groups, an interesting mix of this dominant control and incest avoidance appears to operate. Some 46% of daughters were shown to have ovulated at least once, although none became pregnant because unrelated males were absent and daughters avoided incest (Saltzman *et al*. 1997). Preliminary data from endocrine monitoring of a wild group of *C. jacchus* have shown that usually only one female reproduces in the group even if subordinate females are undergoing ovulatory cycles (Albuquerque *et al*. 2001) or show signs of sexual activity or previous pregnancy (Mendes Pontes & Monteiro da Cruz 1995).

The relatively high proportion of groups identified in this study that contained several matrilines highlights the fact that although kin selection may be an important factor in helping behaviour and group dynamics, reproductive conflicts of interest may occur commonly. We now need to use microsatellite markers to study the patterns of relatedness with respect to observations of altruistic behaviour in the wild. This will enable the contribution of kin-selected altruism to be teased apart from other factors that may explain cooperative breeding in mixed-kin groups, such as reciprocity and by-product mutualism.

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This study is part of a long-term investigation of the genetics of common marmosets by the authors started in 1995. The aim of our project is to use molecular genetic techniques, in conjunction with long-term field studies and ecological data to tackle questions related to the evolution and maintenance of sociality and cooperative breeding in the Callitrichidae.
