Original Article

Folia Primatol 2008;79:79–92
DOI: 10.1159/000108780

Received: June 22, 2006
Accepted after revision: April 22, 2007

Allonursing in Tufted Capuchin Monkeys *(Cebus nigritus)*: Milk or Pacifier?

M. Celia Baldovino[a, b] Mario S. Di Bitetti[a–c]

[a] Asociación Civil Centro de Investigaciones del Bosque Atlántico, Puerto Iguazú,
[b] Laboratorio de Investigaciones Ecológicas de las Yungas, University of Tucumán,
San Miguel de Tucumán, and [c] National Research Council of Argentina CONICET, Argentina

Key Words
Capuchin monkeys · *Cebus nigritus* · Nursing · Allonursing · Allomothering · Milk · Adaptive significance · Kinship · Dominance · Atlantic Forest

Abstract

Allonursing, the behaviour of females nursing offspring that are not their own, is relatively frequent in capuchin monkeys. Using focal-animal sampling and ad libitum observations we describe the pattern of allonursing in a wild group of tufted capuchins, *Cebus nigritus* (4 cohorts, 22 infants), at Iguazú National Park, north-eastern Argentina, and test several hypotheses on the adaptive value of allonursing. During 2,351 contact hours with the group (including 4,207 focal-animal samples totalizing 329 h focused on infants) we observed 39 allonursing bouts. Infants were not allonursed more frequently by close kin than by more distant allomothers. Offspring of dominant females were allonursed more frequently than those of low-ranking females. Nursing bouts were longer than allonursing bouts. Our results suggest that allonursing in tufted capuchins has a social function and is not mainly aimed at providing milk to infants.

Introduction

In mammals, the period of lactation is very costly when compared to non-lactating periods, in terms of an important increase in the energy requirements of the reproductive females [Altmann, 1980; Clutton-Brock et al., 1989; Iverson et al., 1993; Lovelady et al., 1993]. It will thus be expected that lactating females will avoid providing milk to offspring other than their own. However, in several mammal groups (e.g. carnivores [Pusey and Packer, 1994; Boness et al., 1998], bats [Wilkinson, 1992], ungulates [Murphey et al., 1995; Plesner Jensen et al., 1999], and rodents [Hayes,

KARGER
Fax +41 61 306 12 34
E-Mail karger@karger.ch
www.karger.com

0015–5713/08/0792–0079$24.50/0

Accessible online at:
www.karger.com/fpr

María Celia Baldovino
Centro de Investigaciones del Bosque Atlántico
Yapeyú 23, 3370 Puerto Iguazú, Misiones (Argentina)
Tel. +54 3757 421 407, Fax +54 3757 422 370
E-Mail macelia@arnet.com.ar

2000]; for reviews, see Packer et al. [1992] and Roulin [2002]), adult females often provide milk to offspring of other females, a behaviour called allonursing. Among primates, allonursing has been reported in several species of all major radiations (e.g. *Presbytis* sp. [Jay, 1963; Poirier, 1968], *Macaca fuscata* [Tanaka, 2004], *Propithecus candidus* [Patel et al., 2003], howler monkeys, *Alouatta* sp., apes, *Gorilla* sp., cited in Packer et al. [1992], squirrel monkeys, *Saimiri boliviensis boliviensis* [Williams et al., 1994], spider monkeys, *Ateles geoffroyi* [Watt, 1994]). Among capuchin monkeys, allonursing has been reported in several species, the wedged-capped capuchin, *Cebus olivaceus* [Robinson and Janson, 1987; O'Brien and Robinson, 1991], the white-faced capuchin, *Cebus capucinus* [Perry, 1996], and the tufted capuchin, *Cebus apella* [Robinson and Janson, 1987; Fragaszy and Visalberghi, pers. observation cited in Fragaszy et al., 2004].

Several hypotheses have been proposed to explain the adaptive value of allonursing in mammals [Roulin, 2002]. In species with communal caring of offspring or large litter sizes, infants may steal milk from inadvertent mothers and/or females can misdirect nursing bouts to other offspring [Packer et al., 1992; Cameron et al., 1999; Hayes, 2000]. However, the misdirected parental care hypothesis will rarely apply to primates, a taxon characterized by small litter sizes, relatively small group sizes and by the ability of females (usually) to identify their own offspring [Maestripieri, 2001]. Females may allonurse to give up the milk not consumed by their own offspring to reduce weight loads and improve flying (e.g. bats [Wilkinson, 1992]) or swimming (e.g. elephant seals [Beck et al., 2000]) efficiency, another hypothesis that would not apply to primates.

Allonursing may have been favoured by reciprocal altruism [Trivers, 1971] or kin selection [Hamilton, 1964], two competing hypotheses usually used to explain the evolution of apparently altruistic behaviours. The first predicts that females will reciprocate allonursing bouts provided to their respective infants. Another possibility is that adult females reciprocate with other behaviours [Muroyama, 1994], a possibility that is considered under the social benefits hypothesis (see below). We do not have the data required to test the predictions derived from the reciprocal altruism hypothesis. The kin selection hypothesis predicts that allonursing bouts will be preferentially directed to close kin, and in this work we tested the predictions of this hypothesis.

Allonursing by inexperienced females may improve their ability to raise their own offspring, as has been documented for other allomaternal behaviours [Fairbanks, 1990]. This hypothesis requires the capability of producing milk by nulliparous females, which has not been amply documented in primates and still requires empirical evidence [Roulin, 2002]. This hypothesis predicts that nulliparous or inexperienced females will provide allonursing at higher rates than parous females and that allonursing will diminish with the age of the adult females.

Other benefits accrued by allonursing females may include obtaining an optimal stimulation of their nipples and the nervous-endocrine system and thereby maintaining an optimal concentration of prolactin when their own offspring do not provide enough stimuli [Roulin, 2003]. However, it is difficult to make predictions from this hypothesis that could be tested with observational data. Adult females may also receive social benefits (e.g. improved social bonds, increased social status or reduced harassment) by providing allomaternal care to infants of other females [Riedman, 1982; Roulin, 2002]. This hypothesis predicts that females would preferentially allonurse the infants of dominant females. Infants may benefit by improving their immunological system when acquiring a more diverse set of specific immune compounds obtained from the milk provided by different allomothers [Roulin and Heeb, 1999]. Allonursers in this case may bear the costs of pathogen transmission by infants [Roulin and Heeb, 1999]. A test of this hypothesis requires data that were not available in this study. Infants may suck non-mother females to compensate for some nutritional deficiency such as low weight at birth or insufficient supply of maternal milk [Víchová and Bartoš, 2005]. One of the predictions of this hypothesis is that infants that have temporarily or permanently lost their mother will request, and probably receive, more allonursing than other infants in the group. It has even been suggested that, in some instances, the main function of allonursing may be to soothe stressed infants and not to transfer milk to them [Lee, 1987; see review in Cameron, 1998]. This hypothesis predicts an increased probability of an infant receiving allonursing after stressful situations (aggression, predator attack, loss of its mother). These hypotheses have little empirical evidence and they are not mutually exclusive [Roulin, 2002].

The objective of this work is to describe the allonursing behaviour in a wild group of tufted capuchin monkeys, *Cebus nigritus*, and to test some of the hypotheses that have been put forward to explain this behaviour: kin selection, social benefits, improved maternal behaviour, nutritional deficiency and soothing infants. Some of the hypotheses described above will rarely apply to our study animals (milk evacuation, misdirected parental care). To test other hypotheses we require data that we did not obtain during our observational study (reciprocal altruism, immunological function) or require some invasive methods (neuro-endocrine function).

Methods

We conducted this study at Iguazú National Park, in north-eastern Argentina. The study site and study species have been described in Di Bitetti [2001] and Di Bitetti and Janson [2001]. Capuchins at the study site live in multi-male, multi-female groups of between 10 and 40 individuals. Females in this species are philopatric, and males transfer when they approach sexual maturity [Di Bitetti and Janson, 2001]. This study was conducted on the Macuco group of wild tufted capuchin monkeys, *C. nigritus,* that has been studied continuously since 1991 by a team of researchers led by Charles Janson. All individuals in the study group were easily recognized by their body size, sex, colour patterns, shape and size of the tufts and other body features. Female-offspring relationships were known for all individuals born in the group since 1990. From 1999 until 2003, group size ranged between 29 and 40 individuals (including infants) due to births, immigrations and animal losses. The number of adult females in the group during the study period ranged from 10 to 14, due to the disappearance of 5 adult females and the maturation of 5 females.

At Iguazú tufted capuchins give birth between October and February. The mean interbirth interval is about 19 months, and females can produce infants in successive years even when the infant from the previous year has survived [Di Bitetti and Janson, 2001; Ramírez Llorens et al., submitted]. Weaning is a gradual process and there seems to be large variation among infants in the age at which they stop receiving milk from their mothers, ranging from 9 to 23 months. Infants start feeding solid foods at 4 months, and the amount consumed increases gradually from this age until complete independence from the mother’s milk [Baldovino, pers. observation].

We recorded nursing and allonursing sessions on 22 infants of the Macuco group belonging to 4 consecutive cohorts: (1) 1999–2000, (2) 2000–2001, (3) 2001–2002, and (4) 2002–2003.

Table 1. Identity and sociosexual characteristics of the infants included in this study: cohort identity, sampling effort and frequency of nursing and allonursing bouts recorded for each

Infant	Cohort[1]	Sex	Dominance rank of the mother's matriline	Number of focal-animal samples	Total focal-animal hours[2]	Nursing bouts recorded	Allonursing bouts recorded
IB	1	M	5	0	0.0	5	0
PA	1	M	4	0	0.0	8	2
FE	1	M	1	0	0.0	9	0
OR	1	F	4	0	0.0	1	0
ELE	2	F	3	444	37.0	15	0
DUL	2	F	6	376	30.1	22	0
AND	2	M	1	400	30.3	17	9
AT	2	M	4	233	17.9	10	0
GUI	2	M	1	420	34.7	26	5
EST	2	F	2	292	23.5	20	2
CLE	2	M	2	362	27.6	28	3
MT	2	M	6	305	25.2	17	0
OLI	2	F	4	317	25.6	19	1
CAR	3	F	3	0	0.0	6	0
CHI	3	F	1	0	0.0	1	4
JOS	3	F	4	0	0.0	4	4
AGU	3	M	1	0	0.0	1	8
BET	4	F	3	180	12.4	11	0
GAB	4	F	1	271	20.2	12	0
SUS	4	F	5	157	11.4	3	0
PAB	4	M	6	220	18.2	16	1
MEL	4	M	6	230	14.7	11	0

[1] Cohort 1 was born in the 1999–2000 birth season, cohort 2 in the 2000–2001 birth season, cohort 3 in the 2001–2002 birth season and cohort 4 in the 2002–2003 birth season.

[2] The sum of the duration of all the focal-animal samples recorded for this infant.

For cohorts 2 and 4, we followed a randomized sampling protocol to obtain continuous focal-animal samples [Altmann, 1974] from the 14 infants belonging to these cohorts from birth to 10 months of age, trying as much as possible to keep an even representation of all infants in the samples within a cohort. We could not keep the focal animal visible in all the samples, and for this reason the mean duration of the focal-animal samples was 4.6 min. We obtained 4,207 focal-animal samples totalizing 329 h. In each focal-animal sample we recorded, among other behaviours, whether the infant was nursed by its mother during the sample or any other female in the group or not, the identity of the nursing female, and when possible, the duration of the nursing bouts with a precision of a second. For cohorts 1 and 3, focal-animal samples focused on the adult females but we recorded all the instances of nursing or allonursing observed. The number of contact hours with the group ranged from 372 (cohort 4) to 678 (cohort 1) resulting in 2,351 contact hours. The whole data set was collected by one of the authors (M.C.B.).

Differences in sampling protocol and contact hours among years may have introduced some biases in the results. However, infants were evenly represented in the focal-animal samples (vs. non-focal-animal samples) in relation to their sex and the dominance rank of their mother. Table 1 summarizes information on the identity, sex, social rank of the mother and sampling effort for all the cohorts and offspring studied.

In this paper we refer to nursing (or allonursing) as the behaviour of infants putting their mother's (or allomother's) nipple into their mouths. During the time that the infant has the nipple in its mouth, it is not possible to establish whether the infant is actually sucking milk or not. This is because the movements of the mouth and the throat are very subtle and not easy to see from a distance and from below the animals, so we had no way to know if there was transference of milk from the female to the infant during a nursing bout.

In our analysis of nursing and allonursing bout duration, we included only interactions that were observed from the beginning (when the infant established contact with the nipple) until its end. Nursing bouts are brief (the longest ever recorded lasted 111 s), and during a nursing bout, infants switch from one nipple to another in rapid succession until they suddenly and abruptly abandon their mother's breast. Although we do not have estimates of the mean time elapsed between successive nursing bouts, this interval is relatively long (longer than 20 min) in comparison with the brief duration of the nursing bouts. Thus, nursing bouts are clearly distinct and independent events.

The dominance ranks of the females were established on the basis of the results of dyadic aggressive interactions. We built dyadic interaction matrices whose cells represent the frequency and outcome of dyadic interactions among females. Female ranks were ordered such that the frequency of reversals below the diagonal of the matrix was minimized [Lehner, 1996]. Most dyadic aggressions were observed among females that belonged to different matrilines. The paucity of aggressive interactions among females of the same matriline but the consistency of outcomes of females from different matrilines (lack of reversals) allowed us to rank matrilines unambiguously but not the females within matrilines (with the exception of the alpha female). Thus, even though we were not able to build a linear dominance hierarchy among females, the dominance relationships among the different matrilines were unambiguously established. For this reason, for statistical analyses we ranked females according to the hierarchy of their respective matriline. There were 6 matrilines in the group during the whole study period, so female ranks range from 1 (highest) to 6 (lowest) (for details, see Baldovino [2007]).

To test for a kinship effect on the probability of an infant receiving allonursing bouts, we classified potential allomothers into two categories: close kin (same matriline, $r \geq 0.25$) and not closely related individuals ($r < 0.25$). We tallied the frequency of bouts received from each of these groups for each infant that received allonursing bouts, and we compared the frequency of bouts received from each group with the expected frequency based on the number of potential allomothers in each category. Due to the small sample of allonursing bouts observed for each infant, we used a sign test to test this hypothesis. If allonursing bouts received from close kin exceeded (even by a small fraction) the frequency expected by chance alone, we assigned a plus sign to that infant; if the opposite trend was observed, we assigned a minus sign. A sign test [Sokal and Rohlf, 1995] was then used to test whether the number of pluses or minuses exceeded the number expected by chance alone.

For other parametric or non-parametric tests we established a type I error confidence limit (alpha level) of 0.05. For the statistical analyses we used program JMP.IN, version 3.2.6.

Results

We observed 39 allonursing bouts, representing 13% of all the nursing and allonursing events observed (n = 301; table 1). Allonursing was observed in the 4 cohorts of infants under study but was not evenly represented across cohorts and infants, clearly depending on infant identity. The number of nursing bouts was directly dependent on the number of focal-animal hours of observation (linear regression, $R^2 = 0.74$, $F_{1, 20} = 57.5636$, $p < 0.0001$), but this was not the case for the relationship between the number of allonursing bouts and the number of focal-animal hours of observation ($R^2 = 0.002$, $F_{1, 20} = 0.0494$, $p = 0.8264$). There was no correlation between the number of nursing bouts and allonursing bouts observed for each infant

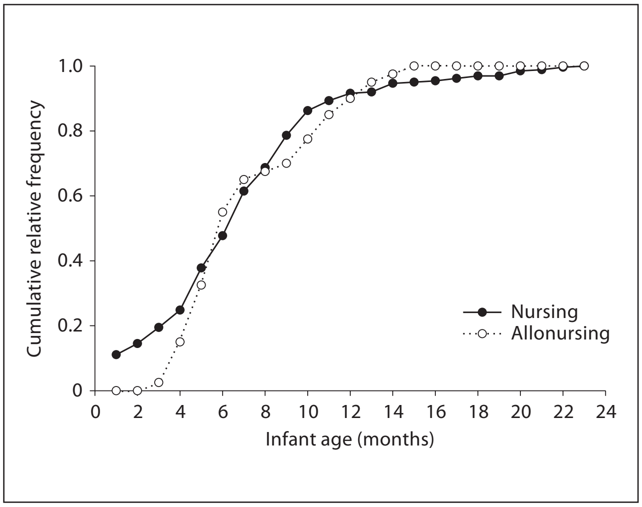

Fig. 1. Cumulative relative frequency of nursing (●) and allonursing (○) bouts in relation to infant age.

(linear regression of allonursing frequency on nursing frequency, $R^2 = 0.002$, $F_{1,20} = 0.0449$, $p = 0.8343$). These results suggest that the frequency of nursing bouts observed is directly dependent on sampling effort but the frequency of allonursing bouts was strongly dependent on other variables that override any potential effects of sampling effort.

Ten out of 22 infants under study were recorded receiving allonursing. All allonursing bouts were observed in immature monkeys of between 3 and 16 months (infants less than 2 months old spend more than 98% of the time with their mother, so allonursing was not expected [Baldovino, 2007]). The frequency of allonursing bouts observed in relation to the age of the infant was bimodal. Compared to nursing bout frequency, there was an increase in the frequency of allonursing bouts observed in infants of between 4 and 6 months and again another increase in observations at 10–12 months (fig. 1).

All the adult females present in the group during the 4 years of this study (14 adult females) were observed nursing 1 or more infants that were not their own. Four of these females had lost their infant before the allonursing bout was observed, and 2 of these were observed allonursing infants more than 6 months after losing their own infant (n = 7 instances of allonursing), which suggests that they may not have been producing milk. Similarly, one of the allonursing bouts we observed was between an infant and a nulliparous female. However, the probability of an adult female allonursing any infant during a study period was independent of her lactational condition (females that were nursing their own infants vs. females that had lost their infants or were nulliparous but ≥6 years old and were presumably not producing milk, likelihood G test of independence = 1.438, d.f. = 1, $p = 0.2304$). The probability of a female providing allonursing to any infant in its cohort was dependent on its parity; nulliparous females ≥6 years old were observed allonursing less fre-

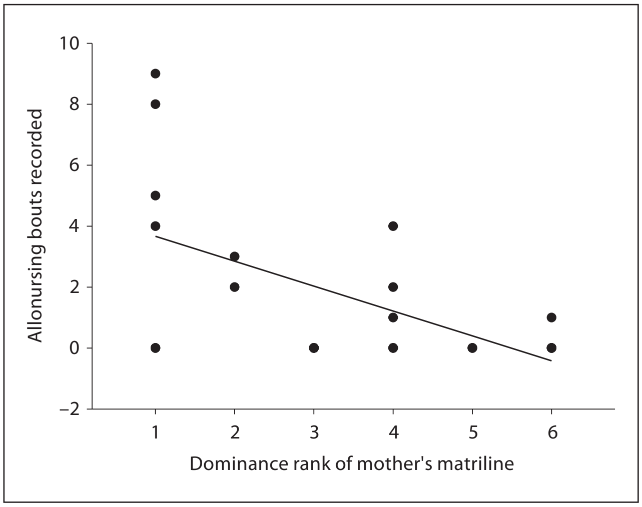

Fig. 2. Relationship between the dominance rank of the matriline to which the infant's mother belongs and the frequency of allonursing bouts we recorded for that infant.

quently than parous females (likelihood G test of independence = 5.304, d.f. = 1, p = 0.0213).

We never observed females rejecting an infant's attempts to nurse or allonurse (e.g. pushing away an infant when it was trying to reach a nipple). On a few occasions (11 nursing bouts and 1 allonursing bout) we observed females trying to finalize a bout by physically rejecting infants from their nipples after ≥30 s of nursing.

Infants received allonursing from females of their own matriline (older sisters, aunts and grandmothers) as frequently as from females of more distant relatedness, after correcting for the different number of potential allomothers in each category (sign test, p = 0.146).

Male and female infants were equally observed receiving allonursing from adult females (likelihood G test of independence = 0.738, d.f. = 2, p = 0.39). Infants of dominant females (matriline dominance ranks 1 and 2) were observed receiving allonursing more frequently than infants of subordinate females (likelihood G test of independence = 0.738, d.f. = 2, p = 0.032). The frequency of allonursing observed for each infant was positively correlated with the dominance rank of its mother's matriline (non-parametric measure of association, Kendall t, b = –0.422, p = 0.0175, fig. 2). For all the cases where the relative rank of the mother and the allonurser could be clearly established (n = 24), on 22 occasions the allonurser was of lower rank than the mother and only on 2 occasions was an allonurser dominant to the mother of the infant.

Nursing bouts were usually brief (less than 1 min). During the bout the infant rapidly switched from one nipple to the other, apparently sucking from both once or twice during the whole nursing session. We found no effect of the sex of the infant ($F_{1, 19}$ = 1.1801, p = 0.2909) or the dominance rank of the mother ($F_{5, 15}$ = 0.0884, p = 0.9929) on the duration of the nursing bouts. Infant age (in months) had no effect on

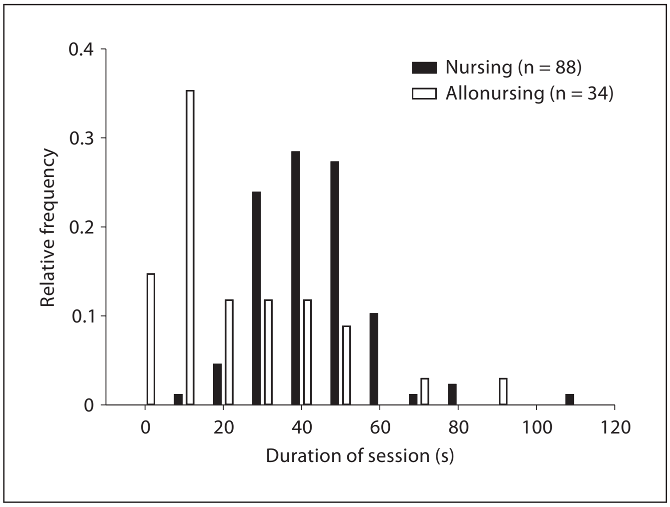

Fig. 3. Duration of nursing and allonursing bouts recorded for the infants of the Macuco group of tufted capuchin monkeys at Iguazú National Park, Argentina, between 1999 and 2003.

the duration of nursing (least-squared regression, $F_{1,86} = 2.771$, $p = 0.100$) or allonursing bouts (least-squared regression, $F_{1,32} = 1.467$, $p = 0.235$).

Mother-offspring nursing bouts were of a longer duration (mean ± SD = 46.95 ± 15.14 s, n = 88) than allonursing bouts (25.65 ± 20.46 s, n = 34, Wilcoxon 2-sample test using normal approximation, S = 1,104, Z = –5.636, $p < 0.0001$). The duration of the nursing bouts showed an almost normal distribution around its mean (it was normal when an outlier session from a 1-week-old infant of a primiparous female that lasted 111 s was omitted, Shapiro-Wilk W test for normality, W = 0.9797, p = 0.5518, fig. 3). The duration of the allonursing bouts showed more variation around its mean (coefficient of variation = 79.8) than mother-offspring nursing bouts (coefficient of variation = 32.2). The distribution of allonursing bout durations was very skewed (with its mode at the 10- to 20-second interval) and strongly deviated from a normal distribution (Shapiro-Wilk W test for normality, W = 0.8542, p = 0.0002, fig. 3). Thus, the duration of allonursing bouts was not only shorter than that of the nursing bouts but also more variable in duration. Allonursing bouts provided by lactating females were not longer (18.58 ± 12.03 min) than those provided by females that were not lactating (nulliparous females plus females that had lost their infants, 28.14 ± 14.84 min, ANOVA, $F_{1,18} = 2.3186$, $p = 0.1452$).

Discussion

Allonursing was a relatively frequent behaviour in wild *C. nigritus*. All the adult females were observed nursing infants other than their own. We observed allonursing in the 4 cohorts under study, and both male and female infants received allonursing bouts. We observed no preference for females to allonurse closely related infants.

The infants of dominant females were allonursed more frequently than those of subordinate females, and allonursers were usually of lower rank than the mother of the recipient infant. Nulliparous females only rarely allonursed, but adult females that presumably were not producing milk because they had lost their infants provided allonursing as frequently as lactating females. Nursing bouts were brief and their duration was normally distributed. In striking contrast, the duration of allonursing bouts was much shorter and more variable than that of nursing bouts and the distribution of this variable was far from normal.

Due to the frequency of reports of allonursing across capuchin monkey species (genus *Cebus*) and sites, Fragaszy et al. [2004] concluded that this is a genus-specific behaviour. In the wedged-capped capuchin, allonursing represents over 13% of the nursing received by infants. Only adult females provide allonursing bouts, and its distribution is not affected by the dominance rank of the mother or the degree of relatedness of females and infants [O'Brien and Robinson, 1991]. In this species the duration of the allonursing bouts was shorter than the duration of nursing bouts and similar to bouts of 'parasitic nursing' among adult or subadult females [O'Brien, 1988]. In the white-faced capuchin, subordinate females allonursed at a higher rate than high-ranking ones, but they did not preferentially allonurse infants of dominant females [Perry, 1996]. Consequently, infant white-faced capuchins were not allonursed more frequently from females whose rank was above their mother's rank. In white-faced capuchins there was no relationship between the grooming frequency and coalition support of pairs of adult females and the frequency with which they provided allonursing to their respective offspring. Since infants may be occasionally separated from their mothers for periods of more than 2 days, Perry [1996] argues that the small costs incurred by adult females when providing milk to infants that are not their own will be more than outweighed by the benefit of their own offspring being nursed by other females if the mother-offspring pair becomes accidentally separated. In this same line of argument, Leighty et al. [2004] argue that allonursing in capuchin monkeys may contribute to the survival of twins both in nature and in captivity.

In our study group, allonursing was a relatively frequent behaviour in the 4 cohorts under study. However, previous studies conducted on this same study group before 1999 did not provide many instances of allonursing behaviour [Di Bitetti, pers. observation]. These differences in the frequency of allonursing among years may be related to differences in group size and the associated social instability (the Macuco group was much smaller during the first years of study).

We did not find a higher frequency of allonursing by females closely related to the infants, which suggests that kin selection is probably not the main driving force behind this behaviour. During the present study, infants of dominant females were observed receiving allonursing more frequently than infants of lower-ranking females and most allonursers were lower in rank than the infant's mother. This observation is clearly consistent with the social benefits hypothesis. An adult female can obtain social benefits by allonursing a dominant female's infant. These benefits could be in the form of a dominant female's higher willingness to share food resources with the allonurser, in the form of lower aggression or harassment to the allonurser or in the form of coalitionary support in aggressive interactions. Alternatively, if an infant from a dominant female does not receive allonursing from another adult female when requested, it may threaten that female by soliciting coalitionary support from its mother and allies with potentially negative consequences for the female that rejected the petition.

The frequency of observed allonursing bouts in relation to the infant's age was bimodal. The first peak, at between 4 and 6 months of age, corresponds to the time when infants are beginning to move around independently of their mothers, which may require higher energy intake. The second, at 10–12 months, may correspond to a critical stage in the weaning process where mothers become more reluctant to provide milk to their infants and it is consistent with both the nutritional hypothesis and the soothing hypothesis. However, better empirical data on both energy requirements and the potential mother-offspring conflict related to weaning is required to test these hypotheses.

The observation that nulliparous females provided allonursing less frequently than parous ones contradicts the hypothesis that allonursing helps improve maternal care behaviours in inexperienced females. However, it is still interesting that nulliparous females were observed providing allonursing even when they were presumably not producing milk. In fact, when comparing the frequency with which adult females that were not lactating allonurse with that of females that were lactating we observed no difference, which suggests that adult females provide allonursing to infants independently of whether they are lactating or not.

Our more striking result is that the duration of allonursing bouts was shorter than the duration of nursing bouts. Not only the duration differed between nursing and allonursing bouts, but also the distribution of bout lengths. If the difference in duration of allonursing bouts was related to the lack of experience, and thus coordination among the infant and the allomother during milk transfer (e.g. having quick and easy access to the nipples), we should have expected the opposite effect, allonursing bouts being of longer duration than nursing ones. This result is similar to the observation of O'Brien [1988] in wedge-capped capuchins. Cameron [1998] provides some evidence that bout length is not necessarily related to the amount of milk transferred during nursing. However, she presents data from only 3 mammal species, of which in one, the fur seal [Trillmich, 1986], there was a clear positive relationship between nursing bout length and weight gain by infants in a large sample of individuals (n = 73). In the other 2 species they did not find a relationship between bout length and amount of milk transferred. One of these was the reindeer [Lavigueur and Barrette, 1992], in a study with only 7 calves and where the response variable was not milk transferred or weight gained, but growth, which is known to be influenced by many variables other than the amount of food (or energy) ingested. Finally, Cameron [1998] reviews several studies conducted on humans, a species in which bout length is composed of both of the time spent by the infant sucking milk and using the nipple as a pacifier (without milk transfer), thus not serving as a good species to compare. Studies combining detailed observations of bout length, sucking rate [Tanaka, 1992], weight gain [like Trillmich, 1986, and several other studies reviewed in Cameron, 1998] and growth rate are necessary to elucidate this question. Given the short duration of the nursing bouts in capuchin monkeys and the magnitude of the difference in nursing bout length observed in our study (a 3-fold difference in modal length), we can tentatively conclude that the amount of milk transferred during allonursing bouts was smaller than the amount transferred during normal, mother-offspring bouts.

Lee [1987] concluded that the main function of allonursing in African elephants was to give comfort to stressed infants rather than providing milk. Her conclusion was mainly based on 2 observations. First, allonursing was performed mostly by nulliparous females. Second, the duration of allonursing bouts was about 1/4 of the duration of nursing bouts. In our capuchin monkey group we also observed allonursing by a nulliparous female (one occasion) and by non-lactating adult females on several occasions. We also observed a marked difference in the length of allonursing and nursing bouts, the modal duration of the former being about 1/3 of the duration of the latter (fig. 3). These observations, along with the relation between the dominance rank of the infant's mother and the frequency of allonursing, suggest that the main function of allonursing in the tufted capuchin monkey is a social one and probably not related to the transfer of milk. We suggest that the main function of allonursing in the tufted capuchin monkey is to soothe infants as was suggested for the African elephants [Lee, 1987] and other species [see references in Cameron, 1998].

Our suggestion that the main function of allonursing in our study group was not the transfer of milk but a social one does not deny other possible functions on some specific occasions. For example, one of the infants in our study group (AGU) permanently lost his mother when he was 6 months old. During the 6 months before his mother disappeared, we did not observe any instance of allonursing directed at this infant but we observed 5 allonursing sessions during the ten first days following the loss of his mother. This infant survived to 2.5 years of age, even though he was well below the typical weaning age when his mother disappeared. His survivorship may have been possible due to the milk provided by other females providing support to the nutritional hypothesis. However, if, as we suggest, one of the main functions of allonursing in tufted capuchins is to soothe stressed infants, we would have also predicted that allonursing frequency would have increased for this infant after the disappearance of his mother. In fact, the mean duration of the allonursing bouts we measured for this infant (23.57 ± 20.61, n = 7) was not longer than other allonursing sessions (26.19 ± 20.77, n = 27, Wilcoxon 2-sample test using the normal approximation, S = 114, Z = –0.342, p = 0.7324), suggesting that transfer of milk was probably not the main function of the allonursing provided to him.

Capuchin monkeys live in stable social groups with complex social relationships [Fragaszy et al., 2004]. The fitness of the individuals in this social context may depend to a high degree on the fate of its group [Robinson, 1988] and thus on the fate of other group members (interdependence [Roberts, 2005]). This interdependence of individuals within social groups may explain the evolution of some apparently altruistic behaviours observed in capuchin monkeys, like allogrooming [O'Brien, 1993; Perry, 1996; Di Bitetti, 1997], group hunting and food-sharing [Rose, 1997], mobbing behaviour [Boinski, 1988; Fragaszy et al., 2004], rescuing group mates from predators [Perry et al., 2003], alarm calling [van Schaik and van Noordwijk, 1989], food calling [Di Bitetti, 2003, 2005; Gros-Louis, 2004] and most allomaternal behaviours, including allonursing [Baldovino, 2007]. Once behaviour becomes established in a population, it may be exploited by cheaters or more dominant individuals or it may take new functions. For example, allogrooming originally served a hygienic function but the importance of this function may be outweighed by its more recent social function [Dunbar, 1991; Di Bitetti, 1997]. The same may have occurred with allonursing in tufted capuchin monkeys, where the soothing function of this behaviour may have outweighed its original milk transfer function.

This soothing function may also increase the infants' survivorship by improving its psychological well-being. Again, we do not deny a flexible, multi-purpose function of this behaviour (including an improvement of the immunological system [Roulin and Heeb, 1999; Roulin, 2002]). Under certain circumstances the main function of allonursing in tufted capuchin monkeys may be to provide milk to the infant and thus allows it to survive the temporary [Perry, 1996] or permanent [this study] loss of its mother.

Conclusion

The relationship between the rank of the infant's mother and that of the allomother suggests that the latter may obtain social benefits when allonursing infants. The duration of allonursing bouts was much shorter and the frequency distribution of bout length was very different from mother-offspring nursing bouts. This difference and observations of allonursing by non-lactating females suggest a sharp difference between nursing bouts directed by females to their own offspring and those directed to infants that are not their own. We suggest that most allonursing bouts may have the main function of soothing infants more than transferring milk, as has been documented for African elephants [Lee, 1987] and other mammals, including humans (see examples in Cameron [1988]) and/or providing social benefits to the donor. We encourage researchers to pay more attention and rigorously test the soothing hypothesis and to estimate the amount of milk transferred during nursing and allonursing bouts before drawing conclusions about the importance of allonursing for the survival of infants and twins in wild capuchin monkeys [Perry, 1996; Leighty et al., 2004].

Acknowledgements

We are grateful to Viviana Benesovsky, Ilaria Agostini, Carlos De Angelo, Ingrid Holzmann, Soledad Díaz, Fermino Silva, Bence von Puttkamer, Kinga Szathmáry and Laura Gadbán for their assistance in the field. Charlie Janson made this project possible and gave invaluable help by providing most of the field equipment. We also acknowledge the authorities of the Argentine National Parks Administration for permission to conduct field work at Iguazú National Park and to use the accommodation of the field station (CIES). This study was supported by a CONICET (Argentine Research Council) fellowship to M.C.B.

References

Altmann J (1974). Observational study of behavior: sampling methods. *Behaviour* 49:227–267.
Altmann J (1980). *Baboons Mothers and Infants*. Chicago, University of Chicago Press.
Baldovino MC (2007). Desarrollo de los infantes de monos caí *(Cebus nigritus):* Ontogenia de la habilidad motora y comportamientos alomaternales. PhD thesis, Universidad Nacional de Córdoba, Argentina.
Boinski S (1988). Use of a club by a wild white-faced capuchin *(Cebus capucinus)* to attack a venomous snake *(Bothrops asper). American Journal of Primatology* 14: 177–180.
Beck CA, Bowen WD, Iverson SJ (2000). Seasonal changes in buoyancy and diving behaviour of adult grey seals. *Journal of Experimental Biology* 203: 2323–2330.
Boness DJ, Craig MP, Honigman L, Austin S (1998). Fostering behavior and the effect of female density in Hawaiian monk seals, *Monachus schauinslandi. Journal of Mammalogy* 79: 1060–1069.

Cameron EZ (1998). Is suckling behaviour a useful predictor of milk intake? A review. *Animal Behaviour* 56: 521–532.

Cameron EZ, Linklater WL, Stanford KJ, Minot EO (1999). A case of co-operative nursing and offspring care by mother and daughter feral horses. *Journal of Zoology* 249: 486–489.

Clutton-Brock TH, Albon SD, Guinness FE (1989). Fitness costs of gestation and lactation in wild mammals. *Nature* 337: 260–262.

Di Bitetti MS (1997). Evidence for an important social role of allogrooming in a platyrrhine primate. *Animal Behaviour* 54: 199–211.

Di Bitetti MS (2001). Home range use by the tufted capuchin monkey, *Cebus apella nigritus*, in a subtropical rainforest of Argentina. *Journal of Zoology, London* 253: 33–45.

Di Bitetti MS (2003). Food-associated calls of tufted capuchin monkeys *(Cebus apella nigritus)* are functionally referential signals. *Behaviour* 140: 565–592.

Di Bitetti MS (2005). Food-associated calls and audience effects in tufted capuchin monkeys *(Cebus apella). Animal Behaviour* 69: 911–919.

Di Bitetti MS, Janson CH (2001). Reproductive socioecology of tufted capuchins *(Cebus apella nigritus)* in northeastern Argentina. *International Journal of Primatology* 50: 109–130.

Dunbar RIM (1991). Functional significance of social grooming in primates. *Folia Primatologica* 57: 121-131.

Fairbanks LA (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour* 40: 553–562.

Fragaszy DM, Visalberghi E, Fedigan LM (2004). *The Complete Capuchin: The Biology of the Genus* Cebus. Cambridge, Cambridge University Press.

Gros-Louis J (2004). The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus*, from the perspective of the signaller. *Animal Behaviour* 67: 431–440.

Hayes LD (2000). To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Animal Behaviour* 59: 677–688.

Hamilton WD (1964). The genetical evolution of social behavior. Parts I, II. *Journal of Theoretical Biology* 7: 1–52.

Iverson SJ, Bowen WD, Boness DJ, Oftendal OT (1993). The effect of maternal size and milk energy output on pup growth in grey seals *(Halichoerus grypus). Physiological Zoology* 66: 61–88.

Jay P (1963). The Indian langur monkey *(Presbytis entellus)*. In *Primate Social Behaviour* (Southwick CH, ed.). New York, Van Nostrand.

Lavigueur L, Barrette C (1992). Suckling, weaning, and growth in captive woodland caribou. *Canadian Journal of Zoology* 70: 1753–1766.

Lee PC (1987). Allomothering among African elephants. *Animal Behaviour* 35: 278–291.

Lehner PN (1996). *Handbook of Ethological Methods,* 2nd ed. Cambridge, Cambridge University Press.

Leighty KA, Byrne G, Fragaszy DM, Visalberghi E, Welker C, Lussier I (2004). Twinning in tufted capuchins *(Cebus apella):* rate, survivorship, and weight gain. *Folia Primatologica* 75: 14–18.

Lovelady CA, Meredith CN, McCrory MA, Nommsen LA, Joseph LJ, Dewey KG (1993). Energy expenditure in lactating women: a comparison of doubly labelled water and heart-rate-monitoring methods. *American Journal of Clinical Nutrition* 57: 512–518.

Maestripieri D (2001). Is there mother-infant bonding in primates? *Developmental Review* 21: 93–120.

Muroyama Y (1994). Exchange of grooming for allomothering in female Patas monkeys. *Behaviour* 128: 103–119.

Murphey RM, Paranhos Da Costa MJR, Gomez da Silva R, De Souza RC (1995). Allonursing in river buffalo, *Bubalus bubalis:* nepotism, incompetence, or thievery? *Animal Behaviour* 49: 1611–1616.

O'Brien TG (1988). Parasitic nursing behaviour in the wedge-capped capuchin monkey *(Cebus olivaceus). American Journal of Primatology* 16: 341–344.

O'Brien TG (1993). Allogrooming behaviour among adult female wedge-capped capuchin monkeys. *Animal Behaviour* 46: 499–510.

O'Brien TG, Robinson JG (1991). Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank and relatedness. *Behaviour* 119: 30–50.

Packer C, Lewis S, Pusey A (1992). A comparative analysis of non-offspring nursing. *Animal Behaviour* 43: 265–281.

Patel ER, Coke CS, Ritchie A, Santorelli C (2003). Alloparental care (including allonursing) in free-ranging silky sifakas *(Propithecus diadema candidus)* in a primary northeastern montane rainforest in Madagascar. *American Journal of Primatology* 60(suppl 1): 71.

Perry S (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus. American Journal of Primatology* 40: 167–182.

Perry S, Manson JH, Dower G, Wikberg E (2003). White-faced capuchins cooperate to rescue a groupmate from a *Boa constrictor. Folia Primatologica* 74: 109–111.

Plesner Jensen S, Siefert L, Okori JJL, Clutton-Brock TH (1999). Age-related participation in allosuckling by nursing warthogs *(Phacochoerus africanus)*. *Journal of Zoology, London* 248: 443–449.

Poirier FE (1968). Nilgiri langur *(Presbytis johnii)* territorial behavior. In *Proceedings of the Second Congress of the International Primatological Society* (Carpenter CR, ed.), vol. 1. Basel, Karger.

Pusey AE, Packer C (1994). Non-offspring nursing in social carnivores: minimizing the costs. *Behavioral Ecology* 5: 362–374.

Ramírez Llorens P, Di Bitetti MS, Baldovino MC, Janson CH (submitted). Infanticide in black capuchin monkeys *(Cebus apella nigritus)* in Iguazú National Park, Argentina. *American Journal of Primatology.*

Riedman ML (1982). The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review of Biology* 57: 405–435.

Roberts G (2005). Cooperation through interdependence. *Animal Behaviour* 70: 901–908.

Robinson JG (1988). Demography and group structure in wedge-capped capuchin monkeys, *Cebus olivaceus*. *Behaviour* 104: 202–232.

Robinson JG, Janson CH (1987). Capuchins, squirrel monkeys, and atelines: socioecological convergence with Old World primates. In *Primate Societies* (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds.), pp 69–82. Chicago, University of Chicago Press.

Rose LM (1997). Vertebrate predation and food-sharing in *Cebus* and *Pan*. *International Journal of Primatology* 18: 727–766.

Roulin A (2002). Why do lactating females nurse alien offspring? A review of hypotheses and empirical evidence. *Animal Behaviour* 63: 201–208.

Roulin A (2003). The neuroendocrine function of allosuckling. *Ethology* 109: 185–195.

Roulin A, Heeb P (1999). The immunological function of allosuckling. *Ecology Letters* 2: 319–324.

Sokal RR, Rohlf FJ (1995). *Biometry,* 3rd ed. New York, Freeman & Co.

Tanaka I (1992). Three phases of lactation in free-ranging Japanese macaques. *Animal Behaviour* 44: 129–139.

Tanaka I (2004). Non-offspring nursing by a nulliparous pregnant female just before first parturition in free-ranging Japanese macaques. *Primates* 45: 205–206.

Trillmich F (1986). Maternal investment and sex allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. *Behavioral Ecology and Sociobiology* 19: 157–160.

Trivers J (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology* 46: 35–57.

Van Schaik CP, van Noordwijk MA (1989). The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. *Behavioral Ecology and Sociobiology* 24: 265–276.

Víchová J, Bartoš L (2005). Allosuckling in cattle: gain or compensation? *Applied Animal Behaviour Science* 94: 223–235.

Watt SL (1994). Alloparental behavior in a captive group of spider monkeys *(Ateles geoffroyi)* at the Auckland Zoo. *International Journal of Primatology* 15: 135–151.

Wilkinson GS (1992). Communal nursing in the evening bat, *Nycticeius humeralis. Behavioral Ecology and Sociobiology* 31: 225–235.

Williams L, Gibson S, McDaniel M, Bazzel J, Barnes S, Abee C (1994). Allomaternal interactions in the Bolivian squirrel monkey *(Saimiri boliviensis boliviensis). American Journal of Primatology* 34: 145–156.