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ARTICLE

Food-sharing behaviour within a group of free-living Endangered Coimbra-Filho's titi monkeys

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Abstract

Socioecological studies related to food-sharing behaviours in titi monkeys are scarce, with no such reports for the Endangered Coimbra-Filho's titi monkey, *Callicebus coimbrai*. We aimed to describe the pattern of food-sharing behaviours during monitoring (444 h) of a wild group of Coimbra-Filho's titi monkeys inhabiting a fragment of Atlantic forest in Northeast Brazil. We reported 43 food-sharing events (23 food-begging and 20 transfer attempt events). For the food-begging events, infants were the main beggars (74 %) while adult males were the main possessors (48 %). High-quality foods were more shared between related and unrelated individuals. Infants were the most successful beggars, receiving most of the high-quality food. Coimbra-Filho's titi monkeys did not require any special skills to access the high-quality or easy-to-process food items related to the food-sharing events, suggesting that food sharing in these monkeys is linked to the kin selection and sharing-under-pressure hypotheses.

Keywords Socioecology · Food transfer · *Callicebus coimbrai* · Parental care · Reciprocity

Introduction

Food sharing or food transfer is characterised in two fashions: (1) when one food-motivated individual (i.e. the possessor) tolerates sharing or transfer of a food resource to another (i.e. the recipient) (Feistner and McGrew 1989), and (2) when one individual tries to take food from another, not necessarily with consent (Brown et al. 2004). This behaviour is often observed in species with high-energy diet requirements, where food acquisition commonly depends on special skills and/or rare opportunities (de Waal et al. 1993). Food sharing has different ultimate functions, which include kin selection, increasing fitness, improving social bonding, reciprocity, coping with harassment (i.e. the "sharing-under-pressure" hypothesis), information gathering and assessing relationship quality (Brown et al. 2004; van Noordwijk and Van Schaik 2009; Yamamoto 2015; Kopp and Liebal 2016). On the other hand, proximate functions of food sharing are relatively unknown, with studies focussing on physiological and prosocial strategies underlying the behaviour (Jaeggi et al. 2013; Liebal and Rossano 2017).

In Neotropical primates such as capuchins, marmosets and tamarins, for example, food sharing may ensure immediate acquisition of food which is rare or hard to access (Feistner and Price 1991; Fragaszy et al. 1997; Ruiz-Miranda et al. 1999). Furthermore, it may facilitate social learning, considering that the individual recipient of the food may learn which foods are appropriate for consumption (de Waal et al. 1993; de Waal 2000). For these primates, complete food sharing has been widely reported between adults and begging infants (Price and Feistner 1993). Sharing among relatives and non-relatives, however, has also been observed (Jaeggi and Van Schaik 2011). In monogamous primates, such as owl monkeys (*Aotus azarai*) and titi monkeys (*Cheracebus torquatus*), for example, parental care and the consequent proximity between adult males and their infants have been considered key factors influencing food sharing (Starin 1978; Wolovich et al. 2007) due to benefit obtained by

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cooperation rather than competition for food (McGrew and Feistner 1992). Other factors such as partner choice hypotheses and formation of coalitions (male–male, male–female, female–female) seem not to be good explicative variables for food sharing in monogamous primates (Kinzey 1981; Norconk 2011). Increased food sharing in monogamous primates (*A. azarai* and *Aotus nancymaae*), aiming at enhanced nutritional intake in infants, is expected to be frequent when offspring are present because of the high degree of parental care performed by the male (Wolovich et al. 2008). Thus, the infant may have earlier independence from its mother, leading to earlier weaning, short inter-birth interval and optimal reproductive success (Starin 1978).

Coimbra-Filho's titi monkey, *Callicebus coimbrai*, is an Endangered primate species distributed in dozens of Atlantic forest fragments in Northeast Brazil (Veiga et al. 2008; Printes et al. 2013). Coimbra-Filho's titi groups are basically formed by a monogamous breeding pair with their offspring (Kobayashi and Langguth 1999). Their diet is primarily frugivorous, although they may consume new leaves and small seeds during periods of low fruit availability (Souza-Alves et al. 2011). As far as we are aware, socioecological studies are scarce, with no reports of food sharing for this species. We aim to describe herein the pattern of food-sharing-related behaviours in a wild Coimbra-Filho's titi monkey group inhabiting a small fragment of Atlantic forest in Northeast Brazil. Owing to the high degree of parental care in social monogamous titi monkeys (Norconk 2011), we expected the rate of food-sharing behaviour between adult males and infants to be higher than between others members of the group. Coimbra-Filho's titi monkeys have been demonstrated to have a highly frugivorous and seasonal diet (Souza-Alves et al. 2011; Souza-Alves 2013), hence it is expected that food items of high quality (fruit, seed, flower) will be shared during periods with high availability of fruit due to easy access and reduced food competition. On the other hand, difficult-to-process food items should be shared during periods of low availability of food to contribute to the daily energy requirement of the members of group.

Materials and methods

The study was conducted in a 14-ha forest fragment at Fazenda Trapsa (11°12′S, 37°14′W), situated in the southern region of Sergipe, Northeast Brazil (see Souza-Alves 2013 for more details). A habituated Coimbra-Filho's titi monkey group was monitored from July 2009 to December 2009 (6 months) and from January 2011 to July 2012 (19 months), from dawn to dusk (05:00 h–18:00 h), during four or five consecutive days/month, totalizing 444 h of monitoring.

Table 1 Study group structure and composition over the observation period

Study chronology	Structure and composition of *Callicebus coimbrai* study group				
July 2009	M1	F1	SB1 (Black face—BF)	I1	
May 2010	M1	F1	BF emigrated	J1	
December 2010	M1	F1	J1	Nb1	
June 2011	M1	F1	SB2	I2	BF returned to the natal group
May 2012	M1		SB2	I2	BF

F adult female; *M* adult male; *SB* sub-adult; *J* juvenile; *I* infant; *Nb* newborn

Group structure and composition varied throughout the study period (Table 1).

Quantitative behavioural data were systematically collected through use of scan sampling protocols (Altmann 1974), with 1-min scans conducted at 5-min intervals. Furthermore, we complemented our observations with ad libitum and all-occurrence sampling methods to obtain detailed information on rare behaviours performed outside the scan periods. Occurrences of food-sharing behaviour were noted in detail whenever they occurred.

In this study, we use the following definitions adapted from Feistner and Price (1990) and Brown et al. (2004) to categorise the food-sharing behaviours observed in Coimbra-Filho's titis: (1) food-begging behaviour, when one individual requested food from another individual either by constantly vocalising while sitting down beside the individual that possessed the food or while locomoting and pursuing it, and (2) attempted transfer, when an individual attempted to take a portion of a food item from another individual.

To verify whether the food shared between the titi monkeys was associated with learning, lack of special skills to acquire the resource or acquisition of highly energetic food, we categorised each item based on its nutritional quality (i.e. high and low quality; Nishida and Turner 1996) and difficulty-to-process (easy and difficult to process; Silk 1978). High-quality resources were rich in calories or protein (i.e. fruits, flowers, and insects), unlike low-quality resources (i.e. leaves, pith, inner bark or other plant parts). Difficult-to-process foods (DPFs) required some strength to open or dexterous manipulation to extract their edible portions efficiently, skills often found only in adult individuals. Easy-to-process foods (EPFs) were any food items that an individual required no special skills to acquire, such as leaves and soft-shelled fruits. High-quality resources and DPFs are expected to be costlier for an individual to give away.

Table 2 Total number of (and successful) begging events observed in the *Callicebus coimbrai* study group

Beggar	Possessor						Total number	Total (% of successful events)
	Adult male	Adult female	Sub-adult	Black face	Juvenile	Infant		
Adult male	–	2 (2)	0	0	0	0	2	9 (100)
Adult female	3 (1)	–	0	0	0	0	3	13 (33)
Sub-adult	0	0	–	0	0	0	0	0 (0)
Black face (BF)	0	0	0	–	0	0	0	0 (0)
Juvenile	1 (0)	0	0	0	–	0	1	4 (0)
Infant	7 (2)	2 (0)	0	0	8 (4)	–	17	74 (35)
Total number	11 (50 %)	4 (67 %)	0	0	8 (80 %)	0	23	
Total %	48	17	0	0	35	0		

Table 3 All identified food sources begged for, shared, or attempted to share by members of the *Callicebus coimbrai* study group, with their nutritional quality and difficulty-to-process

Food source	Total number			Food nutritional quality		Difficulty-to-process	
	Begged	Shared	Transfer attempt	High	Low	EPF	DPF
Adenocalymma comosum new leaf		1	2		×	×	
Pogonophora schomburgkiana seed		1		×			×
Passiflora contracta fruit	1	3	4	×		×	
Simaba cedron new leaf	1		1		×	×	
Tabebuia sp. flower	1		1	×		×	
Tapirira guianensis fruit		1	1	×		×	
Eschweilera ovata flower			1	×		×	
Paypayrola blanchetiana new leaf		1			×	×	
Total	3	7	10				

EPF easy-to-process food, *DPF* difficult-to-process food

To compare the different characteristics of the food items (i.e. high and low quality, or DPF and EPF), as well as the frequencies of successful and unsuccessful sharing, we considered the food items and number of events, respectively, as the sampling unit. Thus, we created contingency tables to verify the possible differences. We tested whether the frequencies of successful and unsuccessful sharing differed between begging and transfer attempt events using a chi-squared test. Also, the frequencies of high- and low-quality items, and DPF and EPF were compared using a chi-squared test. The statistical analyses were performed using R version 3.5.0 software (R Core Team 2018).

Table 4 Frequency of solicitation of different categories of food item in the *Callicebus coimbrai* study group

Food category	Frequency of solicitation by:			χ^2 (p value)*
	Infant	Adult female	Juvenile	
EPF	1	3	3	7.542 (0.02)
DPF	4	0	0	
Low quality	2	1	1	0.052 (0.97)
High quality	3	2	2	

EPF easy-to-process food, *DPF* difficult-to-process food

*$df = 2$

Results

Overall, we recorded 43 food-sharing behavioural events: 23 food-begging and 20 transfer attempt events. While 39 % of food-begging events were successful (i.e. food was shared), the frequencies of success and no success in food-begging behaviour between beggars was similar ($\chi^2 = 5.167$, $df = 3$, $p = 0.16$). I1 was the main beggar (74 %), followed by F1 (13 %), and J1 and M1 (4 % and 9 %, respectively) (Table 2). In 57 % of events, the possessor ignored or avoided the beggar. In 48 % of events, M1 was the possessor of the resource, followed by J1 (35 %) and F1 (17 %). I1 and I2 (67 %) were the main recipients of shared food (Table 3).

Over two-thirds of identified begged food items were high quality (73 %, $N = 8$) and EPF (91 %, $N = 10$). Specifically, infants begged/received more than half (67 %, $N = 4$) of high-quality foods and 83 % ($N = 5$) of EPF. While the solicitation

frequency did not differ between high- and low-quality food, there was a preference for EPF (Table 4). There were three types of food that were begged for: leaf, fruit and flower. *Simaba cedron* young leaves were usually begged for by I1 and I2 when J1 was the possessor of the resource. These plants are tall, thin, have no thorns and are not a limited food supply, thus consumers of these plants need no special skills to obtain them. The liana, *Passiflora contracta*, provides fleshy fruits which were begged for once by I1 when J1 was the possessor of the food. The fruit may be found in either the tree canopy or lower stratum of the forest. White showy flowers from the *Tabebuia* tree were begged for once by F1 when M1 was the possessor of the resource. The latter did not share the resource immediately, and the begging lasted 5 min before M1 actually shared the resource with F1. *Tabebuia* trees are not common in the forest fragment due to intense anthropic disturbance.

The two infants (50 % of total recorded, $N = 6$ events) were those with higher frequency of successful transfer attempts, followed by M1 and BF (17 %, $N = 2$ events) (Table 5). There was no success in 40 % ($N = 8$) of transfer attempts, and M1 ($N = 6$ events) and J1 ($N = 5$ events) presented a higher number of unsuccessful transfer attempts. During the successful transfer attempts, J1 was the main possessor of food (25 %, $N = 3$ events). Of successful transfer attempts, 62 % ($N = 6$) were performed by infants. When comparing the frequency of successful and unsuccessful transfer attempts between individuals, we found no difference ($\chi^2 = 5.763$, $df = 5$, $p = 0.32$). Fruits were the most taken items (50 %), followed by young leaves (37 %) and flowers (13 %). More than half of the taken food items (62 %) were categorised as high-quality food, and 100 % of them as EPF (Table 6). Between individuals we verified no difference when comparing the frequencies of high- and low-quality food taken (Table 6).

All unsuccessful transfer attempt events were associated with agonistic behaviour between individuals. When M1 tried to take food from J1, there was a fight with physical contact. In one event, M1 bit J1's tail, who ended up releasing the food. During another event, J1 was eating *Simaba cedron* (Simaroubaceae) leaves on the tree and did not allow the begging I1 to stay and eat from the same tree. When J1 tried to leave the tree, it was bitten by I1. On two other occasions, I2 tried to take food from BF, but it failed and was bitten. When BF attempted to take I2's food, it was denied, and as a result, I2 was bitten by BF. During another event, the infant requested food from M1 and was not granted it. Thereafter, I2 requested the food again, however it was bitten on the tail and moved away from M1.

Table 6 Frequency of food items taken successfully (transfer attempt) by *Callicebus coimbrai* individuals

Food category	Frequency of food transfer attempted by:				χ^2 (p value)*
	Infant	Adult female	Adult male	Black face	
EPF	5	1	1	1	
DPF	0	0	0	0	–[a]
Low quality	2	0	0	0	1.6 (0.65)
High quality	3	1	1	1	

EPF easy-to-process food, *DPF* difficult-to-process food

*$df = 2$

[a]It was not possible to test any difference between EPF and DPF due to the large number of zeroes in the sample

Discussion

We report the occurrence of food-sharing-related behaviours in wild Coimbra-Filho's titi monkeys, a monogamous Neotropical primate with a high-energy diet. The results demonstrate that the infants were the primary and most successful beggars. On the other hand, the emigrated adult male (BF) was the least tolerated when attempting food sharing, constantly receiving agonistic displays in response to food begging. Also, it was not possible to verify any relationship between food quality and difficulty-to-process with the availability of food resources. In *Cheracebus torquatus*, a large number of food "begging" and "taking" behaviours have been associated with an infant's lack of skill to acquire it (Starin 1978); For example, *Dororia longifolia* fruits were opened by an adult male of *C. torquatus* and immediately begged for by an infant (Starin 1978). On the other hand, in buffy-headed marmosets (*Callithrix flaviceps*), this behaviour may be related to the high energy content of the resource being shared, which was observed when the oldest individuals transferred large insects and vertebrates to infants (Ferrari 1987). Such studies, however, did not demonstrate any robust analysis to assess the influence of shared food on the acquired behaviour by individuals. Nevertheless, food transferred between mother and infant chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus wurmbii*) was, quantitatively, mostly DPF (Nishida and Turner 1996; Jaeggi et al. 2008). In contrast to what was observed

Table 5 Total number of successful and unsuccessful food transfer attempts performed by individuals in the *Callicebus coimbrai* study group

Category	Number of transfer attempts performed by:					
	Infant	Juvenile	Adult male	Adult female	BF	Sub-adult
Successful	6	1	2	1	2	0
Unsuccessful	3	3	0	0	1	1

in a congeneric species (i.e. *C. torquatus*) and other primate species, the preferred type of food begged for or taken by Coimbra-Filho's titis was EPF (i.e. young leaves, fruits and flowers) or high-quality food (fruits and flowers).

We found no association between diet composition/phenology and the type of food resource shared in the study Coimbra-Filho's titi group. The high-quality and EPF plant species shared (Table 3) represent only 13–14 % of the diet composition for this titi group (Souza-Alves et al. 2011; Souza-Alves 2013). Similarly, such food items were equally (50 % for both periods) shared between periods of low and high fruit availability. The less productive months (i.e. November and December) and most productive months (i.e. April and June) presented two events of food sharing each (see Souza-Alves et al. 2011 for fruit availability at the study site). Therefore, it is likely that all the food items were being randomly shared between individuals of the studied Coimbra-Filho's titi group rather than influenced by the high proportion of such food items in the diet or by the productivity of food resources in the study area.

Fathers have been recorded as the main contributors in food sharing with infants (see Table 3 in Brown et al. 2004). This parental relationship can facilitate learning and acquisition of skills by infants to obtain either DPF or high-quality food items (Feistner and McGrew 1989). In this study, such relationships between fathers and infants of Coimbra-Filho's titis are unlikely to be associated with either learning or the necessity to acquire foraging skills. The high frequency of sharing of high-quality food appears to be contributing to increased growth rate and earlier weaning. This explanation is supported by two factors: (1) the Coimbra-Filho's titis inhabit a small and highly disturbed Atlantic forest fragment (Souza-Alves et al. 2014) where a reduced quantity of available food resources is expected (see Zanette et al. 2000), and (2) the longer inter-birth interval (24 months) and reduced weaning time (180 days) recorded for the female in this group are distinct from those recorded in other titi species (see Souza-Alves 2013). On the other hand, the agonistic events recorded may be related to hierarchy in the study group, mainly after the return of BF. Another adult male within a monogamous Coimbra-Filho's titi monkey group can occasionally increase food competition, consequently resulting in a higher aggression rate between individuals. In this sense, the high energy costs usually involved in begging for and defending foods suggest that the food sharing reported in unrelated Coimbra-Filho's titi monkeys may be linked to assessing relationship quality and deliberately coping with harassment. In this case, the possessor of the resource tends to avoid punishment, and any costs of preserving energy and abundant food resources, avoiding risk of injury.

Although Coimbra-Filho's titis exploit a large number of inaccessible food resources such as large seeds (see Souza-Alves 2013), these were not involved in food-sharing events. In contrast to what has been widely observed in other primates (*Cheracebus torquatus*, Starin 1978; *Callithrix flaviceps*, Ferrari 1987), Coimbra-Filho's titis do not depend on other individuals of the group to obtain these foods, resulting in their classification as "un-skilled extractive foragers" (Gibson 1986). Unlike omnivorous and insectivorous primates, such as marmosets and owl monkeys that often engage in food sharing (Ruiz-Miranda et al. 1999; Wolovich et al. 2008), Coimbra-Filho's titis are mostly frugivorous, lacking the need for elaborate foraging strategies such as those required to obtain insects and small vertebrates, for example. Therefore, the food-sharing behaviours observed in this study seem to function for the titi monkeys to gain energy from easy-to-access and high-quality resources instead of being related to a potential lack of skills to obtain the resources. It is likely that the low habitat quality in the small study area and the modification of life history traits across the years may have acted as evolutionary pressures towards food sharing in Coimbra-Filho's titi monkeys. Finally, we believe that food sharing in Coimbra-Filho's titi monkeys may be associated with the kin selection (sharing with offspring) as well as "sharing-under-pressure" hypotheses (sharing between male and female, male and male, and male and juvenile). Both can be used as alternative explanations when animals are aiming to benefit energetically.

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Compliance with ethical standards

Conflict of interest The authors declare that none of them have any conflicts of interest.

Ethical approval All research complied with Brazilian legal requirements. It also adhered to the ASAB/ABS Guidelines for the Use of Animals in Research and American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

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