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BIRD PREDATION AND PREY-TRANSFER IN BROWN CAPUCHIN MONKEYS (*CEBUS APELLA*)

Renata Ferreira, Briseida D. Resende
Massimo Mannu, Eduardo B. Ottoni,
Patrícia Izar

Introduction

In the last decade capuchin monkeys, *Cebus*, have received growing attention in the primatological literature due to some striking convergences between them and chimpanzees, *Pan*, such as: large brain size relative to body size, long life span, tool use skills, and food-sharing among group members (Fragaszy *et al.*, 1990; Visalberghi and McGrew, 1997). These similarities make capuchin monkeys an attractive model for validating hypotheses about the evolution of social life and cognition that are heavily based upon Old World primates (Parr *et al.*, 1997).

Food-sharing tendencies are of interest due to the view that cooperative hunting with subsequent meat sharing was a key factor in the adaptation and organisation of early human societies (Butynski, 1982; Anderson, 1986; McGrew and Feistner, 1992), and many studies have focused on the cooperative hunting and meat sharing of wild chimpanzees (Boesch, 1994). Some authors (e.g., Newcomer and De Farcy, 1985; Fragaszy, 1986) have reported predation on vertebrates by capuchin monkeys in different environmental conditions. However, the relation between predation and prey sharing has only been analysed for wild *C. capucinus*.

Rose (1997) reported predation on birds, coatis (*Nasua narica*), and squirrels (*Sciurus variegatoides*) by two groups of *C. capucinus* at Santa Rosa National Park, Costa Rica. She concluded that, although predation is a common event, food sharing is infrequent. Meat is the most commonly shared food, and the only food shared between adults (usually through falling scraps or abandoned carcasses). Perry and Rose (1994) analysed the sharing of captured coatis in three groups of *C. capucinus* at two sites in Costa Rica. They concluded that: a) among the species normally preyed by capuchins, coatis are riskier because adults are larger than adult capuchins and normally defend their pups; and b) coati pups scream while being eaten, so it is impossible for a monkey to be rapid and furtive when eating them, giving plenty of opportunities for other monkeys to beg from the carcass owner.

The possible social value of food-sharing in captive groups of *C. apella* has been emphasised by de Waal (1997; 2000; de Waal *et al.*, 1993) who observed that the occurrence of this behavior is: a) related to affiliative relations and social tolerance between pairs of individuals, b) linked to previous events of food-sharing between the pair (even after a delayed period) and, c) is more frequent when cooperation

is needed for predation or the acquisition of scraps from other individuals.

Here we describe predation on birds and prey-sharing by a semi-free group of brown capuchin monkeys (*C. apella*). Predation of this sort is rare, but when it does happen, prey transfer is frequent. Due to the small number of observations, the predation and particularly the prey-transfer events are analysed only qualitatively, while examining any relation between the occurrence of transfers and the hierarchical and affiliative relationship between the individuals involved.

Study Site, Group and Data Collection

The capuchin monkey group lives in an area of 18 ha in the Tietê Ecological Park (São Paulo, Brazil). The area was reforested and has two important features: 1) there are no natural predators of *Cebus*, such as *Harpia harpyja*, *Felis pardalis*, *Boa constrictor* or crocodiles (Freese and Oppenheimer, 1981), and 2) the group is provisioned daily with plentiful fruits and vegetables (see Ottoni and Mannu, 2001). Besides the provisioning, the group forages for other foods available in the area, taking up about 50% of an individual's daily activities (RF, unpubl. data). The wet season is from October to March, and the dry season is from April to September (mean monthly rainfall is 178 mm and 69.3 mm, respectively) (São Paulo, DAEE, 2001). The group varied in size from 15 to 25 individuals: five adult males (two castrated), five adult females, three subadult males, one subadult female and 10 juveniles and infants.

Our observations cover a period of five years, and were collected on an *ad libitum* basis during the course of other studies by MM (January 1996 to December 1999, see Ottoni and Mannu, 2001), and BR and RF (2000/2001). The total time of contact with the group was 2768 hours.

Results and Discussion

Table 1 summarises the occurrences of predation and prey-transfers. The data are somewhat biased toward the years 2000/2001 due to an increase in observation hours per week relative to the previous years. For the purposes of calculating the rates of prey sharing we consider two types of predation data: a) the events when predation was actually observed, and b) the predation event was not seen, the animal merely being observed with a carcass.

Twenty-four predation events were recorded; a rate of 0.86 events per 100 observation hours. This is much lower than the bird predation frequency described for *C. capucinus* in a natural environment by Rose (1997); predatory behaviour, however, did not constitute the focus of the studies in this capuchin group as it did in Rose's study. Ten of the events were observed in the first three years of observation (rate of 0.6 every 100 hours) and 14 in the remaining period when the weekly hours of observation of the group were increased

(1.13 every 100 hours). This and the fact that predation, and in many cases the consumption of the prey, is a very fast and almost noiseless behaviour suggests that the frequency is underestimated.

Predation frequency was the same between seasons: Dry season - 0.8 events every 100 hours, wet season - 0.9 every 100 hours. Rose (1997) however, found a higher frequency in the wet season (3.09 per 100 hours) when compared to the dry season (2.04 per 100 hours). The lack of any seasonal difference and the lower predation rates may be a result of provisioning, but also to a reduced availability of prey with our group ranging over a smaller, confined area when compared to the *C. capucinus* of Rose (1997).

The 10 predation events recorded were all by males: six by adults (four of these by the dominant male), three by subadults and one by a juvenile. Of the 14 events in which individuals were found with a carcass, the possessor was a male (adult, subadult or juvenile) in 10 and an adult female in three. In one case an adult male and an adult female eat from the same carcass. Overall, the age/sex predation biases are similar to those described for *C. capucinus*, where adult males (especially the dominant) were the most efficient predators (Perry and Rose, 1994; Rose, 1997).

Some sort of food transfer occurred in 18 of the 24 predation events. The transfers are classed as: *co-feeding* - two individuals eat different prey near to each other (event n° 20); *delayed scrounging* - one individual eats the leftovers of another (events n° 4, 5, 6, 8, 9, 17, 19, 20, 22 and 23); *tolerated scrounging* - the possessor allows another to come near and retrieve dropped scraps (events n° 4, 5, 7, 8, 16, 17 and 19); *facilitated scrounging* - the possessor moves towards an individual, drops food scraps and allows the other to retrieve them (event n° 10); *passive food-sharing* - the possessor permits another to retrieve food items from his/her hands or mouth (events n° 3, 5, 13, 14, 17, 21 and 24); and *theft* - one individual seizes the food from another (event n° 13). Note that different types of food transfer can occur during the same predation event, sometimes involving different individuals. (For a discussion of terms and definitions see Ottoni *et al.*, in prep.) The proportion of prey sharing (in 18/24 predation events) may be even greater if we consider that some of the 'carcass' events may be the result of a previous non-witnessed food-transfer. The predominant type of prey transfer observed in this study was also the most common type observed in *C. capucinus* by Rose (1997), that is, the transfers were generally relaxed involving the collection of leftovers or scraps.

Again, this high rate of prey-sharing that we observed may be related to the food-abundance of the study site. A similar phenomena was described in *C. capucinus*: higher rates of prey-sharing were found in a rich environment (Lomas Barbudal) than in an environment with marked seasonality in food abundance (Santa Rosa, Costa Rica) (Perry and Rose, 1994; Rose, 1997).

Table 1: Events and participants of predation and prey-transfer between individuals in a capuchin monkeys groups, *Cebus apella*, in the Tietê Ecological Park, São Paulo.

	Date	Predation		Prey-transfer	Individuals
		Observed	Carcass		
1.	Sep/97		Juvenile male		Jq or Qz
2.	Sep/97		Juvenile male		Jq
3.	Jun/ 98		Adult male and sub-adult female	Passive sharing of a bird.	Med – Jan
4.	Jan/99		Adult male	Subadult male collects scraps nearby and then remains with the carcass	Mc –Ped
5.	Apr/99	Dominant male		(Encaged bird). Adult male collects scraps nearby. Adult female and infant eating the carcass minutes later.	Bq – Joao– Fis – Man
6.	Oct 99	Dominant male		Juvenile eating the carcass minutes later.	Bq – Frk
7.	Oct/99		Adult female	Subadult male collects falling scraps nearby.	Fis – Eli
8.	Nov/99		Dominant male	Adult male collecting scraps nearby after it remains with the carcass.	Bq – Med
9.	Nov/99		Dominant male	Subadult male collected the discarded carcass. Adult male collecting scraps nearby.	Bq- Qz – Med
10.	Dec/99	Adult male		Adult male discarded carcass in front of adult female.	Med-Jan
11.	Jun/00		Juvenile male	Juvenile male interested.	Frk- Edu
12.	Jul/00	Subadult male			Ped
13.	Jul/00		Adult male	Allows an infant but not a juvenile to take some pieces of the carcass. Later the infant remains with the carcass. Its mother steals the carcass from him.	Med – Joa – Lob – Jan
14.	Aug/00	Subadult male		Avoids an adult male that follows him. After 15 min the carcass' owner approaches and permits a subadult female to take a piece of the carcass.	Qz – Kk – Jq
15.	Sep/00		Adult female		Fis
16.	Oct/00	Adult male		Avoids a juvenile but allows an infant to eat falling scraps nearby.	Sus – Lob – Dw
17.	Nov/00		Subadult male	Subadult avoided adult male, who later collected the carcass. Then subadult female takes pieces of meat from the carcass, collects scraps nearby and eats in contact with adult male.	Qz – Jq – Kk
18.	Nov/ 00	Juvenile male		(Leaves the bird uneaten).	Frk
19.	Jan 01	Subadult male		Allows a juvenile to eat falling scraps. Juvenile collects abandoned carcass.	Ped – Frk
20.	Feb 01	Dominant male		(Predation on nestling birds). Adult male coveeding. Juvenile collects abandoned carcass.	Bq – Med – Joa
21.	Mar/01		Juvenile male	Infant takes pieces of meat from the carcass.	Man – Dw
22.	Apr 01		Adult female	Dominant male collects the discarded carcass.	Fis – Bq
23.	May/01		Juvenile male	Dominant male collects the discarded carcass.	Edu- Bq
24.	Jun/01		Dominant male	Adult female and juvenile taking pieces of the carcass.	Bq – Fis – Man

Prey transfers occurred 12 times between adults or subadults: five from a male to a female (5, 10, 14, 17, 24); two from a female to a male (7, 22); six between males (4, 5, 8, 9, 17, 20) and none between females. In seven events the transfer was from an adult or subadult to a juvenile or infant (5, 6, 13, 16, 19, 20, 24), and in two events in the opposite direction (13, 23). One food transfer event was between juveniles (21). As such, the frequency of sharing between adults is greater than that between adults and youngsters, and sharing occurs mainly between males or from males to females. This contrasts with the observations for *C. capucinus*, in which prey transfer was rarely observed between adults and occurred mainly from mother to infants or between immatures (Perry and Rose, 1994; Rose, 1997).

In 15 events the transfer was from a high to a low ranking individual. In *C. capucinus* the rank of the possessor was either unrelated to the direction of sharing or merely facilitated the theft of the subordinate's prizes by the more dominant individuals. Dominance relationships were inferred by aggression, chasing, cowering, and avoidance, and affiliative relationships were inferred by spatial proximity and grooming (RF and PI, in prep.).

It is noteworthy that in 10 of 18 food transfers there was a close affiliative relationship between the individuals involved: in events 3 and 10, the female and male adults were preferential partners in grooming, sleeping and allocate (see Izar [1997] for descriptions on preferential partnerships in *C. apella*); in events 5, 22 and 24 the transfers were between dominant male and female and their offspring; in event 17 between an adult male and subadult female that belonged to a small subgroup; in event 19, transfer was between subadult and juvenile males which were preferential partners in play. As affiliated individuals stay close to each other, spatial proximity may be the factor influencing the occurrence of transfers in these 10 events. However, in another three events (described in greater detail below) spatial proximity could not have been the only factor, as there were at least three individuals close by, and the possessor shared the prey with only one of them.

(Event 13) 00': Medeiros, an adult castrated male, is seen eating a bird carcass. 10': Joana, an 11-month old infant often carried and groomed by Medeiros, watches him, collecting some scraps nearby. Lobato, a 3-year old juvenile approaches, Medeiros chases him away. Joana bites pieces of the carcass from Medeiros' hands. Medeiros leaves, Joana remains with the carcass. 22': Janete (Joana's mother) steals the carcass from Joana, who then suckles. [Medeiros and Janete are the preferential partners already described in the events 3 and 10].

(Event 16) 00': Noises indicating a fight are heard, and Suspeito (a castrated adult male) leaves the area carrying a bird in its mouth. 02': Suspeito eats the bird in a tree. Lobato, a juvenile, approaches. Suspeito turns his back on Lobato. Lobato approaches Suspeito again. Suspeito pushes

Lobato's head away from the carcass. 04': Lobato is nearby, making some attempts to approach Suspeito. Suspeito repeatedly turns his back or avoids Lobato. 07': Darwin approaches Lobato and tries to play with him. Darwin sees Suspeito. 07'30": Darwin approaches Suspeito and collects some scraps. 09': Darwin takes a small piece of the carcass and eats it. Suspeito moves higher in the tree. 11': Darwin approaches Suspeito, takes another piece of the carcass, and eats it. 12': Darwin starts playing with Lobato, Suspeito remains with the carcass. 25': Suspeito leaves the carcass. [In this event, there is social affinity between Suspeito and Meire (Darwin's mother), similar to that observed between Medeiros and Janete, that is, Suspeito and Meire are preferential partners for sleeping and grooming, although Suspeito does not allocate Darwin as much as Medeiros allocates Joana.]

(Event 14) 00': Quinzinho, a subadult male, catches a bird. Joaquim, an adult male, witnesses the predation. 01': After eating the head of the bird, Quinzinho walks carrying the prey in his mouth. Joaquim follows him for about 50 m. Kika, a subadult female, also begins to follow him. 03': Quinzinho stops in a tree and eats the bird for about 15 minutes. After some failed attempts to approach Quinzinho, Joaquim leaves the area. Meanwhile, Kika remains foraging about 20 m from Quinzinho. 18': Quinzinho, still holding the carcass, approaches to 1 m from Kika. She approaches him, makes an aggressive display (not towards him) and then takes a big piece of the carcass. They both eat in close proximity for another 5 minutes. 23': they leave. [Again, the social relationships data show that Quinzinho and Kika are "preferential partners". In contrast, Quinzinho and Joaquim were seen fighting several times (Joaquim is dominant over Quinzinho)].

In the first two events the carcass owner clearly tolerated the approach and begging of an individual with which it is affiliated but not from another with which it is less affiliated. In the third event, the possessor avoided the approach attempts of one individual and actively approached another, with which it is affiliated, and shared the meat.

We are not sure whether the observed differences between *C. apella* and *C. capucinus* in predation rates and prey transfer rates and directions are due to the type of prey, to the study site or to the species under study. Predation on birds differs from predation on coatis because birds may be easily caught and eaten secretively by the individuals. Robinson (1986) reported that capuchins successfully foraging on nestling birds were discrete in finding a nest, and frequently moved away from the rest of the group. The particular characteristics of this study site make the results difficult to generalise. However, other studies have shown differences in territorial behaviours and hierarchical rigidity of *C. apella* and other capuchins (*C. apella* is a non-territorial and more despotic species) (Janson, 1986; Perry, 1998) which suggests the possibility of specific differences in the dynamics involving social relationships and food sharing.

Recently, Mitani and Watts (2001) compared three hypotheses about the hunting and sharing of meat in wild chimpanzees. Their data did not support the ecological (i.e., in periods of food shortage) or hunting-for-sex hypothesis, but did support the hypothesis that the sharing of meat is used as a social tool to enhance bonding between adult males.

Although the bird predation events described here did not involve cooperative hunts by the group members, sharing does seem to be influenced by the affiliative relationships in the group. There are indications that individuals of *C. apella* are capable of distinguishing and behaving differentially towards other group members. Janson (1984) described non-tolerance by the dominant males towards another males' offspring in feeding trees. The work of de Waal (1997, 2000; de Waal *et al.*, 1993) also suggests this capacity. Overall, the analysis of prey transfer described here, and most especially in three events, suggest that, in *C. apella*, highly valuable food items are preferentially shared with more affiliated individuals.

The drawbacks in data collection and analysis and the many possible proximate variables interfering in these events of meat sharing (for example, recent fights between the individuals involved or how hungry the carcass owner is), do not allow us to be conclusive about the dynamics involving affinity and food sharing. Nevertheless, the apparent refusal to share with some individuals and tolerance towards others in three events raises two questions: to what extent are these tripartite events of food transfer indicative of the social complexity and social knowledge of the capuchin monkeys? Likewise, is preferential prey sharing a tool for improving and maintaining valuable relationships within the *C. apella* groups? Experiments on food transfer in situations involving three individuals, and further observations of other tripartite relations, such as coalitions, could help to answer these questions.

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Renata Ferreira, Department of Biological Anthropology, University of Cambridge, Downing Street, Cambridge CB2 3DZ, England, UK, **Briseida Dogo de Resende**, **Massimo Mannu**, **Eduardo B. Ottoni**, Departamento de Psicologia Experimental, Instituto de Psicologia, Universidade de São Paulo, Avenida Professor Mello Moraes 1721, 05508-900 São Paulo, Brazil, and **Patrícia Izar**, Departamento de Ecologia Geral, Instituto de Biociências, Universidade de São Paulo, 005508-900 São Paulo, Brazil.

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THE BLACK HOWLER MONKEY (*ALOUATTA PIGRA*) AND SPIDER MONKEY (*ATELES GEOFFROYI*) IN THE MAYAN SITE OF YAXCHILÁN, CHIAPAS, MEXICO: A PRELIMINARY SURVEY

Alejandro Estrada, LeAndra Lluecke, Sarie Van Belle
Kirk French, David Muñoz, Yasminda García
Lucía Castellanos, Adrián Mendoza

Introduction

The black howler monkey of Mesoamerica, *Alouatta pigra*, has a restricted geographic distribution in Belize, Guatemala and Mexico. The majority of its range (c. 80%) is in Mexico in parts of the states of Tabasco and Chiapas, and it is the only *Alouatta* species present in the Yucatán peninsula (Smith, 1970; Horwich and Johnson, 1986; Watts and Rico-Gray, 1987). Spider monkeys (*Ateles geoffroyi*) coexist with *A. pigra* in many areas, but because of hunting for food and to obtain pet infants, and the destruction and fragmentation of their forests, they are among the most endangered primates in Mesoamerica (Kinzey, 1998).

Information on population parameters and conservation status for *A. pigra* are available from only a few localities, namely, two sites in Belize in the Bermuda Landing and Cockscomb Wildlife Reserve (Horwich, 1998; Silver *et al.*, 1998; Ostro *et al.*, 1999, 2000), in Tikal, Guatemala (Coelho *et al.*, 1976), in the Muchukux forest in Quintana Roo, Mexico (González-Kirchner, 1998) and in Palenque, Chiapas, Mexico (Estrada *et al.*, 2002). A similar situation prevails in the case of *A. geoffroyi*, with information available only from few localities in Mexico, namely Los Tuxtlas, Veracruz (Estrada and Coates-Estrada, 1996; Silva-López and Jiménez-Huerta, 2000) and the Muchukux and Naji Tucha forests in Quintana Roo, Mexico (González-Kirchner, 1999). Some information is available on populations of *A. geoffroyi* from Tikal, Guatemala (Coelho *et al.*, 1976).

Such paucity of information and the rapid fragmentation and conversion of the natural habitat of *A. pigra* and *A. geoffroyi* to pasture lands and agricultural fields in northern Mesoamerica, coupled with intensive hunting pressure and trafficking of infants as pets, makes the task of protecting these primate species particularly difficult (Estrada and Coates-Estrada, 1988; Rylands *et al.*, 1995). Data on group size, density, and age and sex composition for populations of *A. pigra* and *A. geoffroyi* in large forest tracts and in landscapes modified by man may provide information on the variability of population parameters, and may also improve our understanding of their tolerance of habitat loss and fragmentation (Estrada and Coates-Estrada, 1996; Estrada *et al.*, 1994; Crockett, 1998; Cuarón, 2000).

In this paper we provide preliminary data on group size, population density and demographic structure for populations of *A. pigra* and *A. geoffroyi* in the protected forest surrounding the ruins of the Mayan site of Yaxchilán, Chiapas, Mexico. The data we present are part of a series of surveys of primate populations inhabiting the protected forests surrounding major Mayan archeological sites in southern Mexico (Estrada *et al.*, 2002; in prep.).

Methods

Study area and sites

The study was carried out at the Mayan site of Yaxchilán, Chiapas, Mexico (16°53'N, 90°57'W, 250 m above sea level), near the Río Usumacinta, that marks the international boundary between Mexico and Guatemala (Fig. 1). There is a protected forest of about 2700 ha surrounding the Mayan site, of which 1100 ha are contained within an omega-shaped area by the river, while the rest extends inland (Fig. 1). This forest is connected to 35,000 ha of protected rain forest in the Community Reserve “La Cojolita”. The climate is hot and humid, and average annual precipitation is 1951 mm, with a dry season from December to April (average monthly rainfall = 42.4 ± 12.7) and a wetter period from May to November (average monthly rainfall = 256.0 ± 100.1 mm). Mean annual temperature is 25.5 ± 2.2°C (range 21–28°C).

Tall evergreen rain forest (tree heights between 15–45 m) is the dominant vegetation at the study site (<www.conabio.gob.mx>). Abundant trees in this forest are *Brosimum alicastrum*, *B. costaricanum*, *Poulsenia armata*, *Ficus glabrata* (Moraceae), *Manilkara zapota*, *Pouteria sapota* (Sapotaceae), *Bursera simaruba* (Burseraceae), *Lonchocarpus* sp. (Fabaceae), and *Spondias* spp. (Anacardiaceae) (Meave, 1990).

The Mayan site dates back to about 500 AD (Coe, 1998). Only about 5% of the ruins of the site have been excavated, the rest are covered by rain forest vegetation, and vestiges of buildings can be easily observed amidst the vegetation or roots of trees. Several of the Mayan structures were built at the top of the many hills, while the majority of the largest