



Stone tool use in wild bearded capuchin monkeys, *Cebus libidinosus*. Is it a strategy to overcome food scarcity?

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To determine whether tool use varied in relation to food availability in bearded capuchin monkeys, we recorded anvil and stone hammer use in two sympatric wild groups, one of which was provisioned daily, and assessed climatic variables and availability of fruits, invertebrates and palm nuts. Capuchins used tools to crack open encased fruits, mostly palm nuts, throughout the year. Significant differences between wet and dry seasons were found in rainfall, abundance of invertebrates and palm nuts, but not in fruit abundance. Catulè nuts were more abundant in the dry season. We tested the predictions of the necessity hypothesis (according to which tool use is maintained by sustenance needs during resource scarcity) and of the opportunity hypothesis (according to which tool use is maintained by repeated exposure to appropriate ecological conditions, such as preferred food resources necessitating the use of tools). Our findings support only the opportunity hypothesis. The rate of tool use was not affected by provisioning, and the monthly rate of tool use was not correlated with the availability of fruits and invertebrates. Conversely, all capuchins cracked food items other than palm nuts (e.g. cashew nuts) when available, and adult males cracked nuts more in the dry season when catulè nuts (the most common and exploited nut) are especially abundant. Hence, in our field site capuchins use tools opportunistically.

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Using tools to gain access to food allows expansion of an individual's diet, providing flexibility when food resources fluctuate, and acquisition of energy from resources that cannot be exploited otherwise. Both outcomes increase individual fitness. In vertebrates, tool use occurs in a relatively small number of species (Seed & Byrne 2010; Schumaker et al. 2011) and only a few use tools habitually (sensu McGrew 1992) in the wild. Among the latter are birds (e.g. woodpecker finches, *Cactospiza pallida*: Tebbich et al. 2002; New Caledonian crows, *Corvus moneduloides*: Hunt 1996) and mammals (e.g. bottle-nosed dolphins, *Tursiops* sp.: Mann et al. 2008; sea otters, *Enhydra lutris*: Hall & Schaller 1964), especially nonhuman primates. Among nonhuman primates, some populations of chimpanzees, *Pan troglodytes verus* (reviewed in Whiten et al. 1999), orang-utans, *Pongo pygmaeus* (van Schaik & Knott 2001), bearded capuchin monkeys (Mannu & Ottoni 2009; Spagnoletti et al. 2011; see also Ottoni & Izar 2008) and longtailed macaques,

Macaca fascicularis aurea (Gumert et al. 2009, 2011) use tools regularly. In nonhuman primates, tool use is more plastic than in other vertebrates, present in some populations and absent in others and with geographical variation in forms among different populations (chimpanzees: Whiten et al. 1999; orang-utans: van Schaik et al. 2003a; capuchin monkeys: Ottoni & Izar 2008).

How tool use evolved as behavioural innovation and how it is acquired by individuals and maintained in populations interest a wide variety of scientists concerned with the origin of technological culture (e.g. Fragaszy & Perry 2003). Unfortunately, since tool use in wild populations has been discovered only when already practised by many individuals, it is impossible to determine its history. However, by assessing the interpopulation differences in ecology, social behaviour and tool use that are present today, we can evaluate the role of current ecological and/or social factors in tool use.

To explain variation in tool use among orang-utan populations, Fox et al. (1999) proposed three hypotheses concerning the origins and maintenance of tool use, two of which are relevant for the present study. According to the 'necessity hypothesis', once tool use behaviour is invented, it can be maintained in order to meet

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sustenance needs and deal with resource scarcity. Three predictions follow from this first hypothesis: (1) that tool-using orang-utan populations should have less favourable energy budgets than populations not using tools; (2) that the food acquired with tools should replace foods that decline in abundance seasonally; and (3) that individuals with higher energetic needs (subordinate or pregnant/lactating females) should use tools more than those with lower energetic requirements. In other words, the scarcity of fruits, which are the primary component of orang-utans' diet, could force them to exploit novel food sources that require tools for extraction. According to the 'opportunity hypothesis', propitious ecological conditions facilitate maintenance of tool use through repeated exposure to appropriate circumstances. Two predictions follow from this second hypothesis: (1) that tool-using orang-utan populations live in an environment that provides opportunities to perform this behaviour and (2) that orang-utans of the same population will not use tools in an environment lacking these opportunities. For example, the peat swamp environment of Suaq Balimbing, Sumatra, in which social insects are forced to inhabit tree holes (owing to an ever-wet forest floor) should provide more opportunities to extract social insects with tools than a hilly forest in which social insects are likely to be on the forest floor.

These two hypotheses can be extended to other species and/or other types of tool use. To test whether tool use is maintained by sustenance needs and resource scarcity (the necessity hypothesis) and/or by repeated exposure to appropriate circumstances (the opportunity hypothesis), systematic concurrent data on food availability, availability of items exploited with tools and frequency of tool use are needed. In the Galapagos Islands, woodpecker finches use twigs or cactus spines to pry arthropods out of tree holes. By comparing tool use during wet and dry seasons between two vegetation zones (one arid and one humid), Tebbich et al. (2002) found that in the arid zone, where arthropod availability is higher in the wet season, finches spend more time using tools in the wet season than in the dry season. In contrast, in the humid zone, where arthropod availability is constant all year round, finches use tools for equal amounts of time in wet and dry seasons. In this study the (likely) assumption is that arthropods are the most important food item for the finches, thus making the availability of other food items irrelevant. Thus this study supports the opportunity hypothesis.

At Suaq Balimbing, orang-utans use sticks to extract insects or honey from tree holes, and to gain access to the seeds of *Neesia* fruit, especially during periods of fruit scarcity, indirectly measured as proportion of the time budget spent feeding on tree cambium (van Schaik & Knott 2001); however, across orang-utan sites no support exists for the necessity hypothesis (van Schaik et al. 2003b; see also Fox et al. 2004). Since *Neesia* fruits irregularly and other fruits are not seasonal (C. van Schaik, personal communication), and since this fruit is energy rich and highly preferred by orang-utans, it is plausible in our opinion that orang-utans exploit *Neesia* fruits when present, regardless of the availability of alternative fruit resources.

In the Taï National Park, Ivory Coast, chimpanzees use tools to exploit five species of palm nuts. This behaviour was found to occur more frequently in the major dry season (during which the food is assumed to be scarce on the basis of time spent feeding and on consumption of low-quality food), which is when *Coula* nuts are more abundant (Boesch & Boesch 1984). At Bossou, Guinea, chimpanzees perform two tool-mediated foraging activities (nut cracking to obtain the kernel of oil palms and pestle pounding to obtain the pith of oil palms) more frequently when pulpy fruits, their main foods, are scarce (Yamakoshi 1998). However, in exactly the same period, oil palm nuts are more abundant. Thus, the studies with apes do not provide unambiguous support for the necessity

hypothesis but do provide plausible evidence for the opportunity hypothesis.

For the longtailed macaques living on islands in the Andaman Sea that use stones to process shelled foods, Gumert et al. (2009) suggested that food scarcity promotes tool use, although data on food availability and frequencies of tool use are not yet available. Moura (2004; Moura & Lee 2010) systematically observed provisioned bearded capuchin monkeys living in the dry caatinga habitat of northeastern Brazil (Serra da Capivara National Park, Piauí) digging for tubers, using sticks to probe and stones to crack embedded food. These monkeys displayed a low rate of tool use that did not differ between wet and dry seasons (Moura 2004, page 165). Thus, although both Moura & Lee (2004) and Gumert et al. (2009) suggested that food scarcity promoted tool use, their findings do not support the necessity hypothesis.

We systematically collected data on two wild groups of bearded capuchin monkeys that routinely use hammers and anvils to crack open encased fruits, especially palm nuts (Spagnoletti et al. 2011; see Video 1 in the Supplementary material) and assessed the availability of fruit, invertebrates and nuts. These monkeys live in a semiarid habitat (cerrado; Oliveira & Marquis 2002) in northeastern Brazil. In this area, we expected a high degree of seasonal variability in food resources as reported for similar habitats where other capuchin monkeys have been studied (*Cebus capucinus*, Santa Rosa National Park, Costa Rica, Chapman 1988; Janzen 1988; Chapman & Chapman 1990; *Cebus olivaceus*, Hato Masaguaral, Venezuela, Robinson 1986).

In particular, we investigated the rate of tool use and the proportion of the time budget spent in tool use in relation to climate seasonality and food availability (i.e. fruits, invertebrates and palm nuts) in a provisioned (hereafter, PR) and nonprovisioned (hereafter, NPR) group of capuchins (see Methods for details of food provisioning). According to the necessity hypothesis we predicted that tool use would be more frequent when food resources (i.e. fruit and invertebrates) are less abundant than when more abundant (Prediction N1a and Prediction N1b, respectively), and that the NPR group would use tools more frequently than the PR group, and especially when food is scarce (Prediction N2). According to the opportunity hypothesis tool use frequency would reflect the relative abundance of encased foods (Prediction O3).

METHODS

Site

The study area is located at Fazenda Boa Vista (hereafter, FBV; 9°39'36" S, 45°25'10" W; see map in the Supplementary material) in the northeastern Brazilian state of Piauí, 21 km northwest of the town of Gilbués. The physical geography of the field site is a sandy plain at approximately 420 m above sea level punctuated by sandstone ridges, pinnacles and plateaus (morros) surrounded by cliffs composed of sedimentary rock rising steeply to 20–100 m above the plain. The cliffs and plateaus consist of interbedded sandstone, siltstone and shale. The steep faces of the cliffs shear periodically, producing boulder fields at the base of the cliff close to the plain (for further information about the geology of FBV, see Visalberghi et al. 2007). The sandstone cliffs and plateaus are heavily eroded and there are ephemeral water courses that have running water only after rainfall.

Subjects

From June 2006 to April 2008, we observed the behaviour of 31 wild bearded capuchins (nine adult females, five adult males, two subadult males, eight juveniles and seven infants) living in PR

group ($N = 12$ – 18) and in NPR group ($N = 8$ – 12 ; see Table 1). At the beginning of the study both groups were well habituated to human presence and we could recognize subjects individually. The habituation of the PR group started in 2001 as part of an ecotourism programme, while the habituation of the NPR group started in September 2005. Systematic behavioural data collection started in June 2006 with the present study and two others investigating the ontogeny of tool use (Ramos da Silva 2008) and socioecology (Verderane 2010). During our study the PR group was attracted to visit an area (hereafter, field laboratory) by daily provisioning it with fruit, vegetables and water. On average \pm SD we provided $12\,904 \pm 3802$ kJ/day, which equals approximately 825 ± 234 kJ/day per individual (INRAN's on-line Data Bank, <http://www.inran.it/>). From June 2006 to April 2008, this group visited the field laboratory 53.5% of the days that it was followed.

Behaviours and Other Measures Scored

Each group was followed from dawn to dusk 7–10 days per month by Noemi Spagnoletti (hereafter N.S.), Eduardo D. Ramos da Silva (hereafter E.D.R.S.) or Michele P. Verderane (hereafter M.P.V.), aided by a field assistant (see below), for a total of 3313 h of observation (PR group: 1332 h; NPR group: 1981 h). From June 2006 to May 2007, all occurrences of episodes of tool use (both when in progress or about to begin) were recorded ad libitum. N.S. used focal animal sampling (Martin & Bateson 1993) to collect data on 1052 episodes of tool use. These data were used for all the analyses (see also Spagnoletti et al. 2011). E.D.R.S. contributed 513 episodes recorded ad libitum during a concurrent study on the NPR group using the same behavioural definitions (Ramos da Silva 2008). A tool use episode was defined as starting when the subject (S) approached an anvil site (by definition, an anvil site is a boulder, an exposed stone or log, with a hammer stone on it or within 3 m of it, see Visalberghi et al. 2007 for details) with an encased food item and ending when the item was cracked open, or when S left the anvil without the hammer stone. When S began to crack a new food item, a new episode was recorded. When a cracking episode was in progress or about to begin, we observed it

until the episode ended. If while observing a tool use episode we saw another tool use episode begin, we continued to observe the first episode and the assistant noted the identity of S2 and collected data on this individual. Concurrent episodes beyond two were not recorded. When possible we identified the type of food item exploited with tools. In this paper we focus on the rate of tool use and the foods exploited in the dry and wet seasons. Other aspects of tool use (selectivity, efficiency, transport, etc.) have been reported elsewhere (Liu et al. 2009, 2011; Visalberghi et al. 2009a, b; Frigaszy et al. 2010a, b; Spagnoletti et al. 2011).

From June 2007 to April 2008, M.P.V. recorded data on activity budgets using a 10 min group scan-sampling method at 10 min intervals (hereafter scan; Altmann 1974), for each group, for a total of 4400 scans (PR group: $N = 1728$; NPR group: $N = 2672$). In this paper we focus on the proportion of the time budget that each group spent in feeding behaviours (ingesting, manipulating and searching for food) and in tool use to open encased foods. Detailed analyses of activity budget are reported elsewhere (Verderane 2010).

Food Availability and Climatic Data

The home ranges of the two groups were approximately 9 km² and included four types of vegetation physiognomies according to the terrain and the proximity to water sources (Spagnoletti 2009). The sandy plain is characterized by a high abundance of palms with subterranean stems and medium trees such as *Eschweilera nana* and *Hymenaea courbaril*. The vegetation surrounding the marsh is characterized by a higher diversity of trees forming gallery forests and by the presence of the tall palm tree *Mauritia flexuosa*. Shrubs and small trees dominate the cliff of the hills, whereas in the plateau herbaceous vegetation dominates, especially bromeliads and cactus.

The capuchin monkeys' diet is composed largely of fruit and invertebrates, although they eat many other items (fungi, tubers, vertebrates, etc., Frigaszy et al. 2004a). To estimate the availability of fleshy fruits and seeds (hereafter, fruit), invertebrates and palm nuts in the home range of our study groups, we used a stratified random sampling method combining the two methods described by Izar (2004; Izar et al. 2011): (1) 100 fruit traps and 100 pitfall traps (for invertebrates) placed at 30 m intervals, 1 m to the side of a 3 km trail crossing the different physiognomies of the study area, with collection and weighing of contents every 2 weeks and (2) direct observation of 254 palm trees of the species catulè, *Attalea barreirensis* ($N = 136$) and piassava, *Orbignya* sp. ($N = 118$) selected along the same 3 km trail. Every month the researcher noted the presence/absence of fruits in these palms. This second method was employed because most palm species eaten by the monkeys at FBV have subterranean stems with fruit clusters emerging from the soil (Frigaszy et al. 2004b). Thus, palm fruits would not fall into the fruit traps. Although using fruit/invertebrate traps presents several potential biases it is indicated for comparisons of resource abundance between habitats (Chapman et al. 1994).

For each sample we calculated a food availability index (FAI), expressed as kg/ha, both for fruit and invertebrates based on the dry weight of the material collected from traps and on the cumulative surface area. For catulè and piassava nuts, we calculated a monthly FAI, expressed as number of palms with fruits/ha. We also calculated a monthly FAI for total nuts, as the sum of catulè and piassava palms with fruits/ha.

We recorded rainfall, minimum and maximum temperature and humidity at the field station (Hygro-Thermometer Clock model 445702, EXTECH instruments) daily. Data collection on food availability and climate variables was carried out from June 2006 to April 2008.

Table 1
Group composition

Chicão (provisioned group)				Zangado (nonprovisioned group)			
Individual	Age	Sex	Individual	Age	Sex		
1	Chicão	Adult	M	1	Zangado	Adult	M
2	Segundo-Chefe	Adult	M	2	Moça-Branca	Adult	F
3	Mansinho*	Adult	M	3	Emília	Adult	F
4	Dengoso*	Adult	M	4	Moça-Chita	Adult	F
5	Piassava	Adult	F	5	Dunga	Juvenile	F
6	Chiquinha	Adult	F	6	Catuaba	Juvenile	F
7	Teninha	Adult	F	7	Kico	Juvenile	M
8	Dende	Adult	F	8	Ervília	Juvenile	F
9	Chuchu	Adult	F	9	Elisa	Infant	F
10	Dita	Adult	F	10	Café	Infant	M
11	Teimoso*	Subadult	M				
12	Jatoba*	Subadult	M				
13	Amarelinha	Juvenile	F				
14	Tucum	Juvenile	M				
15	Caboclo	Juvenile	M				
16	Pico	Juvenile	M				
17	Tomate	Infant	M				
18	Catu	Infant	M				
19	Cangaceiro	Infant	M				
20	Pati	Infant	M				
21	Doree	Infant	F				

Individuals are grouped by age and sex. M = male; F = female.

* Individuals that emigrated from the nonprovisioned group to the provisioned group between July and August 2006.

Analyses

Analyses concerning minimum and maximum temperature, minimum and maximum percentage humidity, rainfall and availability of the most abundant palm nuts (catulè and piassava) were based on monthly means ($N = 23$). Analyses of fruit and invertebrate abundance were based on means of bimonthly samples (total $N = 46$).

Thus far, capuchins at FBV have been observed using stones to crack open embedded fruits (nuts or other food items) placed on an anvil; 'tool use' refers exclusively to this behaviour.

From behavioural data collected ad libitum and by focal animal sampling during the first year of the study, we derived monthly rates of tool use. Since groups differed in size, not all the individuals used tools and the number of individuals using tools varied across months (because of emigration/immigration), we calculated the monthly rate of tool use per group as the number of tool use episodes observed in each group divided by the total number of observations/h and the individual monthly rate of tool use as the number of tool use episodes per individual divided by the total number of observation hours. For the latter calculation we distinguished between the individual rate of cracking nuts and the individual rate of cracking other food items.

Data collected by scan sampling during the second year of the study were expressed as mean monthly proportions of individual scans spent in feeding behaviour (including foraging) and in tool use. Since our data did not follow a normal distribution (Lilliefors test: $P < 0.05$), we used nonparametric statistics employing STATISTICA 7, Statsoft (Statsoft, Tulsa, OK, U.S.A.) and SPSS 13.0 for Windows (SPSS Inc., Chicago, IL, U.S.A.).

The region of FBV is seasonally dry, with a wet season lasting from October to April, and a dry season lasting from May to September (see below). To compare climate and food availability across seasons, we used a Mann–Whitney test for independent samples. The Mann–Whitney test was also used to assess whether the monthly rate of tool use per group and per individual and of food cracked differed between PR and NPR groups, as well as to assess whether the monthly proportion of the time budget allocated to feeding and to tool use differed between dry and wet seasons and between groups.

We pooled the data of the two groups to examine how tool use was related to food availability and climatic data. These data were pooled because the groups' monthly rate of tool use did not differ (see below) and 2–3 months after the study began four males (two adults and two subadults) migrated from NPR group to PR group

(see Table 1). Spearman rank correlation was used to examine (1) the relationships between monthly FAI for fruit, invertebrates, catulè nuts, piassava nuts and total nuts and climatic data, (2) the relationships between monthly rates of tool use (group and individual) and food availability and rainfall, (3) the relationships between proportion of the time budget devoted to tool use and food availability and rainfall. Finally, the Wilcoxon signed-ranks test for related samples was run, within individuals, to compare the rate of tool use to open all encased foods, the rate of tool use to open nuts and the rate of tool use to open other food items between dry and wet seasons. Furthermore, since most of the tool use episodes were performed by six adult and subadult males (Chicão, Zangado, Dengoso, Mansinho, Jatoba and Teimoso; see Table 4 in the Results), we ran a separate Wilcoxon signed-ranks test on these subjects to compare rate of tool use between dry and wet seasons to open nuts and other food items and all the encased foods. For all analyses the significance level was set at $P < 0.05$ and for multiple tests on the same variable the Bonferroni correction was applied ($\alpha' = 0.05/\text{number of tests}$; Sokal & Rohlf 1995). Statistical tests were one tailed when a directional prediction was made, and otherwise two tailed.

RESULTS

Seasonality and Food Availability

Annual rainfall at FBV averaged 1290 mm per year. Total rainfall recorded from June 2006 to May 2007 was 1162 mm and from June 2007 to April 2008 1418 mm. Overall, from May to September rainfall averaged 25 mm and from October to April 1266 mm. The annual mean \pm SD of maximum temperature was 32.8 ± 2.2 °C while the annual mean of minimum temperature was 21.5 ± 1.6 °C (see Fig. 1). Table 2 reports the median seasonal values for each climatic variable. Overall our data match the two climatic seasons reported for the region: a dry season lasting 5 months (from May to September) and a wet season lasting 7 months (from October to April).

The FAI for fruit varied across months from 11 to 2786 kg (mean = 337 ± 695 kg), but did not differ significantly between the wet and dry seasons (Table 2). In contrast, the FAI for invertebrates ranged from 2387 to 119 857 kg (mean = $19 079 \pm 28 781$) and was significantly higher in the wet season than in the dry season (Table 2), and was also positively correlated with rainfall (Table 3). Palm nuts were available throughout the year, although their overall abundance differed between seasons (Table 2) and was

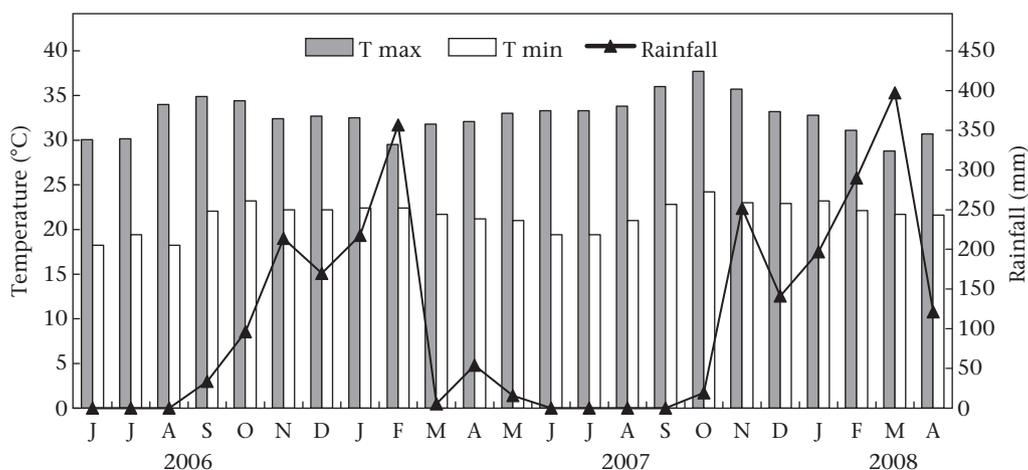


Figure 1. Climatic data (maximum and minimum temperature, rainfall) recorded in the field station from June 2006 to April 2008.

Table 2Seasonal differences (median \pm IQR) for climatic data and food availability index (FAI)

	Dry season	Wet season	Mann–Whitney <i>U</i>	<i>P</i>
Climatic data				
Rainfall (mm)	0.0 \pm 0.0	183.3 \pm 155.5	3	<0.001
T max ($^{\circ}$ C)	33.3 \pm 1	32.4 \pm 2.1	43	0.21
T min ($^{\circ}$ C)	19.4 \pm 1.6	22.3 \pm 1.3	14	<0.01
H max (%)	70.1 \pm 12.8	91 \pm 6.2	11	<0.001
H min (%)	29.2 \pm 13.4	50.5 \pm 12.5	20	<0.01
FAI				
Fruit (kg/ha)	130.6 \pm 139	144.8 \pm 193.5	233	0.66
Invertebrates (kg/ha)	2839.3 \pm 2624.2	6271.5 \pm 23 504.1	152	<0.05
Catulé nuts (no./ha)	25.2 \pm 5.5	10.2 \pm 9.9	3	<0.001
Piassava nuts (no./ha)	4 \pm 2.7	4.4 \pm 5.1	62	0.93
Total nuts (no./ha)	29.1 \pm 4.9	15.6 \pm 7.6	4	<0.001

T max = maximum temperature; T min = minimum temperature; H max = maximum percentage humidity; H min = minimum percentage humidity. Analyses were carried out on 23 samples (dry season $N = 9$, wet season $N = 14$) except for fruit and invertebrates for which analyses were carried out on 46 samples (dry season $N = 18$, wet season $N = 28$).

negatively correlated with rainfall (Fig. 2, Table 3). In particular, the abundance of catulé nuts was higher in the dry season than in the wet season (Table 2) and was negatively correlated with rainfall (Table 3) whereas the abundance of piassava nuts did not differ significantly between seasons (Tables 2, 3).

Tool Use in the Provisioned and Nonprovisioned Groups

From June 2006 to May 2007, during a total of 1709 h of observation, we recorded 1565 tool use episodes performed by adults and juveniles of both sexes, to crack nuts and other encased foods (Table 4). The vast majority occurred on anvil sites located on the ground (boulders or logs), while 0.6% of the episodes (seven nuts and two other encased food items) occurred on tree branches (see Video 2 in the Supplementary material). Capuchins used tools to process four species of palm nut (piassava, catulé, catulé and tucum; see Visalberghi et al. 2008 for a detailed description of these nuts) and four other encased foods: fruta-danta (Icacinaeae), cashew nut, *Anacardium* sp., caroba, *Jacaranda* sp., and mandiaca-brava (Euphorbiaceae). Except for one episode in which an adult male (Zangado) used a stone to mash a root of mucambira (Bromeliaceae) and one episode in which an adult female (Chuchu) used a whole nut to dig in search of tubers or roots, we did not

Table 3

Spearman correlation coefficients between the food availability index (FAI) and climatic variables

FAI	Rainfall	Mean temperature	Mean relative humidity	Sample (<i>N</i>)
Fruit	0.22	0.18	-0.33	46
Invertebrates	0.38*	0.20	0.26	46
Catulé nuts	-0.88*	-0.12	-0.75	23
Piassava nuts	-0.008	0.10	0.01	23
Total nuts	-0.83*	-0.11	-0.70*	23

* Significant after applying the Bonferroni correction for multiple tests ($\alpha = 0.016$).

observe tool use in a feeding context other than stone tool use to crack open encased foods.

The number of individuals observed using stone tools varied monthly from four to 12 in PR group and from two to eight in NPR group. For both groups the median individual rate of tool use was about one episode every 10 h. Individual monthly rates of tool use did not differ significantly between groups (Mann–Whitney test: $U = 64$, $N_1 = N_2 = 12$, $P = 0.32$, one-tailed test; median_{PR} \pm interquartile range, IQR = 0.9 ± 1.19 ; median_{NPR} \pm IQR = 0.71 ± 0.67) and the monthly rate of tool use of the two groups was positively correlated (Spearman $r_s = 0.65$, $N = 12$, $P < 0.05$, one-tailed test).

Most tool use episodes involved palm nuts (89% and 73% in PR and NPR group, respectively). The monthly rate of cracking nuts did not differ between groups (Mann–Whitney test: $U = 65$, $N_1 = N_2 = 12$, $P = 0.35$, one-tailed test; median_{PR} \pm IQR = 0.085 ± 0.09 ; median_{NPR} \pm IQR = 0.07 ± 0.11) whereas the monthly rate of tool use to crack other food items was significantly higher for NPR group than for PR group (Mann–Whitney test: $U = 27$, $N_1 = N_2 = 12$, $P < 0.01$, one-tailed test; median_{PR} \pm IQR = 0.01 ± 0.01 ; median_{NPR} \pm IQR = 0.03 ± 0.02 ; Table 5).

During June 2007 to April 2008 (1604 h of observation), feeding behaviour accounted for $47 \pm 3\%$ of the time budget of PR group (N scans = 1236), and for $50 \pm 7\%$ of the time budget of NPR group (N scans = 814). Tool use accounted for 1% of the time budget in each group (N scans for PR group = 21; N scans for NPR group = 21), which corresponded to 2% of the time budget allocated to total feeding behaviours (Table 6). Neither proportion of the time budget devoted to feeding behaviours nor proportion of the time budget devoted to tool use differed between groups (Mann–Whitney test: $U = 44$, $N_1 = N_2 = 11$, $P = 0.13$, one-tailed test; median_{PR} \pm IQR = 48.3 ± 5.5 ; median_{NPR} \pm IQR = 49.9 ± 9.3 ; Mann–Whitney test:

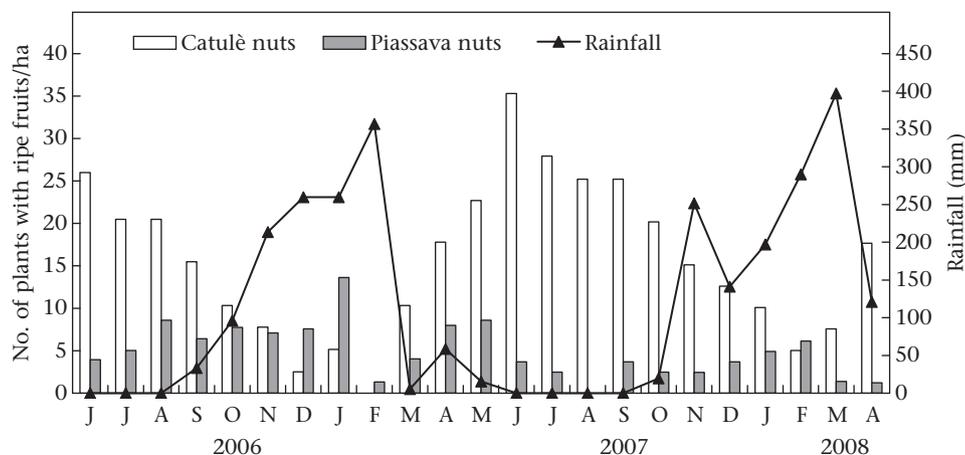
**Figure 2.** Number of catulé and piassava palms with ripe fruits in relation to rainfall from June 2006 to April 2008.

Table 4

Number of tool use episodes performed by each individual to crack palm nuts and other fruit items from June 2006 to May 2007 in the dry (Dry) and wet (Wet) seasons

Individual	Palm nuts			Other fruit items			Total (1+2)
	Wet	Dry	Total 1	Wet	Dry	Total 2	
Chicão	48	68	116	12	12	12	128
Zangado	100	176	276	11	9	20	296
Segundo C.	4	6	10	1		1	11
Dengoso	39	105	144	7	5	12	156
Mansinho	72	114	186	1	2	3	189
Dende	6	5	11	3		3	14
Teninha	14	8	22	1		1	22
Moça-Branca	13	14	27	9	8	17	44
Emília	4	2	6	7	7	14	20
Piassava	21	17	38	13	2	15	53
Chuchu	21	29	50	1	2	3	53
Dita	22	27	49	11	4	15	64
Moça-Chita	42	58	100	22	19	41	141
Jatoba	38	52	90	5	5	10	100
Teimoso	21	40	61	7	5	12	83
Caboclo		2	2	3		3	5
Tucum	30	14	44	20	6	26	70
Catuaba	5	6	11	20	10	30	41
Dunga	15	3	18	11	3	14	32
Ervília	5	5	10	11	2	13	18
Kico	8	4	12	10		10	22
Pico		2	2	1		1	3
Total	527	752	1279	187	89	276	1565

$U = 55$, $N_1 = N_2 = 11$, $P = 0.36$, one-tailed test; median_{PR} \pm IQR = 0.9 ± 1.3 ; median_{NPR} \pm IQR = 0.7 ± 1.2).

Tool Use, Seasonality and Resource Availability

As shown in Table 7, for both groups the individual and group rates of tool use did not correlate with the availability of fruit, invertebrates, piassava nuts and total nuts or with rainfall. In the NPR group, individual rates of tool use (rate to open nuts and total rate) were positively correlated with the availability of catulê nuts (Fig. 3a). This correlation was not significant for the PR group.

The overall individual rate of tool use (nuts plus other encased foods) did not differ between seasons (median_{dry season} \pm IQR = 0.025 ± 0.064 ; median_{wet season} \pm IQR = 0.028 ± 0.035 ; Wilcoxon signed-ranks test: $T = 92$, $N = 22$, $P = 0.13$, one-tailed test). However, the rates of tool use to crack nuts as well as the rates of tool use to crack other food items were higher in the wet season

Table 5

Monthly rate of tool use and annual rate of tool use performed by each individual of the provisioned and nonprovisioned groups to crack nuts and other food items (from June 2006 to May 2007)

Month	Provisioned group		Nonprovisioned group	
	Palm nuts	Other food items	Palm nuts	Other food items
June 2006	0.09	0.02	0.20	0.03
July 2006	0.19	0.01	0.14	0.01
August 2006	0.06	0.00	0.11	0.00
September 2006	0.06	0.01	0.01	0.04
October 2006	0.02	0.07	0.05	0.09
November 2006	0.13	0.01	0.02	0.03
December 2006	0.03	0.01	0.01	0.04
January 2007	0.04	0.00	0.05	0.01
February 2007	0.08	0.00	0.06	0.02
March 2007	0.16	0.00	0.08	0.04
April 2007	0.11	0.00	0.15	0.02
May 2007	0.19	0.01	0.21	0.04
Mean (\pm SD)	0.10 (± 0.06)	0.01 (± 0.02)	0.09 (± 0.07)	0.03 (± 0.02)

Table 6

Monthly proportion of time spent by the provisioned and nonprovisioned groups in feeding behavior and in tool use (from June 2007 to April 2008)

Month	Provisioned group		Nonprovisioned group	
	Feeding*	Tool use	Feeding*	Tool use
June 2007	41.9	0.5	44.9	1.4
July 2007	43.2	2.0	52.2	1.9
August 2007	46.3	0.7	53.8	1.5
September 2007	45.5	1.3	49.3	0.6
October 2007	48.3	1.4	44.5	1.3
November 2007	44.0	1.8	43.3	0.7
December 2007	49.5	0.9	39.1	0.4
January 2008	51.7	2.3	54.9	0.3
February 2008	49.5	0.9	66.3	0.1
March 2008	49.3	0.2	49.6	0.3
April 2008	49.8	0.1	51.3	2.4
Mean (\pm SD)	47.2 (± 3.2)	1.1 (± 0.7)	49.9 (± 7.3)	1.0 (± 0.8)

* Includes time spent in tool use.

than in the dry season (nuts: median_{dry season} \pm IQR = 0.018 ± 0.06 ; median_{wet season} \pm IQR = 0.020 ± 0.036 ; Wilcoxon signed-ranks test: $T = 64$, $N = 22$, $P < 0.05$, one-tailed test; other food items: median_{dry season} \pm IQR = 0.003 ± 0.007 ; median_{wet season} \pm IQR = 0.009 ± 0.008 ; Wilcoxon signed-ranks test: $T = 38$, $N = 22$, $P < 0.01$, one-tailed test).

Since six of the adult and subadult males used tools far more often than most of the females and juveniles (Table 4; see Spagnoletti et al. 2011) we analysed their behaviour separately. Their overall rate of tool use was consistently higher in the dry season than in the wet season (median_{dry season} \pm IQR = 0.113 ± 0.075 ; median_{wet season} \pm IQR = 0.058 ± 0.033 ; Wilcoxon signed-ranks test: $T = 0$, $N = 6$, $P < 0.05$, one-tailed test) and the same held true for their rate of tool use to crack nuts (median_{dry season} \pm IQR = 0.109 ± 0.078 ; median_{wet season} \pm IQR = 0.047 ± 0.037 ; Wilcoxon signed-ranks test: $T = 0$, $N = 6$, $P < 0.05$, one-tailed test). In contrast, their individual rate of tool use to crack other food items did not differ between seasons (median_{dry season} \pm IQR = 0.006 ± 0.004 ; median_{wet season} \pm IQR = 0.007 ± 0.006 ; Wilcoxon signed-ranks test: $T = 7$, $N = 6$, $P = 0.23$, one-tailed test).

We tested whether from June 2007 to April 2008 the monthly proportion of time spent on tool use by PR and NPR groups was affected by food availability and rainfall seasonality. As shown in Table 8, the proportion of time devoted to tool use by PR group did not correlate with the availability of fruit, invertebrates, palm nuts, or with rainfall, whereas the proportion of time devoted to tool use by NPR group was positively correlated with the availability of nuts, and particularly catulê (Fig. 3b), but did not correlate with all the other variables. In both groups, the monthly proportion of time spent in tool use did not differ between dry and wet seasons (median PR_{dry season} \pm IQR = 1 ± 1 ; median PR_{wet season} \pm IQR = 0.9 ± 1.6 ; Mann–Whitney test: $U = 14$, $N_1 = 4$, $N_2 = 7$, $P = 0.5$, one-tailed test; median NPR_{dry season} \pm IQR = 1.4 ± 0.7 ; median NPR_{wet season} \pm IQR = 0.4 ± 1 ; Mann–Whitney test: $U = 6$, $N_1 = 4$, $N_2 = 7$, $P = 0.065$, one-tailed test).

DISCUSSION

Seasonality, Food Availability and Tool Use

Our 2 years of climatic data (rainfall, temperature and percentage humidity) match those provided for previous years for the same region by the Embrapa (Brazilian Agricultural Research Corporation). In FBV we observed a lack of rainfall during several months and this allowed definition of a dry season (5 months with

Table 7

Spearman correlation coefficients between rate of tool use and food availability and between rate of tool use and rainfall in the PR (provisioned) group and NPR (non-provisioned) groups

Group	Tool use	Food availability					Rainfall
		Fruit	Invertebrates	Catulè nuts	Piassava nuts	Total nuts	
PR	Group	0.03	−0.60	0.49	−0.14	0.31	−0.47
	Individual (nuts)	−0.22	−0.68	0.47	−0.28	1.05	−0.47
	Individual (other food items)	−0.45	0.23	0.3	−0.19	0.13	−0.17
	Individual (total)	−0.13	−0.65	0.51	−0.29	0.29	−0.48
NPR	Group	0.22	−0.55	0.60	−0.24	0.39	−0.53
	Individual (nuts)	0.08	−0.65	0.76*	−0.01	0.69	−0.62
	Individual (other food items)	−0.35	0.14	−0.10	−0.18	−0.26	0.15
	Individual (total)	0.09	−0.62	0.74*	0.01	0.64	−0.57

$N = 12$.

* Significant after applying the Bonferroni correction for multiple tests ($\alpha = 0.008$).

mean monthly rainfall of 5.5 mm) and a wet season (7 months with mean monthly rainfall of 181 mm).

Unexpectedly, the indirect assessment of food availability via traps indicates that season had negligible effects on the availability of fruit, and in contrast with other areas (Janzen 1988; Robinson 1986; Chapman & Chapman 1990), the dry season was not associated with less abundant fruit. Invertebrates were more abundant in the wet season. Palm trees and palm nuts are abundant in the capuchins' range (448 individuals/ha, Verderane 2010) and the catulè nuts are 2.5 times more abundant during the dry season than in the wet season. These findings allow us to test all predictions except Prediction N1a concerning fruit seasonality (see Table 9).

Five findings indicate that in FBV capuchin monkeys do not face dramatic periods of food scarcity and that high-quality food is abundant (McCabe & Fedigan 2007). First, systematic comparison based on food availability collected with the same methodology between *C. libidinosus* living in the cerrado–caatinga of FBV and *Cebus nigrinus* living in the Atlantic Forest of Carlos Botelho State Park shows that food scarcity characterized the latter site more than the former (Izar et al. 2011). Fruit is usually considered a limiting resource for the reproductive success of *Cebus* (e.g. Terborgh 1983; Zhang 1995; Di Bitetti 2001; Izar 2004). Strong seasonal variation of fruit availability occurs in the Atlantic Forest, in the primary tropical forest (Zhang 1995; Nakai 2007) and in a semideciduous forest (Galetti & Pedroni 1994). Second, Verderane (2010) showed that females in FBV fed on high-quality foods year-round and that their reproductive success is not related to food scarcity as happens at other field sites, such as Carlos Botelho for *C. nigrinus* (Izar et al. 2011). Third, in FBV capuchins adopted and nursed a marmoset (Izar et al. 2006) and twins were born (one pair in the PR group and one in NPR) and successfully raised by their mother past 1 year of age (L. Biondi, unpublished data). Fourth, average interbirth interval, which reflects food availability

(Izar et al. 2009), was longer in Carlos Botelho than in FBV (Izar et al. 2011). Fifth, the rates of play, a behaviour that decreases when food is scarce (e.g. Lee 1984; Barrett et al. 1992), were higher in FBV than in other populations of capuchins (Spagnoletti 2009; Verderane 2010). Therefore, fruit scarcity in dry season semiarid environments cannot be assumed. Nevertheless, only direct phenological studies, as we plan to do in the future, will allow a proper assessment of the abundance of specific plant species consumed by capuchins.

In FBV, individual rates of tool use varied across months according to the availability of encased foods, as expected by Prediction O3 (see Table 9). The adult males cracked nuts more in the dry season (when catulè nuts are more abundant) than in the wet season. Furthermore, all tool users cracked other encased food (mostly cashew nuts) more in the wet season than in the dry season. Dry cashew nuts are available only at the beginning of the rainy season and typically capuchins use a small stone to get the seed without touching the peel of the fruit, which contains a caustic chemical (Visalberghi & Sirianni, in press). We conclude that capuchins use tools opportunistically when they encounter food items that require this behaviour for access.

Finally, tool use was more frequent in the dry season when invertebrates were less abundant but there was a lack of correlation between monthly invertebrate abundance and both monthly rates of tool use and proportion of time devoted to tool use. Therefore, Prediction N1b is only partially supported (see Table 9).

It is important to stress that frequency of tool use and availability of food resources were consistent across 2 years and tool use data were also consistent across two different methodologies (all occurrences and scans). Overall, our findings indicate that tool use reflects the abundance of nuts in the environment and not the availability of fruits and invertebrates. These findings support the opportunity hypothesis.

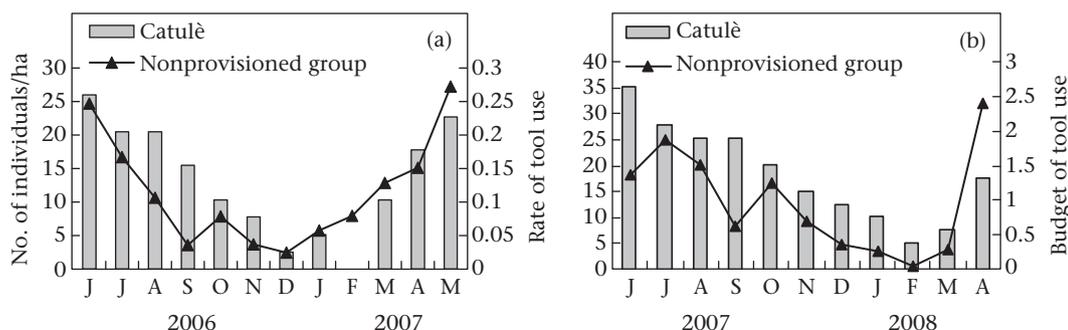


Figure 3. (a) Rate of tool use per individual and (b) budget of tool use for the nonprovisioned group and availability of the catulè nuts per ha.

Table 8

Spearman correlation coefficients between proportion of time spent in tool use and food availability and between proportion of time spent in tool use and rainfall in the PR (provisioned) and NPR (nonprovisioned) groups

Group	Food availability					Rainfall
	Fruit	Invertebrates	Catulé nuts	Piassava nuts	Total nuts	
PR	−0.09	−0.62	0.02	0.42	0.06	−0.05
NPR	0.26	−0.57	0.78*	−0.65	0.75*	−0.70

N = 11.

* Significant after applying the Bonferroni correction for multiple tests ($\alpha = 0.008$).

Tool Use in Provisioned and Nonprovisioned Groups

We now examine whether tool use was less frequent in the PR group than in the NPR group (Prediction N2). Our results show that the food provided did not affect the occurrence of tool use. The individual rates and the proportion of the time budget devoted to this activity did not differ between groups. Overall, the use of tools represents a small proportion of the activity budget (and feeding time) for both PR and NPR groups, as also noted by Verderane (2010; see also Spagnoletti 2009). In both groups there are a few individuals that do not use tools (or do so very rarely) despite being old enough to perform this behaviour and these individuals do not seem to be affected by not using tools (Spagnoletti et al. 2011). Therefore, the above findings do not support Prediction N2 since capuchins do not use tools at different rates in the two groups (see Table 9).

Tool Use in Other Wild Capuchin Populations and in Captivity

The necessity hypothesis is further weakened by the fact that food scarcity per se does not promote tool use in other populations of capuchin monkeys. At least two populations of *C. nigritus* that live in forests overcome low fruit availability by foraging on the leaves of bromeliads (Brown & Zunino 1990; Izar 2004; Izar et al. 2011), although encased food (and/or palm nuts) and stones are also available for at least some study groups (Janson 2006; P. Izar, I. Agostini & B. Wheeler, personal communication). In other areas where fruit seasonality is pronounced, palms are an important alternative resource but no tool use has been reported (Terborgh 1983; Fragaszy 1986; Robinson 1986; Galetti & Pedroni 1994; Zhang 1995). Peres (1994) reported that *Cebus apella* living in the Terra Firme forest of Amazonia overcome the period of fruit scarcity by eating the soft mesocarp of palm fruits, *Oenocarpus bataua*, which does not demand tool use for its acquisition.

Conversely, there is evidence of percussive tool use in provisioned groups living in captivity (reviewed in Visalberghi &

Table 9

Support for the predictions concerning frequency of tool use in relation to food resource availability (fruit, invertebrates, food provisioned and encased food) according to the necessity and opportunity hypotheses

Predictions	Frequency of tool use	Support
Necessity hypothesis	N1a Fruit scarcity > Fruit abundance (not testable in the present study)	–
	Positive correlation with scarcity of fruit	No
	N1b Invertebrate scarcity > Invertebrate abundance	Yes
	Positive correlation with scarcity of invertebrates	No
	N2 Nonprovisioned group > Provisioned group	No
Opportunity hypothesis	O3 Positive correlation with abundance of encased food	Yes

Fragaszy, 2012), in semifree-ranging conditions (e.g. Tietê Ecological Park, São Paulo, Brazil, Ottoni & Mannu 2001; Brasilia National Park, Brasilia, Brazil, Waga et al. 2006) and in the wild (Moura 2004; present study). Percussive tool use seems to be performed opportunistically when nuts are more abundant (this study) and where hammer stones, anvils and encased fruit (including tough seeds) are concurrently present (Visalberghi et al. 2009a). In sum, our findings on the capuchins of FBV do not support Predictions N1b and N2 based on the necessity hypothesis, whereas they do support Prediction O3 based on the opportunity hypothesis. Further studies on populations that do face food scarcity and significant seasonal differences in food resources are necessary to test the validity of Prediction N1a.

Conclusions

Nut cracking is a strenuous activity for capuchins (Liu et al. 2009; Spagnoletti et al. 2011) but still a very advantageous one in terms of energetic gain for all individuals (poster presented at the 23rd Congress of the International Primatological Society, <http://primate-society.com/ips/program.html#poster>). In our population nut-cracking behaviour, although habitual (Spagnoletti et al. 2011), is infrequent. To be a strategy to overcome food scarcity, tool use should represent a major source of energy. This is the case for the chimpanzees in Bossou and in Tai (Yamakoshi 1998; 2001) and for woodpecker finches (Tebbich et al. 2002), but not for capuchins in FBV. During the peak month of tool use, Bossou chimpanzees spend 32% of their total feeding time on tool-using behaviour (nut cracking, pestle pounding, etc.), whereas during the *Coula* season Tai chimpanzees spend 44% of their feeding time cracking these nuts (Yamakoshi 2001). Even more pronounced is the role played by tools for the woodpecker finches living in the arid zone in the Galapagos Islands: these birds spend almost 50% of their foraging time using tools (Tebbich et al. 2002). In contrast, FBV capuchins use stone tools on average for only 2% of their foraging and feeding time. Similarly, in two studies carried out in two different periods at Serra da Capivara National Park where capuchins use both stone and stick tools, Mannu & Ottoni (2009) observed 0.96 tool use events/h per group and Moura & Lee (2010) observed only 0.04 tool use events/h per individual. In conclusion, although we cannot exclude that for a capuchin population living in a poor environment and for which tool use is a major source of energy, the frequency of this behaviour can vary in response to low food availability, so far this scenario has not been reported.

Finally, we must ask whether palm kernels are a keystone food permitting the survival of *C. libidinosus* in our site. At first glance, the low proportion of time spent cracking palm nuts, the fact that their use seems to be opportunistic, and the fact that not all the individuals exhibit this behaviour suggest that, at present and in this population, tool use is not very important for survival. However, placing these findings within the context of fallback foraging theory could help to clarify the role of these foods in the evolution of *C. libidinosus*. According to Marshall & Wrangham (2007) tool use in primates occurs primarily in the context of feeding for fallback foods during periods of low food availability. They distinguished between (1) staple fallback food that is available perennially, usually consumed throughout the year, may seasonally constitute 100% of the diet and is uniformly distributed and (2) filler fallback foods that never make up 100% of the diet, are completely avoided for some time (weeks, months) and are rather patchily distributed. For *C. libidinosus* living in FBV palm nuts appear to constitute a staple fallback food, since tool use to gain access to the nut kernel occurs throughout the year. Moreover, palm fruits appear to be staple fallback food because, throughout the year, capuchins drink their water when unripe and eat their

mesocarp until the woody endocarp of the nut is exposed. However, the role of palms as staple fallback food can only be confirmed by assessing (1) whether the absence of palm fruits from the *C. libidinosus* environment would reduce fecundity and increase mortality and/or (2) whether during periods of extreme food scarcity palms become a staple food for capuchins. In any case it will be necessary to assess the nutrient and energy contribution of the palm fruit tissues to the diet of all individuals in a given group, both tool users and nontool users. If palm fruits are foraged on infrequently, but provide needed nutrients and are major energy contributors, then the argument for their staple fallback role and for their role as the selective agent accounting for tool use in this capuchin species is bolstered.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2012.03.002.

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