RESEARCH ARTICLE

Energetic Payoff of Tool Use for Capuchin Monkeys in the Caatinga: Variation by Season and Habitat Type

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In this paper, we analyze predictions from the energetic bottleneck and opportunity models to explain the use of stones to crack open encased fruit by capuchins in dry environments. The energetic bottleneck model argues that tool use derives from the need to crack open hard-encased fruits which are key resources during periods of food scarcity. The opportunity model argues that tool use by capuchins derives from simultaneous access to stones and encased fruits. The study was conducted in the Caatinga biome, northeastern Brazil, at two areas where capuchin monkeys (*Sapajus libidinosus* and *Sapajus spp.*) regularly use stones to crack open encased fruit of *Syagrus cearensis* and *Manihot dichotoma*. Energetic gains were inferred based on the number of tool-use sites used and the mass of encased fruit consumed per month, and compared across seasons and areas occupied by the two groups. For the drier habitat, a significant increase in frequency of tool use ($N_{dry} = 329$ vs. $N_{wet} = 59$) and in the mean monthly mass of fruits consumed in the dry season (mean$_{dry}$ = 193g vs. mean$_{wet}$ = 13.5 g) offered support for the energetic bottleneck model. However, our inference of low energetic payoffs for tool using individuals (in the drier caatinga habitat from 13 to 193 cal·ind^{-1}·month^{-1} and in the wetter caatinga habitat from 805 to 1150 cal·ind^{-1}·month^{-1}) offer support for the opportunity model. Finally, our analyses indicate that consumption of six *S. cearensis* fruits would equal the daily requirements of capuchins for β-carotene, and the consumption of 1.22 g·day^{-1} of *M. dichotoma* encased fruit or 1.0 g·day^{-1} of *S. cearensis* can supply capuchin's daily requirement of vitamin C. So, specific nutritional requirements may play a role in explaining the continuous consumption of encased fruit and customary use of stones to crack open encased fruit. Am. J. Primatol. 74:332–343, 2012.   © 2011 Wiley Periodicals, Inc.

Key words: Tool use; capuchin monkeys; fallback foods; feeding ecology; energetic payoffs

INTRODUCTION

The robust capuchin monkey (*Sapajus* spp.) is a medium size Neotropical primate that diverged from its sister clade (gracile capuchin, genus *Cebus*) about 6.15 million years ago, and currently occurs in almost all South America biomes [Lynch Alfaro et al., 2012a, b]. *Sapajus* weight between 2 and 4 kg, with males 15–30% heavier and larger than females—depending on the species (eight in total), with a diet comprised mostly of fruits and insects [Fragaszy et al., 2004]. Robust capuchins are known for their dietary flexibility, including the exploitation of bromeliads (meristem and leaf base) in montane forests [Brown & Zunino, 1990] and oysters (*Crassostrea rizophorae*) [Fernandes, 1991] and crabs (*Ucides cordatus*) [dos Santos, 2010] in mangroves. In tropical forests capuchins may consume palm nuts, which they access by banging the nut against bamboo nodes [Izawa, 1979; Janson, 1988]. Galleti and Pedroni [1994] presented data showing that tufted capuchins (*S. nigritus*—according to

Lynch Alfaro et al., 2012a) increase their time on the ground and increase the consumption of nuts during dry periods in the semi-deciduous forest in southeastern Brazil. This dietary variability is linked to a manipulative-destructive foraging strategy [Parker & Gibson, 1977].

Capuchin monkeys are of interest to biological anthropologists because they constitute an

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independent contrast for evolutionary studies of the function of two acclaimed human traits: large neocortex ratio and tool-use behavior [Visalberghi & McGrew, 1997]. The discovery that in dry areas robust capuchins practice customary second-order use of percussive stones (i.e., stones as hammers and as anvils Westergaard, 1999) to consume encased fruit has triggered a series of studies on tool using capuchin groups [see review in Ottoni and Izar, 2008].

Two models have been proposed to explain the relationship between tool-use behavior and large neocortex size in capuchin monkeys. Moura [2004], Moura and Lee [2004], Lee and Moura [2005] proposed the Energetic Bottleneck Hypothesis, that is, encased fruit are "important" resources to capuchins in highly seasonal areas particularly during dry periods. Therefore, food scarcity is expected to constitute a strong selective force resulting in behavioral, morphological, and cognitive changes which could include tool manufacture and manipulation and brain expansion (e.g., "We proposed that the use of embedded resources was associated with habitual food scarcity and that the energetically expensive use of stones and other tools was a vital mechanism for food acquisition," pg. 951, Lee and Moura, 2005).

Conversely, Visalberghi et al. [2005] propose the Opportunity Hypothesis, arguing that the use of tools by capuchins in semiarid areas results from the combined opportunity to exploit resources on the ground (terrestriality), and the availability of encased fruit and stones (e.g., "this [Moura and Lee's] argument is weakened by the frequent observations of spontaneous tool use by capuchins in captivity and in semi–free-ranging, provisioned groups, and by the absence of tool use in wild groups facing energy bottlenecks in many habitats" p 951). In this case, tool use would evolve from a preexisting ability for manipulative foraging. The two models are not mutually exclusive, and both can be seen as capuchins solving a set of foraging problems that result in tool-use behavior (as proposed by van Schaik et al. [1999]). However, these models differ in the importance attributed to food scarcity as a prime mover in the evolution of tool use and, therefore, the intensity of selection acting on adaptations for behavior, morphology, and cognition (sensu Marshall and Wrangham's [2007] distinction on preferred, staple and filler fallback foods).

In this paper, we analyze the monthly net energetic gain afforded by the consumption of encased fruit cracked with stones by two non-provisioned wild groups of capuchins (*Sapajus libidinosus* and *Sapajus spp.*). We infer the energetic gain using data on the weight of encased fruit consumed converted to calories based on the chemical composition of the fruits described by Crepaldi et al. [2001] and Martins et al. [2007]. We infer energetic costs using Liu et al. [2009] indices. In order to compare

the energetic bottleneck and opportunity models, we analyze the number of active tool-use sites and mass of encased fruit consumed across conditions where resource availability differed in two different caatinga areas across two different seasons (see Study Area under Methods section).

We predict that, if capuchins principally use tools during energetic bottleneck conditions, then (1) a higher number of active tool-use sites and (2) a higher mass of encased fruit consumed will be found in drier areas, during the dry season, and when there are no available cultivated crops. We also predict that such encased fruits will provide energetic intake sufficient for capuchins living during energetic bottleneck periods. If, instead, there are no differences in the rates of tool use and encased fruit consumed across seasons and habitat types, this would add support to the opportunity hypothesis.

METHODS

Study Area

The caatinga biome is endemic to northeastern Brazil. It extends over 750,000 km^2 and includes all the northeastern states and part of Minas Gerais [Ab'Saber, 2003]. It is one of the least studied biomes [Prado, 2003] and about 20% of its area is desertified due to anthropogenic processes [Alves et al., 2009]. Caatinga is characterized by a dry climate, following are classification criteria for semiarid regions [MIN, 2005]: (i) mean annual rainfall of less than 800 mm; (ii) aridity index of up to 0.5, calculated by hydric balance, relating rainfall, and potential evapotranspiration, between 1961 and 1990; and (iii) greater than 60% risk of drought, based on the period between 1970 and 1990. Floristic and fauna diversity is low and there is high incidence of endemic plants with adaptations for diminishing water loss, such as the presence of thorns, small leaves, and deep roots in deciduous hardwood trees [Alves et al., 2009]. Compared to other habitat types, there is a reduction in population density for many mammals, including primates [Alves et al., 2009; Ferreira et al., 2009]. Recent reports [MMA, 2003, 2004] have documented the extreme heterogeneity of the caatinga resulting from habitat diversity in water availability, soil composition, altitude, wind forces, solar incidence, and anthropogenic processes.

We monitored indirect evidence of tool-use behavior by capuchins (*S. libidinosus* and *Sapajus spp.*) in two areas representing two different types of caatinga (see Table I). The Serra do Estreito (elevation: 203 m), located in the municipality of Jucurutu (Fig. 1, Figs. S1a and b) exhibits a vegetation pattern classified as open-shrub caatinga, oscaatinga hereafter [Alves, 2007]. The second study area is located in the highland region of Luis Gomes (elevation: 527 m) approximately 300 km southwest

TABLE I. Envirnomnetal Characteristics of the Study Areas: Jucurutu (Open-Shrub Caatinga) and Luis Gomes (Shrub-Arboreal Caatinga)

	Jucurutu study site	Luís Gomes study site
Latitude/longitude	6°12′ 40.2″ S 37°02′ 10.7″W	6°23′ 47.1″S 38°23′ 10.6″W
Type of caatinga	Open shrub	Shrub-arboreal
Average and cumulative annual rainfall in 2009	80.3/963.6 mm^3	84.1/1009.2 mm^3
Sapajus species present (see Fig. S2)	*Sapajus spp.*	*Sapajus libidinosus*
Sampling effort	780 hr	780 hr
Monitored area	361.18 ha	225.40 ha
Average and cumulative parcel area	3/12.32 ha	5/20.35 ha
Type of rocks	Dioritic orthogneiss to granite with remnants of supracrustals [CPRM, 2005a]	Metamorphic rocks forming the crystalline shield, where granite, gneiss, migmatite, schist, and amphibolite predominate occasionally traversed by veins of quartz and pegmatite [CPRM, 2005b]
Presence of encased fruits	*Manihot dichotoma*	*Syagrus cearensis, Manihot dichotoma, Diclea grandiflora*
Flesh fruit producing trees	*Passiflora foetida, Phoradendron affine, Cissus verticillata, Capparis cynophallophora, Commiphora leptophloeos, Pilosocereus gounellei, Cereus jamacaru*	*Capparis cynophallophora, Commiphora leptophloeos, Pilosocereus gounellei, Cereus jamacaru, Pouteria gardneriana*
Presence of cultivar fruits	-	Mango (*Manguifera indica*), corn (*Zea mays*), cashew (*Anacardium occidentalis*)

from Jucurutu (Fig. 1; Figs. S1c and d). This area is classified as shrub-arboreal caatinga, sa-caatinga hereafter [Alves, 2007; MMA, 2003]. This region has been designated as a conservation and research area owing to its biological richness, and it exhibits several indicators of biodiversity, endemism, and, of interest for this study, greater resource availability (both fruits, encased fruits, vertebrates, and invertebrates) for capuchins [MMA, 2003]. These caatinga areas represent the driest and hottest extreme for capuchin monkey habitat. Seasonal variation strongly influences the landscape in both study areas. Lush vegetation is present in the rainy season, with most tree species exhibiting a well-defined reproductive phase (see Fig. S1). Many botanical and ecological studies indicate that the caatinga landscape changes drastically in the dry season, evidenced by trees void of leaves and fleshy fruits [compiled at MMA, 2003; MIN, 2005].

In the wetter sa-caatinga, there are areas with agricultural activity (e.g., mango, corn, cashew fruit) from where capuchins are known to obtain food [Ferreira et al., 2009, 2010].

Study Subjects

The capuchin monkeys that used the tools sampled in this study belong to two non-habituated groups. The group at sa-caatinga is classified as

S. libidinosus [Ferreira et al., 2010], a species formally grouped within *S. apella*, that occupy semiarid areas throughout central and northeastern Brazil. A previous study indicates that only one group with fewer than 30 individuals inhabits this area (Ferreira et al., 2009). The group observed at Serra do Estreito (os-caatinga) was defined as *S. flavius* based on fur color pattern by technicians from the Brazilian Agency for Protection of Primates [Ferreira et al., 2009]. *Sapajus flavius* (blonde capuchin) is a recently rediscovered species occupying northern areas in Coastal Atlantic Forest [Oliveira and Langguth, 2001]. So, the group found at os-caatinga would represent the extreme of *S. flavius* distribution, at the limits of the distribution of *S. libidinosus*. However, in a later study, Silva [2010], one of the co-authors of the previous study [Ferreira et al., 2009], reclassified *S. libidinosus*, and argued that the group at Serra do Estreito is a *S. libidinosus var 07*, with the lightest color fur type of this species (see suplementary material 2). A previous study indicates that only one group composed of about 45 individuals inhabits this area (Ferreira et al., 2009).

Despite such uncertainty on taxonomy, Ferreira et al. [2010] reported that these two groups customarily use tools to crack open two different encased fruit: *Syagrus cearensis* (Palmae/Arecaceae—nut size aproximately 16 cm^3), and *Manihot dichotoma* (Euphorbiaceae—nut size aproximately 0.24 cm^3).
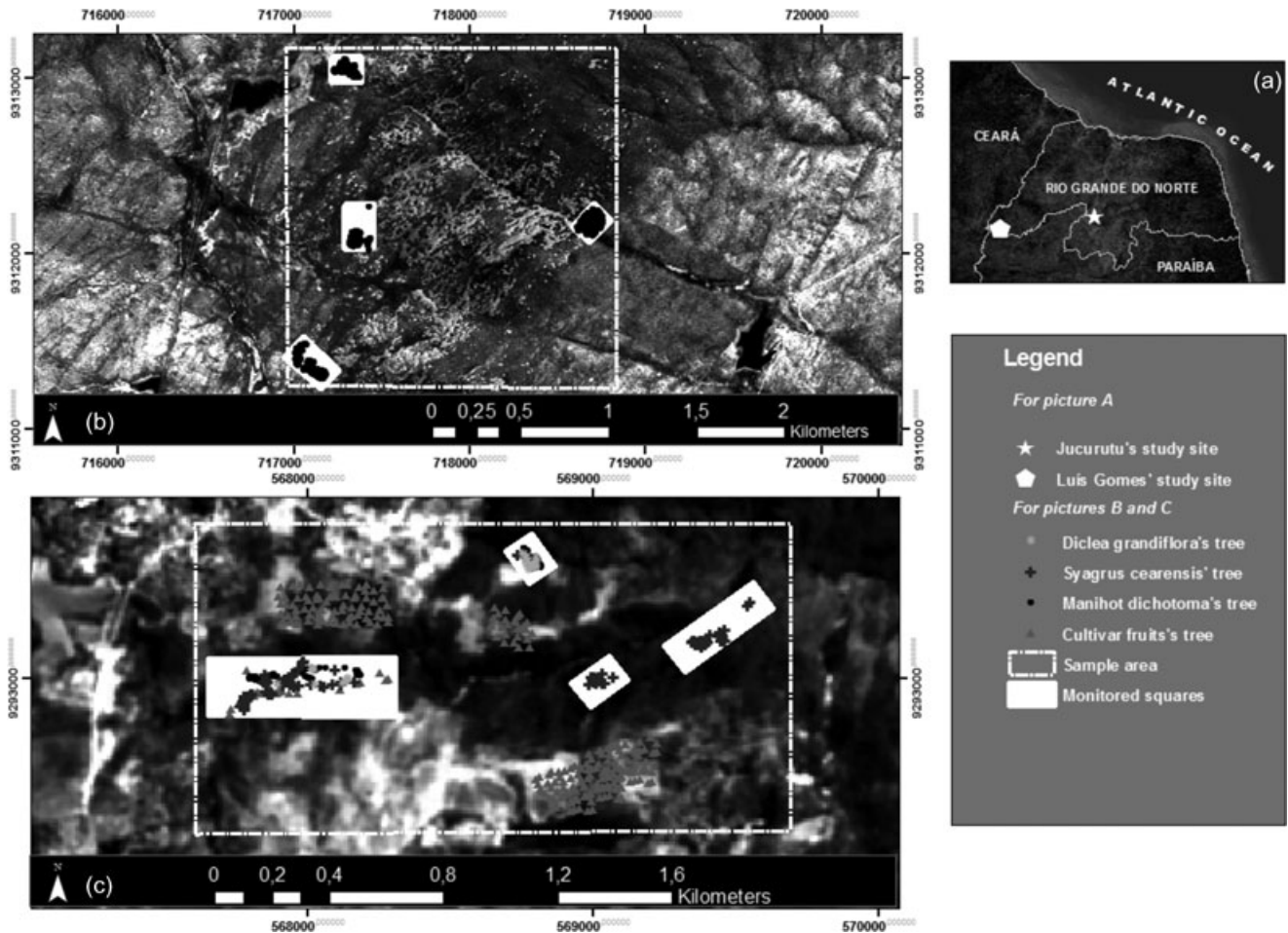
Fig. 1. (a) Satelite image of studied areas. (b) Jucurutu study site, open-shrub caatinga. (c) Luis Gomes study site: Shrub-arboreal caatinga. Squares depict monitored parcels.

Sampling Effort

A total of twenty-six 5-day field excursions were conducted between December 2008 and December 2009 (i.e., one 5-day visit per month to each study area), resulting in 130 days of visits to the caatinga (65 days for each site) and over 1,000 hr of data collection.

Monitored Parcels

Four parcels (pieces of land) within each study area were demarcated for monthly sampling (Fig. 1). Each parcel measured approximately 3 ha in the drier os-caatinga and 5 ha in the wetter sa-caatinga and was located more than 400 m from other parcels and away from human settlements. Although we could not conduct diversity analyses, it is evident from walking through the landscape that the nut producing trees of *S. cearensis* occur in clusters, whereas trees of *M. dichotoma* are more uniformly distributed. Parcels were purposefully located at clusters of *S. cearensis*, and differed in size due to accessibility (many areas are hillsides that make data collection difficult). In our monthly monitoring of the two sites, a total area of 361.18 ha in the drier os-caatinga and of 225.40 ha in the wetter sa-caatinga was traversed. The entire area of the plots monitored was 12.32 ha in drier os-caatinga and 20.35 ha in wetter sa-caatinga. This represents 3.4% of the total os-caatinga area and 9% of the total sa-caatinga area of our study groups. GPS coordinates were taken for all encased fruit-producing plants with diameter at breast height (DBH) of at least 3 cm (total of 1,264 and 401 of encased fruit producing trees inside parcels at os-caatinga and sa-caatinga, respectively). Trails were created inside each parcel to permit systematic data collection, and the trails were inventoried in the same direction for each monthly sampling.

A preliminary investigation [see also Ferreira et al., 2010] showed that stones used as hammers (see tool-use site definition in the next topic) displayed extensive size variation (mean = 10.13 cm; CI 95% = ±7.02 cm—Fig. S3). Also, anvils consisted

of stones or tree trunks, the former ranging from 10 cm to more than 5 m in length (Fig. S3). Unlike the Fazenda Boa Vista (FBV) area studied by Visalberghi et al. [2005, 2007], stones were abundant and readily available to be used as hammers and anvils in both of our sampled areas. Also, due to the different geological formations in these environments, the granitic stones at this caatinga are less friable than are the arenitic stones available to capuchins at FBV cerrado-caatinga ecotone.

Recording Number of Tool-Use Sites

We considered a site to be an active tool-use site when one or more small stones with wear marks (i.e., hammers) were on top of larger stones that also had wear marks (i.e., anvils), with remains of cracked encased fruits on the anvil. While at FBV stones used as anvils present pitted surfaces due to the arenitic origin of stones [Visalberghi et al., 2007], in our study areas, due to the granitic o-ring of stones, wear marks (in anvils and hammers) consisted of white dots or paler patches on stones derived from the friction with nuts (see Fig. S3e).

Each month, we traversed the trails inside each parcel and recorded the geographic location of each active cracking site found, in addition to information on which encased fruit species were cracked. When cracking sites with encased fruits from different species were found, they were classified as mixed cracking sites. A Garmin GPSMAP® 76CSx with UTM grid reader and SAD 69 (South American datum 1969) was used to record global positioning system (GPS) data.

Once data were collected on encased fruit species, the sites were cleaned, so that no encased fruits or hammers remained up to 20 cm from the anvil. When cracked encased fruits were found at inactive cracking sites, they also were removed using the same procedure. The cleaning of cracking sites, which began during the final preliminary excursion (December 2008) prior to the study, enabled us to record the continuous visits by capuchins to these areas and resulted in a record of monthly cracking site use.

Record of Consumed Encased Fruit Weight and Calculus of Energetic Payoff

All GPS points of active sites were collected for analyses of the frequency of tool use. However, given the large number of active sites, we recorded the masses of broken encased fruits sequentially once every ten active sites (i.e., only the encased fruits at the 10th, 20th, 30th site, and so on). All encased fruits within 20 cm of the anvil were collected and weighed with a balance accurate to 1 g (ER2856st model). At mixed sites with more than one encased fruit type, each type was weighed and recorded separately.

Encased fruits of *S. cearensis* differed according to the state of moisture (average weight of an encased fruit unit = 7 g dry, damp = 9 g, and wet = 15 g). We converted wet weight to dry weight for all analyses according to the formula 1 in Table II. For the encased fruits of *M. dichotoma* this type of adjustment was not necessary since moisture did not affect the mass.

Analyses of energy gains, foraging costs, and dietary payoffs are not easy to conduct [Felton et al., 2009]. For this study we calculated mean monthly values of indices measured and gross normalizations in order to tackle the question of the costs and benefits of tool use. These analyses should be considered preliminary estimates.

As we measured the weight of shells at a tool-use site, we calculated monthly energetic gain through tool use by: (i) converting shell weight to kernel weight (formula 2 in Table II); (ii) defining the caloric value per gram of kernel for each encased fruit species based on chemical composition described in literature (formula 3); (iii) multiplying the caloric value per gram by the monthly kernel weight, multiplied by 10, since we measured one of every ten tool-use sites (formula 4).

The cost of tool use was inferred based on the equation presented by Liu et al. [2009, Table III], in which the work to lift a stone is described as the potential energy at maximum height ($\tau = mgh$, where m = stone mass, g = acceleration of gravity, and h = maximum height that stone was lifted—calculated by authors as 35 cm). Liu et al. [2009] detected that capuchins employ force during the downward movement of approximately equal value as the upward movement. Therefore, the total cost of using a stone to crack open an encased fruit includes the energy in upward and downward movements with half of the energy spent during lift, and the other half spent pushing the stone against the nut during the downward phase (see Table III in Liu et al. [2009]).

We calculated the monthly costs of tool use for these two groups by (i) estimating the number of broken encased fruits based on the weight of shells per month (formula 5, Table II); (ii) employing Liu et al. [2009] formula multiplied by the number of broken encased fruits by month, multiplied by 2 (work lift and work push down), multiplied by 10 (since only one out of ten sites were measured). As Work is defined in Joules we converted results in calories by 1 cal = 4.184 j (formula 6, Table II).

The energetic payoff of tool-use behavior can be seen as the difference between energetic gains and costs of tool use (formula 7, Table II). Mean monthly energetic payoff per individual was inferred assuming a group size of 20 individuals, regardless of season (formula 8, Table II). The mean group size of 20 individuals was based on previous observations

TABLE II. Formulas Used to Calculate Energetic Gains, Costs, and Payoffs

Description	Formula	Variables	Unit of equation
(1) Dry shell weight (Dsw)	Dsw = Wet shell weight × *moisture index*	Moisture indexes *M. dichotoma* = 1; *S. cearensis* dry shell = 1, damp shell = 0.777; wet shell = 0.466	g
(2) Kernel weight (Kw)	Kw = Dsw × Kernel index	Kernel indexes *M. dichotoma* = 1 g·shell^{-1}; *S. cearensis* = 0.714 g·shell^{-1}	g
(3) Calorific value (Cv)	$Cv = \frac{4 \times [\%Protein + \%Carbohydrate + 9(\%Lipids)]}{100}$	Cv for *M. dichotoma* = 2.506 and for *S. cearensis* = 5.273	cal·g^{-1}
(4) Energetic gain (EG)	EG = 10 × Cv × Kw		cal
(5) No. of broken seeds (NBs)	NBs = Dsw × Shell index	Shell's index for *M. dichotoma* = 6 μ·g^{-1} and *S. cearensis* = 0.142 μ·g^{-1}	Units
(6) Energetic cost (Ec)	$Ec = \frac{2 \times (Hw \times NBs \times G \times H) \times 10}{Cjc}$	Hammer weight (Hw) for *M. dichotoma* = 0.089 Kg; for *S. cearensis* = 0.612 Kg Gravity acceleration (G) = 9.8 m × s^{-2} H = height of stone lifting (arbitrarily defined as 0.2 m). Conversion joule calories (Cjc) = 4.184	cal
(7) Energetic payoff (EPF)	EPF = EG−Ec		cal
(8) Energetic payoff per individual (EPF/Id)	EPF/Id = EPF/N#Id	No. of individuals in each group (N#Id) = 20	cal·id^{-1}

Notes
(1) *M. dichotoma* dry shell = wet shell = 0.16g. Manihot shells are impermeable, dry and wet shells weight the same. *S. cearensis* dry shell = 7g; damp shell = 9g; wet shell = 15g.
(2) *M.dichotoma* shell = 0,16g; kernel = 0.16g dry weight. *S cearensis* shell = 7g; kernel = 5g, dry weight. For manihot, three unbroken encased fruits weight 1g, from which half is weight of shells and other half is weight of kernel.
(3) Since we could not find the Calorific value (Cv) data for *M dichotoma*, we used the mean Cv of *M. glaziovii* (3.03), *M. spseudoglaziovii* (2.453), and *M. paiuhensis* (2.035), see Martins et al. [2007, Table I, page 635]. Similarly, we assumed that Cv of *S. cearensis* is the same of *S. coronata*, see Crepaldi et al. [2001, Table I, page 156].
(5) *M. dichotoma* 1 g of dry shell = 6 encased fruits. *S. cearensis*: 7 g of dry shell = 1 unit.
(6) Hammer weight data are Emidio and Ferreira (personal observation). This formula is based on the equation of Liu et al. [2009].

of capuchin groups in these areas [Ferreira et al., 2009].

Data Analyses

The values of the dependent variables (number of active tool-use sites, broken encased fruit mass) for each parcel were clustered in monthly unique values. We discarded values on parcels that had no trees producing encased fruits, resulting in 10 monthly samples at the drier os-caatinga (February, April–December 2009) and 11 samples at the wetter sa-caatinga (February–December 2009). The data showed a normal distribution according to Kolmogorov–Smirnov test ($N > 10$, $D > 0.21$, and $P > 0.20$), so parametric tests were applied. Student's t-tests were used to compare areas and seasons. We used Statistica 8, Copyright© StatSoft for data analyses, and the significance level was set at $\alpha \leq 0.05$. This research adhered to the American Society of

Primatologists' principles for the ethical treatment of primates, and complied with the Laws of Brazil that govern animal research.

RESULTS
Overview

We recorded a total of 2,212 active tool-use sites in the drier os-caatinga and 558 sites in the wetter sa-caatinga. This resulted in a mean value of 59 active sites at the os-caatinga during wet periods (or 4.78 active sites/ha), 329 active sites at the os-caatinga during dry periods (or 26.7 active sites/ha), and approximately 70 active tool-use sites per month at the sa-caatinga in either period (or 3.5 active sites/ha—see also Table IV).

In the drier os-caatinga area, all tool-use sites contained manihot broken encased fruits, whereas in the wetter sa-caatinga area, 75% of active sites contained encased fruits of *S. cearensis*, 16% of *M.*

TABLE III. Statistical Results of Seasonal and Habitat Comparisons of the Two Indices Measured: (a) Total Frequency of Active Tool-Use Sites; (b) Total Weight of Encased Fruit

Hypothesis	Dependent variable	N (Number of months)	T	P
Between areas—overall				
N_1 = os-caatinga	Total number of active sites	10,11	2.62	<0.05
N_2 = sa-caatinga	Total mass consumed (g)	10,11	−2.5	<0.05
Between areas—wet season				
N_1 = os-caatinga	Total number of active sites	4,5	0.2	0.85
N_2 = sa-caatinga	Total mass consumed (g)	4,5	−2.01	0.11
Between areas—dry season				
N_1 = os-caatinga	Total number of active sites	6,6	3.5	<0.05
N_2 = sa-caatinga	Total mass consumed (g)	6,6	−1.63	0.13
Season within open-shrub caatinga				
N_1 = wet period	Total number of active sites	4,6	−2.63	0.08
N_2 = dry period	Total mass consumed (g)	4,6	−3.88	<0.05
Season within shrub-arboreal caatinga				
N_1 = wet period	Total number of active sites	5,6	0.2	0.85
N_2 = dry period	Total mass consumed (g)	5,6	0.44	0.67
Cultivar × non-cultivar period	Total number of active sites	7,4	0.3	0.78
	Total mass consumed (g)	7,4	0.58	0.6

dichotoma, 1% of *Diclea grandiflora*, and 8% were mixed tool-use sites.

Comparison Between Areas and Seasons

Our phenological analyses indicate that rainfall affects the availability of native fleshy fruits which are the presumed preferred foods for capuchins in this area (assuming capuchins are primarily frugivorous). Conversely, Syagrus sp and Manihot sp trees produce encased fruits regularly throughout the year (see Fig. 2).

The number of active tool-use sites was higher at the drier os-caatinga, while overall monthly mass consumed was higher at the wetter sa-caatinga (Fig. 3 a x a'; b x b'). Analyses by season showed that this difference between areas exists only during drier periods. During wetter periods there were no significant differences between these two areas regarding these two indices (Table III, Fig. 3).

In comparing between seasons within each area, we found no seasonal variation in the two indices at the wetter sa-caatinga. At the drier os-caatinga,
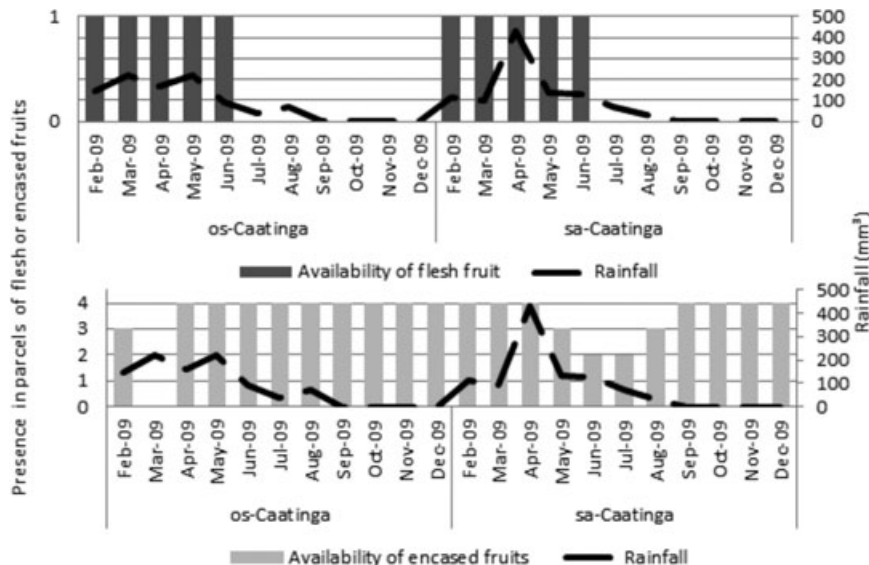

Fig. 2. Presence or absence of fructifying trees at each parcel per month, and its relation to rainfall, at open-shrub caatinga and at shrub-arboreal caatinga. *These data are presented on a binary scale (i.e., presence or absence of flesh fruits or encased fruits at trees, in each parcel). Zero values indicate that none of the trees at any of the four sampled parcel contained fruits that month. For fleshy fruits, only one parcel had fleshy fruit trees (since we purposefully placed our parcels in areas associated with clusters of *Syagrus* and *Maninhot*). For encased fruits, values range from 0 to 4, since all parcels contained encased fruit producing tress.

TABLE IV. Mean Monthly Values of the Number of Active Tool-Use Sites, Mass Consumed, Energetic Gain, Energetic Cost, and Energetic Payoff Inferred for Capuchins Groups in the Two Study Areas: Open-Shrub Caatinga (Jucurutu) and Shrub-Arboreal Caatinga (Luis Gomes) During Wet and Dry Seasons

	os-Caatinga				sa-Caatinga											
	Dry season (N = 6)		Wet season (N = 4)		Dry season (N = 6)						Wet season (N = 5)					
	Manihot		*Manihot*		*Manihot*		*Syagrus*		*Manihot + Syagrus*		*Manihot*		*Syagrus*		*Manihot + Syagrus*	
Area/season/species	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Active tool-use site	329	191	59	42	30	-	41	25	66	50	6	-	63	43	67	46
Dry weight (g)	193	111	13	11	4	-	436	165	438	166	1	-	624	527	624	527
Kernel weight (g)	193	111	13	11	4	-	311	118	313	119	1	-	446	376	446	378
Energetic gain (cal)	4,836	2,803	338	284	100	-	16,430	6,238	16,470	6,255	25	-	23,518	1,984	23,524	19,852
Energetic gain per individual (cal)	241	140	16	14	5	-	821	311	823	312	1	-	1,175	992	1,176	992
Number of broken encased fruits (unit)	1158	671	81	68	24	-	61	23	71	30	6	-	88	74	90	77
Energetic cost (cal)	966	560	67	56	20	-	355	135	363	139	5	-	509	429	510	432
Energetic cost per individual (cal)	48	28	3	2	1	-	17	6	18	6	0	-	25	21	25	21
Energetic payoff (cal)	3,870	2,243	270	227	80	-	16,074	6,103.08	16,106	6,117	20	-	23,009	1,9411	23,014	1,942
Energetic payoff per individual (cal)	193	112	13	11	4	-	803	305	805	306	1	-	1,150	970	1,150	971

. There is no standard deviation for the mean value of *Manihot* at sa-caatinga because its consumption was observed during only two months during the dry season and in one parcel during one month in the wet season.
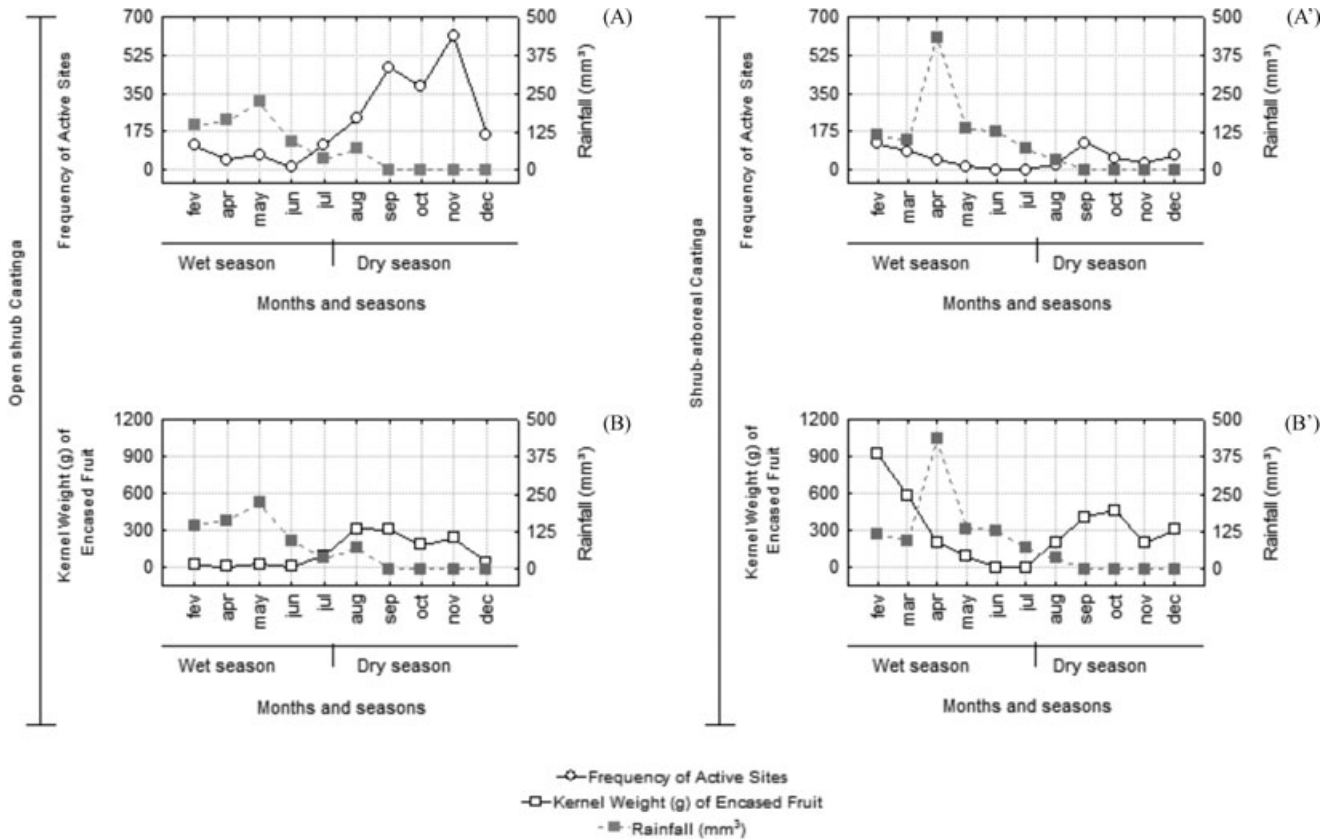. We did not use the values for consumption of *Diclea grandiflora* since the amounts were negligible.

Fig. 3. Measures of the two indices across months in the following order: (a) number of active sites; (b) total mass consumed. Left side displays os-caatinga and right side displays sa-caatinga.

total mass consumed was higher and the number of active tool-use sites was significantly higher during drier periods (Table III and Fig. 3).

In the wetter sa-caatinga, we tested whether the availability of crops (mango, corn, and cashew) influenced tool-use behavior in terms of mean monthly mass of kernels consumed or number of active tool sites. Neither of the two indices were significantly different for months with and without crops (Table III).

Energetic Gains, Costs, and Payoffs of Tool Use

Table IV presents the inferred values of energetic gains, costs, and payoffs of tool-use behavior in each area per season. The inferred mean energetic gain per month within sampled parcels was lower at the drier os-caatinga than the wetter sa-caatinga, ranging from a total of 338 to 4,836 cal per month at drier os-caatinga, and from a total of 16,470 to 23,524 cal per month at wet sa-caatinga. These values are lower if we divide the mean total by an assumed number of 20 individuals per group: from 16 to 241 cal·ind^{-1}·month^{-1} at drier os-caatinga, and from 823 to 1,176 cal·ind^{-1}·month^{-1} at wetter sa-caatinga.

The cost of tool use was relatively low at both sites due to the light weight of the stones used [Ferreira et al., 2010]. The costs of tool use ranged from a mean of 67 to 966 cal per month at dry os-caatinga, and from 363 to 510 cal per month at wet sa-caatinga, or from 3 to 48 cal·ind^{-1}·month^{-1} at dry os-caatinga, and from 18 to 25 cal·ind^{-1}·month^{-1} at wet sa-caatinga. Consequently, the energetic payoff of tool use ranged from 13 to 193 cal·ind^{-1}·month^{-1} at dry os-caatinga and from 805 to 1150 cal·ind^{-1}·month^{-1} at wet sa-caatinga.

DISCUSSION

In this study, we examined predictions concerning tool use in wild capuchins derived from the Energetic Bottleneck and Opportunity hypotheses. Our primary data used to test these hypotheses were based on the number of tool-use sites and weight of encased fruit shells broken by capuchins at two caatinga areas. The density of active tool-use sites at our wetter shrub-arboreal caatinga biome was higher than that described by Visalberghi et al. [2007]: 4.78–26.5 active sites·ha^{-1} versus 1.82 ± 0.82 active sites·ha^{-1} at FBV—an area of ecotone between cerrado and caatinga inhabited by *S. libidinosus*. The density of active tool-use sites in the dry

os-caatinga was 13 times greater than that described at FBV. Although this indicates that capuchins at these caatinga areas frequently use tools, a simple count of the number of tool-use sites is not a reliable indicator of more frequent tool using behavior since capuchins at FBV repeatedly use the same tool-use sites due to the scarcity of appropriate hammers. Canale et al. [2009] describes similar total values (over 2,000 sites mapped) across an area of *S. xanthosternos* occurrence; however, as their sites were not previously cleaned, we do not know how long it took for the *S. xanthosternos* to accumulate these tool-use sites.

Our phenological analyses indicated that trees produce fleshy fruits only during the rainy period (February–June 2010), while trees produce encased fruits regularly throughout the year. Thus, capuchins have the opportunity to crack open encased fruits during all months, but may have a greater need to do so during dry periods. We counted twice as many active tool-use sites in the drier area and, assuming that capuchin group size did not differ between seasons, there was a fivefold increase in the intensity of tool use during dry periods in the dry os-caatinga. This offers support for the energetic bottleneck model, which predicts increased consumption of encased fruits during periods and areas of low resource availability. However, we found no evidence of seasonal variation in tool use frequency in the wetter sa-caatinga. In addition, the rate of tool use and the mass of cracked encased fruit consumed remained constant at sa-caatinga regardless of cultivated crop availability. Thus, data from sa-caatinga offer support to the Opportunity Hypothesis. Taken together, it appears that capuchins opportunistically made use of tools to crack open encased fruits throughout the year, but increased the frequency of such behavior during periods of low food availability, or times of the year of presumed energetic bottlenecks.

Despite the higher use of stone tools by capuchins at the os-caatinga, the total mass consumed from cracked encased fruit was higher in the wetter sa-caatinga (the area with greater abundance of fresh fruits and cultivars). This difference is likely due to the type of encased fruit cracked in each area: small manihot at os-caatinga and medium sized syagrus at sa-caatinga. This means that encased fruit contributes more to the energetic intake of capuchins at the wetter sa-caatinga area than at the dry os-caatinga area, and this contribution was not related to periods of low food availability in the wetter sa-caatinga.

Our analyses reveal that the monthly caloric input obtained from encased fruit accessed with the help of stones is small, from 16 to 241 cal·ind^{-1}·month^{-1} at the drier os-caatinga and from 823 to 1,175 cal·ind^{-1}·month^{-1} at the wetter sa-caatinga. Considering that the daily energetic costs of an adult capuchin are estimated to be approximately 311 cal [Janson 1988], these daily caloric gains are not sufficient to support a capuchin for an entire day at the dry os-caatinga site, although these foods may supply energy for 3–4 days in the wetter sa-caatinga under conditions in which encased fruit is intensively consumed over a short period (and not equally over the month).

The inferred cost of tool use was very low: from 3 to 48 cal·ind^{-1}·month^{-1} at the dry os-caatinga site and from 18 to 25 cal·ind^{-1}·month^{-1} at the wet sa-caatinga site. This low cost is due to the relatively lightweight of stones used. Emidio and Ferreira [submitted] report that the median weight of stones was 46 g at os-caatinga and 429 g at sa-caatinga. The stones at our study areas are lighter than those at the FBV ecotone caatinga-cerrado (ca. 1 kg) where Fragaszy et al. [2004] conducted their studies, and are more similar to stone weight (mean = 150 g) reported by Moura [2004].

It is important to note, though, that both the energetic gains and costs of tool use inferred here are general approximations. First, although the caloric gains per gram are likely to be fairly accurate (based on data of Martins et al. [2007] and Crepaldi et al. [2001]), we used a very restricted definition of active tool-use sites: we marked only those sites where both hammer and encased fruits were found on top of anvils. We did not sample sites with anvils and encased fruit but not hammers, nor sites with anvils and hammers but not encased fruit on top of anvil stones, even though encased fruits were scattered around the anvil. Second, these caloric gains were inferred considering only the area of sampled parcels, and we selected parcels purposefully around clusters of nut producing trees. Thus, this might have inflated the energetic gains. However, our sites did include dispersed nut producing trees with a confirmed presence of tool-use sites. Third, costs were inferred assuming 20 cm as the maximum height that stones were lifted, and these costs refer to one strike per stone/encased fruit. It is reasonable to assume that capuchins will make multiple strikes before cracking a nut, however small the nut is. Fourth, individual gains and costs were inferred considering a mean group size of 20 individuals throughout the year, although it is known that adults perform most of the tool use and on average 50% of individuals in groups are adults/sub-adults [Moura, 2004; Mannu & Ottoni, 2001; Verderane, 2010]. And finally, the year we collected data had higher than average rainfall. It is possible that consumption of encased fruit was diminished due to higher availability of fleshy fruits. Therefore, both the energetic gains and energetic costs of tool use may be higher than the conservative estimates calculated here.

Notwithstanding the above caveats, based on a purely energetic analysis our data do not support the hypothesis that embedded encased fruit

represent key energetic resources to capuchins inhabiting caatinga habitats. It is reasonable to suggest that for these capuchins any caloric gain results in a benefit, and that in the absence of greater floristic diversity and increased opportunity to forage on the ground (as is observed in caatinga), tool use behavior may provide foraging advantages (therefore, favoring the "opportunity" hypothesis).

A second possibility is that encased fruits are important due to their nutritional content. Altmann [2009] suggests that fallback foods can be essential to primates when these foods contain special nutrients, such as vitamin C that is not synthesized by haplorhines. The kernel of *Syagrus* contains 6.36 mg·g^{-1} of vitamin C, and 26.1 ± 0.7 µg·g^{-1} of β-carotenes [each fruit weights a mean of 4.26 g—Crepaldi et al., 2001, Table I]. Similarly, the encased fruit of *Manihot esculenta* contain 26.1% protein and 3.6 mg·g^{-1} of vitamin C [Nartey & Møller 1976]. According to the National Research Council of the National Academies [2003], the daily requirement of β-carotene for non-human primates is 625 µg. Therefore, the consumption of six *S. cearensis* fruits (each fruit weights a mean of 4.26 g per fruit—[Crepaldi et al., 2001]) would equal the daily requirements of capuchins. Nutritional requirements of vitamin C by primates are still imprecisely described; if we take *Callithrix jacchus* as a model [based on National Research Council of the National Academies, 2003], and isometrically regress the requirement to the body weight of capuchins, we obtain a daily requirement of 4.4 mg·g^{-1} of vitamin C. If this is the case, an individual capuchin would need to consume 1.22 g·day^{-1} of *M. dichotoma* encased fruit or 1.0 g·day^{-1} of *S. cearensis* to supply its requirements. In addition, these encased fruits contain larvae of *Tenebrio molitor*, each weighing about 3–4 g, yielding 2.78 cal·g^{-1}, 18% protein [based on National Research Council of the National Academies, 2003]. The possibility that capuchins forage on these nuts to consume the larvae was proposed by Rocha et al. [1998] observing *S. nigritus* at Parque Municipal Arthur Thomas, in southern Brazil. In this case, capuchin tool use would provide an important nutritional reward (protein) and these encased fruits would be best described as a high quality resource and not as a fallback food.

In summary, data on the frequency of tool use by area and by season offer some support for the energetic bottleneck model. However, although we agree with Lee and Moura's [2005, p 951] statement that "First principles suggest that the foraging strategy is a consequence of what is available in the habitat rather than a secondary consequence of changing substrate or mode of locomotion," our estimates of energetic gain indicate that encased fruits are not key energetic resources for the capuchis studied here, and point toward the opportunistic consumption of encased fruit. Finally, analyses of chemical compounds point toward the importance of these encased fruits in supplying specific micronutritional requirements for capuchins.

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