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RESEARCH ARTICLE

Physical Properties of Palm Fruits Processed With Tools by Wild Bearded Capuchins (*Cebus libidinosus*)

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Habitually, capuchin monkeys access encased hard foods by using their canines and premolars and/or by pounding the food on hard surfaces. Instead, the wild bearded capuchins (*Cebus libidinosus*) of Boa Vista (Brazil) routinely crack palm fruits with tools. We measured size, weight, structure, and peak-force-at-failure of the four palm fruit species most frequently processed with tools by wild capuchin monkeys living in Boa Vista. Moreover, for each nut species we identify whether peak-force-at-failure was consistently associated with greater weight/volume, endocarp thickness, and structural complexity. The goals of this study were (a) to investigate whether these palm fruits are difficult, or impossible, to access other than with tools and (b) to collect data on the physical properties of palm fruits that are comparable to those available for the nuts cracked open with tools by wild chimpanzees. Results showed that the four nut species differ in terms of peak-force-at-failure and that peak-force-at-failure is positively associated with greater weight (and consequently volume) and apparently with structural complexity (i.e. more kernels and thus more partitions); finally for three out of four nut species shell thickness is also positively associated with greater volume. The finding that the nuts exploited by capuchins with tools have very high resistance values support the idea that tool use is indeed mandatory to crack them open. Finally, the peak-force-at-failure of the piassava nuts is similar to that reported for the very tough panda nuts cracked open by wild chimpanzees; this highlights the ecological importance of tool use for exploiting high resistance foods in this capuchin species. Am. J. Primatol. 70:884–891, 2008. © 2008 Wiley-Liss, Inc.

Key words: peak-force-at-failure; *Attalea* sp.; *Astrocarium* sp.; *Orbignya* sp.

INTRODUCTION

Tufted capuchins (*Cebus apella*) exhibit craniofacial features and a broad face associated with powerful masticatory muscles that anteriorly can produce and dissipate high masticatory forces [Wright, 2005]; they also have great postcanine occlusal areas, large premolars and square molar teeth with thick enamel and with low cusps that allow cracking tough plant material and nuts [Anapol & Lee, 1994; Kay, 1981]. Habitually, these monkeys access encased foods (nuts, mollusks, etc.) by using their canines and premolars and/or by pounding the food on hard surfaces [Boinski et al., 2001, 2003; Izawa, 1979; Terborgh, 1983]. Furthermore, white-fronted capuchins (*C. albifrons*), which are unable to crack open intact *Astrocaryum* palm nuts with their masticatory system, select and crack nuts that had been infested by bruchid beetles and still contain undamaged endosperm inside [Terborgh, 1983]. In contrast, the wild bearded capuchins (*C. libidinosus*) of Boa Vista (Piauí, Brazil) instead of relying on these latter techniques, routinely crack nuts of several palm species with stone hammers on stone, or wooden anvils [Fragaszy et al., 2004; Visalberghi et al., 2007; see Fig. 1]. Tool use allows access food not available otherwise [Beck, 1980]; in the case of these capuchins it can be argued that the palm fruits are impossible or difficult to open other than with tools.

Nut cracking is an integrated dynamic system with biomechanical and morphological components related to the monkeys' postcranial morphology and

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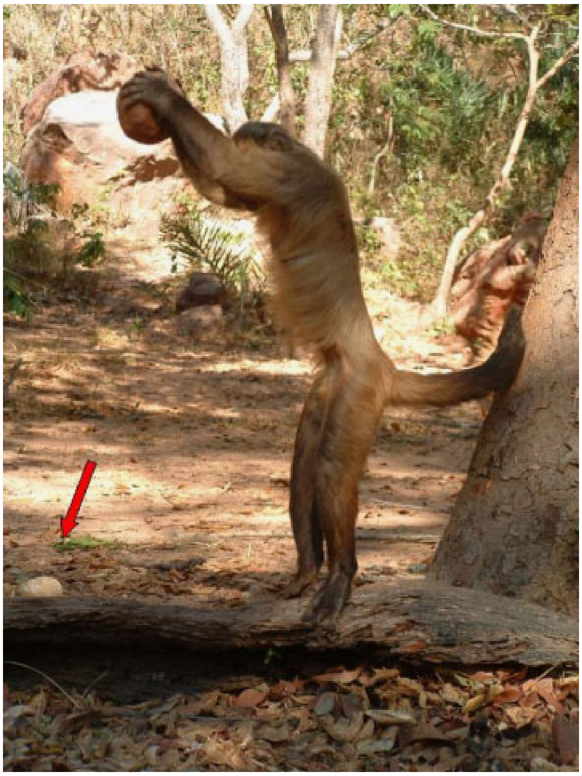

Fig. 1. A male capuchin monkey weighing 3,540 g uses a stone hammer weighing 1,440 g to crack a piassava nut and a wooden anvil. The stone is held with both hands in a bipedal stance. The nut is indicated by the arrow (Photo by Elisabetta Visalberghi).

to environmental components, such as mass and material of the hammer stones (and of the anvil site) and the material and physical properties of the nut. This phenomenon has been approached from a biomechanical and morphological perspective in wild and captive chimpanzees [Foucart et al., 2005; Günther & Boesch, 1993] and very recently in wild capuchin monkeys.

In a study by Liu et al. [submitted] wild capuchins used stones weighing 1.46 kg to crack palm nuts, corresponding to 33–77% of the monkey's body weight. Pickering [2007] has recently shown that to crack open one palm nut the most proficient capuchin male required on average 6.7 strikes and the least proficient one 75.7 strikes, and an adult male (weighing 70 kg) required 6.2 strikes. The phenomenon of nut cracking also has been approached by investigating the characteristics of the hammer stones used by the wild capuchins and providing a petrographic description of them [Visalberghi et al., 2007]. This study suggests that in Boa Vista the hammers suited, in terms of material and weight, to crack nuts are rare and that capuchins transport them to the anvils sites; in fact, episodes of transport ranging from a few meters to more than 50 m have been repeatedly observed [Spagnoletti, unpublished data]. Kiltie [1982] examined the resistance to cracking of several palm nut species eaten by rain forest peccaries (*Tayassu tajacu* and *T. pecari*), but his study did not include those cracked open by capuchins, for which no information is yet available. This information is critical to appreciate fully the environmental components of nut cracking and the constraints imposed on this activity.

Nuts' resistance to cracking constrains tool choices in chimpanzees (*Pan troglodytes verus*) [Boesch & Boesch-Achermann, 2000]: an effective hammer and an effective anvil must each exceed the cracked fruit in their ability to withstand deformation and possibly crack propagation. The nuts (*Panda oleosa*, *Parinari excelsa*, and *Coula edulis*) cracked open by the Taï chimpanzees and elsewhere [Joulian, 1995] differ greatly in terms of impact strength (average breaking impulse) and in terms of compression strength (average peak-force-at-failure) [Boesch & Boesch, 1983; Peters, 1987]. This means that the energy expended to crack the different species of nuts also varies accordingly and this affects the net energy gained (which in turns depends on the number of calories gleaned from the encased endosperm). According to Günther and Boesch [1993] the energy gained from nut cracking by chimpanzees exceeds by 9 to 1 energy expended in transporting nuts and hammers, and cracking, and eating the nut.

In this pilot study, we examined the four nut species most frequently cracked open with tools by wild capuchin monkeys. In particular, we characterized them in terms of size and weight of the nut and of the inner kernel(s), structure of the nut (e.g. number of kernels and shell thickness), and we assessed the nuts' peak-force-at-failure. Our goals were to establish whether the four nut species differ in terms of peak-force-at-failure and to describe the relationship between nut weight/size and peak-force-at-failure. Our hypothesis is that tool use allows capuchins to exploit nuts impossible to crack open otherwise, as suggested by Visalberghi et al. [2007]. We also aimed to compare resistance of various nut species, given that the monkeys can choose among two or more species across the year.

MATERIALS AND METHODS

Our site is located at Fazenda Boa Vista and adjacent lands (hereafter, Boa Vista) in the southern Parnaíba Basin (9°39′S, 45°25′W) in Piauí, Brazil. Boa Vista is a flat open woodland (altitude 420 m asl) punctuated by sandstone ridges, pinnacles, and mesas rising steeply to 20–100 m above it. The flat areas are open woodland; the ridges are more heavily wooded. Palms are abundant in the open woodland; the habit of the palms in this region is to produce fruit at ground level (see Fig. 2a). The nuts most commonly

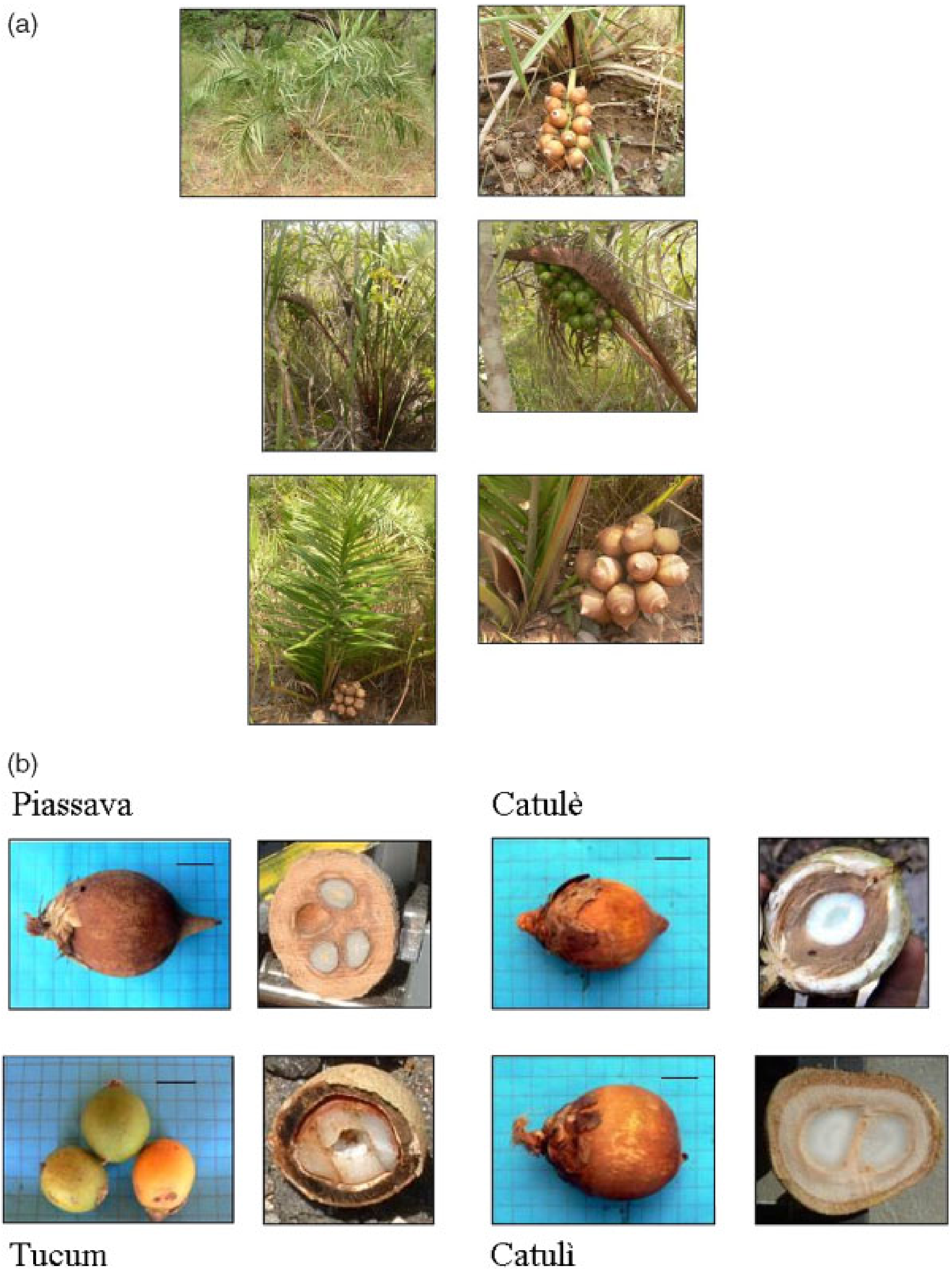

Fig. 2. (**a**) Palms and a close up of their cluster of nuts: piassava (upper photos), tucum (central photos), and catulí (lower photos); (**b**) whole fruit and cross section for each palm nut species. The black line indicates 2 cm. The sections are not from the corresponding whole fruit and are not in scale (Photos of the EthoCebus project).

eaten by capuchins at Boa Vista are: tucum (*Astrocarpum campestre*), catulè (*Attalea barreirensis*), piassava (*Orbignya* sp.), and catulí (*Attalea* sp.). For the latter three fruits the identification of the plant at the species level is still uncertain.

Typically, the capuchins of Boa Vista collect the palm nuts by plucking one nut from the cluster and by pulling and turning it until it comes loose. The mesocarp of catulè, catulí, and piassava (but not of tucum) is thick. Capuchins usually eat the mesocarp until the woody endocarp of the nut is exposed. At this point, they can either immediately look for an anvil site to crack the nut with a hammer, or leave the nut on the ground. In the latter case, the nut may be recovered over the course of days, weeks, or months and then cracked open with a hammer.

The nuts were collected for mechanical analysis by removing them from the clusters of palm trees present in the Boa Vista area (Piauí, Brazil). Collection occurred when the nuts appeared ready to be cracked open and eaten by capuchins; on the basis of our repeated experience with capuchins' behavior we know that at this stage nuts have a brownish color and are easier to twist off. Only nuts that lacked cracks and evidence of beetle infestation were collected. The nuts we collected were tested 2 weeks–3 months after collection. We tested 18 catulè nuts, 35 piassava nuts, 20 catulí nuts, and 12 tucum nuts. Figure 2b shows the woody endocarp and the endosperm of the four species considered. If present, the exocarp and mesocarp (i.e. the external soft part of the nut) were removed before weighing and measuring the nut.

Peak-force-at-failure was measured using a universal tester (TONI COMP III). The tests were carried out at the Associação Brasileira de Cimento Portland (ABCP), São Paulo (Brazil) in November 2006 and July 2007. This machine is normally used to test the compressive strength of concrete. The nut was positioned on the lower metal plate of the apparatus inside a ring of Plasticine® (Acrilex, São Bernardo do Campo, SP, Brazil) (see Fig. 3). For stability, nuts were positioned with the flat side (if there was one flat side) on the metal plate. The load cylinder compressed the nut at a rate of 0.48 kN/s (the machine setup at ABCP). Compression stops when the force abruptly drops, ideally when the first crack(s) are initiated in the shell. The force at failure is stated in kNewton ($1\text{N} = 1\,\text{kg}\,\text{m/s}^2$).

Before testing compressive strength, we took the following measures. Each nut was numbered, weighed in a Mettler Toledo PZ 7001-F professional scale (range: 0.1–7,100 g; precision 0.1 g; Greifensee, Switzerland) and in a Sartorius 1265 MP professional scale (range: 0.001–400 g; precision 0.001 g; Goettingen, Germany). As illustrated in Figure 4, length (l) and diameter (d, for nuts with circular equatorial section) or diameters (d^1 and d^2, for nuts with elliptical equatorial section) were measured by means of a Mitutoyo 500-144B caliper (range 0.01–150 mm; São Paulo, Brazil). After the nuts were cracked open, the weight of the kernel(s) was taken and the thickness of the shell was assessed in its mid position, i.e. as close as possible to its measured diameter. In addition, we counted the number of kernel(s) inside each nut and whether the nut was parasitized (presence of larvae inside the kernel). We estimated the volume of each nut with the following formula for ellipsoids: $\text{volume} = 4/3\pi d^1 d^2 l$ (where $d^1 d^2$ are the diameters and l is length).

The research reported in this manuscript has met the appropriate national and institutional guidelines for collecting data in Brazil. All research reported in this manuscript adhered to the Brazilian legal requirements. All research reported in this manuscript adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

Data Analyses

As data were normally distributed, parametric analyses were carried out. A one-way analysis of variance (ANOVA) was performed to assess whether the resistance of the four species of nuts differed, and post hoc comparisons were carried out with the Tukey HSD test for unequal N. A separate one-way ANOVA was carried out to compare average peak-force-at-failure for larvae infested and nonlarvae infested fruits (this analysis was carried out only for piassava, the only species in which parasites were present).

Pearson's correlations were used to assess the relationship between resistance and weight, between resistance and shell thickness, and between resistance and number of kernels (this latter analysis was not carried out for catulí and tucum, the species that possess only one kernel per nut). The relationship between resistance and volume was not performed because volume and weight were strongly positively correlated. Given that for catulè and tucum species we carried out two comparisons, and for catulí and piassava species we carried out three comparisons; according to the Bonferroni correction the α level was set at $P < 0.025$ for the former species and $P < 0.017$ for the latter species.

RESULTS

Table I reports the values of the measures taken for the four species of nuts and the estimated volume. Mean peak-force-at-failure values were 5.15 ($\pm$0.26; range 3.24–6.71) for catulè, 11.50 ($\pm$0.48; range 6.71–17.06) for piassava, 8.19 ($\pm$0.35; range 4.11–11.17) for catulí, and 5.57 ($\pm$0.25; range 4.55–7.00) for tucum. The ANOVA carried out on the peak-force-at-failure of the four species of nuts showed that they differed in terms of resistance to a continuous pressure (F (3, 81) = 48.6, $P < 0.0001$; Fig. 5). The post hoc comparisons between nut species show that tucum did not differ from catulè, whereas all the other comparisons were statistically different (Table II). Piassava was twice as resistant as catulè and tucum, and catulí had an intermediate position between them and piassava.

The average number of kernels present per palm nut was 1 for catulè and tucum, 3 for piassava (min = 2, max = 6), and 1.85 for catulí (min = 1, max = 3; see Table I). Parasites were found in 48.5% of the piassava nuts and were absent in the other species. Peak-force-at-failure did not differ between larvae-infested and noninfested piassava nuts (F (1, 33) = 0.03, $P = 0.87$).

The species differed in terms of weight of the nut (see Table I). In particular, the tucum nuts contained on average 4 g of meat, the piassava one third more (6.3 g), and catulè and catulí twice as much (8 and 8.1 g, respectively).

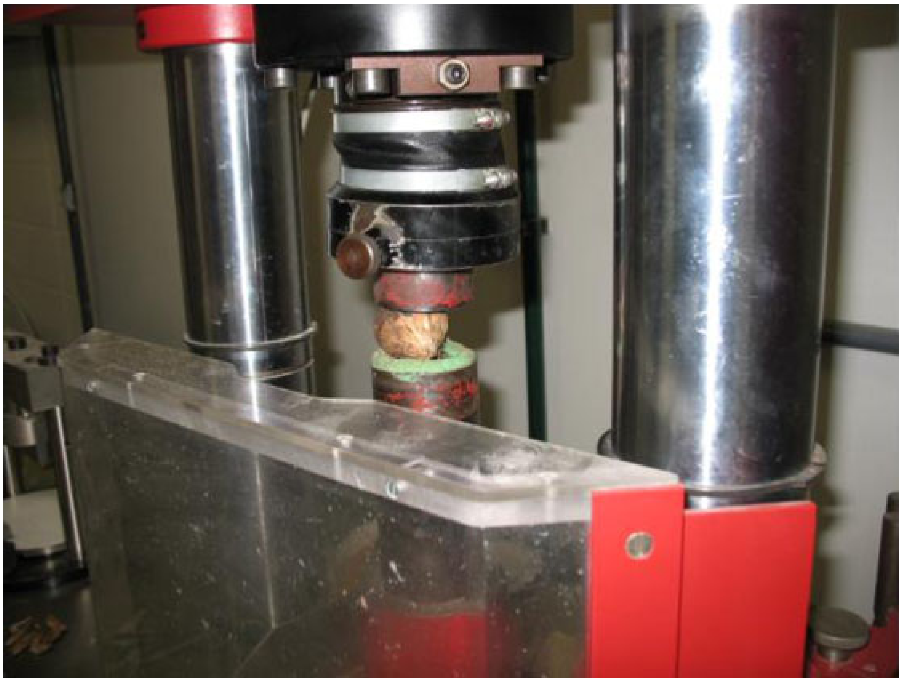

Fig. 3. Universal testing machine used to measure nuts resistance to a continuous pressure. Note the nut (positioned inside a ring of Plasticine® attached to the lower metal plate of the apparatus), which is about to be cracked open.

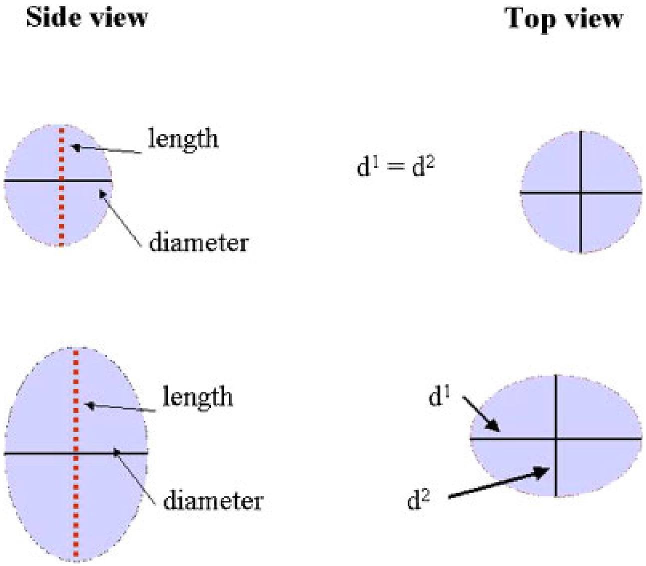

Fig. 4. Illustration of how we measured the nuts. Above: tucum and catulè that are oval, from the side view, and rounded, from the top view. In this case, diameters 1 and 2 are of the same (or almost the same) length. Below: piassava and catulí that are oval both from the side view and from the top view. In this case, diameters 1 and 2 differ. The length is the distance between the point of attachment of the nut to its parent palm tree and its opposite point. The shape of tucum and catulè are rather regular whereas those of the piassava and catulí are more irregular.

Figure 6 shows the bivariate plots of peak-force-at-failure to weight, shell thickness, number of Kernels and of shell thickness to volume. Resistance and weight were significantly positively correlated for catulè ($N = 18$, $r = 0.80$, $P < 0.001$), piassava ($N = 18$, $r = 0.62$, $P < 0.02$), and tucum ($N = 12$, $r = 0.70$, $P < 0.02$); for catulí it was close to significance ($N = 20$, $r = 0.50$, $P = 0.025$). Resistance and shell thickness were also positively correlated for catulè ($N = 18$, $r = 0.60$, $P < 0.01$), but not for piassava, catulí, and tucum (piassava: $N = 18$, $r = 0.55$, $P = 0.02$; catulí: $N = 20$, $r = 0.17$, $P = 0.48$; tucum, $N = 12$, $r = -0.26$, $P = 0.41$). Resistance and number of kernels were significantly positively

TABLE I. Average (±SEM) Peak-Force-at-Failure (Expressed in kNewtons), Diameters, Length, Estimated Volume, Shell Thickness, Weight of the Nut, Number of Kernels, and Weight of the Kernel for Each Species of Nuts

	Peak-force-at-failure (kNewton)	Diam 1 (mm)	Diam 2 (mm)	Length (mm)	Estimated volume (cm^3)	Shell thickness (mm)	Weight (g)	# Kernels	Meat weight (g)
Catulè	5.15	38.89	38.89	49.09	312.74	6.01	32.39	1	8.01
$N = 18$	(±0.26)	(±0.76)	(±0.76)	(±0.63)	(±12.63)	(±0.26)	(±1.38)	(±0)	(±0.21)
Piassava	11.50	40.91	40.60	61.33	339.77	7.66	50.59[a]	3	6.28[a]
$N = 35$	(±0.48)	(±0.72)	(±0.78)	(±0.87)	(±32.11)	(±0.30)	(±2.24)	(±0.18)	(±0.37)
Catulí	8.19	35.25	38.65	50.45	290.92	6.33	36.72	1.85	8.14
$N = 20$	(±0.35)	(±0.72)	(±0.48)	(±1.05)	(±13.00)	(±0.35)	(±1.23)	(±0.13)	(±0.38)
Tucum	5.57	28.33	29.00	46.08	158.91	4.12	15.53	1	4.12
$N = 12$	(±0.25)	(±0.49)	(±0.24)	(±0.41)	(±4.42)	(±0.14)	(±0.39)	(±0)	(±0.11)

[a] Indicates that the average value is based on a smaller sample as the parasitized nuts were excluded; in this case the $N = 18$.

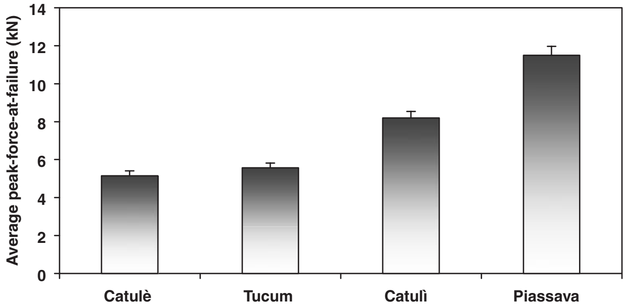

Fig. 5. Average peak-force-at-failure (+SEM) expressed in kN necessary to crack nuts of the four nut species.

correlated for catulí ($N = 20$, $r = 0.56$, $P = 0.01$) but not for piassava ($N = 15$, $r = 0.22$, $P = 0.43$). Finally, whereas in the first three species the thickness and volume were positively correlated (catulè: $N = 18$, $r = 0.64$, $P < 0.01$; piassava: $N = 18$, $r = 0.69$, $P < 0.01$; catulí: $N = 20$, $r = 0.53$, $P < 0.02$), for the tucum nuts it was not ($N = 12$, $r = 0.09$, $P = 0.76$).

DISCUSSION

Our data provide the first objective assessment of the peak-force-at-failure values of the nuts routinely cracked open by wild capuchins in Boa Vista. Resistance of the structure of the nuts differed across nut species and it was positively correlated with weight (and volume). Moreover, for catulè the peak-force-at-failure was positively correlated with shell thickness, whereas this was not true for piassava, catulí, and tucum. As with macadamia nuts (*Macadamia* sp.) [Wang & Mai, 1995], tucum peak-force-at-failure increased with increasing diameter, although shell thickness remained constant at different sizes. Structural complexity (i.e. more kernels and thus more partitions in the fruit) was associated with higher peak force at failure for catulí but not for piassava. The presence of larvae did not affect peak-force-at-failure in the piassava nuts.

TABLE II. Post Hoc Comparisons Between the Nuts

	Catulè	Catulí	Piassava
Catulí	0.0003		
Piassava	0.0001	0.00012	
Tucum	0.9596	0.01368	0.0001

P values are reported for all comparisons.

Chalk et al. [2008] measured the mechanical properties of foods tissues orally processed by *C. libidinosus* at Boa Vista and found that both average toughness and Young's modulus were more than twice those found by Wright [2005] for foods orally processed by *C. apella* and *C. olivaceus* in an evergreen tropical rainforest in Guyana. Although particularly durophageous, the bearded capuchins of Boa Vista did not attempt to crack open the nuts examined in this study with their teeth, or their teeth and hands, but instead used tools. Interestingly, the average Young's modulus of nuts cracked open at Boa Vista appears to be many times higher than that of foods orally processed by capuchins at the same site [Wright et al., 2008]. Therefore, ours as well as Chalk et al.'s and Wright et al's data support the idea that for these primates palm nuts are indeed very difficult to open.

Our methodology allows a straightforward comparison with the data concerning the nuts exploited with tools by capuchins and chimpanzees. When Schrauf et al. [2008] adopted a technique similar to ours to estimate the force necessary to crack nuts usually eaten in Europe and cracked open by captive capuchins they found the following values: 0.37 kN for walnuts (*Juglans regia*), 0.57 kN for Brazil nuts (*Bertholletia excelsa*), and 2.22 kN for macadamia nuts (*M. ternifolia*). Peters [1987] reports the compression force (expressed in kg) required for structural failure for the several African nut species including those exploited by chimpanzees. His values

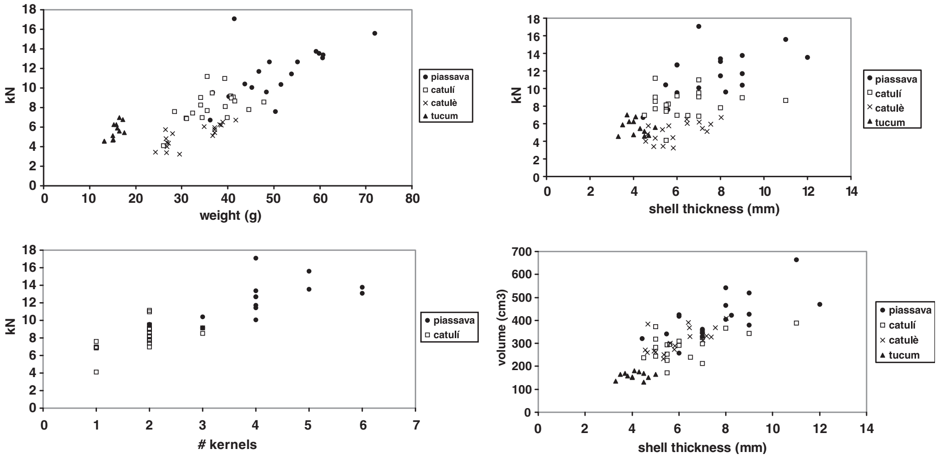

Fig. 6. Bivariate plots illustrating the relationship between peak-force-at-failure and weight (left upper panel), shell thickness (right upper panel), number of kernels (left lower panel), and between volume and shell thickness (right lower panel). The different symbols indicate the four species of nuts.

(transformed by us for sake of comparison in kN) are 2.72 kN for *C. edulis*, 7.98 kN for *P. excelsa*, and vary between 9.57 and 12.22 kN for *P. oleosa*. The mean peak-force-at-failure values of our nut species were 5.15 for catulè, 5.57 for tucum, 8.19 for catulí, and 11.50 for piassava. For example, the maximum peak-force-at-failure for all tested nuts was 13 times that for walnuts (*J. regia*) and between twice (catulè, tucum, catulí) and five times (piassava) that for macadamia nuts. Therefore, relatively high forces are demanded to crack palm nuts exploited by capuchins at Boa Vista. What it is even more interesting is that the small capuchin monkeys [approximately 4 kg, Fragaszy et al., 2004] succeed in opening the piassava nuts that are approximately as resistant as the panda nuts cracked open by chimpanzees [approximately 46 kg, Fleagle, 1999]. The above contrasts provide further strength to the assertion based on biomechanical analyses [Liu et al., submitted] that nut cracking is indeed a strenuous activity for capuchins.

Mammals may not consume large items merely because placing them posteriorly to the molar row would require an intolerable amount of stretch of the adductor muscles [Herring & Herring, 1974; Kiltie, 1982]. The decline of molar surface area from the first to the third molar present in *C. apella* suggests that, contrary to the common assumption that maximum bite force magnitudes increase as the bite point is moved posteriorly, the maximum bite force actually declines moving to the third molar [Spencer, 2003]. All nuts, but tucum, have a diameter of 3–4 cm and our serendipitous observations suggest that capuchins can barely open their mouths wide enough to accommodate nuts of this size on the occlusal surface of their first and second molars, where the bite force is greatest. Future research should test this on the basis of direct measures of the useful space between the upper and lower first and second molars. Therefore, size of the nuts may prompt capuchins to avoid using their teeth, but it cannot explain why they do not pound the nuts directly on hard surfaces. Only very high peak-force-at-failure can account for the lack of direct pounding when bearded capuchins feed on these palm fruits.

The meat content per nut is higher for catulè and catulí, intermediate for piassava, and lower for tucum; therefore, cracking these nuts leads to different amounts of meat. Behavioral and phenological data collected in Boa Vista show that piassava nuts are available seasonally, whereas the other species and especially catulè are available uniformly across the year, and that capuchins crack piassava when the other nut species are available [Spagnoletti et al., unpublished data]. As breaking piassava implies more effort for less meat than is the case for the other nut species, eating piassava should result from a higher encounter rate, and/or it should bring about some special advantage in terms of energy content or micro-elements [Collier & Rovee-Collier, 1981; Krebs & Davies, 1997; Krebs et al., 1981]. In this respect, we found that about half of piassava nuts tested contained grubs of *Coleoptera*, an item highly appreciated by capuchins. Nutritional analyses of the different species of nuts (and of their parasites) and assessments of the distribution of the different palm species with respect to anvil sites are necessary to clarify what parameters affect the monkeys' selection of nuts to crack.

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