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RESEARCH ARTICLE

Factors Affecting Cashew Processing by Wild Bearded Capuchin Monkeys (*Sapajus libidinosus*, Kerr 1792)

ELISABETTA VISALBERGHI[1]*, ALESSANDRO ALBANI[1,2], MARIALBA VENTRICELLI[1], PATRICIA IZAR[3], GABRIELE SCHINO[1], AND DOROTHY FRAGAZSY[4]
[1]*Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, Italy*
[2]*Dipartimento di Scienze, Università degli Studi Roma Tre, Rome, Italy*
[3]*Department of Experimental Psychology, University of São Paolo, São Paolo, Brazil*
[4]*Department of Psychology, University of Georgia, Athens, Georgia*

Cashew nuts are very nutritious but so well defended by caustic chemicals that very few species eat them. We investigated how wild bearded capuchin monkeys (*Sapajus libidinosus*) living at Fazenda Boa Vista (FBV; Piauí, Brazil) process cashew nuts (*Anacardium* spp.) to avoid the caustic chemicals contained in the seed mesocarp. We recorded the behavior of 23 individuals toward fresh (N = 1282) and dry (N = 477) cashew nuts. Adult capuchins used different sets of behaviors to process nuts: rubbing for fresh nuts and tool use for dry nuts. Moreover, adults succeed to open dry nuts both by using teeth and tools. Age and body mass significantly affected success. Signs of discomfort (e.g., chemical burns, drooling) were rare. Young capuchins do not frequently closely observe adults processing cashew nuts, nor eat bits of nut processed by others. Thus, observing the behavior of skillful group members does not seem important for learning how to process cashew nuts, although being together with group members eating cashews is likely to facilitate interest toward nuts and their inclusion into the diet. These findings differ from those obtained when capuchins crack palm nuts, where observations of others cracking nuts and encounters with the artifacts of cracking produced by others are common and support young individuals' persistent practice at cracking. Cashew nut processing by capuchins in FBV appears to differ from that observed in a conspecific population living 320 km apart, where capuchins use tools to open both fresh and dry nuts. Moreover, in the latter population, chemical burns due to cashew caustic compounds appear to be common. The sources of these differences across populations deserve investigation, especially given that social influences on young monkeys learning to open cashew nuts at FBV seem to be nonspecific. Am. J. Primatol. 78:799–815, 2016.

Key words: ***Anacardium* spp.; caustic compounds; age-related ability; social facilitation of eating; tool use**

INTRODUCTION

A food item is worth eating when there is a positive balance between the benefits of eating and the costs of obtaining it. The benefits can be expressed in terms of nutritional value of the food, whereas the costs involve the effort to find the food and process it so as to obtain its edible part. Primates have anatomical, physiological, and behavioral adaptations to overcome the mechanical and chemical challenges of foods [Lambert, 2007].

Capuchin monkeys (genera *Cebus* and *Sapajus*) are omnivorous Neotropical primates that often feed on high quality foods that need to be manipulated and extracted, such as nuts (even if protected by hard shells), invertebrates (including those hidden inside woody substrates), and vertebrates [for a review see Fragaszy et al., 2004a]. The actions of capuchins' feeding repertoire are based on dexterity and physical strength [Fragaszy et al., 2004a]. Both genera are skilled extractive foragers, able to access embedded foods and to overcome plant and animal resistance [Fragaszy et al., 2004a] and extensive laboratory research has been carried out on their grip types, grasping abilities and developmental changes in manipulation [Fragaszy and Adams-Curtis, 1997;

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*Correspondence to: Elisabetta Visalberghi, Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Via Aldrovandi, 16B,00197 Roma (Italy). E-mail: elisabetta.visalberghi@istc.cnr.it

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Spinozzi et al., 2004; Truppa et al., 2016]. Moreover, the masticatory morphology of tufted capuchins (genus *Sapajus*), more robust than in the gracile capuchins (genus *Cebus*), allows the former genus to broaden its dietary niche to include mechanically protected fruits, bromeliads, and other vegetation when fleshy fruit is relatively scarce [Wright, 2005; Wright et al., 2009]. Finally, a few species within the genus *Sapajus* are also habitual tool users in the wild and feed on food items which they could not otherwise obtain [*S. libidinosus*, Canale et al., 2009; De Moraes et al., 2014; Ferreira et al., 2010; Fragaszy et al., 2004b; Mannu and Ottoni, 2009; Mendes et al., 2015; Moura and Lee, 2004; Spagnoletti et al., 2011; Waga et al., 2006; *S. xanthosternos*, Canale et al., 2009; *S. flavius*, Ferreira et al., 2010; Souto et al., 2011].

Complex procedures to process food require practice to develop adult skills that eventually contribute to fitness [Janson and van Schaik, 1993]. White-faced capuchin monkeys (*Cebus capucinus*) become proficient at multi-step extractive foraging techniques following years of practice [Perry and Jiménez, 2012]. White-faced capuchins open *Sloanea terniflora* (a fruit thickly covered with urticating hairs that can be extremely irritating to the eyes and skin) and *Luehea candida* (woody dehiscent pods 5–8 cm long, containing small winged seeds) by performing rubbing, pounding, and fulcrum use (i.e., applying force on an object working against a substrate used as fulcrum) [O'Malley and Fedigan, 2005a; Panger et al., 2002]. These relatively complex behaviors are acquired slowly and age-related differences in feeding competence are evident [O'Malley and Fedigan, 2005a] as well as differences across field sites and individuals [O'Malley and Fedigan, 2005b; Panger et al., 2002]. Juvenile *Sapajus apella* slowly learn to locate and extract invertebrate larvae embedded in bamboo stalks [Gunst et al., 2008, 2010a,b]. Finally, tufted capuchins become able to use stone hammers and stone (or wooden) anvils to open palm nuts after a lot of practice when about 4 years of age or older [Fragaszy et al., 2013; Resende et al., 2008; Spagnoletti et al., 2011].

The cashew tree (*Anacardium* spp.), native to the Northeast of Brazil, produces "double fruits" consisting of an accessory hypocarp (also called pseudo-fruit or apple; hereafter, apple) and a hard drupe [Mitchell and Mori, 1987]. The drupe (hereafter, nut) contains the cashew seed (hereafter, kernel) which is protected by a mesocarp with a honeycomb structure containing the cashew nut shell liquid (hereafter, CNSL), strongly irritant to skin and mucosae [Mitchell and Mori, 1987; Rosen and Fordice, 1994]. The mesocarp contains caustic chemicals both when nuts are immature, soft, and green (hereafter, fresh nuts) and when mature, dry, tough, and gray/brown (hereafter, dry nuts) (Fig. 1). In the fresh nut, the CNSL is more liquid, whereas in the dry nut, it is more viscous. Fresh cashew nuts appear to present no more mechanical demands than other fruits that capuchins bite open, while dry nuts are harder, though adult capuchins of both sexes can still crack them with their teeth [Chalk et al., 2016; J Chalk. Unpublished data; E Visalberghi. Personal observation].

Apparently, humans and bearded capuchins are the only primate species that process cashew nuts to eat the kernels. Traditionally, humans roast or boil the dry nuts to decarboxylate anacardic acid, the main component of CNSL [Gallina Toschi et al., 1993; Mohod et al., 2010]. In modern factories, nuts are cooked and protective clothing, such as gloves and masks, are worn by workers who handle them. So far, reports on *S. libidinosus* accessing the seed of cashew nuts concern two populations living 320 km apart in the State of Piauí (Brazil): namely, the population of Serra da Capivara National Park (hereafter SCNP) for which cashew nuts are the most common encased food exploited with tools [Falótico, 2011] and the population of Fazenda Boa Vista (hereafter, FBV; [Sirianni and Visalberghi, 2013]) for which the most common encased food exploited with tools are several species of palm nuts [Spagnoletti et al., 2011].

Wild bearded capuchin monkeys of FBV exploit cashew trees by eating both the apple and the kernel contained inside the nut. In a pilot study, Sirianni and Visalberghi [2013] reported that the monkeys at FBV use different techniques to access the kernel of fresh and dry nuts. When the nut is fresh, typically capuchins repeatedly rub it on rough surfaces until the shell is partially open and then they extract the kernel with their index finger. In contrast, when the nut is dry, capuchins typically use a tool to crack the shell and expose the kernel. Possibly, these two techniques accommodate the different mechanical and chemical challenges associated with nuts of differing maturational stages. When the nut is fresh, it may be better to perforate the mesocarp by rubbing the nut on a tree limb than cracking it with a tool, since the latter behavior is likely to contaminate the kernel with the caustic liquid. This contamination is indeed risky: for the *S. libidinosus* living in the SCNP that strike fresh cashew nuts with stones, rather than rub them, is not uncommon to have blisters on their lips [Falótico, 2011; Luncz et al., 2015]. So far, there are no reports concerning other populations of *S. libidinosus*, other species of *Sapajus* and *Cebus*, or other non-human primate species consuming the kernels of cashew nuts, although reports of other species of primates eating the fleshy cashew apples are common (e.g., *Alouatta palliata* [Glander, 1982]; *Ateles geoffroyi* [Carpenter, 1935]; *Papio* sp., *Colobus guereza* [Lee and Priston, 2005]; *Cebus olivaceus* [John Robinson. Personal communication]; *C. capucinus*, [Perry and Manson, 2008]). Also chimpanzees raiding cashew plantations eat only the cashew apple and drop the nut on the ground [Hockings and Sousa, 2012].

Fig. 1. Sagittal section of a fresh cashew nut (left); note the white kernel and in the close-up the spongy mesocarp whose tubules contain the CNSL. Cracked dry cashew nuts with the tough mesocarp containing caustic resin (right).

Cashew nuts are high in energy. One hundred grams of cashew kernels collected in FBV correspond to 580 Kcal distributed in a balanced manner across carbohydrates, fat, and protein (value calculated from Peternelli [2015]). Moreover, the cashew kernel contains all the essential amino acids in the right proportions, and the United States Department of Agriculture considers cashews a food of choice for humans [USDA, 2015]. Therefore, we assume that cashews are a food of choice for other omnivorous primates, including capuchin monkeys.

Thus, cashews nuts are a first-rate food protected by a powerful chemical deterrent that can be avoided by using particular processing techniques the acquisition and expression of which may vary in accord with age, body mass, and social influences. The first goal of this study was to corroborate Sirianni and Visalberghi [2013] preliminary findings on the types of processing behaviors used by capuchin monkeys for cashew apples and nuts using targeted sampling of a larger number of individuals, including young ones. The second goal was to determine whether age and body mass influenced success and time spent feeding on cashew apples and extracting the kernels. The third goal was to find out whether social influences were likely to support the acquisition of nut processing skills. For this purpose, we assessed whether the attention paid by youngsters was selectively directed to proficient group members. We also monitored whether the monkeys collected leftovers previously owned by group members and whether they showed evidence of having contacted the caustic CNSL.

Age and Experience

Capuchin monkeys' diet includes many foods that require special handling and extraction techniques [e.g., Agostini and Visalberghi, 2005; Fragaszy, 1986; Gunst et al., 2008, 2010a; Melin et al., 2014; O'Malley and Fedigan, 2005a,b; Panger et al., 2002; Perry and Jiménez, 2012; Wright et al., 2009]. Since cashew nuts require extractive processing as well, we expected the age of an individual (that reflects her/his experience in processing food), will correlate with efficiency, although it is likely that efficiency reaches an asymptote at a certain age, as it does for other foods [Resende et al., 2014]. Many food processing behaviors emerge early in life but need extended practice to be effective or properly executed. Already in the first year of life, capuchins perform rubbing and pounding behaviors, though ineffectively, to modify food items [Fragaszy et al., 2004a]. Although pounding objects on hard surfaces appears already in the first year of life, the effective use of hammer and anvil tools to crack palm nuts does not occur routinely until capuchins are about 4 years of age or older [Eshchar et al., submitted a; Resende et al., 2008]. Finally, the effective behavior used by white-faced capuchins to obtain the seeds of *Luehea candida* are performed more often and are better organized in adults than in youngsters [O'Malley and Fedigan, 2005a].

Therefore, in the present study, we expected that an individual's probability of success at obtaining the kernel increases with age and time spent processing an individual cashew nut decreases with age. Moreover, since cracking a fresh nut with a stone contaminates the kernel with caustic chemicals present in the liquid of the mesocarp [Sirianni and Visalberghi, 2013], we expected proficient capuchins to use tools to exploit dry nuts, but not to exploit fresh nuts. Finally, since rubbing breaches the mesocarp when the nut is fresh but not when it is dry, we expected proficient capuchins to rub only fresh nuts.

Body Mass

To breach the mesocarp and access the kernel of fresh nuts, forceful rubbing is necessary. In contrast, to crack the mesocarp of dry nuts with a tool (and access its kernel) the strikes should not be forceful since the shell is not very hard. Studies carried out on tool use to crack palm nuts in FBV demonstrated that body mass (which correlates positively with the maximum force of an individual's strike) affects success at cracking high resistance nuts but not at cracking low resistance nuts and that, for both types of palm nuts, sex per se does not affect success [Fragaszy et al., 2010; Spagnoletti et al., 2011]. Therefore, we expected body mass to positively correlate with probability of success at opening fresh cashew nuts that need to be rubbed but not to correlate with probability of success at opening dry cashew nuts that do not require forceful strikes.

Attention to Others

In many species, extractive foraging actions and manipulative activities are socially influenced, and social influences appear to contribute to the acquisition of skills in these activities [for a review see Rapaport and Brown, 2008]. The processing techniques used to exploit cashews in FBV are excellent candidates for social influences. Although data collection in the present study was not specifically designed to investigate this topic, as has been done for stone tool use in bearded capuchin monkeys [Eshchar et al., in press; Fragaszy et al., 2013], our method allows us to assess whether youngsters pay more attention to more proficient individuals than to less proficient ones.

Avoidance and Acceptance of Risky Food

Aversive experiences with a novel food induce food aversion [Garcia et al., 1955; for a discussion on the phenomenon in primates, see Visalberghi, 1994]. Therefore, individuals unable to process nuts without contacting the CNSL should be less interested in getting cashew nuts than those who have acquired the proper processing technique. However, as individuals become more proficient, they should overcome their reluctance and exploit this high energy food. Information on wild primates feeding on items containing caustic substances is absent. However, O'Malley and Fedigan [2005a] suggest that the rare consumption of *Sloanea* by juvenile *C. capucinus* may also reflect a form of risk-aversion since the hairs defending these fruits produce irritation. Therefore, we expected infants and young juveniles (i) to contact the "risky" nuts less than adults and (ii) to contact the "non-risky" apples and eat them to the same extent as adults.

METHODS

Study Site, Groups, and Data Collection

The data were collected in FBV (9°39′ S, 45°25′ W), in the State of Piauí, Brazil [for a detailed description, see Visalberghi et al., 2007 and Spagnoletti et al., 2012]. Cashew trees are common in the transition area between *Cerrado* (wooded savannah) and *Caatinga* (thorny bush) [Oliveira and Marquis, 2002] where FBV is situated.

Systematic data were collected in 2012 and 2013 between mid-August and late October, that is, during the cashew season. Subjects belonged to the *Chicao* group, a fully habituated group of *Sapajus libidinosus* (previously *Cebus libidinosus*, [see Lynch Alfaro et al., 2012a,b]). This group consisted of 19 individuals in 2012 and 23 individuals in 2013. Table I reports detailed information about the age of each subject when data were collected. Individuals below 18 months of age (which is the average weaning age at FBV; EthoCebus. Unpublished data) were considered infants, individuals older than 5 years, or about this age in 2012 (as Doree who was already mother [Fragaszy et al., 2016] and Pati who had the same age of Doree) were considered adults, finally individuals in-between were considered juveniles. Note that hereafter when referring to both infants and juveniles, we will use the term youngsters.

The group was followed 6 days a week, from dawn to dusk. Focal animal follows were conducted using continuous recording of behaviors [Martin and Bateson, 1993] on a single subject. Observations started when the focal subject was in a cashew tree (or within 5 m from it and moved into the cashew tree within 3 min). The observations lasted 10 ± 3 min. Whenever the focal subject was out of sight for more than 3 min, the observation ended and the data were excluded. Whenever the subject was engaged in cashew processing within 10 min after the start of the observation, the observation was continued until the food item was exploited; focal sessions spanning less than 7 min were discarded from the analysis. For each subject, we collected 15 observations in 2012 and an average of 19.9 observations in 2013 (range 3–27; all subjects with 18 or more sessions and Pati and Cangaceiro, two peripheral males, with three sessions). We sought to collect a focal observation from all group members before beginning a further observation with any subject. When choosing the subject of the next observation, we actively searched for the least observed individuals, but if the latter were absent or away from a cashew tree, we proceeded to observe other individuals. Within each round of observations, the order in which individuals were sampled was random.

In 2012, data were collected by A.A. and a field assistant (Marino Junior Fonseca de Oliveira). In 2013, data were collected by M.V. and a field assistant (Marcio Fonseca de Oliveira). In 2013, when nuts were dry a second field assistant (Rone Pires de Oliveira) weighed the hammers and identified their material (see below). Observational data were collected using personal digital assistants (Hewlett Packard iPAQ Pocket) equipped with The Observer XT 10 software package (Noldus Information Technology) after a training period during which inter-observer reliability assessed by kappa coefficient for behavioral patterns reached +0.89 between A.A. and M.J.F.O., +0.87 between A.A. and M.V., and +0.84 between M.V. and M.F.O.

The behaviors recorded with The Observer are defined in Table II (see the videos provided as Supplemental Material S1–S7). We recorded the feeding behavior performed by the focal subject and

TABLE I. Subjects. Name, Sex (F, Female; M, Male), Body Mass, Age (Years, Months, and Days), when Observations Started on August 15th 2012 and 2013

		Body mass (kg)		Age (years; months; days)	
Name	Sex	2012	2013	2012	2013
Mansinho	M	3.52	3.41	15; 2; 15[a]	16; 2; 15[a]
Piaçava (Alpha)	F	1.86	1.86	13; 7; 15[a]	14; 7; 15[a]
Teninha	F	2.02	2.10	12; 7; 15[a]	13; 7; 15[a]
Jatobá (Alpha)	M	4.12	4.16	12; 2; 15[a]	13; 2; 15[a]
Teimoso	M	3.48	3.51	12; 2; 15[a]	13; 2; 15[a]
Chuchu	F	1.98	2.04	10; 2; 15[a]	11; 2; 15[a]
Dita	F	2.02	2.12	9; 2; 15[a]	10; 2; 15[a]
Tomate	M	1.99	2.34	5; 7; 16	6; 7; 16
Catu	M	2.07	2.47	5; 5; 10	6; 5; 10
Cangaceiro	M	2.08	2.37	4; 10; 26	5; 10; 26
Pati	M	2.08	2.50	4; 8; 13	5; 8; 13
Doree	F	1.56	1.78	4; 8; 6	5; 8; 6
Paçoca	F	1.44	1.66	3; 7; 13	4; 7; 13
Pamonha	F	1.32	1.57	3; 7; 13	4; 7; 13
Coco	M	1.37	1.65	3; 1; 1	4; 1; 1
Thais	F	1.13	1.34	1; 6; 14	2; 6; 14
Chani	F	0.99	1.17	1; 6; 14	2; 6; 14
Presente	M	1.09	1.45	1; 5; 0	2; 5; 0
Cachaça	M	0.41	1.10	0; 5; 0	1; 5; 0
Divina	F	–	0.97[b]	–	0; 9; 8
Titia	F	–	0.66	–	0; 7; 12
Patrícia	F	–	0.57	–	0; 7; 4
Donzela	F	–	0.40	–	0; 6; 30

For the individuals for which birth dates are unknown, age was estimated. The alpha male and female are indicated.
[a]The age of these subjects was estimated on the basis of several parameters (EthoCebus, Unpublished data).
[b]The weight of this subject was estimated on the basis of infants' growth curve in Fragaszy et al. (in press).

the food target (apple, fresh nut, or dry nut). A cashew nut is fresh when it has an immature green exocarp and a spongy mesocarp. A cashew nut is dry when it has a gray/brown exocarp and a tough mesocarp (see Fig. 1). Success was scored when the apple was eaten and the leftover discarded, or when the seed contained in the nut was eaten and the exocarp discarded. Processing time was the sum of the duration of all the behaviors directed to the target food from when it was collected until the food was consumed or discarded.

When monkeys cracked dry nuts with a tool, we scored whether the anvil they used was on the ground (e.g., a stone, a root) or above the ground (e.g., a tree branch). Moreover, in 92 episodes of tool use, we recorded the tool material (sandstone, siltstone, or palm nut shell). In 80 episodes (out of the 92), we also weighed the tool.

For the purpose of evaluating possible social influences, we recorded all the occurrences in which the focal subject (i) took a food item partially consumed by another individual; (ii) looked (for any duration) at a group member from a distance of 1 m or less while the other processed a nut or an apple (the identity of the group member was also noted). For the purpose of evaluating possible responses to CNSL, we recorded if the focal subject scratched its hands or face, and if she/he drooled. Finally, at the end of each observation, we noted whether the subject's face or hands exhibited evidence of chemical burn, such as blisters.

We adhered to the American Society of Primatologists/Association for the Study of Animal Behaviour guidelines for the treatment of animals in behavioral research and teaching and to the American Society of Primatologists' principles for the ethical treatment of primates. Permits to Etho*Cebus* research were given by IBAMA SISBIO: 28689-3 and CNPq: 002547/2011-2.

Data Analysis

Most analyses were based on generalized linear mixed models. Depending on the nature of the dependent variable, we used logistic regressions (for binary variables), negative binomial regressions (for count variables), and linear regressions (for continuous variables). A first set of analyses compared the probability of success and the time taken to open the food item (apples, fresh nuts, and dry nuts). Other analyses were run separately for the two kinds of nuts.

A second set of analyses focused on the individual and behavioral characteristics that affected success in opening the nuts (binary dependent variable) and

TABLE II. List and Description of the Behaviors Scored

Behavior	Description
Foraging	To search for food while being in a cashew tree, or on the ground below it
Behaviors directed toward the food item	
Eating	To chew the food target and ingest it
Licking/sucking	To contact with the tongue or extract liquid by compressing the lips
Rubbing	To move the food target back and forth (or in one direction only) on a surface
Processing with teeth	To take an encased item with teeth (usually canines) out of its case (without evident contact between lips and food target)
Processing with hands	To exert force on the food target with the hand(s) in order to tear it apart
Extracting with fingers	To take an encased item with one finger/nail (usually index finger) out of its case
Pounding	To bang the food target. The food is held with one or both hands and pounded one or several times in succession against a hard surface
Tapping/shaking	To strike gently with a light blow or blows. Either tap object with fingers or tap object on a surface. Or to move to and fro in short, irregular movements
Rolling	To rotate the food target held between hands by moving them in opposite directions, or to roll the food target over a surface
Tool using	To use a percussor, usually a stone, to access the encased nut
Other behaviors	
Scratch	To scratch hand(s) or to scratch face
Attention	To attend to another individual who is feeding on cashew nut or apple. The focal subject looks at the other from a distance of 1 m or less
Drooling	Abundant salivation due to food ingestion
Other	Includes behaviors not listed above (playing, grooming, resting, mating ...)

the time taken to process and eat them (continuous dependent variable). Independent variables entered into analyses were either individual characteristics (sex, age, and body mass) or the presence/absence of the two most important behavior patterns used to open the cashew nuts, rubbing and tool use. The subject identity was always entered as a random effect to avoid pseudo-replication.

For a third set of analyses, we calculated individual hourly rates of contact with the nuts (calculated separately for the 2 years of observation as a measure of the interest in the different kinds of nuts) and entered them as the dependent variable in a linear regression that included sex and age as the independent variables and the subject identity as a random effect.

We also calculated individual counts of episodes of paying attention to others processing nuts and entered them in a negative binomial regression that included sex and age as the independent variables, observation time as the exposure variable, and the subject identity as a random effect. Finally, we used within-subject conditional negative binomial regressions to evaluate if youngsters paid more attention to other group members processing nuts depending on the latters' sex and age (youngster or adult; a proxy for proficiency), and to evaluate if scratching occurred more often during the manipulation of nuts than of apples. For the former analysis, we estimated the time each individual was available as a potential target of attention on the basis of the proportion of observation time the individual spent processing cashew nuts, and entered this value as the exposure variable.

In the analysis concerning the effects of hammer type on the probability of success, a categorical variable with more than two levels (hammer type: siltstone, sandstone, palm nut shell) was included among the independent variables. We used a Wald test to assess its overall significance.

RESULTS

Success, Behaviors, and Processing Time

For the three types of food items and for each subject, Table III reports the number of food items processed, the percentage of successful episodes, the duration of processing time per item processed, and the percentages of processing time spent performing each behavior.

Success was achieved in 99% of the apple episodes (Table IIIa). Individuals below 1 year of age accounted for most of the failures; however, even them were successful in more than 90% of their episodes (Fig. 5a). The behaviors directed toward the apple consisted mainly in eating and sucking (Fig. 2 and Supplemental Material S1). Other behaviors (pounding, rolling, rubbing, and tapping/shaking) were only occasionally performed, mostly by youngsters, and many were never observed (extracting with fingers, processing with hands, processing with teeth, and tool using).

TABLE III. Apples (a), Fresh Nuts (b), and Dry Nuts (c)

				Percentage of processing time spent performing each behavior									
Subject	# Items processed	% of success	Processing time/item (sec)	Eating	Licking/sucking	Rubbing	Teeth processing	Hand process.	Finger extract.	Pounding	Tapping/shaking	Rolling	Tool using
(a) Apples													
Mansinho	22	100	36	10.7	89.3	0	0	0	0	0	0	0	0
Piaçava	32	100	67	8.5	91.5	0	0	0	0	0	0	0	0
Jatobá	43	100	39	21.5	78.3	0	0	0	0	0	0	0.3	0
Teimoso	25	100	41	32.2	67.8	0	0	0	0	0	0	0	0
Teninha	36	100	50	8.0	92.0	0	0	0	0	0	0	0	0
Chuchu	38	100	46	20.5	79.5	0	0	0	0	0	0	0	0
Dita	18	100	39	14.8	85.2	0	0	0	0	0	0	0	0
Tomate	44	100	47	13.8	85.6	0	0	0	0	0	0.6	0	0
Catu	34	100	38	16.5	75.0	0	0	0	0	0	8.4	0	0
Cangaceiro	16	100	47	14.6	81.1	0.4	0	0	0	2.3	0	1.6	0
Pati	15	100	69	22.2	77.8	0	0	0	0	0	0	0	0
Doree	21	95	43	22.2	77.0	0	0	0	0	0	0.8	0	0
Paçoca	37	100	39	14.5	85.5	0	0	0	0	0	0	0	0
Pamonha	47	100	56	21.0	78.2	0.3	0	0	0	0	0.5	0	0
Coco	63	100	37	23.6	76.4	0	0	0	0	0	0	0	0
Taís	70	99	39	11.3	86.1	0	0	0	0	2.3	0.3	0	0
Chani	57	100	63	13.9	86.1	0	0	0	0	0	0	0	0
Presente	67	100	46	14.2	85.0	0	0	0	0	0	0.8	0	0
Cachaça	58	98	43	12.7	83.2	0.4	0	0	0	3.4	0.2	0	0
Divina	18	94	63	13.4	84.2	2.4	0	0	0	0	0	0	0
Titia	14	93	73	6.5	80.2	8.9	0	0	0	4.5	0	0	0
Patrícia	12	92	117	16.6	65.0	17.1	0	0	0	0	0	1.2	0
Donzela	22	95	92	10.7	72.8	2.1	0	0	0	13.3	0	0.9	0
(b) Fresh nuts													
Mansinho	100	97	75	5.3	0	36.9	7.6	0	50.1	0	0.1	0	0
Piaçava	66	88	84	3.3	0	38.8	9.1	0.2	48.5	0	0.2	0	0
Jatobá	134	96	66	7.9	0	38.1	17.4	0	36.5	0	0	0	0
Teimoso	92	97	68	7.6	0	30.1	24.8	0	37.4	0	0.1	0	0
Teninha	78	95	89	6.5	0	33.9	10.1	0.6	48.2	0	0.7	0	0
Chuchu	116	91	63	4.9	0	35.4	23.7	0	35.8	0	0	0.1	0
Dita	124	98	91	4.8	0	28.2	11.6	0.5	54.9	0	0	0	0
Tomate	82	91	83	5.8	0	40.4	11.7	0	41.1	0	0.7	0.2	0
Catu	95	94	92	4.7	0	33.3	22.7	0	38.9	0	0.3	0	0
Cangaceiro	45	100	95	4.6	0	32.5	21.1	0	41.8	0	0	0	0
Pati	35	86	79	6.9	0.3	35.9	16.1	0	40.6	0	0	0.1	0
Doree	56	86	127	4.8	0	29.3	18.3	0	47.5	0.1	0	0	0
Paçoca	62	89	133	2.7	0	34.8	14.9	0.1	47.4	0.1	0	0	0

TABLE III. Continued

Subject	# Items processed	% of success	Processing time/item (sec)	Percentage of processing time spent performing each behavior									
				Eating	Licking/sucking	Rubbing	Teeth processing	Hand process.	Finger extract.	Pounding	Tapping/shaking	Rolling	Tool using
Pamonha	39	85	131	2.0	0	34.6	20.7	0.1	40.7	1.9	0	0	0
Coco	32	75	111	4.6	0	45.6	12.1	0.7	34.8	1.0	0	1.0	0.2
Taís	23	61	188	1.9	0	37.1	22.3	0	36.2	2.5	0	0	0
Chani	32	47	148	1.8	0	49.5	6.0	0.7	37.8	3.5	0.5	0	0.2
Presente	26	65	125	2.6	0	35.5	18.0	0.1	42.7	0.4	0.6	0	0
Cachaça	17	24	105	0.8	2.8	44.3	23.7	0	16.2	8.5	1.0	0.7	2.0
Divina	5	0	15	0	0	90.6	0	0	0	9.4	0	0	0
Titia	12	0	40	0	0	68.6	6.3	0	0	21.9	0	3.2	0
Patrícia	5	0	22	0	0	12.3	47.4	0	16.0	24.3	0	0	0
Donzela	6	0	30	0	0	44.0	3.0	0	0	46.8	4.7	1.5	0
(c) Dry nuts													
Mansinho	37	76	74	20	0	1.1	20.8	4.5	32.4	1.3	2	11.6	6.3
Piaçava	42	79	70	7.2	0	0	7.6	4.3	28.1	0	1.1	21.9	29.8
Jatobá	39	87	51	14.1	0	0	27.4	2.8	36.4	0.2	1.3	13.3	4.5
Teimoso	14	93	95	14.9	0	0	15.9	3.5	52.9	0	2.9	6.3	3.5
Teninha	28	82	94	10.8	0	0	13.3	3.2	45.1	2.9	1.7	7.8	15.1
Chuchu	27	93	92	9.7	0	0	23.4	0.1	39.1	1.7	2.0	10.2	13.7
Dita	32	91	96	8.9	0	0	6.2	1.8	43.0	0	1.2	22.6	16.3
Tomate	14	64	100	21.0	0	3.6	12.9	7.0	28.0	2.1	7.3	10.0	8.1
Catu	18	72	125	21.1	0	0	10.9	6.0	39.8	1.2	2.1	6.2	12.6
Cangaceiro	32	91	83	18.5	0	0	7.0	2.5	35.0	4.1	0.9	11.2	20.8
Pati	35	83	81	10.0	0	0.2	15.0	3.2	41.9	2.8	4.6	5.8	16.4
Doree	48	69	126	7.0	0	0.1	8.8	3.1	37.4	4.8	1.8	9.8	27.2
Paçoca	38	68	148	2.0	0	0	12.5	2.8	25.4	4.3	1.1	5.1	46.7
Pamonha	27	59	121	5.4	0	0.6	23.4	2.7	46.2	5.5	6.5	4.9	4.9
Coco	43	70	146	6.5	0	0	8.3	4.2	22.7	6.9	1.1	13.8	36.4
Taís	16	38	65	5.3	0	1.3	32.0	4.7	15.9	13.1	8.4	4.3	15
Chani	9	11	105	0.2	0	0	18.4	0	8.7	20.9	3.7	1.8	46.3
Presente	15	33	68	11.2	0	0	26.6	0	24.1	12.3	17.5	8.3	0
Cachaça	12	33	127	2.3	0	4.9	4	2.2	13.8	7.9	0.8	0.5	63.5
Divina	1	0	6	0	0	100	0	0	0	0	0	0	0
Titia	0	–	–	0	0	0	0	0	0	0	0	0	0
Patrícia	2	0	40	0	0	92.6	7.4	0	0	0	0	0	0
Donzela	3	0	37	0	0	5.1	28.5	0	0	66.5	0	0	0

For each subject, we report the number of food items processed, the percentage of successful episodes, the duration of processing time per item processed (based on the time elapsed until success was achieved, or until the item was discarded), and the percentages of processing time spent performing each behavior.

Fig. 2. A young capuchin (*S. libidinosus*) is sucking the cashew apple with his head backward.

Success with fresh nuts was achieved in 87% of the episodes (Table IIIb) and until 1 year of age individuals never succeeded (Fig. 5b). All behaviors were performed: some very often (e.g., rubbing, processing with teeth, and extracting with fingers; [Fig. 3]; see Supplemental Material S2, S3, S5), and some only by a few individuals (licking and to a lesser extent rolling), or only by younger individuals (pounding and tool using).

Success with dry nuts was achieved in 70% of episodes (Table IIIc) and until 1 year of age individuals never succeeded (Fig. 5c). All behaviors, except sucking/licking, were performed. Adults tended to use tools to crack the nut (Fig. 4); see Supplemental Material S7) and they did not perform rubbing. In contrast, until 1 year of age individuals did not perform tool use, rolling, or tapping.

Overall, capuchins were clearly more successful with apples than with fresh or dry nuts ($z = 9.54$, $P < 0.001$ and $z = 11.56$, $P < 0.001$, respectively). They were also more successful in opening fresh nuts than dry nuts ($z = 7.76$, $P < 0.001$). In successful episodes, the total processing time (time needed to open and consume the nuts) was also longer for fresh and dry nuts compared to apples ($z = 10.59$, $P < 0.001$ and $z = 8.80$, $P < 0.001$, respectively), while time needed to open and consume fresh and dry nuts did not differ ($z = 0.82$, $P = 0.425$).

Fig. 3. An adult female is rubbing a fresh cashew nut on the bark of a cashew branch.

Factors Affecting the Opening of Fresh Nuts

As shown in Figure 5b, probability of success gradually increased from 0 at 1 year of age to 0.85 at 5 years, slightly increasing later in life. Among the individual variables examined, only body mass was a significant predictor of probability of success, while sex and age of the subject were unrelated to probability of opening a fresh nut (Table IV). Given the strong correlation between age and body mass (year 2012: $r = 0.803$, $N = 19$, $P < 0.001$; year 2013: $r = 0.810$, $N = 23$, $P < 0.001$), we repeated the analysis excluding the latter. Age became a significant predictor of success ($z = 5.56$, $P < 0.001$; Fig. 5b). Note that here, and below, we report both analyses in order to make our results directly comparable with studies that may have only one of the two variables.

We examined how the use of two behaviors critical for opening nuts (rubbing and tool use) affected the probability of success. When dealing with a fresh nut, success was more likely if the monkey rubbed it ($z = 7.12$, $P < 0.001$) than if the monkey did not; but success was as likely if the monkey used tools than if the monkey did not ($z = 0.75$, $P = 0.456$) (Fig. 6a).

In successful episodes, the total processing time was unrelated to body mass and sex, but was negatively related to age. Older subjects took less time to open a fresh nut (Table V). When the analysis was repeated excluding age, the effect of body mass was significant ($z = -5.16$, $P<0.001$).

Factors Affecting the Opening of Dry Nuts

As shown in Figure 5c, probability of success gradually increased from 0.1 at 2 years of age to 0.69 at 5 years of age; later in life, most of the values remained above this level. The notable exception was the very low probability of success ($=0.33$) at 12 years of age; this value is based on only three episodes performed by Chuchu, in which she opened one nut with tools, and failed once using her teeth and once using a tool. Among the individual variables examined, none significantly predicted the probability of opening a dry nut (Table VI). When the analysis was repeated excluding body mass, age was a significant predictor of success ($z = 4.41$, $P < 0.001$; Fig. 5c).

When dealing with a dry nut, success was more likely if the monkey used tools ($z = 2.88$, $P = 0.004$) than if the monkey did not; but success was as likely if the monkey rubbed the nut than if the monkey did not ($z = -0.89$, $P = 0.140$) (Fig. 6b). When capuchins used a tool, they succeeded in 79% of the episodes

Fig. 4. An adult male uses a stone to crack a dry cashew nut.

(187 episodes out of 236); when capuchins did not use a tool, they succeeded in 61% of the episodes (148 episodes of the 241).

Table VII reports the number of successful and unsuccessful episodes in which youngsters (of both sexes), adult females and adult males used tools or not, to access the kernel of dry nuts. Youngsters used tools to process dry cashew nuts in 37% of the episodes and were successful in 72% of them. Adults used a tool in 54% of the dry nut episodes and were successful in 81% of them. In particular, adult females used tools to process dry cashew nuts in 78% of the episodes and were successful in 80% of them and adult males used tools to process dry cashew nuts in 32% of the episodes and were successful in 82% of them. When using techniques other than tool use, youngsters, adult females, and adult males were successful in 28%, 75%, and 81% of the episodes, respectively.

Total processing time of dry nuts was unrelated to body mass and sex, but was negatively related to age (Table VIII). When the analysis was repeated excluding age, the effect of body mass was significant ($z = -4.37$, $P < 0.001$).

Most tool use episodes occurred when the monkey was on the ground (68%). However, in 32% of the episodes, the monkey was on a tree and used a tree branch as an anvil; the branch could belong to the cashew tree from which the nut was taken or to another nearby tree. In 92 episodes performed by 11 individuals, we were able to record detailed information about the hammers material. The monkeys used sandstone (N = 31), siltstone (N = 16), and palm nut shell (N = 45) and reached success in 87%, 94%, and 80% of the episodes, respectively. In 80 episodes, the mass of the stone was measured: on average sandstone hammers weighed 131 g (min–max: 37–316 g, N = 29), siltstone hammers 496 g (min–max: 170–877 g, N = 16), and palm nut shell hammers 30 g (min–max: 14–72 g, N = 35). Neither the weight nor the type of the hammer affected the probability of opening the nut (hammer weight: $z = 0.44$, N = 80, $P = 0.659$; hammer type: $\chi^2 = 0.00$, df = 2, $P = 0.999$).

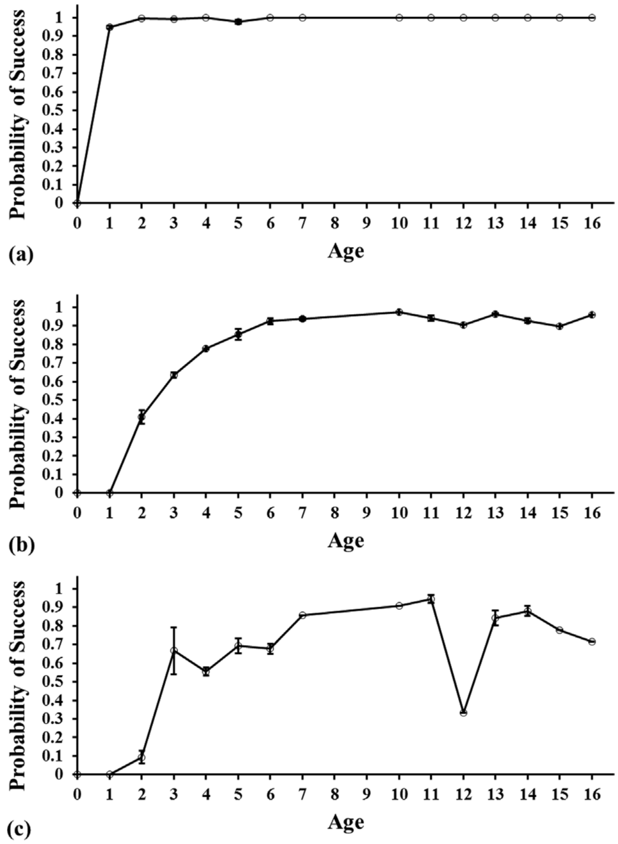

Fig. 5. Probability of success (Mean ± SEM) in relation to age for (a) cashew apples, (b) fresh nuts, and (c) dry nuts.

Chemical Burn, Drooling, and Scratching

During the study, we did not observe any blister on the face or hands of the monkeys, although three events of drooling occurred. In 2012, Catu drooled while processing a fresh nut and in 2013 he drooled (and scratched) while rubbing a fresh nut; in 2013, Pamonha drooled while processing a dry nut (see Supplemental Material S8). Scratching was infrequent: out of the 26 episodes of scratching performed by 11 individuals, 18 were directed to the hands and 8 to the face. Scratching (directed to a hand or the face) occurred in 6 out of 809 apples episodes, 12 out of 1,282 fresh nuts episodes, and 3 out of 477 dry nuts episodes. Monkeys did not scratch more often while processing a nut (either fresh or dry) than an apple ($z = 0.59$, N = 22, $P = 0.555$).

Interest Toward the Different Food

Contact with a food item is a measure of interest independently of success. Contact varied in relation to the type of food items. Younger monkeys contacted apples more often than older ones ($z = -2.19$, N = 42, $P = 0.028$) regardless of sex ($z = 0.23$, N = 42, $P = 0.821$). In contrast, older subjects contacted both fresh nuts and dry nuts more often than

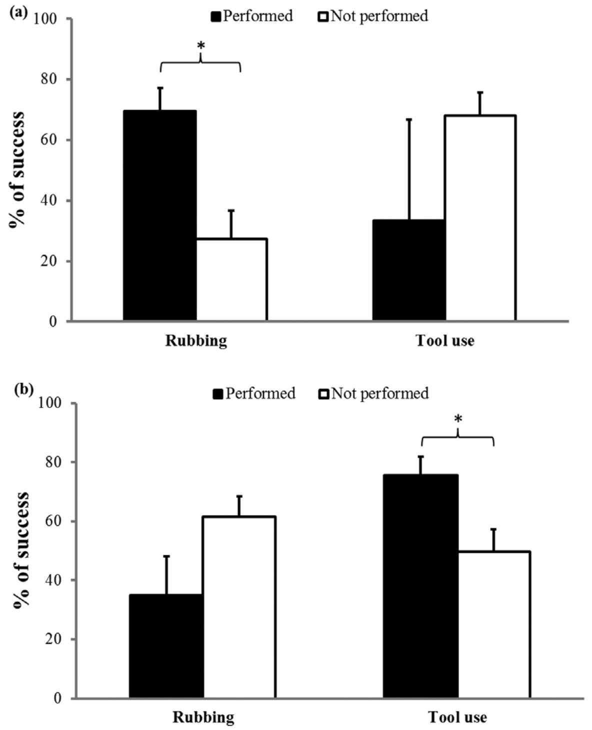

Fig. 6. (a) Fresh nuts. Percent of success when rubbing or tool use behaviors are performed. (b) Dry nuts. Percent of success when rubbing or tool use behaviors are performed.

younger ones (fresh nuts: $z = 4.98$, $N = 42$, $P < 0.001$; dry nuts: $z = 2.55$; $N = 42$, $P = 0.011$), again regardless of sex (fresh nuts: $z = 1.79$, $N = 42$, $P = 0.073$; dry nuts: $z = 0.65$; $N = 42$, $P = 0.514$).

Attending to Others Processing Cashews

Cashew trees produce many fruits at the same time allowing several capuchins to feed concurrently and (possibly) to attend to what others are processing. Notwithstanding this, only three adults and ten youngsters attended to others processing fresh or dry cashews; this behavior was observed in only 4.3% of the episodes (76 times out of 1,759 nut episodes). In a first analysis, we considered all the monkeys as potential targets of attention and we related the rate of paying attention to others manipulating nuts to the subjects' age and sex. Youngsters paid more attention to others manipulating nuts than did adults ($z = -5.10$, $N = 42$, $P < 0.001$), while no sex differences emerged ($z = 0.43$, $N = 42$, $P = 0.666$). In a second analysis, we focused on the target of youngsters' attention. Youngsters did not direct their attention preferentially to adults ($z = 1.51$, $N = 346$, $P = 0.132$) and paid more attention to the behavior of females than to the behavior of males ($z = 1.51$, $N = 346$, $P = 0.033$). We never observed monkeys paying attention to others manipulating apples.

We observed 66 events in which subjects collected a food item previously owned and discarded by a group member. In 68% of them, the leftover was an apple, in 1% a fresh nut, and in 30% a dry nut. Youngsters accounted for 91% of the instances of collection and they collected apples twice as often as nuts.

TABLE IV. Effect of Individual Variables on Probability of Opening a Fresh Cashew Nut

Independent variable	Coefficient	z-value	P-value
Sex	−0.11	−0.17	0.862
Body mass	1.42	2.46	0.014
Age	0.11	1.16	0.246
Intercept	−1.75	2.10	0.036

Results of a random-effects logistic regression based on 1,282 fresh nuts.

DISCUSSION

In FBV, capuchins obtain the nutritious cashew nuts, that are defended by caustic chemicals, by using processing techniques that maximize success and minimize the risk of injury. Interestingly, and as expected, when dealing with a fresh nut, success was more likely if the monkey rubbed the nut than if the monkey did not; in contrast, when dealing with a dry nut, success was more likely if the monkey used tools than if the monkey did not. The use of these different processing techniques also reduces the risk of injury (see below). Thus, we confirm Sirianni and Visalberghi [2013] initial description on how FBV adult capuchins process cashew nuts with a finer methodology.

In addition, we highlight the variation existing across individuals in processing techniques and success. Although capuchins of all ages are nearly always successful in eating the apple, only at 5 years of age, they reach a probability of success higher than 0.85 and 0.68 of obtaining the kernel of fresh nuts and dry nuts, respectively. While adult individuals use different techniques for the two food items, juveniles are less discriminating in their actions toward them. Until 1 year of age, individuals do not perform the same actions as adults do, and they never succeed in obtaining either the fresh or dry nuts.

TABLE V. Effect of Individual Variables on the Time Taken to Open and Consume a Fresh Cashew Nut

Independent variable	Coefficient	z-value	P-value
Sex	−0.17	−1.76	0.078
Body mass	−0.04	−0.37	0.713
Age	−0.07	−3.80	<0.001
Intercept	5.40	36.58	<0.001

Results of a random-effects linear regression based on 1,121 successfully opened fresh nuts.

TABLE VI. Effect of Individual Variables on Probability of Opening a Dry Cashew Nut

Independent variable	Coefficient	z-value	*P*-value
Sex	−0.04	−0.08	0.936
Body mass	0.967	1.82	0.069
Age	0.08	0.96	0.337
Intercept	−1.67	−2.13	0.033

Results of a random-effects logistic regression based on 477 dry nuts.

The Acquisition of Proficiency in Processing Cashew Nuts

Cashew nuts are a challenging food for bearded capuchin monkeys. Thus, foraging on cashew nuts follows the ontogenetic pattern described for other foods requiring extraction (palm nuts in bearded capuchins [Eshchar et al., submitted a]; *Sloanea* seeds by white-faced capuchins [O'Malley and Fedigan, 2005a]), with monkeys progressively mastering the skill needed to succeed routinely.

For fresh nuts, the probability of success increases regularly with age, while for dry nuts, the increase is somehow irregular. Moreover, adults open fresh nuts more reliably and with greater inter-individual consistency than dry nuts. This could reflect (i) our relatively small sample size of dry nuts; (ii) specific characteristics of dry nuts (e.g., resistance, dryness, CNSL viscosity) allowing different strategies to reach success; (iii) different availability of tools near the cashew trees, affecting probability of success when using tools; and (iv) difference in biting force and canine size between adult males and females, affecting the success while using teeth [Plavcan and Kay, 1988]. Further studies should examine the role of these factors in a larger dataset.

Proficiency at processing cashew nuts increases gradually until early adulthood (see Fig. 5b and c). The timeline for dry cashew nuts is similar to that reported for cracking open resistant palm nuts using stone hammers. In FBV striking a palm nut with a stone, an obligatory action to crack a palm nut, first appears in the second year or even later, and young monkeys do not regularly succeed at cracking nuts until their fourth year or later [Eshchar et al., submitted a]. In cashew processing, ineffective actions gradually disappear from youngsters' repertoire as effective actions come to predominate. Similarly, youngsters attempting to crack palm nuts perform actions in a less discriminating manner than do adults. In this respect, it is interesting to note the similar pattern of acquisition despite the fact that cashews are available only for a few weeks, whereas palm nuts are available all year around [Spagnoletti et al., 2012]. Thus, young capuchins gradually learn to tune a variety of species-typical foraging actions (such as pounding and extraction to access embedded food) and use them to obtain different food items that require similar processing techniques. In this way, learning to crack open a hard nut to overcome the resistance of its shell allows the acquisition of skills (such as good aim, regulation of the force, etc.) that are also necessary to crack a cashew nut to avoid its caustic chemical.

TABLE VII. Dry Nuts. Number of Successful and Unsuccessful Episodes in Which Youngsters (of Both Sex), Adult Females, and Adult Males Used Tools, or Did Not Use Tools

	Youngsters	Adult females	Adult males
# of successful episodes with tool use	37	103	47
# of unsuccessful episodes with tool use	14	25	10
# of successful episodes without tool use	24	27	97
# of unsuccessful episodes without tool use	62	9	22
Total # of episodes	137	164	176

When not using tools, capuchins processed the dry nut only with teeth and/or hands.

Factors Affecting Success and Processing Time

Age and body mass were highly correlated in our sample. However, these factors do not align perfectly because, for example, adult females that weigh on average 2.1 kg have more experience than juvenile males that weigh more than 2.1 kg from about 4 years of age [Fragaszy et al., 2016]. As expected, body mass predicted success at opening fresh nuts. Age predicted duration of processing fresh nuts: older individuals processed fresh nuts more quickly. In addition, rubbing significantly contributed to success at opening fresh nuts. Also as expected, body mass did not predict success in opening dry nuts, while duration of processing dry nuts was predicted by age.

Since adult monkeys opened dry nuts in roughly equal percentages by processing techniques with or without tools, tool use appears unnecessary to access the kernel of dry cashew nuts. Moreover, success with tools was reached also with light sandstones, (weighing on average 143 g), or a palm nut shells (weighing on average 32 g) and the average mass of these tools is 15–30 times less than that of the stones used to crack a palm nut [Visalberghi et al., 2009]; thus mass and material of the tool do not play a crucial role to crack open cashew nuts, although they do so to crack open palm nuts at FBV [Visalberghi et al., 2009].

Interestingly, about one-third of the tool episodes occurred when the monkey was on a tree and she/he used a tree branch as an anvil to crack the dry nut.

TABLE VIII. Effect of Individual Variables on the Time Taken to Open and Consume a Dry Cashew Nut

Independent variable	Coefficient	z-value	*P*-value
Sex	−0.03	−0.20	0.840
Body mass	−0.15	−1.36	0.172
Age	−0.04	−2.93	0.003
Intercept	5.24	33.94	<0.001

Results of a random-effects linear regression based on 335 dry nuts.

This is the first report of habitual percussive tool use on tree branch anvils in the genus *Sapajus*. In order to crack hard palm nuts, bearded capuchins in FBV must use heavy stones that are very costly to use and especially to transport [Massaro et al., 2012], and stable wooden or stone anvils located on the ground. The present data demonstrate that when the tool is light, capuchins readily transport and use it in a tree, as the Taï chimpanzees do when cracking the relatively soft coula nuts [Boesch and Boesch-Achermann, 2000].

Males and females processed cashew nuts equally often, and for fresh and dry nuts their rate of success and duration of processing did not differ. However, females used tools to process dry nuts more than twice as often as males, despite the sexes being equally successful both while using tools and while using other processing techniques. The findings that females process dry cashew nuts more often than males and that females use tools to a greater extent than males is in sharp contrast with the pattern reported for the same population using tools to crack palm nuts. In fact, Spagnoletti et al. [2011] found that females performed fewer episodes of tool use to crack palm nuts than males and were less successful than males at cracking high resistance palm nuts. Nut resistance explains these different patterns: while palm nuts require heavy tools and strength [Fragaszy et al., 2010; Spagnoletti et al., 2011], cashew nuts can be opened by both sexes with relatively light tools as well as without them.

Therefore, since tool use is not mandatory to access the kernel of dry cashew nuts, we argue that FBV capuchins use tools (i) to avoid contacting the caustic resin with the lips more than to overcome the resistance of the shell and that (ii) adult males do it to a lesser extent than females because their jaws and canines are bigger and allow them to hold and crack the nuts with their teeth without contacting the resin. These hypotheses could be tested by analyzing videos of males and females orally processing dry cashew nuts.

Social Influences on the Acquisition of Processing Skills

Proximity to and interest toward skilled individuals by others during foraging are common in many species of birds and mammals [e.g., meerkats, Hoppitt et al., 2012] and much effort has been devoted to evaluating the contribution of observing proficient others foraging on the development of foraging skills by the youngsters [Hoppitt and Laland, 2008]. Young capuchin monkeys are usually very interested in adults' processing activities with palm nuts [Coelho et al., 2015; Eshchar et al., in press; Ottoni et al., 2005] and other difficult foods, such as *Sloanea* fruits [O'Malley and Fedigan, 2005a,b] and beetle larvae in bamboo canes [Gunst et al., 2008]. Finally, young-white faced capuchins (*C. capucinus*) show interest toward group members foraging on food items that are rare, difficult to process, or large [Perry and Jiménez, 2012].

However, despite requiring multi-step processing techniques, cashew nuts elicit little interest from less proficient individuals. Young capuchins seldom attend closely to group members processing cashew nuts and very rarely collect discarded parts of the cashew for further inspection or ingestion. Although youngsters pay more attention to others, particularly to females, than do adults, youngsters do not preferentially observe more proficient individuals, that is, those from which something could be learnt. On the whole, this pattern of results indicates that young capuchins do not pay preferential attention to those performing behaviors that they themselves can not yet perform. Finally, it is worthwhile mentioning that we never observed adults intervene in any way with youngsters that were handling cashew nuts.

Youngsters' little attention to others processing cashews contrasts with what they do when adults use stone tools to crack palm nuts. Eshchar et al. [in press] carried out a longitudinal study on stone tool use acquisition in FBV. The study focused on the foraging behavior of youngsters (individuals up to 6 years of age) in relation to others' foraging behavior. The data were collected while the group moved in its habitat including the "outdoor laboratory," an open area where capuchins receive palm nuts for experimental purposes [Visalberghi and Fragaszy, 2013]. In Eshchar et al. [in press] study, youngsters were three times more likely to be near an anvil when others were cracking palm nuts than at other times, and spent 3/4 of their time within 5 m of one or more monkeys when nut-cracking was taking place. Scrounging often occurred: juveniles up to 3 years of age frequently obtained bits of nuts or other desirable leftovers produced by nut-crackers [see also Fragaszy et al., 1997]. Similarly, in a semi-free living group of *Sapajus* spp. that use tools to crack *Syagrus romazoffiana* palm nuts, juveniles commonly observed others cracking nuts and scrounged bits of nuts from others [Coelho et al., 2015].

Several factors can account for the striking difference in the attention devoted to dry cashew nut processing and to palm nut cracking events.

First, tool use for cracking dry cashew nuts occurs both on trees and on the ground and only rarely is the same anvil surface used repeatedly; in contrast, tool use for cracking palm nut occurs over and over again on the same anvils leaving visually salient leftovers [Visalberghi et al., 2013]. Second, one or a few strikes are sufficient to crack the cashew nuts, while many strikes and on average 2–3 min are necessary for palm nuts [Spagnoletti et al., 2011]. Moreover, palm nuts often shatter into multiple pieces with the broken shells still containing small bits of kernel and these leftovers prompt scrounging [Ramos da Silva, 2008]. In contrast, cashew nuts are fully consumed. Cashew nuts can be cracked from a seated posture whereas cracking palm nuts typically involves an erect bipedal posture. Cracking cashew nuts produces less noise than cracking palm nuts, because the strikes are less forceful. All these factors contribute to making cracking cashews with a tool less visually salient than cracking palm nuts with a tool. Finally, retrieving abandoned cracked cashew shells is not profitable since they still contains the caustic resin but little to no edible leftovers.

Nevertheless, social influences may still affect the interest of youngsters toward cashew nuts even though they do not closely watch others processing these nuts. Adults' feeding on nuts may prompt youngsters to stay close by, and possibly facilitates their consumption of this food item and/or helps them overcome their initial disinterest toward nuts (or possible aversion, see Section below).

Risk Aversion and Acceptance of Risky Food

During our data collection, we rarely observed signs of discomfort (drooling and scratching) and we never observed individuals with blisters; however, in 2011, we observed blisters apparently due to CNSL on the lips of a young capuchin in FBV (see Supplemental Material S9). Therefore, it is possible that capuchins that early in life had experienced the CNSL, later avoid this food item until they acquire some of the skills or strength necessary to process it. We assumed that contact is an index of interest and that its absence indicates disinterest or caution. As expected, we found that youngsters contacted the "risky/difficult to process" cashew nuts significantly less than adults do, but both adults and youngsters show equivalent interest in the apples. Young capuchins usually mouth or bite food items that they cannot yet consume, in contrast, the young monkeys in our study did not even try to process the cashew nuts, or did so to a very limited extent. Thus, we propose that they avoided them because of previous noxious experience. In other words, young individuals might have been risk averse, that is, unwilling to consume a food type that had been associated with negative consequences.

This pattern matches that seen in juvenile white-faced capuchins, that rarely consume *Sloanea* seeds, often discard *Sloanea* fruits before opening them and, when they do it, they frequently rub their faces and sneeze [O'Malley and Fedigan, 2005a]. As does CNSL, the urticating hairs present in *Sloanea* fruits produce long-lasting irritation to the skin; moreover, CNSL produces drooling. Perhaps, the initial reluctance of young capuchin monkeys to process *Sloanea* fruits and cashew nuts is due to a few events in which a young individual experiences the aversive effect of the hairs of *Sloanea* or CNSL of cashews. This phenomenon bears a resemblance to the food aversion documented by Garcia et al. [1955] [Garcia and Koelling, 1966] in rats that associated gastrointestinal illness with the novel food consumed earlier.

How juveniles overcome their initial reluctance to handling and eating cashew nuts is not yet understood. We suggest that youngsters' consumption of cashew nuts is socially facilitated by adults eating food in the vicinity. In fact, several studies demonstrated that eating is socially facilitated by seeing/hearing others eating food [Ferrari et al., 2005] and that social facilitation of eating allows tufted capuchin monkeys (*Sapajus* spp.) [Addessi et al., 2007; Visalberghi and Addessi, 2000, 2001] and human children [Galloway et al., 2005] to overcome caution toward novel food.

The Different Approach to Cashews Nuts in Two Populations of Bearded Capuchins

Understanding the benefits and costs of feeding on particular embedded foods requires attention to many facets of the foraging process, including the strength and dexterity required to breach the plant's defenses and the possible costs of doing so ineffectively. Cashew nut processing has an obvious adaptive value, but the nutritious kernel requires processing techniques that minimize the risk of injury. To achieve this goal human beings use fire [Mohod et al., 2010] or, more rarely, tools [Elisabetta Visalberghi, Personal observation]. The ability of FBV capuchins to avoid the caustic liquid/resin present in the cashew mesocarp, which effectively deters most other seed predators, is remarkable.

This study demonstrates that capuchin monkeys at FBV process cashew nuts using different sets of behaviors according to the ripeness of the fruit and state (liquid/resin) of the CNSL present in its mesocarp. Namely, they access the kernel of fresh nuts by rubbing the nut on substrates and use tools or their teeth to open dry nuts. In contrast, the population of bearded capuchins living in SCNP, 320 km from FBV, uses tools to smash/crack both fresh and dry nuts [Falótico, 2011]. Since blisters on the lips are apparently common in SCNP [Falótico, 2011] and rare in FBV (see above), it can be argued that the use of different techniques to access fresh and dry nuts reduces the risk of chemical burns for FBV capuchins. Thus, cashew nut processing in bearded capuchin monkeys may join the list of behaviors related to feeding and to social interactions [e.g., Panger et al., 2002; Perry, 2011] that are distinctively different across groups and that develop over a period of years in supportive social contexts. Future studies should investigate how differences across populations come about, particularly as close observation does not seem a likely contributor to learning how to process cashew nuts for the monkeys at FBV.

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