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# Age-Related Variation in the Mechanical Properties of Foods Processed by *Sapajus libidinosus*

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*KEY WORDS* juvenile primates; mechanically protected foods; toughness; elastic modulus

## ABSTRACT

**Objectives:** The diet of tufted capuchins (*Sapajus*) is characterized by annual or seasonal incorporation of mechanically protected foods. Reliance on these foods raises questions about the dietary strategies of young individuals that lack strength and experience to access these resources. Previous research has demonstrated differences between the feeding competencies of adult and juvenile tufted capuchins. Here we test the hypothesis that, compared to adults, juveniles will process foods with lower toughness and elastic moduli.

**Materials and Methods:** We present data on variation in the toughness and elastic modulus of food tissues processed by *Sapajus libidinosus* during the dry season at Fazenda Boa Vista, Brazil. Food mechanical property data were collected using a portable universal mechanical tester.

**Results:** Results show that food tissues processed by the capuchins showed significant differences in toughness and stiffness. However, we found no relationship between an individual's age and mean or maximum food toughness or elastic modulus, indicating both juvenile and adult *S. libidinosus* are able to process foods of comparable properties.

**Discussion:** Although it has been suggested that juveniles avoid mechanically protected foods, age-related differences in feeding competence are not solely due to variation in food toughness or stiffness. Other factors related to food type (e.g., learning complex behavioral sequences, achieving manual dexterity, obtaining physical strength to lift stone tools, or recognizing subtle cues about food state) combined with food mechanical properties better explain variation in juvenile feeding competency. Am J Phys Anthropol 000:000–000, 2015.

Juvenile mammals are weaned individuals that, by definition, have not reached skeletal or sexual maturity (Borries et al., 2014). They forage independently to meet their nutritional needs, which, because of their small body size and the demands of growth, are greater than those of adult males and females without dependent offspring (Rothman et al., 2008). Obtaining adequate nutrition has been shown to be a critical influence on growth rates, time to sexual maturity, and lifetime reproductive fitness in primates (Altmann, 1998; Altmann and Alberts, 2005). Because of their increased nutritional requirements, juvenile primates may be more vulnerable to spatiotemporal variability in food resources than adults (Chapman et al., 2012).

The development of adult foraging and feeding behaviors varies among primates. Several wild populations exhibit few differences between juveniles and adults with respect to diet or foraging and feeding ability (e.g., Watts, 1985; Tarnaud, 2004; MacKinnon, 2005; Stone, 2006; Nowell and Fletcher, 2008; Schiel et al., 2010; McGraw et al., 2011). For example, squirrel monkeys at 1 year of age achieve prey capture rates comparable to adults (Stone, 2006, 2007). Similarly, juvenile mountain gorillas select similar plant foods as adults to meet the nutritional demands of growth (Watts, 1985; Rothman et al., 2008). However, other taxa show clear age-related variation in time spent foraging or feeding (Janson and

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van Schaik, 1993; Corp and Bryne, 2002; Hanya, 2003; Johnson and Bock, 2004; O'Malley and Fedigan, 2005; Gunst et al., 2008, 2010b), food intake rates (Post et al., 1980; van Schaik and van Noordwijk, 1986; Boinski and Fragaszy, 1989; Janson and van Schaik, 1993; Corp and Bryne, 2002; Hanya, 2003; Johnson and Bock, 2004; Gunst et al., 2008; Jaeggi et al., 2010), or execution of complex food processing behaviors (Boinski and Fragaszy, 1989; Krakauer, 2005; Gunst et al., 2008, 2010a,b). These age differences in foraging and feeding strategies have been explained by differences in body size and strength, inexperience with searching or processing techniques, or the interaction of these factors (Boinski and Fragaszy, 1989; Janson and van Schaik, 1993; Joffe, 1997; Corp and Bryne, 2002; Resende et al., 2008, 2014; Fragaszy et al., 2010, Gunst et al., 2010b).

Tufted capuchins are ideal species to examine the development of foraging and food processing behaviors. They use a physically demanding foraging style to extract relatively soft foods from tough outer tissues, and these mechanically protected foods are important components of their diet (Izawa, 1977; Terborgh, 1983; Janson and Boinski, 1992; Fragaszy et al., 2004a; Gunst et al., 2008, 2010b). Recent reclassification of the genus *Cebus* has elevated the robust morphotype, including the eight tufted capuchin species, into a sister genus *Sapajus* (*S. apella*, *S. libidinosus*, *S. xanthosternos*, *S. nigritus*¸ *S. cay*, *S. robustus*, *S. macrocephalus*, and *S. flavius*) (Lynch Alfaro et al., 2012). While both *Cebus* and *Sapajus* use complex manipulative behaviors to obtain food (e.g., Panger et al., 2002), *Sapajus* species possess craniomandibular traits considered to be adaptations for orally fracturing mechanically demanding food tissues (Daegling, 1992; Dumont, 1995; Spencer, 2003; Wright, 2005; Wright et al., 2009; Wright et al., 2015). It has been argued that this robust masticatory morphology enables tufted capuchins to broaden their dietary niche to include mechanically protected fruits, bromeliads, and other vegetation when fleshy fruit availability declines (Wright, 2005; Wright et al., 2009). Genera-specific differences in mandibular morphology associated with processing mechanically challenging foods emerge during prenatal development, with tufted capuchins exhibiting traits related to increased masticatory force resistance at birth (Cole, 1992).

Both genera also exhibit relatively long juvenile periods (Fragaszy et al., 2004a). In a population of wild black horned capuchins (*S. nigritus*), weaning occurs between 12-18 months of age (Di Bitetti and Janson, 2001). Estrous cycles begin at four years of age; modal age at first birth is seven years, but can be as early as five years of age (Di Bitetti and Janson, 2001; Fragaszy et al., 2004a). Interbirth interval data suggest weaning age is similar in bearded capuchins (*S. libidinosus*), and the age at first birth is around five years for females (Fragaszy et al., Insights into life history of bearded capuchins (*S. libidinosus*). Longitudinal records of body mass and reproduction. Am J Primatol, in review). The termination of the juvenile stage in males is less well defined. Most authors consider males to be sexually mature by 7 years of age, but males do not reach adult body weight until 10 years (Fragaszy et al., 2004a). However, Fragaszy and Adams-Curtis (1998) have reported a male in a captive group sired offspring as early as 4.4 years of age.

The diets of juveniles and adults overlap in terms of food type in both capuchin genera (Fragaszy and Boinski, 1995; Agostini and Visalberghi, 2005; MacKinnon, 2005). However, field studies have demonstrated age-related differences in feeding ability when individuals process mechanically protected foods. The age at which juvenile tufted capuchins reach adult-level efficiency varies among food types. For example, by 3 years of age, tufted capuchins exhibit adult-like foraging success (measured as the percentage of substrates where feeding occurred) when searching for invertebrate prey types embedded in palm fronds or woody substrates (Janson and van Schaik, 1993). At Raleighvallen, Suriname, Gunst et al. (2010b) found that by 1 year of age, *S. apella* juveniles performed the sequence of behaviors required to peel the *Maximiliana maripa* fruit using their dentition and forelimbs, but lacked the body strength required to remove fruits from the infructescence. In the same study group, juveniles younger than 6 years of age lacked the skills to detect and the physical strength to extract invertebrate larvae from bamboo stalks (Gunst et al., 2010a). In *S. libidinosus* populations where individuals use stone hammers and stone or wood anvils to open the endocarps of mature palm fruits (Fragaszy et al., 2004b), juveniles typically begin striking the hard fruits against stones or other palm fruits by 2–3 years of age and become competent tool users by 4–5 years of age (Spagnoletti et al., 2011; Fragaszy et al., 2013). These studies demonstrate that tasks requiring strength alone, such as processing the maripa palm fruit, are mastered well before those requiring cognitive skills or a combination of skill and strength (Gunst et al., 2008, 2010b).

Age-related changes in extractive foraging competence likely coincide with benchmarks of physical growth, such as increased body size and the eruption of the permanent dentition (Galliari, 1985; Gunst et al., 2008; Fragaszy et al., 2010). Studies describing behavioral changes in feeding competence have linked physical strength (including masticatory strength) to the ability to open mechanically protected foods efficiently (e.g., Gunst et al., 2010a,b), suggesting that when reliance on these foods intensifies, younger (and smaller) individuals will be more at risk of not meeting their nutritional goals than older individuals. As a result, young juveniles may select items of lower toughness within a food type, capture smaller prey items, spend more time feeding, or avoid certain food types entirely (Terborgh, 1983; Janson and van Schaik,1993; Hanya, 2003; Johnson and Bock, 2004; Fragaszy et al., 2004a; Venkataraman et al., 2014; Taniguchi et al., 2015). However, there are few quantitative data on the mechanical properties of foods consumed by juveniles.

Here, we describe variation in mechanical properties across food tissues processed by two wild groups of *S. libidinosus*. This species feeds mostly on fruit tissues, including pulp and seeds, and invertebrate prey. The diets of both groups differ between the dry and wet seasons, with groups increasing seed consumption and decreasing fruit and invertebrate consumption during the dry season (Verderane et al., 2013). We then combine these data with known ages of group members to examine how food mechanical properties vary among individuals of different ages. In light of prior studies indicating juvenile tufted capuchins achieve the physical strength required for reaching adult-level efficiency when feeding on certain food types by 3 years of age (e.g., invertebrates embedded in woody substrates, Janson and Boinski, 1992; Maripa palm fruits, Gunst et al., 2010b), we expect to see an age-related increase in the mechanical properties of foods processed by both *S. libidinosus* groups. Specifically, we predict young juveniles less than 3 years of age will consume less mechanically challenging foods than older juveniles and adults.

## MATERIALS AND METHODS

### Study site and subjects

The data were collected at Fazenda Boa Vista (FBV), Gilbués, Piauí, Brazil (9°39′ 36″S, 45° 25′10″W). This site is a semiarid forest habitat located in the transition zone between cerrado and caatinga habitats (Izar et al., 2012; Verderane et al., 2013). Verderane et al. (2013) examined seasonal shifts in the diet of the FBV *S. libidinosus* groups using data collected from 2006 to 2008. They reported both groups decreased their time spent feeding on fleshy fruits and invertebrates and increased time spent feeding on seeds during the dry season (May–September). Given these results, we conducted our study during the dry season because the capuchins were expected to consume more mechanically demanding foods during this period. We assumed similar seasonal diet variation occurred during the 2009 dry season.

We collected feeding behavior data and food samples from two groups (CH and ZA groups) of wild *S. libidinosus* from June to September 2009. Individuals were recognizable and age is known for all individuals born after 2005. The CH group contained nine adults (individuals $\geq 6$ years, four males, five females), three older juveniles ranging in age from 3 to 5 years (all males), and four young juveniles ranging in age from 9 months to 3 years (three males, one female). The ZA group contained eight adults (three males, five females), one older juvenile ranging in age from 3 to 5 years (male), and three young juveniles ranging in age from 9 months to 3 years (two males, one female). There were three nursing infants of undetermined sex in each group that were excluded from the study. These five age-sex classes were used to facilitate comparisons in figures and in the text.

The CH group was provisioned with water, fruits, and corn as part of tool use experiments conducted at FBV during the study period. Spagnoletti et al. (2012) and Verderane et al. (2013) estimated provisions accounted for an increase of approximately 200 kcal/individual/day. In addition, this group's reliance on provisioned foods varied by season. During the wet season, provisioned foods account for 10% of CH group's feeding time, whereas feeding on provisioned foods increased to 30% during the dry season (Verderane et al., 2013). To mitigate the effects of provisioning on our dataset, no data were collected from individuals foraging on provisioned foods.

### Behavioral sampling and food mechanical property testing

Groups were followed from dawn to dusk for 5 consecutive days, and group follows were alternated to distribute observation periods evenly during the study period. Each observation day was divided into three time blocks. Data were collected on all group members, except nursing infants, using continuous focal animal sampling (Altmann, 1974). Focal animals were selected from a randomized list and followed for 15 min until all individuals were observed once within each time block. When focal data were collected for all individuals within a time block during the 5-day group observation period, the randomized list was started again until all individuals were sampled twice.

We recorded all instances of feeding and the plant tissues processed during the focal sample. Focal samples were divided in feeding bouts. Bouts were defined as continuous feeding on a food type within a food patch. Since plant tissue toughness varies when fracturing the tissue with or against the fiber direction (Lucas et al., 1995), we also noted the specific behaviors that individuals used to process food tissues. Behaviors recorded include manual processing of foods (e.g., pounding, tool use) and placement of foods on the tooth row during ingestion. Food specimens for mechanical properties testing were collected from food items dropped or discarded by the focal animal. When possible, whole plant food specimens of comparable phenophase were collected if no food tissue fragments fell to the ground during a feeding bout. We collected 344 focal samples and tested the mechanical properties of food specimens collected during 254 of those focal samples.

Food items were sealed in plastic bags to preserve freshness and tested within 24 h of collection. Storing food samples in bags for a short period of time like this does not affect their properties (Wright et al., 2008). Prior to testing, foods were photographed and assigned to the most exclusive taxonomic category following Lorenzi (2002). Foods that were not taxonomically identified were included in the dataset as unknown. Foods were divided into tissue types (e.g., exocarp, mesocarp, etc.) following a classification scheme adapted from van Roosmalen (1985). Invertebrates are an important component in the capuchin diet accounting for 33% of the annual diet (Norconk et al., 2009). Feeding on invertebrates differs among age classes, contributing 25% of young juvenile female, 17% of young juvenile male, 23% of older juvenile male, 39% of adult female, and 36% of adult male focal samples, respectively (Chalk, unpublished data). However, mechanical testing of this aspect of the diet was unfeasible in this study because we could not acquire and reliably identify samples of prey items as these were being consumed during feeding bouts. We have just one toughness measure of unidentified wasp cuticle and viscera (mean $R = 845.43$ J m$^{-2}$), tested during a previous field season (Chalk, unpublished data). This value is comparable to published fresh cricket cuticle toughness of 1,345.31 J m$^{-2}$ (Williams et al., 2005). As a result, invertebrates are absent from the food mechanics dataset.

The mechanical properties of interest in this study were toughness ($R$) and elastic modulus ($E$). Toughness describes the energy consumed during the creation of a fracture of given area; elastic modulus (also known as Young's modulus) describes a material's ability to resist deformation along the elastic region of the stress-strain curve (Lucas et al., 2001; Williams et al., 2005). Here elastic modulus is used as an estimate of food stiffness since materials with high moduli are also characterized as stiff materials (Ashby, 1992). All tests were conducted in the field using a portable universal mechanical tester kit fitted with 10 N, 100 N, and 1,000 N load cells (Darvell et al., 1996; Lucas et al., 2001), with properties calculated using custom software (LabVIEW, National Instruments, version 7.0). For the majority of food tissues, scissors or wedge tests were used to determine toughness, and three-point bending or compression tests were used to determine elastic modulus (Lucas et al.,

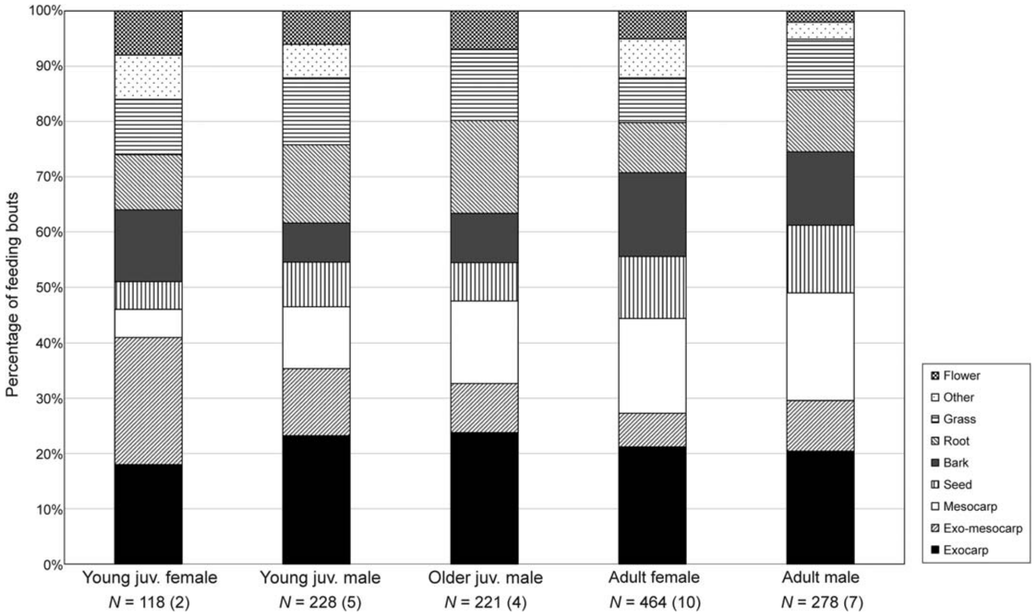

**Fig. 1.** Percentage of bouts devoted to each tissue type according to age-sex class. Sample size (*N*) is the total number of tissues processed for all bouts. The number of individuals within each age-sex class is given in parentheses.

*TABLE 1. Toughness and elastic modulus of food tissues processed by* S. libidinosus

| | $R$ (J m$^{-2}$) | | | | | $E$ (MPa) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Tissue type | *N* | Mean | SE | Max | Min | *N* | Mean | SE | Max | Min |
| Bark | 45 | 1,598.0 | 198.7 | 6,956.9 | 243.3 | 25 | 2,010.8 | 463.5 | 8,886.4 | 0.1 |
| Exocarp | 81 | 1,595.5 | 116.3 | 7,677.8 | 200.4 | 61 | 34.7 | 10.6 | 780.3 | 0.05 |
| Exo-mesocarp | 38 | 1,943.6 | 255.2 | 6,945.3 | 115.6 | 30 | 130.3 | 63.0 | 2,077.7 | 0.06 |
| Flower | 19 | 326.9 | 51.8 | 1,705.6 | 43.4 | | | | | |
| Grass | 38 | 4,007.2 | 629.9 | 15,194.4 | 31.1 | 25 | 3,132.6 | 403.5 | 10,425.7 | 250.9 |
| Mesocarp | 56 | 770.4 | 59.5 | 2,845.6 | 28.7 | 39 | 4.8 | 1.2 | 48.0 | 0.3 |
| Other | 20 | 1,436.6 | 333.9 | 6,740.7 | 112.0 | 11 | 385.7 | 220.8 | 2,431.1 | 0.03 |
| Root | 45 | 2,502.4 | 128.6 | 5,198.6 | 291.4 | 23 | 545.1 | 189.0 | 5,438.4 | 8.6 |
| Seed | 38 | 885.5 | 229.5 | 9,899.4 | 92.1 | 21 | 95.5 | 64.0 | 1,399.1 | 0.3 |

Tissue types include food items not taxonomically identified. See Appendix for descriptive statistics of all taxonomically identified plant foods consumed during the study period.
*N* = number of food tissue specimens. SE = standard error.

2012). We used behavioral data recorded from focal animals to inform how discarded and edible food tissues were tested. For instance, the capuchins processed grasses by stripping portions of the plant off parallel to the fiber direction with the incisors, then biting the grass perpendicular to the fiber direction with the postcanine dentition. As a result, grass toughness was determined by cutting tissues both parallel to and transversely across the fiber direction. Tissues from the same food item were sampled three times.

Both study groups use tools to extract endosperms from palm species, including *Attalea* spp., *Astrocaryum* spp., and *Orbygnia* spp., and tool use accounts for ∼2–5% of feeding time in the wet season and ∼3–6% of feeding time in the dry season (Spagnoletti et al., 2012; Verderane et al., 2013). The objective of this study was to quantify the food material properties of orally processed food tissues. Since palm fruit endocarps were primarily processed with tools, they were not considered here. For toughness, elastic modulus, hardness, and force-to-failure values for palm fruit endocarps see Visalberghi et al. (2008) and Lucas et al. (2009).

## Statistical analysis

Toughness and elastic modulus values were compared among food tissues using Kruskal Wallis tests. Post-hoc Mann-Whitney U tests were used to determine significant pairwise comparisons between food tissues. A Bonferroni correction was applied to all post-hoc pairwise comparisons.

Linear mixed models (LMM) using restricted maximum likelihood were employed to test the relationship between age and food mechanical properties. Following Vogel et al. (2008), if the capuchins processed multiple tissues for a given food item, the food tissue with the highest $R$ and $E$ value was included in the LMMs. Values of mean toughness ($R_{\mathrm{mean}}$), mean elastic modulus ($E_{\mathrm{mean}}$), maximum toughness ($R_{\mathrm{max}}$), and maximum elastic modulus ($E_{\mathrm{max}}$) for all food tissues were used in the analysis. To examine age-related variation in mechanical properties within one species of plant food, we also analyzed a dataset that included only toughness and elastic modulus for *Eschweilera* sp. fruit tissues. We chose *Eschweilera* sp. fruit tissues because of the large number of samples for that food item. For all LMMs, food

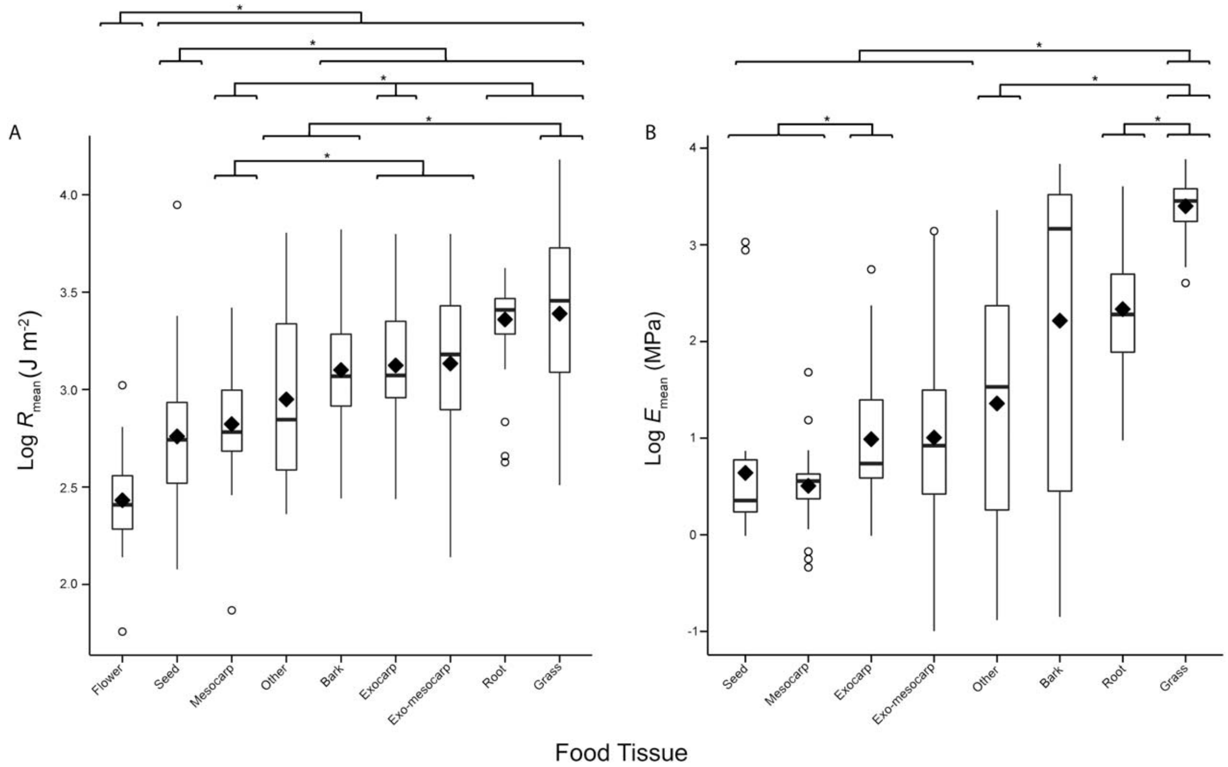

**Fig. 2.** Boxplot of mean log toughness (**A**) and mean log elastic modulus (**B**) of food tissue types. The solid line within the box represents the median and the diamond represents the mean. Asterisks represent significant pairwise differences among tissue types ($P < 0.05$).

mechanical property data were log transformed to normalize the data. We used all available data for each individual and included the individual's identification as a random factor to account for repeated sampling. Age in months, sex, group size, and month of focal sample were included as fixed-effect covariates. Fixed effects included in the models were selected using Akaike's Information Criteria (AIC) (Bolker et al., 2009). Since only one group was observed in September, those data were combined with data from August. Models were fitted using the nlme package in R (Pinheiro et al., 2013). We used post-hoc Kruskal Wallis and Mann-Whitney U tests to compare significant fixed effects. All probability levels are two-tailed; statistical significance for all tests was assessed at $\alpha = 0.05$ level.

## RESULTS

### Comparisons among food tissues

The capuchins processed tissues from 13 identified and several unidentified plant and animal genera. Toughness and elastic moduli of all food tissues processed by the focal individuals during the study period are summarized in Table 1. Overall, age-sex classes processed the same food tissue types (Fig. 1). Fruit exocarp, mesocarp, and seed tissues accounted for more than 50% of focal samples for each age-sex class. Fibrous, non-fruit plant tissues (i.e., roots, grasses, and barks) contributed to 39% of the older juvenile male focal samples, compared with 32% of adult female and 33% of young juveniles and adult male focal samples, respectively. Flowers and other vegetation each accounted for less than 9% of focal samples for all age-sex classes.

Food tissue toughness values ranged from 28.7 to 15,194 J m$^{-2}$ ($n = 380$, mean = 1,714.8 J m$^{-2}$), and elastic moduli ranged from 0.03 to 10,426 MPa ($n = 235$, mean = 653.5 MPa). Food mechanical property data sampled from taxonomically identified plant genera are given in the Appendix. Food tissues processed during the study showed significant differences in toughness (KW $R_{mean}$: $H = 143.9$, $P < 0.001$, Fig. 2A; KW $R_{max}$: $H = 141.1$, $P < 0.001$). Grass stems and roots were the toughest tissues processed by the capuchins. In contrast, flowers had the lowest toughness values of all food tissues tested. Within fruits, outer tissues such as exocarp and exocarp with adherent mesocarp (exo-mesocarp) were significantly tougher than mesocarp and seed tissues (i.e., endocarps excluding palm fruits and endosperms), which themselves did not differ in $R$ values (Fig. 2A). Elastic moduli also differed across plant tissue types (KW $E_{mean}$: $H = 108.4$, $P < 0.001$, Fig. 2B; KW $E_{max}$: $H = 109.8$, $P < 0.001$). Fibrous, non-fruit plant tissues were more resistant to deformation (i.e., with higher elastic moduli) than fruit tissues (exocarps, mesocarps, seed tissues). Among these non-fruit plant tissues, grasses had the greatest values for mean and maximum elastic modulus (Table 1). Within fruits, mesocarp and seed tissues had significantly lower elastic moduli than exocarps (Fig. 2B).

### Comparisons among age classes

Toughness and elastic modulus values for food tissues processed by the FBV capuchins were comparable across age-sex classes (Table 2). For analyses including all food tissues, the best-fit model for mean toughness included group size and age as fixed effects and the best-fit model for maximum toughness included only age as a fixed

*TABLE 2. Comparison of toughness and elastic modulus of foods processed by* S. libidinosus *for the five age-sex classes*

| | $R$ (J m$^{-2}$) | | | | $E$ (MPa) | | | |
|---|---|---|---|---|---|---|---|---|
| Age class | $N$ | Mean | Max | Min | $N$ | Mean | Max | Min |
| Young juvenile female (9 months to 3 years) | 39 | 2,120.2 | 9,346.3 | 68.4 | 16 | 252.4 | 2,985.2 | 1.0 |
| Young juvenile male (9 months to 3 years) | 83 | 1,747.3 | 7,677.8 | 31.1 | 51 | 753.1 | 9,245.8 | 0.0 |
| Older juvenile male (3 to 5 years) | 46 | 1,915.1 | 13,021.2 | 28.7 | 28 | 602.2 | 8,715.6 | 0.3 |
| Adult female (≥ 6 years) | 122 | 1,570.0 | 14,230.1 | 43.4 | 70 | 877.9 | 10,425.7 | 0.1 |
| Adult male (≥ 6 years) | 89 | 1,605.9 | 15,194.4 | 87.7 | 68 | 469.6 | 9,296.9 | 0.1 |

$N$ = number of food tissue specimens.

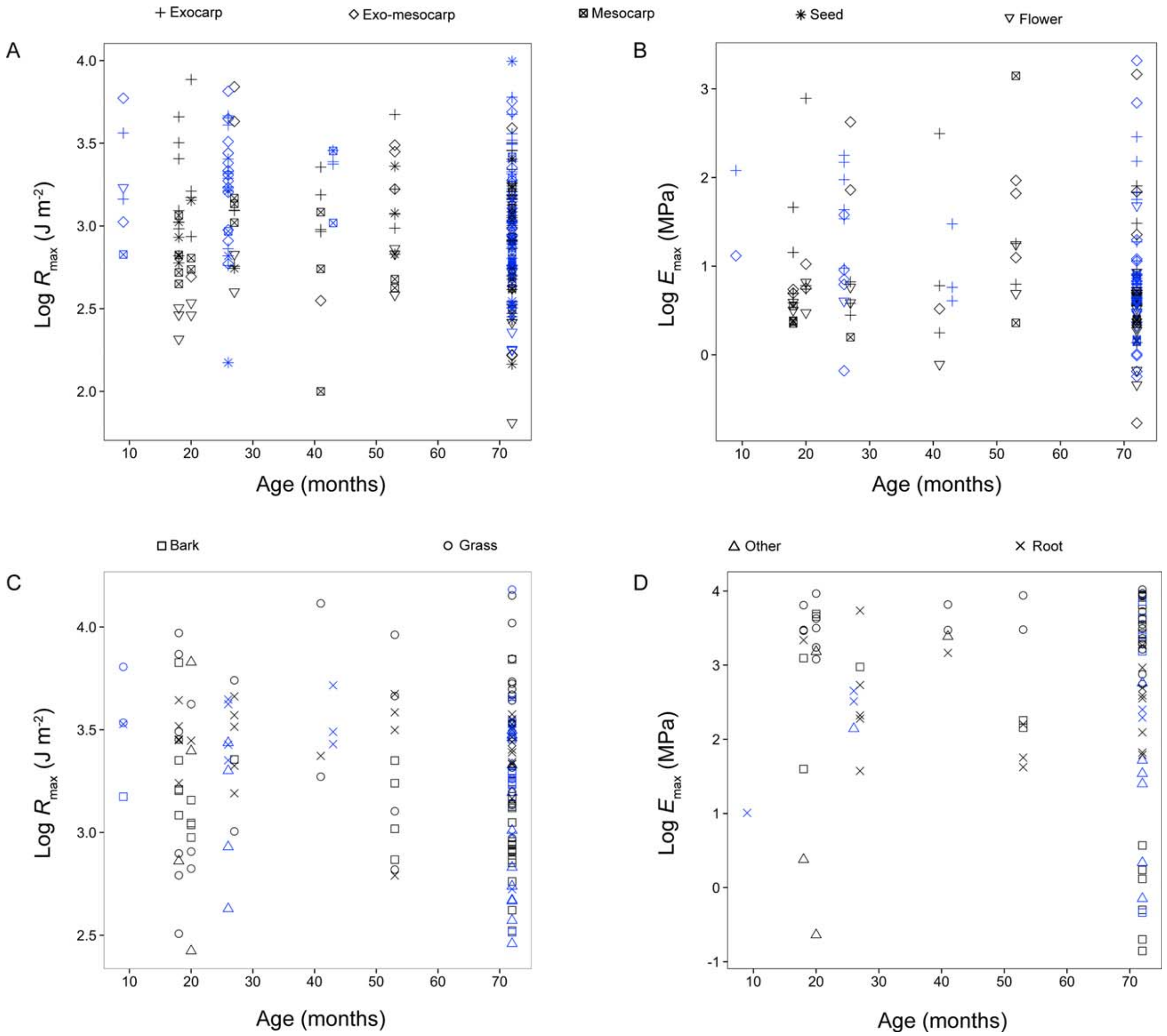

**Fig. 3.** Toughness and elastic modulus values for food tissues processed by focal animals in CH group (black) and ZA group (blue). Each point represents one food tissue sample. Maximum log toughness of fruit tissues (**A**), maximum log elastic modulus of fruit tissues (**B**), maximum log toughness of non-fruit tissues (**C**), maximum log elastic modulus of non-fruit tissues (**D**) did not differ among individuals of different ages. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

effect. The best-fit models for mean and maximum elastic modulus included group, month, and sex as fixed effects. There was no evidence for an effect of age on food mechanical properties, since age in months was not selected as main predictor in the best-fit models for toughness or elastic modulus and was not significant in the best-fit toughness models ($R_{mean}$ LMM: df = 25, $t = -1.6783$, $P = 0.109$; $R_{max}$ LMM: df = 26, $F = 2.787$, $P = 0.107$). Comparisons of maximum toughness and elastic modulus of all food tissues processed by focal animals showed overlap across individuals of different ages (Fig. 3). Similarly, age was not selected as a main predictor in

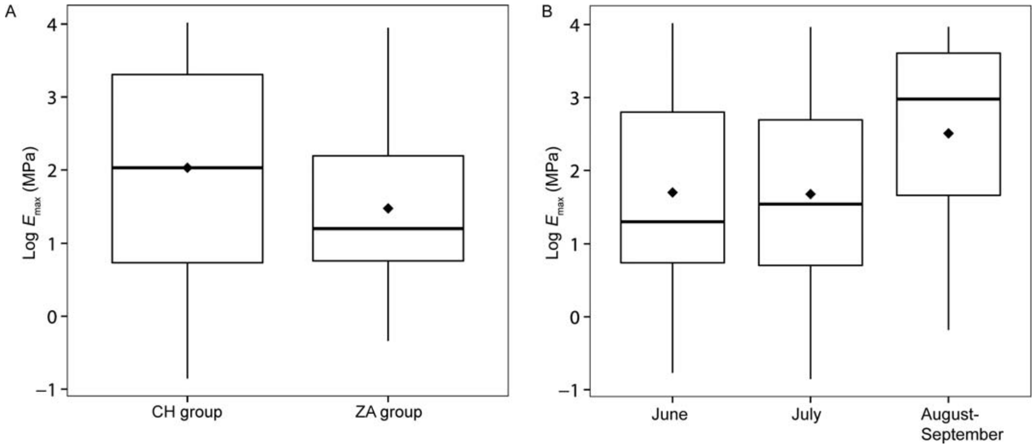

**Fig. 4.** Comparison of elastic modulus of foods processed by the two *S. libidinosus* groups over the duration of the study. CH group processed tissues with greater elastic modulus (**A**). Foods processed in June and July were lower in elastic modulus than those processed in August and September (**B**). Data were collected from only one group in September, and these were included with the August samples for analysis. The solid line within the box represents the median and the diamond represents the mean.

the best-fit models for both mean and maximum toughness or elastic modulus of *Eschweilera* sp. fruit tissues.

There was significant variation in the elastic modulus of all food tissues processed by the two groups (Fig. 4A). The members of the CH group consumed foods with higher mean and maximum elastic moduli than focal animals in the ZA group ($E_{\mathrm{mean}}$ MWU: $T = 2787$, $P = 0.0222$; $E_{\mathrm{max}}$ MWU: $T = 2731$, $P = 0.0139$). We also found a significant relationship between elastic modulus of all food tissues and month (Fig. 4B). Capuchins ate foods with higher mean and maximum elastic moduli in August and September than June and July ($E_{\mathrm{mean}}$ KW: $H = 9.06$, $P = 0.0178$; $E_{\mathrm{max}}$ KW: $H = 9.984$, $P = 0.0068$).

## DISCUSSION

### Food mechanical property variation

During the dry season, the capuchin diet at FBV consists of foods with a mean toughness of 1,715 J m$^{-2}$ and a mean stiffness of 654 MPa. The mean toughness of foods processed by FBV capuchins is comparable to that reported by Wright (2005) for *S. apella* (mean $R = 1{,}110.54$ J m$^{-2}$ for foods processed with the incisors or canines, mean $R = 668.56$ J m$^{-2}$ for foods processed with the postcanine teeth) and for *C. olivaceus* (mean $R = 1{,}042.06$ J m$^{-2}$ for foods processed with the incisors or canines, mean $R = 390.04$ J m$^{-2}$ for foods processed with the postcanine teeth) at Turtle Mountain, Iwokrama Reserve, Guyana and for earlier work with *S. libidinosus* at FBV (Wright et al., 2009). The FBV groups also regularly processed foods exceeding this mean toughness value. The greatest maximum toughness value measured during this study was 15,194.4 J m$^{-2}$, which is nearly 9 times greater than the mean. Similarly, *S. apella* has been shown to ingest food tissues with maximum toughness of 10,908.8 J m$^{-2}$; these maximally tough food tissues processed by both *Sapajus* species are more than three times greater than the maximum toughness of fruit processed by *C. olivaceus* (Wright, 2005).

The inclusion of exceedingly tough or stiff food tissues in the diet is consistent with the feeding strategy previously described for *S. libidinosus* in which mechanically protected foods are important and possibly preferred dietary components (Wright et al., 2009). Our results complement previous work at FBV demonstrating that both groups intensify their feeding on seeds in the dry season (Verderane et al., 2013). The capuchins showed a preference for fruit tissues (>50% of the tested foods). For many fruit species, animals removed and discarded the tough outer tissues to gain access to the pulp or seeds. In the case of *Eschweilera* sp. fruits (~50% of the fruit tissues tested) and palm fruits, the immature seeds appeared to be targeted for water, with individuals opening the seed and drinking the sweet liquid inside (Chalk, personal observations).

Grass, roots, and bark were the food items with the greatest toughness and elastic moduli. Both CH and ZA groups have been shown to increase the proportion of time spent feeding on roots and other fibrous, non-fruit plant foods during the dry season (Verderane et al., 2013). Reliance on these items in later months of the dry season likely explains the observed increase in food tissue elastic modulus from June and July to August and September. Roots were dug from underground and outer tissues were stripped using the anterior dentition. Often the inner tissue was completely consumed; as a result, few samples of this inner root tissue are represented in the dataset. Inner root tissues were tested for three feeding bouts, and the toughness values for these samples ranged from 291.40 to 2,674.7 J m$^{-2}$. Bark was never masticated by the capuchins, but was stripped off tree limbs with the anterior dentition and forelimbs for access to invertebrates. Grasses, particularly the grass stem near the root, constituted the toughest and stiffest items in the diet. Yamashita et al. (2009) reported similar toughness for bamboo processed by species of *Hapalemur*; however, the toughest bamboo tissues were not always masticated. Similarly, the capuchins at FBV removed portions of grass stem with the postcanine dentition, masticating and occasionally fracturing the tissue, then expelling the fibrous remains.

Interestingly, we found individuals in CH group processed foods with higher elastic modulus than those in ZA group. The provisioning of CH group provides a potential explanation for this difference. Verderane et al. (2013) attributed the shorter day ranges and increased time spent resting observed in CH group compared to

ZA group to provisioning. It is possible that, with their hydration and caloric needs met, CH group is free to engage in "snacking" on foods including roots and grasses and stripping bark to locate invertebrate prey during periods of rest. Currently, it is unclear if these foods provide a source of macro- or micronutrients not present in the CH group diet.

## Age-related changes in food mechanical properties

We found no support for the hypothesis that juveniles process less mechanically challenging foods than adults. Juvenile and adult capuchins at FBV breached foods of similar toughness and elastic modulus, indicating that foods processed by adults are accessible by juveniles after weaning. Our results fit with comparable food mechanical property data sampled from multiple age classes, which are available for only a few primate species. For example, dietary toughness was similar between juvenile and adult white faced saki monkeys (*Pithecia pithecia*), and age-related differences in diet were attributed to the lack of masticatory strength of juveniles to access some adult foods (Robl, 2008). Overlap in dietary mechanical properties has also been reported for immature and adult orangutans (van Schaik et al., 2009), red mantled howler monkeys (Raguet-Schofield, 2010), and sooty mangabeys (McGraw et al., 2011). These data provide compelling evidence that juvenile and adult diets are largely similar in terms of mechanical demand in a diverse array of primate taxa. Despite this diversity, some taxa do exhibit significant variation in the mechanical properties of juvenile and adult diets. For example, Venkataraman et al. (2014) reported small and medium juvenile geladas consume foods of lower toughness than large juveniles and adults.

Our findings suggest that masticatory strength alone does not limit juvenile tufted capuchins' access to the majority of foods in their diet. Morphological traits that act to reduce masticatory stress in *Sapajus* relative to *Cebus* are apparent early in development (Cole, 1992). Although the fitness consequences are unknown, the early emergence of robust masticatory traits may be advantageous for processing some mechanically demanding foods from a young age. However, the relationship between food mechanical properties and primate masticatory morphology is far from straightforward, in part because the behavioral flexibility that primates exhibit while feeding plays an important role in an individual's ability to modulate masticatory effort.

Feeding behaviors mitigate the demands of processing tough or stiff food tissues. Prior work has demonstrated that juveniles require years of practice to efficiently access foods requiring motor coordination and dexterity, postcranial strength, and/or the ability to detect cues concerning food state (e.g., larvae embedded in bamboo or palm fruits) (Fragaszy et al., 1994; Boinski et al., 2003; Ottoni et al., 2005; Perry and Jimenez, 2006; Gunst et al., 2008, 2010a,b; Rapaport and Brown, 2008). Our results support the hypothesis that juvenile competence when performing these tasks is constrained by the interaction of food mechanical properties and the mastery of the processing behaviors used to access food types (Gunst et al., 2010a; Fragaszy et al., 2013). For example, grasses were among the toughest plant tissues orally processed by the FBV capuchins, but they did not involve complex harvesting steps and were processed by individuals of all observed age classes. By contrast, competent tool use requires physical strength and motor coordination to lift the stone tool and strike the fruit while standing bipedally and is not achieved until 4–5 years of age (reviewed in Fragaszy et al., 2013). As a result, mechanically protected palm fruits opened using tools were the only food item younger juveniles could not access independently. It is worth noting that their inability to use tools does not completely prevent young juveniles' access to palm fruits because they scrounged small portions of fruits from adults. Capuchin adults tolerate infants and young juveniles investigating their feeding sites. This pattern of harvesting scraps and tolerated food theft from adults is common in *Cebus* and *Sapajus*, but this tolerance generally does not extend to older juveniles (Fragaszy et al., 1997, 2013; MacKinnon, 2005).

In addition to scrounging, other extraoral processing behaviors likely facilitate young juveniles' access to mechanically demanding foods. Both adult and juvenile capuchins engage in strenuous extraoral behaviors, recruiting the use of the fore- and/or hindlimbs and nuchal musculature, to access embedded foods or reduce overall food size prior to ingestion. Furthermore, experimental work has demonstrated that primates adjust bite size in response to food toughness variation (Perry and Hartstone-Rose, 2010; Hartstone-Rose et al., 2015). Smaller bite sizes would allow juveniles to place tough or stiff foods on the postcanine dentition, where masticatory muscles have a greater mechanical advantage. However, ingesting less food per bite could result in lower daily caloric and key nutrient intakes, requiring juveniles allocate more time per day to foraging and feeding. While it is clear that capuchin juveniles and adults process foods of comparable mechanical demand, the data presented here cannot address whether juveniles require additional and/or prolonged oral and manual processing behaviors to access foods of comparable toughness or stiffness or have lower food intake rates. For a species that routinely utilizes mechanically protected foods, the high handling costs of processing those foods may limit daily food intake (Irwin et al., 2014); as a result, young juveniles may find it difficult to consume enough food to buffer themselves from periods of nutritional stress when mechanically challenging resources are significant dietary components. Further research on the nutritional components and food intake rates is needed to address this hypothesis.

## CONCLUSIONS

We have described the variation in the toughness and elastic modulus of food tissues consumed by *S. libidinosus* during the dry season. Although previous studies have documented differences between adult and juvenile tufted capuchin foraging strategies, juveniles did not select foods with significantly lower mean or maximum toughness and elastic modulus, suggesting juveniles and adults are capable of processing foods of comparable food mechanical properties. Juveniles' inability to process mechanically protected foods appears to be more directly linked to the need to master foraging and feeding behaviors requiring fine motor control or complex sequences of actions than food toughness or stiffness.

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## APPENDIX

Descriptive statistics for identified plants processed by *S. libidinosus*

| Plant family | Plant species | Tissue type | $R$ (J m$^{-2}$) | | | | $E$ (MPa) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | $N$ | Mean | Max | Min | $N$ | Mean | Max | Min |
| Anacardiaceae | *Anacardium* sp. | BA | 2 | 4,097.4 | 6,956.9 | 1,072.7 | | | | |
| | | EX | 2 | 491.2 | 637.2 | 381.7 | | | | |
| | | EXM | 5 | 823.5 | 1,597.7 | 299.1 | 4 | 1.1 | 3.3 | 0.6 |
| | | SE | 1 | 128.1 | 149.2 | 111.3 | | | | |
| | | RT | | | | | 1 | 324.5 | | |
| Bignoneaceae | *Jacaranda* sp. | EXM | 3 | 4,285.6 | 6,9453 | 2,741.8 | 3 | 32.1 | 72.3 | 13.1 |
| | | SE | 1 | 1,270.5 | | | 1 | 1.7 | 2.2 | 1.3 |
| Caryocaraceae | *Caryocar* sp. | BA | 1 | 1,369.1 | 1,738.6 | 999.6 | 1 | 2,087.8 | 2,400.0 | 1,775.6 |
| Icacinaceae | *Emmotum nitens* | EX | 1 | 267.1 | 308.2 | 233.3 | | | | |
| Lecythidaceae | *Eschweilera* sp. | EX | 40 | 1,156.1 | 4,735.1 | 235.2 | 36 | 4.9 | 14.3 | 0.0 |
| | | EXM | 2 | 635.1 | 1,069.6 | 462.2 | 2 | 4.9 | 6.8 | 2.7 |
| | | ME | 41 | 793.8 | 2,845.6 | 182.7 | 33 | 3.6 | 8.6 | 1.3 |
| | | SE | 19 | 495.1 | 1,453.3 | 92.1 | 12 | 2.0 | 6.7 | 0.3 |
| | | FL | 6 | 350.9 | 833.0 | 112.3 | | | | |
| Leguminosae - Caesalpinaceae | *Dimorphandra mollis* | BA | 3 | 3,127.0 | 6,709.5 | 949.1 | 1 | 732.8 | 945.0 | 566.5 |
| Leguminosae - Caesalpinaceae | *Hymenaea* sp. | EX | 4 | 2,534.2 | 4,717.7 | 1,565.0 | 4 | 93.6 | 313.0 | 11.2 |
| | | ME | 4 | 478.9 | 1,280.5 | 28.7 | 3 | 5.4 | 17.5 | 0.3 |
| | | SE | 1 | 2,393.9 | 2,533.4 | 2,297.7 | 1 | 4.4 | 5.2 | 3.7 |
| Leguminosae - Caesalpinaceae | *Hymenaea stigonocarpa* | EX | 7 | 1,512.1 | 3,184.3 | 600.1 | 4 | 1.9 | 3.7 | 0.7 |
| | | EXM | | | | | 2 | 10.5 | 22.7 | 1.2 |
| | | ME | 7 | 715.7 | 1,716.1 | 253.4 | 2 | 0.9 | 2.1 | 0.5 |
| | | SE | 2 | 639.6 | 854.3 | 346.3 | 2 | 4.5 | 6.5 | 1.6 |
| Leguminosae - Caesalpinaceae | *Sclerolobium paniculatum* | EX | 4 | 929.1 | 1,623.5 | 200.4 | | | | |
| | | EXM | | | | | 2 | 8.4 | 12.5 | 4.6 |
| | | SE | 3 | 3,731.4 | 9,899.4 | 913.0 | | | | |
| Leguminosae-Mimosoideae | *Parkia pendula* | FL | 1 | 1,052.9 | 1,705.6 | 497.5 | | | | |
| Palmae-Arecaceae | *Mauritia flexuosa* | OT | 1 | 709.0 | 1,023.5 | 536.8 | 1 | 0.5 | 0.7 | 0.3 |
| Palmae-Arecaceae | *Syagrus* sp. | EX | 1 | 906.4 | 1,338.2 | 638.2 | | | | |
| | | ME | 1 | 521.5 | 755.7 | 137.3 | | | | |
| Tiliaceae | *Luehea* sp. | EX | 17 | 2,592.4 | 6,002.5 | 513.7 | 14 | 70.2 | 287.3 | 6.9 |

$N$ = number of food tissue specimens.
Tissue type: BA, bark including cambium and phloem tissues; EX, exocarp; EXM, exocarp and mesocarp; FL, flower; ME, mesocarp; OT, other; RT, root; SE, seed.
For some tissues, collected samples were insufficient for testing both toughness and elastic modulus, and only one property was measured.

## LITERATURE CITED

Agostini I, Visalberghi E. 2005. Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group of wild tufted capuchin monkeys (*Cebus nigritus*). Am J Primatol 65:335–351.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–265.

Altmann J, Alberts SC. 2005. Growth rates in a wild primate population: ecological influences and maternal effects. Behav Ecol Sociobiol 57:490–501.

Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago: University of Chicago Press.

Ashby MF. 1992. Materials selection in mechanical design. Oxford: Pergamon Press.

Boinski S, Fragaszy DM. 1989. The ontogeny of foraging in squirrel monkeys, *Saimiri oerstedi*. Anim Behav 37:415–428.

Boinski S, Quatrone RP, Sughrue K, Selvaggi L, Henry M, Stickler CM, Rose LM. 2003. Do brown capuchins socially learn foraging skills? In: Fragaszy D, Perry S, editors. The biology of tradition: models and evidence. Cambridge: Cambridge University Press. p 365–390.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135.

Borries C, Lu A, Ossi-Lupo K, Larney E, Koenig A. 2014. The meaning of weaning in wild Phayre's leaf monkeys: last nipple contact, survival, and independence. Am J Phys Anthropol 154:291–301.

Chapman CA, Rothman JM, Lambert JE. 2012. Food as a selective force in primates. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB, editors. The evolution of primate societies. Chicago: University of Chicago Press. p 149–168.

Cole TM. 1992. Postnatal heterochrony of the masticatory apparatus in *Cebus apella* and *Cebus albifrons*. J Hum Evol 23: 253–282.

Corp N, Byrne RW. 2002. The ontogeny of manual skill in wild chimpanzees: evidence from feeding on the fruit of *Saba Florida*. Behaviour 139:137–168.

Daegling DJ. 1992. Mandibular morphology and diet in the genus *Cebus*. Int J Primatol 13:545–570.

Darvell BW, Lee PKD, Yuen TDB, Lucas PW. 1996. A portable toughness tester for biological materials. Meas Sci Technol 7: 954–962.

Di Bitetti MS, Janson CH. 2001. Reproductive socioecology of tufted capuchins (*Cebus apella nigritus*) in northeastern Argentina. Int J Primatol 22:127–142.

Dumont ER. 1995. Enamel thickness and dietary adaptation among extant primates and chiropterans. J Mammal 76: 1127–1136.

Fragaszy D, Izar P, Visalberghi E, Ottoni EB, de Oliveira MG. 2004b. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. Am J Primatol 64:359–366.

Fragaszy D, Pickering T, Liu Q, Izar P, Ottoni E, Visalberghi E. 2010. Bearded capuchin monkeys' and a human's efficiency at cracking palm nuts with stone tools: field experiments. Anim Behav 79:321–332.

Fragaszy DM, Adams-Curtis LE. 1998. Growth and reproduction in captive tufted capuchins (*Cebus apella*). Am J Primatol 44:197–203.

Fragaszy DM, Biro D, Eshchar Y, Humle T, Izar P, Resende B, Visalberghi E. 2013. The fourth dimension of tool use: temporally enduring artefacts aid primates learning to use tools. Philos Trans R Soc B 368:20120410-

Fragaszy DM, Boinski S. 1995. Patterns of individual diet choice and efficiency of foraging in wedge-capped capuchin monkeys (*Cebus olivaceus*). J Comp Psychol 109:339–348.

Fragaszy DM, Feuerstein JM, Mitra D. 1997. Transfers of food from adults to infants in tufted capuchins (*Cebus apella*). J Comp Psychol 111:194–200.

Fragaszy DM, Visalberghi E, Fedigan LM. 2004a. The complete capuchin: the biology of the genus Cebus. Cambridge: Cambridge University Press.

Fragaszy DM, Vitale AF, Ritchie B. 1994. Variation among juvenile capuchins in social influences on exploration. Am J Primatol 32:249–260.

Galliari CA. 1985. Dental eruption in captive-born *Cebus apella*: from birth to 30 months old. Primates 26:506–510.

Gunst N, Boinski S, Fragaszy DM. 2008. Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. Behaviour 145:195–229.

Gunst N, Boinski S, Fragaszy DM. 2010a. Development of skilled detection and extraction of embedded prey by wild brown capuchin monkeys (*Cebus apella apella*). J Comp Psychol 124:194–204.

Gunst N, Leca JB, Boinski S, Fragaszy D. 2010b. The ontogeny of handling hard-to-process food in wild brown capuchins (*Cebus apella apella*): evidence from foraging on the fruit of *Maximiliana maripa*. Am J Primatol 72:960–973.

Hanya G. 2003. Age differences in food intake and dietary selection of wild male Japanese macaques. Primates 44:333–339.

Hartstone-Rose A, Parkinson JA, Criste T, Perry JMG. 2015. Comparing apples and oranges—the influence of food mechanical properties on ingestive bite sizes in lemurs. Am J Phys Anthropol 157: 513–518.

Irwin MT, Raharison JL, Raubenheimer D, Chapman CA, Rothman JM. 2014. Nutritional correlates of the "lean season": effects of seasonality and frugivory on the nutritional ecology of diademed sifakas. Am J Phys Anthropol 153:78–91.

Izar P, Verderane MP, Peternelli-dos-Santos L, Mendonça-Furtado O, Presotto A, Tokuda M, Visalberghi E, Fragaszy D. 2012. Flexible and conservative features of social systems in tufted capuchin monkeys: comparing the socioecology of *Sapajus libidinosus* and *Sapajus nigritus*. Am J Primatol 74: 315–331.

Izawa K. 1977. Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). Primates 773–792. 14:

Jaeggi AV, Dunkel LP, van Noordwijk MA, Wich SA, Sura AAL, van Schaik CP. 2010. Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. Am J Primatol 72:62–71.

Janson CH, Boinski S. 1992. Morphological and behavioral adaptations for foraging in generalist primates: the case of the Cebines. Am J Phys Anthropol 88:483–498.

Janson CH, van Schaik CP. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira ME, Fairbanks LA, editors. Juvenile primates: life history, development and behavior. Chicago: University of Chicago Press. p 57–74.

Joffe TH. 1997. Social pressures have selection for an extended juvenile period in primates. J Hum Evol 32:593–605.

Johnson SE, Bock J. 2004. Trade-offs in skill acquisition and time allocation among juvenile chacma baboons. Hum Nat 15: 45–62.

Krakauer, EB. 2005. Development of aye-aye *(Daubentonia madagascariensis)* foraging skills: independent exploration and social learning. PhD thesis Durham, NC: Duke University.

Lorenzi H. 2002. Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil, 2nd ed. Nova Odessa: Plantarum.

Lucas PW, Darvell BW, Lee PC, Yuen TDB, Choong MF. 1995. The toughness of plant cell walls. Philos Trans R Soc Lond B 348:363–372.

Lucas PW, Beta T, Darvell BW, Dominy NJ, Essackjee HC, Lee PKD, Osorio D, Ramsden L, Yamashita N, Yuen TDB. 2001. Field kit to characterize physical, chemical and spatial aspects of potential foods of primates. Folia Primatol 72:11–15.

Lucas PW, Constantino PJ, Chalk J, Ziscovici C, Wright BW, Fragaszy DM, Hill DA, Lee JJW, Chai H, Darvell BW, Lee PKD, Yuen TDB. 2009. Indentation as a technique to assess the mechanical properties of fallback foods. Am J Phys Anthropol 140:643–652.

Lucas PW, Copes L, Constantino PJ, Vogel ER, Chalk J, Talebi M, Landis M, Wagner M. 2012. Measuring the toughness of primate foods and its ecological value. Int J Primatol 33:598–610.

Lynch Alfaro JW, Silva JDSE Rylands AB. 2012. How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. Am J Primatol 74:273–286.

MacKinnon KC. 2005. Food choice by juvenile capuchin monkeys (*Cebus capucinus*) in a tropical dry forest. In: Estrada A, Garber PA, Pavelka M, Luecke L, editors. New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation. New York: Kluwer Press. p 349–365.

McGraw WS, Vick AE, Daegling DJ. 2011. Sex and age differences in the diet and ingestive behaviors of sooty mangabeys (*Cercocebus atys*) in the Tai Forest, Ivory Coast. Am J Phys Anthropol 144:140–153.

Norconk MA, Wright BW, Conklin-Brittain NL, Vinyard C. 2009. Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB, editors. South American primates: comparative perspectives in the study of behavior, ecology, and conservation. New York: Springer Press. p 279–319.

Nowell A, Fletcher A. 2008. The development of feeding behaviour in wild western lowland gorillas (*Gorilla gorilla gorilla*). Behaviour 145:171–193.

O'Malley RC, Fedigan L. 2005. Variability in food-processing behavior among white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. Am J Phys Anthropol 128:63–73.

Ottoni EB, Resende BD, Izar P. 2005. Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. Anim Cogn 24:215–219.

Panger MA, Perry S, Rose L, Gros-Louis J, Vogel E, Mackinnon KC, Baker M. 2002. Cross-site differences in foraging behavior of white-faced capuchins (*Cebus capucinus*). Am J Phys Anthropol 119:52–66.

Perry JMG, Hartstone-Rose A. 2010. Maximum ingested food size in captive strepsirrhine primates: scaling and the effects of diet. Am J Phys Anthropol 142:625–635.

Perry S, Jimenez J. 2006. The effects of food size, rarity, and processing complexity on white-faced capuchins' visual attention to foraging conspecifics. In: Hohman G, Robbins M, Boesch C, editors. Feeding ecology in apes and other primates: ecological, physical, and behavioral aspects. Cambridge: Cambridge University Press. p 203–234.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development CoreTeam. 2013. nlme: linear and nonlinear mixed effects models R package, ver. 3.1-113.

Post DG, Hausfater G, McCuskey SA. 1980. Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender and dominance rank. Folia Primatol 34:170–195.

Raguet-Schofield ML. 2010. The ontogeny of feeding behavior of Nicaraguan mantled howler monkey (*Alouatta palliata*). PhD thesis Urbana, IL: University of Illinois at Urbana-Champaign.

Rapaport LG, Brown GR. 2008. Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. Evol Anthropol 17:189–201.

Resende BD, Nagy-Reis MB, Lacerda FN, Pagnotta M, Savalli C. 2014. Tufted capuchin monkeys (*Sapajus* sp.) learning how to crack nuts: does variability decline throughout development? Behav Process 109:89–94.

Resende BD, Ottoni EB, Fragaszy DM. 2008. Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): a perception-action perspective. Dev Sci 11:828–840.

Robl N. 2008. Ontogenetic resource partitioning in white faced sakis (*Pithecia pithecia*). MA thesis Kent, OH: Kent State University.

Rothman JM, Dierenfeld ES, Hintz HF, Pell AN. 2008. Nutritional quality of gorilla diets: consequences of age, sex, and season. Oecologia 155:111–122.

Schiel N, Souto A, Huber L, Bezerra BM. 2010. Hunting strategies in wild common marmosets are prey and age dependent. Am J Primatol 72:1039–1046.

Spagnoletti N, Visalberghi E, Ottoni E, Izar P, Fragaszy D. 2011. Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. J Hum Evol 61:97–107.

Spagnoletti N, Visalberghi E, Verderane MP, Ottoni E, Izar P, Fragaszy D. 2012. Stone tool use in wild bearded capuchin monkeys, *Cebus libidinosus*. Is it a strategy to overcome food scarcity? Anim Behav 83:1285–1294.

Spencer MA. 2003. Tooth-root form and function in platyrrhine seed-eaters. Am J Phys Anthropol 122:325–335.

Stone AI. 2006. Foraging ontogeny is not linked to delayed maturation in squirrel monkeys (*Saimiri sciureus*). Ethology 112: 105–115.

Stone AI. 2007. Ecological risk aversion and foraging behaviors of juvenile squirrel monkeys (*Saimiri sciureus*). Ethology 113: 782–792.

Taniguchi H. 2015. How the physical properties of food influence its selection by infant Japanese macques inhabiting a snow-covered area. Am J Primatol 77:285–295.

Tarnaud L. 2004. Ontogeny of feeding behavior of *Eulemur fulvus* in the dry forest of Mayotte. Int J Primatol 25:803–824.

Terborgh J. 1983. Five New World primates: a study of comparative ecology. Princeton: Princeton University Press.

van Roosmalen MGM. 1985. Fruits of the Guianan flora. Netherlands: Institute of Systematic Botany.

van Schaik CP, van Noordwijk MA. 1986. The hidden costs of sociality: intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). Behaviour 99:296–314.

van Schaik CP, Van Noordwijk MA, Vogel ER. 2009. Ecological sex differences in wild orangutans. In: Wich SA, Atmoko SSU, Setia TM, Van Schaik CP, editors. Orangutans: geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press. p 255–277.

Venkataraman VV, Glowacka H, Fritz J, Clauss M, Seyoum C, Nguyen N, Fashing PJ. 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). Am J Phys Anthropol 155:17–32.

Verderane MP, Izar P, Visalberghi E, Fragaszy DM. 2013. Socioecology of wild bearded capuchin monkeys (*Sapajus libidinosus*): an analysis of social relationships among female primates that use tools in feeding. Behaviour 150:659–689.

Visalberghi E, Sabbatini G, Spagnoletti N, Andrade FRD, Ottoni E, Izar P, Fragaszy D. 2008. Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). Am J Primatol 70:884–891.

Vogel ER, van Woerden JT, Lucas PW, Atmoko SSU, van Schaik CP, Dominy NJ. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. J Hum Evol 55:60–74.

Watts DP. 1985. Observations on the ontogeny of feeding behavior in mountain gorillas (*Gorilla gorilla beringei*). Am J Primatol 8:1–10.

Williams SH, Wright BW, Truong VD, Daubert CR, Vinyard CJ. 2005. Mechanical properties of foods used in experimental studies of primate masticatory function. Am J Primatol 67:329–346.

Wright BW. 2005. Craniodental biomechanics and dietary toughness in the genus *Cebus*. J Hum Evol 48:473–492.

Wright BW, Ulibarri L, O'Brien J, Sadler B, Prodhan R, Covert HH, Nadler T. 2008. It's tough out there: variation in the toughness of ingested leaves and feeding behavior among four Colobinae in Vietnam. Int J Primatol 29:1455–1466.

Wright BW, Wright KA, Chalk J, Verderane MP, Fragaszy D, Visalberghi E, Izar P, Ottoni EB, Constantino P, Vinyard C. 2009. Fallback foraging as a way of life: using dietary toughness to compare the fallback signal among capuchins and implications for interpreting morphological variation. Am J Phys Anthropol 140:687–699.

Wright KA, Wright BW, Ford SM, Fragaszy D, Izar P, Norconk M, Masterson T, Hobbs DG, Alfaro ME, Lynch Alfaro JW. 2015. The effects of ecology and evolutionary history on robust capuchin morphological diversity. Mol Phylogenet Evol 82:455–466.

Yamashita N, Vinyard CJ, Tan CL. 2009. Food mechanical properties in three sympatric species of *Hapalemur* in Ranomafana National Park, Madagascar. Am J Phys Anthropol 139: 368–381.