**Growing up tough: comparing food-toughness effects on juvenile feeding in *Sapajus*
libidinosus and *Trachypithecus phayrei crepusculus***

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Abstract

Studies of primate feeding ontogeny provide equivocal support for reduced juvenile proficiency. When immatures exhibit decreased feeding competency, these differences are attributed to a spectrum of experience- and strength-related constraints and are often linked to qualitative assessments of food difficulty. However, few have investigated age-related differences in feeding ability relative to mechanical property variation across the diet, both within and among food types. In this study, we combined dietary toughness and feeding behavior data collected in the wild from cross-sectional samples of two primate taxa, *Sapajus libidinosus* and *Trachypithecus phayrei crepusculus*, to test the prediction that small-bodied juveniles are less efficient at processing tough foods than adults. We defined feeding efficiency as the time spent to ingest and masticate one food item (item bout length) and quantified the toughness and size of foods processed during those feeding bouts. To make the datasets comparable, we limited the dataset to foods processed by more than one age class and opened without tools. The overall toughness of foods processed by both species overlapped considerably, and juveniles and adults in both taxa processed foods of comparable toughness. Feeding efficiency decreased in response to increasing food toughness in leaf monkeys and in response to food size in both taxa. Age was found to be a significant predictor of bout length in leaf monkeys, but not in bearded capuchins. Juvenile *S. libidinosus* processed smaller fruits than adults, suggesting they employ behavioral strategies to mitigate the effect of consuming large (and occasionally large and tough) foods. We suggest future intra- and interspecific research of juvenile feeding competency utilize intake rates scaled by food size and geometry, as well as by detailed measures of feeding time (e.g., ingestion vs. mastication), in addition to food mechanical properties to facilitate comparisons across diverse food types and feeding behaviors.

Introduction

Primates exhibit distinctively long juvenile periods relative to similar-sized mammals (Harvey and Clutton-Brock, 1985; Pereira and Fairbanks, 1993; Purvis et al., 2003), and this extended immature period can be a time of learning and skill development, as well as a vulnerable period of high mortality risk (Pereira and Altmann, 1985; Walters, 1987; Janson and van Schaik, 1993; Joffe, 1997; Rapaport and Brown, 2008). The transition to nutritional independence, which defines the start of juvenility, is a particularly critical time because feeding and foraging proficiency may be limited by physical maturity or inexperience (ecological risk aversion hypothesis [ERAH]: Janson and van Schaik, 1993; skill-learning hypothesis: Ross and Jones, 1999). Although some primate taxa exhibit little evidence of discernable age differences in feeding rates and patterns (e.g., gorillas: Watts, 1985; Nowell and Fletcher, 2008; squirrel monkeys: Stone, 2006), many field-based studies highlight some degree of age-related variation, such as juveniles spending more time than adults searching for or processing food items (Post et al., 1980; Boinski and Fragaszy, 1989; Marchetti and Price, 1989; Hauser, 1993; Rolseth et al., 1994; Corp and Byrne, 2002; Hanya, 2003; Johnson and Bock, 2004; Daunt et al., 2007; Gunst et al., 2008, 2010a, b; Raguette-Schofield, 2010; Chalk, 2011; Ossi-Lupo, 2014; O'Mara, 2015).

Age differences in feeding proficiency often are attributed either to skill-related limitations linked to cognitive development or to physical limitations, such as juveniles' smaller size and lesser strength. Evidence for the role of practice and socially mediated learning in skill development has been documented in investigations of complex foraging tasks, such as detecting and extracting embedded resources (Gibson, 1986; Johnson and Bock, 2004; Krakauer, 2005; Gunst et al., 2010a; Eadie, 2015) or tool use (e.g., Lonsdorf, 2005; Sousa et al., 2009; Fragaszy et al., 2013). Together these studies indicate that competency in these cognitively demanding

tasks may develop relatively late in the juvenile period. However, for many food resources, achieving adult-level proficiency ultimately depends on attaining the skeletal, dental, and muscular development required to harvest and efficiently process those foods rather than acquiring complex problem-solving skills (e.g., maripa palms: Gunst et al., 2010b). Across taxa, size-related variables such as body mass, gape, and molar surface area scale positively with feeding variables such as intake rate and bite size (Shipley et al., 1994; Nakagawa, 2009; Perry and Hartstone-Rose, 2010). Although jaw muscle mass and physiological cross-sectional area (PCSA) scale with body size differently across primates, generally, smaller individuals produce absolutely (and for some clades relatively) smaller bite forces (Anapol et al., 2008; Taylor and Vinyard, 2013; Taylor et al., 2015). Growth differs across jaw muscles (Cachel, 1984) and muscle mechanical advantage improves with age (Dechow and Carlson, 1990), suggesting juveniles and adults may engage in disparate jaw muscle recruitment patterns and that juveniles possibly exert less bite force during feeding than adults. As a result, smaller-bodied juveniles are likely to be at a functional disadvantage especially when feeding on tough, hard, or large food items, which may translate to an increased risk of nutritional stress (Janson and van Schaik, 1993).

Food mechanical properties (FMPs) have been used with greater frequency in recent decades as an objective method to compare dietary mechanical demands within and across primate taxa (e.g., Yamashita, 1998; Teaford et al., 2006; Vogel et al., 2008; Wright et al., 2009; Coiner-Collier et al., 2016). One such property, fracture toughness (R), is defined as the energy required to propagate a crack over a given area (Lucas et al., 2001; Williams et al., 2005; Lucas et al., 2012). FMPs, along with other properties such as food size, have been shown to influence food choice, bite size, and food breakdown. In their cross-species comparison, Perry and

colleagues (2015) found that bite sizes tended to be smaller for tougher foods, and food particle breakdown rates in modern humans decline with increasing toughness (Laird et al., 2016). In wild adult primates, processing tough foods has been linked to reduced chewing efficiency as measured by longer feeding bouts (Asian colobines: Wright et al., 2008a) or larger fecal particle size (geladas: Venkataraman et al., 2014).

Given that FMPs represent objective measures for quantifying mechanical demand within and across foods, as well as across different overall diets, these measures are an asset to primate feeding ontogeny studies, which previously relied on age comparisons across broad food categories, focused on one food species, or employed other subjective measures of dietary quality or difficulty. Thus far, results of studies that have explored dietary ontogeny relative to FMPs have been somewhat equivocal. Younger individuals of some species avoid tougher or harder foods (e.g., red uakaris: Bowler and Bodmer, 2011; Japanese macaques: Taniguchi, 2015), while others, including those considered here, exhibit little or no age differences in toughness or hardness of exploited foods (e.g., white-faced saki monkeys: Robl, 2008; howlers: Raguet-Schofield, 2010; sooty mangabeys: McGraw et al., 2011; bearded capuchins: Chalk et al., 2016; Phayre's leaf monkeys: Ossi-Lupo and Koenig, in review). Among taxa that regularly or seasonally exploit tough foods, avoiding these high-toughness foods altogether may not be an option for juveniles. Instead, juveniles may employ behavioral strategies, such as adjusting their feeding time allocation or begging adults for scraps of extracted resources, to meet their nutritional needs (Gunst et al., 2008b). For instance, among gummivorous geladas, cumulative dietary toughness weighted by feeding time was consistently lower for smaller juveniles than for adults or larger juveniles, in part because smaller geladas chose to "focus on more brittle forbs" (Venkataraman et al., 2014: 26). Larger juvenile geladas, in contrast, already exhibited diets that

more closely tracked those of adults, even exceeding adults in cumulative weighted toughness during certain months.

The timing of ontogenetic shifts in feeding proficiency likely is linked, in part, to the pace of hard- and soft- tissue morphological development, and this pacing differs across primate taxa due to body size, dietary category, and life history-related variables. Godfrey et al. (2001) attribute the accelerated dental development of folivorous primate species compared to more frugivorous taxa to selection acting on earlier eruption of the permanent dentition to better equip folivore weanlings for tough, leafy diets. If juvenile folivores have fully occluded permanent dentition at younger ages than frugivores, then folivorous juveniles should likewise achieve earlier adult-level proficiency when processing tough foods. Likewise, species that experience fast somatic growth for their body size may be at a functional advantage when relying on a tougher diet. Early dietary proficiency can have a profound impact on individual lifetime reproductive fitness, as Altmann (1998) demonstrated in yellow baboons (*Papio cynocephalus*). Understanding how juveniles from different species respond to and cope with aspects of their diet informs our understanding of how selection shapes feeding-related morphology and behavior prior to adulthood.

In this paper, we use dietary toughness as a quantitative measure of difficulty (i.e., mechanical demand) to analyze feeding ability across the juvenile period. In addition, we compare two taxa exploiting different diets: *Trachypithecus phayrei crepusculus*, an Asian colobine classified as both a folivore and seed predator (Gupta and Kumar, 1994; Suarez, 2006), and *Sapajus libidinosus*, a frugivorous platyrrhine known for its extractive feeding behaviors (Fragaszy et al., 2004). Previous work has demonstrated that juvenile and adult diets overlap in both taxa, and all weaned age classes consume tough foods items (Chalk et al. 2016; Ossi-Lupo

and Koenig, in review). Furthermore, differences in processing abilities emerge when individuals consume tough items (e.g. Gunst et al., 2010a, b; Venkataraman et al., 2014). We hypothesize that age will impact feeding efficiency, defined here as time spent processing a single food item, as toughness increases. To evaluate this hypothesis, we combine independently collected cross-sectional datasets collected from both taxa. Comparative behavioral data with corresponding data on dietary toughness values collected across a range of age classes are rare. Not only are data currently available for *S. libidinosus* and *T. p. crepusculus*, but these primates also represent examples of primates that routinely consume foods with a broad range of toughness values (Wright et al., 2009; Chalk et al., 2016; Ossi-Lupo and Koenig, in review). If toughness is a primary factor constraining juvenile feeding efficiency in the two study species, we predict that as dietary toughness increases, younger individuals will exhibit longer bout lengths relative to adults because of their smaller masticatory and postcranial strength. As a result, we expect to see an interaction of toughness and age. Alternatively, if juveniles are slower across the range of food toughness (i.e., consistent age differences in the absence of an interaction between toughness and age), this could suggest food characteristics other than toughness are hampering younger individuals. Food geometry and size, for instance, may impact juvenile efficiency independently of toughness (e.g., Janson and Boinski, 1992; Corp and Byrne, 2002). Therefore, we also test whether younger age classes will be less efficient at processing tough foods when accounting for food size. We included this as a separate but complementary test of the main prediction because food-size measures differed between sites (external linear measures for bearded capuchin foods and wet weights for leaf monkey foods) and were available only for a smaller portion of each dataset.

Lastly, we explore species differences in how individuals respond to toughness across ontogeny in the two study species. We expect these species to share the general age-related pattern of reduced juvenile efficiency with increasing food toughness. We refrain from generalizing that the more rapid maturation described for folivores compared to frugivores (e.g., Leigh, 1994; Godfrey et al., 2004) will correspond to ontogenetic feeding patterns between these focal taxa. Instead, we aim only to compare the relationship between feeding efficiency and food toughness between study species.

Materials and methods

For this comparative analysis, we combined datasets from two studies that were designed and carried out separately over different sampling periods. These datasets are suited to investigating the relationship between detailed feeding behavior and dietary toughness across age classes, which warrants combining them in a post hoc manner. In so doing, we have systematically excluded portions of the original data in an effort to make age classes, feeding variables, and toughness measures comparable. Overall toughness is compared between and within species to facilitate the interpretation of age-related variation in feeding efficiency. However, we acknowledge that these data do not represent the full range of dietary toughness in terms of seasonal variation or food types consumed by each focal species.

Study sites

JCW observed bearded capuchins (*S. libidinosus*) at Fazenda Boa Vista (FBV), Gilbués, Piauí, Brazil (9°39'36"S, 45° 25'10"W) from June to September 2009 (510 contact hours, $n = 20$ adults, 8 juveniles). FBV is a semiarid cerrado-caatinga forest with a marked dry season from

May to September (Visalberghi et al., 2007; Verderane et al., 2013). One of two observed groups is provisioned; no data were recorded when animals were feeding on provisioned foods (see Spagnoletti et al. [2012] for provisioning details). In addition, the FBV capuchins use stone hammers to open the woody endocarps of palm fruits; however, the proportion of time spent feeding on foods accessed using tools was less than 3.5 percent of feeding time on average for the non-provisioned group (Verderane et al., 2013). For this reason and because there was no equivalent tool use at the other study site, behavioral and material property data from foods opened using tools were excluded from the current study.

KOL followed three groups of Phayre's leaf monkeys (*T. p. crepusculus*) at the Phu Khieo Wildlife Sanctuary (PKWS) in northeastern Thailand. Within the larger sanctuary, the study site (16°27'N, 101°38'E) was a 1,300 ha area of dry and hill evergreen forest, including patches of dry dipterocarp forest and bamboo (see Koenig and Borries, 2012), with a distinct dry season from November through February (Richter et al., 2016). The data included here were collected from three groups between February and May 2008 (762.3 contact hours; $n = 13$ adults, 14 juveniles).

Age and age class definitions

Traditionally, the juvenile period has been defined as the period between weaning and reproductive maturity (Pereira and Altmann, 1985). Of course, weaning and the transition to nutritional independence is a gradual process (Lee et al., 1991; Lee, 1996, 1999). Each of the juvenile samples tested in this study was comprised mainly of weaned individuals, defined here as having ceased nipple contact (Borries et al., 2001, 2014). Older infants still in occasional nipple contact were included if they were approaching or older than the average weaning age for

that species (*Sapajus* mean age at nipple contact cessation = 12–18 months: Fragaszy et al., 2016, $n = 1$ unweaned subject; *Trachypithecus* = 19 months: Borries et al. 2014, $n = 1$ unweaned subject). Because ages were unknown for many adults of both species, we assigned individuals to one of three age classes for our analysis using the full behavioral and toughness dataset. Younger juveniles (YJs) ranged in age from 10 to 26 months based on ages at the start of each study (*Sapajus* YJs: $n = 4$, mean age = 18.3 months; *Trachypithecus* YJs: $n = 4$, mean age = 19.6 months). Older juveniles (OJs) ranged in age from 27 to 44 months (mean age for *Sapajus* OJs = 32 months, $n = 5$; *Trachypithecus* OJs mean age = 34.6 months, $n = 10$). Adult males and females were grouped together in a single adult age class (*Sapajus*: $n = 19$; *Trachypithecus*: $n = 13$), including older immature males (> 48 months) who had not yet achieved adult male size, but had reached equivalent adult female size (head-body length for *Trachypithecus* or body mass for *Sapajus*).

Ages were known to the birth month for all juvenile subjects and were either known or estimated for a subset of adults. Visalberghi et al. (2016) reported the age in 2012 for seven *Sapajus* adults also included in this study; the published ages were used to calculate age in 2009 for these individuals. In addition, one young adult female was identified as a juvenile during group habituation. We estimated her age from the date of birth of her first presumed offspring and an average age at first birth of 5 years (EthoCebus unpublished data; Fragaszy et al., 2016). For *Trachypithecus*, only one young adult male was known from birth. Three subadult males (classified as adults, see above) were first observed in 2003 as new infants with orange natal coats, and were confidently assigned a birth order in that year's birth season (Borries and Koenig, pers. comm.; see description of orange-to-gray natal coat development in first six months: Borries et al., 2008), which was then used to estimate birth months. Ages for two young

adult females were estimated based on the timing of the birth of their presumed first offspring and the population average age at first birth of 5.3 years (Borries et al., 2011).

Data collection

Feeding behavior and efficiency measure Both studies employed focal animal sampling on individually identified subjects with feeding data recorded continuously (Martin and Bateson, 2007; Table 1). We used food item bout length (IBL), defined as the time in seconds that an individual took to consume a single fruit, leaf, flower, or other food category, as our measure of feeding efficiency. Bouts were initiated when individuals began processing a food item and were terminated when chewing ceased or the item was discarded. Thus, this measure includes handling time for a food item, but excludes search time. For *S. libidinosus*, number of food items was recorded during continuous focal sampling. If an individual consumed more than one food item during a bout, IBL was determined by dividing the total bout length by the number of items consumed during that bout. For *T. p. crepusculus*, IBLs were similarly calculated as time divided by number of whole items, except in the common case of smaller, bite-size items, which were counted as number of items or bites per minute for three continuous minutes, and then the average items per minute was converted back to seconds per item. Contact and focal hours as well as the number of feeding bouts are reported in Table 2.

We restricted the datasets to include plant food items that were taxonomically identifiable (or identifiable to common name) and eaten by more than one age class. Field guides identified plant foods to local names, and identification was confirmed, when possible, using published botanical references; at PKWS, a local botanist from the Royal Forest Department assisted in

plant identification (FBV: Lorenzi, 2002; PKWS: Gardener et al., 2000). In addition, we included only behavioral data with associated toughness data, and only for food items that had been consumed by at least two of the three age classes within each primate species ($n = 69$ foods identified to species or common name with matched behavioral and toughness data for at least two age classes). As a result, the proportions of foods in this study do not reflect the complete observed diet for each separate study. Prior to analysis, we grouped foods into four categories to maximize the overlap in plant parts processed by the focal taxa. These categories were flowers, fruits, leaves and grasses, and roots and barks.

Food mechanical properties Food samples for mechanical properties testing were obtained from food items dropped by focal animals during feeding bouts or collected from the same food patch immediately after focal animals stopped feeding or left the patch. Toughness measures collected at FBV were matched to the food eaten by a particular individual in a single bout, but those collected at PKWS could not be associated with specific individuals or age classes; instead, measures were collected from representative foods from the same patch in which the monkeys fed. Samples were stored in plastic bags and tested within 24 hours of collection. At both field sites, toughness was measured using an HKU portable universal mechanical tester kit fitted with 10N, 100N, and 1000N (FBV only) load cells (Darvell et al., 1996; Lucas et al., 2001). Toughness was calculated using custom software (LabVIEW, National Instruments, version 7.0). We used wedge tests to determine the toughness of fruits and scissor tests to determine the toughness of leaves, flowers, grasses, most seeds, and thin, flat outer tissues of fruits and roots (Lucas et al., 2012).

Toughness typically was calculated for a minimum of two tests per food tissue. As toughness often varies across tissues within a single item, food tissues (e.g., exocarp, mesocarp, endocarp and/or seed casing, and endosperm for fruits or petals, sepal, stamen filaments, and pistil for flowers) were separated and tested individually. For leaves, toughness can vary across different anatomical features (i.e., midvein, secondary veins, and lamina), as well as leaf parts (i.e., tip, middle, base; Lucas et al., 2001; Dominy et al., 2003; Teaforde et al., 2006). The method used for capturing this variation at PKWS followed that described by Lucas and colleagues (2001). Transverse cuts were made at the base, middle, and tip of the leaf, except for very small leaf buds or bipinnate leaves for which only a single cut was made through the center of the leaf. Each cut was further subdivided into anatomical parts. Using the force displacement curve displayed on-screen after each test, the peaks associated with the midvein and secondary vein could be isolated from the lamina part of the curve, resulting in three separate toughness values for a single scissor test (Lucas et al., 2001).

Food size Food size was quantified differently at each field site, and these data were available for a subset of foods eaten by each species (*Sapajus*: $n = 18$ foods, 86 bouts; *Trachypithecus*: $n = 33$ foods, 199 bouts). At FBV, JCW used digital calipers to measure external dimensions (in mm) whenever possible on the actual food eaten or when food remnants could be reconstructed. Measurements were recorded once prior to mechanical testing. The external measurements recorded included diameter for spherical foods, diameters and lengths for ellipsoid foods, and length, breadth, and thickness for sheet-like foods (e.g., bromeliads or root outer tissues). By capturing external dimensions of foods, these values were more consistent at capturing variation

within rather than across food categories. Size measures for *S. libidinosus* foods were specific to individual feeding bouts.

At PKWS, foods were weighed to the nearest tenth of a gram using a small food scale. For very small foods, such as flower buds or some seeds, five to 10 items were placed on the scale together and the combined weight was divided by the number of items to determine an item weight, sometimes resulting in measures to the nearest hundredth of a gram. For each food, wet weight typically was measured for 10 items and then averaged. Unlike at FBV, the food size measure was an average for that food item at the patch or species level and could not be matched with individuals' specific bouts. Therefore, *T. p. crepusculus* wet weights represent size variation across foods but not variation within a particular food species and, therefore, would not indicate any potential age differences in selection preferences within a food species.

Statistical analyses

Food toughness comparisons For all foods, we calculated mean toughness (R_{mean}) by averaging all tissues per food item that were orally processed although not necessarily masticated. Maximum toughness (R_{max}) for each food was the highest value from a single tissue or isolated anatomical part. We used a Welch's t -test for unequal variances to compare R_{mean} and R_{max} between the two focal species. Toughness data for foods processed by all individuals were pooled for this interspecific comparison. Additionally, intraspecific comparisons of R_{mean} and R_{max} among age classes were performed using Welch's ANOVA. For these comparisons of food toughness, data were log-transformed to meet the assumptions of normality and homoscedasticity.

Modeling species differences in feeding efficiency We fit four linear mixed-effect models (LMM) to investigate effects of food toughness on feeding efficiency between and within our two study species (models listed in Supplementary Online Material [SOM] Table S1). The response variable was IBL (seconds); predictor variables included focal species, food toughness (models fit separately for R_{mean} and R_{max}), the interaction of species and toughness, and food category. We included food category as a fixed effect because it likely relates to factors that may influence IBL, such as differences in food-processing techniques or in food geometry (see SOM Table S1). We used an adults-only data subset to determine the relationship between IBL and toughness; immatures were excluded to examine species differences independent of age-related changes in feeding efficiency. To avoid pseudo-replication, we included subject ID, month, and food species or common name as random effects. We were unable to include species as a random slope because there were no common random intercept levels common to both focal taxa on which to allow species slopes to vary. To further account for variation that might otherwise inflate Type I error rates, we included random-slopes terms for food toughness (R_{mean} or R_{max}) on subject ID (Schielzeth and Forstmeier, 2009; Barr et al., 2013).

Modeling the effect of toughness on juvenile and adult feeding efficiency To test our main prediction of whether toughness impacts feeding efficiency in younger individuals more so than in adults, we fit three separate LMMs. The main model was run using the full dataset including both primate taxa, while the two subsequent submodels were tested separately within each primate species. The main model tested the three-way interaction between R (mean and maximum toughness fit separately), age class (adult, older juveniles, and younger juveniles), and

primate species, as well as all two-way interactions between these variables. We also included food category as a fixed effect to account for the influence of factors unique to certain food categories that may influence IBL. Random effects in this main model included subject ID, group, month, and plant species or common name. We included random slope terms for toughness within subject ID and age class within group nested within species. We subsequently refer to this model as the interspecific model (SOM Table S1).

Intraspecific submodels were fit separately on a reduced dataset constructed for each focal taxon to explore age-related effects separate from the potential influence of species-specific differences in food types and processing behaviors. Furthermore, running within-species models allowed for the inclusion of food-size measures (diameter or breadth for the FBV foods, wet weights for the PKWS foods) as a potential additional factor influencing IBLs. Matched food size and toughness data were not available for all bouts, resulting in a smaller dataset than the one included in the age class model described above. Age in months was not known for 10 adults in the *S. libidinosus* dataset and 5 adults in the *T. p. crepusculus* dataset, and these individuals were excluded. These submodels tested a three-way interaction across age in months, *R*, and food size, as well as all two-way interactions. Again, we included food category as a fixed effect. Because of the smaller number of observations included in these submodels, random effects terms differed to avoid overfitting. We included random intercepts of group and subject ID and random-slopes terms for age within group, as well as toughness within subject ID, in both submodels. Subsequently, we refer to these submodels as the intraspecific submodels (SOM Table S1).

If food size affects feeding efficiency, juveniles may process smaller foods than adults. Because *Sapajus* food sizes were specific to individual bouts, we performed one additional non-

parametric test: for each individual, we calculated an average food size for each plant identified. Due to the reduced size of the dataset including food size, we pooled younger and older juveniles into a single juvenile age class. We tested for age class differences in size within food category using Mann-Whitney U tests on untransformed data.

All LMMs were fit using the lme4 package (Bates et al., 2015) in R 3.2.1 (R Development Core Team, 2015). For all models, we checked for normality and homoscedasticity by visual inspection of a q-q plot of the residuals and of the fitted values plotted against residuals. Prior to running all LMMs, we log-transformed continuous predictor variables, including mean or maximum toughness (J m^{-2}), wet weights (g), diameter (mm), and for the known-age models, age (months) was square-root-transformed. Furthermore, to establish comparable estimates, we z-transformed all quantitative predictors to a mean of zero and a standard deviation of one; this also serves to improve interpretation of models that include interactions (Shielzeth, 2010). Box-Cox transformation tests (MASS package: Venables and Ripley, 2002) on a linear model (including all fixed effects but excluding random factors) determined log transformation was the optimal transformation for our response variable, mean IBL. Model stability was assessed by excluding levels of the random effects variables one at a time and comparing the resulting parameter estimates to estimates from the model run with the full dataset. In addition, random effects were dropped from models if the output indicated that term explained none of the variance in the model; in the intraspecific submodels, for *Sapajus*, food species were dropped to avoid problems with model convergence. Influential cases were removed, and models were run again. Variance inflation factors (VIF), derived using the “vif” function in the car package for R (Fox and Weisberg, 2011), were applied to standard linear models excluding random effects and interactions. The significance of each model was

established using a likelihood ratio test (LRT) comparing the full model to a null model, including the random effects structure and food category fixed effect. No multicollinearity issues were found among predictor variables (Field, 2005). Models run with mean and maximum toughness measures produced the same results; therefore, we have limited our presentation of the results and the discussion to include maximum toughness models. Statistical significance for all tests was assessed at $\alpha = 0.05$ level. We conducted Chi-square post hoc pairwise comparisons on significant interactions using the phia package (De Rosario-Martinez, 2015); p -values from post hoc comparisons were adjusted using Holm's correction (Holm, 1979).

Results

Comparisons of food toughness

The overall mean and maximum toughness of foods consumed by *S. libidinosus* and *T. p. crepusculus* (age classes pooled) were comparable (R_{mean} : Welch's $t = 1.468$, $df = 26$, $p = 0.154$, R_{max} : Welch's $t = 1.497$, $df = 28$, $p = 0.146$). For *S. libidinosus*, 21 identified plants were included in the analyses. The average R_{mean} of these foods was $1748.16 \pm 1506.5 \text{ J m}^{-2}$ and an average R_{max} of $3847.1 \pm 3493.36 \text{ J m}^{-2}$. For *T. p. crepusculus*, 48 species of plants were included in the analyses. For these foods, the average R_{mean} was $958.84 \pm 652.68 \text{ J m}^{-2}$ and average R_{max} was $2072.47 \pm 1864.31 \text{ J m}^{-2}$. For both focal species, the toughness of processed foods was comparable across age classes (*Sapajus*: R_{mean} : ANOVA $F = 0.51$, $df = 2$, $p = 0.608$, R_{max} : ANOVA $F = 0.18$, $df = 2$, $p = 0.834$; *Trachypithecus*: R_{mean} : ANOVA $F = 0.11$, $df = 2$, $p = 0.893$, R_{max} : ANOVA $F = 0.13$, $df = 2$, $p = 0.88$, Fig. 1).

Species patterns in feeding efficiency in response to toughness

In the adults-only model, both toughness and primate species were significant predictors of mean IBL (LRT of the full model with the null model: $\chi^2 = 41.19$, $df = 3$, $p < 0.0001$). Bearded capuchin mean IBLs were longer than those of leaf monkeys across the toughness range. While toughness was a positive predictor of IBLs overall, the significant interaction of toughness and species indicated species-specific rates of increase in IBL relative to toughness (Table 3): rates of increase were faster (i.e., steeper slopes) for *Trachypithecus* adults than for *Sapajus* adults. When the relationship between IBL and toughness was tested for each species post hoc, the relationship was significant only for leaf monkeys (post hoc $\chi^2 = 21.5$, $df = 1$, $p < 0.0001$) and not for bearded capuchins (post hoc $\chi^2 = 0.89$, $df = 1$, $p = 0.347$).

Age variation in feeding efficiency in response to toughness

Interspecific model Toughness, age class, and species influenced mean IBL (LRT of the full model with the null model: $\chi^2 = 83.343$, $df = 11$, $p < 0.001$). Since the three-way interaction effect of toughness, age class, and species did not reach significance ($\chi^2 = 5.391$, $df = 2$, $p = 0.068$) for mean IBL, we removed it from the model and ran a new model including the three two-way interactions as well as food category as predictors of mean IBL. The pattern of interspecific differences in mean IBL found for adults—longer IBLs for capuchins, but steeper rates of increase relative to toughness for leaf monkeys—remained consistent in the full dataset including age class in the model (Tables 4 and 5). Like adults, juvenile mean IBL increased with increasing toughness. Furthermore, the significant interaction between age class and toughness indicated differences in the rates of increase, driven by young juveniles, requiring longer bouts for high-toughness foods compared to adults (see post hoc pairwise comparisons: Table 5).

However, this pattern appears to be driven largely by variation among leaf monkey age classes (Fig. 2). In general, the post hoc comparisons revealed that significant age-class differences in mean IBL for the overall model were driven by leaf monkeys, as there was no variation among the bearded capuchin age classes (Table 5). Food category was a significant predictor of mean IBL. Roots, barks, and fruits exhibited the highest mean IBLs, while flowers, leaves, and grasses had shorter mean IBLs (Fig. 3).

Intraspecific submodels We tested predictions concerning age-related variation within species using data subsets that also incorporated a measure of food size. Likelihood ratio tests of the full intraspecific submodels with the null submodels were significant (*S. libidinosus*: $\chi^2 = 28.84$, $df = 7$, $p < 0.001$; *T. p. crepusculus*: $\chi^2 = 108.33$, $df = 7$, $p < 0.001$). The three-way interaction effect of toughness, age, and food size was not significant in either submodel (*S. libidinosus*: $\chi^2 = 1.07$, $df = 1$, $p = 0.3$; *T. p. crepusculus*: $\chi^2 = 0.94$, $df = 1$, $p = 0.332$), and the term was dropped from both submodels.

Among the capuchins, food size had a positive influence on mean IBL, however, toughness was not a positive predictor (Table 6, Fig. 4). As with the interspecific model, age did not predict mean IBL (Fig. 5A); however, the interaction of toughness and age had an influence on mean IBL that approached significance ($p = 0.053$), indicating possible age-specific feeding responses to increasing toughness. Furthermore, food category remained a predictor of mean IBL, such that bout lengths were shorter for grasses than for either fruits or roots and barks, even at high-toughness values (Fig. 4B). A separate Mann-Whitney U test indicated that juvenile capuchins processed smaller fruits than adults, but age classes showed no variation in grass or root and bark sizes (Table 7).

Among the leaf monkeys, all four predictor variables significantly influenced mean IBL (Table 6). Food size and toughness were positive predictors, such that tougher and larger foods required longer bout lengths (Fig. 6A, B). Age was a negative predictor of mean IBL, indicating shorter bout lengths for older leaf monkeys (Fig. 5B), and the significant interaction between age and food toughness ($p = 0.017$) points to greater age differences as foods get tougher (Table 6). There was no age-related effect of food size on mean IBL. Furthermore, there was no interaction between food toughness and size. Similar to the capuchin model, mean IBL varied among food categories with overall longer bouts for fruits than for either leaves or flowers.

Discussion

Contrary to our expectations, dietary toughness did not elucidate strong and consistent ontogenetic differences between species in our measure of feeding efficiency. We found mixed evidence for the effect of age and dietary toughness on feeding efficiency in bearded capuchins and leaf monkeys. Results from the interspecific model and the intraspecific submodel showed food toughness was a consistent positive predictor of bout lengths for immature and adult leaf monkeys. Juvenile leaf monkeys fed less efficiently than adults regardless of toughness (Figs. 2 and 6B), and young juvenile bouts were disproportionately longer than those of adults for high-toughness foods. However, bearded capuchin IBLs did not exhibit a significant positive relationship with toughness. The capuchin intraspecific model confirmed absence of an overall age effect on IBL for capuchins. However, the submodel also indicated a trend ($p = 0.053$) in how younger capuchins respond to toughness, similar to the significant negative interaction of age and toughness in leaf monkeys. These differences in the relationship of feeding efficiency and toughness between study species highlight the importance of a multivariate approach to

characterizing dietary variability and feeding behavioral complexity (e.g., food toughness as well as food geometry, amounts consumed, and nutritional content; manual and oral processing times vs. mastication) whenever possible.

Species differences in toughness and feeding efficiency

The average mean and maximum toughness of foods included here did not differ between primate taxa. Both capuchins and leaf monkeys are known to incorporate tough foods into their diet. Although capuchins processed the highest single toughness value on a food-tissue basis (grass processed by *Sapajus*: 15,194.4 J/m² vs. *Bauhinia saccocalyx* processed by *Trachypithecus*: 10,818.2 J/m²), overall, foods consumed by each focal species exhibited overlap across much of the toughness range. We caution that these data only represent a portion of the annual diet for each taxon, and some of the toughness data collected were excluded because values could not be linked to behavioral bouts. Nonetheless, we expect these datasets capture the extreme end of the toughness range for both taxa. At FBV, food availability has been shown to vary throughout the year, with capuchins increasing the time spent feeding on tough foods (e.g., roots, seeds, palm fruits) during the dry season (sampled here) and decreasing time spent feeding on fleshy fruits (Verderane et al., 2013; Chalk et al., 2016). For PKWS, the data used here are a subset of a larger dataset, which includes five additional months from the previous year. As with the FBV data, we suspect leaf monkeys consume the tougher foods in the dry season, and this dataset does include the toughest food tested at PKWS in those 9 months (Ossi-Lupo and Koenig, in review). While future work based on longer sampling periods may reveal more concrete species differences, comparable dietary toughness between the current datasets allows for a more straight-forward interpretation of our results.

Food toughness was a positive predictor of bout lengths in leaf monkeys. Wright and colleagues (2008a) similarly found that chewing bout lengths increased when captive Asian colobines were provided with tougher leaf bundles. Tougher foods are more resistant to fracture, which should require longer breakdown times prior to swallowing. While bearded capuchin IBLs were far longer than those of leaf monkeys across the sampled toughness range, leaf monkey feeding efficiency suffered greater costs at high toughness, despite their craniodental adaptations for the repetitive loading that comes with masticating tough foods (Wright et al., 2008a, b; Koyabu and Endo, 2010).

The interspecific variation in IBL relative to toughness could be due to straight-forward species differences in morphology and the corresponding effect on feeding efficiency: past studies have demonstrated species differences account for more than 40 percent of the variation in chew-cycle duration (Iriarte-Diaz et al., 2011; Ross and Iriarte-Diaz, 2014). Similar research has documented interspecific variation in chewing speed when controlling for leaf toughness, which Wright and colleagues (2008a) attributed, in part, to genus-level differences in relative molar surface area.

Additionally, the interspecific variation here may be largely attributed to differences in the frequency and variety of ingestive behaviors (i.e., food processing behaviors that occur prior to rhythmic mastication, e.g., Ungar, 1994; Yamashita, 2003) employed by each taxon prior to mastication. *Sapajus* species regularly rely on extractive foraging techniques to access high-quality, easily-digested foods that are often embedded or encased in tough outer tissues (Izawa, 1977; Terborgh, 1983; Janson and Boinski, 1992; Fragaszy et al., 2004). A consequence of this extractive feeding strategy is increased time with a bout that is devoted to processing behaviors, such as pounding or peeling exocarp. In contrast, although *T. p. crepusculus* at PKWS regularly

practices seed predation (Suarez, 2006), individuals employed oral ingestive behaviors to open most seed pods, and these behaviors were relatively brief (i.e., approximately five seconds or less for foods included in this dataset). Similarly, a comparison of sympatric frugivores and folivores in Tai forest demonstrated that colobines exhibited a more limited range of ingestive behaviors and reduced reliance on incisors, even when accessing seeds encased in thick-husked pods (McGraw et al., 2015).

Differences in food geometry within and across food categories further complicate the relationship between toughness and IBL. For example, foods such as leaves or whole small fruits, which are more prevalent in the leaf monkey sample than the bearded capuchin sample, can be placed in the mouth in a single motion, resulting in a bout length that is nearly equivalent to mastication time. For these foods, the relationship between bout length and toughness is a direct one. However, for fruits in which the toughest part is punctured or peeled and discarded to access seeds or fruit pulp, bout lengths include time spent engaged in food processing, as well as mastication. Our feeding efficiency measure captured total bout length to process one item and did not distinguish between food processing and mastication times. Therefore, it seems likely that leaf monkey IBLs largely represented mastication time, while bearded capuchin IBLs reflected their increased temporal investment in ingestive behaviors.

Our intraspecific submodels demonstrate the unequivocal effect of food size on bout length. We did not have a standardized measure of food size between studies and could not include it as a factor in the interspecific models. However, based on qualitative cross-site comparisons of size differences in foods eaten, we suspect that the capuchin diet includes larger foods, particularly larger fruits. If bearded capuchins process larger foods, then it is expected that their IBLs would be longer regardless of toughness given the positive effect of a food's external

dimensions or wet weight on IBL. Unfortunately, the combining of our datasets post hoc prohibits testing this hypothesis directly.

Age variation in the role of toughness for feeding efficiency

Comparisons of food toughness across age classes presented here concur with previous work demonstrating overlap in juvenile and adult dietary toughness for both taxa (Chalk et al., 2016; Ossi-Lupo and Koenig, in review; Fig. 1). We found that juvenile leaf monkey slopes, those of younger juveniles in particular, increased at a faster rate than those of adults in response to increasing food toughness. Age differences in IBL were present for all leaf monkey age class pairs; however, bearded capuchin adults and juvenile age classes exhibited comparable IBLs across the range of dietary toughness (Fig. 2). Although the three-way interaction of R with age and species did not reach significance ($p = 0.068$), the significant two-way interactions of species and R and species and age class suggest species-specific age patterns—that is, interspecific differences in how younger individuals and adults independently responded to toughness, with nearly complete overlap across age classes for capuchins.

Adding food size to our analyses came at the cost of data (i.e., excluding data points lacking corresponding toughness, size, and IBL measures, as well as several adult individuals with unknown ages), but yielded additional clarity as to the drivers of feeding efficiency within species. The results did not suggest that juveniles require disproportionately longer time to consume larger foods (non-significant interaction between age and food size); instead larger foods led to longer bouts across all ages. As in the interspecific model, overall age differences in IBL appear nonexistent for bearded capuchins, but leaf monkey IBLs show a negative relationship, such that bouts become shorter in older individuals. Likewise, the role of toughness

showed a similar overall pattern as in the interspecific model: it remained a positive predictor of bout lengths for leaf monkeys but not for bearded capuchins. Yet, both intraspecific submodels pointed to interactions between toughness and age (albeit a trend for the capuchin model: $p = 0.053$), suggesting younger individuals incurred greater costs to efficiency when consuming tougher foods. For bearded capuchins, it seems possible that any negative effect of toughness on juvenile feeding efficiency may have been obscured by not accounting for food size in the interspecific model. That is, since juveniles consumed smaller fruits than adults, age-related variation in feeding efficiency could be difficult to detect if juveniles were taking just as long as adults to consume absolutely less fruit tissue.

For bearded capuchins, the absence of age differences in IBL is consistent with prior work comparing the duration and feeding behaviors required to pluck and process maripa palms (*Maximiliana maripa*) by *S. apella* (Gunst et al., 2010b). In this study, infants (individuals less than one year of age) were shown to spend more time peeling maripa palms than other age classes; however, while peeling times continued to improve with age, there was no difference in processing duration among individuals older than one year. Of the eight immatures included in this study, only one individual was less than one year of age. It is important to note that age-related changes in tool-use proficiency have been documented in this species (Fragaszy et al., 2013), and this dataset includes only orally processed foods. Nonetheless, this result raises interesting questions about how juvenile *Sapajus* spp. maintain functional equivalence at smaller body sizes.

One possibility is that juvenile bearded capuchins are morphologically equipped to process tough foods at young ages. This explanation is indirectly supported by prior work demonstrating that *Cebus capucinus* juveniles as young as six months engage in adult-like

positional behaviors during feeding and foraging (Bezanson, 2009), suggesting immatures can execute adult-like processing behaviors and still maintain balance. In addition, mandibular traits associated with the ability to resist masticatory loads emerge early during capuchin development (Cole, 1992), implying juvenile mandibles could resist the masticatory forces generated while processing tough foods. However, processing tough foods requires the ability to resist and generate adequate masticatory forces. There are few published juvenile primate jaw muscle architecture or in vivo bite force data; as a result, force production capabilities of juvenile primates are relatively unknown. One study has shown that adult aye-aye jaw muscles exhibit a combination of greater PCSA and long fiber lengths consistent with the ability to generate high bite forces at wider gapes (Perry et al., 2014). When compared to the adult specimen, these authors found that juvenile aye-aye jaw muscles had longer fibers than the adult but a smaller PCSA, indicating juveniles would not be able to generate adult-like bite forces. Similar to aye-ayes, *S. apella* adults also have jaw muscle fiber architecture that facilitates the production of powerful bites when feeding on large foods (Taylor and Vinyard, 2009). Based on results from Perry et al. (2014), it is likely that juvenile bearded capuchin architecture also differs from that of adults. If, like aye-ayes, juvenile bearded capuchins have smaller jaw muscle PCSAs and lack the ability to generate adult-like masticatory forces, they may rely on behavioral strategies to meet their nutritional needs. Opportunistic dissection of juvenile specimens in conjunction with the application of contrast-enhanced micro-CT imaging to visualize soft tissue relationships (e.g., Gignac and Kley, 2014) offer promising avenues for understanding age patterns in muscle size and architecture.

Modifying their feeding behavior may allow juveniles to offset the costs of feeding on large and/or tough foods. Our results show food size influences IBL more so than toughness in a

restricted sample and that juvenile capuchins fed on smaller fruits than adults. Consuming smaller fruits may reflect preference, reduced postcranial strength to harvest large fruits, or exclusion by dominant individuals. Regardless, processing smaller fruits may be sufficient to allow juveniles to maintain adult-level bout lengths, although potentially at the cost of actual wet-weight intake. In addition to food-size selection, capuchin juveniles may also alter the sequence or frequency of ingestive behaviors compared to adults. The capuchin ingestive behavioral repertoire typically involves the use of forelimbs, hindlimbs, and anterior dentition (Wright et al., 2009). Juveniles may employ more combinatorial behaviors (i.e., behaviors using the dentition, forelimbs, and/or hindlimbs) than adults to process foods of comparable toughness, resulting in similar bout lengths using more rigorous behaviors. For example, adults often process *Eschweilera* sp. fruits by pounding the exocarp on tree branches. Once they generate a crack in the exocarp, they use their teeth and forelimbs to split the fruit in half, exposing the ripening seeds. Juveniles adopt a similar strategy and begin these feeding bouts by pounding the fruit on a branch; however, they occasionally use their teeth, forelimbs, and one hindlimb to force the fruit open and access the seeds. These data cannot assess the relative contribution of feeding behavior mode on IBL. Future work using ethograms specifically designed to quantify frequency and range of behaviors (e.g., Gunst et al., 2010a, b), while quantifying food toughness and size, is required to adequately investigate this issue.

By contrast, the persistence of overall age differences in IBLs for leaf monkeys, including reduced feeding efficiency on tough foods for young juveniles, may be a consequence of processing an adult diet using deciduous or mixed dentition. Wright and colleagues (2008a) described *Trachypithecus* spp. as ingestive folivores, relying on the oral as opposed to digestive breakdown of foods relative to other Asian colobines. This description is supported

637 morphologically by their relatively larger second molars and deeper mandibular corpora (i.e.,
638 relative to *Pygathrix* spp.: Wright et al., 2008a, b) and their improved mechanical advantage
639 during postcanine biting (Koyabu and Endo, 2010). Permanent second molars have been
640 estimated to erupt in *T. cristatus* between two and three years of age, and third molars between
641 three to five years of age (Bolter, 2011). Assuming comparable eruption times for *T. p.*
642 *crepusculus*, younger juveniles lacking permanent second or third molars may be at a functional
643 disadvantage given these primates' emphasis on oral food breakdown by posterior dentition.
644 Even individuals with newly-erupted permanent molars may be disadvantaged because unworn
645 molars or those in the early stages of wear appear to be less efficient than molars with
646 compensatory shearing crests formed by exposed dentine with sharp enamel around their
647 perimeter, at least until a certain threshold level of wear (Kay and Hylander, 1978; Mills, 1978;
648 Kono, 2004; King et al., 2005; Elgart, 2010; Venkataraman et al., 2014). Studies quantifying
649 juvenile molar shape (e.g., Glowacka et al., 2016) are needed to determine how deciduous and
650 newly erupted molars wear with use and if these differences track increased feeding (chewing or
651 digestive) efficiency (e.g., Venkataraman et al., 2014).

652   While dental eruption times may affect juvenile masticatory efficiency, differences in
653 young leaf monkeys might also be linked to smaller bite sizes. Food toughness influences bite
654 size across primates, with animals taking smaller bites of tougher foods (Perry et al., 2015). If
655 smaller mouth volumes and gape sizes result in juveniles consistently taking smaller bites than
656 adults (i.e., less food volume per mouthful) regardless of food toughness, then age differences in
657 efficiency should be apparent across the dietary toughness range. Furthermore, Reed and Ross
658 (2010) suggest that animals may adjust bite sizes according to FMPs to minimize feeding time
659 and avoid muscle fatigue, although there is some evidence indicating differences in how bite

sizes are regulated, which may be linked to diet or morphology (folivorous vs. frugivorous strepsirrhines: Hartstone-Rose et al., 2015). It remains to be seen whether juveniles utilize such tactics to a greater extent than adults, adjusting bite sizes to mediate their bout lengths on high-toughness foods. However, experiments such as those conducted by Perry et al. (2015) and Hartstone-Rose et al. (2015) are non-invasive and could be carried out with juvenile subjects.

Conclusions

Detecting fine-grained differences such as age-related variation in feeding behavior is dependent on how well researchers can characterize the diet and its complexity. Toughness and food size negatively impact feeding efficiency; however, the relative importance of these physical properties varies between the focal taxa. Furthermore, toughness appears to constrain juvenile leaf monkey feeding efficiency, whereas juvenile bearded capuchins engage in bout lengths comparable to adults possibly as a result of modifying feeding behavior. Since seasonal increases in dietary mechanical demand have been linked to dry seasons and reduced chewing efficiency for other taxa (Vogel et al., 2009; Raguette-Schofield, 2010; Venkataraman et al., 2014), shifts in dietary toughness or reliance on particularly tough foods during periods of resource shortage could prove especially challenging for juvenile leaf monkeys. Janson and van Schaik (1993) suggested that juvenile risks are higher during lean seasons when increased intra- and intergroup feeding competition lead to reduced tolerance, particularly as body size often determines the outcome of contests over food (Datta, 1986; Janson, 1990; Janson and van Schaik, 1993; Fragaszy and Boinski, 1995). The fact that juvenile leaf monkeys require more time than adults to eat foods of comparable toughness (and size) suggests age-related differences in food intake rates. However, additional work is needed to determine whether the differences in

IBL observed here translate into age differences in meeting nutritional requirements by scaling intake rates by size-related metabolic need.

These results speak to the need for better behavioral and ecological data and additional taxonomic sampling for testing hypotheses aimed at identifying the selective pressures driving feeding behavior ontogeny. Questions that focus on juvenile food selection and feeding competence or those striving to link diet, feeding behavior, and morphology will benefit from incorporating three lines of evidence: an objective measure of food “difficulty,” such as FMPs, food size and/or weight measures, and a temporal measure of time spent foraging, ingesting and masticating. We have demonstrated a relationship between feeding efficiency, toughness, and age for one focal taxon; the addition of food stiffness (i.e., elastic modulus) data will only add to our understanding of dietary mechanical demand across age classes. Second, since food size and geometry varies considerably within and between sites, measures of size (i.e., wet weight) and external dimensions that capture food geometry will facilitate the calculation of intake rates and inform on extra- and intraoral processing of foods of different shapes. Finally, we recommend that temporal measures of foraging and feeding be collected on as fine a scale as visibility permits (e.g., ingestion duration and mastication duration). When possible, filming bouts will facilitate comparisons of whole bouts, times spent ingesting and masticating food items, as well as frequency of feeding behaviors (e.g., McGraw et al., 2015). When visibility precludes quantifying feeding on such a fine temporal scale, valuable results may be gained from measures of single food IBL while accounting for ecological characteristics (e.g., patch size) consistently across sites. Studies that include immature and adult subjects not only inform our understanding of development, but they also provide insight into how animals harness behavioral flexibility to mitigate physical properties of foods.

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1041 **Figure legends**

1042 Figure 1. Log transformed mean (A) and maximal (B) toughness of *S. libidinosus* and *T. p.*
1043 *crepusculus* foods for the three age classes. No difference in mean or maximum toughness was
1044 found among age classes. Solid line within the box represents the median; boxes represent the
1045 first to third quartiles. Outliers were outside 1.5 times the interquartile range.

1046

1047 Figure 2. The relationship between mean item bout length (IBL) and toughness of foods
1048 processed by *S. libidinosus* and *T. p. crepusculus*. Both taxa engage in longer mean IBL with
1049 increasing food toughness. Age-related variation in mean IBL in response to toughness was
1050 apparent in leaf monkeys, but not in capuchins. Lines were fitted on the raw data from the age-
1051 class linear mixed model. Shaded areas represent 95% confidence intervals. Solid line = adults,
1052 dotted line = older juveniles, dot-dash line = young juveniles.

1053

1054 Figure 3. Variation in mean item feeding bout length (IBL) among food categories processed by
1055 *S. libidinosus* and *T. p. crepusculus*. Solid line within the box represents the median; boxes
1056 represent the first to third quartiles. Outliers were outside 1.5 times the interquartile range.

1057

1058 Figure 4. The relationship between mean item bout length (IBL) and size of foods (A) and
1059 maximal toughness (B) processed by *S. libidinosus*. Mean IBL increases when processing larger
1060 foods. The relationship between bout length and toughness appears to vary with food category.
1061 Lines were fitted on the raw data with the intraspecific known-age model. Shaded areas represent

1062 95% confidence intervals. Dotted red line = fruits, solid green line = leaves and grasses, purple
1063 dashed line = roots and barks. Color figure can be viewed in the online issue.

1064

1065 Figure 5. The effect of age on mean IBL when accounting for size of foods processed by *S.*
1066 *libidinosus* (A) and *T. p. crepusculus* (B). Solid line was fitted to age on the raw data with the
1067 intraspecific known-age model. Shaded areas represent 95% confidence intervals. Color gradient
1068 represents $\log_{10}R_{\max}$ values, with cool colors indicating low-toughness foods and hot colors
1069 depicting high-toughness foods.

1070

1071 Figure 6. The relationship between mean item bout length (IBL) and size of foods (A) and
1072 maximal toughness (B) processed by *T. p. crepusculus*. Mean IBL increases when with food size
1073 and toughness. Lines were fitted on the raw data with the intraspecific known-age model. Shaded
1074 areas represent 95% confidence intervals. Dotted red line = fruits, solid green line = leaves and
1075 grasses, blue dashed line = flowers. Color figure can be viewed in the online issue.

1076

Table 1. Summary of focal species diet, group size, weaning age, site details, and feeding behavior data collection methods.

	Adult body size (male, female) ^a	Diet composition ^b	Mean group size	Mean weaning age (months) ^c	Precipitation at field site ^d	Focal sampling method
<i>S. libidinosus</i>	3.5 kg, 2.1 kg	27–36% fruits, 28–35% invertebrates, 12–15% seeds	17	12–18	1289 mm Dry: 24.5 mm; Wet: 1265 mm	15 minute focal animal sampling; continuous recording during feeding
<i>T. p. crepusculus</i>	7.9 kg, 6.3 kg	12–94% leaves, 4–64% fruits, 1–50% flowers	19	19	1347 mm Dry: 60 mm; Wet: 1287 mm	20 minute focal animal sampling; instantaneous recording (1 minute intervals); continuous recording during feeding

^a *S. libidinosus*: Spagnoletti et al. (2011); *T. p. crepusculus*; Smith and Jungers (1997)

^b *S. libidinosus*: Verderane et al. (2013); *T. p. crepusculus*: Suarez (2013)

^c Weaning age defined as age at nipple-contact cessation. *S. libidinosus*: Fragaszy et al. (2004, 2016); *T. p. crepusculus*: Borries et al. (2014)

^d Fazenda Boa Vista (FBV): Verderane et al. (2013); Phu Khieo Wildlife Sanctuary (PKWS): Richter et al. (2016; wet vs. dry calculated from supporting information climate plot)

Table 2. Summary of study group age classes, contact hours, focal hours, and number of feeding bouts.^a

	No. individuals			Contact hours	Focal hours			No. bouts			
	/ age class										
	YJ	OJ	AD		Total	YJ	OJ	AD	YJ	OJ	AD
<i>S. libidinosus</i>	4	5	19	510	86	12.75 (3)	15 (3)	58.25 (3)	39 (7)	31 (6)	89 (5)
<i>T. p. crepusculus</i>	4	10	13	762.3	289.6	69.8 (11.6)	87 (9.7)	132.8 (10.2)	69 (12)	127 (13)	162 (11)

^a *S. libidinosus* focal hours based on focal feeding time. Average focal hours and average number of bouts per individual in each age class are given in parentheses. YJ = younger juveniles, OJ = older juveniles, AD = adults.

Table 3. Comparison of species differences in mean IBL using an adults-only dataset.^a

	Estimate	SE	χ^2	df	<i>p</i> -value
Adults-only model					
Intercept	1.37	0.12			
<i>R</i> max	0.04	0.04	14.48	1	0.0001
Species— <i>Trachypithecus</i>	-0.69	0.11	39.37	1	< 0.0001
Food category			32.67	3	< 0.0001
Fruits	0.37	0.09			
Leaves & grasses	-0.08	0.09			
Roots & barks	0.49	0.30			
<i>R</i> max * Species	0.17	0.06	7.57	1	0.006

^a The estimate and standard error (SE) for species is in relation to *S. libidinosus*. The estimates and SEs for food category are in relation to the flower food category. Random effects: subject, month, and food species or common name. Random slope for toughness within subject was included. The model sample size is 249 observations (89 = *S. libidinosus*, 162 = *T. p. crepusculus*). Toughness was log- and z-transformed. We report significance for fixed effects but did not conduct post hoc pairwise comparisons among food category levels.

Table 4. Influence of maximal toughness ($R_{\max}$), age class, and species on mean IBL (interspecific model).^a

Term	Estimate	SE	<i>t</i> -value	χ^2	df	<i>p</i> -value
Intercept	1.30	0.11	12.26			
$R_{\max}$	0.06	0.03	1.88	49.48	1	< 0.001
Age class				64.15	2	< 0.001
Older juvenile	0.05	0.06	0.87			
Younger juvenile	0.02	0.06	0.38			
Species-- <i>Trachypithecus</i>	-0.62	0.11	-5.67	29.19	1	< 0.001
Food category				41.58	3	< 0.001
Fruits	0.35	0.07	5.17			
Leaves & grasses	-0.04	0.06	-0.71			
Roots & barks	0.41	0.24	1.75			
$R_{\max}$ * Age class				7.15	2	0.02
$R_{\max}$ * Older juvenile	0.04	0.03	1.43			
$R_{\max}$ * Younger juvenile	0.08	0.03	2.61			
$R_{\max}$ * Species	0.11	0.04	2.83	8.02	1	0.005
Species * Age class				19.02	2	< 0.001
Species * Older juvenile	0.12	0.07	1.62			
Species*Younger juvenile	0.29	0.07	4.33			

^a The estimates and standard errors (SE) for age classes are in relation to adults, whereas species is in relation to *S. libidinosus*. The estimates and SEs for food category are in relation to the flower food category. The three-way interaction among $R_{\max}$, species, and age class did not reach significance (estimate = -0.09, SE = 0.07, $\chi^2 = 5.39$, df = 2, $p = 0.068$) and was dropped from the model. Random effects: subject, group, month, food species, or common name. Random slopes for age class within group and $R_{\max}$ within subjects were included. The sample size is 506 observations (148 = *S. libidinosus*, 358 = *T. p. crepusculus*). All continuous variables were log- and z-transformed. We report significance for fixed effects, but did not conduct post hoc pairwise comparisons among food category levels.

Table 5. Results of post hoc multiple comparison tests of fixed effect interactions including age classes from the interspecific linear mixed model.^a

Two-way interactions	χ^2	df	<i>p</i> -value
Age-class * <i>R</i> max			
Adult – OJ	2.169	1	0.282
Adult – YJ	6.608	1	0.030
OJ – YJ	1.610	1	0.282
Age-class * Species			
SAP: Adult – OJ	1.083	1	0.894
SAP: Adult – YJ	0.145	1	1.00
SAP: OJ – YJ	0.331	1	1.00
TRA: Adult – OJ	20.682	1	<0.001
TRA: Adult – YJ	77.490	1	<0.001
TRA: OJ – YJ	11.663	1	0.003
Adult: SAP—TRA	32.408	1	<0.001
OJ: SAP—TRA	18.433	1	<0.001
YJ: SAP—TRA	7.816	1	0.005

^aComparisons made using the phia package for R (De Rosario-Martinez, 2015). *P*-values were adjusted using Holm's correction. Significant *p*-values are bolded. SAP = *S. libidinosus*, TRA = *T. p. crepusculus*, YJ = younger juveniles, OJ = older juveniles, AD = adult.

Table 6. Influence of maximal toughness ($R_{\max}$), age, and food size on mean IBL (intraspecific model).^a

	<i>S. libidinosus</i>						<i>T. p. crepusculus</i>					
	Estimate	SE	<i>t</i> -value	χ^2	df	<i>p</i> -value	Estimate	SE	<i>t</i> -value	χ^2	df	<i>p</i> -value
Intercept	1.67	0.07	24.04				1.02	0.06	17.16			
$R_{\max}$	0.01	0.07	0.18	0.03	1	0.864	0.19	0.03	6.13	35.52	1	<0.001
Food size	0.35	0.07	5.07	23.77	1	<0.001	0.21	0.04	4.672	39.56	1	<0.001
Age (months)	0.08	0.13	0.64	0.23	1	0.632	-0.11	0.01	-10.39	102.9	1	<0.001
Food category				13.35	2	0.001				14.3	2	<0.001
Flowers							-0.24	0.11	-2.11			
Leaves & grasses	0.17	0.17	1.03				-0.31	0.08	-3.65			
Roots & barks	0.40	0.12	3.44									
$R_{\max}$ * Food size	-0.06	0.05	-1.29	1.66	1	0.198	-0.50	0.03	-1.8	3.24	1	0.072
$R_{\max}$ * Age	-0.13	0.07	-1.93	3.74	1	0.053	-0.03	0.01	-2.4	5.74	1	0.017
Food size * Age	-0.05	0.04	-1.26	1.57	1	0.21	-0.05	0.03	-1.8	1.4	1	0.236

^a Food size was measured as external diameter (mm) for *S. libidinosus* foods and as wet weight (g) for *T. p. crepusculus*. The estimate and standard error (SE) for food category is in relation to fruits. The three-way interaction among $R_{\max}$, food size, and age did not reach significance for either species (*S. libidinosus* model: estimate = 0.05, SE = 0.05, $\chi^2 = 1.07$, df = 1, $p = 0.3$; *T. p. crepusculus* model: estimate = 0.01, SE = 0.01, $\chi^2 = 0.94$, df = 1, $p = 0.3$) and was dropped from the model. Random effects included subject and group in both models; the *Trachypithecus* model also included food species. Random slopes for age class within group and $R_{\max}$ within subjects were included in both models. The sample size is 285 observations (86 = *S. libidinosus*, 199 = *T. p. crepusculus*). All continuous variables were log- and z-transformed. Significant p -values are in bold. We report significance for fixed effects but did not conduct post hoc pairwise comparisons among food category levels.

Table 7. Results of Mann-Whitney U comparisons of food size processed by adult and juvenile *S.libidinosus*.^a

Food category	Average food diameter (mm) $\pm$ SD		N identified foods		<i>U</i> statistic	<i>p</i> -value
	Adults	Juveniles	Adults	Juveniles		
Fruits	59.2 $\pm$ 7.6	44.4 $\pm$ 6.9	8	9	4	0.002
Leaves and grasses	3.1 $\pm$ 2	2.6 $\pm$ 0.9	6	5	14	0.855
Roots and barks	11.2 $\pm$ 5.5	14.7 $\pm$ 13.1	5	7	17	0.935

^a SD = standard deviation. Significant *p*-value is bolded.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6