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Growing up tough: Comparing the effects of food toughness 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.

1. 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,

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2002; Hanya, 2003; Johnson and Bock, 2004; Daunt et al., 2007; Gunst et al., 2008, 2010a,b; Raguet-Schofield, 2010; Chalk, 2011; Ossi-Lupo, 2014; O'Mara, 2015).

Age differences in feeding proficiency are often 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 juveniles may 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, 2012; Williams et al., 2005). FMPs, along with other properties such as food size, have been shown to influence food choice, bite size, and food breakdown. For instance, food particle breakdown rates in modern humans have been shown to decline with increasing toughness (Laird et al., 2016) and, in their cross-species comparison, Perry et al. (2015) found that bite sizes tended to be smaller for tougher foods. 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, 2014). 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., 2008). For instance, among graminivorous 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 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 food items (Chalk et al., 2016; Ossi-Lupo, 2014). 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 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, 2014). 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