

Primate dietary ecology in the context of food mechanical properties

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Primate dietary ecology in the context of food mechanical properties

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Abstract

Substantial variation exists in the mechanical properties of foods consumed by primate species. This variation is known to influence food selection and ingestion among non-human primates, yet no large-scale comparative study has examined the relationships between food mechanical properties and feeding strategies. Here we present comparative data on the Young's modulus and fracture toughness of natural foods in the diets of 31 primate species. We use these data to examine the relationships between food mechanical properties and dietary quality, body mass, and feeding time. We also examine the relationship between food mechanical properties and categorical concepts of diet that are often used to infer food mechanical properties.

Traditional dietary categories, such as folivory and frugivory, did not faithfully track food mechanical properties. Additionally, our estimate of dietary quality was not significantly correlated with either toughness or Young's modulus. We found a complex relationship among food mechanical properties, body mass, and feeding time, with a potential interaction between median toughness and body mass. The relationship between mean toughness and feeding time is straightforward: feeding time increases as toughness increases. However, when considering median toughness, the relationship with feeding time may depend upon body mass such that smaller primates increase their feeding time in response to an increase in median dietary toughness, whereas larger primates may even feed for shorter periods of time as toughness increases. Our results emphasize the need for additional studies quantifying the mechanical and chemical properties of primate diets so that they may be meaningfully compared to research on feeding behavior and jaw morphology.

Introduction

Primates feed on a diverse array of plant items and animal tissues to meet their nutritional needs. Variation in the mechanical properties of these items is hypothesized to exert a strong selective pressure on the dental and craniomandibular morphologies and feeding behaviors of primates (Jolly, 1970; Kinzey, 1974, 1992; Hylander, 1975; Kay, 1975; Rosenberger and Kinzey, 1976; Bouvier, 1986 a, 1986 b; Daegling, 1992; Rosenberger, 1992; Silverman et al., 2001; Taylor, 2002; Lucas, 2004; Daegling and McGraw, 2007; Koyabu and Endo, 2009). These properties can influence food selection (Kinzey and Norconk, 1990; Hill and Lucas, 1996; Yamashita, 1996; Teaford et al., 2006), feeding (Ungar, 1995; Hill and Lucas, 1996; Fragaszy et al., 2004; Yamashita et al., 2009; Reed and Ross, 2010; Yamashita et al., 2012), and digestion (Milton, 1981; Milton, 1984; Milton and McBee, 1983; Lambert, 1998). Thus, accurate measurement of food mechanical properties (FMPs) may improve our understanding of observed variation in diet selection among primates (Milton, 1981; Chapman, 1987; Kinzey and Norconk, 1990; Maisels et al., 1994; Ungar, 1995; Palombit, 1997; Wich et al., 2002; Knogge and Heymann, 2003; Lambert et al., 2004; Yamashita et al., 2009; Tombak et al., 2012).

Here, we examine how FMPs relate to feeding time, body mass, and dietary quality (Sailer et al., 1985) in a sample of 31 species of free-ranging primates. We also investigate the extent to which dietary categories (e.g., frugivory, insectivory, folivory) accurately track the mechanical properties of foods eaten by primates. Understanding the relationship among FMPs, dietary ecology, and feeding behavior is essential for informing hypotheses about primate adaptations to diet, and may help to untangle the complex relationship between FMPs and skull morphology (Ross et al., 2012; Ross and Iriarte-Diaz, 2014).

Predictions

In this study, we evaluate the relationships between FMPs and dietary categories, dietary quality, food items, body mass, and time spent feeding. These variables were selected because of their

theoretical and empirical relevance to FMPs and primate dietary ecology (e.g., Clutton-Brock and Harvey, 1977; Gaulin, 1979; Sailer et al., 1985; Ross et al., 2009 b).

1. Dietary categories are distinguishable by their FMPs. If dietary categories accurately reflect variation in the mechanical properties of foods eaten by primate, then FMPs should distinguish among traditional dietary categories (e.g., folivory, frugivory, insectivory). Traditionally, frugivores are predicted to experience relatively smaller masticatory loads, as fruits are often assumed to be soft and present fewer challenges to oral processing (Peters, 1987; Anapol and Lee, 1994; Ravosa, 1996; Taylor, 2006). Frugivory, therefore, and particularly the consumption of ripe pulp, should be associated with low values for toughness and/or Young's modulus, in contrast to the presumably more mechanically challenging diets of folivores.

2. Food items are distinguishable by their FMPs. We predict that broad categories of food items (e.g., fruits, leaves, bark) will separate out by FMPs. If traditional assumptions about the mechanical properties of food items are correct, then leaves should have the highest values for toughness. However, we expect that young leaves will be less tough than mature leaves (Coley, 1981; Choong, 1996; Vogel et al., 2008), and that ripe fruit will be less tough than unripe fruit (Vogel et al., 2008) (although in some cases ripe fruits are known to be tougher than are unripe fruits; see e.g., Yamashita et al., 2012). We predict that ripe fruit will have lower measures of Young's modulus than does unripe fruit.

3. Dietary quality is inversely correlated with FMPs. Because data on the actual nutritional composition of individual food items are limited for most primate species (Chapman et al., 2003; Norconk et al., 2009; Rothman et al., 2011; Rothman et al., 2012; Rothman et al., 2013; Raubenheimer et al., 2015), we used dietary quality (DQ) as a proxy for the nutritional quality of the diet of a given primate

species. Dietary quality approximates the available nutrients within a primate's diet (Sailer et al., 1985), and can be calculated from dietary composition data available in the literature. According to the Jarman-Bell Principle (Bell, 1971; Jarman, 1974; Gaulin, 1979), large-bodied animals are expected to eat large quantities of nutrient-poor (i.e. low-quality) foods while small-bodied animals are expected to eat small quantities of nutrient-rich (i.e. high-quality) foods. In this model, a high value for DQ indicates a diet comprised of sources of readily available energy and nutrients, such as fruit or insects. A low value for DQ indicates reliance on foods that are abundant, such as leaves, but with relatively less available energy and fewer easily accessible nutrients. The DQ model is not intended to capture the full complexity of primate diets; for instance, it ignores nutrient balancing (Gaulin, 1979) and the effect of differential digestive adaptations on nutrient absorption (Milton, 1981, 1998; Milton and McBee, 1983; Lambert, 1998; Chapman et al., 2003; Amato et al., 2014 a, 2014 b). Tough foods contain more fiber (Lucas et al., 2000), which is difficult to digest, thereby limiting access to nutrients (Van Soest, 1994; Lambert, 1998; Rothman et al., 2013). Some researchers have used the terms "low-quality" and "tough" interchangeably (e.g., Remis, 2003; Constantino et al., 2009; Pontzer et al., 2011; Scott, 2011), but the relationship between food toughness and nutrition is uncertain (but see Choong et al., 1992; Hill and Lucas, 1996; Lucas et al., 2000; Huang et al., 2010). Still, despite these limitations, it follows that a negative relationship might exist between DQ and toughness.

4. Body mass is positively correlated with FMPs. Larger-bodied primates consume lower quality foods more frequently than do smaller primates (Bell, 1971; Jarman, 1974; Gaulin, 1979). If FMPs can be used to infer nutritional quality, then, all else being equal, we expect smaller primates with higher metabolic rates to rely on foods with lower toughness and Young's modulus while larger primates will exploit foods with higher values for toughness and Young's modulus.

5. Feeding time is positively correlated with body mass. Body mass is positively related to metabolic

rate (Kleiber, 1947; Elgar and Harvey, 1987; McNab, 2008) and negatively related to dietary nutrient density (Clutton-Brock and Harvey, 1977; Gaulin, 1979; Sailer et al., 1985). Larger-bodied animals can meet their metabolic needs by ingesting more food at once or by devoting more daily time to feeding. Thus, we expect that feeding time may be positively correlated with body mass. Previous studies found a weak relationship between feeding time and body mass that was strongly influenced by phylogeny (Ross et al., 2009 b; Organ et al., 2011). Here, we re-test this relationship with a different data set including different primate species and different values for time spent feeding.

6. Feeding time is positively correlated with FMPs. Experimental studies have shown that jaw movements and chewing patterns vary with mechanical properties within species (Agrawal et al., 1998, 2000; Vinyard et al., 2006; Wright et al., 2008; Thompson et al., 2011), and the ratio of toughness to Young's modulus has been empirically shown to influence the rate at which a food is broken down in humans (Agrawal et al., 1997). Feeding time has been shown to increase with leaf toughness in insects (Williams, 1954; Tanton, 1962), which is probably not surprising, given that tough foods can be higher in fiber and may therefore require more time to break down both orally and within the gut (Van Soest, 1994; Milton, 1984; Lambert, 1998). Thus, an animal that relies on a diet of these tough foods may ultimately increase the proportion of the daily activity budget devoted to feeding time and/or the number of masticatory cycles (i.e. repetitive loading of the mandible) compared with an animal that relies on less mechanically challenging foods. While data are not available to directly test the relationship between FMPs and the number of masticatory cycles, we can use feeding time to explore the relationship between dietary toughness and time devoted to feeding, quantified as time spent orally processing food items.

Materials and Methods

Study species

Our study sample comprises 31 wild primate species, including both haplorhines ($n = 26$) and strepsirrhines ($n = 5$) from a variety of habitats (Table 1). These species represent the majority of primate species for which FMP data have been collected using equivalent mechanical testing protocols and equipment (Darvell et al., 1996; Lucas et al., 2001).

Mechanical properties

For each primate species, we collected FMP data on food items consumed using the Darvell HKU tester. This tester can be used in the field and has become the standard means of measuring FMPs in primates (Williams et al., 2005; Wright, 2005; Teaford et al., 2006; Dominy et al., 2008; Taylor et al., 2008; Vogel et al., 2008; Yamashita et al., 2009; Chalk et al., 2016). All samples were collected during focal feeding bouts or consisted of food items that are known to be included in a primate species' diet, and were tested on the same day as collection when possible. For some primate species (e.g. *Pongo pygmaeus wurmbii*) we were unable to test the most mechanically challenging items due to limitations of our load cell and our inability to reduce the size of certain seeds (see Vogel et al., 2008, 2014 for details).

Toughness (R) was measured for plant foods, including plant parts, eaten by all species, while measurements of Young's modulus (E) were recorded for foods eaten by 21 species (see Supplement). Although fragmentation indices have been hypothesized as a potential driver of feeding adaptations in primates (Agrawal et al., 1997; Lucas et al., 2002), our limited data on Young's modulus prevented us from including these indices in our analyses.

Toughness Toughness (in J m^{-2}) is estimated here as the energy required to extend a unit area of a crack (Gordon, 1978; Lucas and Pereira, 1990; Vincent, 1992; Lucas et al., 2000, 2011). We performed scissors tests for sheet-like items such as leaves (Lucas and Pereira, 1990; Vincent, 1992), and employed wedge tests for thicker items (e.g. >2 mm). In both cases, the blade(s) move progressively

through the material being tested to determine the work done (force x displacement) to force a crack in a specified direction (Lucas et al., 2001).

Young's modulus Young's modulus (in MPa), also termed the elastic modulus, is the ratio of stress to strain throughout elastic deformation, and is defined as an object's ability to resist elastic deformation. The higher the Young's modulus, the more resistant the object is to such deformation (Gordon, 1978; Williams et al., 2005). We measured modulus with both bending and compression tests. Three-point bending was used to measure modulus in food items that could be prepared into the beam-shaped format needed for this type of testing (Vincent, 1992; Yamashita et al., 2009), such as bark or branches. Whenever possible, length to width ratios of 10:1 or greater were maintained. Compression tests entail the extraction of a cuboid or cylindrical sample (Agrawal et al., 1997), which is then placed under compression to measure the associated stress and strain during elastic deformation (Agrawal and Lucas, 2003).

It is unknown whether the mechanical properties of the most common food items in a primate's diet exert greater selective pressures on primate feeding ecology than do the most challenging items (Rosenberger, 1992; Yamashita, 1998; Lambert et al., 2004; Taylor et al., 2008; Wright et al., 2013; Vogel et al., 2014). Consequently, we used estimates designed to quantify both of these aspects of a primate's diet. To estimate the FMPs of a diet at its most challenging, we used maximum estimates of the toughness (R) and Young's modulus (E) of the toughest and most resistant item in the diet, respectively. To illustrate, a fruit may have toughness data available for the exocarp, mesocarp, and endosperm, as these parts were measured separately. The maximum R and E of any eaten food part were used to represent the resistance or toughness of that food item. Thus, for example, if the exocarp had the highest value for R , that value was used to represent maximum toughness for that fruit. If the endocarp were to have the highest R , then that value determined the fruit's maximum toughness.

Scaling up to the level of the whole diet, the maximum values for all foods eaten by a given primate species gave the maximum *E* or *R* for that primate (termed *MaximumE* and *MaximumR*, respectively).

We also generated two estimates—a weighted mean and a median measure—to approximate the typical dietary FMPs for each species. A mean *R* or *E* calculated for all of the food items in a species' diet implicitly assumes that an item eaten infrequently is weighted equally with an item eaten frequently. Certain barks and piths, for example, are extremely tough, but represent only a very small portion of the annual diet composition (Vogel et al., 2008). A robust estimate of the FMPs typically encountered by a primate requires weighting the FMPs of each item in the diet by the frequency of consumption, but these data were not available for every food item. Thus, we weighted FMP data by composition of a species' diet based on food category to avoid over- or under-representing the importance of specific food items. For example, if the proportions of leaves, seeds, flowers, and fruit (pericarp and whole fruit) in a species' diet were available, we calculated the mean *R* and *E* of all foods eaten for each of those categories. We constructed a hierarchical system of categories of food items (detailed in Fig. 1) to reflect data on dietary composition available in the literature as well as variation in how food items were categorized during FMP testing. These category means were then weighted by the proportion of each category in a primate species' diet. The denominator was equal to the total proportion of a primate's diet for which any FMP data were available. Thus, if a primate ate 50% leaves, 20% seeds, 10% pericarp or whole fruit, and 10% insects (and FMP data were not available for insects), the weighted mean *R* for that species was:

$$(0.5 * \text{mean } R \text{ for leaves} + 0.2 * \text{mean } R \text{ for seeds} + 0.1 * \text{mean } R \text{ for pericarp or whole fruit})$$

This process resulted in the variables *WeightedR* and *WeightedE*.

Since extreme outliers minimally influence the median, we also computed medians for *R* and *E* for each food item eaten by a species. We first calculated a mean *R* and *E* of each food item. If a food item comprised multiple parts, we computed the mean across those parts. For example, for a fruit item, we first computed the mean *R* and *E* for exocarp, mesocarp, and endosperm. Finally, we calculated the

median R and E values of all food items in a species' diet, resulting in the variables *MedianR* and *MedianE*, respectively.

[PLEASE PLACE FIG. 1 HERE]

[PLEASE PLACE TABLE 1 HERE]

Dietary categories

We established two dietary categories based on previous classification schemes taken from the literature. Our *general* dietary classification identifies primate species as folivorous, frugivorous, or insectivorous based on dietary composition (Table 1). Following the methodology of Muchlinski (2010), we classified a species as frugivorous if at least 50% of its diet (as measured from time spent feeding on different food items) is comprised of fruit. Once frugivores were classified, the distinction between folivory and insectivory was determined by whether the non-fruit portion of the diet consists of more leaves or more insects. We classified *Callithrix jacchus* as a gummivore (Sussman and Kinzey, 1984).

We also considered a *specific* classification system, following Plavcan and van Schaik (1992), to ensure that the general, higher-level categories do not obscure meaningful biological differences in food properties. This specific classification identified taxa as frugivorous, folivorous, insectivorous, gummivorous, frugivorous-folivorous, frugivorous-insectivorous, or frugivorous-gummivorous (Table 1). Frugivores were given a mixed classification if the secondary component of their diet comprised more than 15% (for leaves) or 25% (for insects and exudates) of the total diet.

Food items

As noted above, we classified food items into the categories listed in Fig. 1 to examine FMP variation across food types. For analyses testing the relationship between FMPs and food items, we set a threshold of $n \geq 15$ individual FMP tests for inclusion. Thus, we included the food items highlighted

in bold (*R*: bamboo, bark, flower, pericarp and whole fruit, leaf, seed, stem/stalk; *E*: bamboo, fruit, leaf, seed) and excluded those that fell below the threshold (cambium, grass, pith, root/tuber/bulb part, shoot). After analyzing variation in FMPs for these food categories, we performed additional analyses to test for differences in FMPs based on food ripeness or maturity. We separated pericarp and whole fruit based on ripeness (ripe and unripe) and leaves based on maturity (young and mature). We categorized seeds separately from pericarp and whole fruit because these items were frequently measured separately, and because seeds and whole fruits often differ in mechanical properties (Lucas et al., 1991; Vogel et al., 2008, 2014; Daegling et al., 2011; Chalk et al., 2016). We used values for *R* and *E* that represented either single tests of individual food items or an average of multiple tests of the same plant species or category of food item, according to how these data were reported.

Dietary quality

Dietary quality (DQ) was calculated by using coefficients to weight the percentages of plant structural parts, plant reproductive parts, and animal material consumed by a primate species (Sailer et al., 1985). Coefficients for dietary quality were taken from Sailer *et al.* (1985): 1 for structural parts, 2 for reproductive parts, and 3.5 for animal matter. One species, *Callithrix jacchus*, consumes large quantities of exudates (Sussman and Kinzey, 1984). Because exudates are not included in the equation of Sailer *et al.* (1985), we elected to give exudates the same coefficient as animal matter for the purpose of calculating DQ for this study, as excluding exudates would vastly underestimate DQ for *C. jacchus*. Principal components analysis of our sample showed that insects and exudates were co-related (Janson pers. comm. to ERV), meaning that they have similar nutritional value within the context of the DQ model. Moreover, available data comparing insects and exudates show that these food types have similar caloric content (Isbell et al., 2013). It is thus probably more appropriate to group exudates with animal matter (as opposed to structural or reproductive parts) in calculating DQ for this study. DQ was calculated as $DQ = 1s + 2r + 3.5(a + e)$. We calculated the DQ index for each primate species using data

on dietary composition (Table 1). Food items were assigned to categories as outlined in Fig. 1 (e.g., pith and shoots were structural; seeds were reproductive). These data included either time spent feeding on different food items or percentage of feeding records devoted to different food items. Data reporting diet as a percentage of total items consumed were excluded. When possible, data on dietary composition were taken from the same populations as FMP data (n = 29). All other data were drawn from the available literature (Table 1). If the reported dietary composition did not add up to 100%, we adjusted the numbers to maintain relative proportions, using the equation:

$$\% \text{ structural (or reproductive, animal, exudate)} * 100 / \text{total recorded diet composition}$$

For example, as dietary composition for *Cebus libidinosus* was only recorded for 86% of its diet, and 51% of its diet was reproductive matter, we calculated an adjusted figure for reproductive matter as: $(0.51 * 100) / 0.86 = 59.3$. The individual DQ values reported in Table 1 are the adjusted values.

Body mass

Body mass data specific to the populations in our sample were used whenever possible (n = 7 of 31), while the remaining body mass estimates were taken from the literature (Table 1). We used species averages that included both males and females. When body mass estimates were presented separately for males and females, we averaged these estimates to achieve a species mean.

Feeding time

Following Ross *et al.* (2009 b), we define feeding time as the percentage of the daily activity budget spent ingesting and orally processing foods. Gut digestion time is known to play an important role in primate diet selection (Milton, 1981; Milton, 1984; Lambert, 1998), but because these data were not available for many species in our sample, we did not consider this variable in our analyses.

Whenever possible, feeding times used here were drawn from the same study populations as those from

which FMP data were collected (n = 18 of 31). When unavailable, we drew on feeding times from the literature (Table 1). For two species (*Chiropotes satanas* and *Ptilocolobus rufomitratu*s), multiple feeding times were available, and none was specific to the sites where FMPs were measured. In these cases, we used the average of the available measures. We preferentially used feeding time data that did not include time spent foraging, as determined by the methodology of each paper (e.g., feeding and foraging were defined and measured separately). Chewing, feeding, and foraging are separate activities, and are not always clearly distinguished in the literature. Ideally, data on feeding times would include an estimate of time spent chewing, but these data are only available for a limited number of captive species (Ross et al., 2009 a; Ross et al., 2009 b).

We specifically excluded any papers that did not clearly define feeding or did not distinguish between feeding and foraging. Excluding foraging time likely underestimates time spent feeding for insectivorous primates, which tend to feed continuously while foraging (e.g., Terborgh, 1983; Robinson, 1986). However, in the absence of fine-grained data that separate insect feeding and foraging, we chose the more conservative approach of excluding foraging time.

Analyses

We used Kruskal-Wallis rank sum tests (Kruskal and Wallis, 1952) to test our predictions that dietary categories and food items are distinguishable by their FMPs. If food items were significantly distinguishable by either toughness or Young's modulus, we performed post-hoc pairwise comparisons using a Wilcoxon rank sum test (Wilcoxon, 1945).

We used correlation analysis to test our predictions relating FMPs to dietary quality, body mass, and feeding time. We used phylogenetic generalized least squares (PGLS) regression (Freckleton et al., 2002) to address the potential influences of phylogeny on the correlations. We used the GenBank consensus tree from 10kTrees (<http://10ktrees.nunn-lab.org/>) (Arnold et al., 2010) to estimate phylogenetic relationships and divergence dates for primate species (Fig. 2). Because not all of the

species in our sample are included in the 10kTrees database, we relied on published phylogenetic positions and divergence estimates for the missing species. We used a divergence date of 400,000 years for *Cebus libidinosus* and *C. apella* (Lynch Alfaro et al., 2012) and 178,000 years for *Pongo pygmaeus wurmbii* and *P. p. morio* (Nater et al., 2011). To test our hypothesis about feeding time and FMPs, we ran PGLS regressions incorporating an interaction between FMPs and body mass. If the interaction was not significant and did not trend toward significance, we then ran the models without the interaction.

[PLEASE PLACE FIG. 2 HERE]

For all analyses, the natural logs of body mass and FMPs were used, and feeding times were logit transformed. We set the significance level for all tests at $\alpha < 0.05$, and noted trends toward significance at $0.05 < p < 0.1$. We used a Bonferroni-Holm correction for multiple comparisons (Holm, 1979) to control for family-wise error rate, applied separately for models of R and E .¹ All analyses were performed using the R Statistical Programming Language version 3.1.0 (<http://www.R-project.org/>). Packages APE (Paradis et al., 2004) and caper (Orme et al., 2013) were used for PGLS.

Results

Dietary categories and FMPs

Dietary categories were not significantly distinguished by any estimate of toughness or Young's modulus (Table 2; Fig. 3).

[PLEASE PLACE TABLE 2. AND FIG. 3 HERE]

Food items and FMPs

Toughness varied significantly among food items across primates (K-W test $\chi^2 = 171.23$, $p < 0.001$) (Fig. 4A). Post-hoc pairwise comparisons yielded several significant differences among food

¹ A stepwise algorithm less conservative than the Bonferroni procedure. First, order p -values from lowest to highest. Calculate α/m (where m is the number of p -values). Reject the first hypothesis and stop the procedure if the first p -value is greater than or equal to α/m . Otherwise, move to the second p -value and compare to $\alpha/(m-1)$, etc.

items; however, food items classified as fruits, seeds, and leaves showed no differences in toughness (Table 3A). Bark and bamboo were not significantly different from each other in toughness, but these items were both tougher than all other food items except for stems, which were significantly less tough than bamboo but not bark. Flowers and seeds were not significantly different.

We also observed a significant difference in Young's modulus across food items (K-W test $\chi^2 = 66.59, p < 0.001$) (Fig. 4B). Here, all food items were significantly different from each other (Table 3B). Bamboo had higher modulus values than fruits or seeds, and fruits had higher values than seeds.

Variation was found in maturity stage in both leaves and fruits (K-W test $\chi^2 = 17.8, p < 0.001$) (Fig. 4C). The toughness of young leaves did not differ from that of mature leaves, ripe fruit, or unripe fruit (Table 3C). Ripe fruit was less tough than unripe fruit and mature leaves. Unripe fruit and mature leaves did not differ.

There was no significant difference in Young's modulus between ripe and unripe fruit (K-W test $\chi^2 = 3.01, p = 0.08$).

[PLEASE PLACE TABLE 3 AND FIG. 4 HERE]

Dietary quality and FMPs

There was no significant correlation between our estimate of dietary quality and any of our estimates of FMPs (Table 4). However, there was a trend towards a negative correlation between *MaximumE* and dietary quality.

[PLEASE PLACE TABLE 4 HERE]

Body mass and FMPs

There was no relationship between body mass and any of our estimates of toughness (Table 5; Fig. 5A-C), although *MedianR* trended towards an inverse relationship with body mass. In contrast, all estimates of Young's modulus were significantly inversely correlated with body mass (Table 5; Fig.

5D-F).

[PLEASE PLACE TABLE 5 AND FIG. 5 HERE]

Feeding time and body mass

Feeding time was significantly correlated with body mass ($F(1, 29) = 5.18, p = 0.03, R^2 = 0.12$) (Fig. 6). This model resulted in a maximum-likelihood estimate of 0 for λ .

[PLEASE PLACE FIG. 6 HERE]

Feeding time and FMPs

We found a complex relationship between feeding time and all three estimates of toughness (Table 6). PGLS models including interactions between body mass and FMPs were run first to consider the possibility that any relationship between FMPs and feeding time might be contingent on body size. If the interaction term was not significant and did not trend toward significance ($0.05 < p < 0.1$), the result without the interaction is presented in Table 6. For *MaximumR* and *WeightedR*, the interaction term was not significant, and we then ran models excluding the interaction. *WeightedR* and feeding time were positively correlated (Table 6A), but the overall significance of the model including *MaximumR* was driven by body mass (Table 6C), and *MaximumR* was not correlated with feeding time.

In the case of *MedianR*, inclusion of the interaction with body mass (Table 6B) resulted in a positive relationship with feeding time for primates with smaller body sizes and a negative one for primates with larger body sizes (Table 6B and Fig. 7B). Thus, as body mass increases, tough foods move from apparently increasing feeding time to potentially reducing feeding time.

The regression lines shown in Fig. 7 suggest an effect of body size on the relationships between feeding time and *WeightedR* (Fig. 7A) and feeding time and *MedianR* (Fig. 7B) by showing the slopes of these relationships for a large primate (the size of *Gorilla beringei*, the largest species in the sample, shown in black) and a small primate (the size of *Callithrix jacchus*, the smallest species in the sample,

shown in gray). In this figure, the body mass of each species is represented by the area of each point, with larger species plotted with larger data points. Both OLS (solid lines) and PGLS (dashed lines) relationships are shown to demonstrate the potential effect of phylogeny. The OLS and PGLS lines for the large body mass slopes (in black) are quite similar, suggesting that among larger primates there may be little in the way of phylogenetic signal. In contrast, the difference between the OLS and PGLS slopes for small body mass (in gray) indicates an effect of phylogeny possibly associated with the smaller-bodied strepsirrhines in the sample.

For the relationship between Young's modulus and feeding time, none of the overall models was significant (Table 6). Body mass was significant for the models including *WeightedE* and *MedianE* (Table 6D, E).

[PLEASE PLACE TABLE 6 AND FIG. 7 HERE]

Discussion

Dietary categories, food items, dietary quality, and FMPs

None of our dietary categories or food items were distinguishable by their FMPs. The lack of significant differences suggests that these categorical descriptions of primate diets do not sufficiently describe a potential relationship between FMPs and primate diets. As noted by previous researchers (Teaford et al., 2006; Vogel et al., 2008; Yamashita et al., 2009), the mechanical properties of foods vary within as well as between specific food items. Thus, for example, categorizing a primate as “folivorous” might fail to characterize the full range of mechanical variation within folivory, given that folivorous primates consume leaves with a wide range of values for toughness and Young's modulus, as well as a variety of non-leaf foods. Similarly, maturity stage may influence FMPs to some extent, and we found that ripe fruits are less tough than are unripe fruits. Contrary to our expectations, there was no difference in toughness between young and mature leaves in our dataset. However, maturity level was

not reported for all leaves in our sample, and the toughest leaves were thus excluded from this analysis (see Fig. 1). Moreover, because our data examine relationships across primates, our results may overlook variation that exists within species. For example, the leaf lamina of mature leaves consumed by Bornean orangutans is tougher than immature leaf lamina (Vogel et al., 2008). At the very least, it is safe to say that, on average, a primate that exclusively consumes leaves does not necessarily ingest tougher foods than does a primate that specializes on fruit. Still, primates do appear to make decisions about food consumption based on detectable properties of foods (Milton, 1984; Kinzey and Norconk, 1990; Hill and Lucas, 1996; Yamashita, 1996; Teaford et al., 2006; Vogel et al., 2008), including toughness. Thus, FMPs may in part determine the range of foods eaten by primates: extremely tough foods, whether leaves or fruits, may be avoided because of their mechanical challenges.

Our results are thus consistent with previous studies that have argued against the use of categorical descriptions of primate diets because they do not adequately track FMPs, and support the continued shift towards more fine-grained studies of feeding behavior that include data on the mechanical properties of the specific food or food part being ingested and masticated (Kay, 1975; Rosenberger and Kinzey, 1976; Lucas et al., 1985; Rosenberger, 1992; Yamashita, 1996, 1998; Wright and Willis, 2012). This impacts broader questions in functional morphology, because if FMPs influence feeding system adaptations in primates (Jolly, 1970; Kinzey, 1974, 1992; Hylander, 1975; Kay, 1975; Rosenberger and Kinzey, 1976; Bouvier, 1986 a, 1986 b; Daegling, 1992; Rosenberger, 1992; Silverman et al., 2001; Taylor, 2002; Lucas, 2004; Daegling and McGraw, 2007; Koyabu and Endo, 2009, but see Ross et al., 2012; Ross and Iriarte-Diaz, 2014), the use of traditional dietary categories as proxies for FMPs will hinder attempts to link FMPs and feeding system morphology in both living and fossil species.

We also found no relationship between dietary quality and FMPs. Foods classified as low quality are typically those with higher fiber content, and fiber contributes to toughness (Hill and Lucas, 1996; Lucas et al., 2000, 2011). However, the relationship between food toughness and nutrition has

received minimal attention (but see Choong et al., 1992; Hill and Lucas, 1996; Lucas et al., 2000; Huang et al., 2010). It is likely that certain mechanically challenging foods may be preferentially selected by primates because of their nutritional composition (Vogel et al., 2008, 2009, 2014; Daegling et al., 2011; Chalk et al., 2016) For example, sooty mangabeys consume mechanically challenging seeds year-round (i.e. not as a fallback food) (Daegling et al., 2011), likely because of the oil content (Cornelius et al., 1970). Moreover, manual and oral processing of foods, as well as gut adaptations related to digestion, may allow primates to extract resources from foods that would otherwise be considered low-quality. The more simplistic DQ index used in this study and others (Sailer et al., 1985; Jaeggi and Van Schaik, 2011) assumes that all primates receive similar energetic benefits from all food items and ignores that different primate species have variable gut morphology and gut passage times. Thus, what may be considered a high quality diet for one species can be considered a low quality diet for another (Milton, 1981; Milton, 1993). Thus, it is conceivable that a mechanically challenging diet may also be characterized as nutritionally high-quality (Daegling et al., 2011). Resolution of the relationship between dietary quality and food mechanical properties requires direct measurement of nutrient composition and FMPs instead of the simple indices used here. While some research has addressed nutrient absorption and calorie intake in primates (Milton, 1981; Milton and McBee, 1983; Lambert, 1998; Chapman et al., 2003; Rothman et al., 2012), none has investigated the question of whether FMPs are related to measurable differences in nutritive quality.

Body mass, feeding time, and FMPs

Food mechanical properties exhibit complex, likely clade-specific relationships with feeding time and body mass. First, with respect to feeding time scaling with body mass, our results are similar to those of previous studies (Ross et al., 2009 b; Organ et al., 2011), and suggest a weak relationship between body mass and feeding time. It may be the case that feeding time is too simplistic of a measure and obscures a meaningful relationship between body mass and food intake. Our measures of feeding

time were drawn from daily activity budgets, which are recorded and reported differently across studies. Alternatively, the relationship between chewing rate and feeding time may be informative. Experimental research has examined this relationship (Ross et al., 2009 a, 2009 b; Thompson et al., 2011), but data remain too limited to enable large-scale, interspecific analysis (but see Williams et al., 2008; Vinyard et al., 2012). Thus, feeding time as drawn from data on daily activity budgets represents the best current measure for comparative study.

Our prediction that larger primates would eat more mechanically challenging foods was not supported, as we found no relationship between toughness and body mass, while dietary Young's modulus actually decreases in larger primates (Fig. 5D-F). This latter result may be a consequence of a sampling bias. FMPs were not always measured for the full range of foods eaten by a primate species; in some cases, the most challenging foods were excluded from analysis, due for example to limitations in the tester apparatus (e.g. Vogel et al, 2008, 2014). Moreover, we found that bamboo has, on average, higher values for Young's modulus than do fruits and seeds (Fig. 4). In our sample, measurements of Young's modulus for bamboo were taken only for *Trachypitecus phayrei* and the relatively small-bodied bamboo lemurs. Further sampling of the high-end range of Young's modulus on food items is critical for drawing conclusions about these relationships. Toughness is not significantly related to body mass after Bonferroni-Holm correction. However, as seen in Fig. 5B and reflected by a significant result prior to Bonferroni-Holm correction (Table 5), the possibility of a weak effect whereby smaller primates consume tougher foods may be worth further investigation. We speculate that, to meet their daily caloric needs, smaller primates may turn to more mechanically challenging—yet nutrient-rich—food items that are avoided by larger primates with slower metabolisms. This result underscores the need to quantify the complete range of food properties from mechanical to chemical to nutritional.

Evaluating whether species with more mechanically challenging diets invest more time in feeding seems to depend in part on the way FMPs are quantified. First, there is clearly no relationship between feeding time and maximum toughness. This result is what we would expect if the toughest

items in a primate's diet represent fallback foods that are important primarily during periods of low availability of preferred food items (Lambert et al., 2004; Laden and Wrangham, 2005; Marshall and Wrangham, 2007; Constantino et al., 2009).

Analysis of median toughness suggests the possibility that the relationship between median toughness and feeding time may be modulated by an interaction with body mass (although Table 6 implies a complex web of weak effects). Feeding time and median toughness appear to scale differently for smaller primates than for larger primates as indicated by the interaction shown in Fig. 7B. For small primates, as median toughness increases, feeding time increases as well. However, for larger primates, feeding time and toughness have a negative relationship (Fig. 7B). In other words, large primates do not respond to increased dietary toughness by increasing the proportion of their activity budget devoted to feeding as much as do smaller primates. While this result is not strong and there is no straightforward relationship between median toughness and feeding time, failure to consider an interaction driven by body mass risks obscuring potentially important relationships. This result may be a consequence of larger primates' hypothesized increased capacity for masticatory force production (Greaves, 1978, 1988; Demes and Creel, 1988; Wroe et al., 2005), or of their slower metabolic rates and thus relatively lower energetic demands (Kleiber, 1947; Gaulin, 1979; Elgar and Harvey, 1987; Lambert, 1998; McNab, 2008). Differences in oral processing and digestion may also play a role. Mountain gorillas (*G. beringei*) excrete long, fibrous strings of minimally processed food (Elgart-Berry, 2000) and are observed to use coprophagy as a method to maximize available energy from fibrous foods (Harcourt et al., 1978; Mahaney et al., 1990).

In contrast, when we examined feeding time and weighted mean toughness, we found a more straightforward relationship with no interaction. As weighted mean toughness increases, feeding time increases as well (Fig. 7A). This relationship aligns with our predictions and suggests that tougher feeds require longer durations of chewing. However, as mentioned, the dietary composition data used to calculate the weighted mean did not always reflect 100% of the diet, and the food items for which

FMPs were measured comprise only a portion of the total diet for most species. Moreover, feeding time is at best a loose proxy for chewing time, and until the relationship between FMPs and chewing time is more fully quantified we can only speculate about the link between toughness and chewing.

Consequently, and in light of the weak interaction with body mass seen for median but not for weighted mean toughness, further research is needed to establish which of these estimates of dietary toughness more accurately represents the true relationship with feeding time.

Our results with median toughness suggest a possible limit on the active time a primate can devote to feeding. Even highly insectivorous tarsiers spend no more than 60% of their daily activity budget foraging and feeding (Gursky, 2000). The demands of social behavior and social grooming may serve to constrain the amount of time primates can dedicate to other behaviors (Aiello and Dunbar, 1993), including feeding. Assuming this upper limit, primates likely cannot rely solely on increased chewing time to process tough diets. Jaw and tooth morphology may be of vital importance, as a limit on feeding time would place an adaptive premium on dental morphology. The lack of a significant relationship between feeding time and maximum toughness may result from selection pressure of fallback foods on tooth morphology. We would then expect to see strong functional relationships between FMPs and cranial and dental morphology. Post-ingestion processing in the form of gut adaptations related to digestion may also be crucially important to limiting feeding time, either as an alternative to dentognathic morphology or in conjunction with it. Further research on primate microbiota (Amato et al., 2014 a, 2014 b; Gomez, 2014; Fogel, 2015) and gut transit time (Milton, 1984; Edwards and Ullrey, 1999) is necessary to quantify the relationship between digestion and FMPs.

Conclusion

Our results deviated from traditional evaluations of primate diets based on the assumed mechanical properties of food items or dietary categories. We found no significant differences in average FMPs between, for example, foods eaten by frugivorous and folivorous primates. Dietary

quality also failed to yield a relationship with FMPs. Moreover, the food items that form the bulk of most anthropoid primates' diets—leaves, fruits, and seeds—are indistinguishable in terms of average toughness.

The complex interrelationships among FMPs, feeding time, and body mass demonstrate that size influences primate feeding ecology in complicated ways that have not been fully characterized by current research. Our analyses were constrained by the availability of feeding data that can be compared across a large sample of primate species. Even commonly recorded and widely available measures such as diet composition were not always available for the specific primate populations for which dietary FMPs were measured. Further study is warranted and will benefit from improved sampling and the integration of nutritional analyses. Thus, primate feeding ecology would benefit from FMPs collected in tandem with detailed measurements of feeding behavior and non-mechanical food properties. Desirable data include measurements of time and frequency of feeding on specific food items, time spent ingesting versus chewing, oral processing versus chewing times and rates, seasonal or even monthly variations in FMPs and feeding behavior, food intake, bite counts, food weight, and nutritional and chemical properties of individual food items. The variation in behavioral data collection across sites (Schuelke et al., 2006) and the lack of site-specific data for all primates in our sample underscore the need for greater consistency in data collection and more detailed fieldwork on the populations in which FMPs were collected.

Finally, we recommend that FMPs be utilized for further investigation of the relationship between diet and jaw and tooth morphology. While some research has addressed the question of possible relationships between FMPs and craniodental morphology (Taylor et al., 2008; Norconk et al., 2009; Vogel et al., 2014), a large-scale comparison of FMPs and craniodental morphology may uncover meaningful form-function interactions that will provide new insight into the evolution of primate mastication.

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Table 1. Species included in the study sample, with body mass, feeding time, dietary quality, and dietary categories.

Species	Source of FMPs ¹	Body mass average (kg)	Feeding time (g time (%))	Dietary quality ²	Diet % animal	Diet % reproductive	Diet % structural	Diet % exudates	Diet category (specific) ³	Diet category (simple) ³
<i>Alouatta clamitans</i>	Carlos Botelho State Park, Brazil (MT & ES)	4.84 ^a	18 ^l	130.3 ^{jj}	0	30.3	69.69	0	FO	FO
<i>Alouatta paliatta</i>	Ometepe, Nicaragua (MRS)	6.25 ^b	11.47^m	145.34^m	0	45.34	54.66	0	FO	FO
<i>Alouatta seniculus</i>	Iwokrama, Guyana (BW)	5.95 ^b	12.7 ⁿ	165.85	0	65.86	34.15	0	FL	FR
<i>Ateles paniscus</i>	Iwokrama, Guyana (BW)	8.78 ^b	18.9 ^o	194.92	0	94.92	5.08	0	FR	FR
<i>Brachyteles arachnoides</i>	Carlos Botelho State Park,	9.25^c	22.2^p	177.62^{kk}	0	77.62	22.38	0	FL	FR

<i>des</i>	Brazil (MT & ES)									
<i>Callithrix jacchus</i>	Pernambuco, Brazil (CV)	0.35 ^d	35 ^q	317.45 ^{ll}	18.9	21.7	0	59.4	G	G
<i>Cebus apella</i>	Iwokrama, Guyana (BW)	3.09 ^b	16 ^f	180.23	0	80.23	19.77	0	FL	FR
<i>Cebus libidinosus</i>	Fazenda Boa Vista, Brazil (JC)	2.44 ^e	17 ^s	249.42^{mmm}	36.05	59.3	4.65	0	FI	I
<i>Cebus olivaceus</i>	Iwokrama, Guyana (BW)	2.91 ^b	34.2 ^t	196.43	0	96.42	3.57	0	FR	FR
<i>Cercopithecus ascanius</i>	Kibale, Uganda (ND)	3.31 ^b	25	171.91ⁿⁿ	8.25	49.48	42.27	0.52	FL	FO
<i>Chiropotes satanas</i>	Iwokrama, Guyana (BW)	2.88 ^b	22.3 ^{u-w}	200	0	100	0	0	FG	FR
<i>Colobus guereza</i>	Kibale, Uganda	11.35 ^b	31	109ⁿⁿ	0	9	91	0	FO	FO

	(ND)									
<i>Colobus vellerosus</i>	Boabeng-Fiema, Ghana (AE)	9.1 ^f	23.7^x	123.71^x	0	23.71	76.29	0	FO	FO
<i>Gorilla beringei</i>	Karisoke, Rwanda (HG)	130 ^b	55.4^y	101.18^{oo}	0	1.18	98.82	0	FO	FO
<i>Hapalemur aureus</i>	Ranomafana, Madagascar (NY)	1.46^g	34.4^z	104.21^{pp}	0	4.21	95.79	0	FO	FO
<i>Hapalemur griseus</i>	Ranomafana, Madagascar (NY)	0.93^g	37.42^z	105.15^{pp}	0	5.15	94.85	0	FO	FO
<i>Hylobates albibarbis</i>	Sabangau, Indonesia (SC)	5.85 ^b	29^{aa}	176.5^{aa}	1	74	25	0	FL	FR
<i>Lemur catta</i>	Beza Mahafaly, Madagascar (NY)	2.1^h	25.77	151.73	0	51.73	48.27	0	FL	FO

<i>Pan troglodytes schweinfurthii</i>	Kibale, Uganda (ND)	38.2 ^b	27.7	196.43ⁿⁿ	0	85.71	14.29	3.06	FR	FR
<i>Papio ursinus</i>	Giant's Castle and Royal Natal, South Africa (PC)	22.3 ^b	56.6^{bb}	110.01^{qq}	0	10	89.9	0	FO	FO
<i>Piliocolobus badius</i>	Kibale, Uganda (ND)	8.29 ^b	39.9	114.9ⁿⁿ	0	13.13	86.87	0.51	FO	FO
<i>Piliocolobus rufomitrus</i>	Tana River, Kenya (PS)	8.44 ^b	27.97 ^{cc} , dd	140.45 ^{cc}	0	40.45	59.55	0	FO	FO
<i>Pithecia pithecia</i>	Iwokrama, Guyana (BW)	1.76 ^b	19 ^{ee}	200	0	100	0	0	FG	FR
<i>Pongo abelii</i>	Ketambe, Indonesia	56.75 ^b	53.9^{ff}	194.03^{ff}	8.89	71.79	19.31	0	FL	FR

	(EV)									
<i>Pongo pygmaeus morio</i>	Kutai, Indonesia (LL)	57.15 ^b	45.9^{gg}	158^{gg}	0.8	56	43.2	0	FL	FO
<i>Pongo pygmaeus wurmbii</i>	Tuanan, Indonesia (EV)	57.15 ^b	56 ^{ff}	191.16^{ff}	6.36	74.25	18.38	0	FL	FR
<i>Prolemur simus</i>	Ranomafana, Madagascar (NY)	2.57^g	41.2^z	100^{pp}	0	0	100	0	FO	FO
<i>Propithecus verreauxi</i>	Beza Mahafaly, Madagascar (NY)	2.8ⁱ	46.83	128.32	0	28.32	71.68	0	FO	FO
<i>Pygathrix nigripes</i>	Ni Chua, Vietnam (BW)	8.46^j	27.1 ^{hh}	144.57^{rr}	0	44.57	54.43	0	FO	FO
<i>Rhinopithecus avunculus</i>	Tonkin Snub-Nosed Monkey Species/Conservation	11.25 ^k	14.78 ⁱⁱ	162.87^{ss}	0	62.87	37.13	0	FL	FR

	Area, Vietnam (BW)									
<i>Trachypithecus phayrei</i>	Phu Khieo, Thailand (KO)	7.09 ^b	27.9	158.1^{tt}	3.65	48.99	47.37	0	FL	FO

Note: Any data without a citation were provided by one of the authors. Data in bold font were taken from the same site where FMP data were collected.

¹Site name with initials of contributing author.

²Dietary quality was calculated from coefficients; see discussion in text. Numbers in columns to the right are the percentage of the diet consisting of animal matter, reproductive parts, structural parts, and exudates, with the source given for dietary composition. The dietary composition data were adjusted to equal 100% (see discussion in text); DQ indices were calculated based on adjusted figures.

³See discussion in text. FO = folivore, FR = frugivore, G = gummivore, I = insectivore, FL = frugivore-folivore, FI = frugivore-insectivore, FG = frugivore-gummivore.

^aChagas *et al.* 2010.

^bSmith and Jungers 1997.

^cTalebi 2005.

^dAraujo *et al.* 2000.

^cFord and Davis 1992.
^fOates *et al.* 1994.
^gVinyard *et al.* 2008.
^hGould *et al.* 2003.
ⁱRichard *et al.* 2006.
^jWright and Willis 2012.
^kRatajszczak *et al.* 1992.
^lChiarello 1993.
^mRaguet-Schofield 2010.
ⁿGaulin and Gaulin 1982.
^oWallace 2001.
^pTalebi and Lee 2010.
^qDigby *et al.* 2006.
^rTerborgh 1983.
^sSabbatini *et al.* 2008.
^tcited in Rímoli *et al.* 2008.
^uBoyle and Smith 2010.
^vSilva and Ferrari 2009.
^wPort-Carvalho and Ferrari 2004.
^xTeichroeb *et al.* 2003.
^yWatts 1988.
^zTan 2000.
^{aa}Cheyne 2010.
^{bb}Dunbar 1992.
^{cc}Decker 1994.

^{dd}Marsh 1981.
^{ee}Vié *et al.* 2001.
^{ff}Morrogh-Bernard 2007.
^{gg}Rodman 1977.
^{hh}Rawson 2009.
ⁱⁱHai 2007.
^{jj}Agostini 2010.
^{kk}Talebi *et al.* 2005.
^{ll}Correa *et al.* 2000.
^{mm}Izar *et al.* 2012.
ⁿⁿDominy and Lucas 2004.
^{oo}Watts 1984.
^{pp}Tan *et al.* submitted.
^{qq}Whiten *et al.* 1987.
^{rr}Duc *et al.* 2009.
^{ss}Le *et al.* 2007.
^{tt}Suarez 2013.

Table 2: The relationship between FMPs and dietary categories using Kruskal-Wallis rank sum tests, where dietary categories are the independent variables and FMPs are the dependent variables. The general diet classification included four categories (folivore, frugivore, insectivore, and gummivore); the specific classification included seven (folivore, frugivore, insectivore, gummivore, frugivore-folivore, frugivore-gummivore, and frugivore-insectivore).

Dependent variable	Independent variable	χ^2	df	<i>p</i>
WeightedR	specific diet category	6.75	5	0.239
WeightedR	simple diet category	3.86	3	0.277
MedianR	specific diet category	4.5	5	0.479
MedianR	simple diet category	3.49	3	0.321
MaximumR	specific diet category	0.86	5	0.973
MaximumR	simple diet category	1.25	3	0.742
WeightedE	specific diet category	3.66	5	0.596
WeightedE	simple diet category	2.82	3	0.421
MedianE	specific diet category	4.53	5	0.476
MedianE	simple diet category	3.69	3	0.297

MaximumE	specific diet category	3.62	5	0.605
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MaximumE	simple diet category	2.48	3	0.479
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Table 3: The relationship between FMPs and categories of food items using a Wilcoxon rank sum test for post-hoc analysis of a Kruskal-Wallis rank sum test, where food items are the independent variables and FMPs are the dependent variables. Significant results are highlighted in bold. Results of Kruskal-Wallis tests were significant for both toughness ($\chi^2 = 122.48, p < 0.001$) and Young's modulus ($\chi^2 = 66.59, p < 0.001$), and for toughness by maturity level ($\chi^2 = 17.8, p < 0.001$).

A. Toughness.

	bark	flower	fruit	leaf	seed	stem
bamboo	0.223	<0.0001	<0.0001	<0.0001	<0.0001	0.005
bark		<0.0001	<0.0001	<0.0001	0.002	0.486
flower			0.031	0.005	0.095	<0.001
fruit				1 ¹	1	0.049
leaf					1	0.068
seed						1

B. Young's modulus.

	fruit	seed

bamboo	<0.0001	<0.0001
fruit		<0.01

C. Toughness by maturity level.

	unripe fruit	ripe fruit	mature leaf
young leaf	0.086	1	0.061
unripe fruit		0.023	1
ripe fruit			0.003

¹Exact *p*-value cannot be computed for ties.

Table 4: The relationship between dietary quality and FMPs using PGLS, where dietary quality is the independent variable. $\lambda = 0$ for all results. After Bonferroni-Holm corrections, no results are significant.

Dependent variable	<i>F</i>	df	slope	Adjusted R^2	<i>p</i>
WeightedR	1.12	29	-0.002	0.004	0.298
MedianR	0.07	29	-0.001	-0.032	0.788
MaximumR	0.13	29	-0.001	-0.029	0.721
WeightedE	2.85	19	-0.007	0.084	0.108
MedianE	2.27	19	-0.007	0.059	0.149
MaximumE	4.57	19	-0.009	0.152	0.046

Table 5: The relationship between body mass and measures of food mechanical properties using PGLS analyses, with body mass as the independent variable. Significant results after performing a Bonferroni-Holm correction for multiple comparisons are indicated in bold. $\lambda = 0$ for all results.

Dependent variable	F	df	slope	Adjusted R^2	p
WeightedR	1.76	1, 29	-0.13	0.025	0.195
MedianR	4.73	1, 29	-0.209	0.11	0.038
MaximumR	<0.01	1, 29	-0.002	-0.034	0.989
WeightedE	22.94	1, 19	-0.572	0.523	0.0001
MedianE	28.12	1, 19	-0.645	0.576	<0.0001
MaximumE	10.75	1, 19	-0.48	0.327	0.004

Table 6: PGLS results for models where feeding time is the dependent variable and body mass and different food material properties are the independent variables. Models including interactions were run first; if the interaction term did not trend toward significance ($0.05 < p < 0.1$), the result without the interaction is presented.

A. Feeding time vs body mass and *WeightedR*, no interaction ($F(2,28) = 5.57, \lambda = 0.242, R^2 = 0.23, p = 0.009$)

Independent variable	<i>t</i>	slope	<i>p</i>
body mass	2.66	0.09	0.013
WeightedR	2.62	0.162	0.014

B. Feeding time vs body mass and *MedianR* ($F(3,27) = 3.51, \lambda = 0.085, R^2 = 0.2, p = 0.029$)

Independent variable	<i>t</i>	slope	<i>p</i>
body mass	2.19	0.827	0.037
MedianR	2.13	0.986	0.043
body mass * MedianR	-1.96	-0.109	0.061

C. Feeding time vs body mass and *MaximumR*, no interaction ($F(2,28) = 4.96, \lambda = 0, R^2 = 0.21, p = 0.014$)

Independent variable	t	slope	p
body mass	2.43	0.086	0.022
MaximumR	2.01	0.125	0.055

D. Feeding time vs body mass and *WeightedE* ($F(3,17) = 2.09, \lambda = 0.12, R^2 = 0.14, p = 0.139$)

Independent variable	t	slope	p
body mass	2.27	0.212	0.036
WeightedE	1.94	0.954	0.071
body mass * WeightedE	-1.9	-0.115	0.074

E. Feeding time vs body mass and *MedianE* ($F(3,17) = 2.24, \lambda = 0.09, R^2 = 0.16, p = 0.12$)

Independent variable	t	slope	p
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body mass	2.29	0.195	0.035
MedianE	1.96	0.843	0.065
body mass * MedianE	-1.93	-0.1	0.07

F. Feeding time vs body mass and *MaximumE*, no interaction ($F(2,18) = 1.61, \lambda = 0.64, R^2 = 0.06, p = 0.228$)

Independent variable	<i>t</i>	slope	<i>p</i>
body mass	1.74	0.095	0.099
MaximumE	0.71	0.048	0.488

Figure 1

Categorization of food items used for this study. Food items were grouped by type according to the second nested level (e.g. leaf, shoot). Sample sizes and min/max ranges for toughness (R) and Young's modulus (E) are provided in parentheses. Each sample corresponds to a specific test of a food item. In some cases, this represents an average of all food items of a particular type for a given species (e.g. the average of all tests for mature leaves eaten by *A. clमितans*) because of how data were reported. In other cases, the sample is a single measurement for a particular plant species. Items in bold are those which were analyzed for variations in FMPs (Table 4).

Figure 2

Phylogenetic tree used for PGLS. The consensus tree was taken from the 10kTrees website (Arnold et al., 2010) and pruned to fit our sample.

Figure 3

Plots by specific dietary category showing distributions of median FMPs. A is toughness and B is Young's modulus. FG = frugivore-gummivore, FI = frugivore-insectivore, FL = frugivore-folivore, FO = folivore, FR = frugivore, and G = gummivore. Species designations are listed in Table 1. No significant results were found.

Figure 4

Plots by food item showing distributions of FMPs. A is toughness and B is Young's modulus. C is toughness by ripeness/maturity. FMP values are not logged, so as to demonstrate clustering of FMPs. The carrot icon in 4C provides context.

Figure 5

Plots of FMPs (log) against body mass (log). A-C represent toughness (A: *WeightedR*, B: *MedianR*, C: *MaximumR*), and D-F represent Young's modulus (D: *WeightedE*, E: *MedianE*, F: *MaximumE*). A-C are not significant, but D-F are significant ($p < 0.01$). Data points are separated by taxon (open red triangles = hominoids, shaded teal triangles = cercopithecoids, purple squares = platyrrhines, blue circles = strepsirrhines). The carrot and almond icons are provided for context.

Figure 6

Plot of feeding time (logit) versus body mass (log). The OLS regression line is shown ($p = 0.03$, $R^2 = 0.12$) as PGLS analysis resulted in $\lambda = 0$. Data points are separated by taxon (open red triangles = hominoids, shaded teal triangles = cercopithecoids, purple squares = platyrrhines, blue circles = strepsirrhines).

Figure 7

Plot of feeding time versus *WeightedR* (A) and *MedianR* (B) intended to visualize the effect of body size on the relationship between feeding time and dietary toughness. The different trend

lines for A and B are caused by the presence of an interaction between body mass and *MedianR* and the absence of an interaction between body mass and *WeightedR* (as seen in Table 6). The area of each data point is scaled to body mass (unlogged). (Red = hominoids, green = cercopithecoids, purple = platyrrhines, blue = strepsirrhines.) The dashed trendlines correspond to the trend expected based on the PGLS model shown in Table 6 for a primate the size of the largest species (*Gorilla beringei*) in the sample (in black) and for a primate the size of the smallest species (*Callithrix jacchus*) in the sample (in gray). The solid trendlines are based on an OLS model (i.e., the model shown in Table 6 with λ set to 0). For A, the trendline shows an increase in feeding time as weighted mean toughness increases. For B, the trendlines describe the nature of the interaction between body mass and median toughness as correlates of feeding time. At smaller body sizes, feeding time increases as toughness increases, but at larger body sizes, the reverse is true.

structural (*R*: N = 563, *E*: N = 54)

leaf (*R*: N = 441, *E*: N = 0) (*R*: 57-10357.18)

mature (*R*: N = 183, *E*: N = 0) (*R*: 57-4301.00)

young (*R*: N = 102, *E*: N = 0) (*R*: 60.7-4505.23)

shoot (*R*: N = 6, *E*: N = 1) (*R*: 243.36-1376.43, *E*: 4.76)

grass (*R*: N = 1, *E*: N = 1) (*R*: 3907.46, *E*: 3132.55)

root/tuber/bulb part (*R*: N = 8, *E*: N = 6) (*R*: 61.83-3327.3, *E*: 0.76-545.13)

stem/stalk (*R*: N = 24, *E*: 4) (*R*: 126.6-6695.65, *E*: 2.25-134.91)

pith (*R*: N = 7, *E*: 1) (*R*: 384-5817.51, *E*: 0.51)

bamboo (non-leaf) (*R*: N = 22, *E*: N = 21) (*R*: 346.5-10584.45, *E*: 52.92-10098.94)

sheath

shoot

culm pith

stalk/rachis

bark (*R*: N = 53, *E*: N = 3) (*R*: 152.9-15097.58, *E*: 1.35-1961.69)

cambium (*R*: N = 1, *E*: N = 1) (*R*: 2786.5, *E*: 282.9)

reproductive (*R*: N = 456, *E*: 234)

fruit

pericarp and whole fruit (*R*: N = 383, *E*: N = 182) (*R*: 15-5418.2, *E*: 0.006-1195)

ripe (*R*: N = 117, *E*: N = 68) (*R*: 24.65-3690.70, *E*: 0.006-1195)

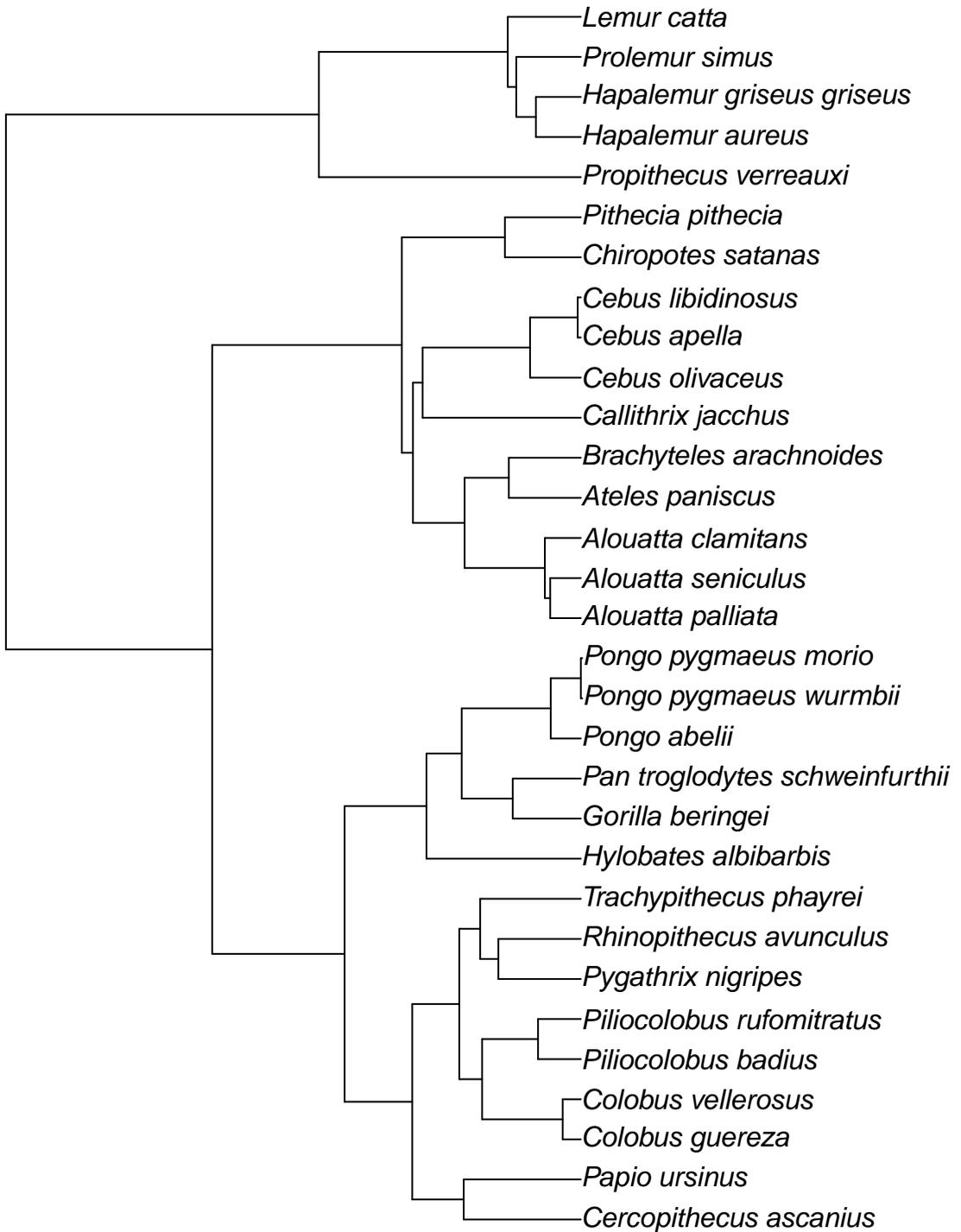
unripe (*R*: N = 59, *E*: N = 55) (*R*: 26.60-3016.17, *E*: 0.106-13.08)

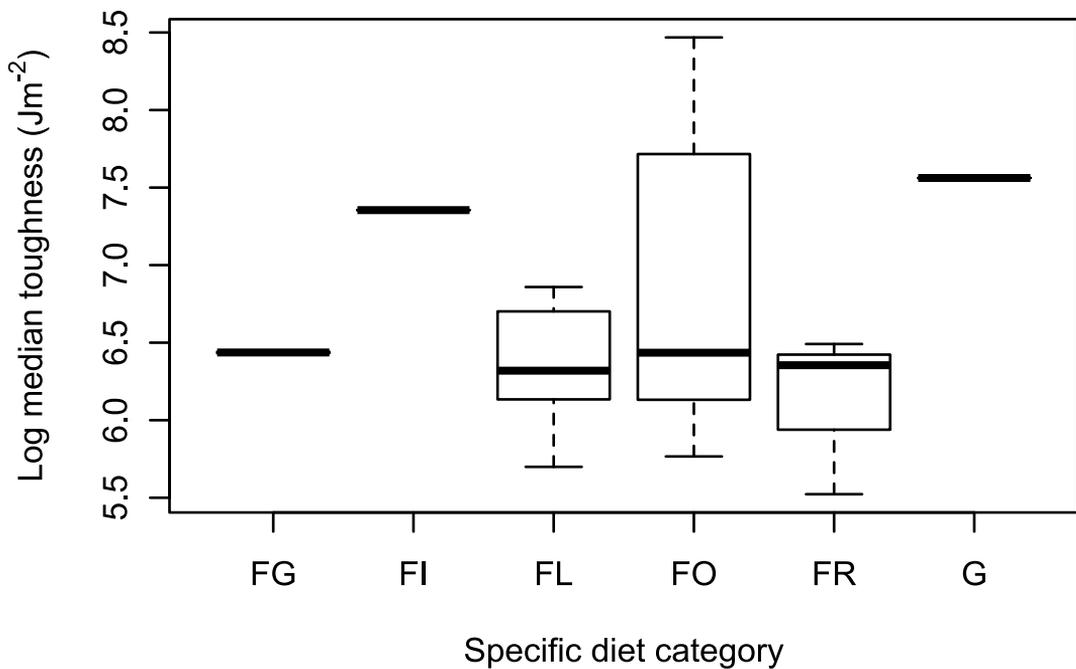
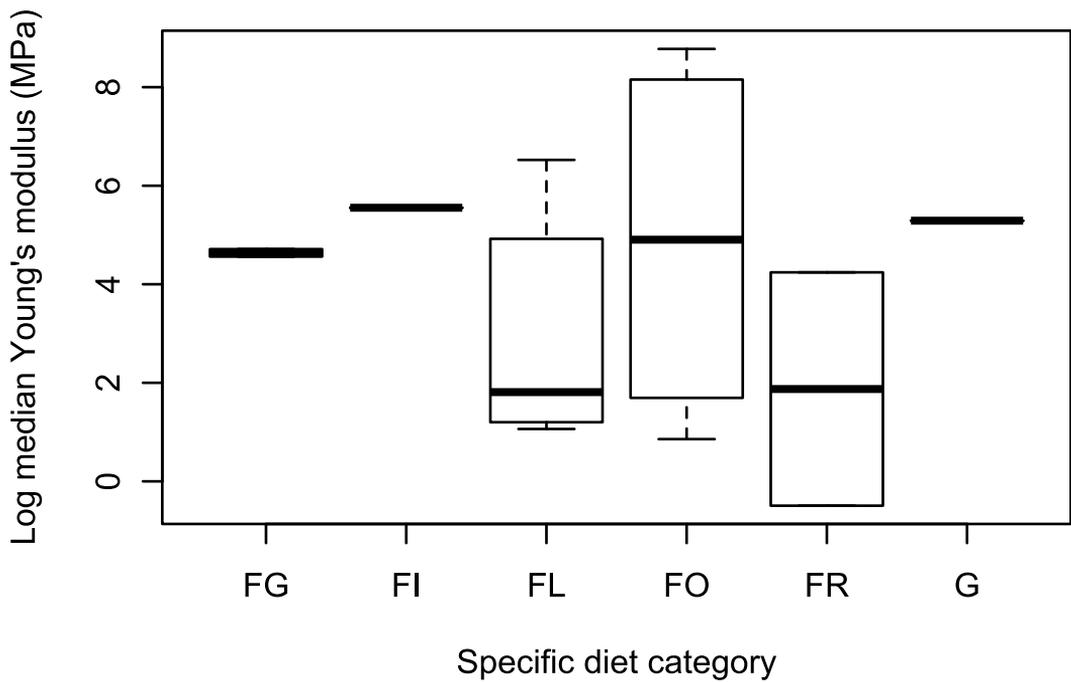
seed (*R*: N = 20, *E*: N = 47) (*R*: 64-2803, *E*: 0.52-169.07)

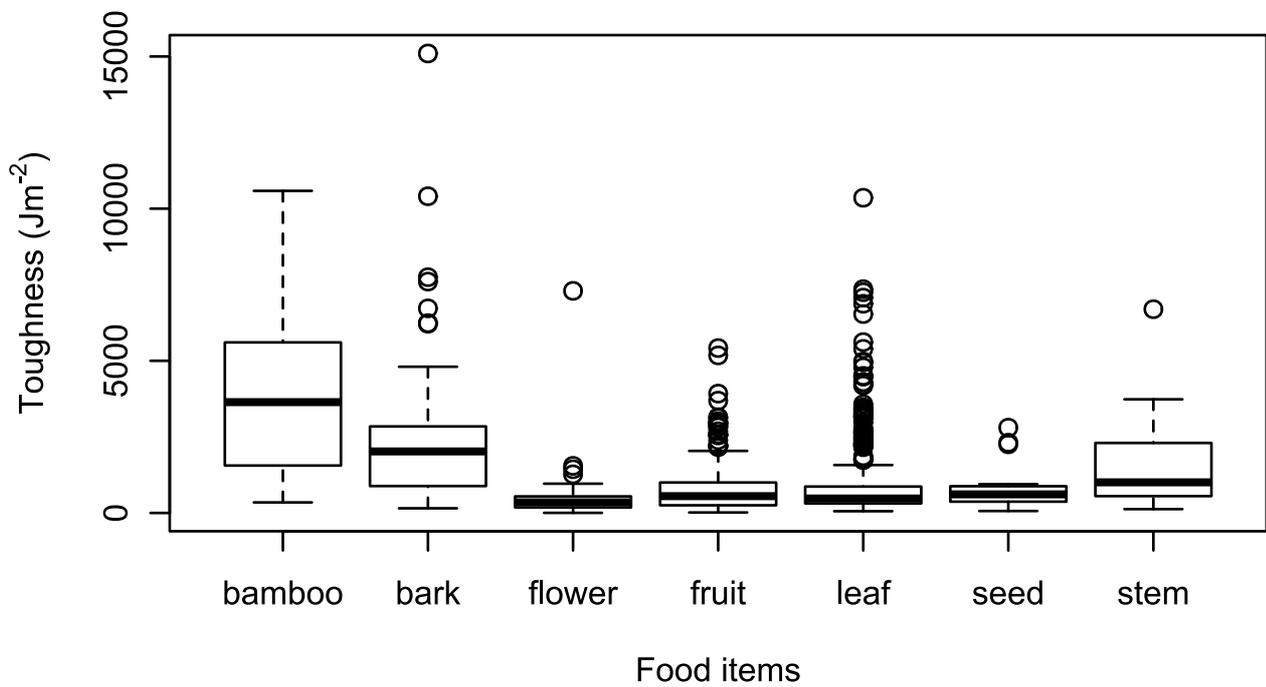
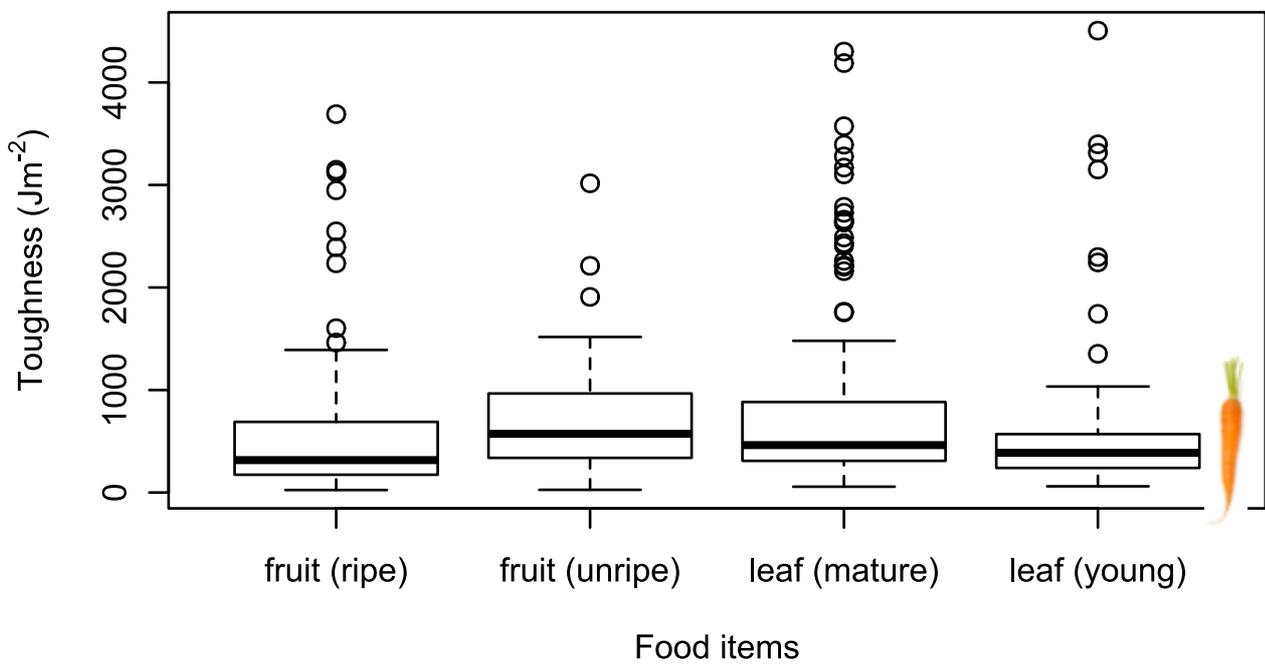
flower (*R*: N = 53, *E*: N = 5) (*R*: 3.1-7298, *E*: 0.21-1475.74)

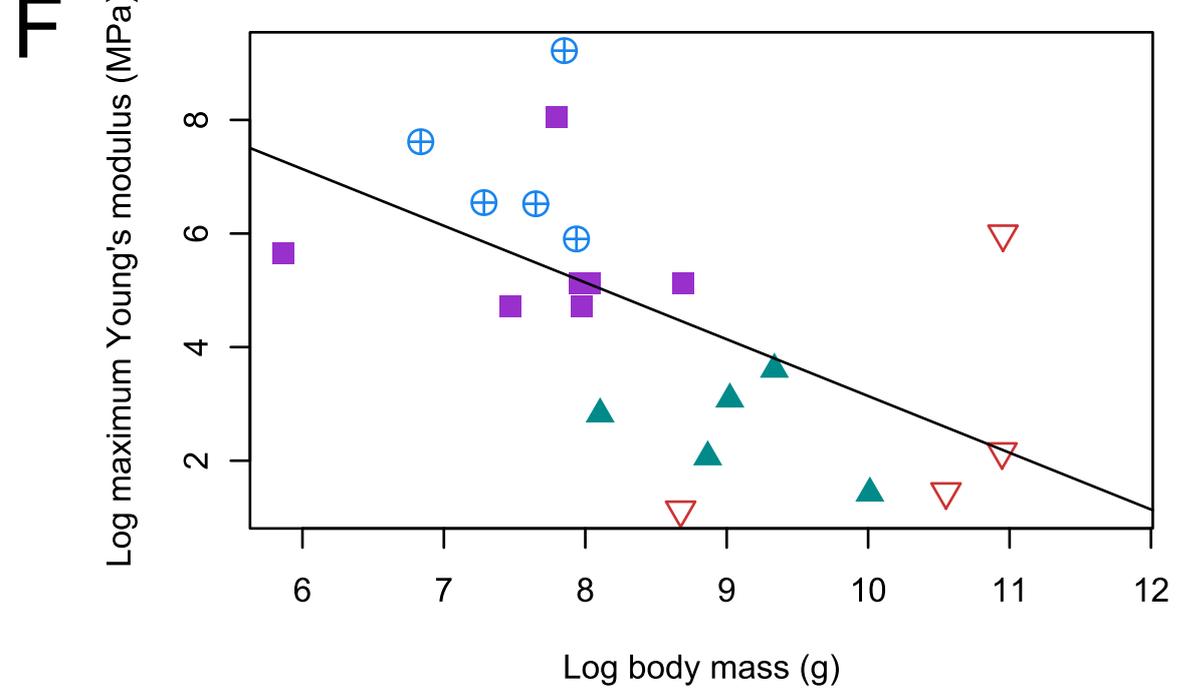
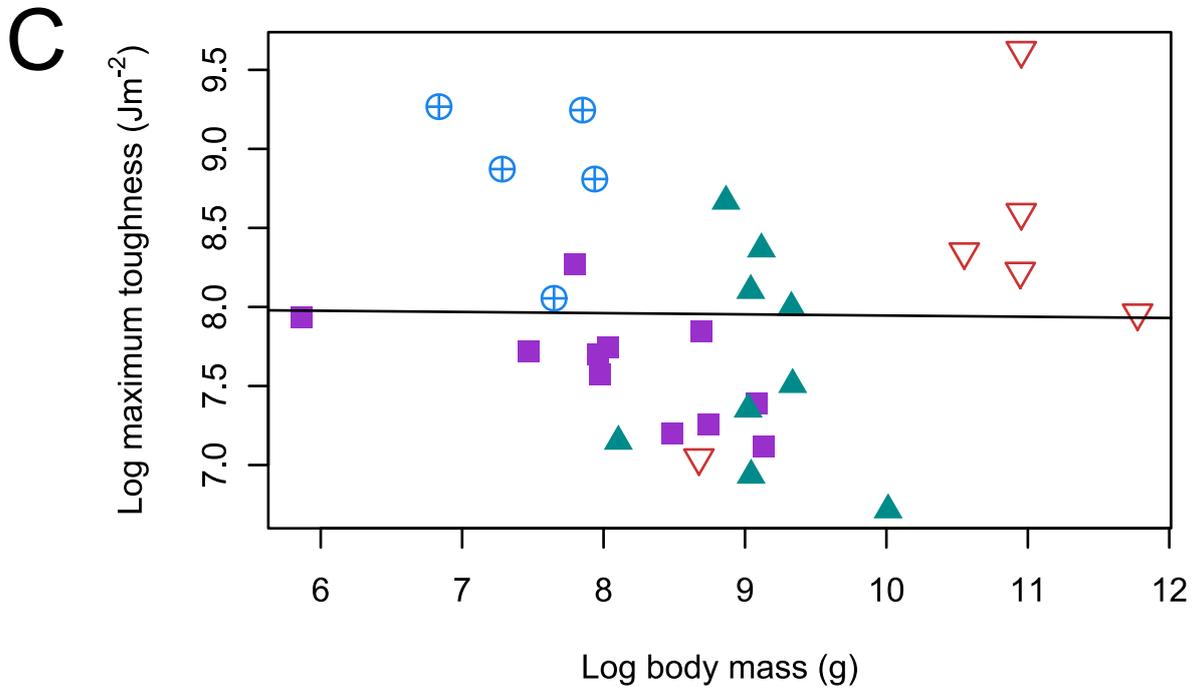
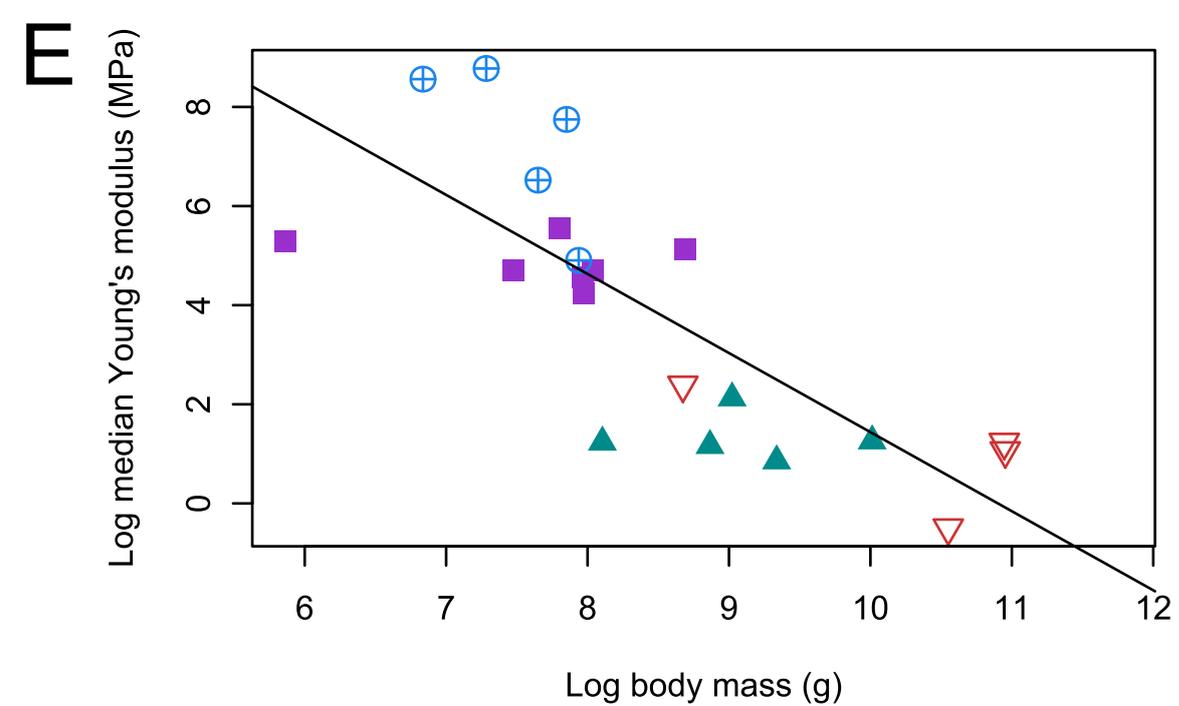
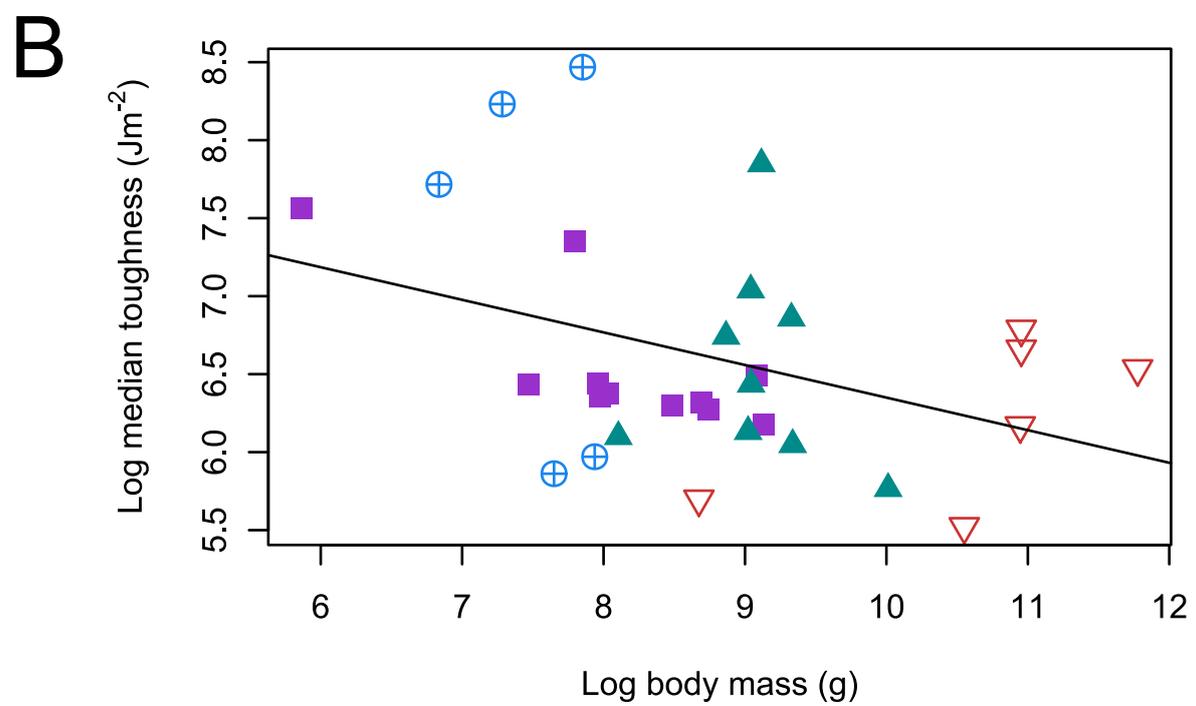
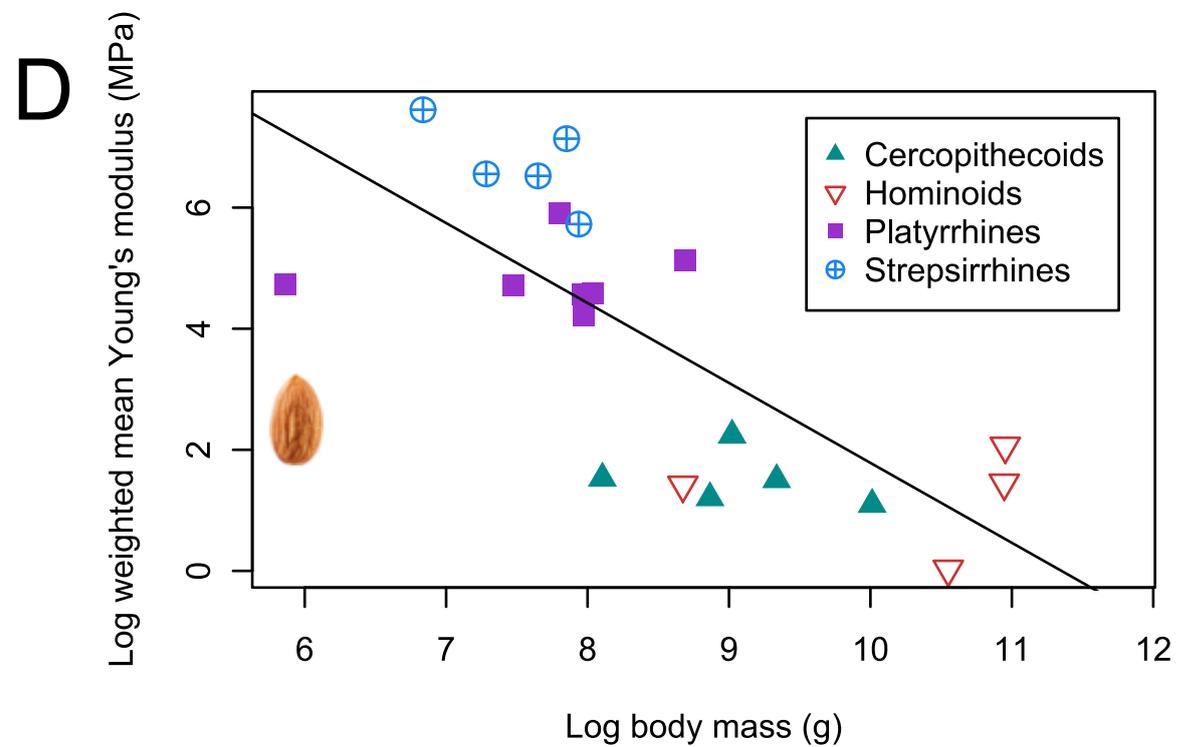
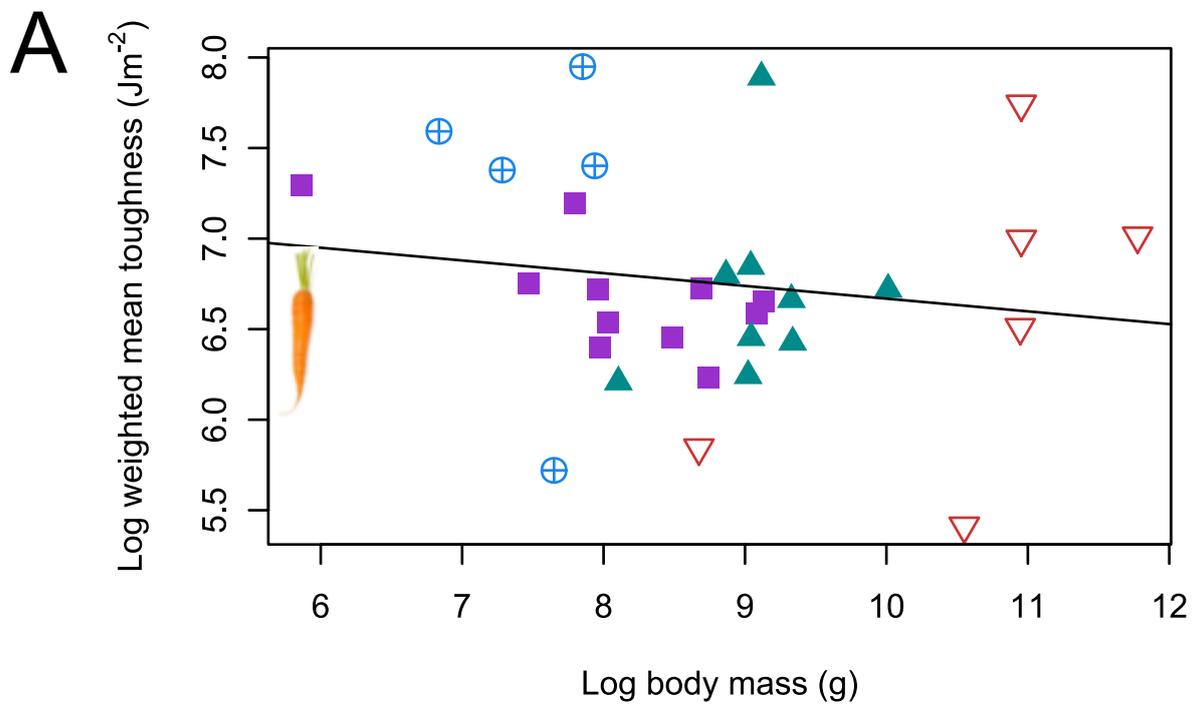
animal (N = 0)

exudate (N = 0)

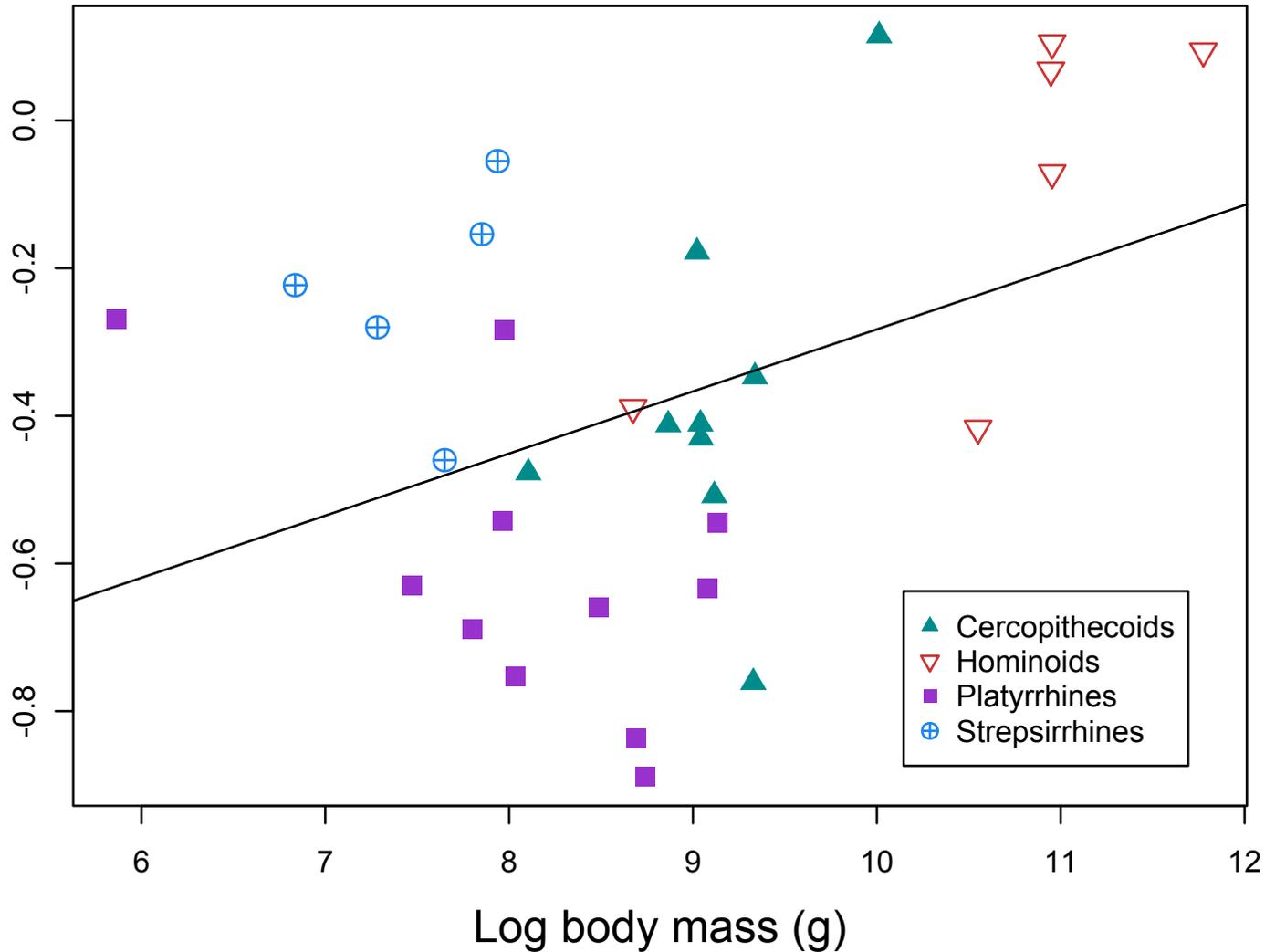


A**B**

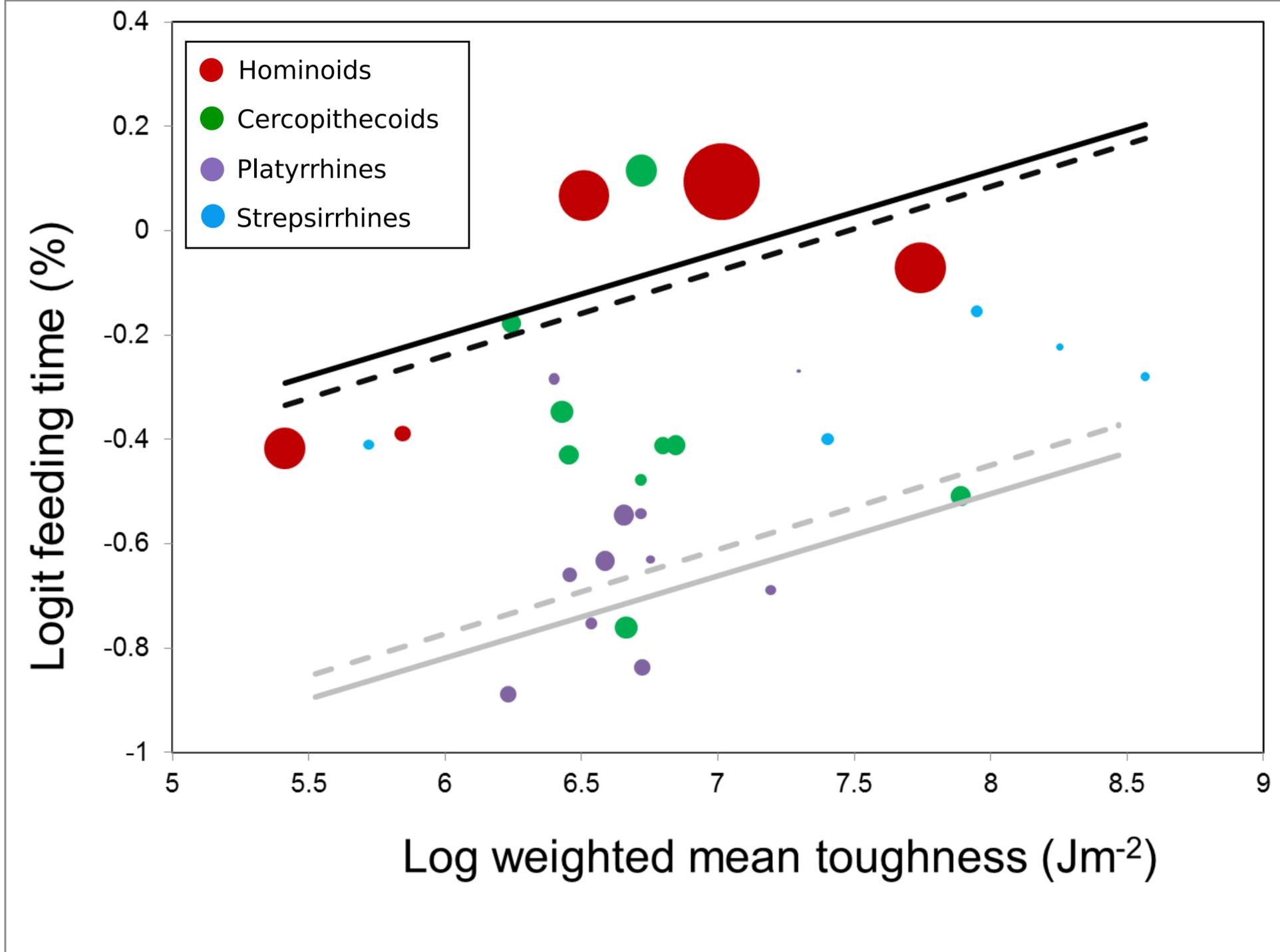
A**B****C**



Logit feeding time



A.



B.

