

RESEARCH ARTICLE

Mechanical Properties of Foods Used in Experimental Studies of Primate Masticatory Function

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In vivo studies of jaw-muscle behavior have been integral factors in the development of our current understanding of the primate masticatory apparatus. However, even though it has been shown that food textures and mechanical properties influence jaw-muscle activity during mastication, very little effort has been made to quantify the relationship between the elicited masticatory responses of the subject and the mechanical properties of the foods that are eaten. Recent work on human mastication highlights the importance of two mechanical properties—toughness and elastic modulus (i.e., stiffness)—for food breakdown during mastication. Here we provide data on the toughness and elastic modulus of the majority of foods used in experimental studies of the nonhuman primate masticatory apparatus. Food toughness ranges from approximately 56.97 Jm^{-2} (apple pulp) to 4355.45 Jm^{-2} (prune pit). The elastic modulus of the experimental foods ranges from 0.07 MPa for gummy bears to 346 MPa for popcorn kernels. These data can help researchers studying primate mastication select among several potential foods with broadly similar mechanical properties. Moreover, they provide a framework for understanding how jaw-muscle activity varies with food mechanical properties in these studies. *Am. J. Primatol.* 67:329–346, 2005. © 2005 Wiley-Liss, Inc.

Key words: mechanical properties; fracture toughness; elastic modulus; electromyography

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INTRODUCTION

In vivo studies of mastication in various mammals, including primates, have employed several techniques (e.g., electromyography, bone strain, and cineradiography) to describe the biomechanics of the masticatory apparatus. In such studies, investigators provide subjects with foods that differ in their structural and mechanical properties in order to elicit a range of functional responses from the jaw muscles. Research has shown that the mechanical and textural properties of different foods influence the magnitude and duration of jaw-muscle activity [Ahlgren, 1966; Crompton, 1989; Horio & Kawamura, 1989; Hylander & Johnson, 1994; Hylander et al., 2000; Oron & Crompton, 1985; Ottenhoff et al., 1996; Mioche et al., 1999; Møller, 1966; Plesh et al., 1986]. Furthermore, changes in the amount and velocity of transverse and vertical jaw movements offer indirect evidence for an association between neuromuscular control of mammalian jaw muscles and food textures [Agrawal et al., 2000; Ahlgren, 1966; Fish & Mendel, 1982; Hiimae & Kay, 1973; Horio & Kawamura, 1989; Hylander et al., 1987; Lucas et al., 1986; Oron & Crompton, 1985; Takada et al., 1994; Thexton et al., 1980].

Jaw-muscle activity during mastication is regulated by the periodontal mechanoreceptors [Anderson et al., 1970; Lavigne et al., 1987]. These mechanoreceptors sense changes in food consistency during mastication through changes in the direction, amplitude, and rate of tooth loading. This information is transmitted to the central nervous system, where muscle activity is adjusted for further comminution of food [Lund, 1991; Ottenhoff et al., 1992; Trulsson et al., 1992; Trulsson & Johansson, 1994, 1996; van der Bilt et al., 1995; Yang & Turker, 1999, 2001]. This neural feedback modulates EMG activity within 20 msec of mechanoreceptor stimulation, suggesting that muscle activity can be altered within a given chew cycle [van der Bilt et al., 1995].

In humans, researchers have performed controlled studies to describe how jaw muscle activity changes with food material properties and textures [e.g., Agrawal & Lucas, 2002; Agrawal et al., 1997, 1998; Lucas et al., 2002; Lucas, 2004; Mioche & Peyron, 1995; Mioche et al., 1999; Plesh et al., 1986; Takada et al., 1994]. However, for most of these studies the mechanical-properties of these foods unknown and thus are not comparable across experiments. To date there has been no quantitative assessment of the link between jaw-muscle activity and food texture in nonhuman primates, although several researchers have identified the need to clarify this relationship [e.g., Agrawal et al., 1997, 1998, 2000; Lucas et al., 2002; Strait & Vincent, 1998; Wang & Stohler, 1990]. This is an important gap in our understanding of primate masticatory mechanics because jaw-muscle activity is thought to have an important role in the evolution of primate masticatory form [Hylander, 1979, 1984, 1985; Hylander et al., 1987, 1998, 2000, 2004, in press; Hylander & Johnson, 1994; Lieberman & Crompton, 2000; Ravosa & Hogue, 2004; Ravosa et al., 2000; Vinyard & Ravosa, 1998; Vinyard et al., 2001, 2005, in press]. Specifically, the jaw muscles exert external loads on the mandible during mastication, and these loads cause internal stresses and strains in the jaws during chewing and biting. Furthermore, numerous comparative studies have relied on studies of jaw-muscle activity and bone strain to gain insight into mandibular loading in order to generate biomechanical hypotheses regarding the influence of diet on primate mandibular form [e.g., Bouvier, 1986a, b; Daegling, 1992; Ravosa, 1991, 1996a, 2000; Taylor, 2002; Williams et al., 2002; Wright, 2001, 2005; Vinyard et al., 2003].

As a first step toward understanding the relationship between primate masticatory function and food properties, we present data on the toughness and elastic modulus of foods consumed by nonhuman primate species in experimental studies of the masticatory apparatus. These data are important for a number of reasons. First, experimentalists are often faced with the dilemma of identifying a broad range of foods of various mechanical properties that a nonhuman primate will chew in the laboratory. Because food material properties have not been measured on experimental foods, it is unknown which foods may be appropriate substitutes for each other during mastication experiments.

Second, several field studies of primate diets have shown that food choice may be related to food texture, and that this may account for morphological differences in the masticatory apparatus between closely-related and/or sympatric species [Dominy & Lucas, 2004; Elgart-Berry, 2004; Happel, 1988; Kinzey & Norconk, 1990, 1993; Lucas et al., 2000; Overdorff & Strait, 1998; Strait, 1993; Vinyard et al., 2004; Wright, 2001, 2004, 2005; Yamashita, 1996, 1998, 2002]. Thus, the current data are also informative for assessing the appropriateness of food choice in the laboratory setting to address evolutionary adaptive explanations for primate jaw forms. These explanations assume that we understand the link between jaw-muscle function and ecologically-relevant foods. While we can accurately describe jaw-muscle function in the laboratory, these data may have limited evolutionary relevance because we do not know whether we are eliciting jaw-muscle activity patterns (particularly with respect to magnitude of recruitment) that are characteristic of primates consuming a natural diet. As field studies that focus on the mechanical properties of primate diets become more common, we can determine which foods used in laboratory studies are more likely to elicit “natural” masticatory responses in the experimental laboratory setting. Matching the material properties of laboratory foods with foods processed in the wild will allow researchers to interpret *in vivo* experimental research in a broader evolutionary context that moves beyond the current functional context. Specifically, it will allow researchers to interpret *in vivo* experimental results on chewing behaviors in the context of the environmentally-dictated selection pressures that conspecifics may experience.

Finally, much of what we know about mammalian jaw-muscle function comes from electromyographic data collected from several nonhuman primate species chewing a variety of foods [e.g., Hylander et al., 1987, 1992, 2000, 2002, 2003, 2004, *in press*; Hylander & Johnson, 1989, 1993, 1994; Luschei & Goodwin, 1974; McNamara, 1973; Miller et al., 1982; Wall et al., 1999; Ross & Hylander, 2000; Vinyard et al., 2001]. While we know that neuromuscular activity varies qualitatively with foods, these data can help us to quantitatively describe how jaw-muscle activity changes with food mechanical properties. Improving our knowledge regarding this relationship will help both laboratory and field primatologists to better understand how variation in the mechanical properties of primate diets relates to variation in the masticatory apparatus and patterns of dietary niche partitioning.

Mechanical Properties and Fracture Mechanics: A Brief Overview

Recently, Agrawal et al. [1997, 1998, 2000] and Lucas et al. [2002] drew on the theory of fracture mechanics to elucidate the relationship between food breakdown and jaw-muscle activity in humans. In order to discuss the relevance of their work, we first provide a brief overview of fracture mechanics and terminology as it relates to mastication.

The fracture of solid particles is determined by two properties: the elastic (or Young's) modulus (E), and toughness (R) [Ashby, 1992]. The elastic modulus describes the rigidity of an object through the ratio of stress (force/unit area over which it acts) to corresponding strain (increase in length/original length) along the linear portion of the stress-strain curve (i.e., $E = \text{stress}/\text{strain}$) (Fig. 1). In lay terms, this value estimates a material's stiffness in either tension or compression, and the higher the modulus the stiffer the material. However, materials can also deform before they form cracks, and therefore the elastic modulus only partially describes the resistance to the initiation of fracture [Ashby, 1992]. Toughness is defined as the energy consumed in growing a crack of a given area, and is measured (in joules per meter squared (Jm^{-2})) as the area under the force-displacement curve produced in growing this crack divided by the crack area [Ashby, 1992; Vincent, 1992; Lucas, 2004] (Fig. 2).

During mastication, fragmentation of food between the teeth is largely dependent on either the food's toughness or a combination of its toughness and stiffness, expressed as fragmentation indices [Agrawal et al., 1997; Lucas et al., 2002]. When food is more or less two-dimensional (e.g., leaves), toughness (R) is probably the most relevant factor that dictates fragmentation [Lucas & Teaford, 1994; Lucas et al., 2000, 2002]. Some food tissues can withstand high strains, or displacements, before crack propagation and subsequent failure begins. Breakdown of such items is displacement-limited. When the size and number of fragments are dictated

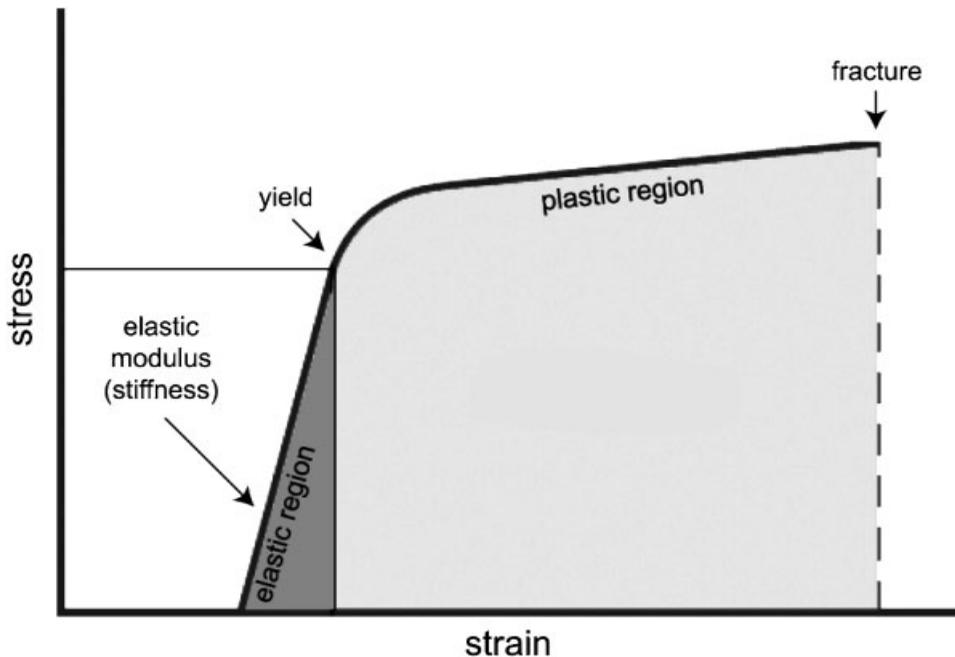


Fig. 1. Hypothetical stress-strain curve showing how the elastic modulus is determined. Elastic deformation occurs prior to the yield point. Once the yield point is reached, all deformation is plastic (i.e., the material does not return to its original dimensions). The elastic modulus, or stiffness, is measured as stress/strain along the linear elastic region of the curve.

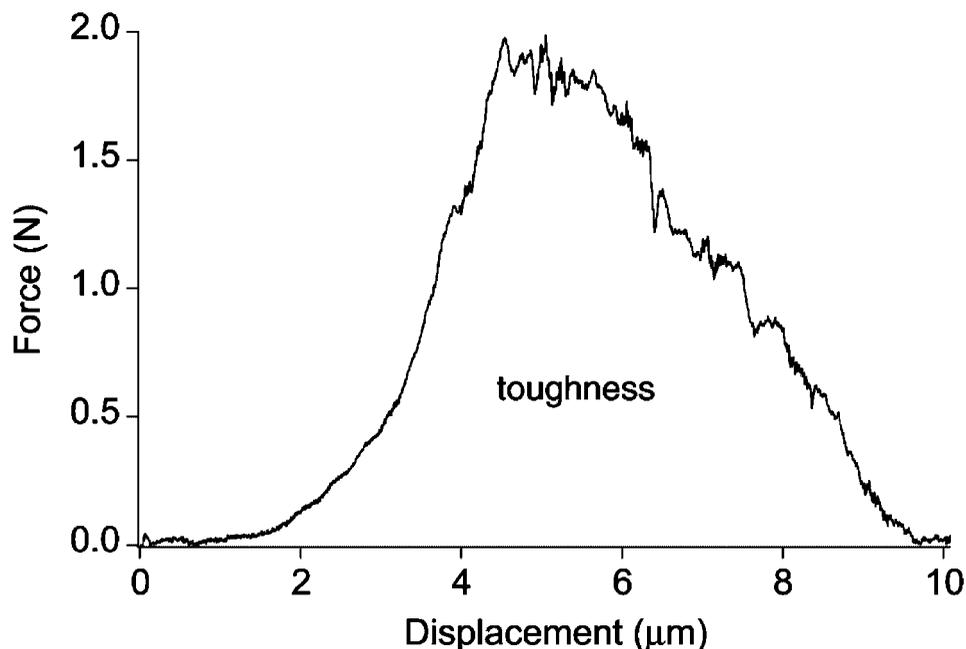


Fig. 2. Force-displacement graph for a raisin sample measured using the scissors test on a portable mechanical-properties tester. Toughness is equivalent to the area under the force-deformation curve divided by the area of new crack growth. It is an indication of the amount of work per unit area (Joules per square meter) done on the material during fracture.

by the displacement available during occlusion, fragmentation is best described by the index $(R/E)^{0.5}$, i.e., $(\text{toughness}/\text{elasticity})^{0.5}$. Foods that exhibit limited strains at high stresses prior to the start of crack formation are stress-limited. The fragmentation index given by $(ER)^{0.5}$ applies when the largest stresses applied to the food dictate fragmentation [Agrawal et al., 1997; Lucas et al., 2002].

Agrawal et al. [1997] showed that the rate of food breakdown between the teeth is inversely related to the fragmentation index given by $(R/E)^{0.5}$ for displacement-limited foods. They further showed that in humans there is a significant inverse relationship between this fragmentation index and 1) the peak magnitude of the integrated surface EMG from the anterior temporalis, 2) the mediolateral deviations of the jaw, and 3) the closing angle of the jaw during mastication [Agrawal et al., 1998, 2000]. This finding is similar to that reported in other studies [e.g., van der Bilt et al., 1995], and suggests that mechanoreceptors send sensory feedback on the rate of food breakdown to the central nervous system in order to modulate jaw-muscle activity during individual power strokes [Agrawal et al., 1998].

MATERIALS AND METHODS

We calculated the toughness and elastic modulus of several food items given to nonhuman primates in experimental studies. The foods included apple pulp (red delicious), apple skin (red delicious), almond, carrot, cherry pit, cricket

cuticle, apricot (dehydrated and dried¹), gummy bear (fresh and dried), raisin (fresh and dried), prune, monkey chow, pear skin, popcorn kernel, prune pit, and sweetgum leaf. We measured toughness using a scissors test on a portable mechanical-properties tester attached to a laptop computer running LabView 6.0 [Darvell et al., 1996; Lucas et al., 2001].

For all toughness tests, the samples were cut to an appropriate size and shape with scalpels or a microtome, and then measured. Apple skin was isolated from the parenchyma (pulp) before it was cut, and the toughness of both tissues was measured separately. In the case of cherry pits and prune pits, only the seed shells were tested. We isolated the seed shells from the pit by removing individual slices (approximately 0.5 mm thick) using a microtome. The cuts for the scissors test were made transversely through the shell from the outer to the inner surface. For sweetgum leaves, cuts were made on isolated sections from the leaf tips without including the major vein in each section. However, cuts were made across multiple secondary veins. To determine the toughness of fresh crickets, we carefully dissected the prothorax cuticle from the remainder of the viscera. We tested only cricket cuticle because the remaining insect tissues (i.e., the viscera) tended toward extreme plastic flow during cutting. This prohibited us from calculating the cut surface area, which is a requirement for measuring toughness in our apparatus. Importantly, the cuticle, which consists largely of chitin, is the toughest structure that a primate would have to break down when chewing an insect of this type.

The elastic modulus of the different foods was measured under either tension and compression. Because tensile and compressive loading may not yield the same values for the elastic modulus, the mode of loading was determined based on the physical characteristics of the specimens and on the likely means that an animal would induce failure (i.e., compression or tension) to the food during chewing. Apricot, gummy bear, raisin, apple skin, pear skin, and prune samples were measured under tension on the portable mechanical-properties tester at cross-head speeds of 15–35 mm/min. For all remaining foods, the elastic modulus was estimated from the load-extension curves produced by compressing the foods in an Instron™ universal testing machine (model 1122; Instron Inc., Canton, MA) in the Rheology Laboratory of the Department of Food Science at North Carolina State University. This second tester was used because several of the remaining items (e.g., prune pit, cherry pit, monkey chow, and popcorn kernel) could potentially have overloaded the load cells on the portable tester, or because the clamps used to hold the specimens in the portable tester compressed the food items before the tensile load (apple pulp, carrot, or almond) was applied. Foods were compressed at a crosshead speed of 10–50 mm/min. Prior to testing, the apple pulp and carrot pieces were cut into uniform shapes and measured. Because the prune pits, cherry pit, almonds, and popcorn kernels could not be cut into a uniform shape, estimates of the elastic modulus required additional calculations, taking into account the convexity of the food surfaces that contacted the plates of the universal testing machine. This was done following the formula for the elastic modulus (E) given by Mohsenin [1986]:

$$E = \frac{0.531F(1 - \mu^2)}{D^{3/2}} \left(\frac{1}{R_1} + \frac{1}{R_1'} \right)^{1/2}$$

¹Food items described as “dried” were allowed to air-dry for 3 or more weeks before they were measured in this study. All other foods were tested on fresh or “out of the package” samples. For example, dehydrated apricots were dehydrated by the manufacturer.

where F is the force, μ is Poisson's ratio, D is the deformation, and R_1 and R'_1 are estimates of the radii of curvatures for the food surfaces contacting the plates of the universal tester. R_1 and R'_1 were determined directly from the specimens [Mohsenin, 1986]. Poisson's ratio, which describes the compressibility of the material perpendicular to an applied stress, was estimated here to be 0.25 for all foods tested. This estimate is based on the fact that the limited estimates of Poisson's ratio for relevant biological materials (e.g., apple flesh and corn stalk) fall within the 0.21–0.32 range [Wainwright et al., 1982]. The elastic modulus for cricket cuticle could not be determined because it was difficult to isolate pieces that were long enough for accurate measurements.

We made as many as 19 estimates of both toughness and elastic modulus for each food item. For each food, we eliminated the largest and smallest measurements because these were often extreme values that could be off by an order of magnitude or more due to measurement error [Leonowicz et al., 2005]. The means and standard deviations (SDs) of the toughness and elastic modulus for each of the food items were calculated based on the remaining cases. We performed statistical comparisons of all of the foods using a one-way ANOVA ($\alpha=0.05$). We identified significant pairwise differences among food items using the a posteriori Tukey's honestly significant difference (HSD) procedure [Sokal & Rohlf, 1995]. We calculated the fragmentation indices $(R/E)^{0.5}$ or $(ER)^{0.5}$ described above for each food using the mean of the elastic modulus and toughness for that food. Because we could not measure both the elastic modulus and toughness on the same specimen, we present only the single displacement-limited index and stress-limited index value based on food means.

RESULTS

Food toughness ranged from approximately 56.97 Jm^{-2} for apple pulp to $4,355.45 \text{ Jm}^{-2}$ for prune pit (Table I, Fig. 3A). While the ANOVA demonstrated significant differences ($F=141.84$; $P<0.001$), several of these foods did not differ significantly in toughness based on Tukey's HSD test (Table I). There was some tendency for tougher foods to be statistically different from one another. Drying the foods had a varying impact on food toughness. For example, dried apricots were not significantly tougher than dehydrated apricots taken immediately from the package, whereas the toughness of gummy bear approximately doubled when the samples were dried. Two fruit pits were tested, and it was found that prune pit was almost twice as tough as cherry pit (Table I).

The elastic moduli of the experimental foods ranged from 0.07 MPa for gummy bears to 346 MPa for popcorn kernels (Table II, Fig. 3B). While the ANOVA again demonstrated significant differences in the elastic moduli ($F=35.94$; $P<0.001$), the Tukey test identified only three statistically significant groupings. Surprisingly, most foods fell into a single group with low elastic moduli. Prune pits and cherry pits, constitute a single group with moderate stiffness (189.50 MPa and 190.08 MPa, respectively). Popcorn kernels are significantly stiffer than any other food item. Prolonged drying of the gummy bear, raisin, and dehydrated apricot samples tended to approximately double their stiffness.

The fragmentation indices for the experimental foods identified several displacement-limited and stress-limited foods (Fig. 4). For example, gummy bears, raisins, and apricots (including fresh, dehydrated, and dried forms) have the highest displacement limited indices due to their high toughness and low stiffness values. However, they have relatively low stress-limited indices

TABLE I. Descriptive Statistics for the Toughness of the Test Foods*

Level ^a	Food	N	Toughness (Jm^{-2})	
			Mean	SD ^b
	Apple pulp	10	56.97	17.76
	Raisin	10	306.60	34.16
	Almond	10	308.62	34.85
	Carrot	11	343.93	48.49
	Prune	10	345.67	35.46
	Dried raisin	10	418.08	106.77
	Pear skin	12	457.49	126.27
	Dehydrated apricot	10	506.33	64.33
	Dried apricot	11	565.24	102.93
	Apple skin	13	662.89	142.39
	Sweetgum leaf	10	697.67	301.28
	Gummy bear	11	887.96	114.15
	Monkey chow	10	1030.55	159.08
	Cricket cuticle	10	1345.31	314.57
	Dried gummy bear	13	1709.72	376.83
	Cherry pit	13	2504.08	630.33
	Popcorn kernel	13	2978.82	678.34
	Prune pit	13	4355.45	711.92

*Foods are presented in ascending order of their mean toughness.

^aThe lines to the left of the food categories represent groups of foods that do not differ significantly based on Tukey's HSD test. Foods not connected by lines are significantly different from each other at $P < 0.05$.

^bSD, standard deviation.

compared to many of the other foods. As expected, cherry pits, popcorn kernels, prune pits, and to a lesser extent monkey chow had high stress-limited indices. Because the fragmentation indices presented in Fig. 4 represent single data points determined from the average toughness and average modulus for each food type, we have no measure of sample variance for these indices, and therefore could not undertake a statistical analysis of these data.

DISCUSSION

Comparisons With Other Published Values

This study presents the most comprehensive data set on the mechanical properties of foods relevant to work on nonhuman primate jaw-muscle function. Agrawal et al.'s [1997, 1998] recent studies on human masticatory function and food mechanical properties provide similar data for some of the same foods. For those foods, in most cases our mechanical-properties data are not markedly different from those of Agrawal et al. [1997, 1998]. For example, they found that the elastic modulus of almond and carrot is 21.57 MPa (SD=4.00) and 4.57 MPa (SD=0.56), respectively. These results are similar to our values of 20.44 MPa (SD=10.63) and 6.77 MPa (SD=0.80), respectively (Table II). The toughness values for the same foods differed slightly between the two studies. Our value for almond (308.62 Jm^{-2} , SD=34.85) was slightly higher than the 245.8 Jm^{-2} (SD=40.2) reported by Agrawal et al. [1997, 1998]. We found the toughness of carrot to be 343.93 Jm^{-2} (SD=48.49) compared to their value of 440.0 Jm^{-2} (SD=47.5).

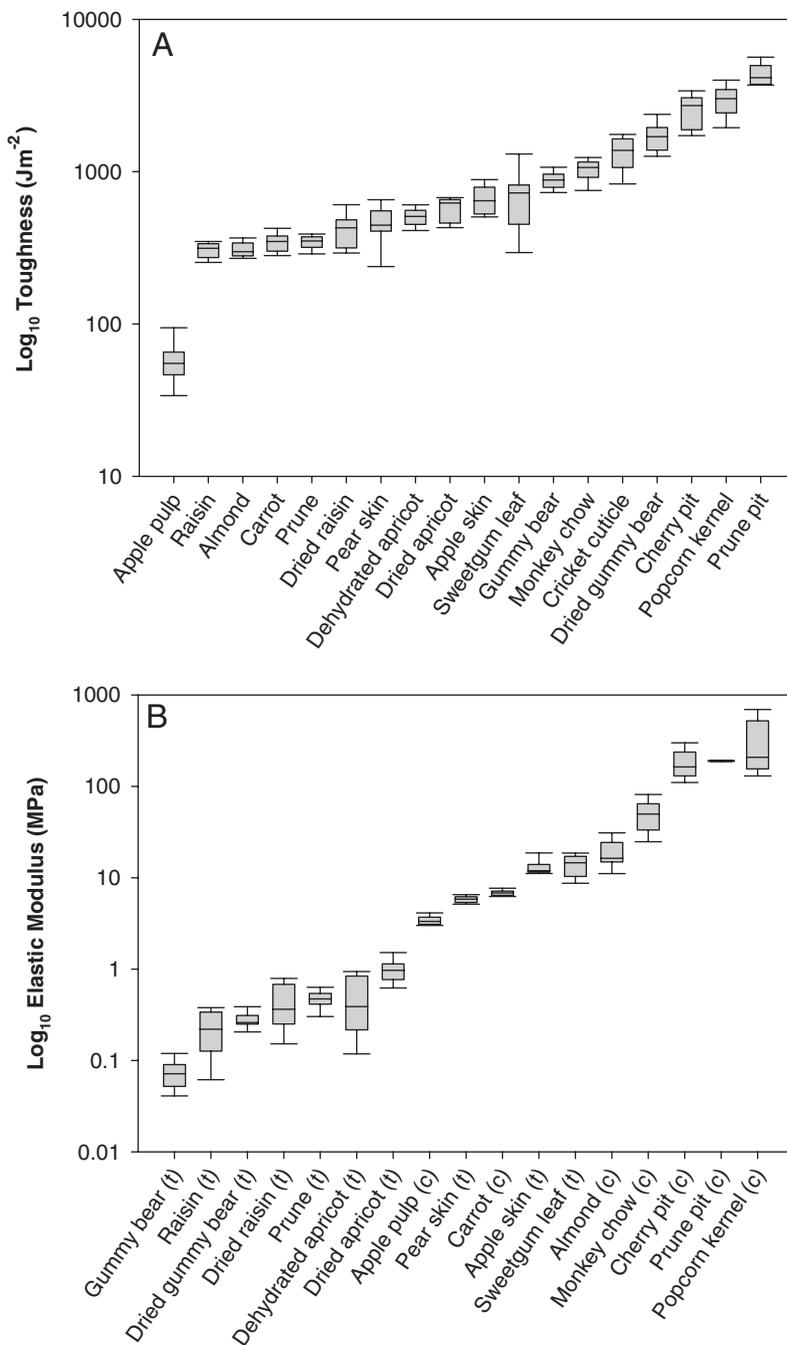


Fig. 3. Boxplots of toughness (A) and elastic modulus (B) for the experimental foods. Means are indicated by the line. The 5th and 95th percentiles are indicated by the whiskers. The data are logged to facilitate the graphical representation.

TABLE II. Descriptive Statistics for the Elastic Modulus of the Test Foods*

Level ^a	Food	N	Elastic Modulus (MPa)	
			Mean	SD ^b
	Gummy bear (t)	12	0.07	0.03
	Raisin (t)	13	0.22	0.11
	Dried gummy bear (t)	11	0.28	0.06
	Dried raisin (t)	13	0.43	0.23
	Prune (t)	10	0.47	0.10
	Dehydrated apricot (t)	13	0.49	0.32
	Dried apricot (t)	13	0.99	0.29
	Apple pulp (c)	16	3.41	0.10
	Pear skin (t)	10	5.80	0.50
	Carrot (c)	15	6.86	0.46
	Apple skin (t)	10	12.89	2.43
	Sweetgum leaf (t)	10	13.88	3.43
	Almond (c)	19	19.42	7.69
	Monkey chow (c)	16	50.44	19.01
	Cherry pit (c)	15	186.92	69.61
	Prune pit (c)	16	189.48	1.20
	Popcorn kernel (c)	16	325.40	218.83

*Foods are presented in ascending order of their mean elastic modulus.

^aThe lines to the left of the food categories represent groups of foods that do not differ significantly based on Tukey's HSD test. Foods not connected by lines are significantly different from each other at $P < 0.05$.

^bSD, standard deviation.

(t), elastic modulus measured in tension on a portable tester.

(c), elastic modulus measured in compression on a universal testing machine.

Our estimate of 663 Jm^{-2} for apple skin toughness is higher than the published estimates, which range from 100 to 450 Jm^{-2} for different varieties [Vincent, 1990, 1991]. This disparity may be due to differences in the way the skin was isolated from the parenchyma, or pulp. According to Vincent [1991], isolating the skin of the apple inevitably leaves layers of parenchyma cells, which can retard the growth of cracks in the skin. This would increase the work required to fracture the skin. The toughness of cherry (2504.08 Jm^{-2} ; $\text{SD}=630.33$) and prune (4355.45 Jm^{-2} ; $\text{SD}=711.92$) pits does not markedly differ from the toughness of *Mezzettia parviflora* seed shells consumed by orangutans. These seed shells range in toughness from 1,204 to $3,113 \text{ Jm}^{-2}$ when measured transversely along their toughest region [Lucas, 1989; Lucas et al., 1991].

Food Mechanical Properties and Primate Mastication Studies

Experimental studies of jaw-muscle function in nonhuman primates are lacking in foods that are stiff but not tough, as well as foods that are tough but not stiff. To some extent, monkey chow fits the "stiff but not tough" texture profile, although there are several stiffer experimental foods. Sweetgum leaves satisfy the "tough but not stiff" profile. The leaves are tough because of the composite nature of the cell wall, which contains cellulose microfibrils embedded in hemicellulose and sometimes lignin [Lucas et al., 1995, 2000; Vincent, 1990]. Although the leaves are consumed by numerous primate species, they have only recently been included in experimental studies

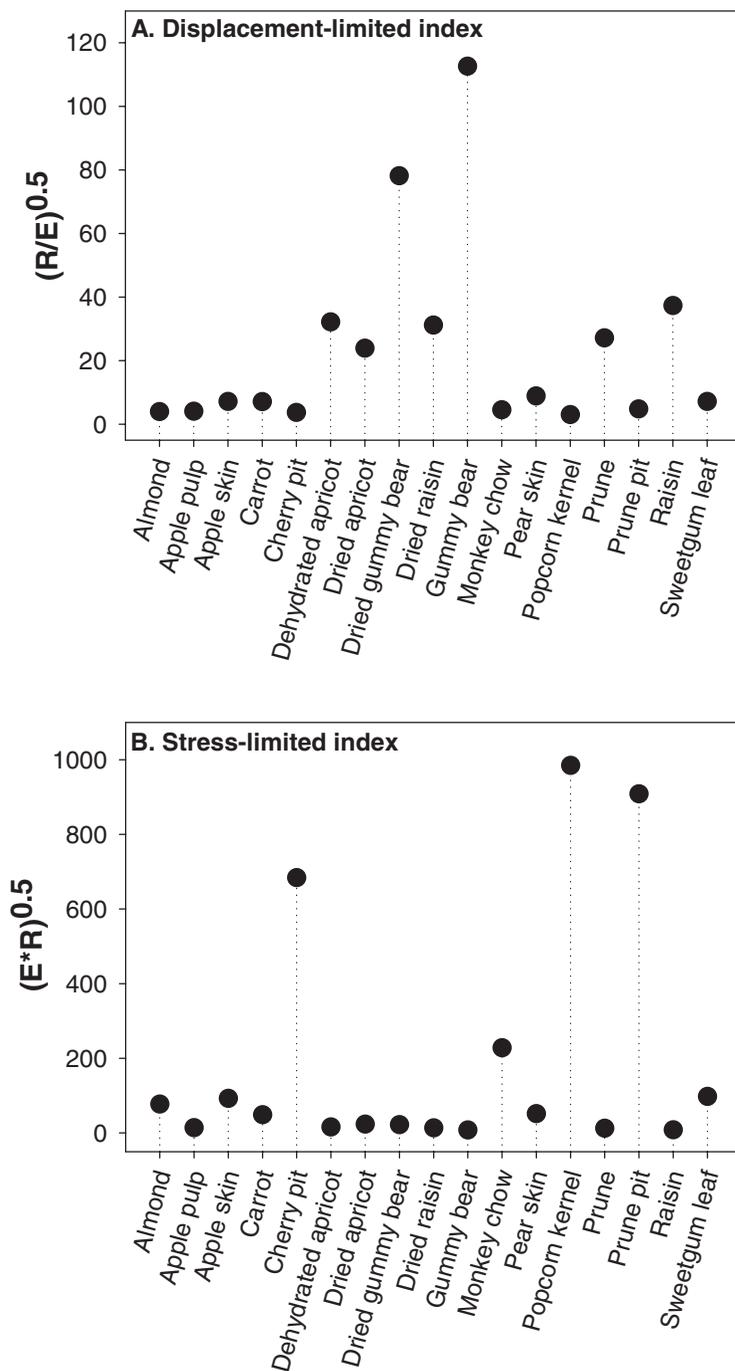


Fig. 4. Fragmentation indices for the experimental foods. **A:** $(R/E)^{0.5}$ applies when the number and size of food particles that result during fragmentation are determined by displacement. **B:** When stress limits fragmentation (e.g., when forces must be high to initiate fracture), the fragmentation index $ER^{0.5}$ applies. Each data point represents a single index for a food type based on the means of the toughness and elastic modulus for that food.

of primate mastication (Hylander et al., unpublished data). The use of leaves in experimental studies is important because in addition to their mechanical properties, their two-dimensional shape may also influence masticatory physiology [Lucas et al., 2002]. Apple skin, which traditionally has been used as a two-dimensional tough item in such studies [Hylander & Johnson, 1994], is surprisingly similar to sweetgum leaf in toughness and stiffness, and thus arguably serves as a suitable alternative.

The results of this study have several implications for laboratory researchers conducting *in vivo* research on mammalian mastication. Given that many of the food items do not differ significantly in either toughness or stiffness, the data presented here suggest that experimentalists can select among several potential foods with broadly similar mechanical properties in their work. Thus, investigators may have more freedom in the future to choose foods that are readily consumed by their primate subjects without significant concern for the differential effects that textural properties may have on jaw-muscle activity. For example, if a subject eats dried raisin but not dehydrated apricot, it is unlikely that significant additional information regarding the relationship between food properties and jaw-muscle activity will be lost, given that these foods are very similar in toughness and stiffness.

The similarity in toughness and stiffness of many of the food items suggests that we may be sampling jaw-muscle activity over only a limited range of mechanical properties for some of the species, particularly those that will not masticate any of the fruit pits or popcorn kernels. One outcome of this finding is that comparing jaw-muscle activity between statistically similar foods may be less relevant than was previously thought. For example, apple skin is well within the range of toughness of some foods that are typically classified as “hard and/or tough” in electromyographic and bone strain studies, such as gummy bear and apricot (both dehydrated and dried). Whereas macaques and baboons in these studies readily masticated apple skin and popcorn kernels, owl monkeys masticated only apricot, gummy bear, or prune. Since apple skin, apricot, gummy bear, and prune do not differ significantly in toughness, the extent to which jaw-muscle activity differences across these foods in owl monkeys relates to differences in toughness remains unclear. In summary, the data presented here provide information that will allow researchers to better contrast jaw-muscle activity patterns with food material properties.

One limitation of this study is that our estimates of toughness and the elastic modulus are representative of foods before they were ingested. We do not consider the effects that saliva and continued processing have on the mechanical properties. It is possible that saliva significantly softens many of the foods tested here, and thus alters their mechanical properties. This would certainly be the case for foods such as monkey chow, dried gummy bear, and dried fruits. Furthermore, we did not control for the effect that multiple simultaneous fractures would have on the food mechanical properties. These properties are likely dynamic throughout the power stroke of mastication. For example, flaws and cracks can occur in the food due to the initial puncture-crushing between occluding teeth, which could ultimately influence how the food material fails during the rest of the power stroke. While some researchers are moving in this direction to understand how materials fail during mastication in humans [e.g., Agrawal et al., 1997; van der Glas et al., 1992], this approach is extremely difficult to replicate in nonhuman primates.

Finally, it remains to be seen how these foods compare with foods that conspecific primates consume in the wild. This will be the true test of whether experimental studies are eliciting the natural range of primate masticatory behaviors. There appears to be a broad correspondence of the properties we measured with the properties of similar biological materials recently published by Lucas [2004] (Fig. 5). Moreover, recent field studies provide examples of how the experimental foods compare with foods that are known to be consumed by wild primates [e.g., Dominy & Lucas, 2004; Teaford et al., in press; Wright, 2005; Yamashita, 2003]. Yamashita [2003] measured the toughness of numerous foods consumed by sifaka and ring-tailed lemurs to determine whether food procurement and ingestion were influenced by toughness and the physical properties of foods. The average toughness of leaves consumed by both species was approximately 300–450 Jm^{-2} , with the toughest foods often exceeding 800 Jm^{-2} . Likewise, Teaford et al. [in press] found that mantled howler monkeys consume leaves that range in average toughness from 250 to 900 Jm^{-2} . Thus, at least in terms of toughness, many of the foods used in

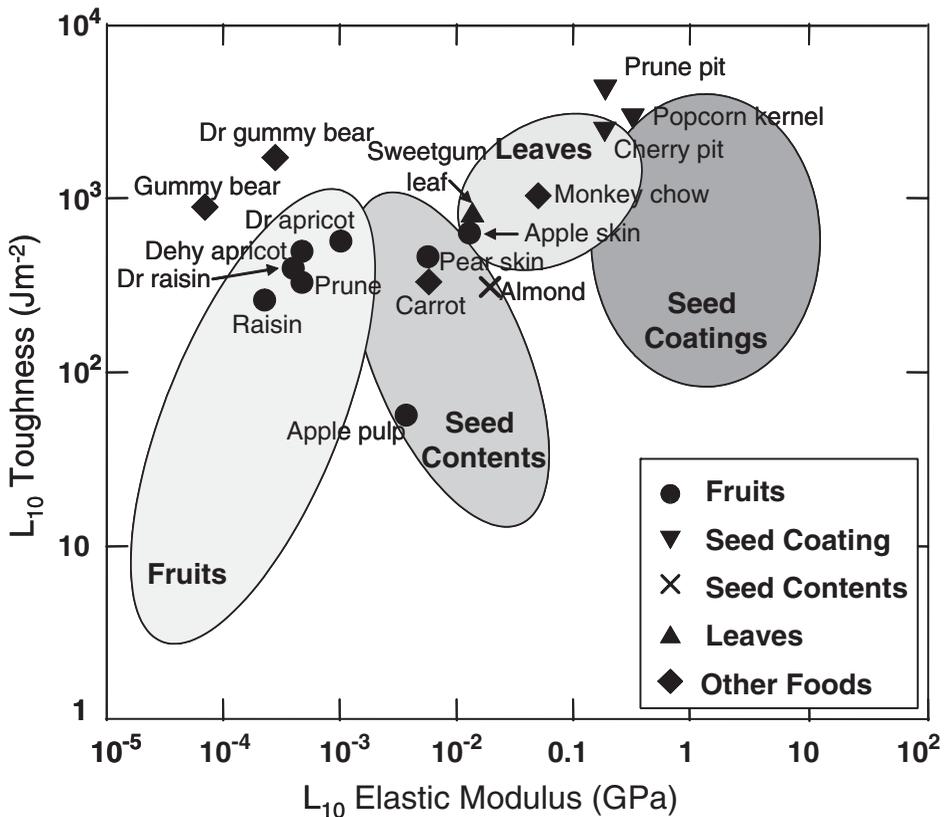


Fig. 5. Bivariate plot showing the range of toughness vs. elastic modulus of foods tested in this study. Shaded ellipses for each of these categories represent the approximate outline of mechanical properties data for various foods within these categories from data compiled by Lucas [2004]. Note that the data collected in this study fall broadly within the published ranges of each food (e.g., leaves and fruits). (Adapted from Lucas [2004].) GPa, gigapascals (1 GPa=0.0001 Mpa); dehy, dehydrated; dr, dried.

experimental studies may be appropriate for animals (e.g., sifaka and howler monkeys) that feed primarily on leaves and fruits. On the other hand, Dominy and Lucas [2003] found that the average toughness of leaves consumed by *Cercopithecus ascanius*, *Colobus guereza*, *Pan troglodytes*, and *Ptilocolobus badius* was significantly lower than that of adjacent leaves that were not consumed. The average toughness of the consumed leaves was about 600 Jm^{-2} , whereas the average toughness of the unconsumed leaves was only about 900 Jm^{-2} . Thus, for some primate species, the toughest foods used in the laboratory-based studies may be tougher on average than the foods rejected by these species in the wild. In such cases, currently used laboratory foods may not be appropriate for addressing adaptive hypotheses regarding masticatory form and function.

The goal of this study was to quantify two of the mechanical properties of foods used in experimental studies of primate mastication. The current data represent the first step toward quantifying the relationship between food mechanical properties and jaw-muscle function in primates. The results show that the foods span a broad range of toughness and stiffness values. This range broadly overlaps the existing mechanical properties of foods consumed by primates in their natural environments. As research on primate feeding ecology becomes increasingly more focused on primate food choices, it would be logical to incorporate mechanical-properties data in studies because these properties can be an important limiting factor to food use. Until recently, experimental and comparative studies of primate masticatory form have not had access to quantitative measures of food texture and have had to rely on qualitative and relative estimates, or simply used broad dietary categories as a basis for comparison [e.g., Daegling, 1992; Daegling & McGraw, 2001; Hylander, 1979, 1985; Ravosa, 1991, 1996a, b; Taylor, 2002]. Clearly, combining both kinds of studies will aid us in determining the effect of food mechanical properties on jaw-muscle activity during mastication, and can ultimately contribute to a more thorough understanding of the evolution of the primate masticatory apparatus.

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