Food material properties and mandibular load resistance abilities in large-bodied hominoids

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ABSTRACT

Numerous comparative studies have sought to demonstrate a functional link between feeding behavior, diet, and mandibular form in primates. In lieu of data on the material properties of foods ingested and masticated, many investigators have relied on qualitative dietary classifications such as "folivore" or "frugivore." Here we provide the first analysis of the relationship between jaw form, dietary profiles, and food material properties in large-bodied hominoids. We employed ratios of area moments of inertia and condylar area to estimate moments imposed on the mandible in order to evaluate and compare the relative ability to counter mandibular loads among central Bornean orangutans (*Pongo pygmaeus wurmbii*), Virunga mountain gorillas (*Gorilla beringei beringei*), and east African chimpanzees (*Pan troglodytes schweinfurthii*). We used data on elastic modulus (E) of fruit, fracture toughness (R) of fruit, leaves, and non-fruit, non-leaf vegetation, and derived fragmentation indices ($\sqrt{R/E}$ and $\sqrt{ER}$), as proxies for bite force. We generated bending and twisting moments (force × moment arm) for various mandibular loading behaviors using food material properties to estimate minimally required bite forces. Based on E and R of foods ingested and masticated, we hypothesized improved resistance to mandibular loads in *Pongo p. wurmbii* compared to the African apes, and in *G. b. beringei* compared to *Pan t. schweinfurthii*. Results reveal that our predictions are borne out only when bite forces are estimated from maximum R of non-fruit, non-leaf vegetation. For all other tissues and material properties results were contrary to our predictions. Importantly, as food material properties change, the moments imposed on the mandible change; this, in turn, alters the entire ratio of relative load resistance to moment. The net effect is that species appear over- or under-designed for the moments imposed on the mandible. Our hypothesis, therefore, is supported only if we accept that maximum R of these vegetative tissues represents the relevant mechanical property influencing the magnitude of neuromuscular activity, food fragmentation, and mandibular morphology. A general implication is that reliable estimates of average and maximum bite forces from food material properties require that the full range of tissues masticated be tested. Synthesizing data on ingestive and masticatory behaviors, the number of chewing cycles associated with a given food, and food mechanical properties, should inform the broader question of which foods and feeding behaviors are most influential on the mandibular loading environment.

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Introduction

Experimental studies of primate masticatory biomechanics have demonstrated that jaw muscles are recruited in coordinated sequences during chewing and unilateral biting (Hylander et al., 1987, 1992, 2000, 2005; Vinyard et al., 2005). Jaw-muscle activity applies external loads to the mandible. These loads, in turn, produce internal stresses and deformations (Hylander, 1979a,b, 1981, 1984, 1985; Hylander et al., 1987). Electromyographic research has shown that magnitude and duration of jaw-muscle activity are modulated by food material properties: incision and chewing of tough and stiff foods require the recruitment of relatively larger amounts of jaw-muscle force compared to less tough or softer foods (Oron and Crompton, 1985; Horio and Kawamura, 1989; Ottenhoff et al., 1992; Hylander and Johnson, 1994; Hylander et al., 2000). The mastication of tough or resistant foods is reflected in increases in physiologic cross-sectional area of the jaw muscles (e.g., Langenbach et al., 2003; Taylor et al., 2006), corroborating that such tissues require greater amounts of muscle force to comminute. Food consistency

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also influences the pattern of jaw movement such that the amplitude of side-to-side movements increases with the chewing of stiff or hard tissues (e.g., Agrawal et al., 2000). Regions of the mandible subjected to elevated loads are presumed to require structural modifications to improve resistance to mandibular loads. Thus, jaw-muscle activity is hypothesized to play an important role in shaping masticatory form in primates and other mammals.

Empirical study of jaw-muscle activity patterns in combination with biomechanical models of masticatory form and function have informed a host of comparative studies seeking to functionally and adaptively link mandibular form, function, and feeding behavior in primates (e.g., Hylander, 1979c, 1988; Bouvier, 1986; Daegling, 1992; Antón, 1996; Ravosa, 1996; Daegling and McGraw, 2001, 2007; Vinyard et al., 2003; Wright, 2005). With few exceptions (e.g., Yamashita, 1998; Lambert et al., 2004; Yamashita et al., 2004; Wright, 2005; Vinyard et al., in press), such investigations have relied on qualitative proxies in lieu of quantitative data on the material properties of the foods ingested and masticated. These descriptions have included broad dietary classifications, such as "folivore" or "frugivore," as well as food classes, such as "leaves," "shrubs," "ripe fruits," etc. The extent to which qualitative dietary descriptions accurately track food material properties remains unknown, but the fact that foods of disparate classes display overlapping material properties (Lucas, 2004; Williams et al., 2005) suggests such data may not always provide powerful substitutes. Discrepancies between qualitative descriptions of foods and actual food material properties may thus confound attempts to functionally and adaptively link mandibular form with masticatory function.

Two internal mechanical characteristics of foods that modulate jaw-muscle activity and influence food fragmentation are fracture toughness (R) and elastic modulus (Young's modulus, E). Fracture toughness represents the energy required to generate a crack of a given area, whereas Young's modulus reflects mechanical stiffness (stiffness scaled for size), or the resistance of a material to deformation (Lucas, 2004). Food material properties data (Elgart-Berry, 2004; Vogel et al., 2008) reveal that large-bodied hominoids differ in E and R of the foods they ingest and masticate (Table 1). Average and maximum R of tissues ingested and masticated is greatest for *Pongo p. wurmbii* and smallest for *Pan t. schweinfurthii*, with Virunga mountain gorillas typically, though not always, intermediate between the two (Table 1). Compared to *Pan t. schweinfurthii*, for example, maximum R of fruits is approximately four times greater in *G. b. beringei* and an order of magnitude greater in *Pongo p. wurmbii*. Maximum E of fruits ingested and chewed by *Pongo p. wurmbii* is about 50% greater than fruits consumed by *Pan t. schweinfurthii*.[1] Notably, average R of whole fruit, exocarp, and endosperm tissues ingested by *Pongo p. wurmbii* is considerably higher than average R of mesocarp reported here, although not all of these tissues are actually chewed and swallowed (Vogel et al., 2008).

Here we provide the first comparative assessment of the relationship between jaw form, dietary profiles, and food material properties in Bornean orangutans (*Pongo pygmaeus wurmbii*), east African chimpanzees (*Pan troglodytes schweinfurthii*), and Virunga mountain gorillas (*Gorilla beringei beringei*). Specifically, we use food material properties as minimum estimates of the average and maximum bite forces these apes generate during chewing and incision. We then evaluate the relative ability of these apes to counter mandibular loads by scaling ratios of area moments of inertia to bending and twisting moments imposed on the mandible. We compare broadly among large-bodied hominoids to address the influence of food material properties (and the derived bite force

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[1] Elastic modulus data (E) were not available for *G. b. beringei*.

Table 1

Means ± standard errors and sample sizes (n) for fracture toughness (R) and Young's modulus (E) of foods tested[a]

	Pan troglodytes schweinfurthii	*Gorilla beringei beringei*	*Pongo pygmaeus wurmbii*[b]
Average fracture toughness, R (J m^{-2})			
Fruits	87.4 ± 19.7 (32)	634.0 ± 255.8 (31)	633.6 ± 112.4 (65)
Leaves	473.4 ± 73.7 (19)	540.0 ± 117.1 (42)	689.5 ± 73.0 (25)
Non-leaf, non-fruit vegetation	677.0 ± 293.0 (4)	1169.2 ± 330.1 (56)	1745.6 ± 356.9 (10)
Maximum fracture toughness, R (J m^{-2})			
Fruits	289.0	1190.0	2464.1
Leaves	1001.0	1330.0	2426.0
Non-leaf, non-fruit vegetation	4223.0	3860.0	3432.0
Average Young's modulus, E (MPa)			
Fruits	0.99 ± 1.17 (99)	N/A	2.40 ± 1.96 (46)
Maximum Young's modulus, E (MPa)			
Fruits	4.30	N/A	6.54[c]
√RE Fruits			
Average	9.30	N/A	39.0
Maximum	35.25	N/A	127.0
√R/E Fruits			
Average	9.40	N/A	16.25
Maximum	8.20	N/A	19.41

[a] Food material properties data derive from two sources: Elgart-Berry (2004) and Vogel et al. (2008). Data were collected as follows: *Pan t. schweinfurthii*, Kibale National Park, Uganda by N. Dominy; *Pongo p. wurmbii*, Tuanan Research Station, Mawas, Kalimantan Tengah, Indonesia, by E. Vogel; *G. b. beringei*, Mgahinga Gorilla National Park, Virunga Volcanoes, by A. Elgart-Berry. To determine R and E of foods ingested, masticated, and eaten (Vogel et al. 2008) relied entirely on field observations of *Pongo p. wurmbii* and *Pan t. schweinfurthii*. Elgart-Berry (2004) measured R of foods masticated as determined by direct observation, reports from previous studies and park rangers. Vogel et al. (2008) and Elgart-Berry (2004) used different portable testers to measure fracture toughness, and Vogel et al. (2008) used a scissors test (rather than the portable tester) to fracture relatively thin foods.

[b] For *Pongo p. wurmbii*, R of fruit is averaged here for mesocarp and represents all stages of ripeness. R of non-leaf, non-fruit vegetation includes bark, root, pith, stem, and fungus. Means are for the various species sampled (cf. Vogel et al., 2008), and sample sizes (n) include multiple samples obtained from the same plant species.

[c] Maximum E of fruits for *Pongo p. wurmbii* represents an underestimate as it excludes exocarp and endosperm, and three species of seeds of ripe fruits that were not measured (*Mezzettia umbellate*, *Mezzettia parviflora*, and *Xylopia fusca*).

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estimates) on the moment demands imposed on the mandibles, and the functional significance of interspecific variation in jaw form. We also address evolutionary trends in load resistance abilities by examining morphological divergence between *Pongo p. wurmbii* and the African apes, and between the African apes. The functional relationship between great ape food mechanical properties and molar enamel is explored in a companion paper (Vogel et al., 2008).

Hypotheses to be tested

We rely on jaw-muscle activity patterns during feeding empirically demonstrated *in vivo* for anthropoid primates (e.g., *Macaca fascicularis, Papio anubis*, and *Aotus trivirgatus*), and the stresses imposed by these muscular forces (Hylander, 1979a,b, 1981, 1984; Bouvier and Hylander, 1981; Hylander and Crompton, 1986; Hylander et al., 1992, 1998, 2000, 2005; Hylander and Johnson, 1994). Our functional hypotheses are predicated on the expectation that the mechanical demands of a tougher or stiffer diet (or both) will be met with a relatively more robust mandible. Virunga gorillas ingest and masticate tougher foods compared to *Pan t. schweinfurthii*, while *Pongo p. wurmbii* ingests and masticates foods that are even tougher, significantly so compared to *Pan t. schweinfurthii* (Vogel et al., 2008). *Pongo p. wurmbii* also ingests and masticates significantly stiffer fruits compared to *Pan t. schweinfurthii*. More resistant foods involve the generation and dissipation of larger and