



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.

We found that 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 feed for shorter

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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.

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1. 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, 1986a, 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, 2012; Reed and Ross, 2010), and digestion (Milton, 1981, 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 traditional 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).

1.1. 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., 2009a).

- Dietary categories are distinguishable by their FMPs.* If dietary categories accurately reflect variation in the mechanical properties of foods eaten by a primate, then FMPs should distinguish among traditional dietary categories (e.g., folivory, frugivory, insectivory). For instance, frugivores are generally 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.
- 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; Teaford et al., 2006; 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 fruits will have lower measures of Young's modulus than does unripe fruits.
- 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, 2012, 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., 2014a, 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.
- 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.
- 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

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