# Novel developments in field mechanics

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## ARTICLE INFO

## ABSTRACT

Our aim is general: we want to illustrate how much can be gleaned from mechanical measurement in the field. We ask how mechanics may constrain foraging and feeding on both plants and animals, and how various aspects of mechanical behavior could affect the feeding choices that primates make. Here, we present novel methods for the measurement of the material properties and also the employment of tried and tested methods in novel settings. This review demonstrates how mechanical investigation methods can quantify the environmental factors affecting primate locomotion to and from food, which makes up a large part of a primate's daily energy budget. We indicate that, despite the accumulation of much data on the material properties of primate foods, the introduction of new methods is allowing researchers to pursue new avenues of research and change paradigms in primate feeding ecology. Field methods are presented that could aid in the understanding of the extra-oral processing of foodstuffs by primates and enrich further studies into cognition and culture surrounding these types of behavior. We conclude that the use of in-field measurements and a greater understanding of the physics of primate environments are vital and exciting themes integral to the continued understanding of primate evolution and biology.

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## 1. Introduction

Primate feeding ecology is a complex subject. Primates, as a group, eat a wide variety of foods gleaned from a range of environments. Understanding the effect of diet on primates can aid researchers in understanding adaptations and niche separation (Robbins and Hohmann, 2006). Added to this, modern primates are often used as a living analogy of our own evolutionary past (Wood and Schroer, 2012). This approach allows us to experimentally investigate and validate theories generated from the fossil record and has led to a greater understanding of the evolutionary path of modern humans and that of our evolutionary relatives. Mechanical field research aims to look at the in vivo biological world in a systematic way, with the intention of understanding the varying physical limits within which an organism survives. Understanding how organism and environment interact physically can lead to novel insights into the evolution of complex traits, sometimes challenging widely held conventions. Primates, in their daily lives, will encounter dangers and survival conundrums presented by the physics of the environment during their daily forage. Judgments of safety during locomotion, the accessibility of optimal food sources, and the readiness of food for ingestion all require a mechanical knowledge of the environment. This technical intelligence has been proposed as one of the possible driving factors behind the evolution of intelligence in the hominin tribe (Byrne, 1997). We believe that quantification of the various mechanical strategies available to a primate in foraging and feeding will provide cost information for each strategy, thus helping to clarify whether the cognitive apparatus of primates is capable of selecting optimal strategies. This is entirely consistent with discussions of form and function in an evolutionary context (Bock and von Wahlert, 1965; Lauder, 1981) and with the quantification needed to establish whether optimal solutions (Alexander, 1989; Johnson, 2013) have been adopted by the animal in question.

What we observe when a primate moves to feed on a plant is a series of mechanical events. This starts with an initial attraction to food and the subsequent locomotion towards and between feeding sites. Foraging generally follows; this is the movement of the body as it interacts with the physical world to acquire foodstuffs. Then,

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finally, feeding encapsulates the stages of ingestion and mastication, right up to a successful swallow. It is physics that plays a vital role throughout these processes. Sadly, the information obtainable from physical measurement in the field has been underutilized, making it difficult to assess its importance to primate behavior and adaptation. Instead, much of the feeding literature focuses on chemistry as the major influence (Freeland and Janzen, 1974). The effectiveness of plant chemical defenses is inferred as, for example, when primates avoid foods with high levels of fiber and polyphenolics (e.g., Milton, 1979; Glander, 1982; Davies et al., 1988; Oates et al., 1990; Rogers et al., 1990; Ganzhorn, 1992; Kool, 1992; Waterman and Kool, 1994; Wrangham et al., 1998; Chapman and Chapman, 2002). We are not doubting this effect, but some of that chemistry may actually owe its behavioral effectiveness to physics. Plant tissues with high fiber levels are disproportionately tough (Choong et al., 1992; Lucas et al., 2000) and so difficult to chew and swallow (Prinz and Lucas, 1997), while tissues loaded with tannins impede salivary lubrication of the mouth. The resultant 'dry' sensation (which is actually high intraoral friction—Prinz and Lucas, 2000) could be responsible for alerting an animal to potential harm and deterring its further feeding.

Any contact by a primate with an object produces a force, which leads to a displacement. What constrains what the primate does? The possibilities are force, displacement, or their product (i.e., the work done). We could factor out parameters such as (a) mechanical properties of both the primate and the object, (b) dimensions, and (c) loading geometry. All of these can have an influence, but knowledge of just one of these groups will not suffice. Suppose, for example, we concentrate on group (a) and measure the toughness of a plant part. Parts with the same toughness, but of different size, will fracture at different loads and displacements and so require very different amounts of work to break. Suppose we ignore group (c) and test a plant part in tension. Is this relevant to chewing it? Pressing on, versus pulling, cellular tissues to the point of 'failure' produces very different responses, as indicated later. So all of the above factors matter, but sometimes the problem is simple enough to reduce the need 'to do everything.'

The aim of this review is to highlight novel methods in field mechanics as they pertain to the travel to and processing of food. Although this issue focuses on primate feeding, we present approaches that help measure the mechanical world that modern primates inhabit and in which extinct members of our own lineage would have lived (Fig. 1). We will explore methods that have been used to gather data on environmental factors that are likely to influence the locomotion of primates to and from their food sources. We will also consider some novel methodologies for measuring the mechanical properties of foods and examine how mechanistic investigations could help us understand extra-oral processing of food by primates. Whilst not all of the methods we highlight here are novel per se, their context may be, thus offering different solutions to research conundrums.

## 2. Getting to food: mechanical factors affecting arboreal locomotion

To eat food, primates must first obtain it, and this can often involve them navigating a wide range of environments and substrates. The distance between food sources varies and usually necessities movement, therefore requiring primates to move varying distances in order to forage for them. The length and intensity of these moves will demand varying amounts of time and energy, which ultimately has to be delivered from digestion of the food obtained. The mechanics of the environment will directly influence these energy and time budgets and drive morphological traits and locomotor behaviors so as to reduce energetic costs associated with
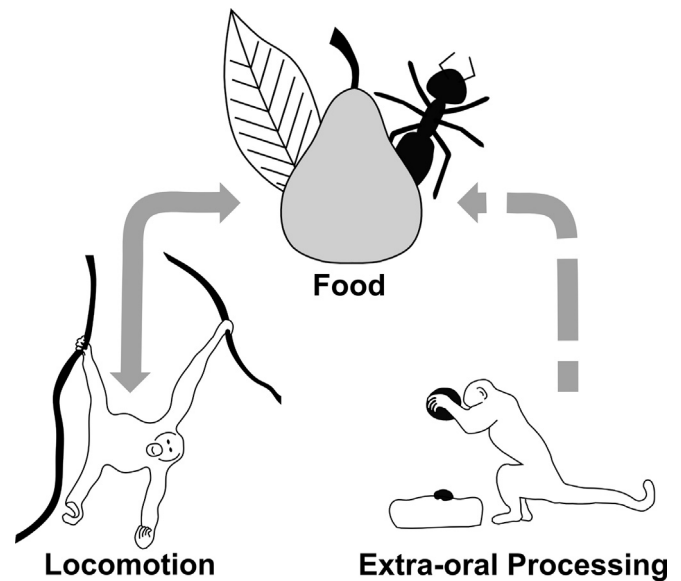


**Figure 1.** Diagram illustrating the wider mechanical world that should be taken into account whilst researching primate foods. Capuchin monkey redrawn from Mannu and Ottoni (2009).

movement. Added to this, food is often found in mechanically-challenging substrates such as the terminal branch niche (Rasmussen, 1990; Sussman, 1991). The ability of a primate to access valuable resources through efficient locomotion will increase its foraging return and ultimately its fitness. The relationship between the arboreal environment and the adaptive radiation of primates has been well researched over the last 50 years, with researchers using studies of locomotor morphology, behavior, and substrates associated with locomotion (Ripley, 1967; Fleagle, 1976; Cartmill and Milton, 1977; Rose, 1977, 1984; Fleagle and Mittermeier, 1981; Cant, 1987, 1992; Demes et al., 1995; Richmond et al., 2001; Thorp, 2005; Channon et al., 2011) to provide a better understanding of the intricate connections between primate locomotion and environmental factors.

This ever-growing field of research has provided evidence and analogies for some of the more contentious issues relating to human evolution, such as the evolution of bipedalism (Rose, 1984; Richmond et al., 2001; Schmitt, 2003; Harcourt-Smith, 2007; Thorpe et al., 2007a, b; Crompton et al., 2008). Understanding locomotion in primates is, therefore, of great importance to those concerned with the emergence of our own species. Whilst there are many studies of the kinematics of primate locomotion, to fully understand the energetics, kinematics, and evolutionary reasoning behind it there is a fundamental requirement to measure their natural mechanical environment. Nonhuman primates are essentially arboreal (Hanna and Schmitt, 2011; Fleagle, 2013) and three major factors will affect their locomotion: the compliance and oscillatory frequency of the substrate and its coefficient of friction. These must also have influenced the postcranial evolutionary trajectory of the primate order. Whilst they have been, and continue to be, investigated in the laboratory, field measurements complement and validate models and theories of primate locomotion arising from laboratory research.

### 2.1. Compliance

Many of the substrates on which primates move are not very rigid and this affects their gait, the best examples being the branches of trees. The less stiff a structure is, the more compliant it

is. So we speak of compliance, the inverse of stiffness. Compliance (Gilman et al., 2011; Gilman and Irschick, 2013; van Casteren et al., 2012a, 2013) is

$$C = \frac{dy}{dF} \tag{1}$$

where $dy$ is the change in displacement (measured in meters) and $dF$ is the change in applied force (in Newtons). Branch compliance can be readily measured, either by deflecting the branch a known distance and measuring the force required, or applying a known force and measuring the displacement this causes. However, either way, the compliance of the testing apparatus has to be known or this will lead to branch compliance being overestimated.

Substrate compliance varies greatly during a primate's daily forage; it is very low for primates on the ground or the boughs of large trees, but can be exceedingly high in terminal branches (Schmitt, 1999; Thorpe et al., 2007b, 2009; van Casteren et al., 2013). High compliance is generally thought to reduce locomotor performance and increase the energetic costs of locomotion for smaller arboreal inhabitants. Small forces can cause large branch perturbations and often energy stored in the branch during loading is lost because the animal has left the branch before it has time to rebound (Alexander, 1991; Demes et al., 1995; Gilman et al., 2011; Gilman and Irschick, 2013). For larger arboreal animals, the importance of compliance is amplified due to their greater mass (van Casteren et al., 2013). In this context, Sumatran orangutans (*Pongo abelii*), the largest habitual tree dwellers, have been shown to use the compliance of vertical supports to their advantage to lower the cost of locomotion in gap crossing (Thorpe et al., 2007a). They may also use stiff-legged bipedalism to save energy whilst moving on small compliant horizontal branches (Thorpe et al., 2007b). Compliance is also an important consideration for primates moving on the ground, although on a terrestrial substrate levels of compliance are orders of magnitudes lower and usually predictably stable. Yet changes in the levels of ground compliance can affect efficiency and gait during terrestrial locomotion (McMahon and Greene, 1979; McMahon, 1985; McMahon et al., 1987; Kerdok et al., 2002), an extreme example of such is the exertion one feels when running over sand (Pinnington and Dawson, 2001). Though the understanding of the role of compliance in animal locomotion is expanding, there are still relatively few good examples of field measurements of locomotor substrates, whether arboreal or terrestrial.

Gilman and Irschick (2013) studied the jumping performance of green anole lizards (*Anolis carolinensis*) using a manual system to measure compliance. For horizontal supports with high compliance, they simply hung a series of small weights (mass $m$ varying between 3.75 and 28.61 g) to generate a force (where $F = mg$, with $g$ being the gravitational constant), measuring the change in displacement at a given point along the horizontal support. This system was adequate for small branches, but the need for ever-increasing dead weights to generate deflection in larger ones makes this method impractical for big branches. For larger horizontal supports and supports of a vertical orientation, they replaced fixed weights with an analog push–pull tension gauge, again measuring deflection under a given load. However, the gauge had a force maximum of 2 N, which restricted its use. This research demonstrated that compliance had an effect on jumping performance and that although perching on a range of perches, green anole lizards selectively tended to jump from sturdier supports. Gilman and Irschick (2013) suggested that compliance is a major ecological factor that affects the behavior and performance of small arboreal inhabitants and the authors advocate direct field measurements of compliance for future research.

van Casteren et al. (2013) were interested in understanding how orangutans perceive levels of compliance as they travel through the jungle canopy. They looked at compliance along larger arboreal supports, measuring the change in compliance in relation to the local diameter of the branch, the distance from the trunk, and the distance from the branch tip. To do this they used a mounted digital force gauge (Mecmesin, Advanced Force Gauge AFG1000N; Fig. 2a) anchored to the ground by human weight (Fig. 2b). At given points along a support, they slung test ropes over branches and lowered their free ends to the ground. At ground level, a series of loops, a known distance apart, were attached to the testing rope via a steel ring (Fig. 2c). Then, for increments of branch displacement as controlled by the loops, the resultant force was measured. The compliance needed to be corrected for the compliance of the testing rope. To estimate this, a series of stretching experiments were performed on different lengths of rope to calculate it as a function of length. This was then subtracted from the apparent compliance to produce the true compliance of the branch. The only complicating factor of this process is that a completely immobile force gauge anchor is impossible to make, mostly because of ground conditions, but the anchor movements are small compared with those of the rope. The results of this study indicated that the best observable trait for the remote estimation of compliance of canopy supports was branch diameter. This is a salient property and has a greater predictive capability than more inconspicuous morphological traits, such as the distance from trunk or branch tip. Using diameter as a proxy for the mechanical properties of branches has already been reported in orangutan nest studies (van Casteren et al., 2012a) and, therefore, the results of van Casteren et al. (2013) add weight to the idea that diameter could be used in such a fashion by orangutans and other arboreal inhabitants. Findings like these have helped validate previous work conducted in the field on primate locomotion, where researchers have used diameter as an estimation for branch compliance (Hunt, 1992; Demes et al., 1995; Thorpe and Crompton, 2005; Thorpe et al., 2009), which has been a tenet of field primatology for many years. Yet direct measurements of compliance are still a preferred approach (Gilman and Irschick, 2013), as although diameter may provide a good rule of thumb (it explains around 60% of the variation; van Casteren et al., 2013), it is still subject to observer inaccuracies and it pales in comparison to the collection and use of quantitative data.

Future investigations into primate locomotion, its evolution, and the environments that have driven these functional and morphological trajectories will most likely be a mosaic of computer simulation, captive observation, and field studies. Computer and captive experimental environments will require quantitative data on levels of substrate compliance if they are to replicate the natural conditions and test hypotheses relating to locomotion. Realistic levels of compliance and the subsequent validation of models outside of natural biomes can only be provided from direct measurements of substrate compliance. Moreover, knowledge of the mechanical world beyond broad categories could help promote a deeper understanding of locomotion. What is the influence of substrate compliance on gait variations? How is a primate utilizing the environment to conserve energy? At what body mass does a hard-to-obtain food become unfeasible to obtain? Questions like these, and many more of a similar vein, all require in-depth and quantitative figures to provide answers that cannot be reached using categories such as bough, branch, or twig.

### 2.2. Branch oscillation

In an arboreal environment, the oscillatory frequency of a support plays a significant role in primate locomotion by producing

**Figure 2.** The method used in van Casteren et al. (2013) to measure the compliance of branches. A) The force gauge (F) was attached via a stud bar to a stand with three steel foot pedals (S) for the weight of a person to anchor the equipment. Loops (L) a known distance apart were then attached to a probe (P) allowing the measurement of the resultant force. B) Photo of the equipment set up used in the field. C) A schematic diagram of a compliance test.

'sway.' The oscillatory frequency will, of course, also be affected by the mass of a primate itself and so in turn will affect its locomotor strategy (Alexander, 1991; Thorpe et al., 2007a; van Casteren et al., 2013). The movement of an arboreal support loaded by a primate can be modeled as a linear, lightly damped harmonic oscillator, swaying at a natural frequency (Thorpe et al., 2007a),

$$f = \left(\frac{1}{2\pi}\right)\sqrt{\frac{K}{m}} \tag{2}$$

The frequency, $f$, is governed by the stiffness, $K$, of the branch (in $Nm^{-1}$) and its effective mass, $m$. If a primate is moving on the branch, then its effective mass is increased by that of the primate. Equation (2) shows that this decreases the frequency of oscillation. One can calculate the effective mass of a branch, $M_b$, using Equation (3) if the stiffness at a given point, $K_1$, and time of oscillation, $T$, is known and both can be readily measured in the field (van Casteren et al., 2013).

$$M_b = \frac{T^2 K_1}{4\pi^2} \tag{3}$$

Using the calculation of $M_b$, it is possible to combine in-field measurements and calculate how the oscillatory time of a branch, $T_b$, will be affected by the weight of a arboreal inhabitant, $M_p$, using Equation (4) (van Casteren et al., 2013).

$$T_b = 2\pi\sqrt{\frac{M_b + M_p}{K_1}} \tag{4}$$

Using the formula mentioned above and combining in-field stiffness measurements and branch oscillatory frequencies, van Casteren et al. (2013) were able to calculate the oscillatory behavior of branches with varying diameters. They showed that with the added weight of an orangutan, the oscillatory frequency of branches is largely unaffected by diameter and only produced a significant change in frequency at smaller branch diameters of 2 cm or below. This quantitative finding was consistent with previous qualitative studies that demonstrated that orangutans had

developed unique locomotor strategies to deal with the high compliance generated by smaller branches of 4 cm and less (Thorpe et al., 2007a, 2009). Arguably the terminal branch niche and its array of available resources have driven the many morphological adaptations of all modern primates (Rasmussen, 1990; Sussman, 1991). However, despite their large size, the ability of orangutans to access and manipulate the terminal branch niche enables them to access the nutrient rich fruits and direct, energy efficient travel routes provided by the smallest inter-tree gaps often found there (Schmitt, 1999; Thorpe et al., 2009). Studies like this bolster the conclusions of morphological and locomotor studies into the influence of the terminal branch niche on primate radiation. In the process, these data enhance our understanding of this vital and mechanically challenging realm.

Some studies, like that of Alexander (1991), have used oscillatory frequencies from previous investigations that had been measured for the purpose of understanding the mechanical design of trees (McMahon and Kronauer, 1976). Whilst these frequencies seem reasonable, the wide variety of architectures of tropical tree species and differences in wood type between trees growing in temperate vs. tropical climates make this procedure inadvisable. Oscillatory frequency can be measured very easily by counting the cycles of branch oscillations over a recorded period of time (van Casteren et al., 2013). It requires only a keen eye and a stopwatch. Other investigations have analyzed video footage of branches oscillating after a study animal has left the branch (Thorpe et al., 2007a), but this requires a clear line of sight and good light. Extensometers have also been used for this purpose in plant biomechanics experiments. Extensometers are relatively small (320 g in Spatz et al., 2007) instruments that can be attached to the outer surface of a branch to measure the amount of stretch that occurs during oscillation. Spatz et al. (2007) used these instruments to measure the difference in oscillations of branched and un-branched trunks. Ropes were used to disturb a stem from resting position; the resultant movement was recorded by the extensometers, placed in two orientations upon the tree trunk. A similar method could also be readily transferred to investigations of the arboreal substrate and would deliver more detailed information about the

oscillatory behavior and dampening of arboreal supports than merely counting oscillations. However, researchers would have to rely on the ability to access and place instruments on focal branches, sometimes not an easy task in a complex tropical environment.

### 2.3. Friction

Friction is the property describing resistance between two objects when moving over each other. It is a ubiquitous yet underappreciated aspect of everyday life for humans (Dowson, 2009). Friction is also a fundamental element of primate locomotion (Cartmill, 1974, 1979, 1985). It is thought that primates have evolved fingerpads, dermatoglyphic ridges (fingerprints), and nails in order to grip small branches (Cartmill, 1974, 1979; Martin, 1990). Friction may play an important role in decision-making by primates during locomotion and feeding. Many of a primate's everyday tasks are influenced by friction: from climbing and walking between food patches, to palpating and harvesting fruits and/or leaves for consumption. In addition, friction plays an important role in intra-oral transport and perception of food and bolus properties. Therefore, one must consider the levels of friction and understand the mechanisms behind its generation to help comprehend the evolution of primate attachment organs and dentition, and their adaptive significance in naturalistic settings. Yet strikingly little observation or experimentation, particularly in a field setting, has been performed to help understand the adaptive significance of friction in primate evolution. We suggest that recent theoretical and empirical advances will eventually establish friction as a major ecological and evolutionary factor in primate evolution. Drawing from materials science and industrial-oriented literature in tribology (the study of friction, lubrication, and wear), we review the theory and methods that are relevant for formulating realistic questions and performing substrate texture measurements and friction tests in a field setting.

#### 2.3.1. Surfaces: the foundation of friction

The role of substrate texture in primate locomotion has received comparatively little attention. Kinematic experiments demonstrate that opossums alter gait on rough versus smooth surfaces by adjusting speed and altering the dynamics of braking and propulsion (Lammers, 2009a, b). These studies suggest that surface texture has significant effects on arboreal locomotor behavior. However, we lack an understanding of how an animal's fingertips actually behave at the interface with the substrate. Surface textures vary wildly in a natural context (Fig. 3) and, therefore, present very different frictional regimes to the moving primate. Yet quantifying the surface texture of plant tissue, along with its effect on primate locomotor behavior in naturalistic settings has not, to our knowledge, been attempted. A first step, when researching the daily influence of friction, could be to measure the texture of substrates that primates move upon, such as branches or bark, and then correlate these variables with locomotor variables such as gait parameters and posture. Molds of contact surfaces or physical in-field measurements could be made. Alternatively electronic hand-held surface roughness analyzers could be employed. These devices measure surface asperities to the micron-level, but can be expensive and will require access to electricity for charging.

#### 2.3.2. Brief introduction to theory

Friction is quantified by the coefficient of friction, $\mu$, between two surfaces. It should be stressed that a single surface does not have an inherent coefficient of friction—only pairs of surfaces do. The frictional force, $F_f$, is typically given by the equation:
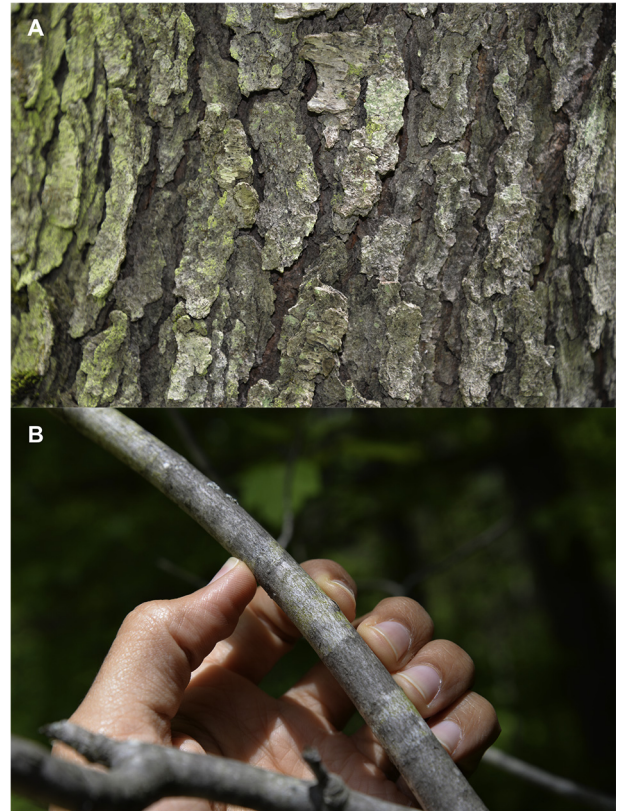


**Figure 3.** An example of how the surface texture of bark can vary. No optical profiler could fully describe a bark surface as rough as (A) with its large asperities, including deep grooves and undercuts. The terminal branch niche often contains smoother bark (B) that will present a very different frictional regime to the sometimes-rougher trunk bark.

$$F_f = \mu N \tag{5}$$

where $N$ is the normal force and $\mu$ is the coefficient of friction. The principle underlying this equation is known as Amonton's law and holds for rigid, amorphous materials. The static coefficient of friction, $\mu_s$, is relevant when stationary objects are set into relative motion, while the dynamic coefficient of friction, $\mu_k$, refers to the resistance between two surfaces during movement. Measurements of the coefficient of friction are therefore relatively straightforward.

However, for biological materials, which are often not rigid and amorphous, the situation is more complex and modifications of this equation are required. In particular, there may be a nonlinear relationship between normal and frictional force (Tomlinson et al., 2009). For example, in rubbery materials, which deform and spread outward under the influence of $N$, $F_f$ is given by the Hertz equation, which has typically been evaluated using a hemispherical piece of rubber against glass. The coefficient of friction under this scenario is:

$$\mu = \pi S \left( \frac{9r}{16E} \right)^{\frac{2}{3}} N^{-\frac{1}{3}} \tag{6}$$

where $E$ is the Young's modulus of the rubber, $r$ is the radius of the sphere, and $S$ is the adhesive shear strength between the contact and the rubber (Warman and Ennos, 2009). This equation demonstrates a potential advantage of soft and rubbery fingerpads, which would deform and form greater contact area, thus increasing friction. There is considerable evidence that human fingertips

behave more like rubbers than inelastic solids (Warman and Ennos, 2009; Derler and Gerhardt, 2012). However, when considering the natural environment of primates, the application of the Hertz equation may be complicated further by the introduction of the varied irregularity of bark surfaces.

More recent work in skin tribology has refined our understanding of how surface textures relate to friction. The coefficient of friction is in fact the summation of two non-interacting terms contributed by two different mechanisms: adhesion and deformation,

$$\mu_{total} = \mu_{adh} + \mu_{def} \qquad (7)$$

Adhesion, $\mu_{adh}$, is produced by the intermolecular forces between two contacting surfaces at the asperity level. Deformation, $\mu_{def}$, is due to the ploughing, or interlocking, of surface features. The regular horizontal and vertical spacings of the contacting surface (i.e., its surface roughness) may increase the coefficient of friction by the 'jamming' of asperities. Here the dermatoglyphic ridges of primates may come into play as a means of increasing friction in an arboreal setting. The reader is referred to the developing theoretical and empirical literature on the influence of surface features on friction (Tomlinson et al., 2009; van der Heide et al., 2013; van Kuilenburg et al., 2013). Merging information on the mechanical properties of primate volar skin with data on the surface texture characteristics of arboreal substrates within this framework may provide a fruitful avenue for research. It is crucial to note that in most studies—usually performed at small loads relevant to human grip and touch—the deformation component is ignored or is negligible but becomes more prominent at higher loads (Derler and Gerhardt, 2012). At the loads experienced by a primate moving upon tree bark, the deformation component of friction is therefore likely to be considerable. Studying the deformation component in relation to naturalistic substrate textures will provide a deeper understanding of the role of friction in primate locomotion.

### 2.3.3. Measuring friction in the field

A researcher faces a difficult task when it comes to measuring frictional quantities in a field setting. This difficulty arises as friction can only be understood relative to the two surfaces moving across each other and many friction models rely on information that is all but impossible to collect in the field (e.g., contact area of primate hand grip on a substrate or the in vivo mechanical properties of primate digital skin). Friction could in principle be measured by observing primate behavior alone, for example by watching the incline of a branch from which a primate falls (e.g., Cartmill, 1979), but this approach is probably unrealistic in the field due to the rarity of primate falls and the difficulty of quickly and accurately measuring branch incline when one does.

For this reason, we suggest that the way forward involves controlled experimentation in the field to isolate variables of interest during friction tests involving biological tissues. By controlling $N$ using static weights whilst recoding the $F_f$, using a force transducer between two interacting surfaces, it is possible to calculate the coefficient of friction. For this approach, researchers must choose the opposing surfaces to reflect the research question, the desired level of biological reality, and scope of inference. In general, the coefficient of friction of human skin (including fingerpads) can vary greatly depending on operational conditions such as environment, materials selection, and even upon the type of motion (van der Heide et al., 2013). In efforts to understand the fundamental mechanisms underlying friction involving human skin, researchers to date have focused on examining skin on surfaces such as glass or metal (reviewed in Derler and Gerhardt, 2012). Experimental field approaches have more bearing on primate evolution because they provide insight on how primate skin

behaves in relation to substrates with more evolutionary relevance (i.e., wood, bark, waxy cuticle of plants). Yet these in-field measurements may necessitate an oversimplification of one of the contacting surfaces (i.e., skin) through the use of surrogate materials, as there is little information about the mechanical properties and surface textures of nonhuman primate volar skin. Using more realistic (but more structurally complex) substrates will also complicate some of the links with developed theory. The study of friction in a field setting—which is still in its infancy—may require researchers to begin by optimizing the function of the system (e.g., determining under which operational conditions the coefficient of friction increases) without necessarily understanding the structure of the system in a detailed fashion (van der Heide et al., 2013). A field researcher, therefore, has to make an informed choice; here we briefly outline two approaches, each with its own advantages and disadvantages, for yielding insight into the role of friction in primate locomotion.

### 2.3.4. Using human skin

Dermatoglyphic patterns on human fingertips look similar (but not identical) to those of nonhuman primates (Martin, 1990). Consequently, in vivo approaches using one's own fingertips contacting bark may be fruitful and can be a justifiable approximation to the interactions occurring between nonhuman primate skin and an arboreal substrate during locomotion. The advantages and disadvantages of this approach are one and the same: the human finger is extremely complex and friction is mediated not only by surface topography of the contacting surfaces, but the sweat and oil on the finger that mediate their tribological interaction. Experimental design can minimize but not completely eliminate this issue. This approach would also benefit from a greater knowledge base surrounding the mechanical characteristics of nonhuman primate volar skin and a comparison with that of humans.

### 2.3.5. Using skin alternatives

To avoid the complexities of in vivo experimental fingerprint measurements, researchers may choose to use skin surrogates contacting bark, provided that the materials used during the friction test sufficiently reflect biological reality. Several synthetic substances appear to match the properties of human skin and may be used (Derler and Gerhardt, 2007). One author (Venkataraman) has had some success using a President Jet® (medium body) vinyl polysiloxane probe with the impression of a human fingertip to perform friction tests on bark. These data (Venkataraman, unpublished data) show that friction perpendicular to fingertip ridges is greater than along them when contacting bark. This finding is contrary to previous studies (e.g., Buck and Bar, 1998) on other substrates involving non-naturalistic contact materials such as metal or glass. These results highlight the advantages of using naturalistic substrates such as bark to test adaptive hypotheses about the putative frictional advantages of primate fingerpads.

The measurement and interpretation of friction in the field is still in its infancy, and novel and exciting methods are currently in development. Given the range of surface textures present in a primate's environment and the paramount role that surface texture and friction may play in the acquisition and processing of food, a greater understanding of the naturalistic tribological landscape will aid in a better understanding of primate evolution and niche adaptation.

## 3. Oral processing—primate food mechanics

Mechanical properties of materials influence two quite different aspects of their behavior—deformation and fracture. Resistance to deformation of a solid object depends on its rigidity, which is the applied force divided by the displacement. This depends on the size of an object; we can control for size by defining an elastic modulus,

$E$, which measures the force per unit area (the stress) that produces a proportional dimensional change (the strain; Ennos, 2012). Once a fracture starts, however, the mechanical analysis needs to change. Cracks are surfaces and their propensity to enlarge depends not on the force, but on the energy released into them. A material's toughness, $R$, is the energy needed to produce a fracture divided by the area of the fracture surface, and is a measure of the resistance of a material to cracking. An alternative measure of toughness is $K_{IC}$. We term this quantity 'fracture toughness' here; it is given approximately by $K_{IC}^2 = ER$. Methods originally designed by engineers (Atkins and Mai, 1985; Calvert and Farrar, 1999; Atkins, 2009) to measure toughness and elastic modulus have found a stable home in biological research; many have become stalwarts of ecological investigations (Vincent, 1992; Beismann et al., 2000; Lucas et al., 2001, 2011b; Lucas, 2004; Vogel et al., 2008; Gilman et al., 2011; Ennos, 2012; van Casteren et al., 2012a, 2013). Mechanical testing has been well utilized in primate feeding ecology and data have been accumulated on the material properties of a range of primate foods such as leaves (Lucas and Pereira, 1990; Choong et al., 1992; Hill and Lucas, 1996; Dominy et al., 2003), fruits (Vogel et al., 2008), insects (Strait and Vincent, 1998), seeds (Lucas et al., 1991, 2012; Daegling et al., 2011), and bark (Vogel et al., 2008).

Experimentally, toughness is estimated by calculating the energy required to propagate a crack through a material. This can be done by two main methods. The first is to generate an artificial defect or notch; this is a weak spot of known dimensions where it is more likely a crack will occur. Cracks can then be initiated and extended through a sample by applying controlled loads in order to estimate a material's toughness (Atkins and Mai, 1985; Lucas, 2004). However, there are some drawbacks to this methodology. During the test, the fracture is under no control and will always take a path of least resistance, whether this be the tissue of interest or not. Frequently notch tests require test-specific shaping of the sample, which can be tricky when targeting certain parts of a food, especially given the often-small sizes of primate foods. The accuracy of results can also sometimes be reliant on notch sharpness and controlling for this, especially in a field scenario, can be troublesome. Due to these reasons, notch tests for measuring food toughness have fallen out of vogue. Thankfully, there are a range of cutting tests that can be employed to measure the toughness of foods. These tests rely on the controlled progression of a crack through a material. They are preferable for investigations into primate foods as they require simple sample preparation and can be used to more easily target specific tissues. In bulk items, such as the flesh of fruit that can be easily shaped into a block, the favored test for field use is a wedge test (Lucas et al., 2011b). The cutting action is achieved by driving a wedge (of ca. 15°) through the material. This prises apart the crack walls and slowly propagates the crack (Khan and Vincent, 1993; Lucas, 2004; Lucas et al., 2011b). In foods consisting of sheets and rods such as the laminar tissues, veins, or the stems of leaves, toughness is usually measured by passing a blade or two crossing blades through the sample causing controlled crack propagation (Ang et al., 2008; Lucas et al., 2011b). In both these cases, the results have to be compensated for the effects of friction. Friction can lead to an overestimation of toughness. The interaction of either a blade against food or two blades moving past one another will generate a frictional force and this force will increase in the measured work done. However, friction can readily be accounted for by performing an empty pass along the same path as the test; this records the amount of work generated by friction, which can be removed from the apparent toughness to give a more accurate estimate (Lucas et al., 2011b).

Testing for the stiffness or Young's modulus of a material involves recording the slope of its initial linear elastic behavior (Fig. 5A). A range of tests can be used to record this, involving tension, compression, or bending. Tension tests are not used as readily as compression or bending when investigating primate food mechanics. This is because to generate tension one must pull on a sample and in order to do so, it must be gripped. Foods are not good candidates for this as they are often soft, moist, or thin, making them hard to clamp (Atkins, 2009). Added to this, samples for tensile tests should ideally be long and dumbbell shaped; this is to encourage failure in the middle away from the disturbing influence of the tensile grips (Lucas, 2004; Ennos, 2012). Unsurprisingly, primate foods do not always oblige these criteria. Because of these reasons, in general, tension tests are not considered ideal for measuring the elastic modulus of primate foods. Testing in compression, discussed in more detail later in this paper, is a good way to measure the modulus of bulk foods such as fruit flesh. It is common practice to destructively sample the flesh, using a cork borer to produce cylinders of a material that can then be easily compressed between two plates (Vogel et al., 2008; Lucas et al., 2011a). For food shaped like rods that cannot be easily formed into a compressible sample, such as plant stems, bending tests similar to those proposed later for prodding tools used by primates are suitable and will generate good results.

### 3.1. Probing primate foods: novel methods

What if a food is a delicate sheet, like the laminae of young leaves? How do we test a fruit that is too small or structurally complex to be cut into workable compression samples? On occasion, in the field, samples may be scarce, so the employment of destructive preparation for testing may not be ideal. Examples like these pose a problem for field mechanical tests and can lead to difficulty in measuring the elastic modulus of some primate foods. Fortunately, one of the biggest improvements in the mechanical testing of biological specimens in recent years has been in
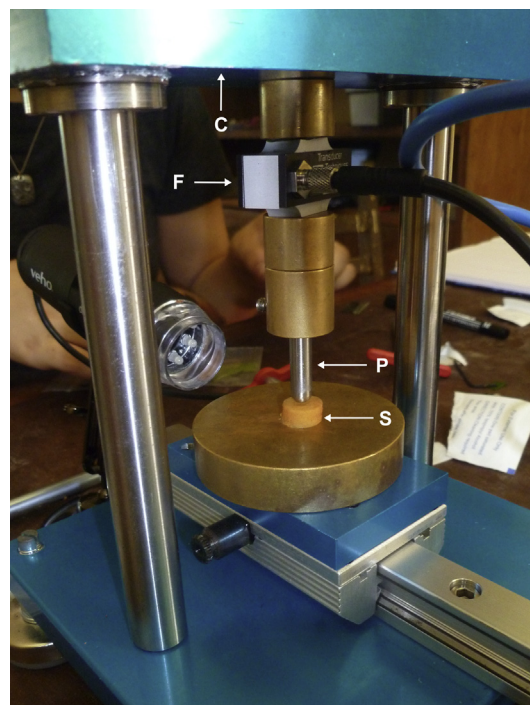


**Figure 4.** The blunt indent method of measuring elastic modulus. A moveable crosshead (C) allows the positioning of the blunt probe (P) onto a sample (S) and the resultant force is measured using a force cell (F).

indentation. Originally, these tests provided measurements just of the hardness of stiff materials that behaved in reasonable accord with an ideal elastic–plastic solid. They generally employed sharp-tipped indenters, such as a Vickers pyramid. About 20 years ago, the addition of displacement control allowed estimation not only of hardness during loading, but the elastic modulus during unloading (Oliver and Pharr, 1992), accurately enough to apply to wood or seed shell. However, the field has really been opened up enormously by the use of spherical indenters to acquire data on the elastic moduli of much softer material such as fruits and leaves. This section deals with the blunt indentation of fruit flesh because application to leaves is detailed in Talebi et al. (2016).

Most moisture-laden materials display time-dependent elasticity. A blunt indentation test provides two important measurements relating to this behavior: an *instantaneous elastic modulus*, which is what would be expected if a material could be loaded instantly, and an *infinite* (fully relaxed) *elastic modulus*, which estimates the elastic behavior under an infinitely slow loading regime. The ratio of the infinite to the instant modulus indicates the rate-sensitivity of a material. This effectively settles a common argument about whether if a specimen were loaded much faster, it would exhibit a completely different value for the modulus. These two measures effectively describe the upper and lower bounds of the modulus with loading rate. Whilst neither measure is a perfect model for what occurs during mastication, the instantaneous measure is probably the more relevant when contextualizing how a food reacts under such loads.

In a typical test, a block of material such as a piece of fruit is loaded slowly and evenly by moving a blunt probe of known radius, $R$, down for a total displacement, $h$, onto the specimen for 10 s (Fig. 4). This period is called the 'load ramp.' The probe is then stopped and the load allowed to decay for a further fixed period (say 90 s). At any given time point, $t$, the decay in the force, $F$, can be assumed to behave according to a series:

$$F(t) = B_0 + B_1\exp(-t/\tau_1) + B_2\exp(-t/\tau_2) + \ldots B_n\exp(-t/\tau_n) \quad (8)$$

where $B_n$ is a fitting constant and $\tau_n$, its time constant (Chua and Oyen, 2009). A parallel series to Equation (8) can be written for the time-dependent shear modulus $G(t)$:

$$G(t) = C_0 + C_1\exp(-t/\tau_1) + C_2\exp(-t/\tau_2) + \ldots C_n\exp(-t/\tau_n) \quad (9)$$

where $C_n$ is termed an amplitude coefficient (Chua and Oyen, 2009). Equations (8) and (9) can be related by

$$C_0 = \frac{B_0}{h^{1.5}\left(\frac{8R^{0.5}}{3}\right)} \quad (10)$$

and

$$C_k = \frac{B_k}{h^{1.5}\left(\frac{8R^{0.5}}{3}\right)RCF_k} \quad (11)$$

The adjustment for the length of time needed to ramp the specimen up to its maximum load, termed $RCF_k$, can be calculated following Oyen et al. (2008) for a standard linear solid. As for leaves (Talebi et al., 2016), if Poisson's ratio is assumed to be 0.5, then $E_0 = 1.5(C_0 + C_1 + \ldots C_n)$ and $E_\infty = 1.5C_0$ (Chua and Oyen, 2009). A multi-coefficient exponential decay model can be used to obtain the fitting and time constants (Talebi et al., 2016).

This novel method can produce modulus results with very little sample preparation and minimal damage to the sample during testing. In this way, we propose that blunt indentation is an ideal way for the rapid characterization of the elastic modulus of primate foods. New methods like this allow the measurement of previously hard to measure mechanical factors. With these new data in hand, it is possible for novel theories on how the salient signals of the food properties may be capitalized upon by primates during foraging (Talebi et al., 2016) and this could have implications for studies into primate cognition and intelligence.

## 4. Preparing a meal: new frontiers in the mechanics of extra-oral processing

On occasion, primates may need to perform some extra-oral processing before food enters the mouth. Many examples of such processing involve tool use and studies in this area have informed reconstructions of the evolution of intelligence and culture in humans (van Schaik et al., 1996; McGrew, 2004). Examples of extra-oral processing in great apes are abundant. In chimpanzees, there are examples of termite fishing using sticks (Sanz et al., 2009; Sanz and Morgan, 2011), hunting using spears (Pruetz and Bertolani, 2007), and the removing of seed cases before eating (Boesch and Boesch, 1982; Luncz et al., 2012). Orangutans remove the irritating hairs from the fruit of the *Neesia* sp. tree using twigs before they eat them (van Schaik et al., 1996, 2003; van Schaik and Knott, 2001). Orangutans use probing wooden tools to extract invertebrates from tree holes or sometimes as a chisel for removing termites from their nests (van Schaik et al., 1996, 2003). Outside the hominid clade, there is evidence that capuchin monkeys crack nuts and use twigs for probes (Fragaszy et al., 2004; Ottoni and Izar, 2008; Mannu and Ottoni, 2009; Norconk et al., 2009; Wright et al., 2009) and that long tailed macaques use stone tools to crush and crack open marine invertebrates (Gumert et al., 2009; Haslam et al., 2013). Much research has investigated the use, production, and material culture surrounding the use of tools for extra-oral processing and there are some lab studies into the cognitive ability of apes to perceive tool rigidity (Manrique et al., 2010; Walkup et al., 2010). However, there are very few examples of good mechanical investigations into these types of behaviors. Taking tried and tested techniques from the world of ecological biomechanical research and applying them to the tools and foods involved in extra-oral processing could provide novel and intriguing insights into how primates select tools and use them when consuming foods. There is a gap in our knowledge on the mechanics of tools. It could be that minor differences in tool structural and material properties are of no consequence to the primate tool user given their relative simplicity and the ease with which they can be fabricated from sometimes local materials. Conversely, though, behaviors such as tool carrying (Ottoni and Izar, 2008; Sanz et al., 2014) and the selection of preferred materials for specific tools (Sanz and Morgan, 2007), amongst other behavioral nuances, may indicate a preference for the way certain tools and materials behave mechanically. This review hopes to encourage further quantification to help understand the influence tool mechanics has on extra-oral processing and on the technical intelligence of primates. Here we look at the techniques that could be applied to two "classic" tool use behaviors seen in both apes and monkeys, the first being the use of sticks as tools and the second the use of anvils and hammers to process nuts and seeds.

### 4.1. Twigs as tools

A range of primates use twigs and sticks during food acquisition as probes (Mannu and Ottoni, 2009; Sanz and Morgan, 2009; Sanz et al., 2009), pounding hammers (Sanz and Morgan, 2009), digging tools (Hernandez-Aguilar et al., 2007), and even spears (Pruetz and

Bertolani, 2007). As they produce their tools, animals show signs of deliberately modifying their chosen tools, indicating capabilities for design complexity and intent (Pruetz and Bertolani, 2007; Mannu and Ottoni, 2009; Sanz et al., 2009). Given that primates are choosing and modifying tools for processing foods and that the mechanical properties of these tools will overtly affect their usefulness, we need to know more about the way the tools behave mechanically. This knowledge will allow researchers to investigate the technical intelligence of tool users, as well as the better-researched social and cultural intelligence traits.

In most cases when probing, pounding, digging, or stabbing, the flexural rigidity (the resistance of a beam to bending) will be influential on the effectiveness of wooden tools. Flexural rigidity is defined as the product *EI*, where *E* is the Young's, or elastic, modulus and *I* is the second moment of area (Ennos, 2012). The second moment of area can be calculated from the cross section area of a tool, while a bending test can be used to estimate *E*. There are two types of bending experiments, the first being three-point bending, where the test specimen is bent between two supports using one central point of contact. This test has previously been successfully used in other primate-based studies (van Casteren et al., 2012a, 2013). However, to limit the effects of shear on the results, the samples must have a span-to-depth ratio of 20 or above (Vincent, 1992; Beismann et al., 2000). Given their smaller size, this may not be tenable with some tools. Fortunately, in the four-point bending test, in which the sample is bent using two central points, placing the beam into pure bending does not require any specific span to depth ratio and can be used to estimate the flexural rigidity (*EI*) of a tool using Equation (12) (Ennos, 2012).

$$EI = \frac{dF}{dy}\frac{a}{48}\left(3L^2 - 4a^2\right) \tag{12}$$

where *a* is the distance between the inner and outer probes and *L* is the distance between the two supporting probes. The flexural strength ($M_{max}$) of a tool can also be estimated using Equation (13) (Ennos, 2012).

$$M_{max} = \frac{F_{max}a}{2} \tag{13}$$

Understanding the rigidity and strength of branch tools will help us understand the way they behave under loading, indicating their effectiveness at their given use. The effectiveness of digging sticks pushed through soil will be limited by their bending strength. In contrast, the effectiveness of a stabbing spear like those seen by Pruetz and Bertolani (2007), which is loaded along its length, will be influenced instead by its rigidity. The point load *F*, such as a spear can take before bowing outwards and undergoing what is known as Euler buckling, is given by the formula.

$$F = \frac{k\pi EI}{L^2} \tag{14}$$

The constant *k* depends on the precise loading conditions. For a spear held at one end and point loaded at the tip, it will equal 2. So the longer and narrower a spear, the less effective it will be at delivering a fatal lunge. Unfortunately, the spears found by Pruetz and Bertolani (2007) were highly tapered, making the mechanical analysis hard to do, so probably the best way to find out the force with which the spears could stab would be to collect the spears after observation and investigate this experimentally. More quantitative studies using this sort of analysis would build upon the largely descriptive research into tool use, selection, and modification.

It has been noted that some primates will modify the ends of some wooden tools to suit the desired application (Pruetz and

Bertolani, 2007; Mannu and Ottoni, 2009; Sanz et al., 2009), whittling away the ends with their teeth. Wood, however, rarely fractures in a uniform manner and can exhibit a range of fracture patterns generally thought to be a product of its density and fine scale anatomy (van Casteren et al., 2012b). It has previously been shown that orangutans, prolific tool users, take advantage of "greenstick" fracture in the construction of arboreal nests (van Casteren et al., 2012a). Do other primates take advantage of these natural fracture mechanisms? Do climate and the growth patterns of plants have an effect on primate tool use and extra-oral processing? Questions like these can only be answered by in-field mechanical tests, probing different anatomies and their corresponding mechanical properties exhibited by the plant material selected by primates in order to process foodstuffs. Laboratory studies have previously used bending, compression, and tensile tests on different orientations of wood to understand the reason for the differing modes of fracture seen in temperate tree species (van Casteren et al., 2012b). Using portable testing rigs, similar tests could be used to investigate the fracture properties of plant species chosen to perform extra-oral food processing tasks.

### 4.2. Bashing it out

Anvils and hammers are simple tools for the processing of food; extant primates use them and there is even evidence to suggest that extinct hominids may also have used similar processes to extract nutrients from hard and tough foods (Peters and Maguire, 1981; Carvalho et al., 2008; Haslam et al., 2009). Using a hammer and anvil places a food item, usually a seed or a nut, in compression, the same basic mechanics as those found during mastication but using dynamically applied loads, rather than static ones, and usually producing a greater force. At first glance it would appear that compression in biological cellular solids or structures is a rather simple affair; under a load there will be a rise in force till a
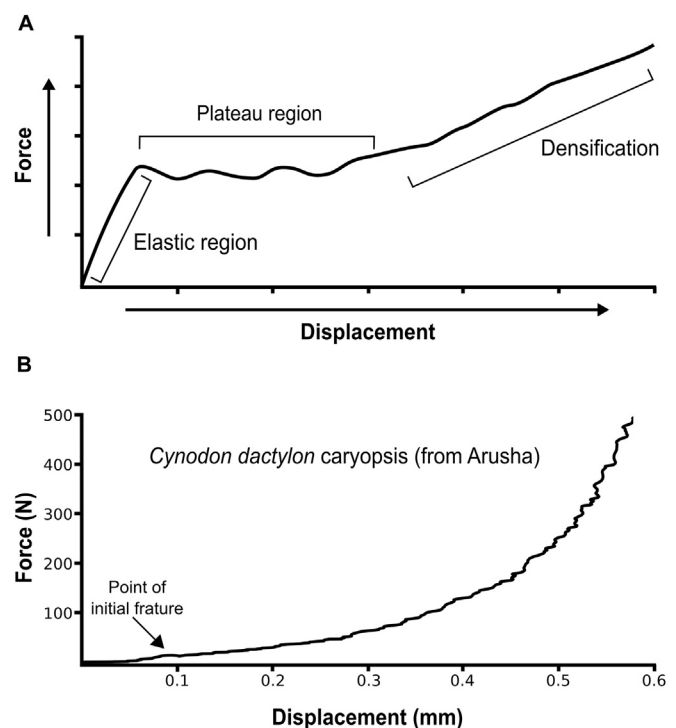


**Figure 5.** A) The stereotypical behavior of a food item under compression. B) A trace of force over displacement during the compressive failure of a single *Cynodon dactylon* seed.

maximum force is achieved, when failure will occur. However, the process can be considered a little more complex in compression as compared to tension, with three distinct stages (Fig. 5A; Gibson and Ashby, 1997). The first is a linear elastic stage during which material shortens reversibly. This is followed by an initial failure in which many of the walls fail under Euler buckling and either multiple fractures or plastic deformation may take place. Finally, as densification occurs, cell walls are pushed together and tissues compressed tightly, dramatically increasing reaction forces. Whether a nut or seed is cracked using a tool or via mastication, this same basic mechanical behavior applies.

Research has indicated that the selection of tools by primates to evoke compressive fracture is a function of the raw materials found in the environment, tool features, tool mobility, and food characteristics (Boesch and Boesch, 1982; Carvalho et al., 2009). There is a growing body of research that is dedicated to the first three factors (Carvalho et al., 2008, 2009; Visalberghi et al., 2009; Haslam et al., 2009, 2013; Luncz et al., 2012), but mechanical knowledge of the foods being processed is often limited. This is a shame, as nuts and seeds are often far from simple structures, regularly displaying a delicate balance of protection from predation whilst still retaining the ability to germinate with ease. Nuts have hard woody shells composed of large, thick-walled cells that resist compressive forces like those in mastication. However, nuts must still retain the ability to germinate, as the radicle must breach through its protective shell. Therefore, adaptations in structure and arrangement of nutshell material must be utilized to provide this delicate balance between protection and germination (Ennos, 2012). A prime example of such structural complexity is that of the *Mezzettia parviflora* (Annonaceae) seed from Southeast Asia. This seed shows varied cellular arrangements and orientations that deliver differing mechanical properties, providing external defenses yet functional weaknesses. This weakness comes in the form of brittle material arranged in a line along one side of the seed; a woody plug at either end accompanies this in order to initiate cracks. This zone of weakness is ideally placed running the length of the long axis of the seed, as its positioning makes it hard for orangutans to take advantage of the weakness due to the limitations of their gape (Lucas et al., 1991, 2011a). Tests have shown, therefore, how the seed fails when subjected to large static loads, as would be delivered by the teeth of an orangutan (Lucas et al., 1994), but how such a seed would behave when loaded dynamically by a hammer is largely unknown.

So far, in the study of compressive extra-oral processing, mechanical investigations seem to be limited to rudimentary field experimentation, where anvils of differing weights are dropped on target nuts. These tests have been successfully used to distinguish apparent differences in the resistance of various species of nut to fracture (Boesch and Boesch, 1982; Luncz et al., 2012). Whilst this gives some knowledge of which food object can withstand the highest initial impact, it tells us little about the forces involved and reveals nothing of the modes or methods of fracture, leaving the literature somewhat lacking in any real knowledge of the fracture mechanics involved. Some studies have previously tackled the compressive failure and fracture of nuts and seeds in the laboratory (Jennings and Macmillan, 1986; Lucas et al., 1991, 1994, 2012; Wang and Mai, 1994), but these concentrate on nuts and seeds that are either orally processed or not touched by primates. Portable field testers have been around for some years and have grown in technical sophistication, now generating accurate and reliable results in in-field scenarios. If equipped with a large force cell, these portable devices can be rigged up using a compression plate to place a whole nut or seed in compression, whilst simultaneously measuring the force and displacement needed to generate wholesale fracture. This allows fuller investigation of the compressive failure and behavior

(Fig. 5) of a food item. Large forces can easily be generated by seeds and nuts in compression. Figure 5B demonstrate how a small grass seed (*Cynodon dactylon*), the properties of which are investigated by Smith et al. (2015), crushed between two plates, may initially fail at low loads (around 10 N in our example). This is a force that can be predicted from mechanical studies of other seeds (Lucas et al., 2012). The seed breaks down further and subsequently densifies at much higher loads without a determinate value—even 500 N to reduce one grass seed in one bite does not produce 'flour.' Such multiple fracture is typical of the effect of a bunodont dentition. Therefore, the need to process foods using such high loads may influence the selection of tools such as hammers and anvils or the evolution of dental form and function.

There are, however, other ways in which the material properties of hard food items can be measured that do not require large (and often expensive) load cells. Both the Young's modulus, $E$, and fracture toughness, $K_{IC}$, of a shell can be calculated by compressing a c-ring or arch of material (Fig. 6a). Using linear isotropic beam theory, it is possible to calculate $E$ from intact arches in compression using Equation (15) (Jennings and Macmillan, 1986; Wang and Mai, 1994)
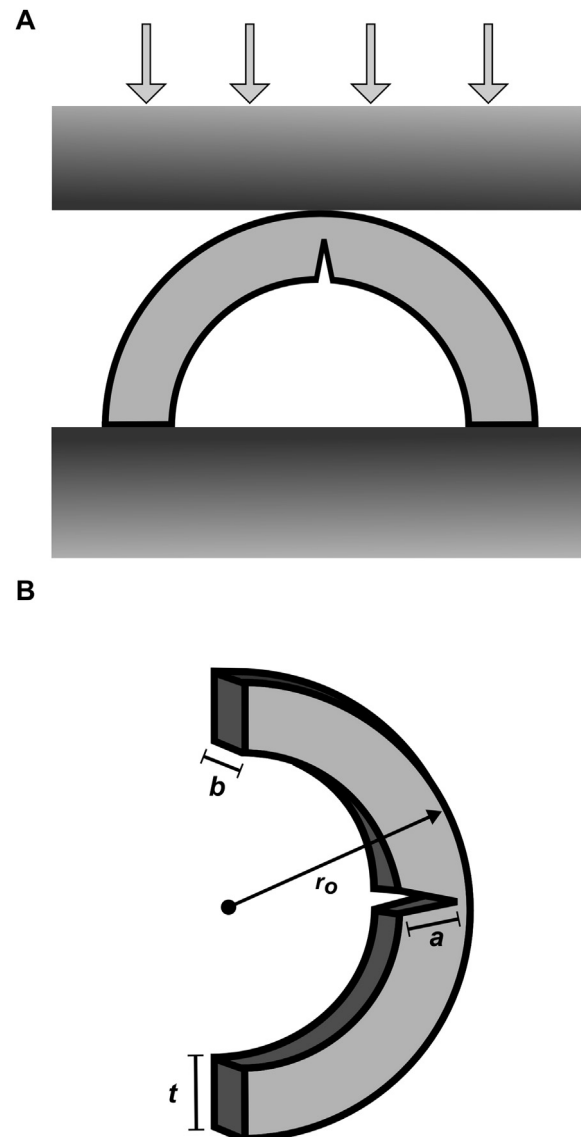
**Figure 6.** The set up (A) and dimensions (B) of a compressive arch test.

$$E = \frac{3\pi(2r_o - t)^2\left(\frac{dF}{dy}\right)}{4bt^2} \qquad (15)$$

where $t$ is the thickness and $r_o$ is the outer radius of the arch (Fig. 6b). Notched arches can be used to calculate the fracture strength, $\sigma_f$, and fracture toughness, $K_{IC}$, using Equations (16) and (17), respectively (Wang and Mai, 1994). However, accurate measurement of the notch length, $a$ (Fig. 6b), will vastly affect the validity of the results, so it is advisable to use digital photography and image analysis software to enhance the precision of this measurement.

$$\sigma_f = 2F\frac{3r_o - 2t}{bt^2} \qquad (16)$$

$$K_{IC} = \left(1.1215 - 1.365\frac{a}{t}\right)\sigma_f\sqrt{\pi a} \qquad (17)$$

These equations have been used before to describe the material properties of nuts in laboratory settings (Jennings and Macmillan, 1986; Wang and Mai, 1994), yet their usefulness has failed to cross over into a field context. One advantage of cut samples is that a researcher can target specific regions or orientations of a hard food object. This type of method would produce a well-rounded and definitive characterization of the nuts and seeds that are consumed by primates, allowing primatologists to truly understand the significance food characteristics have on the social, cognitive, and cultural aspects of this interesting behavior.

## 5. Conclusions

Primates live in a complex physical world and face a multitude of mechanical pressures. Understanding the mechanical parameters of primate environs can aid and inform on morphological and behavioral adaptations.

Here, we have presented ways to measure and interpret the physical traits of an environment and we suggest that this line of investigation, although currently active, can be expanded and presents novel and exciting avenues of investigation in primatology. Using these methods, it will be possible to expand beyond field descriptions of the mechanical environment into the quantitative sphere. Subjective impressions of objects such as 'young leaves,' 'ripe fruit,' 'hard objects,' or 'flexible branches' can now be given a more precise definition via in vivo measurement. The level of resolution that we suggest is intended to help an understanding of the relations between the environment, morphology, function, and behavior of extant primates and also to help more accurately to piece together the paleoenvironment of fossil forms from fragmented and indirect evidence. The mechanical testing toolkit presented in this review can build upon and invigorate topics within field primatology, generating a deeper understanding of human evolution and that of our close evolutionary relatives.

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