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Novel developments in field mechanics

Adam van Casteren [a,*], Vivek Venkataraman [b], A. Roland Ennos [c], Peter W. Lucas [d]

[a] Max Planck Weizmann Center for Integrative Archeology and Anthropology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103, Leipzig, Germany
[b] Department of Biological Sciences, Dartmouth College, Hanover, NH, 03755, USA
[c] School of Biological, Biomedical and Environmental Sciences, The University of Hull, HU6 7RX, UK
[d] Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, Panama

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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.

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,

* Corresponding author.
E-mail address: adam.vancasteren@gmail.com (A. van Casteren).

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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.

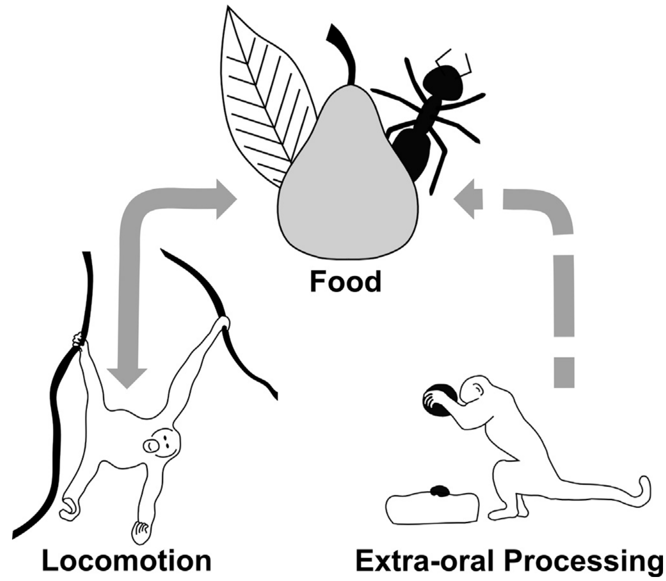

Figure 1. Diagram illustrating the wider mechanical world that should be taken into account whilst researching primate foods. Capuchin monkey redrawn from Mannu and Ottoni (2009).

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 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