Primate Fauna: Physical Properties of Prey Items

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INTRODUCTION

Numerous studies have noted the relationship between primate mastoid sphenoid, and food habits. The use of mastoid sphenoid, mandible, and skull properties of the different species of primate can be used to identify food habits, and infer the physical properties of the dietary items. Our goal is to explore the physical properties of a few of the items of food found in primates. We present new data after

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summarizing the physical property data in the literature on insects, muscle, and bone.

Faunivores are organisms that regularly include invertebrate and vertebrate prey in their diets (Pielage, 1988). Many primates, especially the nocturnal, small-bodied species, are highly faunivorous, with the majority of prey being insects (Haddow and Elliffe, 1964; Amerasinghe et al., 1971; Charles-Dominique, 1977; Hadik, 1979; Doyle, 1979; Hadik et al., 1980; Pages, 1980). Additionally, insects are a significant component of many anthroploid diets (Rcns, 1996). However, with respect to their physical properties, insects are quite heterogeneous. For instance, although all insects have exoskeletons, their degrees of hardness vary considerably. Some primates specialize on certain portions of the insect community, for example, *Arctocebus calabarensis* eats soft-bodied prey such as moths, whereas *Galagooids demidovii* prefers harder-bodied insects such as beetles (Charles-Dominique, 1977). Although most prime faunivores consume mostly insects, some species also include vertebrate muscle and bone in their diets. For example, Coquerel's mouse lemur, *tarsiers, baboons, macaques, and chimpanzees*, prey on vertebrates (Pages, 1980; Butynski, 1982; Niemitz, 1984; Richard, 1985).

Morphological studies have demonstrated that differences in the physical properties of insects, muscle, and bone are reflected in the form of the masticatory apparatus of the predator. Freeman's (1979, 1981a,b) craniodental morphological study on microchiropterans bats demonstrated that characters such as the robustness of the jaw and the size of cranial crests vary predictably and positively with the hardness of insects eaten. Strait (1993a,b) showed that specific responses to different physical properties characterize the dentitions of faunivorous mammals that typically consume either hard insects such as beetles or soft insects such as caterpillars or moths. Faunivores feeding on hard objects have relatively less development of shearing crests on their molar teeth (an those of closely related faunivores that feed on soft objects (Strait, 1993a). Additionally, dental microwear analysis (Strait, 1993b) revealed that faunivores that eat hard objects consistently exhibit more pitted occlusal surfaces than soft-object feeders. Moreover, Dumont (1995) showed that inverteous hard-object feeding primates and bats exhibit relatively thicker enamel on their teeth than congers that feed on softer food items.

In order to understand more thoroughly these anatomical correlates to faunivorous dietary adaptations, it is necessary to discriminate between the physical properties of different prey species. Relative little is known about the physical properties of species that are common food sources for faunivorous primates. Entomologists have reported on the physical properties of the cuticle of insects from various taxa and anatomical regions relevant to flight, feeding, defense, development, and reproduction (Table 1). Relative stiffness is the most commonly reported physical property of arthropod cuticle. Stiffness is the resistance to a solid to deformation within its elastic range (Strait, 1997). However, most stiffness studies were not performed in a controlled environment and, therefore, are inaccurate (Vincent, 1980). Among taxa that are frequently chosen as prey by inverteous primates the only cuticular stiffness values from controlled studies are for coleopterans, orthopterans, and lepidopterans (Table 1), and they vary greatly among taxa. For instance, even one of the most plant parts of a coleopteran, the intersegmental membrane, is stiffer and stronger, by over an order of magnitude, than the abdominal region of a lepidopteran (Table 1).

Plasticity—nonreversible deformation—must also be considered. The noncorticalized abdominal tergite cuticle of caterpillars deforms plastically, while many beetle exoskeletons are quite brittle (Heinburn and Jolle, 1976). The cuticle of some insects is considered tough (Lucas and Luke, 1984); however, the data on toughness of invertebrate cuticles is sparse. Toughness is defined as a solid's resistance to crack propagation. The only available toughness value for insects is for the intersegmental membrane of Locusta (Vincent, 1990b), an insect that is only occasionally eaten by primates.

Some primates also consume small vertebrate prey, including reptiles, birds, and other mammals (Niemitz, 1984; Richard, 1985). Vertebrate muscle, skin, and connective tissue are usually described in the functional morphological literature as soft (Lucas and Luke, 1984; Freeman, 1984; van Valkenburgh, 1988), compliant (Frazzetta, 1988), or tough (Lucas and Luke, 1984).

**Table 1. Summary of Quantitative Data in the Literature on the Physical Properties—Stiffness, Strength, and Toughness (Work per Unit Area)—of Animals that Are Frequent Food Sources for Faunivorous Primates**

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Stiffness (Pa)</th>
<th>Strength (Pa)</th>
<th>Toughness (kJ m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beetle*</td>
<td>5.05 × 10⁸</td>
<td>2.1 × 10⁹</td>
<td>0.2-0.6*</td>
</tr>
<tr>
<td>Locusta*</td>
<td>7.4 × 10⁹</td>
<td>1.6 × 10¹</td>
<td>2-3</td>
</tr>
<tr>
<td>Caterpillar*</td>
<td>2.2 × 10⁹</td>
<td>9.2 × 10⁸</td>
<td>-</td>
</tr>
<tr>
<td>Insect muscle</td>
<td>2.3 × 10⁸</td>
<td>1.0 × 10⁹</td>
<td>-</td>
</tr>
<tr>
<td>Skin</td>
<td>1.0³</td>
<td>1.0 × 10⁹</td>
<td>-</td>
</tr>
<tr>
<td>Bone</td>
<td>0.6-2.6 × 10⁹</td>
<td>0.4-2.94 × 10⁹</td>
<td>1.7-2.6*</td>
</tr>
</tbody>
</table>


*Intersegmental membrane.

*Tearing energy.

*Local abdominal tergite.

*Work to fracture from each test in bending.
and Luke, 1984), while bone is described as hard and brittle (Lucas and Luke, 1984; Freeman, 1988; van Valkenburgh, 1988). The physical properties of some vertebrate tissues have been better documented than invertebrate tissues (Table 1). Relative to muscle and skin, bone is considered stiff and strong. Skin, aside from being exceedingly tough, is much softer and stronger than muscle (Table 1).

This brief review demonstrates that there are some physical property suitable data for modeling biomechanically optimal masticatory morphologies for habitually faunivorous primates. Although some taxonomic groups and physical properties have been sufficiently sampled, there are outstanding gaps. The primary deficiency is the lack of toughness values or proper descriptions of fracture behavior for invertebrate taxa that are common today's primates (Table 1). To rectify this situation by qualifying fracture toughness and describing fracture behavior more completely in representative hard-bodied and soft-bodied insects, as well as in vertebrate muscle tissue.

**MATERIALS AND METHODS**

We measured the toughness of potential animal foods by means of a scissors test similar to that described by Lucas and Pereira (1990), which is a modification of the guillotine test of Atkins and Mai (1979; Wright, 1992; Vincent, 1992). This particular test was designed to measure toughness, one of the most important but most neglected physical properties. The resultant force-deflection charts also have sufficient information to allow inference to be drawn on the relative plasticity of the test specimens.

We selected experimental specimens represent only animal species that are frequent prey choices of primates and clearly exhibit extremes in their physical properties. Test specimens include larval lepidopterans (Spodoptera; n = 10) to represent soft insects, and adult coleopterans (Tenebrio; n = 10), as hard food. To approximate a more carnivorous diet, we examined bovine muscle [m. semitendinosus (n = 10), chosen because of the relatively unpenetrable orientation of its fibers]. We also tested paper cotton (85-g m-2, single and double thickness; n = 1) as a baseline for comparison and accessibility to other workers with similarly designed testing machinery.

It can be very difficult to measure toughness, and indeed, other physical properties in biological materials because they are frequently anisotropic, viscoelastic, structurally complex, irregularly shaped, and heterogeneous. These variables contribute to difficulties with the implicit assumptions and methods of many conventional tests (Lucas and Pereira, 1990; Vincent, 1990a, 1992). Scissors or guillotine tests have many advantages when testing biological materials (Atkins and Vincent, 1984; Atkins and Mai, 1985; Vincent, 1990a, 1992; Lucas and Pereira, 1990). Results from them are minimally affected by different sizes or shapes of specimens, they can register very small increments of work, and they direct the propagating crack so that the energy exerted by the load is solely directed to fracture. This last aspect of scissors/guillotine mechanisms is important because (1) it confines the deformation to a limited area so that the stress generated by the deformation detects fewer of the imperfections [Griffith cracks (Gordon, 1978; Vincent, 1990b)] which act as stress concentrators, and (2) it produces resultant curves including only fracture energy. As Vincent (1990a, p. 240) noted, “Great care is necessary to ensure that the curve encloses only the fracture energy and does not include . . . stored elastic strain energy. The easiest way to ensure this. . . . is to use a test in which the crack grows in a stable fashion.” Finally, scissors or guillotine tests also have the ability to record variations in texture (Vincent, 1990a, 1992), a consideration that is especially relevant when testing complex biological structures that are generally anything but homogeneous.

Additionally, an important factor in compliant and extensible materials such as muscle tissue is that fracture at places remote from the site where the load is imposed requires the transmission of strain energy from the area where the load is imposed to the fracture site. In general, such transmission is difficult in soft tissues as a result of the J-shaped stress-strain curve (Purslow, 1989) or because, in muscle, the material is made of fibers that are not particularly well stuck together laterally. This makes the material insensitive to damage and therefore difficult to break (Purslow, 1987). For such tissues it is necessary to feed the force in to the fracture zone more directly. This is achieved by either cutting, e.g., with a knife or guillotine, or shearing, as between scissor blades.

The testing machinery consisted of a pair of dissection scissors affixed to a universal testing machine (Instron 4202) (Fig. 1). Although the action of the scissors generally resembles the action of jaws during mastication, we did not attempt to mimic an actual chewing cycle, i.e., all forces were applied vertically. The insects were affixed to a piece of cardboard, with a V-shaped wedge removed where the scissors could pass through unrestricted. The free end of the cardboard was then set in a clamp, and its height was adjusted to the level of the scissor blades. The long axis of the specimen was set perpendicular to the scissor blades. Caterpillars were cut through their midsections and beetles, with their more heterogeneous external morphology, were positioned so that the scissors contacted just distal to the beginning of the elytra. We cut beef muscle into rectangular pieces with 3 samples oriented so that the fibers were parallel to the scissor blades, and 5 samples with the fibers perpendicular to the blades. The start-
All force-deflection output was displayed on a chart recorder (force on the Y axis and deflection on the X axis). Before each experiment we recorded 2 free passes of the scissors to establish the forces and work performed due to the friction of the blades. After the experiments were completed we digitized the deflection curves for the specimens and free passes and used a program that subtracts the free-pass baseline from the experimental line so that the remaining curve represents only the work to fracture. Accordingly, all analyses and figures represent transformed data.

we compared the specific work of cutting—toughness—as the area under the force–displacement curve divided by the original cross-sectional area of the specimen.

For many measurements of physical properties, some estimate of original specimen dimensions is required. Therefore, before each experiment we measured the cross section (height and width) of each specimen with dial calipers. The cross-sectional area for a caterpillar is modeled after a circle, while the cross sectional area of a beetle is approximated as an ellipse. Since the bovine muscle was cut into rectangular pieces the product of height and width provided an estimate of its cross-sectional area.

We used nonparametric statistical tests in lieu of single-classification analysis of variance to test for differences in toughness between sampled taxa or, for muscle tissue, between fiber orientations. We employed the Games and Howell test when variances were heterogeneous, and the Kruskal–Wallis test when the samples were neither homoscedastic nor normally distributed (Sokal and Rohlf, 1981).

**RESULTS**

The toughness values represent the lowest possible work to fracture. The beetles were substantially tougher (2.77 kJ m$^{-2}$) than the caterpillars (0.39 kJ m$^{-2}$) ($P < 0.01$) (Table II). Muscle tissue (1.26 kJ m$^{-2}$) was intermediate between them, though significantly different from both insect samples ($P < 0.01$). Additionally, there is no significant difference ($P < 0.05$) between the fiber orientations (parallel or perpendicular to scissor blades) for the muscle tissue (Table II).

From visual examination of the force–deflection charts we obtained an estimate of relative plasticity. Brittle solids typically demonstrate very spiked patterns, whereas ductile solids show smoother curves. Accordingly, beetles display brittle fracture, while caterpillars and muscle demonstrate considerable flow (plastic behavior) (Fig. 2).
Table II. Means and Standard Deviations (in Parentheses) for the Original Cross-Sectional Area, Fracture Toughness, and Strength (Ultimate Stress) in the Test Samples of Paper, Beetles, Caterpillars, and Bovine Muscle*

<table>
<thead>
<tr>
<th>Sample</th>
<th>n</th>
<th>Area (mm²)</th>
<th>Toughness (kJ m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beetles</td>
<td>10</td>
<td>14.66 (1.59)</td>
<td>2.77 (0.34)</td>
</tr>
<tr>
<td>Caterpillars</td>
<td>10</td>
<td>14.60 (3.77)</td>
<td>0.39 (0.11)</td>
</tr>
<tr>
<td>Bovine muscle</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pooled sample</td>
<td>10</td>
<td>27.30 (11.61)</td>
<td>1.26 (0.41)</td>
</tr>
<tr>
<td>Perpendicular</td>
<td>5</td>
<td>1.40 (0.22)</td>
<td></td>
</tr>
<tr>
<td>Parallel</td>
<td>5</td>
<td>1.11 (0.33)</td>
<td></td>
</tr>
<tr>
<td>Copper paper</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 layer</td>
<td>1</td>
<td>0.73</td>
<td>38.61</td>
</tr>
<tr>
<td>2 layer</td>
<td>1</td>
<td>1.14</td>
<td>36.88</td>
</tr>
</tbody>
</table>

*Sample size.

Fig. 2. Representative force/deflection tracings for caterpillars, beetles, and beef muscle. Force in newtons and deflection in millimeters. All three samples of approximately the same original cross-sectional area (caterpillar, 16.62 mm²; beetle, 13.85 mm²; beef muscle, 14.96 mm²).

Discussion

The only other comparable toughness values for primate food items are from studies of the toughness of certain dicotyledonous leaves (Lucas and Pereira, 1990; Lucas et al., 1991). Toughness values from Lucas and Pereira's (1990) study of 8 species of leaves at different stages of maturity range from 0.089 to 2.24 kJ m⁻². The beetle samples demonstrate a mean toughness value in the midrange of the leaf values, while caterpillars have values close to the lowest values for young leaves. Beef muscle toughness values fall within the upper range of Lucas and Pereira's (1990) leaf values. In a more detailed study of variation in fracture toughness in a single species of leaf at uniform maturity Lucas et al. (1991) found that within a single leaf the toughness of different anatomical regions ranges considerably, from a low of 0.022-0.30 kJ m⁻² for the mesophyll and the epidermis and its cuticle to 6 kJ m⁻² for secondary veins. In the same way the values quoted for the two types of the whole insects are means of the outer cuticle, which may be expected to be relatively resistant, and the more delicate internal organs. The effect of the outer covering is then very obvious, since there is no reason to think that the toughness of internal organs of the sample caterpillars and beetles—both herbivores—is very different. Just as the veins of a leaf can dictate fracture by deflecting free-running cracks or making cutting difficult, it appears that beetle cuticle dictates its properties when the insect is being chewed.

The fact that muscle shows no anisotropy when being cut, though it does when fractured in tension (Purslow, 1987), reinforces the observation that a crack propagated by cutting does not necessarily detect the structure since the forces are being applied in such a small zone. Thus many biomaterials, e.g., seaweed, wood, fruit, some leaves, have vastly different work to fracture values when tested at different orientations (Vincent, 1990a; Lucas et al., 1991). But when cut on a microtome, wood (Vincent, unpublished) and meat (Dobraszczyk, 1987) show no anisotropy, because the toughening structures that give rise to the anisotropy are not allowed to express their effects under such localized cutting forces. In contrast, the toughening effects of leaf veins are due to the relatively large scale inhomogeneity.

Interestingly, beetles can be considered both tough and brittle. Lucas and Luke (1984) and Lucas and Teaford (1994) consider tough and brittle to be opposite properties, since materials that are ductile and demonstrate a plastic response tend to increase fracture energy and therefore fracture toughness. However, the important distinction to be made here is between a material and a structure. Homogeneous isotropic materials cannot be both brittle and tough, but beetles, being composite structures—i.e., composed of mechanically isolated plates—exhibit both brittleness and toughness in terms of the ability to stop cracks.

Caterpillars and muscle are fragile and ductile. It is also apparent that they are too compliant either to store or to transmit significant amounts of strain energy. Thus fracture occurs only at the point where the scissor
blades are shearing past each other, and the sharpness of the blades and the precision of their occlusion become much more important factors.

In order for primatologists and paleontologists to understand and more rigorously to explain the interaction between an animal's masticatory apparatus and its dietary habits, the physical properties and fracture mechanics of food items themselves must be better understood. The two types of fracture behavior that we described dictate the type of tooth that is necessary. With restricted brittle fracture, the fracture is fed by globally available strain energy so the teeth are not crucial for directing the path of the crack and need not have elaborate shearing crests (Strait, 1993a, 1993b). But compliant foods have to be cut and with teeth developed shearing crests to initiate tearing or to cut through the material or both. In these types of solids cracks are not self-propagating, therefore teeth have to be continuously driven through the material in order to subdivide it.

In order to characterize the physical properties of primate diets, it is necessary to conduct large-scale comparative studies in the field. Practically, insects are the only primate animal foods that can be tested in the laboratory because a prerequisite of physical property testing is that items must be fresh (food physical properties can be drastically altered as the specimen dries out during transport) (Kinzevsky and Norconk, 1990). However, the laboratory methods discussed in this paper can also be performed in the field (Strait, 1997; Darvell et al. 1996).

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REFERENCES


Primate Fossil


