

Hardness of Cercopithecine Foods: Implications for the Critical Function of Enamel Thickness in Exploiting Fallback Foods

Joanna E. Lambert,^{1*} Colin A. Chapman,² Richard W. Wrangham,³ and Nancy Lou Conklin-Brittain³

¹Department of Anthropology, University of Oregon, Eugene, Oregon 97403

²Department of Zoology, University of Florida, Gainesville, Florida 32611 and Wildlife Conservation Society, Bronx, New York 10460

³Department of Anthropology, Harvard University, Cambridge, Massachusetts 02138

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ABSTRACT We evaluate the hardness of foods consumed by sympatric *Cercopithecus ascanius* (redtail guenons) and *Lophocebus albigena* (grey-cheeked mangabeys), and consider how selection might operate to influence foraging adaptations. Since *L. albigena* has among the thickest dental enamel in extant primates and is commonly referred to as a hard-object consumer, we predicted that their diet would be harder than that of the guenon. Data on diet and food hardness (as measured by resistance to puncture and crushing) were collected between June–October of 1997 at Kibale National Park, Uganda, and were compared to similar data collected in Kibale between 1991–1994. Contrary to what we pre-

dicted, there was no difference in dietary hardness when the puncture resistance of all fruit consumed by the two species was compared (31 tree species in both study periods). However, in June–October 1997, *L. albigena* exploited a diet more resistant to puncture and crushing than *C. ascanius*. This difference is largely explained by the higher percentage of bark and seeds consumed by the *L. albigena* during this period. We suggest that it is the difference in the mechanical properties of fallback foods during critical periods that may have served as the selective pressure for thick enamel in *L. albigena*. *Am J Phys Anthropol* 125:363–368, 2004. © 2004 Wiley-Liss, Inc.

Dental enamel is hard, varies in its thickness, and has a structure subject to natural selection (Maas and Dumont, 1999). Since thick dental enamel resists wear longer than thin enamel, and since diets resistant to fracture are more likely to wear enamel, the appearance of thick dental enamel in fossil and extant species is presumed to indicate adaptation to a hard-object diet comprising seeds and unripe fruit (Kay, 1981; Dumont, 1995; Teaford et al., 1996). This generalization is supported to varying degrees. For example, Dumont (1995) demonstrated that hard food-consuming primate species have significantly thicker enamel than soft food-consumer counterparts, especially in congeneric comparisons. Similarly, *Cebus apella* has the thickest molar enamel known among extant primates, and consumes hard palm nuts that no other primate can open (Kay, 1981; Terborgh, 1983). However, there is no evident enamel thickness threshold separating hard-object feeders from soft-object feeders (Maas and Dumont, 1999). Moreover, there are few analyses of the hardness of food items in primate diets.

Lophocebus albigena (the grey-cheeked mangabey) has among the thickest molar enamel of any extant primate (Kay, 1981). And, since some of its earliest descriptions (Hadow, 1952; Chalmers,

1968; Kingdon, 1974; Waser, 1975, 1977), this species has been classified as a “hard-object consumer” (Kay, 1981; Dumont, 1995; Kinzey and Norconk, 1990; Teaford et al., 1996). Kay (1981) suggested that *L. albigena* consumes food (e.g., hard nuts, seeds, and fruits) unavailable to thinner-enameled, sympatric cercopithecines (e.g., *Cercopithecus*). Thus, the case of *L. albigena* appears to offer further support for the hypothesis that thick dental enamel facilitates a diet resistant to fracture. However, such characterization of feeding behavior easily becomes reified. Indeed, there exist very few (if any) quanti-

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*Correspondence to: Joanna E. Lambert, Department of Anthropology, University of Oregon, Eugene, OR 97403.
E-mail: jlambert@oregon.uoregon.edu

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field data on whether grey-cheeked mangabeys actually do consume foods that are significantly more resistant to fracture than foods consumed by thinner-enamelled primates, such as sympatric *Cercopithecus* monkeys (guenons).

Like all cercopithecines, guenons and mangabeys are noted for their omnivorous and flexible dietary strategy (Chapman et al., 2002; Lambert, 2002a,b). Yet in addition to differences in molar enamel thickness (although not in microstructure), there are evident differences in overall foraging strategy between sympatric *Cercopithecus* monkeys and *L. albigena* (Haddow, 1952; Waser, 1977; Struhsaker, 1978; Wrangham et al., 1998; Conklin-Brittain et al., 1998; Olupot, 1998). For example, it is apparent that *Cercopithecus* spp. and *L. albigena* differ in terms of their exploitation of fallback foods (Wrangham et al., 1998). Moreover, as indicated in other foraging-related suites of traits (e.g., locomotion; Gebo et al., 1994), adaptations may be selected for during relatively short (but critical) periods of stress (Rosenberger, 1992; Kinzey, 1978). Thus, generalizations about what a species does on average may not lend the greatest insight into the evolution of a trait. Bearing this in mind, here we address the following questions:

- 1) Are the fallback foods consumed by *L. albigena* significantly more resistant to fracture (via puncture and crushing) than foods consumed by sympatric cercopithecines? And,
- 2) How do fallback foods compare to favored food items (e.g., fruit) in their hardness properties?

We measure the hardness properties of foods consumed by *L. albigena* and *Cercopithecus ascanius*, and interpret these data in light of information on overall feeding patterns and fallback diets. Our ultimate goal is to shed light on the relationships among enamel thickness, feeding behavior, and the timing of selection.

METHODS

The study was conducted at the Kanyawara site of the Kibale National Park in western Uganda. The park has an area of 766 km² and is situated roughly 25 km east of the Ruwenzori Mountains at an elevation of approximately 1,500 m. *C. ascanius* and *L. albigena* are common in Kanyawara, and occur at a density of approximately 184 individuals/km² and 11.48 groups/km² and 45 individuals/km² and 2.41 groups/km², respectively (Chapman and Lambert, 2000).

With the help of one full-time research assistant, we collected feeding data on focal animals from one *C. ascanius* group and one *L. albigena* group during all-day follows (0700–1800 hr; July–October, 1997). Focal animals were followed for half-hour intervals. During these intervals, we recorded all occurrences of a feeding event in which the entire process of food acquisition, processing, and ingestion could be ob-

served fully and without interruption. We defined a feeding event as all ingestion that took place over the course of a 60-sec interval.

Samples were collected of as many as possible of the foods consumed by the two monkey species during July and October 1997. Plant parts were obtained by using an aluminum tree-pruning saw that extended to approximately 12 m. The canopy of the Kanyawara site is dense and fairly continuous at approximately 10–30 m, with emergent trees that achieve heights of up to 50 m (Skoropa, 1988; Struhsaker, 1997). In some cases, climbing trees was necessary to reach peripheral branches. In other cases, tree height precluded sample collection. Only those plant portions that animals were observed to consume were assessed for mechanical properties. Samples were placed in a plastic bag, transported from the forest back to the field station, and processed as soon as possible to avoid distorted scores due to desiccation. In addition to assessing the hardness of foods consumed by both monkey species during 1997, we also include hardness measurements of food consumed by these two species during 1991–1994.

Mechanical properties of fruit, seeds, and bark were measured following the methods described by Kinzey and Norconk (1990). We use their terminology of “puncture” and “crushing resistance.” We measured resistance to puncturing using a portable agricultural fruit and vegetable tester (Model 719-40MRP). This instrument was equipped with a pin and plunger, and was used to determine the hardness of bark, seeds, and fruit flesh (i.e., the meso- and exocarp portion of the fruit’s pericarp). We measured resistance to crushing using a soil compression tester (Rimac Spring Tester). This instrument was used to determine the force required to crush seeds and bark. No attempt was made to quantify the hardness of animal matter, gums/saps, and flower or leaf buds, as preliminary trials indicated that they were too soft for the instruments to detect resistance.

RESULTS

Data were collected during ca. 400 observational/contact hours which resulted in 582 complete feeding records; 391 complete feeding records were collected for *L. albigena*, and 191 for *C. ascanius*. The two monkey species were observed to consume 56 parts of 36 plant species. During the 1997 study period, fruit made up a low percentage in each of the species’ diets relative to earlier studies (Waser, 1977; Struhsaker, 1978; 33.5% for *L. albigena*, and 17.3% for *C. ascanius*), although *L. albigena* ate more fruit ($\chi^2 = 16.2$; $P < 0.01$) than did *C. ascanius*. *C. ascanius* ate significantly more insects (48.7%) than *L. albigena* (36.4%) ($\chi^2 = 7.67$; $P < 0.01$), and more leaves (24.1% vs. 9.8%, $\chi^2 = 53.7$; $P < 0.01$). *L. albigena* consumed more bark ($\chi^2 = 5.25$; $P = 0.02$; 8.9% vs. 3.6%) and seeds ($\chi^2 = 10.8$; $P = 0.01$; 8.6% vs. 1%) than *C. ascanius*.

TABLE 1. List of species, plant part, fruit form, puncture resistance score, crushing score, and consumer¹

Species	Plant part	Fruit form	Puncture score (kg/mm ²)	Crushing score (kg)	Consumer (includes 1991–1994 and 1997 reports)
<i>Aphania senegalensis</i>	Fruit	Drupe	3.0		RT, MG
<i>Aphania senegalensis</i>	Bark ²		NA	14.8	MG
<i>Balanites wilsoniana</i>	Bark ²		NA	13.9	MG
<i>Celtis africana</i>	Fruit ⁴	Drupe	0.25		RT, MG
<i>Celtis africana</i>	Bark ²		4.0	7.0	MG
<i>Celtis durandii</i>	Fruit ⁴	Drupe	1.25	2.2	RT, MG
<i>Chaetacme aristata</i>	Fruit	Drupe	0.7		RT, MG
<i>Cordia abyssinica</i>	Fruit	Drupe	1.1		RT, MG
<i>Cordia abyssinica</i>	Bark ²		9.0		MG
<i>Cordia milleni</i>	Fruit ³	Drupe	1.7		RT, MG
<i>Cordia milleni</i>	Bark ²		NA	3.0	MG
<i>Croton macrostachys</i>	Fruit ²	Dry, indehiscent	3.0		MG
<i>Croton macrostachys</i>	Seed ²		NA	1.0	MG
<i>Dasylepis eggingii</i>	Fruit	Berry	1.7		RT, MG
<i>Diospyros abyssinica</i>	Fruit ²	Berry	3.6		RT, MG
<i>Diospyros abyssinica</i>	Seed ²		16.5	19.25	MG
<i>Ehretia cymosa</i>	Fruit	NA	0.25		MG
<i>Fagaropsis angolensis</i>	Fruit ⁴	Drupe	1.0		RT, MG
<i>Ficus bracteata</i>	Fruit ⁴	Syncarp	0.1		RT, MG
<i>F. capensis</i>	Fruit	Syncarp	1.7		RT, MG
<i>F. cyathistipula</i>	Fruit	Syncarp	0.27		MG
<i>F. dawei</i>	Fruit	Syncarp	0.01		RT, MG
<i>F. exasperata</i>	Fruit ²	Syncarp	0.01		RT, MG
<i>F. exasperata</i>	Bark ²		NA	6.0	MG
<i>F. natalensis</i>	Fruit	Syncarp	2.0		RT, MG
<i>Funtumia africana</i>	Fruit ⁴	Dry, dehiscent	1.9		RT, MG
<i>Hippocratea sp.</i>	Fruit ⁴	Dry, dehiscent	9.0		MG
<i>Hippocratea sp.</i>	Seed ⁴		NA	NA	MG
<i>Linociera johnsonii</i>	Fruit ²	Drupe	0.01		RT, MG
<i>Linociera johnsonii</i>	Bark ²		1.75	6.9	MG
<i>Millettia dura</i>	Fruit ²	Dry, dehiscent	7.0		MG
<i>Millettia dura</i>	Seed ²		17	17.0	MG
<i>Mimusops bagshawei</i>	Fruit ⁴	Drupe	0.01		RT, MG
<i>Mitragyna sp.</i>	Bark ²		NA	11.1	MG
<i>Neoboutonia africana</i>	Bark ²		NA	2.0	MG
<i>Olea welwitschii</i>	Fruit	Drupe	0.01		RT, MG
<i>Pancovia turbinata</i>	Fruit	NA	0.01		RT, MG
<i>Premna angolensis</i>	Bark ²		NA	6.1	MG
<i>Pseudospondias microcarpa</i>	Fruit ⁴	Drupe	0.27		RT, MG
<i>Rauwolfia oxyphylla</i>	Fruit	NA	0.9		RT, MG
<i>Secamon sp.</i>	Fruit ²	Dry, dehiscent	7.1		MG
<i>Secamon sp.</i>	Seed ²		NA		MG
<i>Strychnos mitis</i>	Fruit	Drupe	2.01		RT
<i>Symphonia globulifera</i>	Bark ²		NA	6.5	MG
<i>Uvariopsis congensis</i>	Fruit	Berry	4.0		RT, MG
<i>Vangueria acutiloba</i>	Fruit	Drupe	2.35		RT, MG
<i>Warburgia ugandensis</i>	Fruit	NA	0.2		RT, MG

¹ RT, redbelt monkey (*C. ascanius*); MG, mangabey (*L. albigena*).

² Consumed by *L. albigena* in 1997.

³ Consumed by *C. ascanius* in 1997.

⁴ Consumed by both species in 1997; all others reported to consume during 1991–1994. Drupe, fleshy fruit containing one or more seeds, each of which is surrounded by a stony layer; Berry, fleshy fruit without stony layers, containing many seeds; Dry, fleshless; Dehiscent, opening to shed seeds; Indehiscent, dry (fleshless) fruits that do not open to release seeds; Syncarp, ¹false fruit composed of two or more united ovaries. Sources: Howard (1991); Friis (1992); Hamilton (1981); Flora of Tropical East Africa (1952–1976); Eggeing and Dale (1951). NA, information not available or not recorded; n = 1 for all plant parts.

Table 1 lists the 1991–1994 and 1997 puncture and crushing scores. There was no difference in the puncture resistance of fruits (n = 31; including both 1991–1994 and 1997 data sets; Fig. 1) consumed by *C. ascanius* and those consumed by *L. albigena* (Mann-Whitney U = 342.5; P = 0.58). The mean (n = 30 spp.) *L. albigena* fruit puncture score was 1.81 kg/mm² (median = 1.05; SD = 2.31), while the mean (n = 25) *C. ascanius* fruit puncture was 1.19 kg/mm² (median = 1.0; SD = 1.18). However, exam-

ining the upper end of the hardness distribution reveals a different picture of puncture resistance; indeed, the mean of the top five hardest foods punctured by *C. ascanius* is 2.9 (median = 3.0; SD = 0.91), and by *L. albigena* 11.72 (median = 9.0; SD = 4.66) (Mann-Whitney U = 0; P = 0.008).

When the scores from the 1997 diet are evaluated (i.e., including fruit, seeds, and bark), *L. albigena* exploited a more puncture-resistant diet (mean = 4.22 kg/mm²; median = 1.82; SD = 5.2; n = 20; Fig.

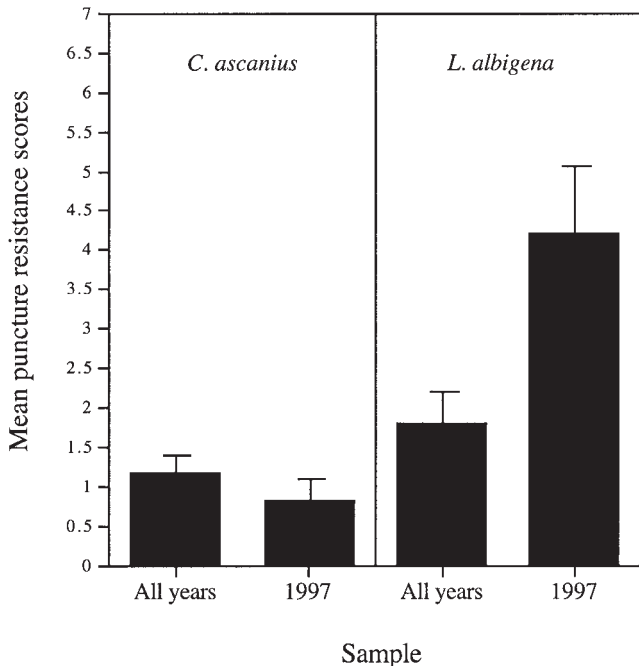


Fig. 1. Mean puncture scores (with error bars) for *C. ascanius* and *L. albigena* during two study samples. All years = 1991–1994, 1997.

1) than *C. ascanius* (mean = 0.84 kg/mm²; median = 0.26, SD = 1.11; n = 12) ($U = 65.0$; $P = 0.03$). This difference is likely due to the higher percentage of bark and seeds consumed by *L. albigena* during 1997. These results may represent an underestimate of the hardness of the total diet for 1997, as the puncture resistance of the bark and/or seeds of nine species were not included in the analysis because of unavailable data. In this analysis, results stem from the puncture resistance of 15 fruit species, three bark species, and two seed species.

With regard to crushing results, Kinzey and Norconk (1990) determined the crushing resistance of the seeds of all fruit species consumed by *Chiroptes* and *Ateles*, despite the fact that *Ateles* monkeys do not crush seeds but instead typically either spit or swallow seeds whole after removing fruit pulp. In contrast, we consider that if an animal masticates only the fleshy portions of fruit and then discards or swallows the seed, it makes more sense biologically to determine the resistance of the food parts that the animals actually crush. *C. ascanius* do not crush as many seed species as *L. albigena*, and they rarely consume bark. In addition, because of the constraints of removing foods from high-canopy trees, we were only able to get a few samples of crushed foods, and there were not enough samples in the *C. ascanius* sample for statistical analysis. Considering only crushed foods, *L. albigena* foods had a mean crushing of 8.3 kg (median = 6.7, SD = 5.89, n = 14, mean of top five hardest foods = 13.21). The crushing score for *C. ascanius* was 2.2 kg (seeds of *Celtis durandii*).

DISCUSSION

Our results are consistent with the hypothesis that thick dental enamel facilitates a diet resistant to fracture. However, these results are best understood in light of broader patterns of diet and feeding strategies, i.e., beyond a simple annual percentage of dietary categories. During some periods, *L. albigena* consumes a high percentage of soft ripe fruit and can exhibit extensive dietary overlap with sympatric, thinner-enamelled cercopithecines. For example, Lambert (2002a) found considerable overlap in the plant species consumed by the Kibale cercopithecine community between 1999–2001. During this time, *L. albigena* consumed a majority of fruit (40%) and had a diet that overlapped extensively with the thinner-enamelled *Cercopithecus mitis* and *C. ascanius*. *Lophocebus albigena* overlapped with the two guenon species in 32 of the 38 plant species they consumed (80%), and shared 2 of 5 top plant species. Reporting on data collected during a 12-month period (1992–1993), Wrangham et al. (1998) indicated that *L. albigena* had a diet comprising 25.1% and 21.4% of ripe and unripe fruit (46.5% total fruit) in one group, and 24.2% and 21.4% in another group (45.6% total fruit). Of 21 ripe fruit species consumed by either *L. albigena* or *C. ascanius* during this period, these two species shared 12 (57.1%).

While there is overlap in these two species' diets, and while *L. albigena* can be highly frugivorous, *L. albigena* also consumes foods not eaten by sympatric guenons: hard seeds and bark. For example, *L. albigena* is noted for its exploitation of the particularly hard *Diospyros abyssinica* seeds (19.25 kg = hardest food in the sample). Unlike other cercopithecines in Kibale that only infrequently consume this fruit (and do not crush seeds), *L. albigena* consumes the seeds and discards the exocarp. Waser (1977) indicated that the sound of *L. albigena* masticating the hard seeds of *D. abyssinica* is species-specific and can be heard from a considerable distance.

Lophocebus albigena also eats bark, which, like *D. abyssinica* seeds, is very hard. Bark consumption has been observed in mangabeys since their earliest descriptions (Waser, 1977). Bark is particularly hard, and may be surprisingly high in nutrients, such as protein and soluble sugars (Rogers et al., 1994). Indeed, Rogers et al. (1994) argued that the bark of *Milicia excelsa* may be an important fallback resource for *G. gorilla gorilla* in the Lope Reserve, Gabon, during seasons of low fruit availability. A similar argument was made for Barbary macaques (*Macaca sylvanus*; Menard and Qarro, 1999). Of note is that in an earlier study, Wrangham et al. (1998) found no evidence that *L. albigena* focused on any particular class of plant type for fallback food. Nonetheless, in this earlier research, *L. albigena* was the only species (of four: *C. mitis*, *C. ascanius*, *L. albigena*, and *Pan troglodytes*) that consumed an appreciable amount of bark (3.2% and 3.9% for the

two study groups). The two other cercopithecines (*C. mitis* and *C. ascanius*) ate no bark, and *Pan troglodytes* had a diet comprising only 0.4% bark.

These results suggest that it is not so much what is consumed most commonly (i.e., soft, fleshy fruit) that selects for enamel thickness, but the hardness of foods that are consumed infrequently, when other, more preferred foods are not available. Of course, *L. albigena* is a larger species with more robust mandibles and a broader gape than *C. ascanius* (and other guenons). Indeed, thick dental enamel should be viewed as only one attribute among a larger suite of traits that facilitates a hard diet and the occupation of a perhaps previously unrealized hard-fall-back-food niche during seasonally stressful periods. However, the data presented here suggest that it is more complicated than lumping *L. albigena* into a broad category of "hard-food consumer," as has been done commonly in the interpretation of enamel thickness. The fact that for the most part *L. albigena* consumes similar food to that fed on by sympatric cercopithecines, but also has a diet comprising a small (but probably very important) percentage of foods such as bark and seeds, suggests that thick enamel in *L. albigena* serves a critical function (sensu Rosenberger, 1992; Kinzey, 1978). That is, thick dental enamel was selected for because of its benefits during periods when preferred foods are unavailable. Such data have implications for understanding diet and dental adaptations in early human ancestors (Teaford and Ungar, 2000), and can be understood in light of recent work of Robinson and Wilson (1998), who pointed out that some resources are intrinsically easy to use and are widely preferred, while others require specialized phenotypic traits (in this case, thick dental enamel) on the part of the consumer. This allows consumers to evolve phenotypic specialization for nonpreferred resources without greatly compromising their ability to use preferred resources.

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