

BRIEF COMMUNICATION

Unexpected hard-object feeding in Western lowland gorillas

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Abstract

Objectives: Gorilla diets are characterized by large amounts of fruit and tough fibrous plant material. Hard-object feeding is not generally associated with this genus as the high crests on their molar teeth would be at risk of damage from the mechanically challenging woody endocarp. This study aims to demonstrate that at least one population of western lowland gorillas are seasonal hard-object feeders, orally processing the seeds of *Coula edulis*.

Materials and methods: Feeding behavior of habituated western lowland gorillas and phenology of fruiting trees was observed over a 4-year period to determine the extent they exploited the seeds of *C. edulis*. Additionally, the endocarps of *C. edulis* were subjected to testing to determine their mechanical properties.

Results: Our results demonstrate that during the fruiting season (January, February, and December) gorillas consistently opened the seeds of *C. edulis* using their postcanine dentition. The protective endocarp is composed of a very stiff material, presenting a substantial mechanical challenge to a gorilla. However, the high ratio between elastic modulus and toughness will facilitate brittle, cataclysmic fracture of the seed shell given a high enough load.

Discussion: Although a rich energy source, *C. edulis* likely tax gorilla dentitions to their upper limit. The rarity of such behavior at sites where it could be observed may indicate a degree of social learning or culture driving its occurrence. This shows a greater breadth of gorilla diets than previously described and suggests gorillas may be a useful model for interpreting the dietary mechanics that necessitated robust craniodental morphology in australopiths.

KEYWORDS

food mechanical properties, gorilla, hard-object feeding

1 | INTRODUCTION

The internal endosperm of angiosperm seeds makes a tempting food, as it is an easily digestible energy source, rich in proteins and lipids (Lucas et al., 2011; Peters, 1987). For this reason, many plants encase such seeds within a thick hard endocarp (seed shell), usually made up

of heavily lignified tissues providing a considerable mechanical challenge to a would-be consumer (Peters, 1987; Figure 1). Such mechanically protected seeds are therefore not a major dietary item for most primates, as access to the internal nutrients requires either specialized craniodental morphology or the cultural traits and cognitive skills for tool use. To orally process such a resource not only requires a primate

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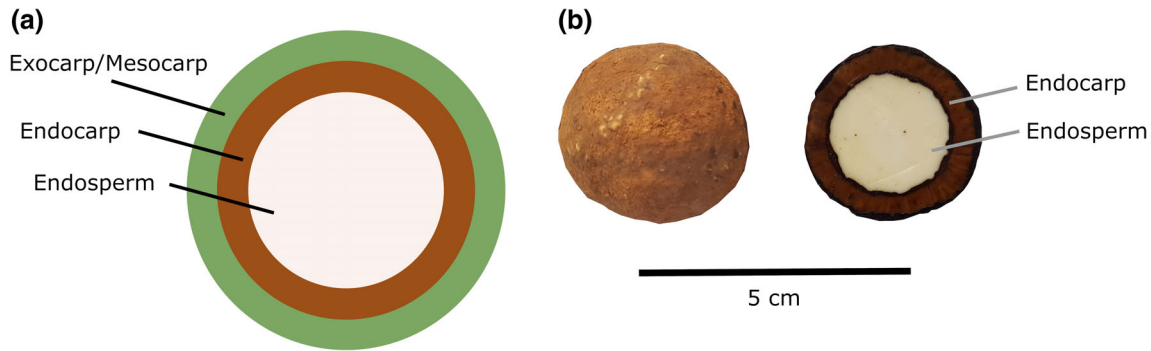


FIGURE 1 (a) A schematic drawing depicting the basic anatomy of a *C. edulis* fruit. (b) A photograph of the woody endocarp and internal endosperm

to produce the necessary and often substantial bite force but additionally requires resilient teeth. The postcanine dentition involved in the processing of hard objects are commonly characterized by low rounded cusps, with thickened enamel containing microstructural adaptations to limit enamel fracture; thus enabling efficient crack production and long-term tooth survival (Lucas, 2004; Ziscovici, Lucas, Constantino, Bromage, & van Casteren, 2014). However, some primate molars can be spared from the functional demands of hard-object feeding via behavioral mechanisms, such as the use of tool technology. Primates such as bearded capuchin monkeys (*Sapajus libidinosus*), long tailed macaques (*Macaca fascicularis*), and chimpanzees (*Pan troglodytes*), rely on the mechanical advantage afforded to them through the use of hammer stones and anvils to extract nutritious endosperms from woody endocarps. This ingenuity permits access to highly nutritious food sources without the prerequisite morphological adaptations (Boesch & Boesch-Achermann, 2000; Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004; Proffitt et al., 2018).

Gorillas are considered to be folivorous/frugivorous, consuming more herbaceous vegetation and less fruit than other members of the great ape family. Mountain gorillas (*Gorilla gorilla beringei*) consume relatively little fruit (Wright et al., 2015), whereas the diet of western lowland gorillas (*Gorilla gorilla gorilla*) is approximately 30% fruit and they incorporate a large amount of tree leaves into their diet when fruit is less abundant (Doran-Sheehy, Mongo, Lodwick, & Conklin-Brittain, 2009; Masi, Cipolletta, & Robbins, 2009). It is thought that gorillas are able to consume fibrous and mechanically challenging foods due to their large size and the morphological robusticity of their masticatory apparatus (Eng, Lieberman, Zink, & Peters, 2013; Taylor, 2002). In both species of gorilla, their teeth have large tooth crowns and roots, absolutely thick enamel and increased shearing crests compared to other great apes (Eng et al., 2013; Kupczik & Dean, 2008; Skinner, Alemseged, Gaunitz, & Hublin, 2015; Uchida, 1996). These dental and gnathic traits have been assumed to facilitate the processing of large amounts of tough fracture resistant foods. Although seed predation by western gorillas was reported anecdotally in one group of semi-habituated gorillas in the Lopé Forest (Tutin, Ham, White, & Harrison, 1997; Williamson, Tutin, Rogers, & Fernandez, 1990), it has not been recorded elsewhere (Rogers et al., 2004) and hard food items are still considered an insignificant part of their diet (Constantino, Markham, & Lucas, 2012; Rogers et al., 2004; Scott, Teaford, & Ungar, 2012; Tutin et al., 1997).

Here we report the first instance of consistent, seasonal, large hard-object feeding in habituated western lowland gorillas in Loango National Park, Gabon. We combine videos of the oral processing and mechanical testing of the endocarps of *Coula edulis* to show how gorillas orally process such foods and indicate the stresses this may impact on their masticatory apparatus.

2 | METHODS

One group of habituated western gorillas in Loango National Park, Gabon was observed for 6,303 hr on 1,043 days between January 2015 and June 2018. The group consisted of 14–16 individuals (1 silverback male, 4–6 adult females, 7 juveniles/subadults, and 2–4 infants). We conducted instantaneous scan samples every 10 min, recording the activity (feed, rest, or travel) of all individuals in view, including what plant species and part was consumed. Phenology data were collected once per month for the presence and ripeness of fruit of an average of 263 trees along 35 km within the study area (Head, Boesch, Makaga, & Robbins, 2011). Videos were collected opportunistically during daily follows of the gorilla group.

Mechanical testing of *C. edulis* endocarp (Figure 1) was performed using a portable universal testing machine (Lucas Scientific FLS-1). As a measure of the woody endocarps resistance to fracture, we measured the critical stress intensity factor (K_{IC}) of the material. This in itself is really two properties combined $K_{IC} = (ER)^{0.5}$. The fracture toughness (R , $J\ m^{-2}$), which is a materials resistance to crack propagations and the elastic (Young's) modulus (E , GPa) which is a materials resistance to elastic deformation or, effectively it's stiffness. Both K_{IC} and E were measured by compressing a C-ring of endocarp material at an increasing force (F) to failure. C-rings of endocarp material were cut using a circular saw at circa 4 mm in thickness (b). C-rings were then either kept intact or intentionally notched at a given length (a). Using isotropic beam theory, it is possible to estimate E using Equation (1) (Wang & Mai, 1994).

$$E = \frac{3\pi(2r_o - t)^2 \left(\frac{dF}{dy}\right)}{4bt^2} \quad (1)$$

Where r_o is the outer radius, t is the width of the C-ring, and dF/dy is the linear region of the force displacement curve. The fracture

strength (σ_f) can be calculated using Equation (2) and K_{IC} can be calculated from Equation 3 (Wang & Mai, 1994). The K_{IC} of the endocarp was measured in two directions, cracks were either propagated from the external surface inwards or from the internal outwards. This represents the two main directions that fracture will likely occur when the endocarp is being cracked orally by gorillas. Either a crack is initiated and propagated by a gorilla tooth cusp, therefore running from the external surface inwards. Alternatively, as a gorilla increases the bite force on the woody endocarp, this material may flex and bend. Such movements will cause tensile stresses to rise on the concave side of the curved endocarp. In this scenario, cracks are likely to propagate from the internal to the external surface.

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

$$K_{IC} = \left(1.1215 - 1.365 \frac{a}{t} \right) \sigma_f \sqrt{\pi a} \quad (3)$$

Hardness (H) of endocarp was measured using the sharp indent test. Samples were cut to a flat surface and a tungsten carbide Vickers pyramid was driven into the sample for circa 1 mm and the resultant force displacement data allowed the calculation of H from Equation (4) (McGraw et al., 2015). F_{max} is the force required to make a permanent plastic deformation in the material and A_p is the area of contact that can be estimated from the indenter geometry.

$$H = F_{max} / A_p \quad (4)$$

3 | RESULTS

The gorillas were observed eating *C. edulis* seeds on 77 of the 237 days of observation (37%) during the months that *C. edulis* was available (January, February, and December; Figure 2). We observed 10 individuals of both sexes (age range 5 to ~28 years) feeding on

C. edulis seeds. The mean feeding bout duration (calculated as time spent feeding on *C. edulis* during consecutive instantaneous scans) was 17 min for the silverback male and 10 min for the adult females (Table 1), with a maximum feeding time of 180 and 70 min in any given day for the silverback male and adult females, respectively. Seed cracking generally followed a similar pattern. External exocarp/mesocarp flesh was removed by the anterior teeth and discarded. The endocarp was then cracked by the postcanine teeth. Once opened, the endosperm seems to be separated from the endocarp and this woody tissue is then generally expelled from the oral cavity whilst the endosperm is consumed (Figure 3a and Video S1).

Fracture toughness (K_{IC}) differed significantly (Mann-Whitney U test, $W = 187$, $p < 0.001$) depending on the direction a crack is traveling. Cracks running from the interior to the exterior of the endocarp measured 1.03 (SD 0.29) MPa m^{0.5} ($n = 14$) compared to 0.62 (SD 0.19; $n = 15$) MPa m^{0.5} in the opposite direction (Figure 3b). The endocarp material is stiff demonstrating a mean elastic modulus of

TABLE 1 *C. edulis* seed feeding behavior, displayed for the silverback male (SB) and adult females (AF)

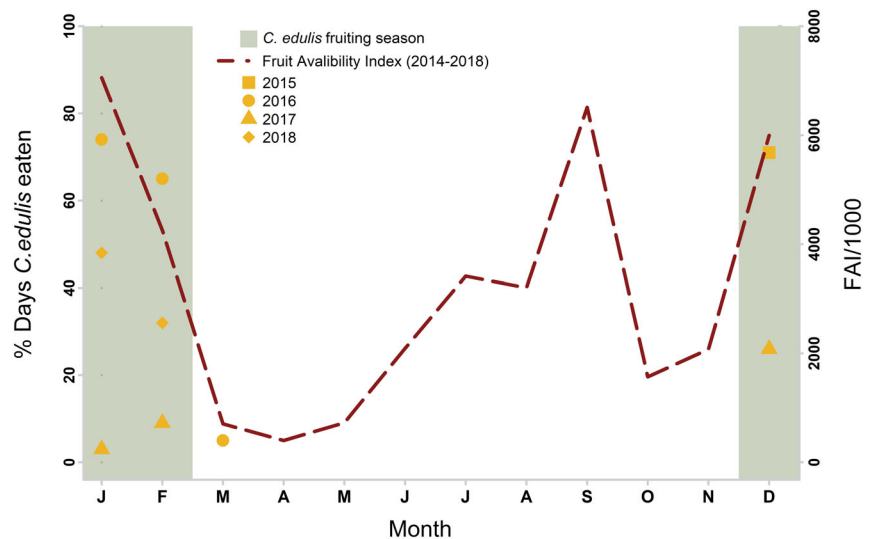
	SB ($n = 1$)	AF ($n = 6$)
Number of recorded <i>C. edulis</i> feeding bouts ^a	40	49
Mean (range) of <i>C. edulis</i> feeding bout duration (min) ^a	17 (10–80)	10 (10–30)
Mean (range) of <i>C. edulis</i> feeding duration (min/day) ^a	28 (10–180)	10 (10–70)
Duration to consume one <i>C. edulis</i> seed (s) ^b	69.5	84.8
Feeding rate (seeds/hr) ^b	52	42
Energy intake (kJ/hr) ^c	3,318	2,680

^aCalculated using instantaneous scan samples. A feeding bout is defined as uninterrupted *C. edulis* feeding (consecutive 10 min scans).

^bCalculated using video data.

^cEnergy intake is the product of the energy content per seed (63.8 kJ; Kalan, Mundry, & Boesch, 2015) and the seed feeding rate.

FIGURE 2 The percentage of observation days in each month for a given year where *C. edulis* was eaten. *C. edulis* was consumed when available in the gorilla habitat (shaded rectangles), even when other fruit is readily available. The fruit availability index was a compilation of phenology (% fruit trees with ripe fruit), density of fruit trees in study area, and size (DBH) of fruit trees (Head et al., 2011)



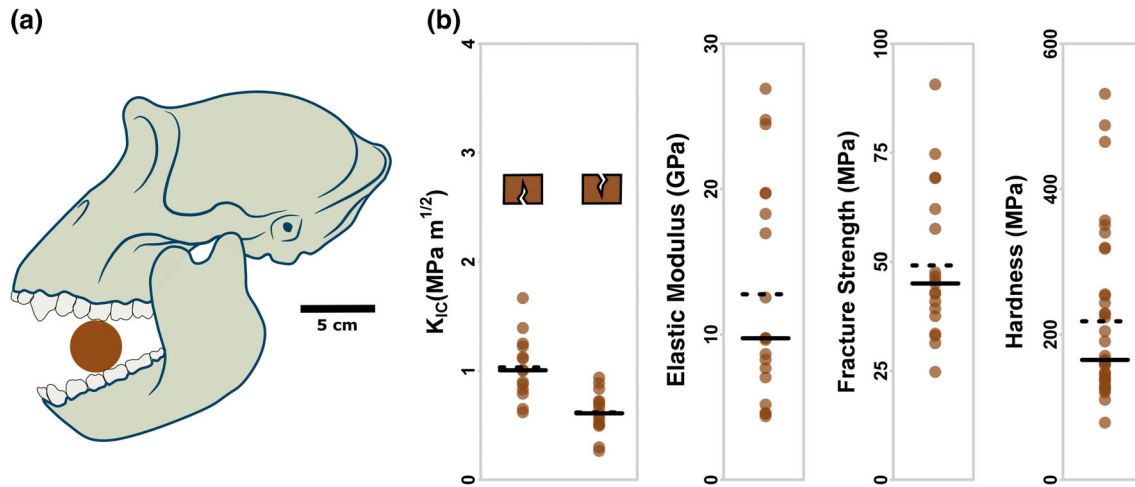


FIGURE 3 (a) Illustrating the method of seed breaking by gorillas, in all cases whole seeds were cracked on the postcanine teeth. (b) The results of the mechanical testing of the endocarp of *C. edulis*, solid bars represent medians and dashed bars represent means

Species	Diameter (mm)	K_{IC} (MPa m ^{1/2})	E (GPa)	σ_f (MPa)	H (MPa)
<i>Mezzettia parvifolia</i> ^a	25	3.4	9.4	67.0	210
<i>Schinziophyton rautanenii</i> ^b	26	2.1	5.2	45.7	–
<i>Macadamia ternifolia</i> ^c	24	0.78	6.2	57.8	190

TABLE 2 Comparable mechanical properties from other hard objects found in primate diets

^aData taken from Lucas, Peters, and Arrandale (1994) and Lucas et al. (2011).

^bData taken from Williamson and Lucas (1995).

^cData taken from Jennings and Macmillan (1986) and Wang and Mai (1994).

12.8 (SD 7.5) GPa ($n = 20$) and exhibited a mean fracture strength of 49.1 (SD 17.1; $n = 20$) MPa and hardness of 218.2 (SD 113; $n = 35$) MPa.

4 | DISCUSSION

We present the first evidence of routine, seasonally driven, large hard-object feeding in western gorillas. This is surprising as seed predation by gorillas has only rarely been observed at one study site, contributing negligible amounts to the gorilla diet (Rogers et al., 2004; Tutin et al., 1997). However, we show that at Loango, gorillas consistently consume *C. edulis* when it is available during an annual fruiting season (Figure 2). The endosperm of *C. edulis* is a rich source of energy as one seed contains 63.8 kJ (Kalan et al., 2015). Therefore, 3,318 kJ of energy, or around 16% of an adult male's daily budget, would be consumed during a 1 hr feeding bout (Table 1; Masi et al., 2015). These observations of routine consumption of seeds by western gorillas expand our knowledge of their dietary breadth beyond their primary folivory/frugivory patterns and begin to question traditional interpretations of gorilla craniofacial morphology.

Does oral seed breaking tax the dental apparatus of lowland gorillas? Despite being often referred to as the “softest” seed in the chimpanzee nut cracking literature (Boesch & Boesch-Achermann, 2000), *C. edulis* does present a considerable mechanical challenge. The seeds are large (circa 3–4 cm in diameter; Peters, 1987) with an

endocarp material comparable mechanically to other hard objects found in primate diets (Table 2) such as *Mezzettia parvifolia* seeds consumed by orangutans (Lucas et al., 1994; Lucas, Lowery, Pereiras, Sarafis, & Kuhn, 1991) or *Macadamia ternifolia* and *Schinziophyton rautanenii* seeds consumed by humans but requiring tool assisted opening (Wang & Mai, 1994; Williamson & Lucas, 1995). One noticeable difference between *C. edulis* and other seeds protected by a woody endocarp is the rather high ratio (14:1) between elastic modulus and toughness (Table 2); such a condition will facilitate brittle fracture. Therefore, the endocarp of *C. edulis* appears somewhat conducive to cracking actions, oral or otherwise when loaded with high force. Previous research supports this; compression tests recorded a mean peak force of 2,717.4 N (range 1,882.8–3,167.5) to break *C. edulis* seeds, which often failed cataclysmically (Peters, 1987). Such a number is remarkably close to the predicted limits of gorilla bite force and exceeds those of *Pan* and *Pongo* (Table 3). It therefore seems implicit that the consumption of *C. edulis* by gorillas at Loango is regularly taxing their masticatory apparatus to its upper limits. There does appear to be a sex difference in *C. edulis* feeding. The silverback male tends to spend more time feeding on *C. edulis* and was generally quicker in processing the fruits than the females of the group (Table 1). While the reasoning behind this is not clear it seems likely that the larger size, increased muscle mass and higher bite forces of male gorillas (Eng et al., 2013) may allow quicker and easier oral processing of *C. edulis* endocarp. Western gorilla males have been

TABLE 3 The predicted maximal bite forces (N) for the great apes estimated from chipping analysis of teeth (Constantino et al., 2010) or masticatory morphology (Eng et al., 2013)

Species	Chipping analysis	Morphological estimates
<i>Pan troglodytes</i>	1,766	1,780
<i>Pan paniscus</i>	-	1,245
<i>Pongo sp.</i>	2,460	2,560
<i>Gorilla sp.</i>	2,865	3,420

documented to have higher food intake than adult females (Masi et al., 2015).

We have observed oral-cracking behaviors in gorillas as young as 5 years and as old as approximately 28 years. Smaller jaw abductor muscles and gape in young gorillas would make it unlikely that such immature individuals are routinely successful at orally processing the endocarp of *C. edulis*. At such a young age, success is likely limited to the endocarps that possess mechanical properties on the lower end of the natural variation (Figure 3b, Peters, 1987). However, it would appear that experimentation and some success is seen early in gorilla development (video S2), although the ontogenetic incorporation of hard objects into the gorilla diet warrants further investigation. Such a longitudinal time period of oral endocarp processing is indicative that the gorilla masticatory system is quite capable of supporting prolonged seasonal hard-object feeding.

The craniodental morphology of gorillas is thought to represent a functional adaptation to the consumption of tough fibrous foods (Taylor, 2002; Taylor, Vogel, & Dominy, 2008). Here we show that such morphological adaptations afford gorillas a degree of dietary plasticity, indicating that some craniodental characteristics associated with repetitive mastication may also equip gorillas to seasonally consume large hard objects, negating the need to resort to tool use strategies employed by some seed-consuming chimpanzees (Boesch & Boesch-Achermann, 2000). *C. edulis* is found throughout the range of western and central chimpanzees as well as western gorillas. Tool use by chimpanzees to crack the seed casings is not a ubiquitous behavior across all populations, being observed only in a few locations in West Africa (Whiten et al., 1999). Similarly, the lack of oral nut cracking by other populations of western gorillas suggests the possibility that social learning and culture may be responsible for such consumption at Loango. Behavioral variants that may be cultural traits have already been documented in other aspects of gorillas' diet (Robbins et al., 2016).

The discovery of seasonal hard-object feeding in gorillas, who traditionally represent craniodental adaptations to the processing of large volumes of foliage, will have an influence on the interpretation of the dietary ecology of human ancestors. There is a temporal trend toward increased robusticity of the masticatory apparatus in early hominins (eventually reversed in *Homo*) that presumably accommodates a diet of more mechanically challenging foods (Sponheimer et al., 2013). Yet there is much disagreement about which foods may have been the main evolutionary driver of such adaptations (Strait et al., 2013; Ungar & Sponheimer, 2011). The debate focuses on

whether these derived features are to produce high bite forces (Smith et al., 2015) or for the production of sustained repetitive masticatory loads (Ungar & Sponheimer, 2011). In the light of our findings in gorillas, we suggest that the framework of this debate may need to be re-assessed. We show that the diet of gorillas encompasses a broad dietary spectrum and they can produce and maintain the high bite forces required for seasonal hard-object feeding, despite their derived morphology and reputation as quintessential repetitive feeders. This considerably confounds conventional interpretations of form-function relationships pertaining to feeding behaviors in primates and may call for a readdressing of the interpretation of some fossil hominin remains.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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