

1 Grass leaves as potential hominin dietary resources

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3 Oliver C. C. Paine^{a,*}, Abigale Koppa^b, Amanda G. Henry^c, Jennifer N. Leichliter^a,
4 Daryl Codron^{d,e}, Jacqueline Codron^f, Joanna E. Lambert^{a,g}, Matt Sponheimer^a

5
6 a Department of Anthropology, University of Colorado Boulder, Boulder, CO 80309 USA

7 b Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794,
8 U.S.A.

9 c Faculty of Archaeology, Leiden University, Einsteinweg 2, 2333CC Leiden, The Netherlands.

10 d Florisbad Quaternary Research Department, National Museum, PO Box 266, Bloemfontein, 9300,
11 South Africa

12 e Centre for Environmental Management, University of the Free State, PO Box 339, Bloemfontein, 9300,
13 South Africa

14 f Institut für Geowissenschaften, AG für Angewandte und Analytische Paläontologie, Johannes
15 Gutenberg–Universität Mainz, 55128 Mainz, Germany

16 g Department of Environmental Studies, University of Colorado Boulder, Boulder, CO 80309 USA

17
18 * Corresponding Author: oliverpaine@colorado.edu (Oliver Paine)

19 20 Abstract

21 Discussions about early hominin diets have generally excluded grass leaves as a staple
22 food resource, despite their ubiquity in most early hominin habitats. In particular, stable
23 carbon isotope studies have shown a prevalent C₄ component in the diets of most taxa,
24 and grass leaves are the single most abundant C₄ resource in African savannas. Grass
25 leaves are typically portrayed as having little nutritional value (e.g., low in protein and
26 high in fiber) for hominins lacking specialized digestive systems. It has also been
27 argued that they present mechanical challenges (i.e., high toughness) for hominins with
28 bunodont dentition. Here, we compare the nutritional and mechanical properties of
29 grass leaves with the plants growing alongside them in African savanna habitats. We
30 also compare grass leaves to the leaves consumed by other hominoids and demonstrate
31 that many, though by no means all, compare favorably with the nutritional and
32 mechanical properties of known primate foods. Our data reveal that grass leaves exhibit
33 tremendous variation and suggest that future reconstructions of hominin dietary
34 ecology take a more nuanced approach when considering grass leaves as a potential
35 hominin dietary resource.

36
37 Keywords: grass; dietary fiber; protein; toughness; hominin diet

38 39 Introduction

40 Diet has long been considered a prime mover in hominin evolution, but links
41 between diet and early hominin differentiation have become more debatable as new

42 methods and data have become available. A growing body of evidence is challenging
43 many traditional interpretations of hominin dietary behavior (for discussion, see Ungar
44 and Sponheimer, 2011). For instance, *Paranthropus boisei* exhibits some of the starkest
45 morphological adaptations to diet of any known hominin species (Rak, 1983, 1988),
46 and some have argued that its hyper-robust craniodental architecture was necessary for
47 the habitual consumption of hard, obdurate foods such as nuts and seeds (Leakey, 1959;
48 Tobias, 1967; Jolly, 1970; Rak, 1983; Demes and Creel, 1988; Strait et al., 2008, 2013;
49 Constantino et al., 2010, 2011; Smith et al., 2015), yet dental microwear evidence
50 reveals no hard-object consumption by *P. boisei* (Ungar et al., 2008, 2012; Grine et al.,
51 2012). Moreover, some argue that craniodental robusticity can result from the
52 mechanical challenge posed by diets of tough, low quality foods requiring prolonged
53 and repetitive loading of the chewing apparatus (Ungar and Hlusko, 2016; Daegling
54 and Grine, 2017; see also Hylander, 1988, for earlier arguments about craniodental
55 robusticity as an evolutionary response to repetitive loading).

56 Additionally, stable carbon isotope studies show that C₄ foods (i.e., foods
57 enriched in ¹³C) became increasingly significant portions of hominin diets beginning at
58 least 3.7 Ma—culminating with *P. boisei*, whose diet was 75–80% C₄ (van der Merwe
59 et al., 2008; Cerling et al., 2011; Ungar and Sponheimer, 2011; Lee-Thorp et al., 2012;
60 Sponheimer et al., 2013; Levin et al., 2015). Moreover, the degree of postcanine
61 megadontia and mandibular robusticity exhibited by early hominin species is positively
62 correlated with the amount of C₄ foods they consumed, suggesting that the inherent
63 properties of these foods may have contributed to australopith craniodental adaptations
64 (Sponheimer et al., 2013).

65 Hominins may have consumed foods enriched in ¹³C either as primary
66 consumers of plants using the C₄/CAM photosynthetic pathway and/or as secondary
67 consumers eating animals that consume significant quantities of C₄ vegetation (e.g.,
68 grazing ungulates such as wildebeest and zebra). However, while faunal resources were
69 a likely source of dietary carbon, few would argue that meat consumption was a major
70 component of early hominin diet, despite recent discoveries revealing hominin tool use
71 before 3 Ma (McPherron et al., 2010; Harmand et al., 2015). Similarly, plants using
72 CAM photosynthesis (e.g., succulents) were potentially consumed, but are relatively
73 scarce within most savanna habitats. Thus, despite contributions from faunal and CAM
74 resources, it is most likely that C₄ plants were the primary source of dietary carbon for
75 early hominins with high C₄ isotopic signatures such as *P. boisei*, *Paranthropus*
76 *aethiopicus*, and *Australopithecus bahrelghazali*.

77 Of the roughly 7500 species of plants that use the C₄ photosynthetic pathway,
78 most (~80%) are monocots in the families Poaceae and Cyperaceae—tropical grasses
79 (~4500 species) and sedges (~1500 species), respectively (Sage et al., 1999; Sage,
80 2004). Thus, the bulk of C₄ plant biomass available to African herbivores is located in

81 savanna and/or wetland habitats. While definitions of ‘savanna’ can be debated, it is
82 generally agreed upon that a mostly continuous layer of grasses is a key, if not
83 definitive component of savanna habitats (for discussion, see Scholes and Archer,
84 1997).

85 We are now faced with the task of determining which C₄ plants contributed to
86 hominin diets (grasses and/or sedges) and how they were utilized. Specifically, were
87 certain plant parts such as seeds and storage organs targeted for consumption? These
88 questions become particularly important for species with highly derived craniodental
89 morphology, such as *P. boisei* (Wood and Constantino, 2007; Ungar and Sponheimer,
90 2011; Daegling and Grine, 2017).

91 Grass and sedge species possess several anatomical structures that may serve as
92 food for a consumer, including underground storage organs (USOs such as tubers,
93 rhizomes, and corms), seeds, and leaves (which include the blade, collar, and sheath).
94 Scholars have more readily accepted some of these anatomical elements of grasses and
95 sedges as hominin foods. For example, some (e.g., van der Merwe et al., 2008;
96 Dominy et al., 2012) have argued that C₄ sedges were a likely resource because they
97 often have relatively large USOs that are unavailable to most African herbivores. This
98 underutilized resource would be available to hominins with rudimentary tools, such as
99 digging sticks, and thus would have represented a novel feeding niche ripe for hominin
100 exploitation (Hatley and Kappelman, 1980; Hernandez-Aguilar et al., 2007). Also,
101 sedge (and other) USOs are available year-round and are often portrayed as being both
102 nutrient-dense and mechanically suitable for hominin dental adaptations (Hatley and
103 Kappelman, 1980; Laden and Wrangham, 2005; Dominy et al., 2008; Wrangham et al.,
104 2009; Dominy, 2012; Lee-Thorp et al., 2012).

105 Similarly, the seeds of C₄ grasses have been proposed as a hominin food by
106 some researchers (Jolly, 1970; Peters and Vogel, 2005). Like sedge USOs, they are
107 perceived as nutritionally adequate and possessing physical properties (small and
108 somewhat hard) well suited for hominin consumption. It is also worth noting that
109 modern humans consume vast quantities of grass seed today (e.g., maize, rice, wheat)
110 and have done so for millennia (van Oudtshoorn, 2012).

111 In contrast, grass leaves are not considered a viable hominin food by most
112 because they are generally regarded as offering little nutritional value (low in protein
113 and high in fiber) and having mechanical properties (particularly, measures of
114 toughness) that are ill-suited for hominins lacking the occlusal relief and/or hypsodonty
115 seen in leaf-eating primates or grazing herbivores (Yeakel et al., 2007; Lee-Thorp et
116 al., 2012; Fontes-Villalba et al., 2013; Macho, 2014; Yeakel et al., 2014). However, it is
117 noteworthy that grammivory is observed in other omnivorous taxa exhibiting bunodonty
118 such as black bears (*Ursus arctos*), which are known to eat 31 species of graminoids in
119 Yellowstone National Park (Raia, 2004; Gunther et al., 2014).

120 Moreover, because C₄ grasses are generally dominant components of savanna
121 landscapes, their leaves often represent the most abundant and accessible biomass for
122 herbivores (Jacobs et al., 1999). Unsurprisingly, grasses represent a major source of
123 nutrition for *Papio* living in these environments (DeVore and Washburn, 1963;
124 Altmann and Altmann, 1970; Post, 1982; Altmann et al., 1987; Norton et al., 1987;
125 Barton et al., 1993; Barton and Whiten, 1994; Altmann, 1998). From this standpoint, it
126 is possible that grass leaf has been prematurely excluded from reconstructions of
127 hominin diet by some and that when it is considered it is often treated as a monolithic
128 entity in a manner that fails to account for taxonomic, seasonal, and habitat effects
129 which may potentially affect its nutritional and mechanical palatability (e.g., Peters and
130 Vogel, 2005; Lee-Thorp et al., 2012; Yeakel et al., 2014; Macho, 2015).

131 While no one disputes that many ungulates have dental and digestive
132 adaptations specifically enabling them to subsist on a grass-based diet (Stirton, 1947;
133 White, 1959; Langer, 1974; Janis, 1976; Janis and Fortelius, 1988; Robbins, 2012),
134 Poaceae are incredibly diverse with species ranging from tree-like bamboo with woody
135 growth to softer, strictly herbaceous and ‘carpet-like’ grasses. This suggests that we
136 should adopt a more nuanced understanding of the diversity of consumption patterns
137 and dietary niches adopted by primary consumers of grasses and that we reassess many
138 assumptions about the potential role of grasses in early hominin dietary ecology.

139 Here, we investigate the nutritional and mechanical properties of African C₄
140 grass leaves. We wish to make it clear that we are not attempting to describe what
141 hominins did, or did not eat, we are simply interested in testing the hypothesis that
142 grass leaves could have been a significant source of nutrition for early hominins.
143 Moreover, we are not investigating hypotheses concerning the potential evolutionary
144 link between australopith craniodental morphology and the consumption of grass
145 leaves. Clearly, these are important avenues of research but they will ultimately be of
146 limited value if there is a lack of nutritional and mechanical data to support or reject
147 any given hypothesis. It is the goal of this paper to begin to provide these data and to
148 help inform future debates.

149

150 **Methods**

151 We collected plant samples from the Cradle Nature Reserve, South Africa (July,
152 2014, and January, 2015) and Amboseli National Park, Kenya (May, 2016), from
153 transects located in distinct microhabitats (e.g., grassland, woodland, and wetland).
154 Microhabitats were defined according to Reed et al. (2013: Table 1.1). We sampled the
155 most abundant grass, sedge, tree, and forb species as determined according to methods
156 outlined in Stohlgren et al. (1995) (‘forbs’ in our study represent plants that are neither
157 grasses, sedges, nor trees). All grass species we sampled are C₄ and sedges are mixed
158 C₃/C₄ species. Samples were separated into their constituent organs for analyses (e.g.,

159 seed, leaf, and stem).

160 We grouped these samples into broad categories of potential hominin plant
161 foods based on organs/structures known to be eaten by primates: grass leaf, sedge leaf,
162 tree leaf, forb leaf, fruit, inflorescence (from grasses and sedges), and USOs (e.g.,
163 rhizomes, bulbs, and corms from grasses, sedges, and forbs). Here, we present mature
164 leaf and inflorescence samples collected only during the wet season to capture
165 nutritional values that best represent the bulk of their growth phase. Newly grown
166 leaves (particularly among grasses) are known to be higher in protein and lower in fiber
167 than mature leaves. Thus, we do not include data for any new growth samples we
168 collected to ensure that our results reflect the properties of leaves during the majority of
169 their life cycles and when they are most abundant. Fruit and USO samples are from
170 both wet and dry seasons as their collection is subject to availability.

171 Toughness was measured in the field on fresh samples using the scissors test on
172 a Lucas Scientific FLS-I portable mechanical tester. Toughness (R) is a measure (J/m^2)
173 of the force necessary to propagate a crack through a material (for discussion, see Lucas
174 et al., 2012). When applicable, we performed scissors tests perpendicular to veins
175 and/or midribs within plant tissues in order to capture maximum toughness values. For
176 the same reason, we did not remove exocarps, sheaths, and/or rinds of organs such as
177 fruits and USOs prior to testing. We replicated the scissors test three times per
178 specimen and used the median value for statistical analyses. We could not test some
179 fruit samples due to their small size and heterogeneous structural properties. We dried
180 wet samples in the field in Excalibur® dehydrators at 40° C, sealed dried samples in
181 paper bags with desiccant, and exported them to the Nutritional and Isotopic Ecology
182 Lab (NIEL) at the University of Colorado Boulder for nutritional analyses.

183 We present results for crude protein (CP) and acid detergent fiber (ADF) as a
184 percentage of dry weight. We chose these measures because they are a widely used
185 proxy for overall forage quality (Robbins, 1983; McNaughton and Georgiadis, 1986;
186 but see discussion for the important factors such as micronutrients and water content).
187 Crude protein was measured with a LECO® FP 528 nitrogen analyzer using the
188 standard %N x 6.25 conversion to obtain %CP. ADF was measured with an ANKOM®
189 2000 fiber analyzer.

190 We performed nonparametric comparisons using the Wilcoxon/Kruskal-Wallis
191 test in JMP® Pro 13.0.0 as few of our datasets are normally distributed. Multiple
192 comparisons were performed using the Steel-Dwass all pairs test. See Supplementary
193 Online Material (SOM) 1 for summary statistics of all samples and measures recorded.

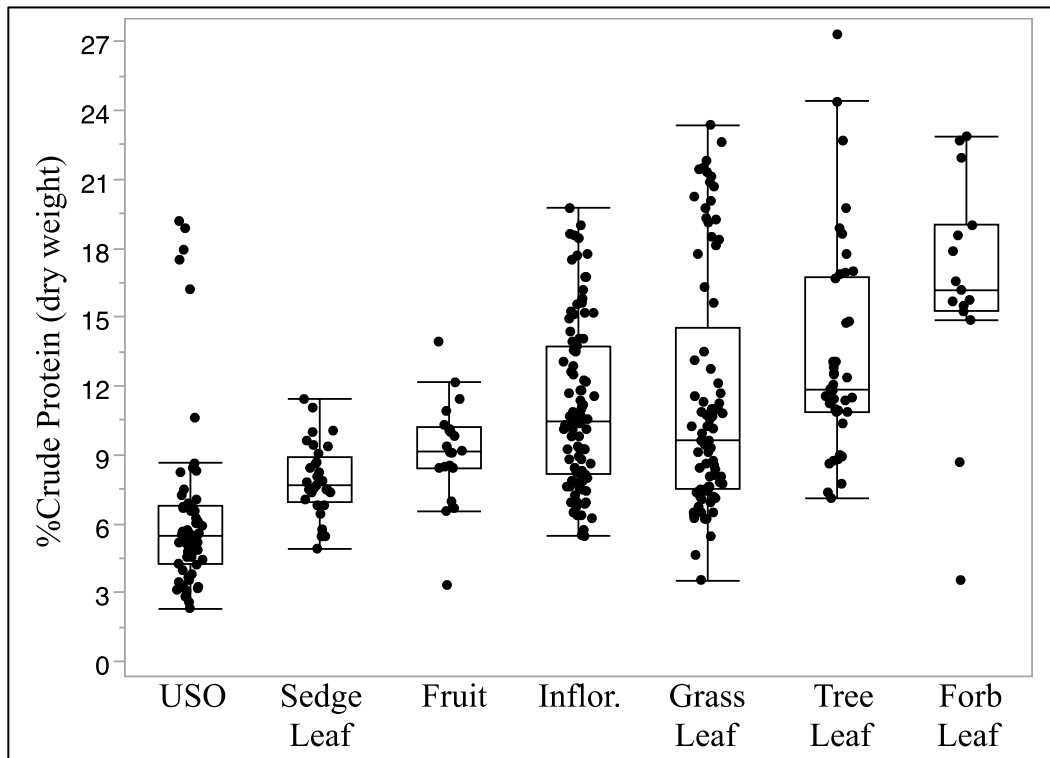
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195 **Results**

196 *Nutritional data*

197 Plant foods differed significantly in protein content ($p < 0.0001$). Grass leaves

198 have lower protein levels than forb ($p = 0.0438$) and tree leaves ($p = 0.0397$), but higher
 199 levels than sedge leaves ($p = 0.0083$) and USOs ($p < 0.0001$) (Figure 1). Four of the
 200 five extreme outliers in the USO category are the stolons of *Cynodon plectostachyus*;
 201 the fifth is from the rhizome of *Typha capensis*. Grass leaves, fruits, and inflorescences
 202 do not differ significantly in protein content. Grass leaves exhibit a wide range of
 203 values: ranging from protein deficient ($< 5\%$) to relatively protein-rich ($>15\%$), with
 204 some samples having higher values than the leaves of trees growing alongside them ($>$
 205 20%). Indeed, protein values for grass leaves span almost the entire range of all other
 206 values combined, although the distribution is bimodal with each mode normally
 207 distributed (Shapiro-Wilk test: lower mode, $p = 0.5682$; higher mode, $p = 0.7985$). The
 208 four species representing the higher cluster have mean CP as follows: *Panicum* sp.
 209 (17.4%), *Sporobolus ioclados* (19.5%), *C. plectostachyus* (20.9%), and *Setaria*
 210 *verticillata* (21.0%).

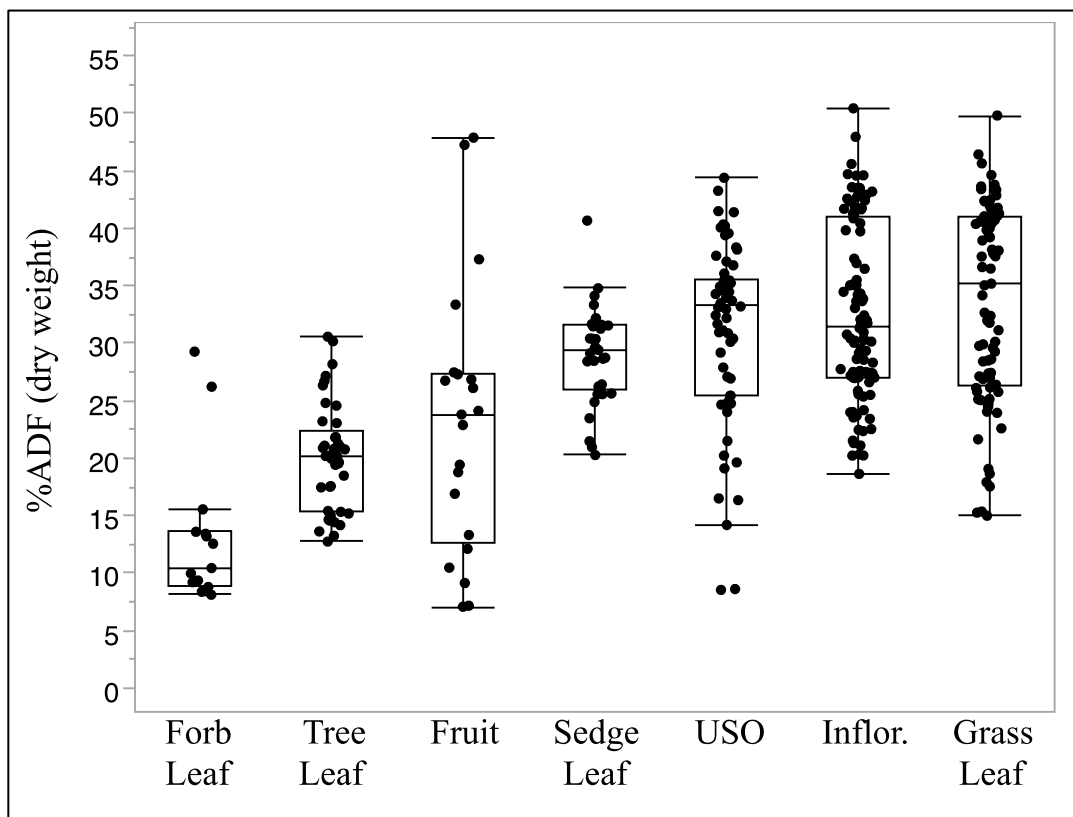


211
 212 Figure 1. Crude protein content (%) of plant parts within savanna habitats known to be
 213 consumed by primates. (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). Categories are
 214 arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles,
 215 the lines within them are the medians, the whiskers show data within 1.5 times the
 216 interquartile ranges, and the dots outside of the whiskers are outliers. “Inflor.” is the
 217 abbreviation of inflorescence.

218
 219

Grass leaves have the highest median value for ADF content (35.9%) compared

220 to all other categories, and that they are significantly higher than forb and tree leaves (p
 221 < 0.0001) and fruit ($p < 0.0001$; Figure 2). However, once again, grass leaves exhibit a
 222 high degree of variation. The distribution of grass leaf ADF values is bimodal, though it
 223 is less pronounced than observed in our protein values. The four grass leaf species with
 224 the highest crude protein among grass leaves analyzed also have the lowest levels of
 225 ADF with their mean values as follows: *C. plectostachyus* (16.1%), *Se. verticillata*
 226 (22.4%), *Sp. ioclados* (24.4%), and *Panicum* sp. (25.5%).



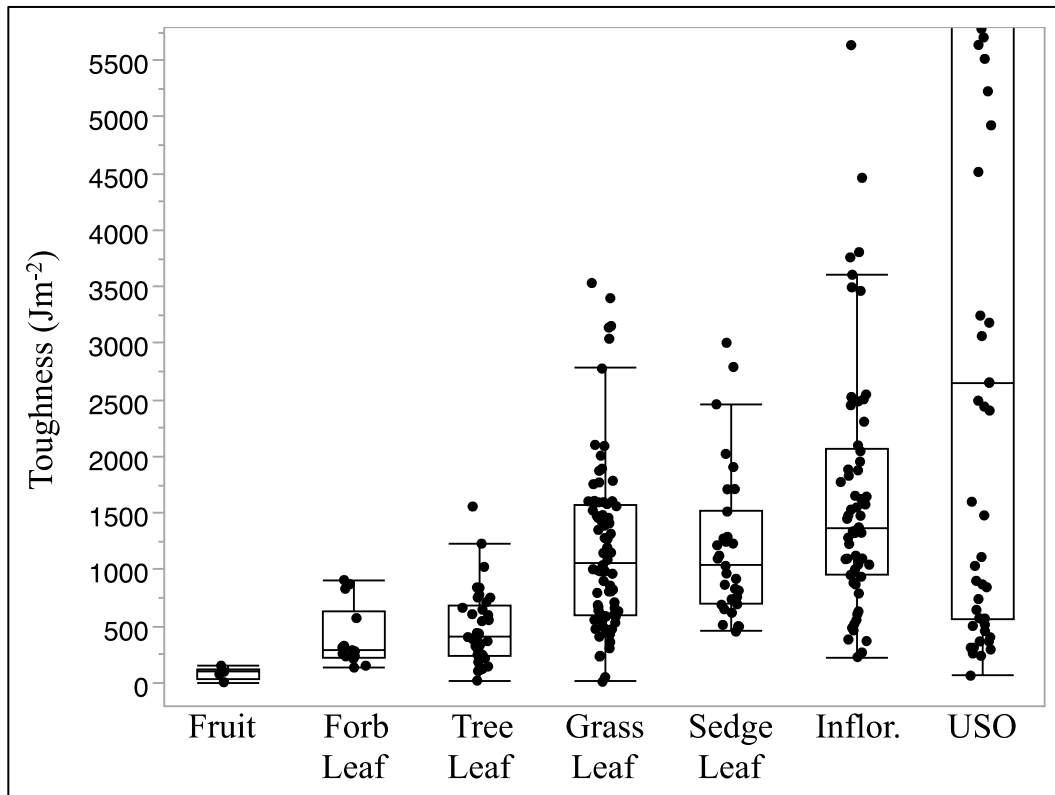
227
 228 Figure 2. Acid detergent fiber content (%) of plant parts within savanna habitats known
 229 to be consumed by primates (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). Categories are
 230 arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles,
 231 the lines within them are the medians, the whiskers show data within 1.5 times the
 232 interquartile ranges, and the dots outside of the whiskers are outliers. “Inflor.” is the
 233 abbreviation of inflorescence.

234

235 *Mechanical data*

236 Mechanically, grass leaves are significantly tougher than fruit ($p = 0.0062$), forb
 237 leaves ($p = 0.0002$), and tree leaves ($p < 0.0001$). Only USOs are significantly tougher
 238 than grass leaves ($p = 0.0175$; Figure 3). Yet, similar to CP and ADF, grass leaf
 239 toughness values span almost the entire range of our samples (with the exception of

240 USOs), with some having values in line with tree leaves and fruits known to be primate
241 foods.



242
243 Figure 3. Toughness values (J/m^2) of plant organs within savanna habitats known to be
244 consumed by primates (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). The y-axis has been
245 capped at 6000 J/m^2 as primates rarely consume foods beyond this limit. Categories are
246 arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles,
247 the lines within them are the medians, the whiskers show data within 1.5 times the
248 interquartile ranges, and the dots outside of the whiskers are outliers. “Inflor.” is an
249 abbreviation of inflorescence.

250
251 **Discussion**

252 Grass leaves within our transects, taken as a whole, have relatively low crude
253 protein content, high fiber content, and high toughness values. At this broad scale,
254 common assumptions about their merit as potential hominin foods appear to be
255 warranted. However, it is clear that grass leaves—like many plant species and plant
256 foods commonly consumed by primates—are diverse with regard to their nutritional
257 and mechanical properties and our data indicate that ~25% of our samples (*C.*
258 *plectostachyus*, *Se. verticillata*, *Sp. ioclados*, *Panicum sp.*) potentially represent high-
259 quality resources within their respective habitats. As with many other generalizations
260 about diet and nutrition, this suggests that we rethink earlier assumptions about what

261 constitutes a ‘quality food’. Many generalizations have been made, for example, about
262 the nutritional properties of fruit versus leaves, with fruit representing a ‘high-quality’
263 food high in easily digested mono- and disaccharides and low in fiber. Leaves,
264 conversely, have been classically generalized as being low in simple sugars and high in
265 fiber. Despite these assumptions (prevalent throughout the literature), nutritional
266 analyses have revealed extreme variance in fruit and leaf nutritional composition. For
267 example, analyses of the sugar and fiber composition of leaves and fruits consumed by
268 catarrhines in Kibale National Park, Uganda, have demonstrated that fruit can have
269 similar (or lower) sugars than the mean sugar value for leaves, and that the variance in
270 monosaccharides of leaves overlaps that of fruit (Danish et al., 2006). Indeed, as more
271 nutritionally explicit analyses are conducted on wild foods, it is increasingly evident
272 that we should revisit all such generalizations, including those made about grasses
273 (Simpson and Raubenheimer, 2012; Lambert and Rothman, 2015; Rothman et al.,
274 2015).

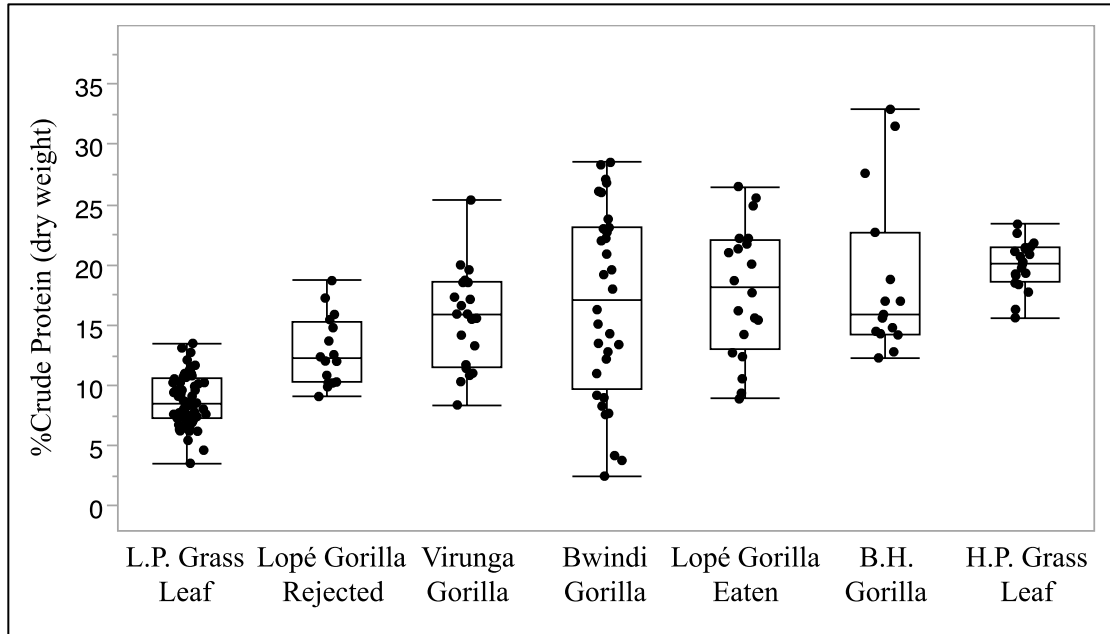
275 As noted above, grass leaf is generally the most abundant plant biomass in
276 savanna ecosystems (Jacobs et al., 1999). Thus, if we cast aside earlier generalizations
277 made about grass leaf macronutrient composition, and consider that 25% of the grass
278 leaves within any given habitat can be palatable to species without specialized digestive
279 strategies, this further increases their value to herbivore consumers because encounter
280 and harvesting rates will be relatively high. At the very least, the notion that all grass
281 leaves growing on savanna landscapes were unsuitable for hominin consumers needs
282 reconsideration, particularly when we compare our samples with published values for
283 other hominoid foods.

284

285 *Hominoid comparisons*

286 When we divide our samples into ‘high-protein’ and ‘low-protein’ categories based
287 on their bimodal distribution for crude protein content, we find that our high-protein
288 grasses (SOM 1) compare very favorably against other hominoid leaf foods. In the
289 figures below, we compare CP (Figure 4) and ADF (Figure 5) of the leaves consumed
290 by gorillas from the Virunga Mountains of Rwanda and Zaire (Waterman et al., 1983),
291 the Lopé Reserve, Gabon (Rogers et al., 1990), Bai Hokou, Central African Republic
292 (Remis et al., 2001), and the Bwindi Impenetrable National Park, Uganda (Rothman et
293 al., 2006). We also include data provided by Rogers et al. (1990) for leaf foods rejected
294 by the Lopé Reserve gorillas. These comparisons reveal that our high-protein grasses
295 have protein contents equivalent to, and in one instance higher than, the leaves
296 consumed by gorillas (CP in high quality grass leaves is significantly higher than in the
297 leaves eaten by the Virunga gorillas; $p = 0.0019$).

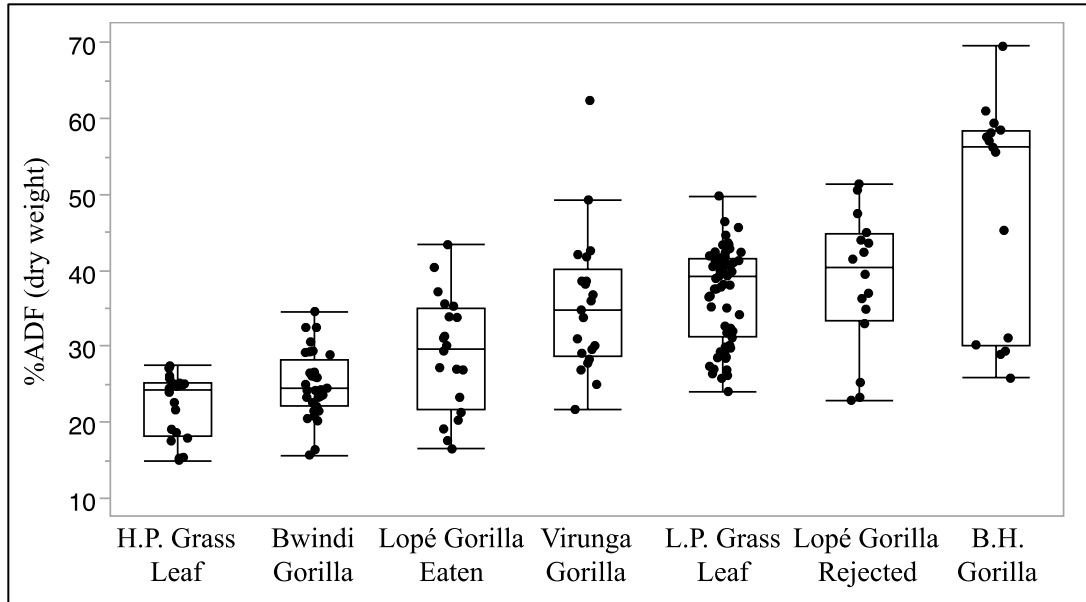
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Figure 4. Crude protein (%) of low-protein (L.P.) and high-protein (H.P.) grass leaves compared to leaves eaten, and rejected, by gorillas arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles, the lines within them are the medians, the whiskers show data within 1.5 times the interquartile ranges, and the dots outside of the whiskers are outliers (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). Low-protein grasses are significantly different than all other categories ($p < 0.0001$) and high-protein grasses are significantly different than Virunga gorilla leaf foods ($p = 0.0019$) and leaves that Lopé gorillas reject (Steel-Dwass all pairs). Gorilla data from Waterman et al., 1983; Rogers et al., 1990; Remis et al., 2001; Rothman et al., 2006.

Our comparisons of ADF reveal a similar trend, albeit more complex (Figure 5). Our high-protein grass leaves are significantly lower in ADF content than all categories ($p < 0.05$) except the leaves eaten by the Bwindi gorillas. Our low-protein grasses have significantly higher ADF than the high-protein grasses and the leaves eaten by the Bwindi and Lopé gorillas ($p < 0.01$) but they are not statistically different from the rejected leaf foods and the leaves eaten by the Virunga and Bai Hokou gorillas. As noted, low levels of ADF have been argued to drive food choice in some primate species and in fact, the leaves of the eight species with the lowest ADF content within our samples are documented foods for the baboons in Amboseli (Altmann, 1998).

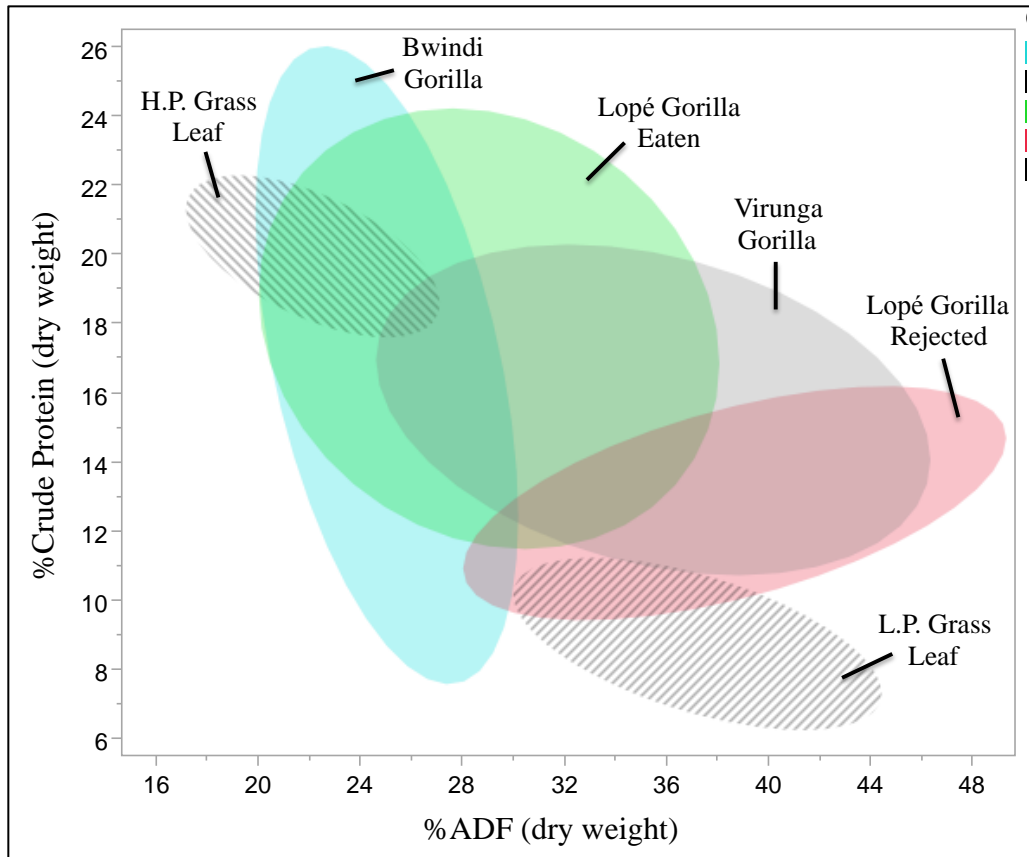


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321 Figure 5. Acid detergent fiber content (%) of high-protein (H.P.) and low-protein (L.P.)
 322 grass leaves compared to leaves eaten, and not eaten, by lowland and mountain gorillas
 323 arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles,
 324 the lines within them are the medians, the whiskers show data within 1.5 times the
 325 interquartile ranges, and the dots outside of the whiskers are outliers
 326 (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). Low-protein grass ADF values are
 327 significantly higher than high-protein grasses ($p < 0.0001$), Bwindi gorilla leaf foods (p
 328 < 0.0001), and Lopé gorilla leaf foods ($p = 0.0029$). High-protein grasses are
 329 significantly different than the leaves that Lopé gorillas reject ($p = 0.0004$), leaves Lopé
 330 gorillas eat ($p = 0.0410$), Virunga gorilla leaf foods ($p < 0.0001$), and Bai Hokou gorilla
 331 leaf foods ($p < 0.0001$; Steel-Dwass Method). Gorilla data from Waterman et al., 1983;
 332 Rogers et al., 1990; Remis et al., 2001; Rothman et al., 2006.

333

334 The ratio of protein to fiber content (protein/fiber) has been proposed as a useful
 335 index to gauge the palatability of vegetation for primates (Milton, 1979; Barton et al.,
 336 1993; Chapman et al., 2002). Figure 6 combines the data from Figures 4 and 5 to
 337 create a spatial representation of these ratios for each food category. As can be seen,
 338 high protein/fiber grasses skew higher in nutritional space compared to most gorilla
 339 foods whereas our low protein/fiber grasses only intersect with the leaf foods rejected
 340 by the Lopé gorillas.

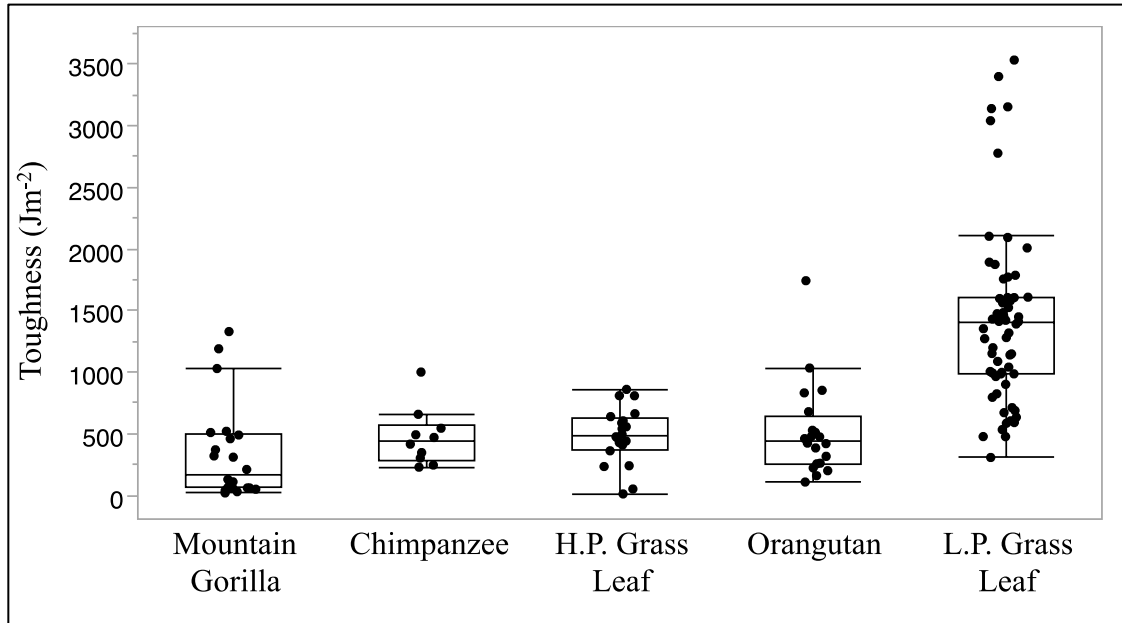


341
 342 Figure 6. Protein/fiber ratios of the leaf foods of gorillas and high-protein (H.P.) and
 343 low-protein (L.P.) grass leaves. Higher protein/fiber ratio foods plot nearer to the upper
 344 left corner, foods with lower ratios plot nearer to the bottom right corner. Ellipses
 345 represent 50% of each category's distribution. Gorilla data from Waterman et al., 1983;
 346 Rogers et al., 1990; Rothman et al., 2006. The Bai Hokou gorilla data have been omitted
 347 for clarity.

348
 349 Toughness can also influence dietary selection for primates and other
 350 mammalian herbivores (O'Reagain and Mentis, 1989; O'Reagain, 1993; Hill and
 351 Lucas, 1996; Wright, 2005). For instance, O'Reagain (1993) found that the
 352 acceptability of grass leaves to grazing sheep at the Dundee Research Station, South
 353 Africa, was inversely correlated with tensile strength. Venkarataman et al. (2014)
 354 recorded a mean fracture toughness of 2686 J/m² (maximum 4197 J/m²) for tall grass
 355 leaves consumed by geladas. Presumably, hominins lacking cercopithecoid dentition
 356 would have a toughness threshold considerably lower.

357 Figure 7 shows the toughness values recorded for our low and high protein
 358 grasses compared with those for the leafy vegetation consumed by chimpanzees from
 359 Kibale National Park, Uganda (Vogel et al., 2008), orangutans from the Ketambe

360 Research Station, Sumatra (Vogel et al., 2014), and gorillas from the Bwindi
 361 Impenetrable and Mgahinga Gorilla National Parks in Uganda (Elgart–Berry, 2004).
 362 There are no significant differences in toughness between the leaves of our high–
 363 protein grass samples and the leaves eaten by chimpanzees, gorillas, and orangutans.



364
 365 Figure 7. Toughness values of grass leaves compared to the values for leaves consumed
 366 by chimpanzees, gorillas, and orangutans arranged in ascending order by mean value.
 367 Boxes represent the 25th–75th percentiles, the lines within them are the medians, the
 368 whiskers show data within 1.5 times the interquartile ranges, and the dots outside of the
 369 whiskers are outliers. Low-protein (L.P.) grasses have values significantly higher than
 370 all other categories ($p < 0.0001$ for all comparisons; Steel-Dwass all pairs).

371
 372 *Primate grass consumption*

373 The vast majority of primate species, including those used for comparison
 374 above, do not rely on grasses as a major source of nutrition mainly due to the fact that
 375 most primates live in forested environments where grasses are less abundant, if present
 376 at all. Yet, even when grasses are present they are rarely a preferred food. For example,
 377 the Fongoli chimpanzees of Senegal that inhabit woodland savanna generally eat few
 378 grasses despite their ubiquity within their habitat (Sponheimer et al., 2006).
 379 Chimpanzees in Kibale National Park, Uganda, are known to consume the pith of
 380 elephant grass (*Pennisetum purpureum*) when preferred fruits are unavailable, but grass
 381 leaves are rarely, if ever eaten (Wrangham et al., 1991, 1998; Conklin-Brittain et al.,
 382 1999).

383 Nonetheless, there are primate species that rely heavily on grass as a source of
 384 nutrition. It has long been known that many baboon populations consume almost all

385 parts of various grass species: seeds, stem bases, rhizomes, and leaves (DeVore and
386 Washburn, 1963; Altmann and Altmann, 1970; Post, 1982; Altmann et al., 1987;
387 Norton et al., 1987; Barton et al., 1993; Barton and Whiten, 1994; Altmann, 1998). For
388 example, during the Amboseli dry seasons, baboons utilize the stem bases and rhizomes
389 of many grass species but in the weeks after the rains when the grass is in flush, their
390 diet (adults and juveniles) consists of 90% grass leaves (Altmann and Altmann, 1970;
391 Dougalle et al., 1964). Altmann (1998:82) noted that the fresh leaves of *Se. verticillata*
392 are a “baboon favorite” and listed many of the species we sampled as being major
393 sources of nutrition for Amboseli baboons including *C. plectostachyus*, *Cynodon*
394 *dactylon*, *Sp. ioclados*, and *Sporobolus spicatus*. Similarly, Barton et al. (1993) and
395 Barton and Whiten (1994) observed baboons in Laikipia, Kenya, spending 10.7% of
396 their average monthly feeding time on the grass leaves of *C. dactylon*, *C.*
397 *plectostachyus*, and *Pennisetum* spp. With the exception of *Pennisetum*, which we did
398 not sample, all of the above grasses are relatively high in protein with low toughness
399 values compared to the many of the other plant tissues in our study.

400 Also, the gelada, whose diet is often dominated by grass leaf (~90%), clearly
401 demonstrates that large-bodied primates can subsist on grasses (Crook and Aldrich-
402 Blake, 1968; Dunbar and Dunbar, 1974; Dunbar, 1976; Iwamoto, 1979; Fashing et al.,
403 2014).

404

405 *The dietary value of grasses beyond their mechanical and nutritional properties*

406 Poaceae are the fourth largest plant family globally and roughly a tenth of all
407 grass species occur in eastern and southern Africa (van Outdshoorn, 2012). The
408 dominance of grasses in many savannas can be seen when measures of net primary
409 production (NPP) are compared. Grasses often double aboveground NPP compared to
410 trees, particularly in nutrient rich savannas where grass NPP represents two thirds of
411 total NPP. While there is considerable morphological variation among grass species,
412 leaf tissue generally accounts for over 50% of the aboveground biomass (O'Reagain,
413 1993). In this sense, it is not surprising that 75–90% of the large mammal biomass
414 living in savanna habitats is supported by grass (Owen-Smith and Danckwerts, 1997).

415 Altmann (1998) noted that *C. dactylon*, a major food resource for the baboons
416 of Amboseli, is not only valuable from a nutritional standpoint, but also because it is a
417 rhizomatous grass that occurs in thick ‘carpets’ across large stretches of ground. As
418 such, encounter and harvesting rates are high leading to high energetic yield per
419 invested harvesting time. *Sp. spicatus*, another species of great importance to both the
420 baboons of Amboseli and Laikipia, forms thick mats in saline soils and is similarly
421 dominant in areas where it is found. In fact, the two wetland transects we sampled in
422 Amboseli are differentiated by the fact that one is bordered by *Sp. spicatus* and the
423 other by *C. dactylon* mats.

424 The fact that *C. dactylon* and *Sp. spicatus* are known to be major baboon foods
425 is telling in light of the fact that, among our samples, they do not fall within the
426 distribution of high-protein grasses. That being said, these two species (along with
427 *Dactyloctenium aegyptium*) have the highest protein/fiber ratios within our low-protein
428 category and their consumption by baboons is likely a function of availability as much
429 as it is a result of their inherent nutritional and mechanical properties. It is worth noting
430 that many of our high-protein grasses are the dominant grasses within their respective
431 transects, at least seasonally.

432

433 *Grass consumption and dental morphology*

434 It can be argued that specialized dentition with high occlusal relief and
435 pronounced shearing crests is necessary for the efficient and effective comminution of
436 leaves (Lucas, 2004; Atkins, 2009; Ungar, 2010). Indeed, colobine primates (which can
437 be leaf-eating specialists) exhibit ‘blade-like’ teeth (Kay, 1975; Lucas, 2004; Atkins,
438 2009; Ungar, 2010). Gelada teeth exhibit increased hypsodonty compared to *Papio*,
439 their more generalist sister taxon, and this dental morphology is diagnostic for
440 *Theropithecus* in the fossil record (Eck and Jablonski, 1984; Leakey, 1993).

441 However, current research is beginning to investigate whether the lack of
442 occlusal relief necessarily indicates a lack of tough, leafy foods in their diets.
443 Winchester et al. (2014) argued that increases in enamel thickness and megadontia are
444 functionally equivalent to hypsodonty in that the increased absolute amount of enamel
445 similarly resists wear over the course of an animal’s lifetime. Moreover, australopith
446 dental morphology may be the result of the genetic inability to adopt hypsodonty over a
447 relatively short period of evolutionary time (Grine et al., 2012; Ungar and Hlusko,
448 2016; Daegling and Grine, 2017). Ungar and Hlusko (2016) noted that the dental
449 adaptations seen in the robust australopiths (molar inflation and thickened enamel)
450 could represent “the evolutionary path of least resistance,” arguing that an adaptive
451 shift towards hypsodonty would have required a higher degree of genetic restructuring
452 for such a radical reorganization of dental morphology. Indeed, temporal lags between
453 behavioral shifts and morphological adaptations are seen in other clades such as the
454 East African proboscideans. The fossil record shows a clear and profound dietary shift
455 to C₄ grass dominated diets among late gomphotheres and early elephants ~8 Ma and
456 yet, significant increases in lamellar number and hypsodonty do not appear until ~5 Ma
457 (Lister, 2013, 2014; but see Jardine et al., 2012, for discussion of how dietary grit,
458 rather than grass itself, may have selected for mammalian hypsodonty).

459 What is more, Rabenold and Pearson (2011) examined the phytolith content in
460 the diets of several primates and used the data to predict the molar enamel thickness
461 needed to adequately resist dental attrition. When they compared their predicted values
462 with the observed enamel thickness, they found a strong correlation ($R^2=0.87$),

463 suggesting that a diet focused on plants with high phytolith content (such as the leaves
464 of grasses) may have selected for the hyper thick dental enamel found in species such
465 as *P. boisei*.

466

467 *Digestive constraints on the consumption of grass leaf*

468 Though there are exceptions, the majority of mammalian grazers have
469 specialized digestive systems that enable them to extract energy from the structural
470 carbohydrates found in plant cell walls using both autoenzymatic and alloenzymatic
471 processes. While we will never fully know the digestive capabilities of extinct
472 hominins, the ‘funnel-shaped’ australopith torso has been argued to indicate a larger
473 gut, and thus the ability to consume more difficult-to-digest (higher fiber) plant foods
474 compared to *Homo* (Aiello and Wheeler, 1995). While the specialized, multi
475 chambered stomachs of the colobines are clearly adaptations that aid fiber fermentation,
476 other non-colobine primates have an excellent capacity for so-called hind-gut
477 fermentation. Chimpanzees, for example, are considered ‘high fermenters’ of fiber
478 (particularly hemicelluloses) among the hominoids (Conklin-Brittain et al., 2006) and it
479 is probably fair to assume that ancient hominins had some ability to extract energy from
480 dietary fiber. Regardless, many of the grasses we examined are relatively low in ADF
481 and when protein/fiber ratios are taken into account, it becomes clear that many grass
482 leaves fall within the ranges of non-grass leaf foods consumed by other hominoids
483 (Figure 6).

484

485 *Future considerations*

486 We recognize that levels of protein and fiber alone do not dictate food choice in
487 herbivores and that the nutritional quality of any potential food is more difficult to
488 quantify. Other macronutrients such as non-structural carbohydrates (e.g., starches,
489 sugars) and lipids as well as water content and essential minerals such as calcium,
490 phosphorous, and sodium are important factors to consider when assessing the potential
491 value of any given food resource (Sniffen et al., 1992; McDowell and Valle, 2000).
492 Nutritional quality is also impacted by antifeedants such as lignin and tannins, plant
493 secondary metabolites (true toxins), and biogenic silica that can both impede nutrient
494 uptake and cause toxic effects for herbivore consumers (Robbins, 1993; Reed et al.,
495 2000). Grass leaves, while generally lower in secondary compounds than tree leaves,
496 can accumulate high amounts of silica in their leaf tissues (Coughenour, 1985), and can
497 increase concentrations in response to grazing pressure (Jones and Handreck, 1967;
498 Van Soest and Jones, 1968). Future research should attempt to account for as many of
499 these variables as possible in order to obtain a more accurate picture of dietary quality.

500

501 Furthermore, the effects of season and habitat play a role in determining the
nutritional and mechanical properties of plant foods throughout their life cycle. Here,

502 we only present data for leaf foods during the wet season (see Methods). Any
503 assessment of the potential for plant foods to act as staple components of diet need to
504 incorporate these spatial and temporal effects, notably the tendency for the nutritional
505 quality of leafy vegetation in savanna habitats to decline during dry seasons (Cooper et
506 al., 1988; Georgiadis and McNaughton, 1990). Seasonal effects on leafy vegetation are
507 among the reasons that USOs are often argued to have been important foods for
508 hominins because they are thought to be relatively resistant to temporal fluctuations in
509 nutritional quality (Laden and Wrangham, 2005). However, it must be noted that ‘USO’
510 is a somewhat artificial category considering the wide range of forms that underground
511 storage organs can take (e.g., fleshy, starch filled tubers vs. tough rhizomes) and further
512 study requires separating USOs into multiple categories. From a spatial perspective,
513 habitat differences at both the local and regional level almost certainly affect the
514 nutritional and mechanical properties of vegetation and this may be particularly
515 important for our understanding of hominin dietary ecology. Could it be possible that
516 the different carbon isotopic compositions of *P. boisei* and *P. robustus* are the result of
517 nutritional and mechanical differences between the available C₄ vegetation within their
518 respective habitats? Though we suspect that this might be the case, our understanding
519 of the paleolandscapes on which these hominins lived and, particularly, the mechanical
520 and nutritional properties of the available vegetation, is not sufficiently advanced at this
521 point to address this question.

522

523 **Conclusion**

524 Stable carbon isotope analyses have revealed that C₄ foods were consumed by
525 many hominin species and it is a fair assumption that the bulk of those resources came
526 in the form of plant tissues. Early hominins were likely to be generalist feeders that
527 opportunistically consumed resources based on their seasonal availability (Knott,
528 2005).

529 The USOs of C₄ sedges and C₄ grass seeds were almost certainly part of the
530 broader hominin dietary repertoire just as they are for baboons today (Jolly, 1970;
531 Norton et al., 1987; Altmann, 1998; Dominy et al., 2008). However, a combination of
532 the limited seasonal availability of grass seeds, the lack of dental microwear evidence
533 supporting USO consumption, and their nutritional/mechanical properties reported
534 here, make it unlikely that they could solely account for all of the C₄-derived carbon in
535 high-C₄ species like *P. boisei*. Our data show that grass leaves should not be treated as
536 a ‘one size fits all’ category as many are less tough, higher in protein, and lower in fiber
537 than other potential plant foods on some savanna landscapes. This, coupled with their
538 great abundance, means we should not summarily exclude grass leaves from
539 reconstructions of hominin diets. Indeed, we know of no living large-bodied mammal
540 (excepting carnivores that prey heavily on grazing herbivores) with a C₄ isotopic

541 signature like the one seen in *P. boisei* that does not eat grass leaf extensively, if not
542 exclusively. It is not clear to us that hominins are exceptions to this mammalian rule.
543 Regardless, if we hope to build better models of early hominin dietary behavior, the
544 inherent variation of grass leaf properties (and of other potential foods), as
545 demonstrated here, needs to be considered.

546

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559

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