Grass leaves as potential hominin dietary resources

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

a Department of Anthropology, University of Colorado Boulder, Boulder, CO 80309 USA
b Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794, U.S.A.
c Faculty of Archaeology, Leiden University, Einsteinweg 2, 2333CC Leiden, The Netherlands.
d Florisbad Quaternary Research Department, National Museum, PO Box 266, Bloemfontein, 9300, South Africa
e Centre for Environmental Management, University of the Free State, PO Box 339, Bloemfontein, 9300, South Africa
f Institut für Geowissenschaften, AG für Angewandte und Analytische Paläontologie, Johannes Gutenberg–Universität Mainz, 55128 Mainz, Germany
g Department of Environmental Studies, University of Colorado Boulder, Boulder, CO 80309 USA

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

Abstract

Discussions about early hominin diets have generally excluded grass leaves as a staple food resource, despite their ubiquity in most early hominin habitats. In particular, stable carbon isotope studies have shown a prevalent C_4 component in the diets of most taxa, and grass leaves are the single most abundant C_4 resource in African savannas. Grass leaves are typically portrayed as having little nutritional value (e.g., low in protein and high in fiber) for hominins lacking specialized digestive systems. It has also been argued that they present mechanical challenges (i.e., high toughness) for hominins with bunodont dentition. Here, we compare the nutritional and mechanical properties of grass leaves with the plants growing alongside them in African savanna habitats. We also compare grass leaves to the leaves consumed by other hominoids and demonstrate that many, though by no means all, compare favorably with the nutritional and mechanical properties of known primate foods. Our data reveal that grass leaves exhibit tremendous variation and suggest that future reconstructions of hominin dietary ecology take a more nuanced approach when considering grass leaves as a potential hominin dietary resource.

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

Introduction

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

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

Additionally, stable carbon isotope studies show that C_4 foods (i.e., foods enriched in ^{13}C) became increasingly significant portions of hominin diets beginning at least 3.7 Ma—culminating with *P. boisei,* whose diet was 75–80% C_4 (van der Merwe et al., 2008; Cerling et al., 2011; Ungar and Sponheimer, 2011; Lee-Thorp et al., 2012; Sponheimer et al., 2013; Levin et al., 2015). Moreover, the degree of postcanine megadontia and mandibular robusticity exhibited by early hominin species is positively correlated with the amount of C_4 foods they consumed, suggesting that the inherent properties of these foods may have contributed to australopith craniodental adaptations (Sponheimer et al., 2013).

Hominins may have consumed foods enriched in ^{13}C either as primary consumers of plants using the C_4/CAM photosynthetic pathway and/or as secondary consumers eating animals that consume significant quantities of C_4 vegetation (e.g., grazing ungulates such as wildebeest and zebra). However, while faunal resources were a likely source of dietary carbon, few would argue that meat consumption was a major component of early hominin diet, despite recent discoveries revealing hominin tool use before 3 Ma (McPherron et al., 2010; Harmand et al., 2015). Similarly, plants using CAM photosynthesis (e.g., succulents) were potentially consumed, but are relatively scarce within most savanna habitats. Thus, despite contributions from faunal and CAM resources, it is most likely that C_4 plants were the primary source of dietary carbon for early hominins with high C_4 isotopic signatures such as *P. boisei, Paranthropus aethiopicus,* and *Australopithecus bahrelghazali*.

Of the roughly 7500 species of plants that use the C_4 photosynthetic pathway, most (~80%) are monocots in the families Poaceae and Cyperaceae—tropical grasses (~4500 species) and sedges (~1500 species), respectively (Sage et al., 1999; Sage, 2004). Thus, the bulk of C_4 plant biomass available to African herbivores is located in

2

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 C_4 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 C_4 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 C_4 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 gramnivory 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 C_4 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 C_4
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 C_4 and sedges are mixed
158   C_3/C_4 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.
194
195   **Results**
196   *Nutritional data*
197   Plant foods differed significantly in protein content ($p < 0.0001$). Grass leaves

5

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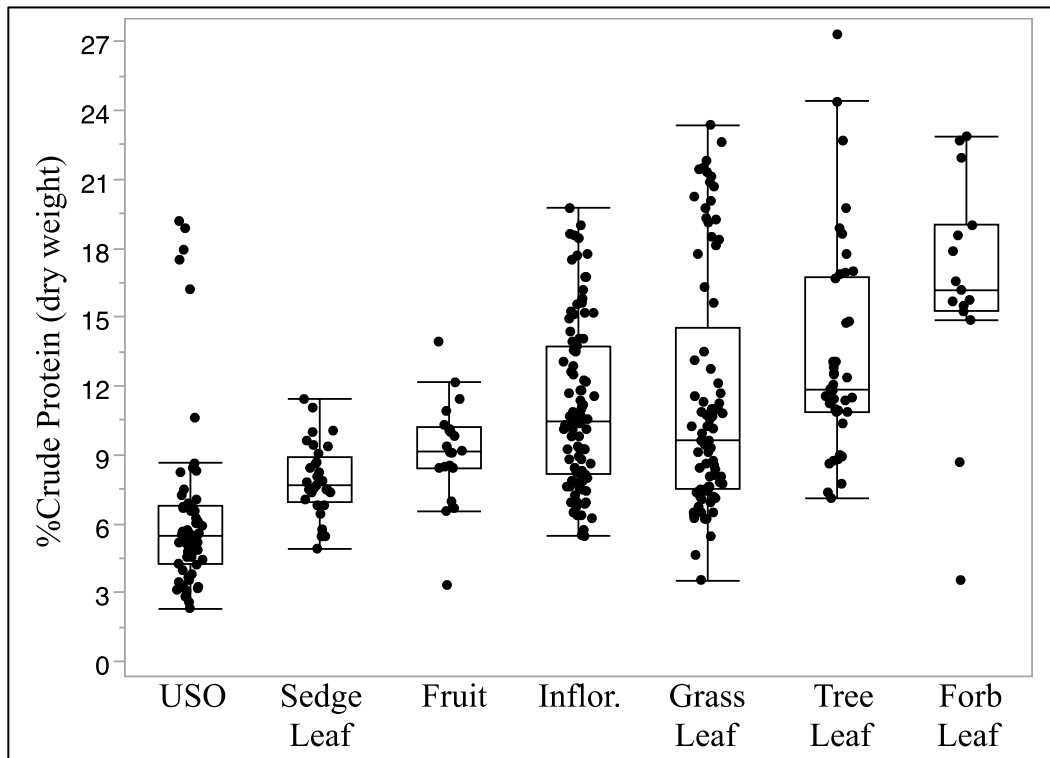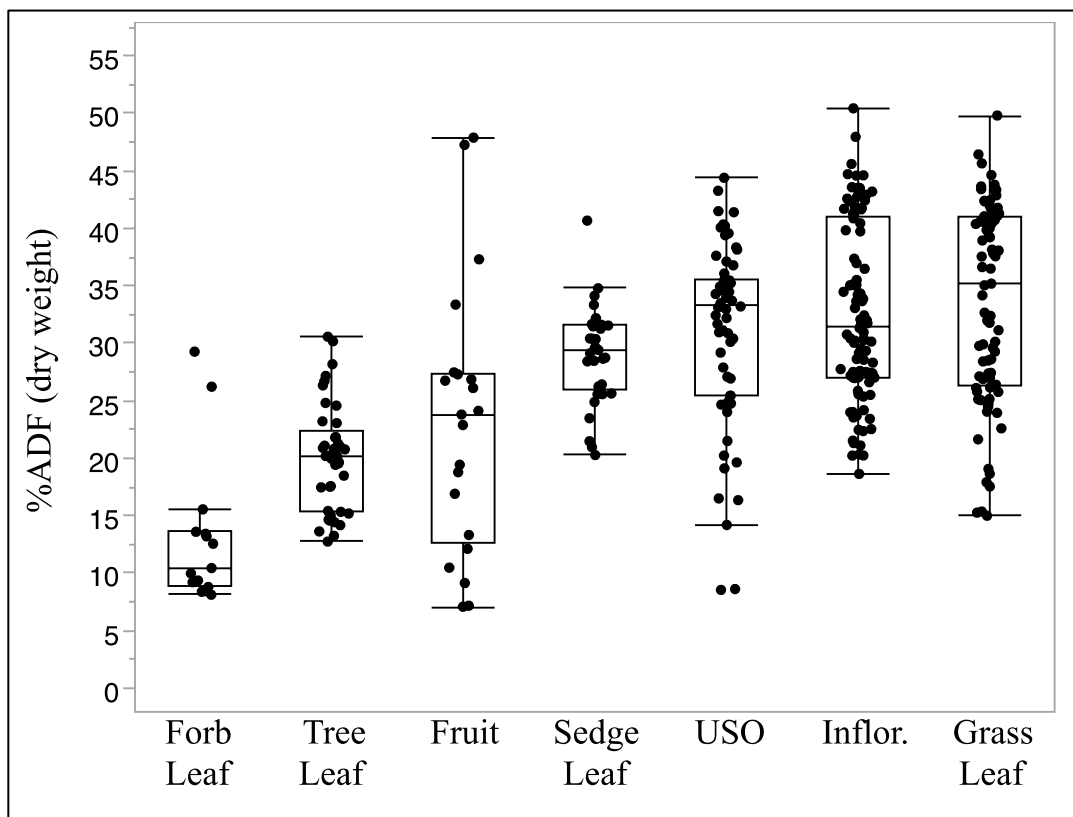

Figure 1. Crude protein content (%) of plant parts within savanna habitats known to be consumed by primates. (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). Categories are arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles, the lines within them are the medians, the whiskers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

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

6

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.
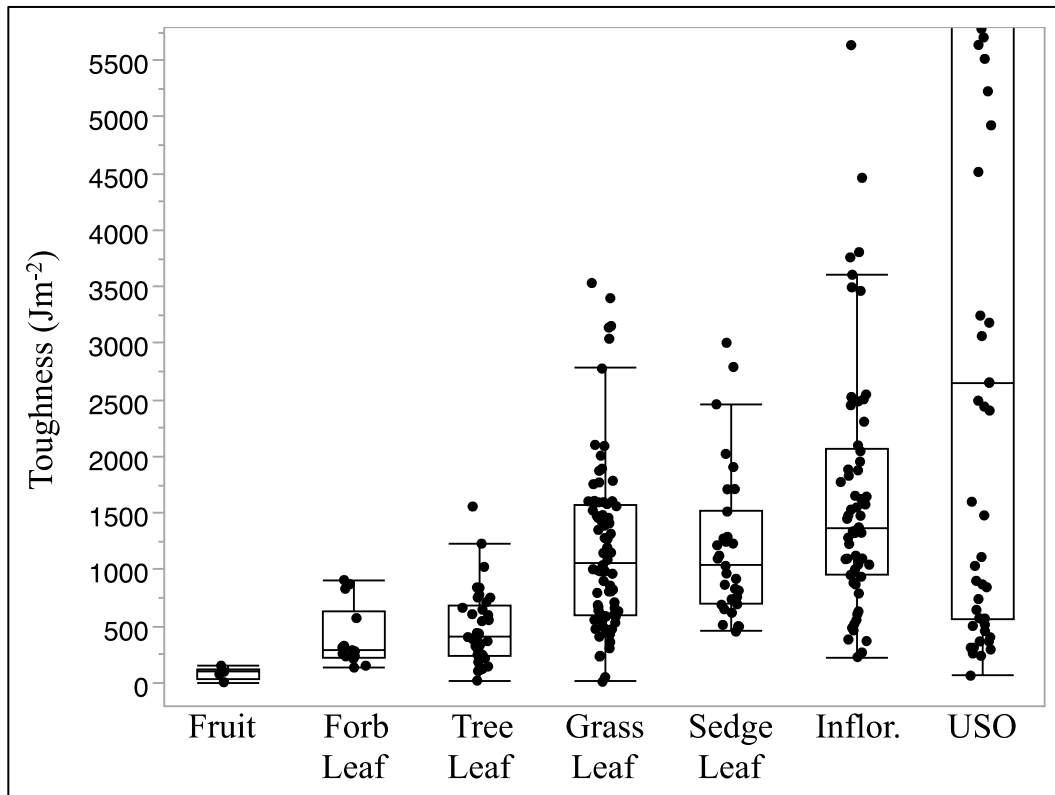
242
243   Figure 3. Toughness values (J/m^2) of plant organs within savanna habitats known to be
244   consumed by primates (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). The y-axis has been
245   capped at 6000 J/m2 as primates rarely consume foods beyond this limit. Categories are
246   arranged in 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

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

8

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; $p = 0.0019$).
298
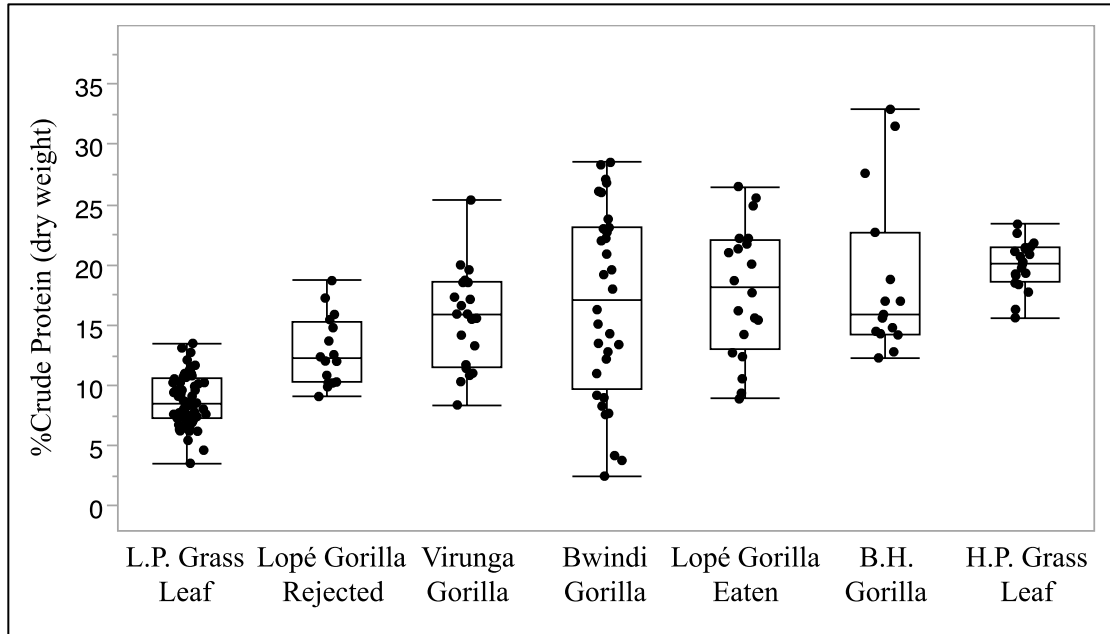
Figure 4. Crude protein (%) of low-protein (L.P.) and high-protein (H.P.) grass leaves compared to leaves eaten, and rejected, by gorillas arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles, the lines within them are the medians, the whiskers show data within 1.5 times 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).
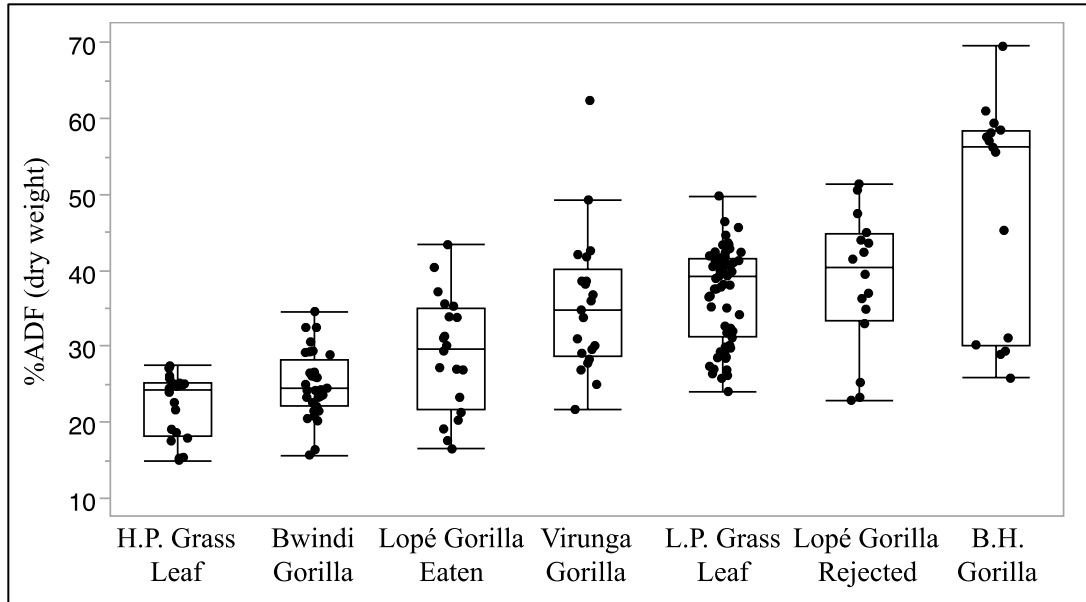
Figure 5. Acid detergent fiber content (%) of high-protein (H.P.) and low-protein (L.P.) grass leaves compared to leaves eaten, and not eaten, by lowland and mountain gorillas arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles, the lines within them are the medians, 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 grass ADF values are significantly higher than high-protein grasses ($p < 0.0001$), Bwindi gorilla leaf foods ($p < 0.0001$), and Lopé gorilla leaf foods ($p = 0.0029$). High-protein grasses are significantly different than the leaves that Lopé gorillas reject ($p = 0.0004$), leaves Lopé gorillas eat ($p = 0.0410$), Virunga gorilla leaf foods ($p < 0.0001$), and Bai Hokou gorilla leaf foods ($p < 0.0001$; Steel-Dwass Method). Gorilla data from Waterman et al., 1983; Rogers et al., 1990; Remis et al., 2001; Rothman et al., 2006.

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

11
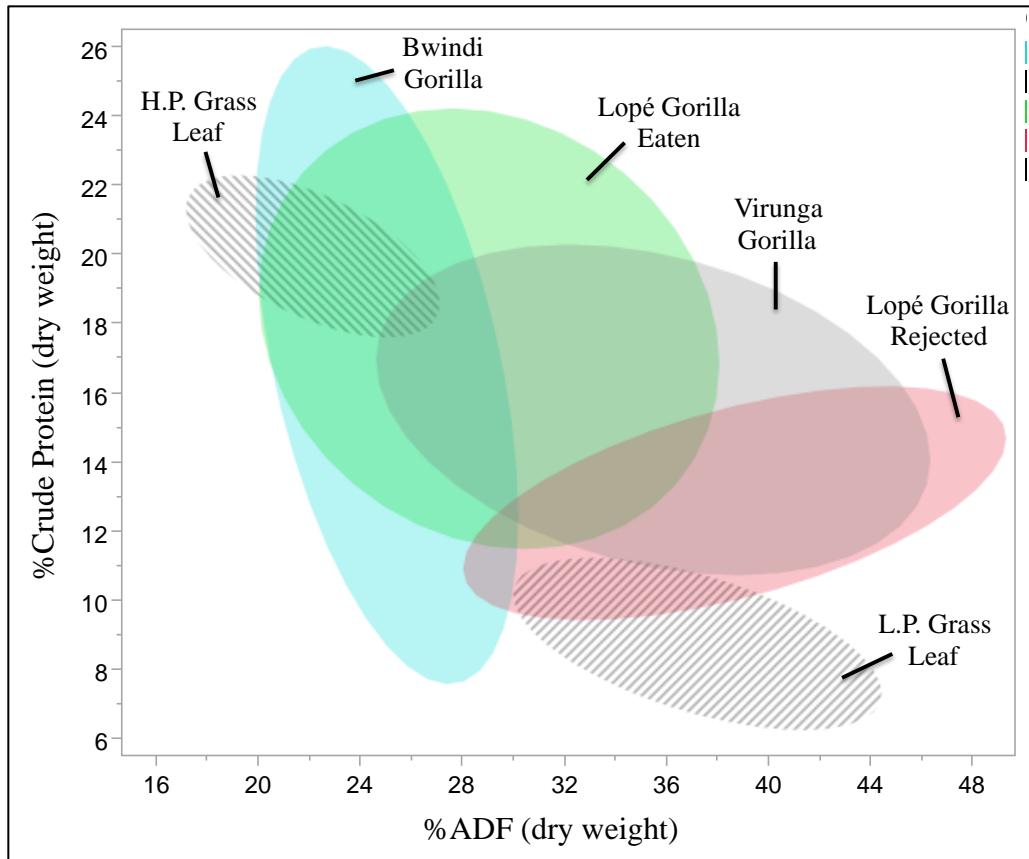
Figure 6. Protein/fiber ratios of the leaf foods of gorillas and high-protein (H.P.) and low-protein (L.P.) grass leaves. Higher protein/fiber ratio foods plot nearer to the upper left corner, foods with lower ratios plot nearer to the bottom right corner. Ellipses represent 50% of each category's distribution. Gorilla data from Waterman et al., 1983; Rogers et al., 1990; Rothman et al., 2006.The Bai Hokou gorilla data have been omitted for clarity.

Toughness can also influence dietary selection for primates and other mammalian herbivores (O'Reagain and Mentis, 1989; O'Reagain, 1993; Hill and Lucas, 1996; Wright, 2005). For instance, O'Reagain (1993) found that the acceptability of grass leaves to grazing sheep at the Dundee Research Station, South Africa, was inversely correlated with tensile strength. Venkarataman et al. (2014) recorded a mean fracture toughness of 2686 J/m^2 (maximum 4197 J/m^2) for tall grass leaves consumed by geladas. Presumably, hominins lacking cercopithecoid dentition would have a toughness threshold considerably lower.

Figure 7 shows the toughness values recorded for our low and high protein grasses compared with those for the leafy vegetation consumed by chimpanzees from 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.
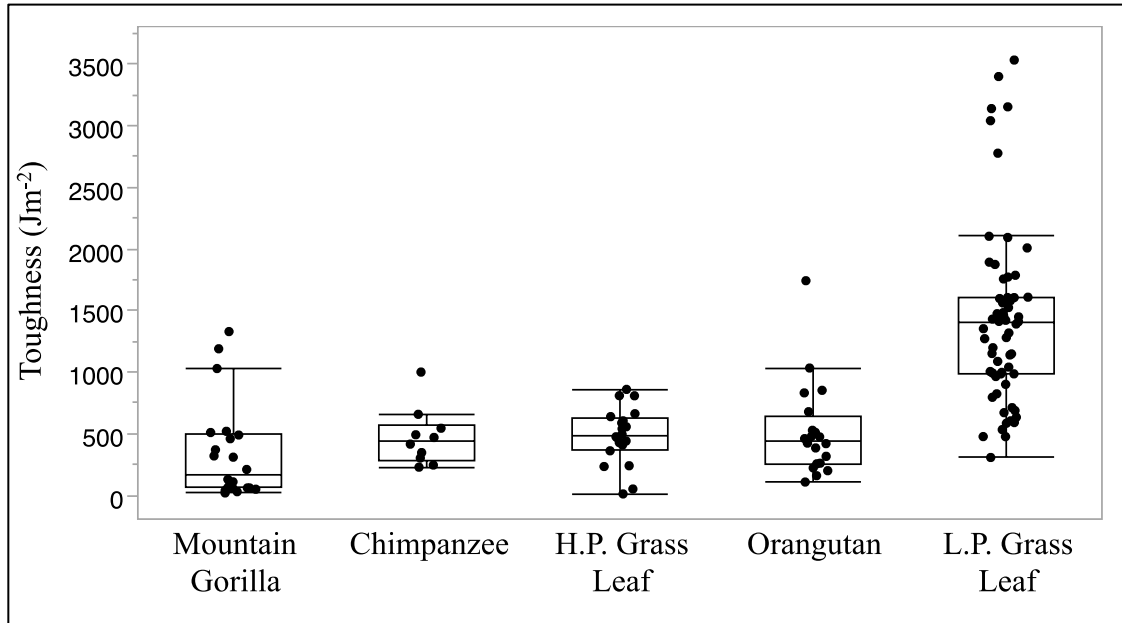
364
365 Figure 7. Toughness values of grass leaves compared to the values for leaves consumed
366 by chimpanzees, gorillas, and orangutans arranged in ascending order by mean value.
367 Boxes represent the 25th–75th percentiles, the lines within them are the medians, the
368 whiskers show data within 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

13

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 C_4 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   Furthermore, the effects of season and habitat play a role in determining the
501   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 C_4 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 C_4 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 C_4 sedges and C_4 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 C_4-derived carbon in
535   high-C_4 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 C_4 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

559

560 **References**
561 Aiello, L.C., Wheeler, P., 1995. The expensive–tissue hypothesis: the brain and the
562 digestive system in human and primate evolution. Curr. Anthropol. 36, 199–221.
563 Altmann, S., Post, D., Klein, D., 1987. Nutrients and toxins of plants in Amboseli,
564 Kenya. African J. Ecol. 25, 279–293.
565 Altmann, S.A., 1998. Foraging for Survival: Yearling Baboons in Africa. University of
566 Chicago Press, Chicago.
567 Altmann, S.A., Altmann, J., 1973. Baboon Ecology. University of Chicago Press,
568 Chicago.
569 Atkins, T., 2009. The Science and Engineering of Cutting: The Mechanics and
570 Processes of Separating, Scratching and Puncturing Biomaterials, Metals and Non–
571 Metals. Butterworth–Heinemann, Oxford, UK.
572 Barton, R., Whiten, A., Byrne, R., English, M., 1993. Chemical composition of baboon
573 plant foods: implications for the interpretation of intra–and interspecific differences in
574 diet. Folia Primatol. 61, 1–20.
575 Barton, R.A., Whiten, A., 1994. Reducing complex diets to simple rules: food selection
576 by olive baboons. Behav. Ecol. Sociobiol. 35, 283–293.
577 Cerling, T.E., Mbua, E., Kirera, F.M., Manthi, F.K., Grine, F.E., Leakey, M.G.,
578 Sponheimer, M., Uno, K.T., 2011. Diet of *Paranthropus boisei* in the early Pleistocene
579 of East Africa. Proc. Natl. Acad. Sci. 108, 9337–9341.

580   Chapman, C.A., Chapman, L.J., Bjorndal, K.A., Onderdonk, D.A., 2002. Application of
581   protein-to-fiber ratios to predict colobine abundance on different spatial scales. Int. J.
582   Primatol. 23, 283–310.

583   Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol.
584   9, 129–136.

585   Conklin-Brittain, N., Knott, C., Wrangham, R., 2006. Energy intake by wild
586   chimpanzees and orangutans: methodological considerations and a preliminary
587   comparison. Cm. S. Bio. Evol. Anth. 1, 445–472.

588   Conklin-Brittain, N.L., Wrangham, R.W., Hunt, K.D., 1998. Dietary response of
589   chimpanzees and cercopithecines to seasonal variation in fruit abundance. II.
590   Macronutrients. Int. J. Primatol. 19, 971–998.

591   Constantino, P.J., Lee, J.J.–W., Chai, H., Zipfel, B., Ziscovici, C., Lawn, B.R., Lucas,
592   P.W., 2010. Tooth chipping can reveal the diet and bite forces of fossil hominins. Biol.
593   Letters 6, 826–829.

594   Constantino, P.J., Lee, J.J.–W., Morris, D., Lucas, P.W., Hartstone–Rose, A., Lee, W.–
595   K., Dominy, N.J., Cunningham, A., Wagner, M., Lawn, B.R., 2011. Adaptation to
596   hard–object feeding in sea otters and hominins. J. Hum. Evol. 61, 89–96.

597   Cooper, S.M., Owen-Smith, N., Bryant, J.P., 1988. Foliage acceptability to browsing
598   ruminants in relation to seasonal changes in the leaf chemistry of woody plants in a
599   South African savanna. Oecologia 75, 336–342.

600   Coughenour, M.B., 1985. Graminoid responses to grazing by large herbivores:
601   adaptations, exaptations, and interacting processes. Ann. Mo. Bot. Gard. 72, 852–863.

602   Crook, J.H., Aldrich-Blake, P., 1968. Ecological and behavioural contrasts between
603   sympatric ground dwelling primates in Ethiopia. Folia Primatol. 8, 192–227.

604   Daegling, D.J., Grine, F.E., 2017. Feeding behavior and diet in *Paranthropus boisei*:
605   the limits of functional inference from the mandible. In: Marom, A., Hovers, E. (Eds.),
606   Human Paleontology and Prehistory: Contributions in Honor of Yoel Rak. Springer
607   International Publishing, Cham, pp. 109–125.

608   Demes, B., Creel, N., 1988. Bite force, diet, and cranial morphology of fossil hominids.
609   J. Hum. Evol. 17, 657–670.

610   DeVore, I., Washburn, S.L., 1963. Baboon ecology and human evolution. In: Howel,
611   F.C., Bourlière, F. (Eds.), African Ecology and Human Evolution. Viking Fund
612   Publications in Anthropology No. 36, New York, pp. 335–367.

613   Dominy, N.J., 2012. Hominins living on the sedge. Proc. Natl. Acad. Sci. 109, 20171–
614   20172.

615   Dominy, N.J., Vogel, E.R., Yeakel, J.D., Constantino, P., Lucas, P.W., 2008.
616   Mechanical properties of plant underground storage organs and implications for dietary
617   models of early hominins. Evol. Biol. 35, 159–175.

618   Dunbar, R., Dunbar, E., 1974. Ecological relations and niche separation between
619   sympatric terrestrial primates in Ethiopia. Folia Primatol. 21, 36–60.

620   Eck, G.G., Jablonski, N.G., 1984. A reassessment of the taxonomic status and phyletic
621   relationships of *Papio baringensis* and *Papio quadratirostris* (Primates:
622   Cercopithecidae). Am. J. Phys. Anthropol. 65, 109–134.

623   Elgart-Berry, A., 2004. Fracture toughness of mountain gorilla (*Gorilla gorilla*
624   *beringei*) food plants. Am. J. Primatol. 62, 275–285.

625   Fashing, P.J., Nguyen, N., Venkataraman, V.V., Kerby, J.T., 2014. Gelada feeding
626   ecology in an intact ecosystem at Guassa, Ethiopia: variability over time and
627   implications for theropith and hominin dietary evolution. Am. J. Phys. Anthropol. 155,
628   1–16.

629   Grine, F.E., Sponheimer, M., Ungar, P.S., Lee-Thorp, J., Teaford, M.F., 2012a. Dental
630   microwear and stable isotopes inform the paleoecology of extinct hominins. Am. J.
631   Phys. Anthropol. 148, 285–317.

632   Grine, F.E., Sponheimer, M., Ungar, P.S., Lee-Thorp, J., Teaford, M.F., 2012b. Dental
633   microwear and stable isotopes inform the paleoecology of extinct hominins. Am. J.
634   Phys. Anthropol. 148, 285–317.

635   Gunther, K.A., Shoemaker, R.R., Frey, K.L., Haroldson, M.A., Cain, S.L., Van Manen,
636   F.T., Fortin, J.K., 2014. Dietary breadth of grizzly bears in the Greater Yellowstone
637   Ecosystem. Ursus 25, 60–72.

638   Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boës, X.,
639   Quinn, R.L., Brenet, M., Arroyo, A., 2015. 3.3–million–year–old stone tools from
640   Lomekwi 3, West Turkana, Kenya. Nature 521, 310–315.

641   Hatley, T., Kappelman, J., 1980. Bears, pigs, and Plio–Pleistocene hominids: a case for
642   the exploitation of belowground food resources. Hum. Ecol. 8, 371–387.

643   Hernandez-Aguilar, R.A., Moore, J., Pickering, T.R., 2007. Savanna chimpanzees use
644   tools to harvest the underground storage organs of plants. Proc. Natl. Acad. Sci. 104,
645   19210–19213.

646   Hill, D.A., Lucas, P.W., 1996. Toughness and fiber content of major leaf foods of
647   Japanese macaques (*Macaca fuscata yakui*) in Yakushima. Am. J. Primatol.38, 221–
648   231.

649   Hylander, W.L., 1988. Implications of in vivo experiments for interpreting the
650   functional significance of "robust" australopithecine jaws, in Grine, F. (Ed.),
651   Evolutionary History of the "Robust" Australopithecines. Transaction Publishers, New
652   York, pp. 55–83.

653   Iwamoto, T., 1979. Ecological and sociological studies of gelada baboons. Feeding
654   ecology. Contrib. Primatol. 16, 279–330.

655   Jacobs, B.F., Kingston, J.D., Jacobs, L.L., 1999. The origin of grass–dominated
656   ecosystems. Ann. Mo. Bot. Gard. 86, 590–643.
657   Janis, C., 1976. The evolutionary strategy of the Equidae and the origins of rumen and
658   cecal digestion. Evolution, 30, 757–774.
659   Janis, C.M., Fortelius, M., 1988. On the means whereby mammals achieve increased
660   functional durability of their dentitions, with special reference to limiting factors. Biol
661   Rev. 63, 197–230.
662   Jardine, P.E., Janis, C.M., Sahney, S., Benton, M.J., 2012. Grit not grass: concordant
663   patterns of early origin of hypsodonty in Great Plains ungulates and Glires.
664   Palaeogeogr. Palaeoclimatol. Palaeoecol. 365, 1–10.
665   JMP®, Version 13.0. SAS Institute Inc., Cary, NC, 1989–2017.
666   Jolly, C.J., 1970. The seed–eaters: a new model of hominid differentiation based on a
667   baboon analogy. Man 5, 5–26.
668   Jones, L., Handreck, K., 1967. Silica in soils, plants, and animals. Adv. Agron. 19,
669   107–149.
670   Kay, R.F., 1975. The functional adaptations of primate molar teeth. Am. J. Phys.
671   Anthropol. 43, 195–215.
672   Kay, R.F., 1985. Dental evidence for the diet of *Australopithecus*. A. Rev. Anthropol.
673   14, 315–341.
674   Knott, C.D., 2005. Energetic responses to food availability in the great apes:
675   implications for hominin evolution, in: Brockman, D.K., van Schaik, C.P. (Eds.),
676   Seasonality in Primates: Studies of Living and Extinct Human and Non–Human
677   Primates, Cambridge University Press, New York, pp. 351–378.
678   Laden, G., Wrangham, R., 2005. The rise of the hominids as an adaptive shift in
679   fallback foods: plant underground storage organs (USOs) and australopith origins. J.
680   Hum. Evol. 49, 482–498.
681   Lambert, J.E., Rothman, J.M., 2015. Fallback foods, optimal diets, and nutritional
682   targets: Primate responses to varying food availability and quality. A. Rev. Anthropol.
683   44, 493–512.
684   Langer, P., 1974. Stomach evolution in the Artiodactyla. Mammalia 38, 295–314.
685   Leakey, L.S., 1959. A new fossil skull from Olduvai. Nature 184, 491–493.
686   Leakey, M.G., 1993. Evolution of *Theropithecus* in the Turkana basin, in: Jablonski,
687   N.G. (Ed.), *Theropithecus*: The Rise and Fall of a Primate Genus. Cambridge
688   University Press, New York, pp. 85–123.
689   Lee-Thorp, J., Likius, A., Mackaye, H.T., Vignaud, P., Sponheimer, M., Brunet, M.,
690   2012a. Isotopic evidence for an early shift to C4 resources by Pliocene hominins in
691   Chad. Proc. Natl. Acad. Sci. 109, 20369–20372.

692 Lee-Thorp, J., Likius, A., Mackaye, H.T., Vignaud, P., Sponheimer, M., Brunet, M.,
693 2012b. Isotopic evidence for an early shift to C4 resources by Pliocene hominins in
694 Chad. Proc. Natl. Acad. Sci. 109, 20369–20372.
695 Levin, N.E., Haile-Selassie, Y., Frost, S.R., Saylor, B.Z., 2015. Dietary change among
696 hominins and cercopithecids in Ethiopia during the early Pliocene. Proc. Natl. Acad.
697 Sci. 112, 12304–12309.
698 Lister, A.M., 2013. The role of behaviour in adaptive morphological evolution of
699 African proboscideans. Nature 500, 331–334.
700 Lister, A.M., 2014. Behavioural leads in evolution: evidence from the fossil record.
701 Biol. J. Linn. Soc. 112, 315–331.
702 Lucas, P.W., 2004. Dental Functional Morphology: How Teeth Work. Cambridge
703 University Press, New York.
704 Macho, G.A., 2014. Baboon feeding ecology informs the dietary niche of *Paranthropus*
705 *boisei*. PLoS One 9, e84942.
706 Macho, G.A., 2015. Pliocene hominin biogeography and ecology. J. Hum. Evol. 87,
707 78–86.
708 McDowell, L., Valle, G., 2000. Major minerals in forages, in: Givens, D.I., Owen, E.,
709 Axford, R.F.E., Omed, H.M. (Eds.), Forage Evaluation in Ruminant Nutrition. CABI
710 Publishing, New York, pp. 373–397.
711 McNaughton, S., Georgiadis, N.J., 1986. Ecology of African grazing and browsing
712 mammals. Annu. Rev. of Ecol. Syst. 17, 39–66.
713 McPherron, S.P., Alemseged, Z., Marean, C.W., Wynn, J.G., Reed, D., Geraads, D.,
714 Bobe, R., Béarat, H.A., 2010. Evidence for stone-tool-assisted consumption of animal
715 tissues before 3.39 million years ago at Dikika, Ethiopia. Nature 466, 857–860.
716 Milton, K., 1979. Factors influencing leaf choice by howler monkeys: a test of some
717 hypotheses of food selection by generalist herbivores. Am. Nat. 114, 362–378.
718 Norton, G.W., Rhine, R.J., Wynn, G.W., Wynn, R.D., 1987. Baboon diet: a five-year
719 study of stability and variability in the plant feeding and habitat of the yellow baboons
720 (*Papio cynocephalus*) of Mikumi National Park, Tanzania. Folia Primatol. 48, 78–120.
721 O'Reagain, P., Mentis, M., 1989. The effect of plant structure on the acceptability of
722 different grass species to cattle. Journal of the Grassland Society of Southern Africa 6,
723 163–170.
724 O'Reagain, P.J., 1993. Plant structure and the acceptability of different grasses to sheep.
725 J. Range Manage. 46, 232–236.
726 Oates, J.F., Whitesides, G.H., Davies, A.G., Waterman, P.G., Green, S.M., Dasilva,
727 G.L., Mole, S., 1990. Determinants of variation in tropical forest primate biomass: new
728 evidence from West Africa. Ecology 71, 328–343.
729 Oudtshoorn, F.v., 1999. Guide to Grasses of Southern Africa. Briza Publications,
730 Pretoria.

731 Peters, C.R., Vogel, J.C., 2005. Africa's wild C_4 plant foods and possible early hominid
732 diets. J. Hum. Evol. 48, 219–236.
733 Post, D.G., 1982. Feeding behavior of yellow baboons (*Papio cynocephalus*) in the
734 Amboseli National Park, Kenya. Int. J. Primatol. 3, 403–430.
735 Prize, C., Workings, I., Classics, P., Portals, P., Statements, S., 2013. African hominin
736 stable isotopic data do not necessarily indicate grass consumption. Poc. Natl. Acad. Sci.
737 110, 17163–17164.
738 Rabenold, D., Pearson, O.M., 2011. Abrasive, silica phytoliths and the evolution of
739 thick molar enamel in primates, with implications for the diet of Paranthropus boisei.
740 PLoS One 6, e28379.
741 Raia, P., 2004. Morphological correlates of tough food consumption in large land carnivores.
742 Ital. J. Zool. 71, 45–50.
743
744 Rak, Y., 1988. On variation in the masticatory system of *Australopithecus boisei*. in Grine, F.
745 (Ed.), Evolutionary History of the "Robust" Australopithecines. Transaction Publishers, New
746 York, pp.193–198.
747 Rak, Y., 2014. The Australopithecine Face. Academic Press, New York.
748 Reed, J., Krueger, C., Rodriguez, G., Hanson, J., 2000. Secondary plant compounds and
749 forage evaluation. in, Givens, D.I., Owen, E., Axford, R.F.E. (Eds.), Forage Evaluation
750 in Ruminant Nutrition. CABI Publishing, New York, pp. 433–448.
751 Reed, K.E., Spencer, L.M., Rector, A.L., 2013. Faunal approaches in early hominin
752 paleoecology. in, Sponheimer, M. (Ed.), Early Hominin Paleoecology. University
753 Press of Colorado, Boulder, pp. 3–34.
754 Remis, M.J., Dierenfeld, E., Mowry, C., Carroll, R., 2001. Nutritional aspects of
755 western lowland gorilla (*Gorilla gorilla gorilla*) diet during seasons of fruit scarcity at
756 Bai Hokou, Central African Republic. Int. J. Primatol. 22, 807–836.
757 Robbins, C., 2012. Wildlife Feeding and Nutrition. Academic Press, New York.
758 Rogers, M.E., Maisels, F., Williamson, E.A., Fernandez, M., Tutin, C.E., 1990. Gorilla
759 diet in the Lopé Reserve, Gabon. Oecologia 84, 326–339.
760 Rothman, J.M., Chapman, C.A., Struhsaker, T.T., Raubenheimer, D., Twinomugisha,
761 D., Waterman, P.G., 2015. Long-term declines in nutritional quality of tropical leaves.
762 Ecology 96, 873–878.
763 Rothman, J.M., Dierenfeld, E.S., Molina, D.O., Shaw, A.V., Hintz, H.F., Pell, A.N.,
764 2006. Nutritional chemistry of foods eaten by gorillas in Bwindi Impenetrable National
765 Park, Uganda. Am. J. Primatol.68, 675–691.
766 Sage, R.F., 2004. The evolution of C4 photosynthesis. New Phytol. 161, 341–370.
767 Sage, R.F., Sage, T.L., Pearcy, R.W., Borsch, T., 2007. The taxonomic distribution of
768 C_4 photosynthesis in Amaranthaceae sensu stricto. Am. J. Bot. 94, 1992–2003.

769   Scholes, R., Archer, S., 1997. Tree-grass interactions in savannas 1. Annu. Rev. Ecol.
770   Syst. 28, 517–544.

771   Simpson, S.J., Raubenheimer, D., 2012. The Nature of Nutrition: A Unifying
772   Framework from Animal Adaptation to Human Obesity. Princeton University Press,
773   Princeton.

774   Sniffen, C., O'connor, J., Van Soest, P., Fox, D., Russell, J., 1992. A net carbohydrate
775   and protein system for evaluating cattle diets: II. Carbohydrate and protein availability.
776   J. Anim. Sci. 70, 3562–3577.

777   Sponheimer, M., Alemseged, Z., Cerling, T.E., Grine, F.E., Kimbel, W.H., Leakey,
778   M.G., Lee-Thorp, J.A., Manthi, F.K., Reed, K.E., Wood, B.A., 2013. Isotopic evidence
779   of early hominin diets. Proc. Natl. Acad. Sci. 110, 10513–10518.

780   Sponheimer, M., Loudon, J., Codron, D., Howells, M., Pruetz, J.D., Codron, J., De
781   Ruiter, D., Lee–Thorp, J.A., 2006. Do "savanna" chimpanzees consume C_4 resources?
782   J. Hum. Evol. 51, 128–133.

783   Stirton, R., 1947. Observations on evolutionary rates in hypsodonty. Evolution 1, 32–
784   41.

785   Stohlgren, T.J., Falkner, M., Schell, L., 1995. A modified–Whittaker nested vegetation
786   sampling method. P. Ecol. 117, 113–121.

787   Strait, D.S., Constantino, P., Lucas, P.W., Richmond, B.G., Spencer, M.A., Dechow,
788   P.C., Ross, C.F., Grosse, I.R., Wright, B.W., Wood, B.A., Weber, G.W., Wang, Q.,
789   Byron, C., Slice, D.E., Chalk, J., Smith, A.L., Smith, L.C., Wood, S., Berthaume, M.,
790   Benazzi, S., Dzialo, C., Tamvada, K., Ledogar, J.A., 2013. Viewpoints: diet and dietary
791   adaptations in early hominins: the hard food perspective. Am. J. Phys. Anthropol. 151,
792   339–355.

793   Strait, D.S., Wright, B.W., Richmond, B.G., Ross, C.F., Dechow, P.C., Spencer, M.A.,
794   Wang, Q., 2008. Craniofacial strain patterns during premolar loading: implications for
795   human evolution. in, Vinyard, C., Ravosa, M.J., Wall, C. (Eds.), Primate Craniofacial
796   Function and Biology. Springer, New York, pp. 173–198.

797   Tobias, P.V., 1967. Olduvai Gorge. Cambridge University Press, Cambridge.

798   Ungar, P., Hlusko, L., 2016. The evolutionary path of least resistance. Science 353, 29–
799   30.

800   Ungar, P.S., 2010. Mammal teeth: origin, evolution, and diversity. JHU Press.

801   Ungar, P.S., Grine, F.E., Teaford, M.F., 2008. Dental microwear and diet of the Plio–
802   Pleistocene hominin *Paranthropus boisei*. PLoS One 3, e2044.

803   Ungar, P.S., Krueger, K.L., Blumenschine, R.J., Njau, J., Scott, R.S., 2012. Dental
804   microwear texture analysis of hominins recovered by the Olduvai Landscape
805   Paleoanthropology Project, 1995–2007. J. Hum. Evol. 63, 429–437.

806   Ungar, P.S., Sponheimer, M., 2011. The diets of early hominins. Science 334, 190–193.

807 van der Merwe, N.J., Masao, F.T., Bamford, M.K., 2008. Isotopic evidence for
808 contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of
809 Tanzania. S. Afr. J. Sci. 104, 153–155.
810 Van Soest, P., Jones, L., 1968. Effect of silica in forages upon digestibility. J. Dairy
811 Sci. 51, 1644–1648.
812 Venkataraman, V.V., Glowacka, H., Fritz, J., Clauss, M., Seyoum, C., Nguyen, N.,
813 Fashing, P.J., 2014. Effects of dietary fracture toughness and dental wear on chewing
814 efficiency in geladas (*Theropithecus gelada*). Am. J. Phys. Anthropol. 155, 17–32.
815 Vogel, E.R., van Woerden, J.T., Lucas, P.W., Atmoko, S.S.U., van Schaik, C.P.,
816 Dominy, N.J., 2008. Functional ecology and evolution of hominoid molar enamel
817 thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. J. Hum. Evol.
818 55, 60–74.
819 Vogel, E.R., Zulfa, A., Hardus, M., Wich, S.A., Dominy, N.J., Taylor, A.B., 2014.
820 Food mechanical properties, feeding ecology, and the mandibular morphology of wild
821 orangutans. J. Hum. Evol. 75, 110–124.
822 Waterman, P.G., Choo, G.M., Vedder, A.L., Watts, D., 1983. Digestibility, digestion–
823 inhibitors and nutrients of herbaceous foliage and green stems from an African montane
824 flora and comparison with other tropical flora. Oecologia 60, 244–249.
825 White, T.E., 1959. The endocrine glands and evolution, no. 3: os cementum
826 hypsodonty, and diet. Contributions from the Museum of Paleontology, The University
827 of Michigan. 13, 211–265.
828 Wood, B., Constantino, P., 2007. *Paranthropus boisei*: fifty years of evidence and
829 analysis. Am. J. Phys. Anthropol. 134, 106–132.

830 Wrangham, R., Cheney, D., Seyfarth, R., Sarmiento, E., 2009. Shallow-water habitats

831 as sources of fallback foods for hominins. Am. J. Phys. Anthropol. 140, 630–642.
832 Wrangham, R., Conklin-Brittain, N., Chapman, C., Hunt, K., Milton, K., Rogers, E.,
833 Whiten, A., Barton, R., 1991. The significance of fibrous foods for Kibale Forest
834 chimpanzees [and discussion]. Phil. Trans. R. Soc. B. 334, 171–178.
835 Wrangham, R.W., Conklin–Brittain, N.L., Hunt, K.D., 1998. Dietary response of
836 chimpanzees and cercopithecines to seasonal variation in fruit abundance. I.
837 Antifeedants. Int. J. Primatol. 19, 949–970.
838 Wright, B.W., 2005. Craniodental biomechanics and dietary toughness in the genus
839 *Cebus*. J. Hum. Evol. 48, 473–492.
840 Yeakel, J.D., Bennett, N.C., Koch, P.L., Dominy, N.J., 2007. The isotopic ecology of
841 African mole rats informs hypotheses on the evolution of human diet. Proc. R. Soc.
842 Lond. B. 274, 1723–1730.
843 Yeakel, J.D., Dominy, N.J., Koch, P.L., Mangel, M., 2014. Functional morphology,
844 stable isotopes, and human evolution: a model of consilience. Evolution 68, 190–203.