Seasonal and habitat effects on the nutritional properties of savanna vegetation: potential implications for early hominin dietary ecology

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Abstract

The African savannas that many early hominins occupied likely experienced stark

seasonality and contained mosaic habitats (i.e., combinations of woodlands, wetlands,

30 grasslands, etc.). Most would agree that the bulk of dietary calories obtained by taxa such

as *Australopithecus* and *Paranthropus* came from the consumption of vegetation growing

across these landscapes. It is also likely that many early hominins were selective feeders

that consumed particular plants/plant parts (e.g., leaves, fruit, storage organs) depending

on the habitat and season within which they were foraging. Thus, improving our

35 understanding of how the nutritional properties of potential hominin plant foods growing

in modern African savanna ecosystems respond to season and vary by habitat will

improve our ability to model early hominin dietary behavior. Here, we present nutritional

analyses (crude protein and acid detergent fiber) of plants growing in eastern and

southern African savanna habitats across both wet and dry seasons. We find that many

40 assumptions about savanna vegetation are warranted. For instance, plants growing in our

woodland habitats have higher average protein/fiber ratios than those growing in our

wetland and grassland transects. However, we find that the effects of season and habitat

are complex, an example being the higher protein levels we observe in the grasses and

sedges growing in our Amboseli wetlands during the dry season. Also, we find

45 significant differences between the vegetation growing in our eastern and southern

African field sites, particularly among plants using the C_4 photosynthetic pathway. This

may have important implications for the contrasting dietary interpretations that stable

carbon isotope and dental microwear analyses have suggested for eastern and southern

African *Paranthropus* species.

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Introduction

Many early hominin species are understood to have inhabited landscapes that

were characterized by stark seasonality and mosaic habitats, just as modern African

savannas are today (Dart, 1925; Howell and Bourliere, 1963; Wolpoff, 1980; Huntley,

55 1982; Vrba, 1995; Reed et al., 2013; Domínguez-Rodrigo, 2014). Though recent

evidence suggests that eastern African *Australopithecus* likely consumed faunal resources

(McPherron et al., 2010; Harmand et al., 2015), most agree that the bulk of dietary

calories obtained by these early hominins came from plants. Additionally, many early

hominins (i.e., pre-*Homo*) were probably eclectic feeders that consumed a variety of plant

60 types and plant parts (e.g., leaves, fruits, seeds, flowers, underground storage organs), and

there is evidence that diets varied both between and within species (Ungar and

Sponheimer, 2011). These variations were potentially driven, at least in part, by the

effects that habitat and season have on the nutritional chemistry of savanna vegetation.

Furthermore, due to inherent differences in climate and geology, these effects were likely

65 to have manifested in different ways across the eastern and southern African landscapes

known to have been occupied by fossil hominins.

While no modern savanna ecosystem can serve as a direct analog for the African

Plio-Pleistocene, an understanding of how the nutritional properties of modern savanna

vegetation vary across habitats and seasons will ultimately improve models of early

70 hominin dietary ecology. Indeed, there is long history of using modern savanna plants to

investigate hominin feeding behavior (e.g., Carr, 1976; Peters and Maguire, 1981; Peters and O'Brien, 1981; Sept, 1986, 1996; Peters and Blumenschine, 1995; Andrews and Bamford, 2008; Copeland, 2009), and previous researchers have also investigated the seasonal and/or habitat variation of potential hominin plant foods (e.g., Peters and

75 Maguire, 1981; Sept, 1986, 2001; Peters et al., 1984; Peters and Blumenschine, 1995; Copeland 2007, 2009). For example, Sept (2001) developed hypothetical plant diets for baboons, chimpanzees, modern hunter-gatherers, australopiths, and early *Homo* based on the adaptations and foraging capabilities each taxon may, or may not have had (e.g., increased craniodental robusticity, the use of tools, the use of fire). She then assessed

80 abundance and seasonal availability of plant foods assigned to each taxon in one-hectare plots within two Kenyan semiarid riparian ecosystems, one located in the Turkana basin, northern Kenya, and the other in the Tsavo region of southern Kenya. While these sites are similar in vegetation, they differ in terms of rainfall and geological substrate. In particular, Sept (2001) found that non-megadont australopiths (e.g., *Australopithecus*

85 *anamensis, Australopithecus afarensis*), without the aid of rudimentary digging tools to access underground plant organs, would have struggled to gain enough calories across seasons in the southern Kenyan site. In contrast, megadont australopiths (e.g., *Paranthropus aethiopicus, Paranthropus boisei*) using digging sticks to access underground foods (Brain, 1993; Sussman, 1998) would have fared reasonably well. Sept

90 (2001) concluded that both taxa would have been successful at the Turkana site, despite lower precipitation, due to the fact that its volcanic soils allowed for more productive vegetative growth and thus less of a need to rely on underground plant organs for dietary calories.

In another study, Copeland (2009) examined the diets of chimpanzees living in

95 relatively high-rainfall savannas (750–1200 mm/yr) and contrasted them with the plants

available in semiarid savannas in northern Tanzania, under the premise that hominin

fossils from the region are generally associated with more open, drier habitats. Copeland

(2009) noted that fruit is scarce in semiarid savannas and that if early hominins habitually

occupied these landscapes, as the fossil record suggests, they were unlikely to have been

100 able to maintain the level of frugivory exhibited by moist-savanna chimpanzees, let alone

those living in forested habitats such as Mahale National Park, Tanzania, and Kibale

National Park, Uganda. Interestingly, despite the high prevalence of resources such as

grasses within their habitats, savanna chimpanzees do not heavily utilize them but instead

increase their home ranges to compensate for the patchier distribution of preferred fleshy

105 fruits (Pruetz, 2006; Sponheimer et al., 2006). In this regard, Copeland (2009) concluded

that hominins were probably not as dependent on fruit as savanna chimpanzees are today,

and instead may have consumed grasses and *Acacia* (*Vachellia*) spp. in a manner more

similar to baboons (*Papio* spp.; DeVore and Washburn, 1963; Altmann and Altmann,

1970; Post, 1982; Altmann et al., 1987; Norton et al., 1987; Barton et al., 1993; Barton

110 and Whiten, 1994; Altmann, 1998). She also suggested that the exploitation of

underground organs (as proposed by Conklin-Brittain et al., 2002; Sponheimer et al.,

2005; Wrangham, 2005) might have been an important component of hominin feeding

behavior.

The studies highlighted above, and others, offer valuable insight into the way the

115 heterogeneous nature of savanna landscapes likely influenced early hominin feeding

behavior. However, they do not directly investigate how the nutritional chemistry (e.g.,

crude protein, dietary fiber, non-structural carbohydrates, lipids) of savanna vegetation varies across habitats and seasons, and in response to the inherent regional differences between eastern and southern Africa (e.g., soil types, rainfall modality, seasonal

120 temperature fluctuations). To be sure, studies of African ungulate diets have investigated how the nutritional properties of graze and browse are affected by season and habitat, and have demonstrated that certain habitats offer higher quality resources at different times of the year due to factors such as rainfall patterns/levels, soil chemistry, and elevation (see Robbins, 1993; Prins and Van Langervelde, 2008, Searle and Shipley, 2008). However,

125 while these studies are informative, many ungulates have specialized dentition and/or digestive capabilities that hominins most likely lacked. Thus, these studies do not speak directly to hominin feeding behavior. Also, these studies generally do not include plant organs that are specifically targeted by many primates such as inflorescences and underground storage organs.

130   Here, we begin to address these gaps by examining the spatiotemporal variation of two nutritional measures—crude protein and dietary fiber—in plants growing in savannas of eastern and southern Africa. The questions we address include: 1) does our eastern African site, with its volcanic soil and tropical climate, contain plants with higher protein/fiber ratios, on average, compared to those growing in our South African site? 2)

135 do plant categories have different protein/fiber ratios in different habitats? For example, do grasses growing in woodlands have higher protein-ratios than those growing in more open environments? 3) do habitats with higher dicot/monocot ratios, such as woodlands, contain plants with higher protein/fiber ratios than monocot-dominated habitats, such as

grasslands and wetlands? 4) are the effects of seasonality habitat specific, such as in

140 wetlands where plants have year-round access to water?

Methods

We collected plant samples from wet and dry seasons in The Cradle Nature

Reserve (The Cradle), South Africa (July 2014 and January 2015), and Amboseli

145 National Park (Amboseli), Kenya (May 2016 and August 2017). The Cradle was chosen

because it sits in the Sterkfontein Valley, which is home to several of the major hominin

fossil bearing sites in South Africa. Its dolomitic soils and unimodal rainfall contrast with

Amboseli, which was chosen because its volcanic soils, bimodal rainfall pattern, and

extensive wetlands likely characterized many of the environments inhabited by eastern

150 African hominins, including *P. boisei*.

For this study, we have grouped our transects (five in The Cradle and four in

Amboseli) into three broad habitat categories—grassland, woodland, and wetland

(following Reed et al., 2013)—that are representative of landscapes that early hominins

are thought to have inhabited. Grasslands had <10% woody cover, woodlands contained

155 trees 8–20 m in height that covered >40% of the transect, and wetlands were treeless

transects containing permanent water sources. The transects were randomly placed within

each habitat type and consisted of Modified-Whittaker sampling plots measuring 20m by

50m, with subplots of varying sizes nested within (see Stohlgren et al., 1995). Most

transects within each field site were many kilometers away from each other, with the

160 closest two roughly half a kilometer apart—a wetland and woodland within The Cradle.

We collected four individual samples of the most abundant grass, sedge, tree, and forb

species (when available) as determined according to methods outlined in Stohlgren et al. (1995). 'Forbs' in this study are non-woody plants that are neither grasses nor sedges. Samples were separated into their constituent organs for analyses (e.g., seed, leaf, fruit,

165 and storage organ). All fruit within our transects was sampled regardless of abundance because most fruit, though generally scarce on savanna landscapes, represents a resource that was likely targeted and exploited by hominins (Suzuki, 1969; Dunbar, 1976; McGrew et al., 1981; Nishida and Uehara, 1983; Peters and Vogel, 2005).

In addition to designating three broad habitat categories, we grouped our samples

170 into three categories of plant foods based on organs/structures known to be eaten by primates: leaves, reproductive organs (inflorescences of grasses and sedges, fruit, and flowers), and storage organs (tubers, rhizomes, and stolons). We do not include stems or roots in this current study. We analyzed our fruits whole, including the exocarp, flesh, and seeds, as this is how baboons typically consume them. All of our fruits are relatively

175 small (<3 cm in diameter) and none had a thick rind. Similarly, grass and sedge seeds were analyzed as whole inflorescences, which for species with panicles include primary and secondary axes and spatheoles. Underground storage organs (USOs) were harvested when present in association with their above ground parts.

We dried wet samples in the field in Excalibur® dehydrators at 40° C, sealed dried

180 samples in paper bags with desiccant, and exported them to the Nutritional and Isotopic Ecology Lab (NIEL) at the University of Colorado Boulder for nutritional analyses. We present results for crude protein (CP) and acid detergent fiber (ADF) as a percentage of dry weight in the form of protein/fiber ratios (CP/ADF; Supplementary Online Material (SOM) File S1). We chose this ratio measurement because it is a widely used proxy for

185 overall forage quality (Robbins, 1993; McNaughton and Georgiadis, 1986). Crude

protein was measured with a LECO® FP 528 nitrogen analyzer using the standard %N ×

6.25 conversion to obtain %CP. ADF was measured with an ANKOM® 2000 fiber

analyzer within a sequential series of dietary fiber analyses—i.e., a single sample was

analyzed for neutral detergent fiber (NDF), ADF, and acid detergent lignin (ADL) in that

190 order (see Terrill et al., 2010). We chose ADF as a measure of fiber (as opposed to NDF

or crude fiber) because it theoretically represents the fiber fraction without

hemicelluloses, which are at least partially digested by primates (Lambert, 1998). Thus,

ADF is a more appropriate measure of the dietary fiber that is largely indigestible to

mammals, such as hominins, without specialized digestive systems.

195   Our protein/fiber ratios were natural log-transformed and two three-factor

analysis of variance (ANOVA) tests were performed. One analyzed the effects of plant

category, habitat, and season on protein/fiber ratios and the other analyzed the effects of

field site, habitat, and season. We could not run a four-factor ANOVA with all variables

combined due to the fact that not all plant categories are represented seasonally in each

200 field site. Kruskal-Wallis tests with multiple comparisons using the Steel-Dwass method,

when appropriate, were run for single factor comparisons. Our figures include the

average protein/fiber ratios reported by Rothman et al. (2006) for foods consumed by

eastern gorillas (*Gorilla berengei*) in Bwindi Impenetrable National Park, Uganda. We

use gorilla foods, as opposed to chimpanzee foods, because chimpanzee diets are heavily

205 reliant on fleshy fruits, and we have relatively few fruits in our sample given their

scarcity in savanna habitats. That being said, the gorilla protein/fiber ratios are meant to

situate our data in a hominoid dietary context, and are not meant to imply anything about

what hominins did, or did not, eat. All statistical analyses were performed in JMP® Pro

13.0.0 (SAS Institute, 2016). We set our significance level at α = 0.05.

210   Importantly, we note that Amboseli (and most of the surrounding region) was in

the midst of a historic drought when we collected our dry season samples. Thus, the

samples we collected during this time potentially represent the extremes of variation for

any given plant taxon.

215 **Results**

Our three-factor ANOVA examining plant categories, habitat, and season shows

that protein/fiber ratios are significantly influenced by plant category (p = 0.0001) and

habitat (p = 0.0002), but, unexpectedly, not by season (p = 0.4282). None of the

interactions were significant, though the interaction between plant category and habitat

220 was the strongest and closest to reaching significance (p = 0.0556; Table 1). Leaves and

reproductive organs have higher protein/fiber ratios than storage organs and vegetation in

woodland habitats skews higher than vegetation found in wetlands and grasslands.

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Our three-factor ANOVA examining field site, habitat, and season reveals that

field site and habitat strongly influence our protein/fiber ratios (p < 0.0001), yet their

interaction is not significant (p = 0.1354; Table 2). Once again, season does not

significantly influence protein/fiber ratios, but its interactions with habitat and field site

230 do. On the whole, the vegetation in Amboseli has higher protein/fiber ratios and, once

again, our woodland transects are driving the differences between habitats.

235 **Discussion**

Our study illuminates the nutritional properties of an array of taxonomic and

functional plant groups that are directly relevant to primate and hominin feeding behavior

and quantifies temporal differences across habitats at two spatial scales—regional and

local. For the most part, our results are consistent with received wisdom about savanna

240 plant nutrients. First and foremost, our data reveal strong differences between eastern and

southern African field sites, an expected result due to inherent climatic and geological

differences between the two regions. Other results were also expected, such as the higher

protein/fiber ratios of woodland plants and lower ratios for storage organs. However,

some results, such as the lack of seasonal differences within habitats, were less expected.

245 We discuss these issues in more detail below.

Field site comparisons

Our study cannot speak comprehensively to the broader, regional differences that

exist between eastern and southern African savanna ecosystems and how they may have

250 influenced differences in hominin feeding behavior across large geographical ranges. We

have only sampled the vegetation from one field site within each region of the continent,

and each field site has its own biogeographical history and local patterns of biodiversity

that set it apart from neighboring landscapes as much as they do from one another. For

example, the South African Highveld is a distinct geological and floral region within

255 southern Africa—one only needs to travel a few hundred kilometers from the fossil-

bearing sites to reach the Lowveld, which does not experience freezing temperatures

(Acocks, 1953; Mucina and Rutherford, 2011).

Nonetheless, the strong differences we found between the two fields sites (Table

2) are certainly influenced by broader, regional differences between eastern and southern

260 Africa. For one, soil chemistry, which heavily affects the plants growing upon them

(Anderson and Talbot, 1965; Cole, 1982; McNaughton, 1983; Mutanga et al., 2004), is

very different at the two sites. The Cradle is characterized by dolomitic soils whereas

Amboseli is located in a volcanic basin, and, as noted in the Introduction, volcanic soils

were cited by Sept (2001) as the reason for increased soil fertility in her more productive

265 transects. Also, the seasonality each site experiences differs at a regional level. There are

two annual rainy and dry seasons in many parts of eastern Africa, including Amboseli,

whereas the Highveld experiences only one of each (Herrmann and Mohr, 2011). Perhaps

most importantly, the Highveld, with an elevation of ~1480 m, experiences a dry season

marked by occasional temperatures below freezing, which result in areas of measurable

270 frost (Schulze, 1997). Amboseli, although at an elevation of ~1130 m, is roughly 200 km

south of the equator and does not experience such pronounced temperature fluctuations

across seasons (Williams, 1972).

Habitat comparisons

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275   We find that woodland habitats have vegetation with higher protein/fiber content

than vegetation in grassland and wetland habitats (Figure 1; Table 3). This was expected

as woodlands, by definition, have higher dicot/monocot ratios and tree leaves generally

have higher protein levels compared to monocots such as grasses and sedges. However, it

is important to note that woodlands also provide shade and water storage for plants

280 growing in the understory, which in turn can lead to higher nutrient content. Also, there

are complex relationships between grasses and trees that can positively affect the

abundance and nutrient levels of grasses, particularly in certain *Acacia*-dominated

woodlands (Knoop and Walker, 1985; Scholes and Archer, 1997). In fact, our wet season

Acacia woodland grass leaves (one transect in Amboseli and one in The Cradle) have

285 significantly higher protein/fiber ratios compared to grass leaves growing in other

habitats (Kruskal-Wallis: $p < 0.0001$). This would tend to support arguments that

woodland habitats represented preferred hominin feeding locations (Sikes 1994).

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Seasonal comparisons

Neither ANOVA reveals significant seasonal effects on the protein/fiber ratios of

295 our plant samples. This is unexpected because seasonal climate changes are known to

have some of the biggest effects on phenological, and hence, biochemical changes in

plants throughout their life cycle (Schulze, 1997). However, the significant interactions

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among season, habitat, and field site in our second ANOVA (Table 2) suggest underlying

seasonal complexities that are masking larger scale, landscape-wide differences. When

300 we dig more deeply into our dataset, we find several anomalies that are driving our

ANOVA results, suggesting that our data do, in fact, reveal some strong seasonal

differences but that their occurrence and direction are mediated by field site, habitat, and

plant category. We highlight two examples below.

305 <u>The leaves of wetland grasses and sedges in Amboseli</u> In our Amboseli wetland transects,

the protein/fiber ratios of the leaves of grass and sedge species for which we have wet

and dry season data (five species) show an increase in protein/fiber ratios during the dry

season (p = 0.0118; Fig. 2), a reversal of the trend we observe in most other plants.

310

Because our Amboseli wetland transects offer a stable water source year-round,

one might assume that many of the plants growing within them are buffered against

seasonal changes at a fundamental level. Yet, the significant increase in dry season crude

315 protein content (as opposed to a decrease in ADF; p = 0.0197) that is driving the

increased protein/fiber ratios in our samples is perhaps surprising in light of the fact that

Amboseli was experiencing a historic drought during our collections. This increase in

crude protein content may actually be an indirect result of the broad scale seasonal

stresses that affect the large mammalian fauna in the park. During the dry season in

320 Amboseli, and elsewhere, the larger mammals understandably tend to congregate near the

permanent wetlands. As such, this concentration of fauna can lead to an increase in soil nitrogen due to higher amounts of urea being added to the wetland habitats (Ruess and McNaughton, 1984), which in turn increases soil fertility. The increase in protein that we see in dry season wetland monocots likely reflects this higher soil fertility.

325

Storage organs in The Cradle. Because storage organs contain the caloric reserves a plant maintains for regrowth after dormancy, one might hypothesize that they are also somewhat buffered against seasonal effects. When we examine the storage organs in our analyses, we find that those we sampled in The Cradle show significant increases in
330 protein/fiber ratios during the dry season (Fig. 3; p = 0.0002), whereas those in Amboseli remain unchanged (p = 0.4589). The increased protein/fiber ratios of samples from The Cradle are driven by both lower ADF levels and significantly higher protein content (Kruskal-Wallis: p = 0.0004). This may be the effect of the starker seasonality we see in the Highveld whereby larger energy reserves may be necessary for survival across the
335 longer, colder dry season. There is one species that does not fit this trend, *Hypoxis hemerocallidea*, which represents the extreme outlier in our wet season sample and the second highest value in our dry season sample (Fig. 3). However, it is toxic when eaten raw and is only used by humans medicinally, though several of its congeners are known to be human and primate foods (Peters et al., 1992; van Wyk and Gericke, 2000). It is
340 also worth noting that there are significantly higher protein/fiber ratios (Kruskal-Wallis: p < 0.0001; no overlapping values) in dry season storage organs growing in our wetland transect, including the rhizomes of *Typha capensis* and *Juncus effusus.*

345

Implications for hominins

<u>Habitat, season, abundance, and selectivity</u> Our analyses reveal that vegetation with the

highest protein/fiber ratios is generally found in the woodland habitats at both field sites,

and woodlands are a consistent, if not dominant component of australopith

350 paleoenvironmental reconstructions (e.g., Sikes, 1994; Reed, 1997; Bobe et al., 2002;

Reynolds et al., 2007; de Ruiter et al., 2008; Behrensmeyer and Reed, 2013).

Nonetheless, wetlands appear to seasonally offer resources with relatively high

protein/fiber ratios, potentially on landscapes where other dry season habitats show a

decline. In this regard, while the wet season plants in our study are generally 'better'

355 candidates for hominin foods from a protein/fiber ratio perspective, it is clear that the dry

season vegetation is not necessarily 'worse' across the board.

For instance, if we use the protein/fiber ratios of Bwindi gorilla foods as a gauge

(mean ln CP/ADF= –1.15, SD = 0.89; Rothman et al., 2006), we find that vegetation

within these parameters exists across seasons, within all habitats (Fig. 1). Of course, we

360 are not suggesting that all plants in our study within this range would have been edible

for hominin foragers. However, these data demonstrate that adequate, if not preferred

dietary resources can be obtained across habitats and seasons for highly selective,

generalist herbivores, which many hominins may have been. Indeed, savanna baboons,

which are generalist feeders, take advantage of the rarer, preferred resources when they

365 are available while eating more ubiquitous foods year-round, such as the leaves and

corms of grasses and sedges (Barton et al., 1993; Barton and Whiten, 1994; Altmann,

1998). For example, Barton et al. (1993) analyzed the protein/fiber ratios (CP/ADF) of acacia seeds eaten by baboons in the Laikipia Plateau, Kenya, and reported an untransformed value of 12.89—almost five times higher than the highest untransformed

370   value from our samples. However, these seeds represented only 3.3% of their total diet and are not indicative of the general protein/fiber content of baboon foods. In fact, by looking at the food groups that each account for 10% or more of Laikipia baboon diet (*Acacia* flowers, 18%; grass blades, 12.4%; fruits, 11.7%; sedge bulbs, 11.4%), we find a mean, untransformed protein/fiber ratio of 0.75. Within our study, 75 samples (~14%)

375   fall above this protein/fiber threshold representing all habitats and plant types, as well as both seasons.

It is important to note that the relative abundance of food resources is a crucial factor to incorporate when studying the dietary behavior of an organism. The behavioral calculus that many generalist herbivores have to make is essentially a cost/benefit

380   analysis. On average, high-nutrient, energy-rich foods are found in low densities within savanna landscapes (Suzuki, 1969; Dunbar, 1976; McGrew et al., 1981; Nishida and Uehara, 1983; Peters, 1987) and their exploitation requires more energy and time directed towards their discovery and harvesting (Altmann and Altmann, 1970, Altmann, 1974). Conversely, while savanna habitats are replete with lower-nutrient foods, more energy

385   and time must be directed towards their consumption and digestion (Searle and Shipley, 2008).

Relative abundance is accounted for in our study, as we focused our sampling on the most abundant taxa; however, certain items are undoubtedly overrepresented in our dataset. As noted, we sampled any and all fruits we found in our transects, regardless of

390 abundance, because such items are actively sought after by baboons and were likely to

have been readily exploited by hominins. Nonetheless, relative abundance is a key factor

to incorporate when reconstructing hominin dietary behavior. For example, grasses are

often overlooked or dismissed as potential resources for hominins yet their nutritional

properties are highly variable, with many having some of the highest protein/fiber ratios

395 within their respective habitats (Paine et al., 2018). What is more, grasses are not only

ubiquitous, they are a requirement for any definition of a savanna landscape so at the very

least, their sheer abundance must preclude their removal from hominin dietary models.

Hominins and C_4 foods Since many of the earlier studies of potential hominin plant foods

400 were concluded (e.g., Carr, 1976; Peters and Maguire, 1981; Peters and O'Brien, 1981;

Sept, 1986; Peters and Blumenschine, 1995; Andrews and Bamford, 2008; Copeland,

2009), new factors to incorporate in our exploration of early hominin diet have emerged.

Most notably, stable carbon isotope analyses reveal that hominins began to incorporate

significant amounts of C_4 foods into their diets beginning ~3.75 Ma (Cerling et al., 2013;

405 Sponheimer et al., 2013; Wynn et al., 2013; Levin et al., 2015). Thus, if the bulk of early

hominin dietary carbon was derived from the direct consumption of vegetation, these C_4

resources were most likely to have been the grasses and/or sedges that represent the vast

majority of C_4 plants on African savanna landscapes (Ungar and Sponheimer, 2011;

Sponheimer et al., 2013). C_4 forbs and plants using CAM photosynthesis may also have

410 influenced the isotopic signatures of early hominins, but they were likely only a minor

component of their diets as they are fairly scarce within these habitats (Lüttge, 2004).

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Given the above, a central question facing researchers studying early hominin

dietary ecology is why *P. boisei* and *Paranthropus robustus,* which share highly derived

craniodental adaptations believed to be directly related to diet, have such fundamentally

415 different results from isotopic and dental microwear analyses. The stable carbon isotope

compositions for the southern African species, *P. robustus,* suggest a mixed diet of C_3

and C_4 foods (Sponheimer et al., 2006) and dental micro- and macrowear analyses reveal

a significant degree of hard object feeding (Scott et al., 2005; Towle et al., 2017). This

evidence aligns with morphological interpretations suggesting that the large, thickly

420 enameled molars and robust craniomandibular morphology of *Paranthropus* were direct

adaptations to a diet consisting of hard, obdurate foods that may have included C_3 tree

nuts and hard 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).

In stark contrast, the microwear of *P. boisei,* the hyperrobust eastern African species,

425 shows no evidence of hard object feeding and the results from stable carbon isotope

analyses indicate a diet of ~80% C_4 foods (Ungar et al., 2008; van der Merwe et al., 2008;

Cerling et al., 2011). The question then becomes: why did C_4 foods dominate the diet of

P. boisei, but not its congener, *P. robustus*?

If we isolate all of the C_4 plants in our analyses and compare them across seasons

430 within each field site, we find clear differences between the C_4 vegetation in Amboseli

versus The Cradle (Fig. 4). Among the four categories in Figure 4, all differences are

significant except for the plants collected during the wet and dry seasons at Amboseli

(Table 4). This suggests that C_4 plants represent a more stable food resource throughout

the year for herbivores in Amboseli compared to The Cradle. If we assume that the

435 regional differences between eastern and southern Africa today existed, to some degree,

in the past, then our data suggest that these differences between C_4 plants may have

important implications for the diet of *Paranthropus.*

440

If one accepts the monophyly of *Paranthropus,* with *P. aethiopicus* as a potential stem

ancestor (Strait et al., 1997; Wood and Constantino, 2007), the robust craniodental

445 adaptations that characterize the genus would have been present in the *Paranthropus*

species that dispersed southward from eastern Africa. Could it be that the ancestor of *P.*

robustus was simply unable to find nutritionally adequate C_4 foods in the Highveld year-

round, and thus had to alter its diet accordingly? This is certainly plausible based on the

data we have presented but, again, our study is not comprehensive enough to legitimately

450 test such a hypothesis. Also, it is important to note that some *Australopithecus africanus*

specimens living in the Highveld ate significant amounts of C_4 foods, with stable carbon

isotope compositions that overlap the lower range of *P. boisei* (Ungar and Sponheimer,

2011; Sponheimer et al., 2013). This attests to the potential of C_4 plants in the Pliocene

Highveld as staple resources for hominins. However, there is considerable variation

455 among the carbon isotopic data for *A. africanus* and *P. robustus* (unlike the relative lack

of variation in *P. boisei* carbon isotope compositions across large spatial and temporal

scales; Lee-Thorp et al., 1994; Sponheimer and Lee-Thorp, 1999; van der Merwe et al.,

2003; Cerling et al., 2011; Sponheimer et al., 2006b, 2013), which may indicate that C_4

resources were consumed mostly in the wet season and/or woodlands, as our data

460 suggest, with open grassland C_4 foods being rejected. This certainly makes sense in the

context of other research positing that woodlands, in addition to offering higher quality

food, may have offered better protection from predators and safe sleeping sites for early

hominins (Susman et al., 1984; Sept, 1994; Sikes, 1994).

A woodland-based dietary reconstruction for *P. robustus* also fits with the habitat

465 reconstructions proposed by de Ruiter et al. (2008), who argued that this species was

more strongly associated with closed habitat taxa and thus may have adhered to more

wooded habitats within savanna landscapes. Modern chimpanzees living in savannas

spend most of their time in the wooded portions of their home ranges (Pruetz, 2006;

Yoshikawa and Ogawa, 2015), though they largely avoid eating the C_4 plants among

470 them, which contrasts with our understanding of most hominin feeding behavior in

similar environments (Sponheimer et al., 2006). However, the predominantly C_3,

chimpanzee-like stable isotopic signatures of *A. anamensis* and *Ardipithecus ramidus*

(White et al., 2009; Cerling et al., 2013; Sponheimer et al., 2013) might indicate that

they, like contemporary chimpanzees, favored tree-based resources in woodland (or

475 other) habitats.

Limitations and future directions

While protein/fiber ratios employed here are a useful and important proxy for the

palatability of primate plant foods, they by no means represent a complete nutritional

480 analysis. For instance, they do not account for the antifeedants found in many savanna

plants that may have potentially hindered their palatability for hominin consumers. For example, savanna grasses tend to have higher amounts of silica in their tissues whereas tree leaves are generally more lignified, and contain higher amounts of secondary compounds that are potentially toxic to mammalian herbivores (Robbins, 1993; Skarpe

485 and Hester, 2008). Also, season and habitat may strongly influence other important nutritional components within plant types such as monosaccharides, lipids, micronutrients, and water content. These factors are undeniably important to account for when investigating hominin dietary behavior and will be investigated in future analyses.

It is also important to note that protein/fiber content is not always the appropriate

490 nutritional currency to use when exploring hominin feeding behavior, particularly given the recent emphasis on underground storage organs as potentially important hominin foods (e.g., Laden and Wrangham, 2005; Dominy et al., 2008; Wrangham et al., 2009; Dominy, 2012; Lee-thorp et al., 2012). Many underground storage organs are principally consumed as a source of energy (starch), rather than a source of protein, and energy

495 content is a crucial parameter to incorporate into investigations of hominin dietary ecology. That being said, it is interesting that our data show seasonal increases in storage organ protein/fiber ratios in The Cradle, suggesting that their importance to hominins in similar environments may have been cyclical, as others have suggested (e.g., Laden and Wrangham, 2005; Wrangham et al., 2009).

500

Conclusions

22

In a broad sense, our study suggests that the variation in the protein/fiber ratios of savanna vegetation can be reliably predicted by habitat, plant type, and field site in a

505 manner that conforms to expected patterns. Most clearly, plants growing in the volcanic soils and tropical climate of Amboseli have higher protein/fiber ratios, on average, when compared to plants growing in The Cradle. Particularly, there are highly significant differences between the C_4 plants at the two sites, which may have important implications for the isotopic and microwear differences observed between eastern and southern

510 *Paranthropus* species. Also, our woodland transects contain plants, both dicots and monocots, with higher protein/fiber ratios compared to those growing in other habitats, regardless of season.

However, though we generally observe declines in protein/fiber ratios during the dry season, our analyses reveal that seasonal variations are complex. The manner in

515 which wet and dry seasons affect the vegetation in our eastern and southern African field sites is significantly different, and certain habitats and/or plant parts do not respond to seasonality in a way that mirrors others in our study—a case in point being the increase in protein/fiber levels from wet season to dry season of the grass and sedge leaves growing in our Amboseli wetland transects, and in the storage organs sampled from The Cradle.

520 If we are to assume that most hominin species were eclectic feeders living within savanna landscapes, future models of their dietary behavior will need to incorporate these complexities. No reconstruction of hominin feeding behavior will ever be completely accurate just as no modern landscape can serve as a perfect analog for Plio-Pleistocene hominin habitats. Yet, by investigating how habitat and seasonal dynamics play out in

525 modern ecological systems, we can only improve our understanding early hominin

dietary behavior. In particular, we must acknowledge the regional differences between eastern and southern African savannas as a means to better understand the potential ecological differences between the hominin species that inhabited them.

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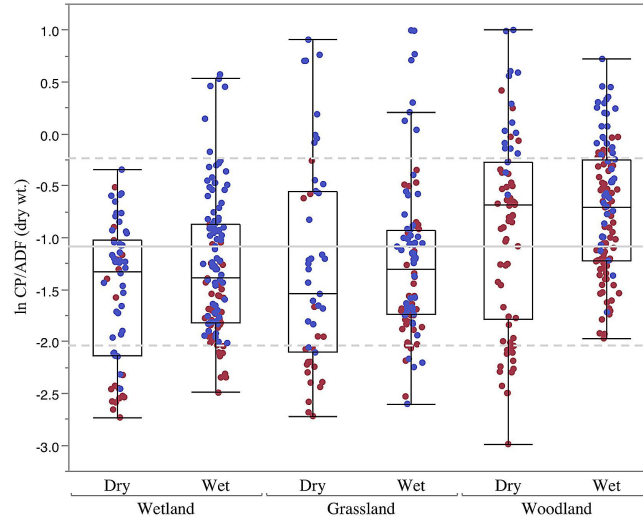
Figure Captions

Figure 1. Protein/fiber ratios of all plant parts (dry matter) grouped by habitat and season (Kruskal-Wallis: $p < 0.0001$). Solid gray line represents the mean ln CP/ADF for 119 foods eaten by gorillas in Bwindi Impenetrable National Park, Uganda (–1.15) and dotted lines represent the standard deviation (0.89). Gorilla data from Rothman et al. (2006).

815 Legend: blue dots = Amboseli; red dots = The Cradle. For statistical results of comparisons, refer to Table 3.
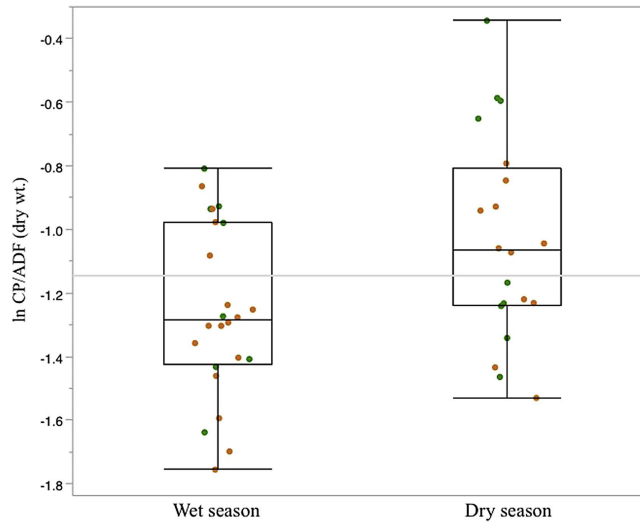
Figure 2. The protein/fiber ratios (dry matter) of the leaves of sedges (*Cyperus*

820 *immensus*, *Cyperus rotundus*,and *Pycreus mundtii*) and the two dominant grass species

(*Cynodon dactylon* and *Sporobolus spicatus*) within Amboseli wetlands. Seasons differ

significantly (Kruskal-Wallis: p = 0.0118). Legend: green = grass leaves; orange = sedge

leaves. Solid gray line represents the mean ln CP/ADF for 119 foods eaten by gorillas in

Bwindi Impenetrable National Park, Uganda (–1.15 with a standard deviation of 0.89).

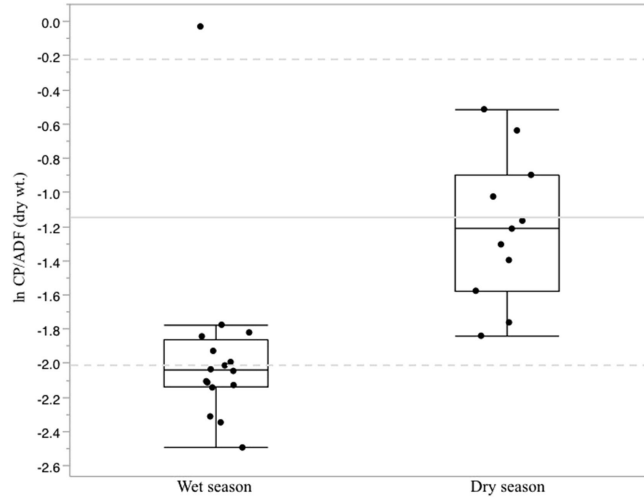825 Gorilla data from Rothman et al. (2006).

Figure 3. Protein/fiber ratios of storage organs (dry matter) in The Cradle. Seasons differ significantly (Kruskal-Wallis: $p = 0.0002$). Solid gray line represents the ln CP/ADF for 119 foods eaten by gorillas in Bwindi Impenetrable National Park, Uganda (-1.15) and dotted line represent the standard deviation (0.89). Gorilla data from Rothman et al. (2006).
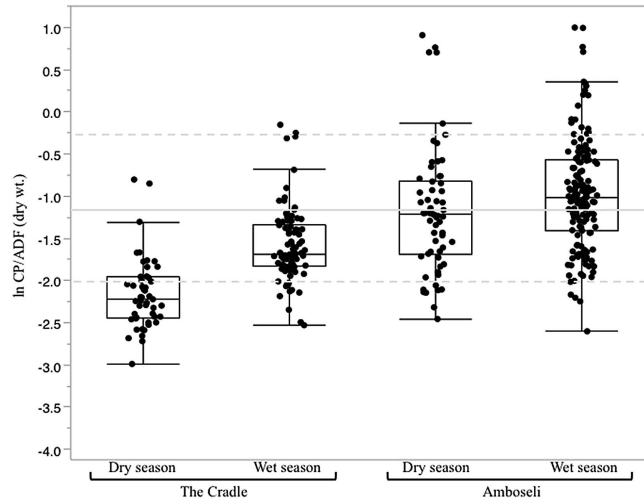
835 **Figure 4.** Protein/fiber ratios for all C_4 samples (dry matter) by season and field site
(Kruskal-Wallis: $p < 0.0001$). Solid gray line represents the mean ln CP/ADF for 119
foods eaten by gorillas in Bwindi Impenetrable National Park, Uganda (–1.15) and dotted
line represent the standard deviation (0.89). Gorilla data from Rothman et al. (2006). For
pairwise comparisons, refer to Table 4.

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Table 1
Results of three-factor ANOVA exploring plant category, habitat, and seasonal effects on log-transformed protein-fiber ratios.[a]

Effect source	F ratio	p[b]
Plant category	9.0868	**0.0001**
Habitat	8.9526	**0.0002**
Season	0.6287	0.4282
Plant category*Habitat	3.3235	0.0556
Plant category*Season	1.6764	0.1881
Habitat*Season	0.6853	0.5044
Plant category*Habitat*Season	1.075	0.3682

[a] $p < 0.0001$; $R^2 = 0.188$.
[b] Significant results are depicted in bold type.

Table 2
Results of three-factor ANOVA exploring field site, habitat, and seasonal effects on log-transformed protein-fiber ratios.[a]

Effect Source	F ratio	p[b]
Field Site	178.6225	**<0.0001**
Habitat	81.9881	**<0.0001**
Season	1.9727	0.1608
Field Site*Habitat	2.0070	0.1354
Field Site*Season	10.8202	**0.0011**
Habitat*Season	3.0897	**0.0464**
Field Site*Habitat*Season	4.8072	**0.0085**

[a] $p < 0.0001$; adjusted $R^2 = 0.344$.
[b] Significant results are depicted in bold type.

Table 3
Statistical comparisons of habitats across seasons (Steel-Dwass method).[a]

	Wet WL	Dry WL	Wet GL	Dry GL	Wet WO
Dry WL	0.5276	–			
Wet GL	0.9996	0.5290	–		
Dry GL	0.9572	0.9775	0.8792	–	
Wet Wood	**<0.0001**	**<0.0001**	**<0.0001**	**0.0010**	–
Dry Wood	**0.0173**	**0.0002**	0.0520	0.2838	0.8889

Abbreviations: GL = grassland; WL = wetland; WO = woodland.
[a] Significant results are depicted in bold type. 'Wet' and 'Dry' refer to seasons.

845

Table 4

Statistical comparisons of C$_4$ plants across seasons (Steel-Dwass method).[a]

	Dry Cradle	Wet Cradle	Dry Amboseli
Wet Cradle	**<0.0001**	–	
Dry Amboseli	**<0.0001**	**0.0007**	–
Wet Amboseli	**<0.0001**	**<0.0001**	0.0747

[a] Significant results are depicted in bold type. 'Wet' and 'Dry' refer to seasons.