

1 **Nutritional characteristics of wild and cultivated foods for chimpanzees (*Pan***
2 ***troglodytes*) in agricultural landscapes**

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21 **ABSTRACT**

22 Primate habitats are being transformed by human activities such as agriculture. Many wild primates
23 include cultivated foods (crops) in their diets, calling for an improved understanding of the costs and
24 benefits of crop feeding. We measured the macronutrient and antifeedant content of 44 wild and 21
25 crop foods eaten by chimpanzees (*Pan troglodytes schweinfurthii*) in a mosaic habitat at Bulindi,
26 Uganda, to evaluate the common assertion that crops offer high nutritional returns compared to
27 wild forage for primates. Additionally, we analysed 13 crops not eaten at Bulindi but which are
28 consumed by chimpanzees elsewhere, to assess whether nutritional aspects explain why
29 chimpanzees in Bulindi ignored them. Our analysis of their wild plant diet (fruit, leaves and pith)
30 corresponds with previous chemical analyses of primate plant foods. Compared to wild food
31 equivalents, crops eaten by the chimpanzees contained higher levels of digestible carbohydrates
32 (mainly sugars) coupled with lower amounts of insoluble fiber and antifeedants. Cultivated fruits
33 were relatively nutritious throughout the ripening process. Our data support the assumption that
34 eating cultivated foods confers energetic advantages for primates, although crops in our sample
35 were low in protein and lipids compared to some wild foods. We found little evidence that crops
36 ignored by the chimpanzees were less nutritious than those which they did eat. Non-nutritional
37 factors (e.g., similarity to wild foods) probably also influence crop selection. Whether cultivated
38 habitats can support threatened but flexible primates like chimpanzees in the long-term hinges on
39 local people's willingness to share their landscape and resources with them.

40

41 **Keywords:** agroecosystems; cultivars; crop foraging; dietary flexibility; human-dominated
42 landscapes; nutritional ecology

43 **INTRODUCTION**

44 Conversion of forests for subsistence and commercial agriculture is continuing apace throughout the
45 World's most biodiverse regions (Gibbs et al. 2010; Laurance et al. 2014; Tilman et al. 2001). While
46 agricultural expansion erodes wild foods, ecologically and behaviourally flexible species may exploit
47 these new environments and their novel foods (McLennan and Hockings 2014). Crop feeding by
48 wildlife (commonly termed 'crop raiding') receives considerable attention because it can cause
49 conservation conflicts through impacts on local livelihoods (Conover 2001; Hill 1997; MacKenzie and
50 Ahabyona 2012; Redpath et al. 2013). Understanding the attractiveness of crops (i.e., cultivated
51 foods) to wildlife thus has strong relevance for conservation management (Dostaler et al. 2011;
52 Osborn 2004; Rode et al. 2006).

53 Nonhuman primates (hereafter 'primates') feature prominently in the literature on crop
54 damage by wild tropical vertebrates (Paterson and Wallis 2005). The propensity of generalist
55 primate foragers to exploit areas of human settlement and cultivation is well documented, e.g.,
56 members of *Macaca*, *Papio* and *Chlorocebus* in Asia and Africa (Brennan et al. 1985; Hill 2000;
57 Priston and McLennan 2013; Strum 2010), and *Alouatta*, *Cebus* and *Sapajus* in the Neotropics (Bicca-
58 Marques and Calegario-Marques 1994; McKinney 2011; Spagnoletti et al. 2016). However, with the
59 expansion of agroecosystems in primate habitats a broad range of other taxa have been found to eat
60 crops (Estrada et al. 2012). These include species not usually regarded as generalist, omnivorous
61 feeders (e.g., *Trachypithecus vetulus*, Nijman 2012; *Procolobus kirkii*, Nowak and Lee 2013; *Gorilla*
62 *beringei beringei*, Seiler and Robbins 2016), suggesting that more 'specialist' primates can also
63 respond flexibly to agricultural encroachment, albeit if only in the short-term (Nowak and Lee 2013).

64 Humans have selected agricultural foods to be easily digestible, energy rich, and low in plant
65 secondary compounds which impede digestion or include harmful toxins (Milton 1999). Including
66 crops in the diet has far-reaching consequences for primates. Frequent crop consumption is
67 associated with major changes in activity budgets with primates typically spending more time resting
68 and in social behaviour, and less time travelling and foraging, apparently due to energetic benefits of

69 crops which allow metabolic demands to be met sooner (e.g., *Papio cynocephalus*, Altmann and
70 Muruthi 1988; *P. anubis*, Strum 2010; Warren et al. 2011; *Chlorocebus aethiops*, Saj et al. 1999).
71 Crop feeding has further been linked to reduced physiological stress (*P. anubis*, Lodge et al. 2013)
72 and possibly enhanced immune responses (*Colobus guereza*, Chapman et al. 2006; *P. anubis*,
73 Weyher et al. 2006). Despite significant costs (i.e., injury or mortality from pest management),
74 frequent crop consumption may confer life history and reproductive advantages to primates, for
75 example improved body condition and increased adult weight, reduced infant mortality, shorter
76 interbirth intervals and earlier reproductive onset (*Macaca fuscata*, Sugiyama and Ohsawa 1982; *P.*
77 *anubis*, Lodge et al. 2013; Strum 2010; Warren et al. 2011). Even so, elevated serum insulin and
78 cholesterol levels in refuse foraging *P. anubis* and *P. cynocephalus* has been reported (Kemnitz et al.
79 2002).

80 High nutritional returns of crops compared to wild forage are usually assumed. Few studies
81 have quantified nutritional characteristics of both wild and cultivated foods in diets of crop foraging
82 primates. Cultivated cacao (cocoa) eaten by *Macaca tonkeana* was higher in digestible
83 carbohydrates and lower in insoluble fiber compared to wild fruits in their diet (Riley et al. 2013).
84 Similarly, maize and potato eaten by *Papio anubis* had markedly lower insoluble fiber and thus
85 greater digestibility compared to many of their wild plant foods (Forthman Quick and Demment
86 1988).

87 Chimpanzees (*Pan troglodytes*) offer a useful model for examining nutritional attributes of
88 'natural' versus cultivated foods in diets of wild primates. While varying by habitat and season, their
89 natural diets are consistently dominated by ripe fruits which they seek out even when scarce,
90 leading some authors to label them ripe fruit specialists (Ghiglieri 1984; Watts et al. 2012;
91 Wrangham et al. 1998). In general, chimpanzee food selection reflects a preference for higher levels
92 of macronutrients, particularly easily digestible sugars, and lower amounts of insoluble fiber and
93 digestion-inhibiting antifeedants (i.e., polyphenols and condensed tannins), which characterise ripe
94 fruit (Hohmann et al. 2010; Matsumoto-Oda and Hayashi 1999; Remis 2002; Reynolds et al. 1998;

95 Sommer et al. 2011; Wrangham et al. 1998). Unripe fruits may be eaten but are usually lower in
96 sugar and higher in fiber and antifeedants than ripe ones (Houle et al. 2014; Wrangham and
97 Waterman 1983), although chimpanzees seem to tolerate moderate levels of tannins (Remis 2002;
98 Reynolds et al. 1998; Sommer et al. 2011). Fibrous piths and stems provide an additional source of
99 carbohydrate energy, particularly during fruit shortages (Matsumoto-Oda and Hayashi 1999;
100 Wrangham et al. 1991, 1998). Young leaves are probably selected for high protein content (Carlson
101 et al. 2013; Takemoto 2003), which is generally low in fruits. High concentrations of tannins in leaves
102 are avoided (Takemoto 2003). Overall, chimpanzees are considered to have high quality diets
103 (Conklin-Brittain et al. 1998).

104 Chimpanzees are found in habitats transformed by agriculture across their geographic range
105 in equatorial Africa (Hockings and McLennan 2012, 2016). Crop feeding by these great apes reflects
106 their species-typical preference for ripe sugary fruits, though a variety of non-fruit crops are also
107 exploited (Hockings and McLennan 2012). At the borders of large uncultivated habitats chimpanzees
108 target particular crops in adjacent farmland (e.g., mango and sugarcane around Budongo Forest
109 Reserve, Uganda: Tweheyo et al. 2005; maize and banana around Kibale National Park, Uganda: Krief
110 et al. 2014; Naughton-Treves et al. 1998). In some areas, chimpanzees survive in mosaic habitats
111 within agroecosystems (Bessa et al. 2015; McLennan 2008) where crops can become integral to their
112 feeding ecology (Bossou, Guinea: Hockings et al. 2009; Bulindi, Uganda: McLennan 2013).

113 Assimilation of cultivated foods into chimpanzee diets is a dynamic process (Takahata et al.
114 1986) and intriguing differences exist among populations in which crops are eaten and which are
115 ignored, even where local crop assemblages are similar (McLennan and Hockings 2014). The extent
116 to which nutritional factors drive chimpanzee foraging decisions in cultivated habitats, including
117 which crops they exploit, remains unknown.

118 In this study, we examined nutritional composition in a broad selection of wild and cultivated
119 foods consumed by a population of wild East African chimpanzees (*Pan troglodytes schweinfurthii*)
120 inhabiting a farm–forest mosaic habitat in Bulindi, Uganda. Our primary objective was to identify

121 potential nutritional benefits of eating crops over wild foods for these chimpanzees. We first
122 examined macronutrients and antifeedants in major categories of wild foods (fruits, piths and
123 leaves) to characterise nutritional properties of their natural diet. We then compared wild and
124 cultivated foods eaten by these chimpanzees. A secondary aim was to determine if nutritional
125 factors explain why they ignore certain crops exploited by one or more chimpanzee populations
126 elsewhere. Thus, we compared nutrient and antifeedant concentrations in crops eaten and not
127 eaten. We predicted that crops eaten would offer nutritional advantages over wild food equivalents
128 (i.e., by being higher in digestible carbohydrates such as sugars and lower in insoluble fiber and
129 antifeedants). We also predicted that crops fed on by the chimpanzees would likewise offer
130 nutritional advantages over those crops which they ignored.

131

132 **METHODS**

133 ***Study site***

134 Bulindi (1°28'N, 31°28'E) is situated in Hoima District, western Uganda, midway between the
135 Budongo and Bugoma forest reserves – two main forest blocks with >500 chimpanzees each
136 (Plumptre et al. 2010). These reserves are separated by about 50 km. The intervening landscape is
137 densely populated by people (>150 persons per km²; Uganda Bureau of Statistics 2014) and
138 dominated by subsistence and commercial agriculture (McLennan and Hill 2015). A genetic survey
139 revealed that 260–320 chimpanzees from nine or more resident 'communities' inhabit small
140 fragments of unprotected forest across this cultivated landscape (McCarthy et al. 2015).
141 Chimpanzees in Bulindi represent one of these communities. Local farmers practice a combination of
142 subsistence farming and cash-cropping. Staple food crops include cassava, potato, maize and
143 groundnuts, while major cash crops are tobacco, rice and sugarcane (McLennan and Hill 2015).
144 Domestic fruits including mango, jackfruit, banana and papaya are grown around homes. Since the
145 1990s, forest clearance for timber and farming has been extensive throughout the landscape
146 separating Budongo and Bugoma (McLennan and Hill 2015; Mwavu and Witkowski 2008;

147 Twongyirwe et al. 2015). Primates including chimpanzees are not traditionally hunted for food in
148 western Uganda, which enables them to persist in modified habitats near people. Consumption of
149 agricultural crops by chimpanzees occurs throughout this region (McLennan 2008).

150 Chimpanzees in Bulindi were studied first in 2006–2008 (McLennan and Hill 2010). In 2012,
151 the first author resumed research on the chimpanzees. The community numbered 18–21 individuals
152 during the present study in 2014–2015. Their home range exceeds 20 km² but they usually used a
153 core area of c.5 km², comprising small patches of degraded riverine and swamp forest amid
154 agricultural gardens and villages, and dissected by a main road (McLennan and Asiimwe 2016)
155 (Figure 1). Common forest trees include *Phoenix reclinata*, *Pseudospondias microcarpa* and
156 members of the Moraceae including figs (McLennan and Plumptre 2012). About 80% of forest within
157 the chimpanzees' core area was cleared for farming between 2006 and 2014 (Lorenti 2014).

158 Although the chimpanzees' diet is dominated numerically by wild plants, they forage
159 frequently on cultivated foods in gardens and by homes, as well as from abandoned or naturalised
160 sources (McLennan 2013; McLennan and Hockings 2014). Local tolerance of chimpanzees varies
161 from person-to-person but crop loss to the apes is considered a worsening problem by many
162 villagers (McLennan and Hill 2012). The chimpanzees have never been actively provisioned.

163

164 < **Figure 1 here** >

165

166 ***Plant food collection***

167 We collected plant foods during January–April 2014, September–November 2014, March–June 2015,
168 and October–December 2015. The chimpanzee diet at Bulindi has been well-studied using a
169 combination of indirect methods (faecal analysis and feeding trace evidence) and direct observation.
170 A least 139 different plant food items from 103 identified species have been recorded eaten to date
171 (McLennan 2013, and unpublished data). During daily tracking we observed feeding behaviour
172 opportunistically and did not record feeding rates. We avoided observing chimpanzees feeding on

173 crops from non-abandoned or naturalised sources, though we sometimes encountered them
174 foraging in gardens. During observations, we paid careful attention to food items selected and how
175 these were processed. Similarly, we examined chimpanzee feeding traces carefully to determine the
176 part consumed. We confirmed that the chimpanzees ate certain fruits by faecal analysis. Methods
177 used to analyse chimpanzee feeding traces and faecal samples are detailed in McLennan (2013).

178 We collected 78 plant foods for this study including 44 wild and 34 cultivated items
179 (Appendix Tables 2–4). Wild foods are predominantly native plants which are not usually planted or
180 domesticated by humans; exceptions in the sample include native figs (*Ficus natalensis* and *F.*
181 *thonningii*) which are sometimes planted around homes, and paper mulberry (*Broussonetia*
182 *papyrifera*), an exotic shrub introduced previously into nearby Budongo Forest. Its occurrence in
183 Bulindi is presumably the result of dispersal by birds; thus we treated it as wild. Cultivated foods
184 (synonymous with ‘crops’, ‘cultivars’ or ‘cultigens’) are domesticated plants selectively bred by
185 people; several in our sample also occur as naturalised specimens in Bulindi (e.g., guava, tamarillo)
186 (see Spencer and Cross 2007 for a discussion of cultivated versus wild plant definitions).

187 We collected three major categories of plant food: fruits (ripe and unripe), leaves (young
188 and emerging), and piths (terrestrial herbaceous stems and leaf petioles or stems). While
189 chimpanzees usually ate fruits ripe, they consumed some fruits throughout the ripening process,
190 including fully unripe. For eight such fruits, we collected ripe and unripe samples. Though the precise
191 stage of maturity varied (Houle et al. 2014), unripe fruits were small compared to mature fruits, firm,
192 and/or with green or pale skin and pulp. We considered leaf petioles and stems ‘piths’ when the
193 manner of processing by chimpanzees corresponded to that of terrestrial stem feeding rather than
194 leaf feeding (i.e., leaves discarded and only the inner part of the petiole/stem eaten). Other minor
195 food categories (e.g., seeds, tubers, flowers, cambium) were represented by 1–2 foods only. Life
196 forms of plants sampled included trees, shrubs, climbers and vines, herbs, and grasses.

197 Plants collected included both commonly and occasionally eaten items (as indicated by
198 faecal analysis, direct observation and feeding trace records; McLennan 2013). Thirteen items were

199 crops grown at Bulindi which are reportedly eaten by ≥ 1 population of wild chimpanzees elsewhere
200 (Hockings and McLennan 2012), including several eaten by nearby communities in Hoima District (M.
201 McCarthy, pers. comm.), but for which no evidence suggests Bulindi chimpanzees eat them
202 (Appendix Table 4). An exception is tamarillo fruit for which feeding traces were twice attributed to
203 chimpanzees in 2007 (McLennan 2013). However, no further evidence has suggested the
204 chimpanzees eat tamarillo (e.g., absence of seeds in faeces, and absence of feeding traces at
205 numerous naturalised tamarillo shrubs in the forest). Thus, we consider it very unlikely that
206 chimpanzees ate tamarillo in the present study. For all other crops 'not eaten' (including fruits such
207 as pineapple and staple food crops like cassava and maize cob), there has been no evidence of
208 consumption by the chimpanzees since research was initiated. Moreover, local farmers maintain
209 chimpanzees do not eat these crops in Bulindi (McLennan and Hill 2012).

210 Wherever possible, we collected samples from actual plants which chimpanzees ate from,
211 including intact items from feeding patches after chimpanzees fed or which fell to the ground
212 incidentally while they fed (e.g., a fruiting or leafing branch), and partially-eaten items such as large
213 cultivated fruits (e.g., jackfruit), which are often not consumed in their entirety. We collected all
214 partially-eaten items in the same morning that chimpanzees ate them. Otherwise, we collected
215 samples from conspecific plants showing a similar phenophase. We collected intact cultivated foods
216 from local gardens with permission. For several crops, we failed to obtain a sample in the desired
217 stage of maturity from local gardens, so we bought them at a market in Hoima town, 12 km from
218 Bulindi, assuming they were of similar quality to ones consumed by the chimpanzees. Where
219 possible, we collected samples from multiple plants of the same species.

220 We collected food samples in plastic bags and processed them on the same day to include
221 only parts fed on by chimpanzees. For example, we removed outer layers of piths, leaving only the
222 soft inner part. We removed fruit seeds and tough skins, but retained the soft fruit skins if these
223 were normally ingested. Faecal analysis showed that chimpanzees sometimes chewed the soft bean-
224 like seeds of *Parkia filicoidea*, suggesting they obtained nutrients from them. Occasionally, they ate

225 immature seeds and pods of cultivated beans (*Phaseolus vulgaris*); thus, we retained a portion of the
226 seed content for these two fruits. We took samples from crops not eaten by the chimpanzees from
227 parts likely to be most palatable (e.g., soft fruit pulp, inner portion of piths).

228 After processing, we dried samples at 50–55°C using a Shef® food dehydrator. Once dry, we
229 weighed samples, stored them in plastic bags with silica gel, and shipped 5–15 g dry weight per item
230 to University of Hamburg, Germany, for biochemical analyses.

231

232 ***Nutritional analyses***

233 We analysed samples for macronutrients and antifeedants via standard methods (for reviews of
234 laboratory procedures see Ortmann et al. 2006; Rothman et al. 2012). We ground samples in a
235 Retsch mill to a homogenous powder and dried to 50°C in the laboratory overnight. We estimated
236 nutrient concentrations on a dry matter (DM) basis. We measured total nitrogen (TN) by the Kjeldahl
237 method (Association of Official Analytical Chemists 1990) and determined crude protein (CP) as TN x
238 6.25. While this conversion factor should be adapted for different food categories, especially tropical
239 fruits (Milton and Dintzis 1981), we use it here to allow for comparison with other studies. Since CP
240 does not necessarily reflect protein available for digestion (Rothman et al. 2008; Wallis et al. 2012),
241 we also assessed soluble protein via the photometric BioRad assay after extraction of plant material
242 with 0.1 N NaOH for 15 h at room temperature. A meta-analysis of primate leaf selection found that
243 soluble protein had a greater effect on selection than TN (or CP), suggesting these protein measures
244 differ in ecological relevance (Ganzhorn et al. 2016). Even so, TN and soluble protein were highly
245 correlated in our sample of foods (Pearson’s correlation: $r = 0.593$, $N=78$, $P<0.0001$). Further, TN in
246 leaves from Uganda correlated well with available protein (Wallis et al. 2012). Therefore, we used CP
247 as our measure of protein in the analysis, but we also report soluble protein in the Appendices.

248 We analysed neutral detergent fiber (NDF) and acid detergent fiber (ADF) using an ANKOM
249 fiber analyser (Van Soest et al. 1991). NDF represents the insoluble fiber (hemicellulose, cellulose
250 and lignin) with ADF representing the cellulose and lignin fractions; hemicellulose (HC) is thus

251 determined by weight difference (NDF-ADF). We determined fat content (lipids) using ether extract,
252 and measured ash via combustion (Rothman et al. 2012). We extracted soluble carbohydrates and
253 procyanidin (condensed) tannins with 50% methanol, and determined soluble sugars as the
254 equivalent of galactose after acid hydrolyzation of the methanol extract.

255 We measured concentrations of procyanidin tannins as equivalents of quebracho tannin
256 using the buthanol-method, and measured total phenolics (simple phenols and polyphenols) using
257 the Folin-Ciocalteus reagent (Stolter et al. 2006). Tannins inhibit digestion by making some nutrients
258 (e.g., proteins) unavailable for digestion. Simple phenols are small molecules that enter the cell and
259 can act as poisons; these components are volatile and are likely to be lost during the drying process.
260 We based analyses of polyphenols on water extracts. Standard chemical assays of these components
261 represent poor proxies of their actual biological relevance, as both groups of chemicals comprise a
262 plethora of substances with differing properties (e.g., Rothman et al. 2009). Nevertheless, we used
263 these analyses to allow comparisons with other studies.

264 We calculated total non-structural carbohydrate (TNC) content, i.e. the digestible
265 carbohydrates, by subtraction following Conklin-Brittain et al. (2006):

$$266 \quad \%TNC = 100 - (\%lipids + \%CP + \%ash + \%NDF).$$

267 Following Conklin-Brittain et al. (2006), we applied standard conversions to nutritional fractions to
268 calculate metabolizable energy (ME), assuming a high capacity of chimpanzees to ferment NDF,
269 using the fiber digestion coefficient (0.543) provided by Milton and Demment (1988):

$$270 \quad ME \text{ (kcal/100 g DM)} = 4 \times \%TNC + 4 \times \%CP + 9 \times \%lipids + 1.6 \times \%NDF.$$

271 With the exception of ME (expressed as kcal/100 g DM), we present all values as % DM.

272

273 ***Statistical analysis***

274 We examined differences between food categories in CP, lipids, soluble sugars, TNC, fiber (NDF and
275 ADF), polyphenols and tannins, and ME. Because of unequal samples sizes and non-normality of
276 some distributions, we used non-parametric statistics. We compared nutritional attributes of major

277 wild food categories (ripe fruits, piths, young leaves) using Kruskal–Wallis ANOVAs followed by
278 Dunn–Bonferroni pairwise comparisons. We compared ripe and unripe samples from fruits which
279 chimpanzees ate in both maturity stages using Wilcoxon signed rank tests. We used Mann–Whitney
280 tests to assess differences between (i) crops eaten and wild food equivalents, and (ii) cultivated
281 fruits eaten and not eaten; reported z-scores inform about the group with the lowest distribution.
282 We only compared wild and cultivated foods for fruit and pith since the chimpanzees ate leaves from
283 one crop only (yam leaves; not collected for this study). We used one-sample Wilcoxon signed rank
284 tests to assess differences between individual non-fruit crops which were not eaten (but eaten
285 elsewhere) and medians of wild food equivalents.

286 To control for multiple testing we applied a Holm–Bonferroni sequential adjustment to P-
287 values in all groups of tests. This procedure is considered more powerful than the conventional
288 Bonferroni approach, while still controlling the family-wise Type I error (Abdi 2010). Nevertheless,
289 we also report unadjusted P-values in some tests where the adjustment was likely too conservative
290 given small sample sizes, but these should be interpreted with caution. We performed statistical
291 analyses using SPSS version 23 (SPSS Inc., Chicago, IL, USA) and set statistical significance at $P < 0.05$;
292 all tests were two-tailed.

293

294 ***Ethical note***

295 This research involving wild chimpanzees was non-invasive and adhered strictly to the legal
296 requirements of Uganda, and to ethics guidelines detailed by the Association for the Study of Animal
297 Behaviour (UK) and the American Society of Primatologists Principles for the Ethical Treatment of
298 Nonhuman Primates. The study was approved by the Uganda National Council for Science and
299 Technology, the President’s Office and the Uganda Wildlife Authority.

300

301 **RESULTS**

302 ***Wild foods compared***

303 Wild food categories (ripe fruits, piths and young leaves) differed broadly in nutritional content
304 (Figure 2; Appendix Table 2). Kruskal–Wallis tests indicated differences among categories in
305 concentrations of CP (H = 21.25, P<0.001), lipids (H = 8.30, P=0.047), soluble sugars (H = 21.73,
306 P<0.001), total non-structural carbohydrates (TNC) (H = 21.63, P<0.001), fiber (NDF: H = 18.43,
307 P<0.001; ADF: H = 16.01, P=0.001), polyphenols (H = 8.17, P=0.047), and in metabolizable energy
308 (ME) (H = 16.64, P=0.001; df=2 in all tests; Holm–Bonferroni adjustments applied). Pairwise
309 comparisons showed that young leaves had significantly higher protein and lipid concentrations than
310 both ripe fruits and piths (Figure 2). Ripe fruits were significantly higher in soluble sugars than young
311 leaves and tended to have higher sugar concentrations than piths, though this difference was non-
312 significant after adjusting for multiple comparisons. The TNC content of fruits was higher than in
313 both leaves and piths. Piths contained highest levels of fiber, with significantly greater NDF content
314 than fruits and greater ADF content than both fruits and leaves. Young leaves generally had higher
315 NDF concentrations than ripe fruits, though not significantly so after adjustment. ME was highest in
316 ripe fruit and lowest in piths. Regarding antifeedants, leaves had significantly higher polyphenol
317 concentrations than both fruits and piths. Tannins tended also to be highest in young leaves,
318 although the overall Kruskal–Wallis test was non-significant (H = 5.13, P=0.077 with adjustment).

319

320 < **Figure 2 here** >

321

322 ***Wild and cultivated foods compared***

323 **Fruits**

324 Chemical composition of ripe fruits eaten by the chimpanzees differed markedly between wild and
325 cultivated items (Figure 3; Appendix Tables 2 and 3). Ripe wild fruits had significantly higher
326 concentrations of CP (z = -2.599, P=0.047) and lipids (z = -2.747, P=0.042), whereas ripe cultivated
327 fruits were higher in sugar (z = -2.726, P=0.042) and TNC (z = -3.381, P=0.006; Holm–Bonferroni
328 adjustments applied). Other differences were marginally non-significant after adjustment: ME was

329 generally higher in cultivated fruits ($z = -2.493$, $P=0.051$), while wild fruits showed a tendency to be
330 higher in insoluble fiber (NDF: $z = -2.282$, $P=0.054$; ADF: $z = -2.324$, $P=0.054$) and polyphenols ($z = -$
331 2.368 , $P=0.054$) (Figure 3). While tannins were found in 10 of 21 (48%) wild fruits (range: 0.13–0.55%
332 DM), they were found in only 2 of 10 (20%) ripe cultivated fruits eaten by the chimpanzees (0.32%
333 DM in both cocoa and guava).

334

335 < Figure 3 here >

336

337 All 8 fruits analysed in both ripe and unripe stages (6 crop fruits and 2 wild fruits; see
338 Appendix Tables 2 and 3) had higher concentrations of CP and NDF when unripe compared to when
339 they were ripe. Conversely, ripe samples all had higher TNC content. Differences were significant
340 prior to adjusting for multiple tests only ($P=0.008$ in each case; Table 1). As predicted, sugar
341 concentrations were higher when fruits were ripe, with one exception: sugar content in cocoa was
342 marginally higher in the unripe sample. ADF content was higher in unripe samples except for
343 plantain banana, which had marginally more ADF in the ripe sample. Concentrations of lipids and
344 antifeedants were similar in unripe and ripe stages of the fruits tested.

345

346 < Table 1 here >

347

348 Since few wild unripe fruits were analysed, we could not compare unripe fruits from wild
349 and cultivated sources. However, no significant differences were apparent between wild *ripe* fruits
350 and cultivated *unripe* fruits eaten by the chimpanzees (Figure S1 in the electronic supplementary
351 material).

352

353 **Piths**

354 Wild and cultivated piths eaten also varied in chemical composition (Appendix Tables 2 and 3). Sugar
355 and TNC concentrations, and ME, were generally higher in cultivated compared to wild piths, while
356 ADF and polyphenol concentrations were generally lower (Figure 4). Cultivated piths were all quite
357 low in protein whereas some wild piths (i.e., *Aframomum* sp. and *Marantochloa leucantha*) had
358 relatively high CP concentrations. Differences were significant only for sugars ($z = -2.268$, $P=0.024$)
359 and polyphenols ($z = -2.462$, $P=0.009$), and only before correcting for multiple tests (adjusted P-
360 values = 0.17 and 0.07, respectively). Tannins were not found in any cultivated pith analysed.

361

362 < Figure 4 here >

363

364 ***Crops eaten and not eaten compared***

365 Some differences were apparent between the 10 ripe cultivated fruits eaten and six which were not
366 eaten (Appendix Table 3 and 4). Those eaten were lower in CP ($z = -2.768$, $P=0.039$; Figure 5) but
367 higher in TNC ($z = -2.820$, $P=0.038$; Holm–Bonferroni adjustment applied). Crop fruits eaten also
368 tended to have lower lipid and NDF concentrations than those not eaten, but these differences were
369 non-significant after correcting for multiple tests ($P = 0.10$ and 0.11 , respectively). No differences
370 were apparent in other nutrients tested, including sugars. Small concentrations of tannins were
371 found in only 3 of the 16 ripe cultivated fruits: cocoa and guava (eaten) and soursop (not eaten).

372

373 < Figure 5 here >

374

375 Papaya leaf, which the chimpanzees did not eat, was higher in CP (29% DM) than all 10 wild
376 young leaf species which they did eat (Mdn = 22.7%; one-sample Wilcoxon signed rank test: $P =$
377 0.040 with Holm-Bonferroni adjustment). In fact, papaya leaf was highest in protein of all 78 foods
378 analysed (Appendices). Papaya leaves were also low in polyphenols (0.78%) compared to most wild
379 leaf foods (Mdn = 1.48%) though this difference was non-significant after adjustment (unadjusted P
380 = 0.028 ; adjusted $P = 0.196$). While tannins were not found in papaya leaf, they were present in 7 of

381 10 wild young leaf foods. Papaya pith, also not eaten, was lower in fiber (NDF = 18.35%, ADF =
382 13.42%) than all 7 wild piths analysed (Mdn = 37.64% and 23.37%, respectively), while its ME
383 content was highest (305.14 Kcal/100 g versus 264.70 Kcal/100 g [Mdn] for wild piths). A second
384 cultivated pith not eaten at Bulindi (rice) was lower in polyphenols (0.15%) than all wild piths
385 analysed (Mdn = 0.61%). Only unadjusted P-values were significant (P=0.018 in each case). Notably,
386 both rice and papaya pith had considerably higher levels of CP (13.4% and 14.2%, respectively) than
387 the 4 cultivated piths which the chimpanzees did eat (1.8–8.4%; Appendix Table 3 and 4).
388 Conversely, sugar concentrations in rice and papaya pith were lower and more similar to those in
389 wild piths eaten. The fiber and polyphenol content was overall similar in cultivated piths eaten and
390 not eaten. None of the cultivated piths contained tannins.

391 Four additional crops analysed – not eaten by the chimpanzees – are staple foods for local
392 people: cassava and sweet potato (tubers), maize cob (caryopsis) and ground nuts (seed crop).
393 There were no wild food equivalents for these in our sample. These crops were generally low in
394 soluble sugars (Appendix Table 4). However, cassava and maize cob in particular are high in starch
395 (United States Department of Agriculture 2016), which we did not assay. Fiber concentrations in
396 cassava, maize cob and ground nuts were within the range of other non-fruit items eaten by the
397 chimpanzees. However, sweet potato was high in NDF (59%) – almost all hemicellulose. The fiber
398 content of cassava and maize similarly comprised mostly hemicellulose. Ground nuts were rich in
399 protein and contained an exceptionally high lipid concentration. All staple food crops were low in
400 antifeedants.

401

402 **DISCUSSION**

403 Our results support the common assertion that crops offer certain nutritional advantages over wild
404 plants for primates in human-modified environments. Chimpanzees within the forest–agricultural
405 mosaic in Bulindi supplement a ‘natural’ diet with various cultivated foods which compared to wild
406 food equivalents, and in accord with our prediction, had higher levels of easily digestible

407 carbohydrates (mainly sugars) coupled with reduced amounts of insoluble fiber and antifeedants.
408 Conversely, however, crops eaten by the chimpanzees were not a good source of protein or lipids
409 relative to some wild foods, which may be true of cultivars generally (Milton 1999). Additionally,
410 compared to crops, wild plants may contain higher concentrations of essential micronutrients
411 (vitamins and minerals) which we did not assay here (Milton 1999; cf. Rode et al. 2006). Whether
412 crop feeding primates balance their nutrient intake (e.g., with protein or lipid-rich wild foods) is
413 largely unknown. However, Johnson et al. (2013) demonstrated nutrient balancing in a female *Papio*
414 *ursinus*, which included exotic plants and other 'human-derived' foods in its diet. Since we did not
415 measure feeding time or food intake by the chimpanzees, we could not estimate nutrient intake.
416 Thus, further research is needed to determine how the chimpanzees prioritise and regulate nutrient
417 intake through their choice of wild and cultivated foods to better understand the role of crops in
418 meeting their nutritional requirements (Felton et al. 2009; Lambert and Rothman 2015).

419 Besides chemical properties, other characteristics of crops suggest they offer enhanced
420 foraging efficiency over many wild foods. When grown in fields, orchards and plantations, crops
421 present a predictable, spatially abundant and concentrated food source, requiring little search time.
422 Crops also frequently come in large 'packages'. Jackfruits, for example, are the largest tree-borne
423 fruit, weighing up to 35 kg (Prakash et al. 2009); a single large jackfruit easily satisfies an adult
424 chimpanzee (McLennan, pers. observ.) (Figure 6). Additionally, crop fruits usually have low seed-to-
425 pulp ratios relative to wild fruits (Milton 1999). Overall, crops are easier to find, process, and digest
426 than many wild foods, providing more energy for less effort (Forthman Quick and Demment 1988;
427 Strum 2010).

428 Our analysis of the chimpanzees' wild plant diet at Bulindi corresponds with previous
429 chemical analyses of primate plant foods (Lambert and Rothman 2015): ripe fruits provided energy
430 from easily digestible carbohydrates (i.e., sugars); piths were an alternative source of carbohydrate
431 energy, particularly from fiber; while young leaves provided protein, which was low in fruits. Plants
432 eaten by wild primates generally contain low amounts of lipids (Lambert and Rothman 2015;

433 Rothman et al. 2012), as was true of wild plants analysed here. While previous studies found that
434 ripe fruits eaten by apes contained most fat (Conklin-Brittain et al. 1998; Reiner et al. 2014), lipids
435 were highest in young leaves in our sample. However, this high “lipid” content likely includes non-
436 nutritive components like wax and cutin which are also extracted by ether (Palmquist and Jenkins
437 2003). Nevertheless, individual plants within major food categories – both wild and cultivated –
438 varied considerably in chemical properties (Appendix Table 2 and 3).

439

440 < Figure 6 here >

441

442 Though unripe fruit contained less digestible carbohydrates and more fiber compared to
443 when fully ripe, it offered a supplementary source of protein and energy. We found no differences in
444 antifeedant content between unripe and ripe samples. However, most fruits sampled in both
445 maturity stages were crops which, relative to wild foods, had small concentrations of polyphenols
446 generally and rarely contained tannins (Appendices). While our sample of unripe fruits was small,
447 the absence of strong differences between unripe cultivated fruits and ripe wild fruits suggests
448 agricultural fruits are relatively nutritious throughout the ripening process. Indeed, chimpanzees
449 often ate unripe fruits of cocoa, mango, jackfruit and guava when available (McLennan, unpublished
450 data) (Figure 6). Again, however, nutrient concentrations in unripe fruits varied considerably. For
451 example, unripe fruit of cocoa, mango and papaya had sugar levels comparable to ripe fruits of many
452 wild species. Conversely, unripe plantain banana contained very little soluble sugar, but may have
453 instead provided energy from hemicellulose (Appendix Table 3).

454

455 ***Why did chimpanzees ignore certain crops?***

456 Contrary to prediction, we found little evidence that crops ignored by the chimpanzees were less
457 nutritious than those which they did eat. Compared to cultivated fruits eaten, ignored fruits
458 (avocado, pineapple, pumpkin, soursop, tamarillo and tomato) tended to be lower in non-structural

459 carbohydrates and more fibrous, which might have influenced whether chimpanzees chose to eat
460 them or not. Conversely, the ignored fruits were a better source of protein and lipids – although
461 chimpanzees probably select ripe fruits primarily for their digestibility and high sugar content. Still,
462 pineapple had among the highest sugar content of all fruits analysed and should have been highly
463 attractive to chimpanzees. Moreover, all ignored fruits are highly palatable to humans, with the
464 exception of pumpkin which – while edible raw – is considered too fibrous to eat uncooked by local
465 people, although other primates in Bulindi readily eat it (e.g., *Chlorocebus tantalus*).

466 Two cultivated piths not eaten by the chimpanzees (rice stem and papaya leaf petiole)
467 offered a good source of protein with low concentrations of fiber and antifeedants. Still, the greater
468 sugar content of cultivated piths which were eaten (especially sugarcane and yam pith, which had
469 sugar concentrations comparable to crop fruits; Appendix Table 3), suggests chimpanzees at Bulindi
470 selected cultivated piths mainly for their sweet taste (or carbohydrate energy), not protein. Young
471 leaves of papaya had the highest amount of crude protein of all foods analysed. But no evidence
472 suggested the chimpanzees exploit this protein-rich resource (as chimpanzees do at Bossou, for
473 example; Hockings and McLennan 2012) – although they often ate papaya fruit.

474 Non-nutritional factors probably also influence crop selection by primates. In this study, we
475 did not compare availability or abundance of different crops, which might influence whether
476 chimpanzees eat them or not (McLennan and Hockings 2014). With regards to fruits, soursop trees
477 were rare at Bulindi and chimpanzees probably had limited opportunities to encounter the sweet
478 fruits. But other crop fruits not eaten such as pineapple, pumpkin, tamarillo and tomato were more
479 common than several which were eaten (e.g., lemon, orange, passion fruit). Other non-fruit crops
480 which were ignored – particularly staple foods for local people like cassava, maize, sweet potato and
481 rice – were highly abundant and chimpanzees encountered these foods daily when seasonally
482 available. Thus, availability cannot explain why they did not eat them. In particular, maize cob is
483 among the crops most commonly targeted by chimpanzees across Africa (Hockings and McLennan
484 2012). Crops which are comparable to wild foods in shape, colour and/or odour, and requiring

485 similar processing, are most likely to be recognised as edible by wildlife (McLennan and Hockings
486 2014). Chimpanzees probably recognise many fruit crops as palatable from ripeness cues, but some
487 fruits ignored at Bulindi (e.g., avocado and pineapple) are harvested by humans before fully ripe and
488 thus lack a strongly sweet odour, or are encased within a tough exocarp such as pumpkin. However,
489 chimpanzees readily consume cocoa pods which are similarly tough and not strongly-scented. In
490 Bulindi, chimpanzees seem not to have parallels in their natural diet for crops such as cassava tuber,
491 sweet potato and groundnuts (which are embedded), and maize cob (which is concealed). Such
492 characteristics may help explain why they do not currently exploit them.

493 A previous study showed that chimpanzees at Bossou, where apes have exploited crops for
494 generations, ate a greater variety of cultivated foods (including staple food crops like cassava, rice
495 and maize cob) compared to Bulindi where major habitat encroachment is more recent (McLennan
496 and Hockings 2014). Fast-changing mosaic landscapes may generate dynamic feeding patterns in
497 wild animals, involving complex interactions between local anthropogenic and environmental factors
498 (e.g., farming practises and the relative availability and nutritional quality of wild and cultivated
499 foods) (McLennan and Hockings 2014). Thus, chimpanzees in Bulindi may yet 'discover' that certain
500 crops not currently exploited are good to eat in time, as illustrated by Takahata et al. (1986) who
501 described the gradual assimilation of mango, guava and lemon into the diet of wild chimpanzees at
502 Mahale, Tanzania.

503

504 ***Sustainability of primate crop feeding***

505 On-going human settlement and cultivation, especially in the tropics, means that primates should
506 adjust their behaviour to survive in modified landscapes, or else go locally extinct (Anderson et al.
507 2007; Estrada et al. 2012; Nowak and Lee 2013). Supplementing a natural diet with energy-rich crops
508 is one such adjustment, but crop foraging inevitably brings primates into competition with humans
509 (Paterson and Wallis 2005). The relative costs and benefits of eating crops will differ according to
510 species and habitat and, perhaps most importantly, human cultural attitudes and socioeconomic

511 conditions which define tolerance of wildlife, but are subject to change (Hill and Webber 2010;
512 McLennan and Hill 2012; Naughton-Treves and Treves 2005; Riley 2010). Like many primates,
513 chimpanzees show a high level of behavioural and dietary flexibility which enables them to survive in
514 cultivated habitats, providing they are not hunted or persecuted (Hockings et al. 2015; Hockings and
515 McLennan 2016). Despite the tolerance sometimes afforded apes by human cultural beliefs,
516 persistent crop losses and associated problems (i.e., aggression towards people; McLennan and
517 Hockings 2016) can instigate retributive killings and use of lethal control methods (Hyeroba et al.
518 2011; McLennan et al. 2012; Meijaard et al. 2011). Chimpanzees have slow life histories and even
519 occasional trappings and killings cause population declines (Hockings and McLennan 2016). Whether
520 agricultural and other matrix habitats can support populations of threatened but flexible primates
521 like chimpanzees in the long-term is uncertain. Ultimately, it hinges on the willingness and capacity
522 of local people to share their landscape and resources with them.

523

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533

534 < **Appendix Table 2 here** >

535 < **Appendix Table 3 here** >

536 < **Appendix Table 4 here** >

537

538 **Electronic Supplementary Material**

539 Supporting Information (Figure S1) is available online.

540

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789

790 **FIGURE LEGENDS**

791 **Fig. 1** Home range of chimpanzees in Bulindi (Hoima District, western Uganda) during this study
792 (2014–2015), adapted from Google Earth 7.1.5, 2015. Dark green areas are fragments of riverine
793 forest, *Cyperus papyrus* swamp and wooded grassland; the surrounding matrix comprises
794 smallholder farmland and homes. The yellow polygon shows the most commonly used portion of the
795 home range which is dissected by a main road (at centre); the chimpanzees cross this road on a
796 frequent basis (McLennan and Asiimwe 2016). Main trading centres with shops, schools, local
797 government offices and a police post are indicated by red ovals.

798
799 **Fig. 2** Chemical properties in three major categories of wild food eaten by chimpanzees in Bulindi in
800 this study (2014–2015): ripe fruits (F; N=21), piths (P; N=7) and young leaves (L; N=10). Horizontal
801 lines are medians (% DM except ME, expressed as Kcal/100 g); rectangles span first to third quartiles;
802 whiskers show maximum and minimum values; open circles are outliers. Comparisons include
803 macronutrients (crude protein, lipids, soluble sugars, total non-structural carbohydrates [TNC]), fiber
804 fractions (NDF, ADF), antifeedants (tannins, polyphenols) and metabolizable energy (ME). Solid
805 horizontal lines with asterisks indicate results of post hoc Dunn–Bonferroni pairwise comparisons: *
806 $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; dashed horizontal lines indicate pairs that differed ($P < 0.05$) only
807 prior to the Dunn–Bonferroni adjustment; (ns) = overall Kruskal–Wallis test non-significant.

808
809 **Fig. 3** Chemical properties in ripe wild fruits (W; N=21) and ripe cultivated fruits (C; N=10) eaten by
810 chimpanzees in Bulindi in this study (2014–2015). For details see Figure 2. Tannins were not
811 detected in many fruits (not shown). Solid horizontal lines with asterisks indicate results of Mann–
812 Whitney tests with Holm–Bonferroni adjustment: * $P < 0.05$, ** $P < 0.01$; dashed horizontal lines
813 indicate pairs that differed ($P < 0.05$) only prior to adjustment.

814

815 **Fig. 4** Chemical properties of wild (W; N=7) and cultivated (C; N=4) pith foods eaten by chimpanzees
816 in Bulindi in this study (2014–2015). For details see Figure 2. Tannins (not shown) were not detected
817 in any cultivated pith analysed, but were present in 3 of 7 wild piths eaten. Dashed horizontal lines
818 indicate pairs that differed ($P < 0.05$) prior to applying a Holm–Bonferroni adjustment.

819

820 **Fig. 5** Chemical properties of ripe cultivated fruits eaten (N=10) and not eaten (N=6) by the
821 chimpanzees in this study (2014–2015). For details see Figure 2. Tannins were not detected in most
822 cultivated fruits (not shown). ^ lipid content of avocado fruit was exceptionally high: 40.3% DM (not
823 shown to scale for readability); all other crop fruits had lipid concentrations 0.3–2.4% DM. Solid
824 horizontal lines with asterisks indicate results of Mann–Whitney tests with Holm–Bonferroni
825 adjustment: * $P < 0.05$; dashed horizontal lines indicate pairs that differed ($P < 0.05$) only prior to
826 adjustment.

827

828 **Fig. 6** Some crops in the diet of chimpanzees in Bulindi, 2014–2015. (a) Adult male eating ripe
829 jackfruit; (b) subadult female eating unripe jackfruit; (c) adult males from a nearby community eating
830 pith of commercially grown sugarcane; (d) damage to banana plants after chimpanzees ate the inner
831 pith; (e) naturalised guava, a common food for chimpanzees in Bulindi; (f) partially-eaten unripe
832 cocoa pods; (g) partially-eaten unripe mangos; (h) subadult male eating ripe mango; (i) partially-
833 eaten semi-ripe papaya fruit; (j) adult male in a cassava field; cassava is a staple food crop for
834 humans but chimpanzees in Bulindi do not feed on any part of the plant; (k) adult male by a field of
835 ripening maize, also a staple food crop. While chimpanzees in Bulindi ignore the cob, they
836 occasionally eat pith from young maize plants (l). Photographs by Matthew McLennan except (h) and
837 (k) by Georgia Lorenti.

Table 1 Chemical properties of ripe and unripe fruits of 8 species (6 crops and 2 wild species) eaten by chimpanzees at Bulindi in both stages of maturity during this study (2014–2015)

		CP	Lipid	NDF	ADF	Sugar	TNC	CT	PP	ME
Ripe	Mdn	3.78	0.76	8.20	4.61	59.57	83.59	0.00	0.51	372.92
	Quartiles	2.77– 4.85	0.64– 0.84	5.71– 15.58	3.13– 7.44	48.91– 70.63	76.55– 87.01	0.00– 0.32	0.16– 1.50	353.36– 378.96
Unripe	Mdn	5.35	0.80	19.78	9.36	22.39	60.35	0.39	0.51	333.85
	Quartiles	3.72– 9.28	0.34– 2.31	12.69– 40.22	4.58– 17.24	16.98– 49.95	50.77– 77.13	0.00– 0.91	0.24– 1.95	293.23– 364.45
	P	**	ns	**	*	*	**	ns	ns	*

Medians (in bold) and quartiles are shown for ripe and unripe fruits. Values are expressed as % DM except for metabolizable energy (ME), expressed as Kcal/100g. CP = crude protein; NDF = Neutral detergent fiber; ADF = acid detergent fiber; Sugar = soluble sugars; TNC = total non-structural carbohydrates; CT = condensed tannins, PP = polyphenols. Ripe and unripe fruits were compared with Wilcoxon signed rank tests. Unadjusted P-values are shown: * P<0.05, **P<0.01 (adjusted P-values are >0.05); 'ns' indicates that the unadjusted P-value was non-significant.

Appendix

Table 2 Chemical properties of some wild plant foods eaten by chimpanzees in Bulindi, 2014–2015 ^a

Wild plant food species	Family	Life form ^b	Part eaten	TN	CP	SP	Lipid	Sugar	TNC	Ash	NDF	ADF	HC	CT	PP	ME
(A) WILD FRUITS																
<i>Aframomum</i> sp.	Zingiberaceae	H	Ripe Fruit	0.73	4.56	1.33	1.65	33.10	66.81	9.08	17.90	10.36	7.54	0.13	0.29	329.0
<i>Allophylus africanus</i>	Sapindaceae	T	Ripe Fruit	1.62	10.13	8.95	1.26	38.30	77.32	3.76	7.54	4.70	2.84	0.23	2.80	373.2
<i>Allophylus ferrugineus</i>	Sapindaceae	S	Ripe Fruit	1.47	9.19	4.71	1.55	38.58	71.62	6.01	11.63	5.58	6.05	0.52	1.86	355.8
<i>Dovyalis macrocalyx</i>	Flacourtiaceae	S	Ripe Fruit	1.09	6.81	0.91	1.16	32.43	83.63	4.28	4.12	2.23	1.89	0	0.25	378.8
<i>Ficus asperifolia</i>	Moraceae	S	Ripe Fruit	1.13	7.06	1.94	4.10	42.51	67.42	6.54	14.88	9.76	5.12	0.27	0.31	358.6
<i>Ficus exasperata</i>	Moraceae	T	Ripe Fruit	2.07	12.94	3.74	5.19	26.16	55.45	10.97	15.45	11.37	4.08	0	0.65	345.0
<i>Ficus mucuso</i>	Moraceae	T	Ripe Fruit	0.71	4.44	2.33	3.81	44.41	69.28	5.48	16.99	12.23	4.76	0.19	0.65	356.4
<i>Ficus natalensis</i>	Moraceae	T	Ripe Fruit	0.84	5.25	1.73	1.77	24.79	61.34	6.14	25.50	17.86	7.64	0	0.69	323.1
<i>Ficus sansibarica</i>	Moraceae	T	Unripe Fruit	2.18	13.63	5.76	1.30	25.04	59.08	5.24	20.76	12.82	7.94	0.74	4.91	335.7
<i>Ficus sur</i>	Moraceae	T	Ripe Fruit	0.83	5.19	2.04	4.22	28.78	62.61	8.43	19.55	15.17	4.38	0.17	0.39	340.5
<i>Ficus thonningii</i>	Moraceae	T	Ripe Fruit	0.82	5.13	2.22	1.91	29.46	53.74	6.74	32.49	23.80	8.69	0	0.35	304.6
<i>Ficus vallis-choudae</i>	Moraceae	T	Ripe Fruit	0.58	3.63	2.53	3.16	18.97	60.71	7.95	24.56	19.21	5.35	0	0.80	325.1
<i>Lantana camara</i>	Verbenaceae	S	Ripe Fruit	1.07	6.69	3.21	0.63	43.86	68.67	4.77	19.24	15.55	3.69	0	1.14	337.9
<i>Marantochloa leucantha</i>	Marantaceae	H	Ripe Fruit	0.76	4.75	1.56	1.58	3.13	21.96	17.22	54.49	24.82	29.67	0	0.42	208.2
<i>Momordica calantha</i>	Cucurbitaceae	C	Ripe Fruit	0.81	5.06	1.98	1.52	59.36	74.54	10.07	8.81	3.33	5.48	0	0.16	346.2
<i>Monanthes ferruginea</i>	Annonaceae	S	Ripe Fruit	1.46	9.13	3.30	2.41	44.61	67.10	3.51	17.86	11.04	6.82	0	0.44	355.1
<i>Morus mesozygia</i>	Moraceae	T	Ripe Fruit	1.45	9.06	4.24	2.40	53.56	74.46	4.71	9.37	5.40	3.97	0	0.47	370.7
<i>Parkia filicoidea</i>	Fabaceae	T	Ripe Fruit	1.55	9.69	5.24	0.62	30.88	69.01	2.78	17.90	7.04	10.86	0.49	0.31	349.0
<i>Phoenix reclinata</i>	Arecaceae	T	Ripe Fruit	0.52	3.25	5.98	0.85	51.50	74.96	3.47	17.47	7.74	9.73	0	1.75	348.4
–	–	–	Unripe Fruit	1.00	6.25	8.43	0.74	16.34	50.52	3.71	38.78	17.89	20.89	5.26	5.42	295.8
<i>Pseudospondias microcarpa</i>	Anacardiaceae	T	Ripe Fruit	0.69	4.31	8.97	0.38	48.05	87.62	2.53	5.16	2.90	2.26	0.55	4.41	379.4
–	–	–	Unripe Fruit	0.71	4.44	7.41	0.17	24.17	79.29	3.58	12.52	4.44	8.08	0.24	2.40	356.5
<i>Toddalia asiatica</i>	Rutaceae	S	Ripe Fruit	1.10	6.88	1.90	1.46	37.18	73.67	4.00	14.00	8.76	5.24	0.14	0.94	357.7
<i>Vitex doniana</i>	Lamiaceae	T	Ripe Fruit	0.36	2.25	7.46	2.14	36.75	74.69	3.97	16.95	13.94	3.01	0.14	1.39	354.1
(B) WILD PITHS																
<i>Aframomum</i> sp.	Zingiberaceae	H	Pith	3.29	20.56	3.31	3.08	8.19	24.72	13.40	38.24	20.81	17.43	0.60	0.61	270.0
<i>Alchornea cordifolia</i>	Euphorbiaceae	S	Pith	0.94	5.88	3.04	1.03	17.07	50.91	4.55	37.64	27.14	10.50	0	4.08	296.6
<i>Antiaris toxicaria</i>	Moraceae	T	Pith	0.54	3.38	3.10	0	33.11	56.01	4.60	36.02	23.37	12.65	0.59	2.38	295.2
<i>Marantochloa leucantha</i>	Marantaceae	H	Pith	2.70	16.88	2.57	2.50	4.89	22.28	20.99	37.36	20.08	17.28	0	0.63	238.9
<i>Pennisetum purpureum</i>	Poaceae	G	Pith	2.20	13.75	4.64	1.97	8.69	22.52	18.10	43.66	22.64	21.02	0	0.17	232.7
<i>Phoenix reclinata</i>	Arecaceae	T	Pith ^c	0.37	2.31	1.13	0	28.36	38.29	2.05	57.35	36.13	21.22	0.20	0.23	254.2
<i>Piper umbellatum</i>	Piperaceae	H	Pith	1.52	9.50	1.15	2.41	13.01	37.08	15.58	35.43	26.41	9.02	0	0.23	264.7
(C) WILD LEAVES																
<i>Antiaris toxicaria</i>	Moraceae	T	Young Leaf	3.14	19.63	9.38	2.13	13.34	54.23	6.01	18.01	9.86	8.15	2.60	5.27	343.4
<i>Broussonetia papyrifera</i>	Moraceae	S	Young Leaf	4.09	25.56	5.24	3.19	7.32	41.64	9.00	20.61	11.37	9.24	0	0.77	330.5
<i>Ficus asperifolia</i>	Moraceae	S	Young Leaf	3.49	21.81	2.97	4.72	4.97	37.67	10.57	25.23	16.68	8.55	0	0.67	320.8

<i>Ficus mucoso</i>	Moraceae	T	Young Leaf	3.77	23.56	8.78	2.23	3.80	47.82	7.89	18.50	13.14	5.36	0.90	2.85	335.2
<i>Ficus natalensis</i>	Moraceae	T	Young Leaf	2.33	14.56	4.55	4.34	4.93	41.84	8.75	30.51	18.79	11.72	0.31	0.72	313.5
<i>Illigera pentaphylla</i>	Hernandiaceae	C	Young Leaf	3.95	24.69	4.21	7.31	3.29	9.65	9.52	48.83	19.61	29.22	0.17	0.90	281.3
<i>Piper guineense</i>	Piperaceae	C	Young Leaf	4.01	25.06	4.08	2.11	4.23	28.80	11.87	32.16	20.69	11.47	0	1.30	285.9
<i>Pseudospondias microcarpa</i>	Anacardiaceae	T	Young Leaf	3.31	20.69	8.67	3.11	3.91	53.74	4.32	18.14	11.27	6.87	0.75	6.38	354.7
<i>Sterculia dawei</i>	Sterculiaceae	T	Young Leaf	4.26	26.63	9.31	2.35	4.84	34.93	8.06	28.04	11.38	16.66	0.94	1.65	312.2
<i>Trichilia dregeana</i>	Meliaceae	T	Young Leaf	2.84	17.75	8.71	4.34	7.92	55.06	5.11	17.74	11.97	5.77	2.72	6.58	358.7
(D) WILD 'OTHER'																
<i>Entandrophragma</i> sp.	Meliaceae	T	Cambium	0.87	5.44	1.31	3.45	22.79	46.52	6.55	38.04	28.67	9.37	0.15	0.38	299.8
<i>Hibiscus calyphyllus</i>	Malvaceae	S	Flower	2.87	17.94	5.55	2.32	27.49	45.74	5.27	28.73	9.01	19.72	2.14	1.22	321.6
<i>Phoenix reclinata</i>	Arecaceae	T	Young Seed	1.03	6.44	6.76	5.94	11.52	26.62	1.42	59.58	31.25	28.33	1.74	1.56	281.0

^a TN = total nitrogen, CP = crude protein (TN x 6.25), SP = soluble protein (BioRad), Sugar = soluble sugars, TNC = total non-structural carbohydrates, NDF = neutral detergent fiber, ADF = acid detergent fiber, HC = hemicellulose, CT = condensed tannins, PP = polyphenols, ME = metabolizable energy (see Methods for calculations). Values are presented as % DM, except ME (Kcal/100 g).

^b Life form: C = climber of vine, G = grass, H = herb, S = shrub, T = tree

^c Pith from *Phoenix reclinata* leaf fronds is typically 'wadged' (i.e., chewed and compressed to extract the juice) before being spat out; thus the fibrous portion is not usually ingested

Appendix

Table 3 Chemical properties of cultivated plant foods eaten by chimpanzees in Bulindi, 2014–2015 ^a

Cultivated plant food species (common name)	Family	Life form ^b	Part eaten	TN	CP	SP	Lipid	Sugar	TNC	Ash	NDF	ADF	HC	CT	PP	ME
(A) CULTIVATED FRUITS																
<i>Artocarpus heterophyllus</i> (Jackfruit)	Moraceae	T	Ripe Fruit	1.03	6.44	2.29	1.16	75.88	83.13	3.69	5.58	3.85	1.73	0	0.16	377.6
–	–	–	Unripe Fruit	1.79	11.19	4.77	2.66	20.60	55.01	5.37	25.77	15.30	10.47	0.97	0.54	330.0
<i>Carica papaya</i> (Papaya)	Caricaceae	T	Ripe Fruit	0.73	4.56	1.81	0.79	71.30	84.05	3.58	7.02	5.37	1.65	0	0.15	372.8
–	–	–	Unripe Fruit	1.05	6.56	1.51	0.86	61.47	70.65	8.72	13.21	10.14	3.07	0	0.20	337.7
<i>Citrus limon</i> (Lemon)	Rutaceae	S	Ripe Fruit	0.75	4.69	0.74	0.86	19.64	84.94	2.64	6.87	4.79	2.08	0	0.17	377.3
<i>Citrus sinensis</i> (Orange)	Rutaceae	S	Ripe Fruit	0.78	4.88	1.65	0.67	33.18	76.35	3.67	14.44	8.92	5.52	0	0.46	354.0
<i>Mangifera indica</i> (Mango)	Anacardiaceae	T	Ripe Fruit	0.45	2.81	1.89	0.68	67.63	85.17	1.96	9.38	3.80	5.58	0	0.16	373.0
–	–	–	Unripe Fruit	0.58	3.63	1.55	1.26	39.73	80.51	2.58	12.03	5.01	7.02	0	0.37	367.1
<i>Musa</i> sp. (Plantain banana)	Musaceae	H	Ripe Fruit	0.41	2.56	2.41	0.63	68.60	88.79	1.91	6.11	1.25	4.86	0	0.45	380.8
–	–	–	Unripe Fruit	0.64	4.00	2.03	0.57	1.06	51.53	3.20	40.70	0.80	39.90	0	0.13	292.4
<i>Musa</i> sp. (Sweet/dessert banana)	Musaceae	H	Ripe Fruit	0.43	2.69	2.62	0.34	81.73	86.91	1.66	8.40	1.77	6.63	0	0.38	374.9
<i>Passiflora edulis</i> (Passion fruit)	Passifloraceae	C	Ripe Fruit	0.66	4.13	2.07	2.39	59.37	78.69	3.20	11.60	4.10	7.50	0	0.12	371.3
<i>Phaseolus vulgaris</i> (Bean)	Fabaceae	S	Unripe Fruit	2.18	13.63	4.94	0.85	16.53	51.12	4.09	30.32	11.56	18.76	0.13	0.16	315.1
<i>Psidium guajava</i> (Guava)	Myrtaceae	T	Ripe Fruit	0.44	2.75	1.46	0.72	43.34	67.69	3.60	25.24	19.06	6.18	0.32	0.57	328.6
–	–	–	Unripe Fruit	0.56	3.50	2.14	0.26	18.88	39.61	3.99	52.64	36.05	16.59	0.53	0.47	259.0
<i>Theobroma cacao</i> (Cocoa)	Sterculiaceae	T	Ripe Fruit	0.79	4.94	1.50	0.80	51.50	81.33	3.03	9.90	6.55	3.35	0.32	0.75	368.1
–	–	–	Unripe Fruit	1.63	10.19	4.55	5.60	53.36	65.69	4.74	13.78	8.57	5.21	0.74	0.61	376.0
(B) CULTIVATED PITHS																
<i>Dioscorea alata</i> (Water yam)	Dioscoreaceae	H	Pith	1.10	6.88	1.73	0.42	66.39	71.98	9.42	11.31	8.06	3.25	0	0.13	337.3
<i>Musa</i> sp. (Plantain banana)	Musaceae	H	Pith	1.34	8.38	2.44	1.10	23.48	35.76	13.09	41.68	25.29	16.39	0	0.14	253.1
<i>Saccharum officinarum</i> (Sugarcane)	Poaceae	G	Pith ^c	0.28	1.75	0.74	0.74	76.56	75.41	1.62	20.48	10.17	10.31	0	0.10	348.1
<i>Zea mays</i> (Maize)	Poaceae	G	Pith	1.08	6.75	3.65	1.22	34.7	41.10	5.34	45.59	22.75	22.84	0	0.21	275.3

^a TN = total nitrogen, CP = crude protein (TN x 6.25), SP = soluble protein (BioRad), Sugar = soluble sugars, TNC = total non-structural carbohydrates, NDF = neutral detergent fiber, ADF = acid detergent fiber, HC = hemicellulose, CT = condensed tannins, PP = polyphenols, ME = metabolizable energy (see Methods for calculations). Values are presented as % DM, except ME (Kcal/100 g).

^b Life form: C = climber of vine, G = grass, H = herb, S = shrub, T = tree

^c Pith from sugarcane is typically 'wadded' (i.e., chewed and compressed to extract the juice) before being spat out; thus the fibrous portion is not usually ingested

Appendix

Table 4 Chemical properties of some cultivated plant foods grown in Bulindi but *not* eaten by the chimpanzees ^a

Cultivated plant food not eaten (common name)	Family	Life form ^b	Part eaten	TN	CP	SP	Lipid	Sugar	TNC	Ash	NDF	ADF	HC	CT	PP	ME
(A) CULTIVATED FRUITS																
<i>Ananas comosus</i> (Pineapple)	Bromeliaceae	H	Ripe Fruit	1.34	8.38	1.09	1.79	78.78	75.63	1.20	13.01	3.81	9.20	0	0.12	372.9
<i>Annona muricata</i> (Soursop)	Annonaceae	T	Ripe Fruit	1.24	7.75	2.21	1.58	54.55	79.00	2.76	8.91	5.85	3.06	0.22	0.33	375.5
<i>Cucurbita</i> sp. (Pumpkin)	Cucurbitaceae	C	Ripe Fruit	1.33	8.31	2.01	0.99	27.72	58.66	5.34	26.70	3.99	22.71	0	0.11	319.5
<i>Persea americana</i> (Avocado)	Lauraceae	T	Ripe Fruit	0.73	4.56	1.60	40.28	26.50	22.05	2.04	31.07	19.23	11.84	0	0.08	518.7
<i>Solanum betaceum</i> (Tamarillo)	Solanaceae	H	Ripe Fruit	2.19	13.69	2.87	0.99	27.99	59.07	11.13	15.12	9.84	5.28	0	0.19	324.1
<i>Solanum lycopersicum</i> (Tomato)	Solanaceae	S	Ripe Fruit	1.51	9.44	1.86	0.95	52.29	63.58	9.72	16.31	13.34	2.97	0	0.29	326.7
(B) CULTIVATED 'OTHER'																
<i>Arachis hypogaea</i> (Ground nut)	Fabaceae	H	Seed (nut)	3.53	22.06	20.52	42.02	9.17	5.29	1.79	28.84	8.91	19.93	0.10	0.32	533.7
<i>Carica papaya</i> (Papaya)	Caricaceae	T	Pith	2.27	14.19	3.62	1.82	20.47	50.66	14.98	18.35	13.42	4.93	0	0.23	305.1
–	–	–	Young Leaf	4.78	29.88	7.62	3.60	4.61	35.43	9.31	21.79	12.30	9.49	0	0.78	328.5
<i>Ipomoea batatas</i> (Sweet potato)	Convolvulaceae	C	Tuber	0.60	3.75	1.30	1.83	9.64	34.87	0.70	58.85	2.03	56.82	0	0.07	265.1
<i>Manihot esculenta</i> (Cassava) ^c	Euphorbiaceae	S	Tuber	0.21	1.31	0.50	0	3.89	62.97	0.54	35.18	1.34	33.84	0	0.05	313.4
<i>Oryza</i> sp. (Rice)	Poaceae	G	Pith	2.14	13.38	3.98	1.60	15.45	27.43	11.53	46.07	22.14	23.93	0	0.15	251.3
<i>Zea mays</i> (Maize)	Poaceae	G	Caryopsis (cob)	1.48	9.25	3.57	4.58	4.20	53.82	1.35	31.00	3.81	27.19	0	0.08	343.1

^a TN = total nitrogen, CP = crude protein (TN x 6.25), SP = soluble protein (BioRad), Sugar = soluble sugars, TNC = total non-structural carbohydrates, NDF = neutral detergent fiber, ADF = acid detergent fiber, HC = hemicellulose, CT = condensed tannins, PP = polyphenols, ME = metabolizable energy (see Methods for calculations). Values are presented as % DM, except ME (Kcal/100 g).

^b Life form: C = climber of vine, G = grass, H = herb, S = shrub, T = tree

^c Cassava cultivated in Bulindi is of the 'sweet' variety (i.e., without toxic levels of cyanogenic glucosides) and can be eaten by humans uncooked