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**The macronutrient composition of wild and cultivated plant foods of West African chimpanzees (*Pan troglodytes verus*) inhabiting an anthropogenic landscape**

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Indicate which taxonomic group was the subject of your study (select all that apply or type another option)::	Apes (non-human)
Keywords:	human-primate coexistence, anthropogenic landscape, crop-foraging, oil palm, nutritional ecology

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Manuscripts

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4 1 **The macronutrient composition of wild and cultivated plant foods of West African**  
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6 2 **chimpanzees (*Pan troglodytes verus*) inhabiting an anthropogenic landscape**  
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8  
9 3 Short title: Nutrient content of chimpanzee foods  
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41  
42 20 **ABSTRACT**

43 21 Agricultural expansion encroaches on tropical forests and primates in such landscapes  
44 22 frequently incorporate crops into their diet. Understanding the nutritional drivers behind crop-  
45 23 foraging can help inform conservation efforts to improve human-primate coexistence. This  
46 24 study builds on existing knowledge of primate diets in anthropogenic landscapes by estimating  
47 25 the macronutrient content of 24 wild and 11 cultivated foods (90.5% of food intake) consumed  
48 26 by chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea, West Africa. We also compared  
49 27 the macronutrient composition of Bossou crops to published macronutrient measures of crops  
50 28 from Bulindi, Uganda, East Africa. The composition of wild fruits, leaves and pith were  
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4 29 consistent with previous reports for primate diets. Cultivated fruits were higher in  
5  
6 30 carbohydrates and lower in insoluble fibre than wild fruits, while wild fruits were higher in  
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8 31 protein. Macronutrient content of cultivated pith fell within the ranges of consumed wild pith.  
9  
10 32 Oil palm food parts were relatively rich in carbohydrates, protein, lipids, and/or fermentable  
11  
12 33 fibre, adding support for the nutritional importance of the oil palm for West African  
13  
14 34 chimpanzees. We found no differences in the composition of cultivated fruits between Bossou  
15  
16 35 and Bulindi, suggesting that macronutrient content alone does not explain differences in crop  
17  
18 36 selection. Our results build on current understanding of chimpanzee feeding ecology within  
19  
20 37 forest-agricultural mosaics and provide additional support for the assumption that crops offer  
21  
22 38 primates energetic benefits over wild foods.  
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30 40 **Key words:** human-primate coexistence; *Pan troglodytes verus*; anthropogenic landscape;  
31  
32 41 crop-foraging; oil palm; nutritional ecology  
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## 39 43 INTRODUCTION

40 44 The world's most biodiversity rich forests are increasingly being converted to agriculture for  
41  
42 45 subsistence and large-scale industrial farming to meet the demands of an ever-growing human  
43  
44 46 population (Laurance, Sayer, & Cassman, 2014). Such agricultural expansion brings new  
45  
46 47 challenges for wildlife aiming to meet their nutritional and energetic needs from the  
47  
48 48 surrounding environment. Deforestation reduces the distribution and availability of wild food  
49  
50 49 resources while agricultural practises introduce spatially clumped and often predictably  
51  
52 50 available cultivated foods, i.e. crops. Many wildlife species respond to these changes by  
53  
54 51 altering their foraging strategies to incorporate crops into their diets, allowing them to exploit  
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56 52 anthropogenic landscapes, (e.g. African elephant (*Loxodonta africana*) Hoare, 2001; baboon  
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4 53 (*Papio* spp.) Hill, 2000; macaque (*Macaca* spp.) Priston & McLennan, 2013; and other non-  
5  
6 54 human primates (hereafter ‘primates’) Humle & Hill, 2016; wild boar (*Sus scrofa*) Keuling,  
7  
8 55 Stier, & Roth, 2009; and raccoon (*Procyon lotor*), Beasley & Rhodes, 2008). Crop-foraging  
9  
10 56 (also often termed “crop-raiding”) affects local livelihoods through crop losses and damages  
11  
12 57 (Hill, 1997; 2005), while species that consume cultivated foods frequently face significant risks  
13  
14 58 from crop protection and foraging deterrent methods and/or hostile behaviours from farmers  
15  
16 59 (Hockings & Humle, 2009). As a result, crop-foraging is one of the principle threats to human-  
17  
18 60 wildlife coexistence within anthropogenic landscapes (e.g. Hoare, 2001; Hockings & Humle,  
19  
20 61 2009; Mackenzie & Ahabyona, 2012; Redpath, et al., 2013). Understanding the nutritional  
21  
22 62 drivers behind crop consumption by wildlife is therefore essential for effective conservation  
23  
24 63 planning and mitigation strategies (Osborn, 2004; Rode, Chiyo, Chapman, & McDowell, 2006;  
25  
26 64 Dostaler, Ouellet, Therrien, & Cote, 2011).

31  
32 65 The behavioural and ecological flexibility and broad dietary repertoire of many primate  
33  
34 66 species means that they readily exploit crops when available (e.g. baboon (*Papio* spp.) Hill,  
35  
36 67 2000, Strum, 2010; macaque (*Macaca* spp.) Priston & McLennan, 2013; vervet (*Chlorocebus*  
37  
38 68 spp.) Brennan, Else, & Altmann, 1985; capuchin (*Cebus* spp.) McKinney, 2011; orangutan  
39  
40 69 (*Pongo* spp.) Campbell-Smith, Campbell-Smith, Singleton, & Linkie, 2011). Studies  
41  
42 70 examining primate feeding ecology within human-impacted environments have revealed  
43  
44 71 diverse crop-foraging strategies depending on various factors such as availability, proximity  
45  
46 72 and type of cultivated resources, habitat quality and wild food availability, and perceived risks  
47  
48 73 associated with crop-foraging (Naughton-Treves, Treves, Chapman, & Wrangham, 1998;  
49  
50 74 Reynolds, 2005; Hockings, Anderson, & Matsuzawa, 2009; Strum, 2010; McKinney, 2011;  
51  
52 75 McLennan, 2013; Bryson-Morrison, Tzanopoulos, Matsuzawa, & Humle, 2017). Where crops  
53  
54 76 are fully incorporated into the diets, primates often display changes to activity budget and  
55  
56 77 ranging patterns, spending less time foraging and travelling and more time resting (e.g.

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4 78 Altmann & Muruthi, 1988; Saj, Sicotte, & Paterson, 1999; Strum, 2010; Warren, Higham,  
5  
6 79 MacLarnon, & Ross, 2011; Cancelliere, Chapman, Twinomugisha, & Rothman, 2018). Crop  
7  
8 80 consumption by primates has also been associated with a more effective immune response to  
9  
10 81 parasite infections (e.g. Chapman, Speirs, Gillespie, Holland, & Austad, 2006) and, where  
11  
12 82 crop-foraging by wildlife is tolerated, a reduction in physiological stress (e.g. Lodge, Ross,  
13  
14 83 Ortmann, & MacLarnon, 2013). Finally, some crop-foraging populations also show differences  
15  
16 84 in life history variables, such as shorter inter-birth intervals, younger age at first parturition,  
17  
18 85 reduced infant mortality, increased longevity, and heavier bodyweight in adulthood (e.g.  
19  
20 86 Strum, 2010; Sugiyama & Fujita, 2011; Warren, et al., 2011; Lodge, et al., 2013). These  
21  
22 87 behavioural, ecological and physiological advantages to crop-foraging primates are often  
23  
24 88 attributed to the greater nutritional and energetic value of crop foods compared to wild plant  
25  
26 89 foods (e.g. Altmann & Muruthi 1988; Saj, et al., 1999; Strum, 2010; Warren, et al., 2011;  
27  
28 90 Lodge, et al., 2013).

33  
34 91 Humans have selected cultivated foods to be palatable, easily digestible and energy rich  
35  
36 92 with low levels of potentially toxic and/or digestion inhibiting secondary compounds (Milton,  
37  
38 93 1999). Cultivated potato and maize consumed by baboon (*Papio anubis*) were found to be  
39  
40 94 easier to digest than wild plant foods due to lower levels of insoluble fibre (Forthman-Quick &  
41  
42 95 Demment, 1988). Similarly, cultivated cacao fruit consumed by Tonkean macaques (*Macaca*  
43  
44 96 *tonkeana*) were lower in insoluble fibre and higher in carbohydrate energy than wild fruit foods  
45  
46 97 (Riley, Tolbert, & Farida, 2013). The first comprehensive study to quantify the macronutrient  
47  
48 98 content of multiple cultivated and wild foods in the diets of wild primates, found that cultivated  
49  
50 99 fruits and pith consumed by chimpanzees (*Pan troglodytes*) in Bulindi, Uganda, East Africa  
51  
52 100 were lower in insoluble fibre and secondary compounds and higher in carbohydrates than wild  
53  
54 101 food equivalents (McLennan & Ganzhorn, 2017). However, crops were found to be low in  
55  
56 102 other macronutrients, particularly protein and lipids, compared to wild foods (McLennan &

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4 103 Ganzhorn, 2017). Furthermore, wild and cultivated foods consumed by vervet monkeys  
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6 104 (*Cercopithecus aethiops*) at Lake Nabugabo, Uganda were found to differ in the relative  
7  
8 105 proportions of macronutrients they contained, with cultivars containing higher proportions of  
9  
10 106 carbohydrates and proteins relative to lipids compared to wild foods (Cancelliere, et al., 2018).  
11  
12 107 These results suggest that crops are indeed high-quality foods in that they provide a rich source  
13  
14  
15 108 of energy from easily digestible carbohydrates.

16  
17  
18 109 Chimpanzees are found in anthropogenically disturbed habitats throughout their range  
19  
20 110 in West, Central and East Africa (Humle, Maisels, Oates, Plumptre, & Williamson, 2016) and  
21  
22 111 frequently incorporate crops into their diets (Hockings & Humle, 2009; Hockings &  
23  
24 112 McLennan, 2012). However, crop selection differs between chimpanzee populations, even  
25  
26 113 when similar crop varieties are available (McLennan & Hockings, 2014). Chimpanzees  
27  
28 114 consume a diverse range of plant food types (Nishida & Uehara, 1983; Sugiyama & Koman,  
29  
30 115 1992; Tutin & Fernandez, 1993; Reynolds, 2005), as well as varying amounts of animal  
31  
32 116 products (ranging between 3 - 13% of the total diet of seven different chimpanzee populations:  
33  
34 117 Pruetz, 2006). Nevertheless, regardless of habitat type, chimpanzees are predominantly  
35  
36 118 frugivorous and maintain a high proportion of fruit in their diets even when fruit availability is  
37  
38 119 low (Ghiglieri, 1984; Wrangham, Conklin-Brittain, & Hunt, 1998; Watts, Potts, Lwanga, &  
39  
40 120 Mitani, 2012). Generally, the macronutrient composition of chimpanzee diets reflects their  
41  
42 121 preference for ripe fruits, with relatively high levels of easily digestible carbohydrates and  
43  
44 122 lower levels of insoluble fibre and secondary compounds, such as condensed tannins and  
45  
46 123 polyphenols (Conklin, Wrangham, & Hunt, 1998; Reynolds, Plumptre, Greenham, &  
47  
48 124 Harborne, 1998; Wrangham, et al., 1998; Matsumoto-Oda & Hayashi, 1999; Hohmann, et al.,  
49  
50 125 2010). Pith, particularly from terrestrial herbaceous vegetation (THV), also provides  
51  
52 126 chimpanzees with moderate to high levels of carbohydrates, as well as energy from digestible  
53  
54 127 fibre fractions (Wrangham, et al., 1991; Wrangham, et al., 1998; Matsumoto-Oda & Hayashi,

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4 128 1999). Young leaves provide the greatest amounts of protein of plant foods frequently  
5  
6 129 consumed by chimpanzees (Takemoto, 2003; Carlson, Rothman, & Mitani, 2013). Chimpanzee  
7  
8 130 diets are considered high quality (i.e. generally higher in macronutrients and lower in  
9  
10 131 indigestible fibre and secondary compounds) (Conklin, et al., 1998). However, the  
11  
12 132 macronutrient and secondary compound content of wild fruits and leaves varies between  
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14  
15 133 chimpanzee study sites (Hohmann, et al., 2010).

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17  
18 134 In the present study, we aimed to build on existing knowledge of primate diets in  
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20 135 anthropogenic landscapes by describing the macronutrient content of wild and cultivated foods  
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22 136 consumed by a chimpanzee community inhabiting the forest-agricultural mosaic of Bossou,  
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24 137 Guinea, West Africa. Such information is necessary to help increase current understanding of  
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26 138 chimpanzee crop-foraging decisions and differences in crop selection both within and between  
27  
28 139 populations. Presently, there is limited information on the nutritional characteristics of foods  
29  
30 140 in the diets of West African chimpanzees inhabiting anthropogenic landscapes (Takemoto,  
31  
32 141 2003). This chimpanzee community is ideally situated for our study as Bossou has been rated  
33  
34 142 as the long-term study site facing the greatest degree of human-impact, due to the extreme  
35  
36 143 proximity between chimpanzees and people (Wilson, et al., 2014). Furthermore, over 30 years  
37  
38 144 of research has produced a comprehensive list of over 200 plant food species (246 plant parts)  
39  
40 145 known to be consumed by the chimpanzees (Humle, Koops, & Cherif, 2011). They also eat  
41  
42 146 some animal products including insects, larvae, honey, bird eggs, and tree pangolin (*Manis*  
43  
44 147 *tricuspis*). However, faunivory is relatively rare at Bossou compared to other known  
45  
46 148 chimpanzee sites (Pruetz, 2006). All animal products combined contribute less than 3% to total  
47  
48 149 feeding bouts at Bossou (2.3%: Hockings, unpublished data; 1.9%: Bryson-Morrison,  
49  
50 150 unpublished data), which is likely due to the scarcity of mammalian prey species (Humle,  
51  
52 151 2011), and the relatively negligible consumption of *Dorylus* ants, (0.8 – 1.2% of total feeding  
53  
54 152 bouts: Yamakoshi, 1998; Hockings, unpublished data; Bryson-Morrison, unpublished data).



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4 153 The Bossou chimpanzees have foraged on crops for generations and consume 17 different fruit  
5  
6 154 and non-fruit varieties (Hockings, et al., 2009; Hockings, 2011). Crops account for a relatively  
7  
8 155 large proportion of overall feeding time (6.4 - 20% per annum: Takemoto, 2002; Hockings, et  
9  
10 156 al., 2009; Bryson-Morrison, 2017). The chimpanzees also frequently feed from the semi-  
11  
12 157 domesticated or wild oil palm (*Elaeis guineensis*), exploiting more food parts (i.e. fruit, nut  
13  
14 158 kernel, pith, petiole, flower, and heart) than any other known chimpanzee community (Humle  
15  
16 159 & Matsuzawa, 2004). Oil palm is native to West Africa and is found at high densities in human-  
17  
18 160 impacted landscapes where it is maintained and utilised by people predominantly to produce  
19  
20 161 palm oil for domestic and commercial use (Humle & Matsuzawa, 2004). Bossou chimpanzees  
21  
22 162 heavily depend on the oil palm for food (up to 15.9% of annual feeding time: Yamakoshi, 1998)  
23  
24 163 and nesting (Humle & Matsuzawa, 2004). Recent evidence suggests that oil palm trees are also  
25  
26 164 an important food and nesting resource for other chimpanzee communities residing in human-  
27  
28 165 impacted areas across West Africa (Guinea-Bissau: Sousa, Barata, Sousa, Casanova, &  
29  
30 166 Vicente, 2011; Bessa, Sousa, & Hockings, 2015; Côte d'Ivoire: Humle & Matsuzawa, 2004;  
31  
32 167 Sierra Leone: Garriga, et al., 2019; Guinea: Leciak, Hladik, & Hladik, 2005). The  
33  
34 168 macronutrient content of the oil palm fruit and nut kernel, both of which are used in the  
35  
36 169 production of palm oils, has been previously described (Agunbiade, Wiseman, & Cole, 1999;  
37  
38 170 Akpanabiatu, Ekpa, Mauro, & Rizzo, 2001; Bora, Rocha, Narain, Moreira-Monteiro, &  
39  
40 171 Moreira, 2003; Kok, Ong-Abdullah, Ee, & Namasivayam, 2011). However, there are no  
41  
42 172 published data detailing the nutritional composition of other oil palm parts, i.e. petiole, pith,  
43  
44 173 flower, and palm heart (inner core of the trunk), that also serve as potentially important food  
45  
46 174 sources for chimpanzees.

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54 175 Specifically, in this study, we examined and compared the macronutrient and estimated  
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56 176 metabolizable energy content of wild and cultivated foods, including oil palm food parts, which  
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58 177 constituted the bulk of the Bossou chimpanzee diet. Following findings from the Bulindi  
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4 178 chimpanzee community which also resides in a forest-agricultural mosaic in Uganda, East  
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6 179 Africa (McLennan & Ganzhorn, 2017), we predicted that cultivated foods consumed by Bossou  
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8 180 chimpanzees would be higher in easily digestible carbohydrates, and lower in insoluble fibre,  
9  
10 181 protein, and lipids, than equivalent wild foods. Bossou chimpanzees are also known to consume  
11  
12 182 more fruit and non-fruit crop species than the Bulindi chimpanzees (e.g. pineapple, maize,  
13  
14 183 cassava, rice), despite similar crops being available at both sites (McLennan & Hockings,  
15  
16 184 2014). Therefore, to investigate if nutritional differences influence crop selection between  
17  
18 185 chimpanzee sites, we compared the macronutrient and energy content of cultivated foods at  
19  
20 186 Bossou with published results for cultivated foods at Bulindi (McLennan & Ganzhorn, 2017).  
21  
22 187 McLennan & Ganzhorn, (2017) found little nutritional differences between crops consumed  
23  
24 188 and those ignored by the Bulindi chimpanzees. However, plant chemistry is influenced by  
25  
26 189 many environmental factors including temperature variability, light intensity, water  
27  
28 190 availability, salt levels, soil type, seasonality, and plant maturation stage (Sams, 1999; Woolf  
29  
30 191 & Ferguson, 2000; Chapman, Chapman, Rode, Hauck, & McDowell, 2003). Consequently, the  
31  
32 192 nutritional composition of wild plant parts in primate diets varies spatially and temporally both  
33  
34 193 within and between habitats (Ganzhorn, 1995; Chapman, et al., 2003; Worman & Chapman,  
35  
36 194 2005; Rothman, Chapman, Hansen, Cherney, & Pell, 2009; Houle, Conklin-Brittain, &  
37  
38 195 Wrangham, 2014), including between chimpanzee study sites (Hohmann, et al., 2010).  
39  
40 196 Therefore, we predicted that there would be differences in the macronutrient composition of  
41  
42 197 cultivated foods between Bossou and Bulindi.  
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## 50 198 **METHODS**

### 51 52 53 199 **Study site and population**

54  
55 200 We present data collected from April 2012 to March 2013 from the habituated chimpanzee (*P.*  
56  
57 201 *t. verus*) community, which inhabits the anthropogenic landscape surrounding the village of  
58  
59 202 Bossou, Republic of Guinea, West Africa (latitude 7°38'71.7"N and longitude 8°29'38.9"W)

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4 203 (Matsuzawa, Humle, & Sugiyama, 2011). During our study, the community size ranged  
5  
6 204 between 12-13 individuals with six adult females and four adult males. The chimpanzee  
7  
8 205 community's home range is approximately 15 km<sup>2</sup>, although they spend the majority of their  
9  
10 206 time in the four small hills (70-150 m high) that surround Bossou village and constitute their 6  
11  
12 207 km<sup>2</sup> core area (Humle, 2011). Local people practise slash and burn agriculture within and at  
13  
14 208 the edges of these small hills, resulting in a highly heterogeneous forest-agricultural mosaic  
15  
16 209 composed of regenerating, riverine, and mature forest as well as fallow land, coffee plantations  
17  
18 210 and cultivated fields (Humle, 2011; Bryson-Morrison, Matsuzawa, & Humle, 2016). The  
19  
20 211 climate in this region is classified as tropical wet seasonal with a long rainy season from March  
21  
22 212 to October, when wild fruit availability is low, and a short dry season from November to  
23  
24 213 February, when wild fruit availability is high (Yamakoshi, 1998; Takemoto, 2002; Hockings,  
25  
26 214 2007; Humle, 2011; Bryson-Morrison, et al., 2016).

### 215 **Sample collection and nutritional analyses**

216 Our sample collection protocols and nutritional analyses followed Rothman, Chapman, & Van  
217 Soest (2012). We collected food samples during focal feeding bout observations of adult  
218 individuals (N = 10) (total observation: 568 hours), and endeavoured to collect samples from  
219 the same tree, plant or food patch fed on by the focal individual. When this was not possible,  
220 we selected nearby conspecific plants and collected parts of the same maturation stage as those  
221 consumed. With permission from farmers, we also collected fruits from cultivated fruit trees  
222 and food parts from banana plants grown in coffee plantations. However, we did not collect  
223 field crops, such as pineapple, maize or rice, from cultivated areas. Instead, crops were either  
224 donated to us by our local research assistants or were bought from the Bossou village market.  
225 All sampled crops were grown in Bossou and were known to have been harvested within 1-2  
226 days of us buying and processing them. Oil palm petiole from young leaf fronds and palm heart  
227 were collected opportunistically from trees that were known to have recently fallen (<3 days).

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4 228 For wild foods, we sampled ripe fruits and pith, and used previously reported macronutrient  
5  
6 229 concentrations for leaves (Takemoto, 2003). We sampled all cultivated plant parts that were  
7  
8 230 observed to be eaten (i.e. ripe fruits, pith, nut kernel, petiole, palm heart, and tuber). We did  
9  
10 231 not sample unripe fruits or other plant parts, such as bark, as these constituted a negligible part  
11  
12 232 of the diet during our study period. In total, we gathered nutritional data for foods representing  
13  
14 233 90.5% of overall food intake (measured as g dry matter) (Table 1). We collected 209 food parts  
15  
16 234 (135 wild parts; 74 crop parts) representing 35 species (24 wild species; 11 crop species) (Table  
17  
18 235 1). We combined fruit samples from all *Ficus* species (i.e. 6 species), as we were unable to  
19  
20 236 obtain large enough sample sizes of individual species for nutritional analyses. However,  
21  
22 237 studies have shown that fruits from different *Ficus* species are relatively uniform in  
23  
24 238 macronutrient composition (Wrangham, et al., 1993; Conklin & Wrangham, 1994; McLennan  
25  
26 239 & Ganzhorn, 2017).

31  
32 240 We processed samples in the same way as the chimpanzees by only selecting parts  
33  
34 241 observed to be eaten and swallowed. We therefore removed all plant parts seen to be discarded  
35  
36 242 by the chimpanzees, such as the tough outer skins of some fruits and the outer herbaceous  
37  
38 243 covering of stems, and retained all parts observed to be swallowed, including fruit pulp and the  
39  
40 244 soft inner pith portion of stems. We kept fruit seeds when these were observed to be consumed  
41  
42 245 and regularly swallowed by the chimpanzees (Table 1), as limited time and resources meant  
43  
44 246 that we were unable to collect faecal samples to establish which seeds remained typically  
45  
46 247 undigested. It must therefore be noted that the inclusion of seeds in some of our fruit samples  
47  
48 248 may have elevated fibre, protein, and/or lipid estimates (Conklin & Wrangham, 1994; Milton,  
49  
50 249 2008). Chimpanzees also make wadges from some fruits and pith, whereby they suck out the  
51  
52 250 juices and discard the fibrous portions (Goodall, 1986; Malenky & Wrangham, 1994;  
53  
54 251 Reynolds, et al., 1998). However, Bossou chimpanzees swallowed partially or all sampled and  
55  
56 252 analysed fruits and piths during observed feeding bouts, with wadging occurring occasionally

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4 253 near the end of a feeding bout for some species (for example pith from terrestrial herbaceous  
5  
6 254 vegetation), and as such we did not analyse discarded wadges.  
7  
8

9 255 We weighed all samples as soon as possible after collection (wet weight) and dried in  
10  
11 256 a dehydrator set at 45°C. We reweighted samples after drying and stored them in the dark in  
12  
13 257 sealed and labelled plastic bags with desiccant. Once transported back to the UK, we ground  
14  
15 258 all samples through a 1 mm screen using a Fritsch Pulverisette 19 at Sparsholt College  
16  
17 259 Nutritional Laboratory, Hampshire, England. Particularly oily samples were freeze dried in  
18  
19 260 order to aid in the grinding process. We mixed all samples representing the same plant part and  
20  
21 261 species prior to analyses to account for spatial and temporal variation in chemical composition  
22  
23 262 (Rothman, et al., 2012).  
24  
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26  
27

28 263 We used standard wet chemistry procedures (Association of Official Analytical  
29  
30 264 Chemists, 1990) to estimate macronutrient content. A portion of each sample was dried at  
31  
32 265 105°C in an oven for 24 hours to calculate dry matter before nutritional analyses were  
33  
34 266 performed. We estimated total nitrogen (N) content using Kjeldahl digestion (using a Gerhardt  
35  
36 267 Vapodest 50) and calculated crude protein (CP) by multiplying N by 6.25 (Rothman, et al.,  
37  
38 268 2012). Crude protein values overestimate the amount of available protein within food samples  
39  
40 269 as total nitrogen includes digestible and indigestible fibre-bound protein (Rothman, Chapman,  
41  
42 270 & Pell, 2008). As we did not have the facilities to determine available protein (AP), we used  
43  
44 271 CP measures instead. However, McLennan & Ganzhorn (2017) found that CP and AP were  
45  
46 272 highly correlated in their sample of wild and cultivated chimpanzee foods. Furthermore, CP  
47  
48 273 and AP were correlated in leaves from Uganda (Wallis, et al., 2012). We determined neutral  
49  
50 274 detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) using  
51  
52 275 detergent fibre analysis (Van Soest, Robertson, & Lewis, 1991). We determined ash by burning  
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54 276 a portion of the sample at 500°C. We used ether extract (extracted using a Gerhardt Soxtherm)  
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4 277 to estimate lipid content. As we did not have the facilities to extract soluble carbohydrates, we  
5  
6 278 calculated total non-structural carbohydrates (TNC) using the following formula:

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8  
9 279  $\%TNC = 100 - (\%CP + \%Lipid + \%Ash + \%NDF)$

10  
11 280 This calculation is widely used to give a crude estimate of TNC, but it could contain errors as  
12  
13  
14 281 it does not subtract vitamins and secondary compounds; and errors from other analyses can be  
15  
16 282 compounded (Rothman, et al., 2012).

17  
18  
19 283 We estimated energy gain using the standard physiological metabolisable energy (ME)  
20  
21 284 equation:

22  
23  
24 285  $ME = ((4 \text{ Kcal/g} \times TNC) + (4 \text{ Kcal/g} \times CP) + (9 \text{ Kcal/g} \times Lipid) + (1.6 \text{ Kcal/g} \times NDF))/100$

25  
26  
27 286 where components were multiplied by their physiological fuel values derived from human diets  
28  
29  
30 287 (National Research Council 2003), while NDF was multiplied by the high fermentation  
31  
32 288 physiological fuel value for fibre digestion in chimpanzees (Conklin-Brittain, Knott, &  
33  
34 289 Wrangham, 2006). All macronutrient values are expressed as % dry matter and ME values are  
35  
36 290 expressed as Kcal/100g.

### 37 38 39 40 291 **Nutritional comparisons of Bossou and Bulindi cultivated foods**

41  
42 292 For comparison, we used macronutrient and energy content data from McLennan & Ganzhorn  
43  
44 293 (2017) for cultivated fruits and pith (N = 15) consumed by the Bulindi chimpanzee community.  
45  
46  
47 294 We also used macronutrient and energy data for crops grown at both sites, that the Bossou  
48  
49 295 chimpanzees consumed and that the Bulindi chimpanzees ignored (N = 4 i.e. pineapple,  
50  
51 296 cassava, rice, maize).

### 52 53 54 55 297 **Statistical analysis**

56  
57 298 For analyses, we included oil palm food parts with crops given that a large majority of trees  
58  
59 299 found at Bossou are semi-domesticated and actively maintained and utilised by local people.  
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4 300 We used SPSS version 22.0 to conduct non-parametric Mann-Whitney U tests throughout due  
5  
6 301 to the small sample sizes, and set the significance level at  $p \leq 0.05$ . Specifically, we compared  
7  
8 302 the macronutrient and energy content between cultivated (N = 9) and wild (N = 16) fruits eaten  
9  
10 303 by the Bossou chimpanzees. We also compared the macronutrient and energy content of crop  
11  
12 304 fruits consumed at Bossou with those consumed at Bulindi (N = 11), as well as between crops  
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14 305 grown at both sites that are consumed at Bossou but ignored at Bulindi (N = 4). We were unable  
15  
16 306 to conduct statistical tests to compare the macronutrient content of pith due to the small number  
17  
18 307 of crop pith species consumed by the chimpanzees (Bossou: N = 3; Bulindi: N = 4). We  
19  
20 308 therefore describe and visually display the macronutrient and energy content of crop and wild  
21  
22 309 (N = 8) pith.

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26  
27 310 All research protocols reported in this manuscript were ethically reviewed and approved  
28  
29 311 by the School of Anthropology and Conservation, University of Kent, UK, as well as the  
30  
31 312 Institut de Recherche Environnementale de Bossou and the Direction Nationale de la Recherche  
32  
33 313 Scientifique et Technologique, Guinea, West Africa. This research also adhered to the ASP  
34  
35 314 Principles for Ethical Treatment of Non-Human Primates.

## 36 37 38 39 40 315 **RESULTS**

41  
42 316 The macronutrient (i.e. NDF, ADF, ADL, Lipid, Ash, CP, and TNC) and ME composition of  
43  
44 317 all examined cultivated (N = 12) and wild (N = 24) foods are presented in Table 1.

45  
46  
47 318 < **Insert Table 1 here** >

### 48 49 50 319 **Bossou chimpanzee cultivated and wild fruit foods compared**

51  
52 320 Cultivated fruits were significantly higher in TNC than wild fruits (Mann-Whitney U test, U =  
53  
54 321 27.0, P = 0.010), whereas wild fruits were significantly higher in ADF, ADL, NDF, and CP  
55  
56 322 (ADF: U = 19.0, P = 0.002; ADL: U = 20.0, P = 0.002; NDF: U = 25.0, P = 0.007; CP: U =  
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58 323 21.5, P = 0.003) (Figure 1). We found no significant difference in ME, lipid, or ash composition

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4 324 between cultivated and wild fruits (ME:  $U = 41.5$ ,  $P = 0.084$ ; Lipid:  $U = 43.0$ ,  $P = 0.108$ ; Ash:  
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6 325  $U = 47.0$ ,  $P = 0.169$ ) (Figure 1).

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8  
9 326 <Insert Figure 1 here>

10  
11  
12 327 < Insert Figure 2 here >

### 13 14 15 328 **Bossou chimpanzee cultivated and wild pith foods compared**

16  
17 329 Median NDF, ADF and TNC values for cultivated pith were higher than those for wild pith,  
18  
19 330 while wild pith was higher in CP (Figure 2). Overall, examined cultivated pith fell within the  
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21  
22 331 ranges of wild pith for NDF, ADF, ADL, lipids, TNC, and ME content, while *Musa sinensis*  
23  
24 332 (banana) pith was higher in ash content than all examined wild piths (Table 1).

### 25 26 27 28 333 **Oil palm food parts**

29  
30 334 The macronutrient composition of oil palm nut kernel and fruit from Bossou falls within the  
31  
32 335 range reported by other studies (Appendix 1). Although the exact composition of nut kernel  
33  
34 336 varies, all were high in lipids and moderate to high in CP and TNC (Appendix 1). Oil palm  
35  
36 337 fruit was high in NDF, lipids, and TNC (Appendix 1). Pith was relatively low in lignin (ADL)  
37  
38 338 and high in fermentable fibre fractions (NDF) and TNC (Table 1). Both the petiole and heart  
39  
40 339 were high in ash, CP, and TNC and lower in fibre than other oil palm parts (Table 1). Oil palm  
41  
42 340 nut kernel and fruit were particularly high in ME, while petiole, pith and heart contained similar  
43  
44 341 amounts of ME, which were within the ranges found for other sampled foods (Table 1).

### 45 46 47 48 49 342 **Comparisons of Bossou and Bulindi cultivated foods**

50  
51 343 We did not find any significant differences in the macronutrient fractions or ME content for  
52  
53 344 cultivated fruits (Mann-Whitney U test: CP:  $U = 42$ ,  $P = 0.569$ ; Lipids:  $U = 44$ ,  $P = 0.676$ ;  
54  
55 345 TNC:  $U = 36$ ,  $P = 81$ ; Ash:  $U = 41$ ,  $P = 0.552$ ; NDF =  $38$ ,  $P = 0.412$ ; ADF =  $U = 35$ ,  $P = 0.295$ ;  
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57 346 ME:  $U = 38$ ,  $P = 0.412$ ) consumed by Bulindi and Bossou chimpanzees (Figure 3). Median  
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4 347 values of NDF, ADF, lipids, and ash for cultivated pith consumed at Bossou were higher than  
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6 348 cultivated pith consumed at Bulindi, while the median values of CP, TNC and ME for Bulindi  
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8 349 pith were higher than Bossou pith (Figure 4).  
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10  
11 350 Finally, we did not find any significant differences in macronutrient fractions or ME  
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13 351 content in the crop varieties grown at both sites that Bossou chimpanzees consumed and  
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15 352 Bulindi chimpanzees ignored (Mann-Whitney U test: CP: U = 6, P = 0.564; Lipids: U = 6, P  
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17 353 = 0.564; TNC: U = 6, P = 0.564; Ash: U = 3, P = 0.149; NDF: U = 8, P = 1.000; ADF: U = 7,  
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19 354 P = 0.772; ME: 8, P = 1.000).  
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23 355 < **Insert Figure 3 here** >

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26 356 < **Insert Figure 4 here** >  
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## 30 357 **DISCUSSION**

31 358 Our results add further support to the widespread view that crop-foraging has energetic benefits  
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33 359 by providing primates with access to foods low in insoluble fibre and high in easily digestible  
34  
35 360 carbohydrates (e.g. Lodge, et al., 2013; Naughton-Treves et al., 1998; Hockings et al., 2009).  
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39 361 Although the inclusion of seeds in some of our fruit samples (Table 1) may have  
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41 362 elevated protein, lipid and/or fibre estimates (Conklin & Wrangham, 1994; Milton, 2008), our  
42  
43 363 results for the nutritional composition of wild plant parts consumed by the Bossou chimpanzees  
44  
45 364 were similar to those reported previously for other chimpanzee communities (Conklin, et al.,  
46  
47 365 1998; Matsumoto-Oda & Hayashi, 1999; Hohmann, et al., 2010) and for primates more  
48  
49 366 generally (Lambert & Rothman, 2015). Foods varied in their nutrient content; ripe fruits  
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51 367 provided easily digestible carbohydrates (TNC), pith provided carbohydrate energy mostly  
52  
53 368 from fermentable fibre (i.e. NDF) (Wrangham, et al., 1991), while leaves provided high  
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55 369 amounts of protein (Takemoto, 2003). Fruit contained the highest proportions of lipids of wild  
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4 370 foods, as is consistent with other studies of great ape diets (Conklin, et al., 1998; Reiner,  
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6 371 Petzinger, Power, Hyeroba, & Rothman, 2014; but see McLennan & Ganzhorn, 2017).

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9 372 Primate diets are generally considered to contain limited amounts of lipids (Lambert &  
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11 373 Rothman, 2015). However, the Bossou chimpanzees frequently consume oil palm fruit and nut  
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13 374 kernel (Yamakoshi & Sugiyama, 1995; Humle & Matsuzawa, 2004; Bryson-Morrison, 2017),  
14  
15 375 both of which were extremely high in lipids. Oil palm fruit and nut kernel likely constitute high  
16  
17 376 quality foods for the chimpanzees given that lipids provide twice the energy of carbohydrates  
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19 377 and protein (National Research Council, 2003). Pith from oil palm leaf fronds were similar to  
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21 378 wild pith in providing good sources of energy from fermentable fibre. Bossou chimpanzees  
22  
23 379 also frequently consume the petiole, from young leaf fronds, and the palm heart (up to 9.6% of  
24  
25 380 feeding time, Yamakoshi, 1998). Our results showed that these parts are nutrient dense foods  
26  
27 381 rich in both protein and carbohydrates and relatively low in insoluble fibre. Oil palm trees  
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29 382 clearly provide the chimpanzees with high quality food sources, all of which are available year-  
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31 383 round (Bryson-Morrison, et al., 2016). These findings provide nutritional support for the oil  
32  
33 384 palm serving as a potentially critical resource for chimpanzees residing in human-impacted  
34  
35 385 landscapes across West Africa, particularly as emerging evidence suggests that oil palm trees  
36  
37 386 are utilised extensively for food by such populations (Yamakoshi, 1998; Humle & Matsuzawa,  
38  
39 387 2004; Brncic, Amarasekaran, & McKenna, 2010; Bessa, et al., 2015; Garriga, et al., 2019).  
40  
41 388 Nevertheless, differences have been reported in the extent of oil palm use and the number of  
42  
43 389 parts consumed by chimpanzee populations in varying habitat types across Africa, and these  
44  
45 390 differences are not always readily explained by environmental variables (Humle & Matsuzawa,  
46  
47 391 2004). For example, despite the presence of oil palm in some chimpanzee habitats across East  
48  
49 392 Africa, there is little evidence of its use for food or nesting, except for the chimpanzee  
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51 393 community in Gombe National Park, Tanzania (Humle & Matsuzawa, 2004). As such, the  
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4 394 extent of chimpanzee oil palm use may in part be driven by culturally learned preferences in  
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6 395 food selection and differences in tool use repertoires (Humle & Matsuzawa, 2004).  
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9 396 Similarly to Bulindi, we found that Bossou chimpanzee wild fruit were generally higher  
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11 397 in protein and fibre than cultivated fruit. However, unlike Bulindi, we found that cultivated and  
12  
13 398 wild pith consumed by Bossou chimpanzees were nutritionally similar. Furthermore, we found  
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15 399 that Bossou and Bulindi cultivated pith differed in most macronutrients. Bulindi chimpanzees  
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17 400 consumed pith from sugar cane and yam, crops not grown at Bossou, both of which contained  
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19 401 particularly high levels of sugar akin to cultivated fruits (McLennan & Ganzhorn, 2017).  
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21 402 Bulindi chimpanzees may be selecting cultivated pith for carbohydrate energy (McLennan &  
22  
23 403 Ganzhorn, 2017), while Bossou chimpanzees may be consuming cultivated pith for their  
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25 404 micronutrient rather than macronutrient content. Rice pith, which Bossou chimpanzees  
26  
27 405 consume when seasonally available (Hockings et al., 2009), may serve as an important source  
28  
29 406 of sodium, as has been found for crops consumed by elephants in Kibale National Park, Uganda  
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31 407 (Rode et al., 2006), and for plant food parts that grow in wet areas, such as the pith of  
32  
33 408 herbaceous swamp plants (gorilla: Magliocca & Gautier-Hion, 2002; chimpanzee: Reynolds,  
34  
35 409 Lloyd, Babweteera, & English, 2009, 2012; black and white colobus: Oates, 1978). The  
36  
37 410 sodium content of *Dorylus* ants was also found to be greater than all examined plant foods in  
38  
39 411 the diet of the chimpanzee population in Gombe National Park, Tanzania (O'Malley & Power,  
40  
41 412 2014; Shimwa, Murray, Power & O' Mallet, 2019). However, we did not examine  
42  
43 413 micronutrient content in the present study, and such analyses for rice pith, other foods  
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45 414 consumed from wet areas, such as algae, and *Dorylus* ants are necessary to understand the  
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47 415 drivers of consumption based on micronutrient intake and requirements.  
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55 416 Finally, we found no differences in the nutritional composition of cultivated fruits from  
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57 417 Bossou and Bulindi, unlike previous findings for wild foods between chimpanzee study sites  
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59 418 (Hohmann, et al., 2010). The variety of crops grown at Bossou and Bulindi are similar  
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4 419 (McLennan & Hockings, 2014) and the lack of differences in macronutrient components is  
5  
6 420 likely due to high genetic selectivity (Milton, 1999). The similarity in crop fruit macronutrient  
7  
8 421 and energy content between sites suggest that it is unlikely that differences in chimpanzee crop  
9  
10 422 selection is driven solely by nutritional composition. Similarly, it is unlikely that availability  
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12 423 accounts for crop selection given that all of the crops eaten by the Bossou chimpanzees but  
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14 424 ignored by the Bulindi chimpanzees (i.e. pineapple, cassava, rice, and maize) are highly  
15  
16 425 abundant at both sites (Hockings et al., 2009; McLennan & Hockings, 2014; McLennan &  
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18 426 Ganzhorn, 2017). Therefore, the decision to exploit specific crop varieties is likely driven by  
19  
20 427 multiple behavioural and ecological factors such as the degree to which crops are integral to  
21  
22 428 the diet, the relative abundance and nutritional quality of available wild and cultivated foods,  
23  
24 429 in addition to the perceived risks involved in acquiring specific crops, and the cultural  
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26 430 differences in the dietary repertoire of chimpanzee communities (McLennan & Hockings,  
27  
28 431 2014). Notably, the similarities in crop species availability and nutritional composition  
29  
30 432 between Bossou and Bulindi raise the possibility that human-induced changes drive cultural  
31  
32 433 adaptations in food selection and feeding behaviours in chimpanzee populations residing in  
33  
34 434 anthropogenic environments (Gruber, et al., 2019).

### 41 435 **Conclusions and future directions**

42 436 Our study adds to knowledge on the nutritional composition of foods consumed by  
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44 437 chimpanzees in a range of different habitats. We reported on the nutritional characteristics of  
45  
46 438 both wild and cultivated foods, building on our current understanding of chimpanzee feeding  
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48 439 ecology and diet within forest-agricultural mosaics. Such information is essential to help  
49  
50 440 unravel if crop-foraging decisions are driven by the relative nutritional composition of wild  
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52 441 and crop foods, the availability and accessibility of foods within the environment, and/or  
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54 442 cultural differences in food species selection. Understanding the primary drivers of crop-  
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56 443 foraging at the local level is necessary for the effective management of human-wildlife

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4 444 coexistence and the development of conservation initiatives for chimpanzees, and other primate  
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6 445 populations, residing in anthropogenic landscapes. Furthermore, the nutritional profiles of  
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8 446 foods selected by wild primates are important for informing captive facilities on species-  
9  
10 447 specific dietary needs. Future studies should aim to estimate soluble carbohydrates (simple  
11  
12 448 sugars) in crop and wild foods to provide a more accurate measure of easily digestible  
13  
14 449 carbohydrates, as these may also influence chimpanzee foraging decisions (McLennan &  
15  
16 450 Ganzhorn, 2017). Additionally, examining the nutritional composition of wild and crop foods  
17  
18 451 across temporal and spatial scales could provide key insights into primate feeding behaviours  
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20 452 and crop-foraging choices, such as variations in the timings of crop-foraging bouts.  
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25 453         Nevertheless, knowledge of the nutritional compositions of consumed foods alone do  
26  
27 454 not provide details of how primates balance and prioritise their nutrient intake (Felton, Felton,  
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29 455 Lindenmayer, & Foley, 2009; Garber, Righini, & Kowalewski, 2015; Righini, Garber, &  
30  
31 456 Rothman, 2015; Cancelliere, et al., 2018). Such information is also important if we are to  
32  
33 457 understand fully the strategies primates employ to meet their nutrient and energetic needs from  
34  
35 458 the surrounding environment (Righini, et al., 2015). Thus, our future priorities are to use  
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37 459 nutritional geometry to examine the effects of seasonal fruit availability and crop consumption  
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39 460 on chimpanzee nutrient intake and prioritisation (Simpson & Raubenheimer, 2012;  
40  
41 461 Raubenheimer, Machovsky-Capuska, Chapman, & Rothman, 2015).  
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13  
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15 473

16  
17 474 The data that support the findings of this study are available in Table 1 of the manuscript.

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765 **Table 1** Macronutrient and energy composition of cultivated and wild foods consumed by Bossou chimpanzees, Guinea, West Africa

<b>Cultivated Species</b>	<b>Part</b>	<b>NDF</b>	<b>ADF</b>	<b>ADL</b>	<b>Lipid</b>	<b>Ash</b>	<b>CP</b>	<b>TNC</b>	<b>ME</b>	<b>No. samples</b>
<i>Citrus sinensis</i> (Orange)	Ripe Fruit	8.62	7.87	5.75	2.29	3.75	5.68	79.66	376	4
<i>Zea mays</i> (Maize)	Ripe Fruit	53.81	3.26	2.11	2.54	1.63	10.30	31.72	277	2
† <i>Theobroma cacao</i> (Cacao)	Ripe Fruit	22.70	20.88	5.40	31.45	3.51	10.93	31.42	489	3
<i>Ananas comosus</i> (Pineapple)	Ripe Fruit	9.06	4.28	3.52	0.09	2.83	2.49	85.53	367	2
<i>Musa sinensis</i> (Banana)	Ripe Fruit	4.65	2.62	0.65	0.19	3.89	5.66	85.62	374	3
	Pith	41.28	27.47	3.42	2.80	18.63	20.08	17.21	240	9
<i>Citrus reticula</i> (Mandarin)	Ripe Fruit	12.80	11.03	6.39	6.23	4.80	7.55	68.61	381	2
<i>Mangifera indica</i> (Mango)	Ripe Fruit	7.80	2.88	2.32	0.62	2.14	2.29	87.15	376	10
<i>Carica papaya</i> (Papaya)	Ripe Fruit	12.60	11.70	6.49	0.09	8.26	3.94	75.11	337	3
<i>Oryza</i> sp. (Rice)	Pith	54.93	34.79	3.65	1.18	12.87	3.45	27.56	223	3
<i>Manihot esculenta</i> (Cassava)	Tuber	8.44	2.37	1.89	0.40	1.39	1.34	88.44	376	5
<i>Elaeis guineensis</i> (Oil palm)	Ripe Fruit	50.29	40.97	16.89	30.32	2.00	4.42	12.98	423	4
	Heart	30.94	20.18	2.39	4.03	12.13	18.56	34.35	297	9
	Petiole	30.64	20.66	1.69	3.68	12.65	20.11	32.92	294	9
	Pith	51.28	41.69	7.93	1.15	2.89	1.55	43.13	271	3
	Nut	57.48	/	/	42.82	2.00	11.12	23.20‡	615	3

**Wild Species**

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5	† <i>Parkia bicolor</i>	Ripe Fruit	14.50	5.94	3.53	14.04	3.59	18.83	49.04	421	6
6	† <i>Megaphrynium macrostachyum</i>	Ripe Fruit	68.62	23.38	10.55	1.11	6.46	12.61	11.20	215	4
7	† <i>Ficus</i> sp.	Ripe Fruit	59.41	55.27	22.51	4.33	8.23	10.30	17.74	246	28
8	† <i>Pseudospondias microcarpa</i>	Ripe Fruit	38.81	33.46	15.60	4.64	9.31	9.78	37.46	293	13
9	† <i>Canarium schwenfurthii</i>	Ripe Fruit	60.96	50.09	17.72	12.30	3.05	5.65	18.05	303	2
10	<i>Spondias mombin</i>	Ripe Fruit	51.36	41.75	22.07	4.17	5.02	10.03	29.43	278	5
11	† <i>Myrianthus libericus</i>	Ripe Fruit	44.86	37.25	17.16	11.47	2.88	19.18	27.35	310	2
12	<i>Myrianthus arboreus</i>	Ripe Fruit	41.08	33.65	13.93	22.69	2.30	19.35	14.59	406	2
13	† <i>Macaranga barteri</i>	Ripe Fruit	40.26	32.95	8.52	19.46	4.16	8.98	27.14	384	1
14	† <i>Morus mesozygia</i>	Ripe Fruit	20.29	19.26	7.77	9.58	7.16	13.27	49.70	371	1
15	† <i>Monodora tenuifolia</i>	Ripe Fruit	48.17	32.97	16.35	23.34	1.81	12.17	14.51	394	1
16	† <i>Discoreophyllum cumminsii</i>	Ripe Fruit	35.68	31.72	5.30	18.03	11.23	14.92	20.14	360	2
17	<i>Musanga cecropioides</i>	Ripe Fruit	64.26	60.54	14.97	3.56	3.72	8.67	23.52	258	13
18	† <i>Antiaris africana</i>	Ripe Fruit	32.67	15.80	7.10	2.99	5.15	12.18	47.01	316	5
19	† <i>Aningeria altissima</i>	Ripe Fruit	33.33	19.92	8.39	12.38	3.79	8.72	41.77	367	7
20	<i>Landolphia</i> sp.	Ripe Fruit	32.94	24.33	13.21	1.64	3.04	4.52	57.87	317	2
21	<i>Aframomum latifolium</i>	Pith	61.21	43.57	5.15	0.66	12.84	6.70	18.59	205	11
22	<i>Costus afer</i>	Pith	48.43	32.34	7.67	1.35	8.86	10.15	31.21	244	5
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4	<i>Gongronema latifolium</i>	Pith	34.09	27.61	8.49	3.22	13.38	3.82	45.49	281	2
5	<i>Hypselodelphis</i> sp.	Pith	31.29	25.13	5.95	1.88	9.96	18.25	38.62	294	11
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7	<i>Maranthochloa macrophylla</i>	Pith	37.64	24.71	3.91	2.67	13.93	22.54	23.22	267	2
8											
9	<i>Megaphrynium macrostachyum</i>	Pith	33.57	19.36	2.38	3.50	13.67	26.47	22.80	282	1
10											
11	<i>Pennisetum purpureum</i>	Pith	53.79	33.80	1.72	1.98	15.24	15.29	13.69	220	6
12											
13	<i>Thaumatococcus daniellii</i>	Pith	36.69	22.46	2.02	2.53	13.99	23.82	22.96	269	3
14											
15	Species combined	Leaf <sup>□</sup>	37.00	/	/	2.70	12.00	25.00	23.30	277	/
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17 766 ADF = acid detergent fibre, ADL = acid detergent lignin, NDF = neutral detergent fibre, CP = crude protein, TNC = total non-structural  
 18 767 carbohydrates, ME = metabolisable energy. Macronutrients expressed on a percentage dry matter basis. Energy = Kcal/100g. † = seeds included.  
 19 768 ‡Mean TNC value of oil palm nuts taken from Akpanabiatu et al. (2001). □ Overall mean values for young leaves consumed by the chimpanzee at  
 20 769 Bossou taken from Takemoto (2003)

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4 778 **FIGURE LEGENDS**

5 779 **Figure 1** Macronutrient density and ME (metabolizable energy) of wild (N = 16) and cultivated  
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7 780 (N = 9) fruit consumed by Bossou chimpanzees, Guinea, West Africa. Horizontal lines are  
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10 781 medians; boxes span first to third quartiles; whiskers depict minimum and maximum values;  
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12 782 circles are outliers; \* indicate statistically significant differences. CP = crude protein; TNC =  
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14 783 total non-structural carbohydrates; fibre fractions = NDF (neutral detergent fibre), ADF (acid  
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16 784 detergent fibre), ADL (acid detergent lignin). Macronutrients expressed as % dry matter; ME  
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18 785 expressed as Kcal/100g

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25 787 **Figure 2** Macronutrient density and ME (metabolizable energy) of wild (N = 8) and cultivated  
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27 788 (N = 3) pith consumed by Bossou chimpanzees, Guinea, West Africa. Horizontal lines are  
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29 789 medians; boxes span first to third quartiles; whiskers depict minimum and maximum values;  
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31 790 circles are outliers. CP = crude protein; TNC = total non-structural carbohydrates; fibre  
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33 791 fractions = NDF (neutral detergent fibre), ADF (acid detergent fibre), ADL (acid detergent  
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35 792 lignin). Macronutrients expressed as % dry matter; ME expressed as Kcal/100g

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43 794 **Figure 3** Macronutrient and ME (metabolizable energy) comparison of cultivated fruits eaten  
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45 795 by chimpanzees in Bossou, Guinea (N = 9) this study (2012-2013) and Bulindi, Uganda (N =  
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47 796 11) taken from McLennan and Ganzhorn (2017). Horizontal lines are medians; boxes span first  
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49 797 to third quartiles; whiskers depict minimum and maximum values; circles are outliers. CP =  
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51 798 crude protein; TNC = total non-structural carbohydrates; fibre fractions = NDF (neutral  
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53 799 detergent fibre), ADF (acid detergent fibre), ADL (acid detergent lignin). Macronutrients  
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55 800 expressed as % dry matter; ME expressed as Kcal/100g

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4 802 **Figure 4** Macronutrient and ME ( metabolizable energy) comparison of cultivated pith eaten  
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6 803 by chimpanzees in Bossou, Guinea (N = 3) this study (2012-2013) and Bulindi, Uganda (N =  
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8 804 4) taken from McLennan and Ganzhorn (2017). Horizontal lines are medians; boxes span first  
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10 805 to third quartiles; whiskers depict minimum and maximum values; circles are outliers. CP =  
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12 806 crude protein; TNC = total non-structural carbohydrates; fibre fractions = NDF (neutral  
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14 807 detergent fibre), ADF (acid detergent fibre), ADL (acid detergent lignin). Macronutrients  
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16 808 expressed as % dry matter; ME expressed as Kcal/100g  
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20 809 **Graphical Abstract** Comparison of macronutrient and energy content of cultivated fruits eaten  
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22 810 by chimpanzees in Bossou, Guinea this study and Bulindi, Uganda taken from McLennan &  
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24 811 Ganzhorn (2017)  
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3 **RESEARCH HIGHLIGHTS**  
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- 5
- 6 • Crop fruits have higher carbohydrates and lower fibre content than wild fruits which
- 7 contain comparatively more protein
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- 11 • Oil palm food parts are nutrient dense, highlighting their critical importance as a food
- 12 resource for Western chimpanzees
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For Peer Review

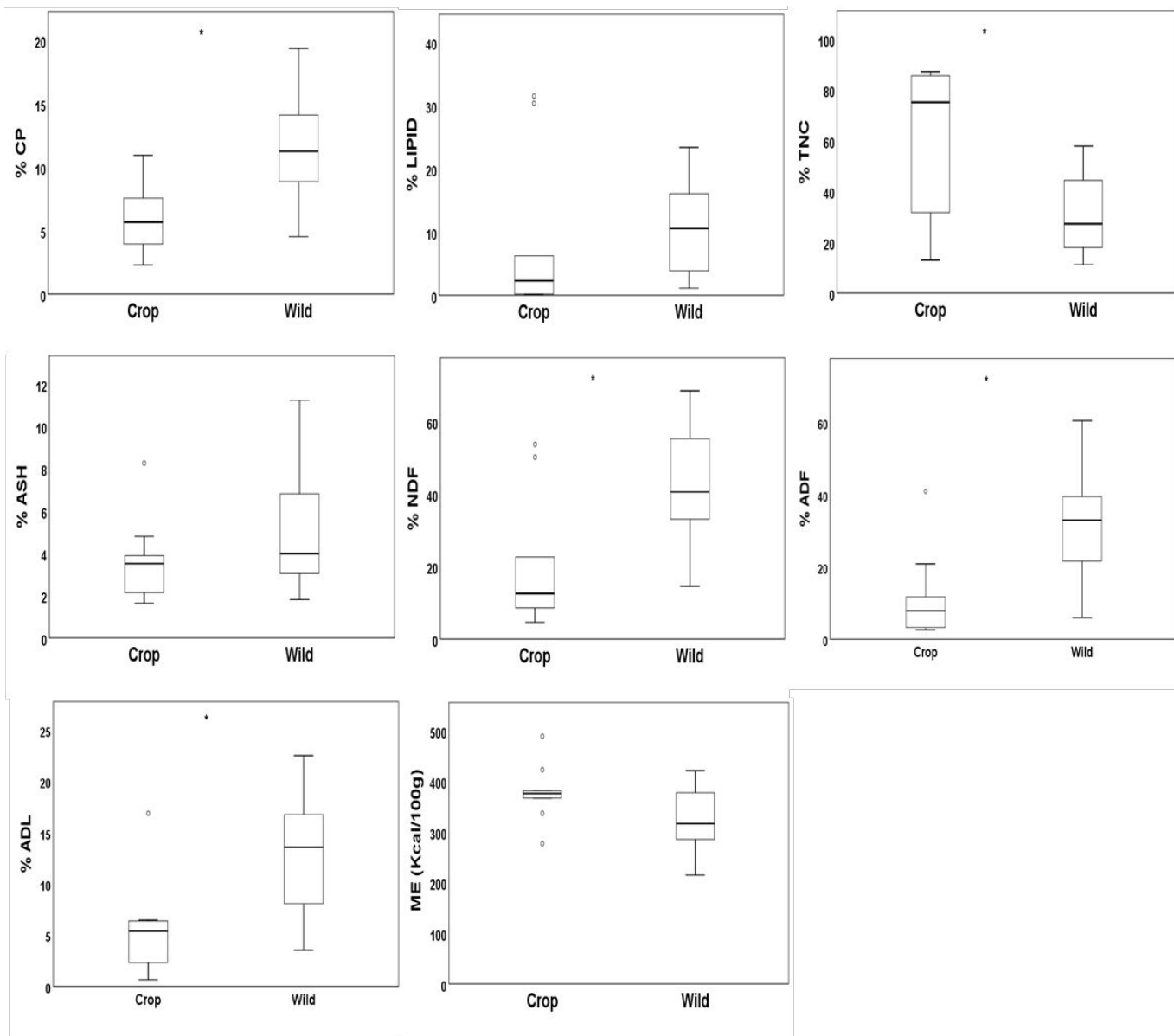


Figure 1

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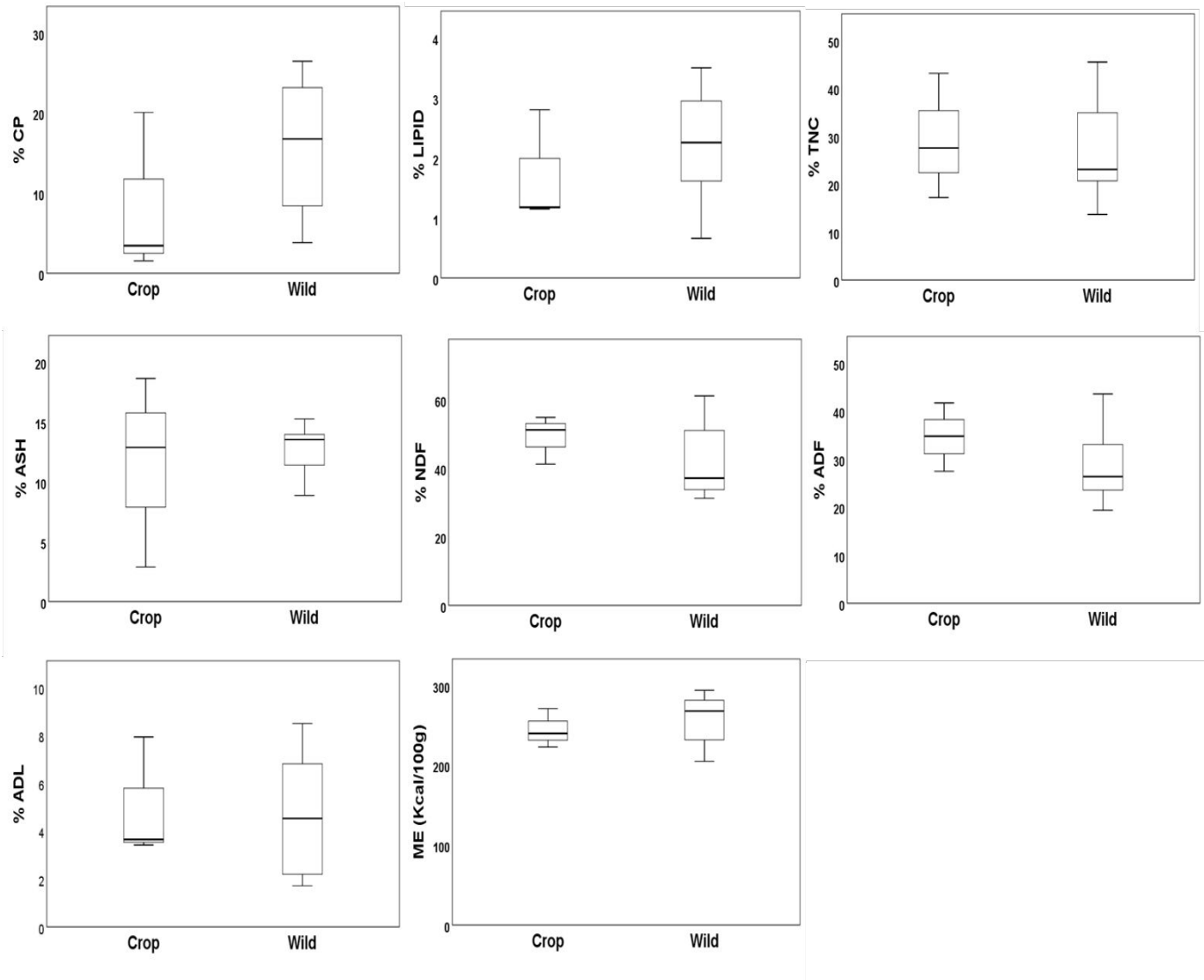


Figure 2

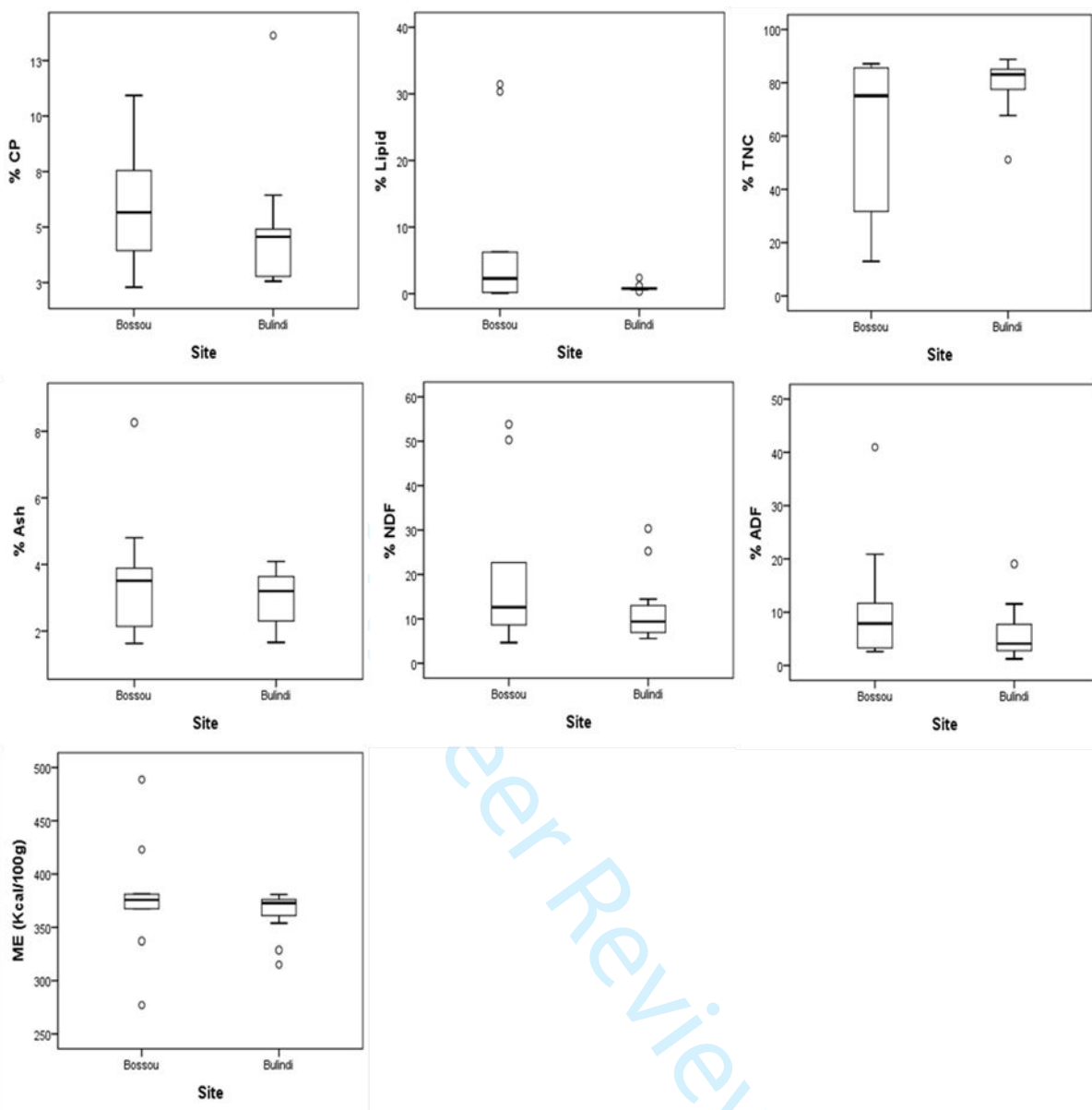


Figure 3

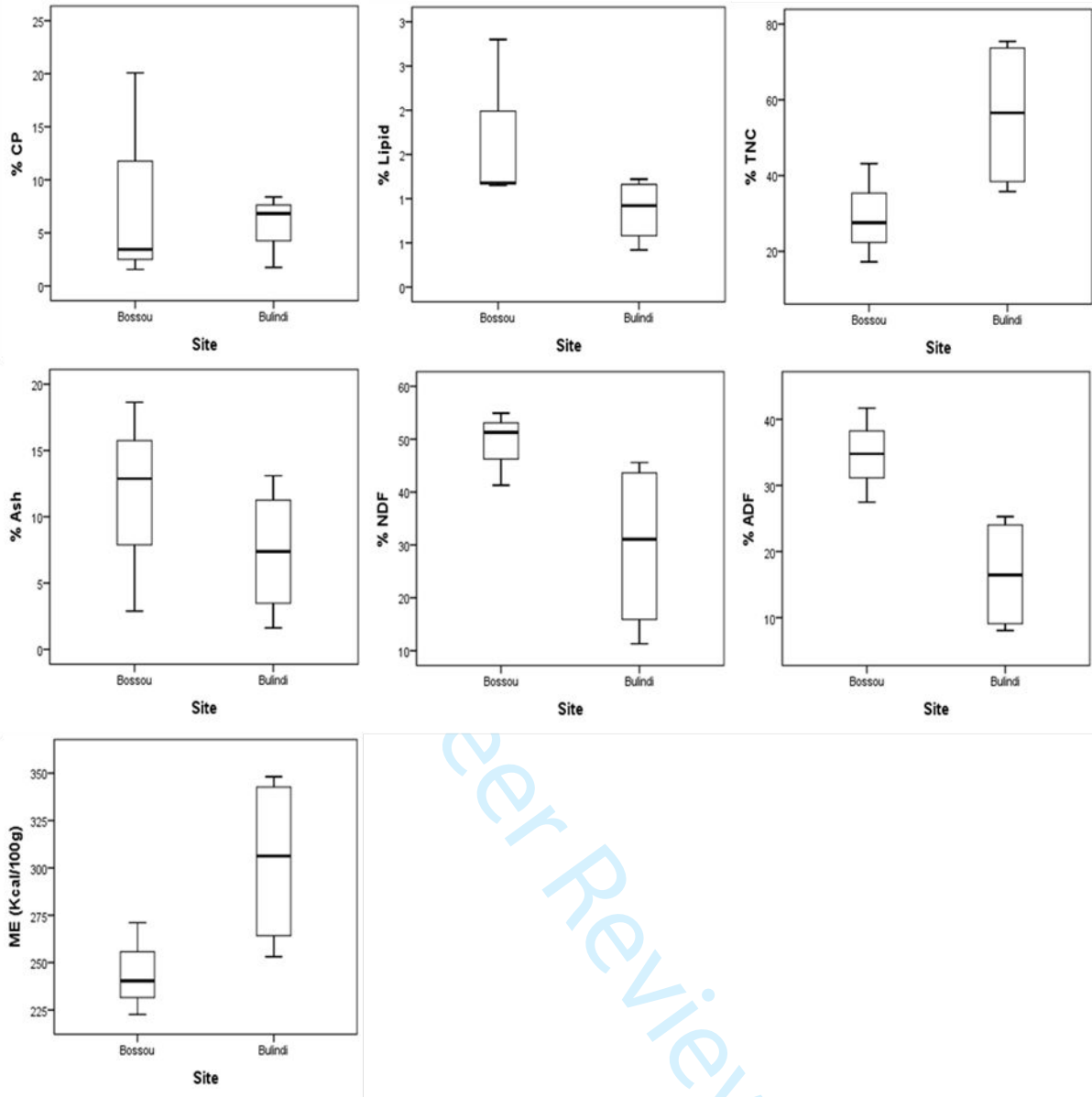


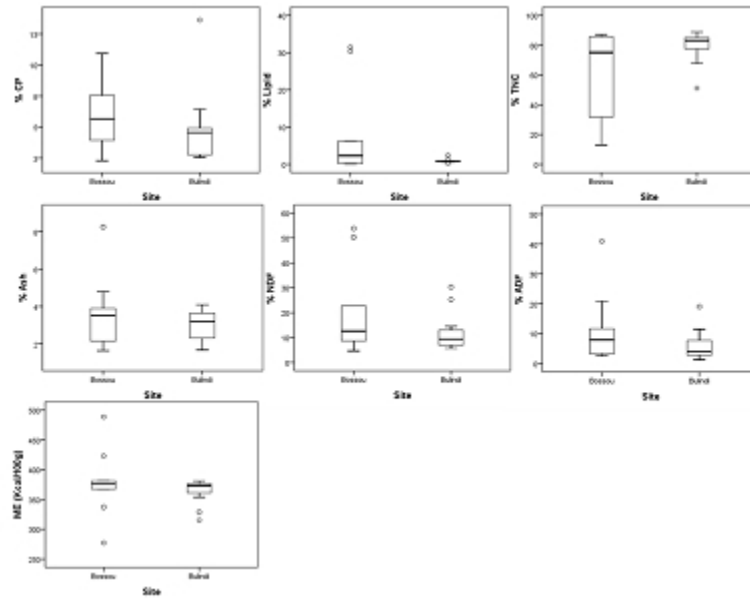
Figure 4

**Appendix 1** Published results of the nutritional composition of oil palm (*Elaeis guineensis*) nut kernel and fruit

	Sample origin	NDF	Lipid	Ash	CP	TNC	
<b>Kernel</b>	Commercial <sup>†</sup>	45.6	47	2.6	13.6	/	Agunbiade et al (1999)
	Nigeria <sup>‡</sup>	/	42	1.8	8.1	25.4	Akpanabiatu et al (2001)
	Nigeria <sup>‡</sup>	/	41	1.5	7.9	21	Akpanabiatu et al (2001)
	Malaysia <sup>□</sup>	/	54.9	1.9	7.8	18.1	Kok et al (2011)
	Brazil	/	32.6	1.7	10.9	35.1	Bora et al (2002)
	Bossou, Guinea	57.5	42.8	2.0	11.1	/	This study
<b>Fruit</b>	Brazil	/	73.2	1.9	3.4	13.3	Bora et al (2002)
	Bossou, Guinea	50.3	30.3	2.0	4.4	13.0	This study

NDF = neutral detergent fibre, CP = crude protein, TNC = total non-structural carbohydrates. Macronutrients expressed on a percentage dry matter basis. <sup>†</sup>Commercial sample of West African origin. <sup>‡</sup>Dura variety. <sup>□</sup>Tenera hybrid.





Graphical Abstract Comparison of macronutrient and energy content of cultivated fruits eaten by chimpanzees in Bossou, Guinea this study and Bulindi, Uganda taken from McLennan & Ganzhorn (2017)

70x53mm (144 x 144 DPI)