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

Journal:	*American Journal of Primatology*
Manuscript ID	AJP-19-0153.R3
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	17-Jan-2020
Complete List of Authors:	Bryson-Morrison, Nicola; University of Kent, Durrell Institute of Conservation and Ecology Beer, Andy; Royal Zoological Society of Scotland Gaspard Soumah, Aly; Institut de Recherche Environmentale de Bossou (IREB) Matsuzawa, Tetsuro; Kyoto University, Primate Research Institute Humle, Tatyana; DICE, School of Anthropology and Conservation
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

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

Short title: Nutrient content of chimpanzee foods

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ABSTRACT

Agricultural expansion encroaches on tropical forests and primates in such landscapes frequently incorporate crops into their diet. Understanding the nutritional drivers behind crop-foraging can help inform conservation efforts to improve human-primate coexistence. This study builds on existing knowledge of primate diets in anthropogenic landscapes by estimating the macronutrient content of 24 wild and 11 cultivated foods (90.5% of food intake) consumed by chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea, West Africa. We also compared the macronutrient composition of Bossou crops to published macronutrient measures of crops from Bulindi, Uganda, East Africa. The composition of wild fruits, leaves and pith were consistent with previous reports for primate diets. Cultivated fruits were higher in carbohydrates and lower in insoluble fibre than wild fruits, while wild fruits were higher in protein. Macronutrient content of cultivated pith fell within the ranges of consumed wild pith. Oil palm food parts were relatively rich in carbohydrates, protein, lipids, and/or fermentable fibre, adding support for the nutritional importance of the oil palm for West African chimpanzees. We found no differences in the composition of cultivated fruits between Bossou and Bulindi, suggesting that macronutrient content alone does not explain differences in crop selection. Our results build on current understanding of chimpanzee feeding ecology within forest-agricultural mosaics and provide additional support for the assumption that crops offer primates energetic benefits over wild foods.

Key words: human-primate coexistence; *Pan troglodytes verus*; anthropogenic landscape; crop-foraging; oil palm; nutritional ecology

INTRODUCTION

The world's most biodiversity rich forests are increasingly being converted to agriculture for subsistence and large-scale industrial farming to meet the demands of an ever-growing human population (Laurance, Sayer, & Cassman, 2014). Such agricultural expansion brings new challenges for wildlife aiming to meet their nutritional and energetic needs from the surrounding environment. Deforestation reduces the distribution and availability of wild food resources while agricultural practises introduce spatially clumped and often predictably available cultivated foods, i.e. crops. Many wildlife species respond to these changes by altering their foraging strategies to incorporate crops into their diets, allowing them to exploit anthropogenic landscapes, (e.g. African elephant (*Loxodonta africana*) Hoare, 2001; baboon

(*Papio* spp.) Hill, 2000; macaque (*Macaca* spp.) Priston & McLennan, 2013; and other non-human primates (hereafter 'primates') Humle & Hill, 2016; wild boar (*Sus scrofa*) Keuling, Stier, & Roth, 2009; and raccoon (*Procyon lotor*), Beasley & Rhodes, 2008). Crop-foraging (also often termed "crop-raiding") affects local livelihoods through crop losses and damages (Hill, 1997; 2005), while species that consume cultivated foods frequently face significant risks from crop protection and foraging deterrent methods and/or hostile behaviours from farmers (Hockings & Humle, 2009). As a result, crop-foraging is one of the principle threats to human-wildlife coexistence within anthropogenic landscapes (e.g. Hoare, 2001; Hockings & Humle, 2009; Mackenzie & Ahabyona, 2012; Redpath, et al., 2013). Understanding the nutritional drivers behind crop consumption by wildlife is therefore essential for effective conservation planning and mitigation strategies (Osborn, 2004; Rode, Chiyo, Chapman, & McDowell, 2006; Dostaler, Ouellet, Therrien, & Cote, 2011).

The behavioural and ecological flexibility and broad dietary repertoire of many primate species means that they readily exploit crops when available (e.g. baboon (*Papio* spp.) Hill, 2000, Strum, 2010; macaque (*Macaca* spp.) Priston & McLennan, 2013; vervet (*Chlorocebus* spp.) Brennan, Else, & Altmann, 1985; capuchin (*Cebus* spp.) McKinney, 2011; orangutan (*Pongo* spp.) Campbell-Smith, Campbell-Smith, Singleton, & Linkie, 2011). Studies examining primate feeding ecology within human-impacted environments have revealed diverse crop-foraging strategies depending on various factors such as availability, proximity and type of cultivated resources, habitat quality and wild food availability, and perceived risks associated with crop-foraging (Naughton-Treves, Treves, Chapman, & Wrangham, 1998; Reynolds, 2005; Hockings, Anderson, & Matsuzawa, 2009; Strum, 2010; McKinney, 2011; McLennan, 2013; Bryson-Morrison, Tzanopoulos, Matsuzawa, & Humle, 2017). Where crops are fully incorporated into the diets, primates often display changes to activity budget and ranging patterns, spending less time foraging and travelling and more time resting (e.g.

Altmann & Muruthi, 1988; Saj, Sicotte, & Paterson, 1999; Strum, 2010; Warren, Higham, MacLarnon, & Ross, 2011; Cancelliere, Chapman, Twinomugisha, & Rothman, 2018). Crop consumption by primates has also been associated with a more effective immune response to parasite infections (e.g. Chapman, Speirs, Gillespie, Holland, & Austad, 2006) and, where crop-foraging by wildlife is tolerated, a reduction in physiological stress (e.g. Lodge, Ross, Ortmann, & MacLarnon, 2013). Finally, some crop-foraging populations also show differences in life history variables, such as shorter inter-birth intervals, younger age at first parturition, reduced infant mortality, increased longevity, and heavier bodyweight in adulthood (e.g. Strum, 2010; Sugiyama & Fujita, 2011; Warren, et al., 2011; Lodge, et al., 2013). These behavioural, ecological and physiological advantages to crop-foraging primates are often attributed to the greater nutritional and energetic value of crop foods compared to wild plant foods (e.g. Altmann & Muruthi 1988; Saj, et al., 1999; Strum, 2010; Warren, et al., 2011; Lodge, et al., 2013).

Humans have selected cultivated foods to be palatable, easily digestible and energy rich with low levels of potentially toxic and/or digestion inhibiting secondary compounds (Milton, 1999). Cultivated potato and maize consumed by baboon (*Papio anubis*) were found to be easier to digest than wild plant foods due to lower levels of insoluble fibre (Forthman-Quick & Demment, 1988). Similarly, cultivated cacao fruit consumed by Tonkean macaques (*Macaca tonkeana*) were lower in insoluble fibre and higher in carbohydrate energy than wild fruit foods (Riley, Tolbert, & Farida, 2013). The first comprehensive study to quantify the macronutrient content of multiple cultivated and wild foods in the diets of wild primates, found that cultivated fruits and pith consumed by chimpanzees (*Pan troglodytes*) in Bulindi, Uganda, East Africa were lower in insoluble fibre and secondary compounds and higher in carbohydrates than wild food equivalents (McLennan & Ganzhorn, 2017). However, crops were found to be low in other macronutrients, particularly protein and lipids, compared to wild foods (McLennan &

Ganzhorn, 2017). Furthermore, wild and cultivated foods consumed by vervet monkeys (*Cercopithecus aethiops*) at Lake Nabugabo, Uganda were found to differ in the relative proportions of macronutrients they contained, with cultivars containing higher proportions of carbohydrates and proteins relative to lipids compared to wild foods (Cancelliere, et al., 2018). These results suggest that crops are indeed high-quality foods in that they provide a rich source of energy from easily digestible carbohydrates.

Chimpanzees are found in anthropogenically disturbed habitats throughout their range in West, Central and East Africa (Humle, Maisels, Oates, Plumptre, & Williamson, 2016) and frequently incorporate crops into their diets (Hockings & Humle, 2009; Hockings & McLennan, 2012). However, crop selection differs between chimpanzee populations, even when similar crop varieties are available (McLennan & Hockings, 2014). Chimpanzees consume a diverse range of plant food types (Nishida & Uehara, 1983; Sugiyama & Koman, 1992; Tutin & Fernandez, 1993; Reynolds, 2005), as well as varying amounts of animal products (ranging between 3 - 13% of the total diet of seven different chimpanzee populations: Pruetz, 2006). Nevertheless, regardless of habitat type, chimpanzees are predominantly frugivorous and maintain a high proportion of fruit in their diets even when fruit availability is low (Ghiglieri, 1984; Wrangham, Conklin-Brittain, & Hunt, 1998; Watts, Potts, Lwanga, & Mitani, 2012). Generally, the macronutrient composition of chimpanzee diets reflects their preference for ripe fruits, with relatively high levels of easily digestible carbohydrates and lower levels of insoluble fibre and secondary compounds, such as condensed tannins and polyphenols (Conklin, Wrangham, & Hunt, 1998; Reynolds, Plumptre, Greenham, & Harborne, 1998; Wrangham, et al., 1998; Matsumoto-Oda & Hayashi, 1999; Hohmann, et al., 2010). Pith, particularly from terrestrial herbaceous vegetation (THV), also provides chimpanzees with moderate to high levels of carbohydrates, as well as energy from digestible fibre fractions (Wrangham, et al., 1991; Wrangham, et al., 1998; Matsumoto-Oda & Hayashi, 1999). Young leaves provide the greatest amounts of protein of plant foods frequently consumed by chimpanzees (Takemoto, 2003; Carlson, Rothman, & Mitani, 2013). Chimpanzee diets are considered high quality (i.e. generally higher in macronutrients and lower in indigestible fibre and secondary compounds) (Conklin, et al., 1998). However, the macronutrient and secondary compound content of wild fruits and leaves varies between chimpanzee study sites (Hohmann, et al., 2010).

In the present study, we aimed to build on existing knowledge of primate diets in anthropogenic landscapes by describing the macronutrient content of wild and cultivated foods consumed by a chimpanzee community inhabiting the forest-agricultural mosaic of Bossou, Guinea, West Africa. Such information is necessary to help increase current understanding of chimpanzee crop-foraging decisions and differences in crop selection both within and between populations. Presently, there is limited information on the nutritional characteristics of foods in the diets of West African chimpanzees inhabiting anthropogenic landscapes (Takemoto, 2003). This chimpanzee community is ideally situated for our study as Bossou has been rated as the long-term study site facing the greatest degree of human-impact, due to the extreme proximity between chimpanzees and people (Wilson, et al., 2014). Furthermore, over 30 years of research has produced a comprehensive list of over 200 plant food species (246 plant parts) known to be consumed by the chimpanzees (Humle, Koops, & Cherif, 2011). They also eat some animal products including insects, larvae, honey, bird eggs, and tree pangolin (*Manis tricuspis*). However, faunivory is relatively rare at Bossou compared to other known chimpanzee sites (Pruetz, 2006). All animal products combined contribute less than 3% to total feeding bouts at Bossou (2.3%: Hockings, unpublished data; 1.9%: Bryson-Morrison, unpublished data), which is likely due to the scarcity of mammalian prey species (Humle, 2011), and the relatively negligible consumption of *Dorylus* ants, (0.8 – 1.2% of total feeding bouts: Yamakoshi, 1998; Hockings, unpublished data; Bryson-Morrison, unpublished data).

The Bossou chimpanzees have foraged on crops for generations and consume 17 different fruit and non-fruit varieties (Hockings, et al., 2009; Hockings, 2011). Crops account for a relatively large proportion of overall feeding time (6.4 - 20% per annum: Takemoto, 2002; Hockings, et al., 2009; Bryson-Morrison, 2017). The chimpanzees also frequently feed from the semi-domesticated or wild oil palm (*Elaeis guineensis*), exploiting more food parts (i.e. fruit, nut kernel, pith, petiole, flower, and heart) than any other known chimpanzee community (Humle & Matsuzawa, 2004). Oil palm is native to West Africa and is found at high densities in human-impacted landscapes where it is maintained and utilised by people predominantly to produce palm oil for domestic and commercial use (Humle & Matsuzawa, 2004). Bossou chimpanzees heavily depend on the oil palm for food (up to 15.9% of annual feeding time: Yamakoshi, 1998) and nesting (Humle & Matsuzawa, 2004). Recent evidence suggests that oil palm trees are also an important food and nesting resource for other chimpanzee communities residing in human-impacted areas across West Africa (Guinea-Bissau: Sousa, Barata, Sousa, Casanova, & Vicente, 2011; Bessa, Sousa, & Hockings, 2015; Côte d'Ivoire: Humle & Matsuzawa, 2004; Sierra Leone: Garriga, et al., 2019; Guinea: Leciak, Hladik, & Hladik, 2005). The macronutrient content of the oil palm fruit and nut kernel, both of which are used in the production of palm oils, has been previously described (Agunbiade, Wiseman, & Cole, 1999; Akpanabiatu, Ekpa, Mauro, & Rizzo, 2001; Bora, Rocha, Narain, Moreira-Monteiro, & Moreira, 2003; Kok, Ong-Abdullah, Ee, & Namasivayam, 2011). However, there are no published data detailing the nutritional composition of other oil palm parts, i.e. petiole, pith, flower, and palm heart (inner core of the trunk), that also serve as potentially important food sources for chimpanzees.

Specifically, in this study, we examined and compared the macronutrient and estimated metabolizable energy content of wild and cultivated foods, including oil palm food parts, which constituted the bulk of the Bossou chimpanzee diet. Following findings from the Bulindi chimpanzee community which also resides in a forest-agricultural mosaic in Uganda, East Africa (McLennan & Ganzhorn, 2017), we predicted that cultivated foods consumed by Bossou chimpanzees would be higher in easily digestible carbohydrates, and lower in insoluble fibre, protein, and lipids, than equivalent wild foods. Bossou chimpanzees are also known to consume more fruit and non-fruit crop species than the Bulindi chimpanzees (e.g. pineapple, maize, cassava, rice), despite similar crops being available at both sites (McLennan & Hockings, 2014). Therefore, to investigate if nutritional differences influence crop selection between chimpanzee sites, we compared the macronutrient and energy content of cultivated foods at Bossou with published results for cultivated foods at Bulindi (McLennan & Ganzhorn, 2017). McLennan & Ganzhorn, (2017) found little nutritional differences between crops consumed and those ignored by the Bulindi chimpanzees. However, plant chemistry is influenced by many environmental factors including temperature variability, light intensity, water availability, salt levels, soil type, seasonality, and plant maturation stage (Sams, 1999; Woolf & Ferguson, 2000; Chapman, Chapman, Rode, Hauck, & McDowell, 2003). Consequently, the nutritional composition of wild plant parts in primate diets varies spatially and temporally both within and between habitats (Ganzhorn, 1995; Chapman, et al., 2003; Worman & Chapman, 2005; Rothman, Chapman, Hansen, Cherney, & Pell, 2009; Houle, Conklin-Brittain, & Wrangham, 2014), including between chimpanzee study sites (Hohmann, et al., 2010). Therefore, we predicted that there would be differences in the macronutrient composition of cultivated foods between Bossou and Bulindi.

METHODS

Study site and population

We present data collected from April 2012 to March 2013 from the habituated chimpanzee (*P. t. verus*) community, which inhabits the anthropogenic landscape surrounding the village of Bossou, Republic of Guinea, West Africa (latitude 7°38′71.7″N and longitude 8°29′38.9″W)

(Matsuzawa, Humle, & Sugiyama, 2011). During our study, the community size ranged between 12-13 individuals with six adult females and four adult males. The chimpanzee community's home range is approximately 15 km^2, although they spend the majority of their time in the four small hills (70-150 m high) that surround Bossou village and constitute their 6 km^2 core area (Humle, 2011). Local people practise slash and burn agriculture within and at the edges of these small hills, resulting in a highly heterogeneous forest-agricultural mosaic composed of regenerating, riverine, and mature forest as well as fallow land, coffee plantations and cultivated fields (Humle, 2011; Bryson-Morrison, Matsuzawa, & Humle, 2016). The climate in this region is classified as tropical wet seasonal with a long rainy season from March to October, when wild fruit availability is low, and a short dry season from November to February, when wild fruit availability is high (Yamakoshi, 1998; Takemoto, 2002; Hockings, 2007; Humle, 2011; Bryson-Morrison, et al., 2016).

Sample collection and nutritional analyses

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

For wild foods, we sampled ripe fruits and pith, and used previously reported macronutrient concentrations for leaves (Takemoto, 2003). We sampled all cultivated plant parts that were observed to be eaten (i.e. ripe fruits, pith, nut kernel, petiole, palm heart, and tuber). We did not sample unripe fruits or other plant parts, such as bark, as these constituted a negligible part of the diet during our study period. In total, we gathered nutritional data for foods representing 90.5% of overall food intake (measured as g dry matter) (Table 1). We collected 209 food parts (135 wild parts; 74 crop parts) representing 35 species (24 wild species; 11 crop species) (Table 1). We combined fruit samples from all *Ficus* species (i.e. 6 species), as we were unable to obtain large enough sample sizes of individual species for nutritional analyses. However, studies have shown that fruits from different *Ficus* species are relatively uniform in macronutrient composition (Wrangham, et al., 1993; Conklin & Wrangham, 1994; McLennan & Ganzhorn, 2017).

We processed samples in the same way as the chimpanzees by only selecting parts observed to be eaten and swallowed. We therefore removed all plant parts seen to be discarded by the chimpanzees, such as the tough outer skins of some fruits and the outer herbaceous covering of stems, and retained all parts observed to be swallowed, including fruit pulp and the soft inner pith portion of stems. We kept fruit seeds when these were observed to be consumed and regularly swallowed by the chimpanzees (Table 1), as limited time and resources meant that we were unable to collect faecal samples to establish which seeds remained typically undigested. It must therefore be noted that the inclusion of seeds in some of our fruit samples may have elevated fibre, protein, and/or lipid estimates (Conklin & Wrangham, 1994; Milton, 2008). Chimpanzees also make wadges from some fruits and pith, whereby they suck out the juices and discard the fibrous portions (Goodall, 1986; Malenky & Wrangham, 1994; Reynolds, et al., 1998). However, Bossou chimpanzees swallowed partially or all sampled and analysed fruits and piths during observed feeding bouts, with wadging occurring occasionally near the end of a feeding bout for some species (for example pith from terrestrial herbaceous vegetation), and as such we did not analyse discarded wadges.

We weighed all samples as soon as possible after collection (wet weight) and dried in a dehydrator set at 45°C. We reweighted samples after drying and stored them in the dark in sealed and labelled plastic bags with desiccant. Once transported back to the UK, we ground all samples through a 1 mm screen using a Fritsch Pulverisette 19 at Sparsholt College Nutritional Laboratory, Hampshire, England. Particularly oily samples were freeze dried in order to aid in the grinding process. We mixed all samples representing the same plant part and species prior to analyses to account for spatial and temporal variation in chemical composition (Rothman, et al., 2012).

We used standard wet chemistry procedures (Association of Official Analytical Chemists, 1990) to estimate macronutrient content. A portion of each sample was dried at 105°C in an oven for 24 hours to calculate dry matter before nutritional analyses were performed. We estimated total nitrogen (N) content using Kjeldahl digestion (using a Gerhardt Vapodest 50) and calculated crude protein (CP) by multiplying N by 6.25 (Rothman, et al., 2012). Crude protein values overestimate the amount of available protein within food samples as total nitrogen includes digestible and indigestible fibre-bound protein (Rothman, Chapman, & Pell, 2008). As we did not have the facilities to determine available protein (AP), we used CP measures instead. However, McLennan & Ganzhorn (2017) found that CP and AP were highly correlated in their sample of wild and cultivated chimpanzee foods. Furthermore, CP and AP were correlated in leaves from Uganda (Wallis, et al., 2012). We determined neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) using detergent fibre analysis (Van Soest, Robertson, & Lewis, 1991). We determined ash by burning a portion of the sample at 500°C. We used ether extract (extracted using a Gerhardt Soxtherm) to estimate lipid content. As we did not have the facilities to extract soluble carbohydrates, we calculated total non-structural carbohydrates (TNC) using the following formula:

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

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

We estimated energy gain using the standard physiological metabolisable energy (ME) equation:

$$ME = ((4\ Kcal/g \times TNC) + (4\ Kcal/g \times CP) + (9\ Kcal/g \times Lipid) + (1.6\ Kcal/g \times NDF))/100$$

where components were multiplied by their physiological fuel values derived from human diets (National Research Council 2003), while NDF was multiplied by the high fermentation physiological fuel value for fibre digestion in chimpanzees (Conklin-Brittain, Knott, & Wrangham, 2006). All macronutrient values are expressed as % dry matter and ME values are expressed as Kcal/100g.

Nutritional comparisons of Bossou and Bulindi cultivated foods

For comparison, we used macronutrient and energy content data from McLennan & Ganzhorn (2017) for cultivated fruits and pith (N = 15) consumed by the Bulindi chimpanzee community. We also used macronutrient and energy data for crops grown at both sites, that the Bossou chimpanzees consumed and that the Bulindi chimpanzees ignored (N = 4 i.e. pineapple, cassava, rice, maize).

Statistical analysis

For analyses, we included oil palm food parts with crops given that a large majority of trees found at Bossou are semi-domesticated and actively maintained and utilised by local people.

We used SPSS version 22.0 to conduct non-parametric Mann-Whitney U tests throughout due to the small sample sizes, and set the significance level at $p \leq 0.05$. Specifically, we compared the macronutrient and energy content between cultivated (N = 9) and wild (N = 16) fruits eaten by the Bossou chimpanzees. We also compared the macronutrient and energy content of crop fruits consumed at Bossou with those consumed at Bulindi (N = 11), as well as between crops grown at both sites that are consumed at Bossou but ignored at Bulindi (N = 4). We were unable to conduct statistical tests to compare the macronutrient content of pith due to the small number of crop pith species consumed by the chimpanzees (Bossou: N = 3; Bulindi: N = 4). We therefore describe and visually display the macronutrient and energy content of crop and wild (N = 8) pith.

All research protocols reported in this manuscript were ethically reviewed and approved by the School of Anthropology and Conservation, University of Kent, UK, as well as the Institut de Recherche Environmentale de Bossou and the Direction Nationale de la Recherche Scientifique et Technologique, Guinea, West Africa. This research also adhered to the ASP Principles for Ethical Treatment of Non-Human Primates.

RESULTS

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

< **Insert Table 1 here** >

Bossou chimpanzee cultivated and wild fruit foods compared

Cultivated fruits were significantly higher in TNC than wild fruits (Mann-Whitney U test, U = 27.0, P = 0.010), whereas wild fruits were significantly higher in ADF, ADL, NDF, and CP (ADF: U = 19.0, P = 0.002; ADL: U = 20.0, P = 0.002; NDF: U = 25.0, P = 0.007; CP: U = 21.5, P = 0.003) (Figure 1). We found no significant difference in ME, lipid, or ash composition between cultivated and wild fruits (ME: U = 41.5, P = 0.084; Lipid: U = 43.0, P = 0.108; Ash: U = 47.0, P = 0.169) (Figure 1).

<Insert Figure 1 here>

< Insert Figure 2 here >

Bossou chimpanzee cultivated and wild pith foods compared

Median NDF, ADF and TNC values for cultivated pith were higher than those for wild pith, while wild pith was higher in CP (Figure 2). Overall, examined cultivated pith fell within the ranges of wild pith for NDF, ADF, ADL, lipids, TNC, and ME content, while *Musa sinensis* (banana) pith was higher in ash content than all examined wild piths (Table 1).

Oil palm food parts

The macronutrient composition of oil palm nut kernel and fruit from Bossou falls within the range reported by other studies (Appendix 1). Although the exact composition of nut kernel varies, all were high in lipids and moderate to high in CP and TNC (Appendix 1). Oil palm fruit was high in NDF, lipids, and TNC (Appendix 1). Pith was relatively low in lignin (ADL) and high in fermentable fibre fractions (NDF) and TNC (Table 1). Both the petiole and heart were high in ash, CP, and TNC and lower in fibre than other oil palm parts (Table 1). Oil palm nut kernel and fruit were particularly high in ME, while petiole, pith and heart contained similar amounts of ME, which were within the ranges found for other sampled foods (Table 1).

Comparisons of Bossou and Bulindi cultivated foods

We did not find any significant differences in the macronutrient fractions or ME content for cultivated fruits (Mann-Whitney U test: CP: U = 42, P = 0.569; Lipids: U = 44, P = 0.676; TNC: U = 36, P = 81; Ash: U = 41, P = 0.552; NDF = 38, P = 0.412; ADF = U = 35, P = 0.295; ME: U = 38, P = 0.412) consumed by Bulindi and Bossou chimpanzees (Figure 3). Median values of NDF, ADF, lipids, and ash for cultivated pith consumed at Bossou were higher than cultivated pith consumed at Bulindi, while the median values of CP, TNC and ME for Bulindi pith were higher than Bossou pith (Figure 4).

Finally, we did not find any significant differences in macronutrient fractions or ME content in the crop varieties grown at both sites that Bossou chimpanzees consumed and Bulindi chimpanzees ignored (Mann-Whitney U test: CP: $U = 6$, $P = 0.564$; Lipids: $U = 6$, $P = 0.564$; TNC: $U = 6$, $P = 0.564$; Ash: $U = 3$, $P = 0.149$; NDF: $U = 8$, $P = 1.000$; ADF: $U = 7$, $P = 0.772$; ME: 8, $P = 1.000$).

< Insert Figure 3 here >

< Insert Figure 4 here >

DISCUSSION

Our results add further support to the widespread view that crop-foraging has energetic benefits by providing primates with access to foods low in insoluble fibre and high in easily digestible carbohydrates (e.g. Lodge, et al., 2013; Naughton-Treves et al., 1998; Hockings et al., 2009).

Although the inclusion of seeds in some of our fruit samples (Table 1) may have elevated protein, lipid and/or fibre estimates (Conklin & Wrangham, 1994; Milton, 2008), our results for the nutritional composition of wild plant parts consumed by the Bossou chimpanzees were similar to those reported previously for other chimpanzee communities (Conklin, et al., 1998; Matsumoto-Oda & Hayashi, 1999; Hohmann, et al., 2010) and for primates more generally (Lambert & Rothman, 2015). Foods varied in their nutrient content; ripe fruits provided easily digestible carbohydrates (TNC), pith provided carbohydrate energy mostly from fermentable fibre (i.e. NDF) (Wrangham, et al., 1991), while leaves provided high amounts of protein (Takemoto, 2003). Fruit contained the highest proportions of lipids of wild foods, as is consistent with other studies of great ape diets (Conklin, et al., 1998; Reiner, Petzinger, Power, Hyeroba, & Rothman, 2014; but see McLennan & Ganzhorn, 2017).

Primate diets are generally considered to contain limited amounts of lipids (Lambert & Rothman, 2015). However, the Bossou chimpanzees frequently consume oil palm fruit and nut kernel (Yamakoshi & Sugiyama, 1995; Humle & Matsuzawa, 2004; Bryson-Morrison, 2017), both of which were extremely high in lipids. Oil palm fruit and nut kernel likely constitute high quality foods for the chimpanzees given that lipids provide twice the energy of carbohydrates and protein (National Research Council, 2003). Pith from oil palm leaf fronds were similar to wild pith in providing good sources of energy from fermentable fibre. Bossou chimpanzees also frequently consume the petiole, from young leaf fronds, and the palm heart (up to 9.6% of feeding time, Yamakoshi, 1998). Our results showed that these parts are nutrient dense foods rich in both protein and carbohydrates and relatively low in insoluble fibre. Oil palm trees clearly provide the chimpanzees with high quality food sources, all of which are available year-round (Bryson-Morrison, et al., 2016). These findings provide nutritional support for the oil palm serving as a potentially critical resource for chimpanzees residing in human-impacted landscapes across West Africa, particularly as emerging evidence suggests that oil palm trees are utilised extensively for food by such populations (Yamakoshi, 1998; Humle & Matsuzawa, 2004; Brncic, Amarasekaran, & McKenna, 2010; Bessa, et al., 2015; Garriga, et al., 2019). Nevertheless, differences have been reported in the extent of oil palm use and the number of parts consumed by chimpanzee populations in varying habitat types across Africa, and these differences are not always readily explained by environmental variables (Humle & Matsuzawa, 2004). For example, despite the presence of oil palm in some chimpanzee habitats across East Africa, there is little evidence of its use for food or nesting, except for the chimpanzee community in Gombe National Park, Tanzania (Humle & Matsuzawa, 2004). As such, the extent of chimpanzee oil palm use may in part be driven by culturally learned preferences in food selection and differences in tool use repertoires (Humle & Matsuzawa, 2004).

Similarly to Bulindi, we found that Bossou chimpanzee wild fruit were generally higher in protein and fibre than cultivated fruit. However, unlike Bulindi, we found that cultivated and wild pith consumed by Bossou chimpanzees were nutritionally similar. Furthermore, we found that Bossou and Bulindi cultivated pith differed in most macronutrients. Bulindi chimpanzees consumed pith from sugar cane and yam, crops not grown at Bossou, both of which contained particularly high levels of sugar akin to cultivated fruits (McLennan & Ganzhorn, 2017). Bulindi chimpanzees may be selecting cultivated pith for carbohydrate energy (McLennan & Ganzhorn, 2017), while Bossou chimpanzees may be consuming cultivated pith for their micronutrient rather than macronutrient content. Rice pith, which Bossou chimpanzees consume when seasonally available (Hockings et al., 2009), may serve as an important source of sodium, as has been found for crops consumed by elephants in Kibale National Park, Uganda (Rode et al., 2006), and for plant food parts that grow in wet areas, such as the pith of herbaceous swamp plants (gorilla: Magliocca & Gautier-Hion, 2002; chimpanzee: Reynolds, Lloyd, Babweteera, & English, 2009, 2012; black and white colobus: Oates, 1978). The sodium content of *Dorylus* ants was also found to be greater than all examined plant foods in the diet of the chimpanzee population in Gombe National Park, Tanzania (O'Malley & Power, 2014; Shimwa, Murray, Power & O' Mallet, 2019). However, we did not examine micronutrient content in the present study, and such analyses for rice pith, other foods consumed from wet areas, such as algae, and *Dorylus* ants are necessary to understand the drivers of consumption based on micronutrient intake and requirements.

Finally, we found no differences in the nutritional composition of cultivated fruits from Bossou and Bulindi, unlike previous findings for wild foods between chimpanzee study sites (Hohmann, et al., 2010). The variety of crops grown at Bossou and Bulindi are similar

(McLennan & Hockings, 2014) and the lack of differences in macronutrient components is likely due to high genetic selectivity (Milton, 1999). The similarity in crop fruit macronutrient and energy content between sites suggest that it is unlikely that differences in chimpanzee crop selection is driven solely by nutritional composition. Similarly, it is unlikely that availability accounts for crop selection given that all of the crops eaten by the Bossou chimpanzees but ignored by the Bulindi chimpanzees (i.e. pineapple, cassava, rice, and maize) are highly abundant at both sites (Hockings et al., 2009; McLennan & Hockings, 2014; McLennan & Ganzhorn, 2017). Therefore, the decision to exploit specific crop varieties is likely driven by multiple behavioural and ecological factors such as the degree to which crops are integral to the diet, the relative abundance and nutritional quality of available wild and cultivated foods, in addition to the perceived risks involved in acquiring specific crops, and the cultural differences in the dietary repertoire of chimpanzee communities (McLennan & Hockings, 2014). Notably, the similarities in crop species availability and nutritional composition between Bossou and Bulindi raise the possibility that human-induced changes drive cultural adaptations in food selection and feeding behaviours in chimpanzee populations residing in anthropogenic environments (Gruber, et al., 2019).

Conclusions and future directions

Our study adds to knowledge on the nutritional composition of foods consumed by chimpanzees in a range of different habitats. We reported on the nutritional characteristics of both wild and cultivated foods, building on our current understanding of chimpanzee feeding ecology and diet within forest-agricultural mosaics. Such information is essential to help unravel if crop-foraging decisions are driven by the relative nutritional composition of wild and crop foods, the availability and accessibility of foods within the environment, and/or cultural differences in food species selection. Understanding the primary drivers of crop-foraging at the local level is necessary for the effective management of human-wildlife coexistence and the development of conservation initiatives for chimpanzees, and other primate populations, residing in anthropogenic landscapes. Furthermore, the nutritional profiles of foods selected by wild primates are important for informing captive facilities on species-specific dietary needs. Future studies should aim to estimate soluble carbohydrates (simple sugars) in crop and wild foods to provide a more accurate measure of easily digestible carbohydrates, as these may also influence chimpanzee foraging decisions (McLennan & Ganzhorn, 2017). Additionally, examining the nutritional composition of wild and crop foods across temporal and spatial scales could provide key insights into primate feeding behaviours and crop-foraging choices, such as variations in the timings of crop-foraging bouts.

Nevertheless, knowledge of the nutritional compositions of consumed foods alone do not provide details of how primates balance and prioritise their nutrient intake (Felton, Felton, Lindenmayer, & Foley, 2009; Garber, Righini, & Kowalewski, 2015; Righini, Garber, & Rothman, 2015; Cancelliere, et al., 2018). Such information is also important if we are to understand fully the strategies primates employ to meet their nutrient and energetic needs from the surrounding environment (Righini, et al., 2015). Thus, our future priorities are to use nutritional geometry to examine the effects of seasonal fruit availability and crop consumption on chimpanzee nutrient intake and prioritisation (Simpson & Raubenheimer, 2012; Raubenheimer, Machovsky-Capuska, Chapman, & Rothman, 2015).

ACKNOWLEDGMENTS

We are grateful to the Institut de Recherche Environnementale de Bossou and the Direction Nationale de la Recherche Scientifique et Technologique for permission to conduct research in Bossou, Guinea. We thank all field guides at Bossou who assisted with data collection. We are grateful to Roy Niblett for his help with chemical analyses. We also thank Jessica Rothman and two anonymous reviewers for their helpful comments on an earlier version of this manuscript. This study was funded by a MEXT-JSPS grants #24000001, #16H06283; core-to-core CCSN; the leading graduate program U04 to T. Matsuzawa, and a Copenhagen Zoo conservation research grant and a grant in aid of research from Sigma-Xi the Scientific Research Society to N. Bryson-Morrison.

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

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

Cultivated Species	**Part**	**NDF**	**ADF**	**ADL**	**Lipid**	**Ash**	**CP**	**TNC**	**ME**	**No. samples**
Citrus sinensis (Orange)	Ripe Fruit	8.62	7.87	5.75	2.29	3.75	5.68	79.66	376	4
Zea mays (Maize)	Ripe Fruit	53.81	3.26	2.11	2.54	1.63	10.30	31.72	277	2
†*Theobroma cacao* (Cacao)	Ripe Fruit	22.70	20.88	5.40	31.45	3.51	10.93	31.42	489	3
Ananas comosus (Pineapple)	Ripe Fruit	9.06	4.28	3.52	0.09	2.83	2.49	85.53	367	2
Musa sinensis (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
Citrus reticula (Mandarin)	Ripe Fruit	12.80	11.03	6.39	6.23	4.80	7.55	68.61	381	2
Mangifera indica (Mango)	Ripe Fruit	7.80	2.88	2.32	0.62	2.14	2.29	87.15	376	10
Carica papaya (Papaya)	Ripe Fruit	12.60	11.70	6.49	0.09	8.26	3.94	75.11	337	3
Oryza sp. (Rice)	Pith	54.93	34.79	3.65	1.18	12.87	3.45	27.56	223	3
Manihot esculenta (Cassava)	Tuber	8.44	2.37	1.89	0.40	1.39	1.34	88.44	376	5
Elaeis guineensis (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										
†*Parkia bicolor*	Ripe Fruit	14.50	5.94	3.53	14.04	3.59	18.83	49.04	421	6
†*Megaphrynium macrostachyum*	Ripe Fruit	68.62	23.38	10.55	1.11	6.46	12.61	11.20	215	4
†*Ficus* sp.	Ripe Fruit	59.41	55.27	22.51	4.33	8.23	10.30	17.74	246	28
†*Pseudospondias microcarpa*	Ripe Fruit	38.81	33.46	15.60	4.64	9.31	9.78	37.46	293	13
†*Canarium schwenfurthii*	Ripe Fruit	60.96	50.09	17.72	12.30	3.05	5.65	18.05	303	2
Spondias mombin	Ripe Fruit	51.36	41.75	22.07	4.17	5.02	10.03	29.43	278	5
†*Myrianthus libericus*	Ripe Fruit	44.86	37.25	17.16	11.47	2.88	19.18	27.35	310	2
Myrianthus arboreus	Ripe Fruit	41.08	33.65	13.93	22.69	2.30	19.35	14.59	406	2
†*Macaranga barteri*	Ripe Fruit	40.26	32.95	8.52	19.46	4.16	8.98	27.14	384	1
†*Morus mesozygia*	Ripe Fruit	20.29	19.26	7.77	9.58	7.16	13.27	49.70	371	1
†*Monodora tenuifolia*	Ripe Fruit	48.17	32.97	16.35	23.34	1.81	12.17	14.51	394	1
†*Discoreophyllum cumminsii*	Ripe Fruit	35.68	31.72	5.30	18.03	11.23	14.92	20.14	360	2
Musanga cecropioides	Ripe Fruit	64.26	60.54	14.97	3.56	3.72	8.67	23.52	258	13
†*Antiaris africana*	Ripe Fruit	32.67	15.80	7.10	2.99	5.15	12.18	47.01	316	5
†*Aningeria altissima*	Ripe Fruit	33.33	19.92	8.39	12.38	3.79	8.72	41.77	367	7
Landolphia sp.	Ripe Fruit	32.94	24.33	13.21	1.64	3.04	4.52	57.87	317	2
Aframomum latifolium	Pith	61.21	43.57	5.15	0.66	12.84	6.70	18.59	205	11
Costus afer	Pith	48.43	32.34	7.67	1.35	8.86	10.15	31.21	244	5

Gongronema latifolium	Pith	34.09	27.61	8.49	3.22	13.38	3.82	45.49	281	2
Hypselodelphis sp.	Pith	31.29	25.13	5.95	1.88	9.96	18.25	38.62	294	11
Maranthochloa macrophylla	Pith	37.64	24.71	3.91	2.67	13.93	22.54	23.22	267	2
Megaphrynium macrostachyum	Pith	33.57	19.36	2.38	3.50	13.67	26.47	22.80	282	1
Pennisetum purpureum	Pith	53.79	33.80	1.72	1.98	15.24	15.29	13.69	220	6
Thaumatococus daniellii	Pith	36.69	22.46	2.02	2.53	13.99	23.82	22.96	269	3
Species combined	Leaf□	37.00	/	/	2.70	12.00	25.00	23.30	277	/

ADF = acid detergent fibre, ADL = acid detergent lignin, NDF = neutral detergent fibre, CP = crude protein, TNC = total non-structural carbohydrates, ME = metabolisable energy. Macronutrients expressed on a percentage dry matter basis. Energy = Kcal/100g.† = seeds included. ‡Mean TNC value of oil palm nuts taken from Akpanabiatu et al. (2001). □Overall mean values for young leaves consumed by the chimpanzee at Bossou taken from Takemoto (2003)

FIGURE LEGENDS

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

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

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

Figure 4 Macronutrient and ME (metabolizable energy) comparison of cultivated pith eaten by chimpanzees in Bossou, Guinea (N = 3) this study (2012-2013) and Bulindi, Uganda (N = 4) taken from McLennan and Ganzhorn (2017). Horizontal lines are medians; boxes span first to third quartiles; whiskers depict minimum and maximum values; circles are outliers. CP = crude protein; TNC = total non-structural carbohydrates; fibre fractions = NDF (neutral detergent fibre), ADF (acid detergent fibre), ADL (acid detergent lignin). Macronutrients expressed as % dry matter; ME expressed as Kcal/100g

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)

RESEARCH HIGHLIGHTS

- Crop fruits have higher carbohydrates and lower fibre content than wild fruits which contain comparatively more protein
- Oil palm food parts are nutrient dense, highlighting their critical importance as a food resource for Western chimpanzees

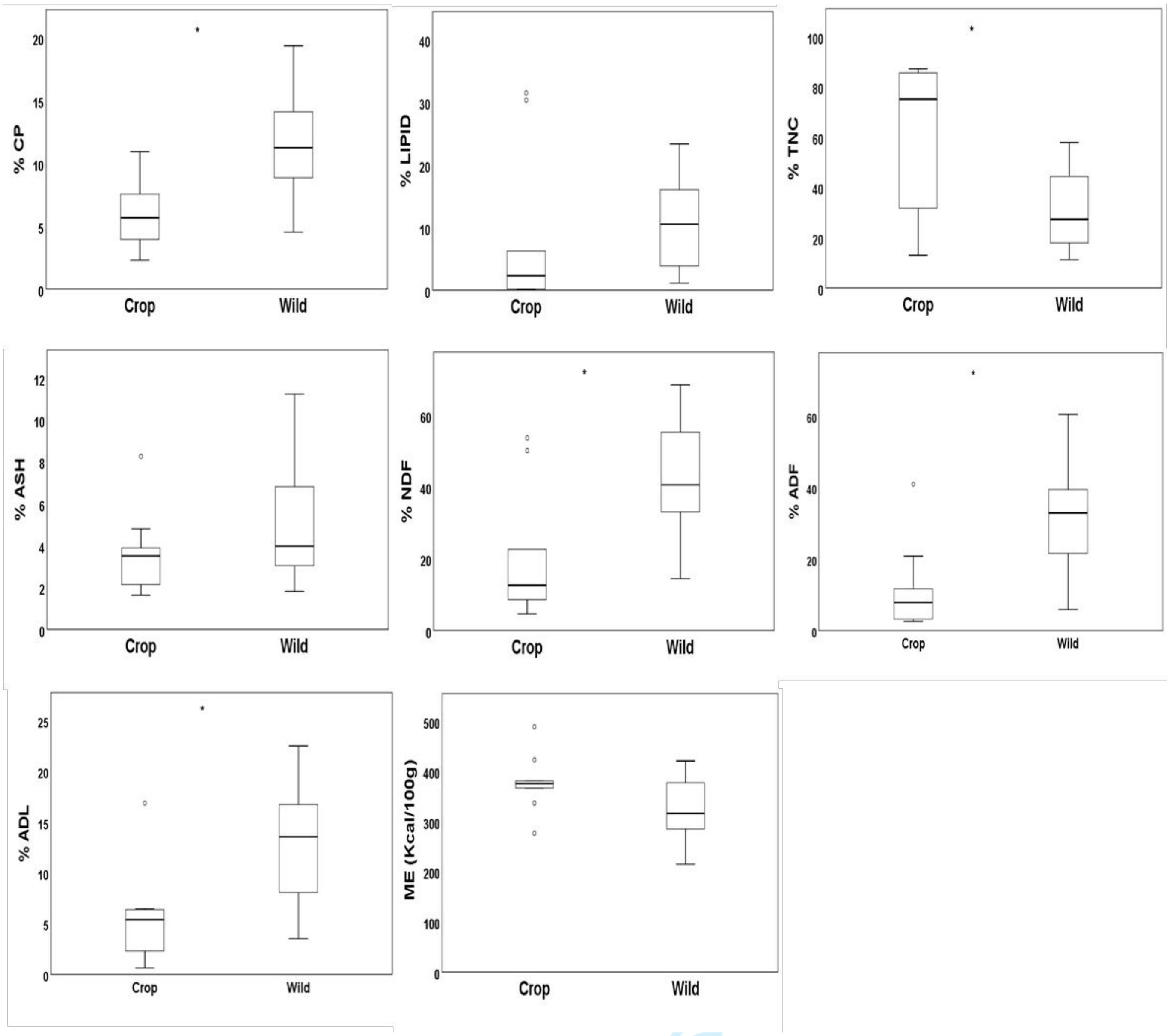

% CP
0
5
10
15
20
*
Crop
Wild
% LIPID
0
10
20
30
40
Crop
Wild
% TNC
0
20
40
60
80
100
*
Crop
Wild
% ASH
0
2
4
6
8
10
12
Crop
Wild
% NDF
0
20
40
60
*
Crop
Wild
% ADF
0
20
40
60
*
Crop
Wild
% ADL
0
5
10
15
20
25
*
Crop
Wild
ME (Kcal/100g)
0
100
200
300
400
500
Crop
Wild

Figure 1

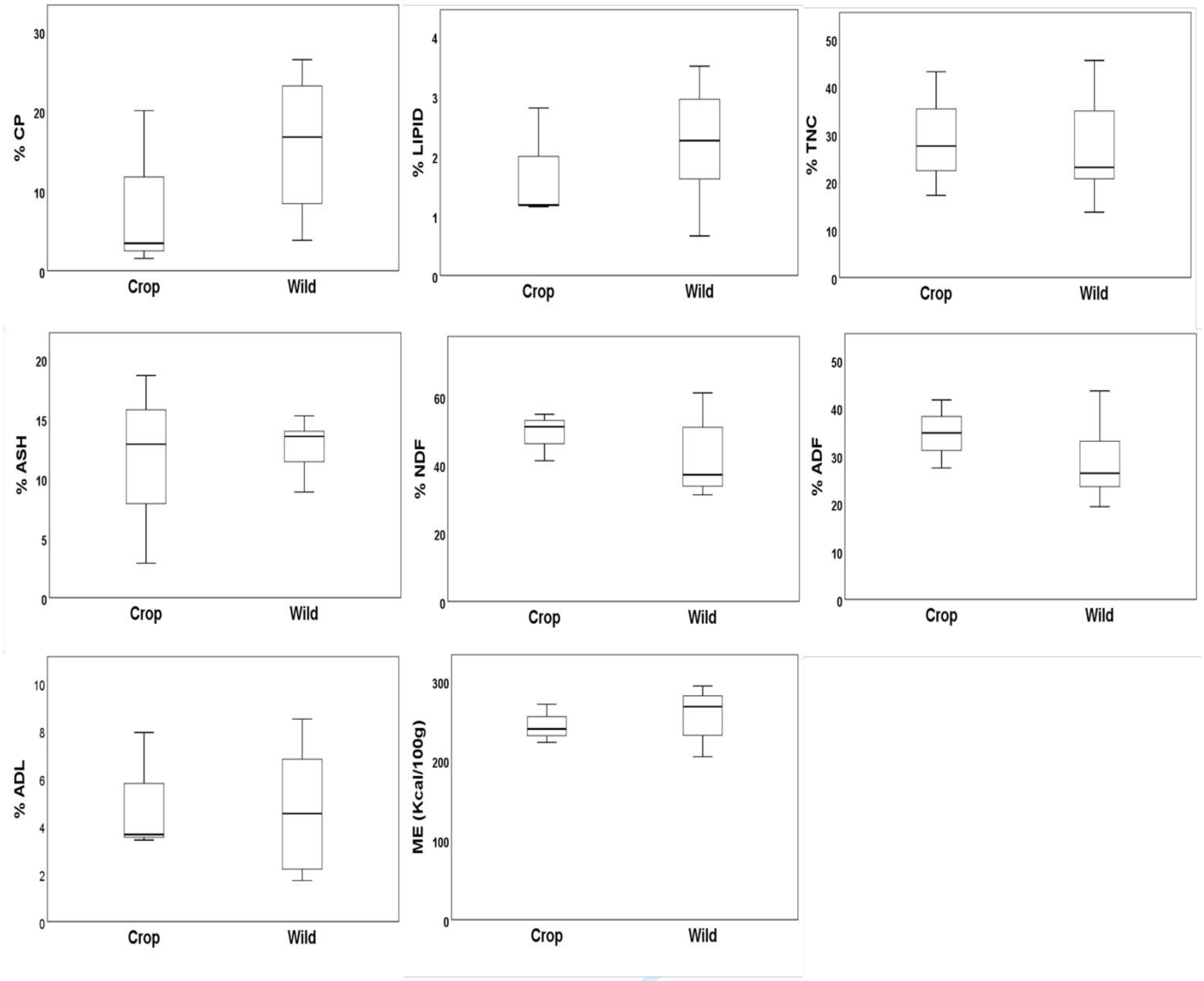

% CP
0
10
20
30
Crop
Wild
% LIPID
0
1
2
3
4
Crop
Wild
% TNC
0
10
20
30
40
50
Crop
Wild
% ASH
0
5
10
15
20
Crop
Wild
% NDF
0
20
40
60
Crop
Wild
% ADF
0
10
20
30
40
50
Crop
Wild
% ADL
0
2
4
6
8
10
Crop
Wild
ME (Kcal/100g)
0
100
200
300
Crop
Wild

Figure 2

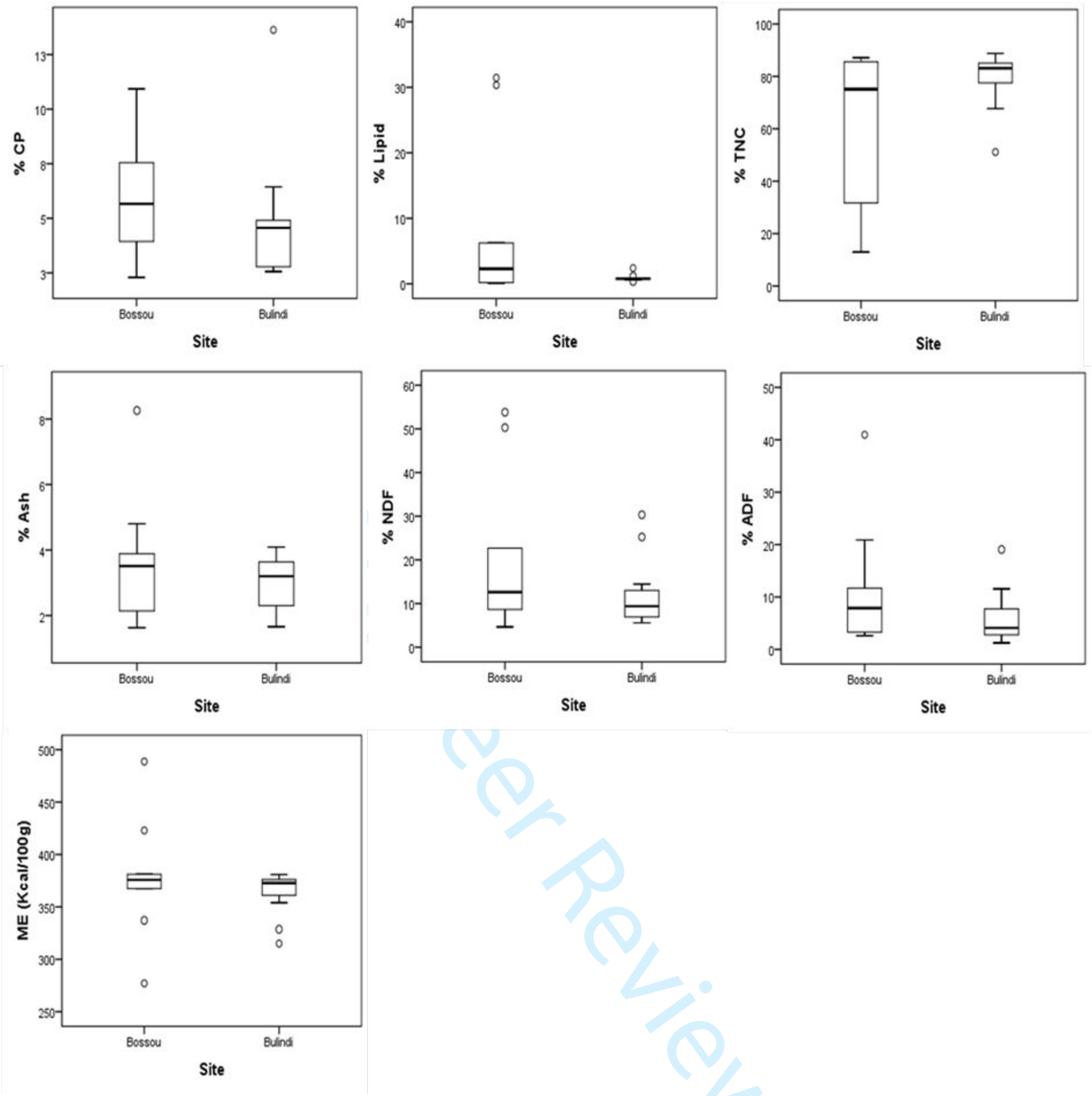

% CP
13
10
8
5
3
Bossou
Bulindi
Site
% Lipid
40
30
20
10
0
Bossou
Bulindi
Site
% TNC
100
80
60
40
20
0
Bossou
Bulindi
Site
% Ash
8
6
4
2
Bossou
Bulindi
Site
% NDF
60
50
40
30
20
10
0
Bossou
Bulindi
Site
% ADF
50
40
30
20
10
0
Bossou
Bulindi
Site
ME (Kcal/100g)
500
450
400
350
300
250
Bossou
Bulindi
Site

Figure 3

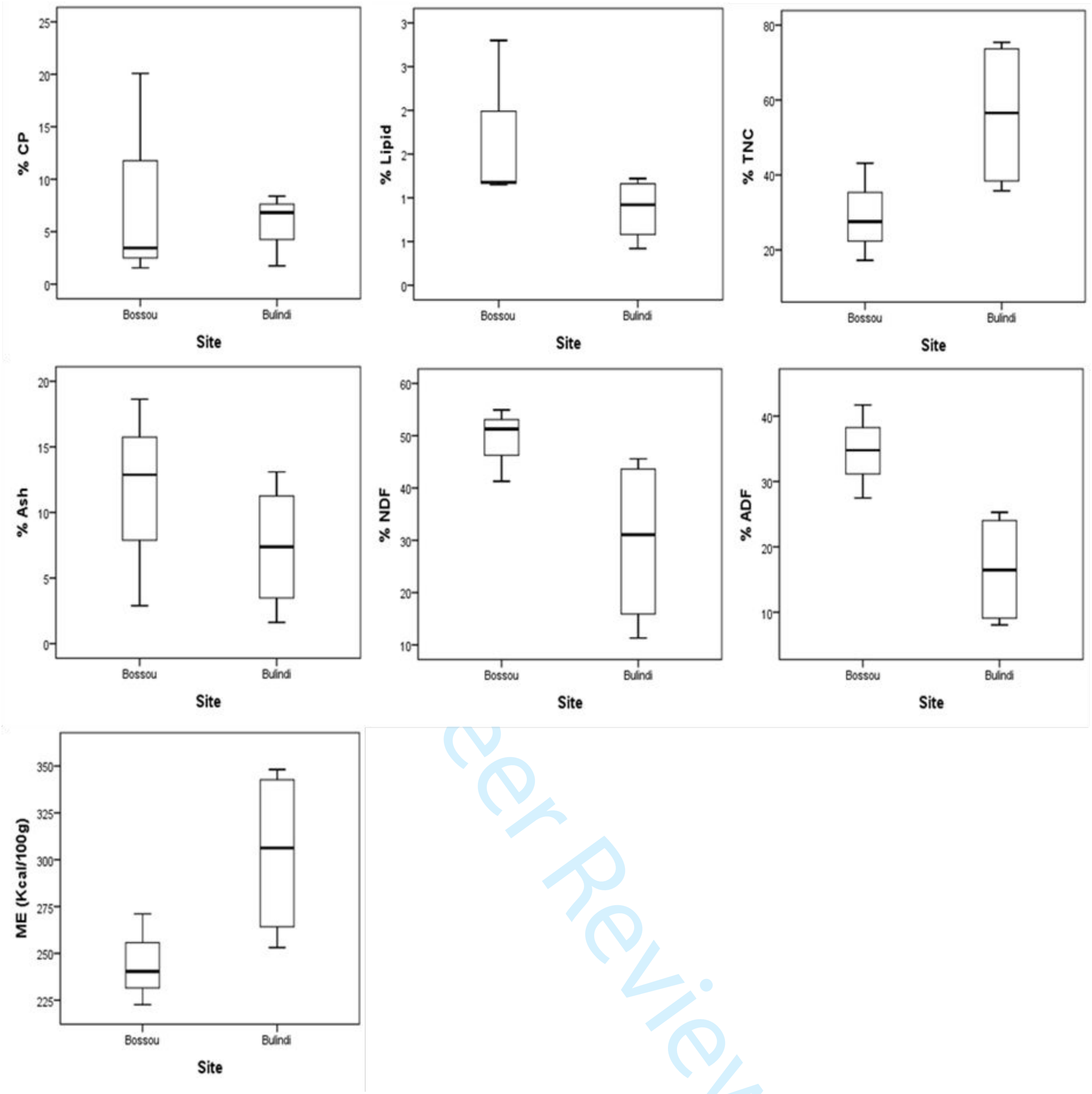
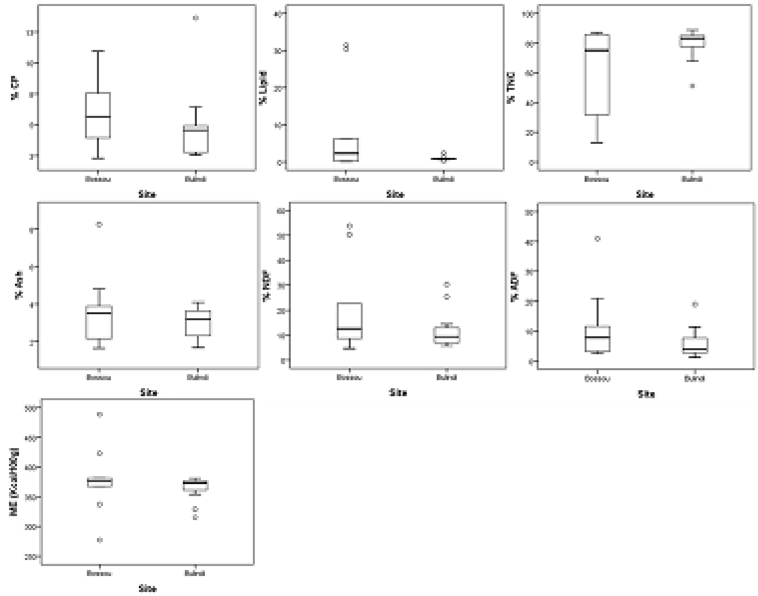

% CP
0
5
10
15
20
25
Bossou
Bulindi
Site
% Lipid
0
1
1
2
2
3
3
Bossou
Bulindi
Site
% TNC
20
40
60
80
Bossou
Bulindi
Site
% Ash
0
5
10
15
20
Bossou
Bulindi
Site
% NDF
10
20
30
40
50
60
Bossou
Bulindi
Site
% ADF
10
20
30
40
Bossou
Bulindi
Site
ME (Kcal/100g)
225
250
275
300
325
350
Bossou
Bulindi
Site

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**	
Kernel	Commercial[†]	45.6	47	2.6	13.6	/	Agunbiade et al (1999)
	Nigeria[‡]	/	42	1.8	8.1	25.4	Akpanabiatu et al (2001)
	Nigeria[‡]	/	41	1.5	7.9	21	Akpanabiatu et al (2001)
	Malaysia[□]	/	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
Fruit	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. [†] Commercial sample of West African origin. [‡] Dura variety. [□] 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)

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