Diet Composition and Feeding Ecology of Chimpanzees (*Pan troglodytes troglodytes*) in a Lowland Tropical Forest in Moukalaba-Doudou National Park, Gabon

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ABSTRACT   Characterizing the diet of wild chimpanzees is fundamental to understanding ecological variation, flexibility, and adaptation within and among populations. Here, we describe the diet composition of central chimpanzees (*Pan troglodytes troglodytes*) in Moukalaba-Doudou National Park, southwestern Gabon. The chimpanzee diet in this area has not previously been described. Based on a macroanalysis of 809 fecal samples and 1,119 minutes of direct observation of their foraging, we showed that they consume fewer insects and more vertebrate prey than those in other study sites. No evidence for the consumption of termites or driver ants was found. Fruits of *Ficus* spp. was the most frequently identified plant food and appeared in the diet of Moukalaba chimpanzees throughout the year. Chimpanzees at Moukalaba, like at other study sites, exhibit a preference for a small number of fruit species, including *Ficus* spp., among the foods available at any given period or area while flexibly changing the foods they eat in response to seasonal changes in fruit quantity in the habitat.

KEYWORDS: Chimpanzee; Diet; Feeding ecology; Moukalaba-Doudou.

INTRODUCTION

The diet of wild chimpanzees (*Pan troglodytes*) has been described in various habitats across equatorial Africa, from savanna/woodlands open habitats (Tutin et al. 1997; Piel et al. 2017) to tropical rainforests (Newton-Fisher 1999; Furuichi et al. 2001; Basabose 2002; Head et al. 2011). Wherever chimpanzees have been studied, they have been reported to be primarily frugivores (Sugiyama & Koman 1987; Sugiyama et al. 1988; Newton-Fisher 1999; Basabose 2002). The aforementioned studies revealed high diversity in the diet of chimpanzees inhabiting different environments, suggesting ecological flexibility. Behavioral and social flexibility may also be needed to exploit resources with varied conditions of access (Tutin 1994; McLennan 2014). Thus, the description of the chimpanzee diet in a new site is helpful for site-based research, conservation, and meta-analyses at the species, genus, and family levels. In the present study, we describe the diet composition of the chimpanzee

inhabiting a forest-savanna mosaic in Moukalaba-Doudou National Park, Gabon, for the first time.

Moukalaba is an appropriate place to assess the dietary composition flexibility of chimpanzees for several reasons. First, this area is composed of multiple vegetation types —old secondary forest, swamp forest, gallery forest, young secondary forest, and savanna —that provide a variety of potential food sources for chimpanzees (Takenoshita et al. 2008; Nakashima et al. 2013; Nakashima 2015). Second, chimpanzees, as well as sympatric gorillas, have not suffered from the high hunting pressure for the bushmeat trade, and thus their density is higher compared to other areas in Gabon (Thibault and Blaney 2003; Kuehl et al. 2009).

Previous studies conducted in other locations have shown general patterns in chimpanzee diet. They tend to prefer ripe fruit year-round, but their reliance on fruit changes in response to variations in fruit availability in their habitat (e.g., Kuroda et al. 1996; Tutin 1999). Certain types of fruit are highly favored and consumed consistently, while others are only eaten during specific seasons or when preferred fruits are scarce (e.g., Tutin & Fernandez 1993a; Tweheyo & Lye 2003). Additionally, chimpanzees consume more non-fruit foods during periods of low fruit availability (e.g., Takemoto 2003; Marshall & Wrangham 2007). Therefore, we examined their diet in terms of the following hypothesis. 1) the fruit feeding of chimpanzees would show seasonal changes related to changes in fruit availability; 2) there are two types of preferred food for chimpanzees: those that have a steady supply throughout the year and those that are concentrated at specific seasons/periods of the year, and 3) animal consumption increases when the fruit is scarce.

METHODS

I. Study site

We conducted a field study in the Moukalaba-Doudou National Park, Gabon. The park covers an area of 5,028 km^2, constituted by the mosaic of tropical seasonal forest and savanna grassland (Vande Weghe et al. 2016). Our study site is an area of about 280 km^2, located in the northern area of the park (2°2'–2°4'S, 10°2'–10°6'E). Kyoto University has conducted a long-term field project for primatology with the Institute de Recherche en Ecologie Tropical (IRET) since 2001 (see Ando et al. 2008; Takenoshita et al. 2008; Akomo-Okoue et al. 2015). The area typically experiences two seasons: the rainy season from October to April and a dry season (monthly rainfall below 100 mm) from May to September. It seldom rains during the three months in the middle of the dry season (June, July, and August). Mean annual rainfall (2002–2006) was 1,777 mm (range: 1,583–2,163 mm). The mean monthly minimum and maximum temperatures varied from 21.3°C to 24.1°C and from 29.3°C to 33.7°C, respectively (Takenoshita et al. 2008).

The study areas have been known to have high densities of chimpanzees and gorillas since the 1980s (Tutin & Fernandez 1984; Walsh et al. 2003; Nakashima et al. 2013). While gorillas have been habituated (Ando et al. 2008), chimpanzees were not yet habituated. Nevertheless, we could often observe them for several minutes before they moved off and record directly observed feeding behavior in trees and on the ground.

The study site comprised two sectors: Boutsiana-Dougetsi (hereafter BTS) and Mont Doudou (hereafter MDD; Figure 1). The BTS sector had a low elevation, about 68 m (Sosef et al. 2004), and included young secondary forest: *Musanga cecropioides*-dominated forest regenerated from old plantations, temporarily inundated forest, and savanna (Iwata
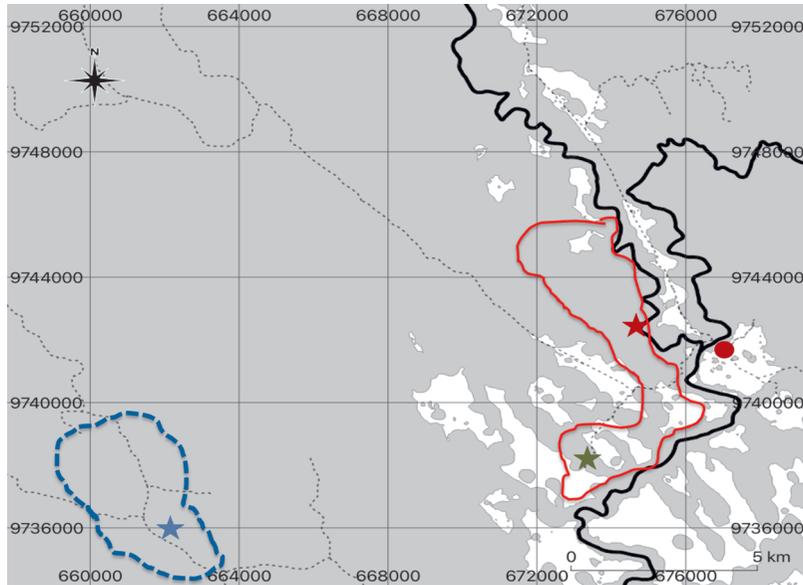
Figure 1 Study site. Thick black line: river; dashed line: logging road; solid red circle: Boutsiana-Dougetsi sector; dashed blue circle: Mont Doutou sector; red star: Boutsiana camp; green star: Dougetsi camp; blue star: Mont Doutou camp, red circle: Doussala village.

& Ando 2007). The density of ground vegetation was high, and the canopy cover was low compared to other forests in Gabon (Lewis et al. 2013). The BTS sector was very close to the village of Doussala. The MDD sector consisted of the Doudou mountain range, which runs north-south at altitudes up to 900 m (Sosef et al. 2004). The vegetation of the MDD sector included mixed-species primary forest that had been selectively logged and old closed-canopy secondary forest with sparse ground vegetation.

II. Data collection

To gather information about the diet of chimpanzees in our study site, we used macroscopic analysis of their feces. While direct observation of feeding behavior is generally considered the most accurate way to determine an animal's diet, indirect methods such as fecal analysis, food trace observation, and examination of stomach contents of dead animals can be used when direct observation is not feasible (Tutin & Fernandez 1993b; McGrew et al. 2009). In the case of chimpanzee studies, fecal analysis has been a popular method for a long time (e.g., Goodall 1986; Nishida & Uehara 1983). It is beneficial for detecting fruit and insect consumption, which often leave remnants in feces. However, a limitation lies in detecting plants' herbaceous and fibrous components such as leaves, pith, bark, and flowers. Such food items are often too fragmented to identify remnants at the species level (Tutin & Fernandez 1993b). Nonetheless, fecal analysis can still provide insights into the consumption of broad food categories such as whole leaves or fibrous foods, which can be quantitatively described. Furthermore, the method of primate fecal analysis is well standardized (McGrew et al. 2009), making it easier to compare results across sites.

We collected chimpanzee feces that had fallen on the nest site, defecated during direct observation, or were found by chance while walking through the forest. Chimpanzee feces

were readily distinguishable from those of sympatric western lowland gorillas (*Gorilla gorilla gorilla*) by size, color, form, and smell (Tutin & Fernandez 1993b). At the nest sites, we collected one sample per nest to reduce the likelihood of individuals contributing multiple samples daily.

The data used in this study was collected during two different survey periods. The first survey period (Period 1) lasted 48 months, from April 2003 to March 2007, and was conducted by Takenoshita, Ando, and Iwata in the BTS area. During Period 1, we did not exclusively focus on chimpanzees, i.e., we also engaged in the habituation and ecological study of sympatric gorillas in the same area, and whenever chimpanzee feces were encountered, they were collected.

The second survey period (Period 2) spanned 14 months, from April 2013 to June 2014, and was conducted solely on chimpanzees by Ebang. During this period, Ebang walked through the forest in the MDD and BTS areas to locate chimpanzees and collect their feces.

As a result, we obtained two different types of datasets. The data collected during Period 1 (DS1) consisted of a small number of feces collected per season in the BTS area, covering multiple years of data. On the other hand, the data collected during Period 2 (DS2) was for a single year but covered two different areas, BTS and MDD, and had a larger number of feces collected per season than DS1.

We washed fecal samples through a 1-mm mesh sieve. After drying, we identified and recorded the contents as fruit (seeds, skins, pulp, and whole fruit), leaf (green leaf fragment, whole undigested leaves), fiber (pith, bark), invertebrate, vertebrate, and other items. Then we evaluated the relative volume of these food categories at 5% intervals for the total mass of the washed sample (Kuroda et al. 1996, adapted from Tutin & Fernandez 1993b). Thus, the percentage of fruit per sample is the combined percentage of fruit, seeds, and other fruit remains, the percentage of the leaf is the combined percentage of all foliage remains, and the percentage of fiber is the combined percentage of pith and bark (Tutin & Fernandez 1993b). We identified seeds and other fruit remains to species level where possible and calculated the number of fruit species per sample. For invertebrate contents, all identified matter were those of insects, so hereafter we refer to them as insect to clarify that we did not detect non-insect invertebrates. We did not identify the vertebrate remains to species level, recording skin, bone, and hair in the samples as 'vertebrates' (Phillips & McGrew 2013). Regarding insects and vertebrates, it is often the case that their bodies make up less than 5% of fecal volume. Therefore, if they are detected even when their volume percentage is less than 5%, they are counted as feces containing them, but we recorded the relative volume as 0%.

In addition to fecal analysis, we recorded food items consumed by chimpanzees during opportunistic observations (1,119 minutes of observation in total). Also, additional data came from fresh feeding traces when these could be attributed with certainty to chimpanzees, based on associated fresh signs (feces, knuckle marks, nests) or the recently observed departure of chimpanzees from the same locality (McGrew et al. 1988).

Samples of insects and vertebrates found in feces were preserved in 100% ethanol. Insect specimens were identified at the Biology Laboratory of Masuku University, Franceville, Gabon. Some insect species were easy to identify with their unique characteristics. For example, weaver ants (*Oecophylla longinoda*) have reddish heads and black eyes; honeybees (*Apis* spp.) have triangular heads or black and yellow banded chitinous strips of the abdomen; worker ants of the genus *Pheidole* (known as the 'Big-headed' ants) have a unique head-thorax ratio. Others could not be reliably identified at the species level by the macroscopic methods employed in this study. Thus, groups such as 'small ants' and 'unidentified' in the analyses below were classes known to include two or more species.

III. Data analysis

We compiled a list of all plants consumed during the study from fecal data and direct observations. We first described diet composition in terms of the number of plant foods and species eaten and the number of species of non-plant foods. We then classified fruit foods into two types: Type 1, frequently consumed in both the dry and rainy seasons each year; Type 2, frequently consumed only within either season (see below).

To investigate the hypothesis 1 and 3, we used Wilcoxon rank-sum tests to compare the relative volume of each food category (fruit, leaf, fiber, insects, and vertebrates) and the number of fruit species per fecal sample between seasons and sectors for each dataset.

To address the hypothesis 2, we characterized the consumption of each food and described its contribution to the diet as a proportion of all foods consumed in each season. We operationally defined 'major fruits' as species detected in more than 20% of fecal samples in DS1 and more than 10% in DS2 due to the lower dominance of single foods in the latter dataset in DS1.

Additionally, we investigated the seasonal variation on identified species of insects. We used Fisher's exact probability test, setting the significant level at $p < 0.05$. We performed statistical analyses on fecal data using R software version 4.2.2 (R Core Team 2022); data from direct observations are presented for supplementary purposes.

Results

I. Overall diet

We identified at least 73 fruit species; 71 of which were identified to at least the genus level, two were identified to the family level (Table 1). In addition, we distinguished at least 18 species that we could not identify even at the family level.

Table 2 provides a summary of the fecal analysis results. In the total sample of 809 independent fecal samples, fruits were found in 99.6% (n = 806), leaves in 74.7% (n = 604), fiber in 28.4% (n = 230), insects in 7.3% (n = 59), vertebrates in 4.7% (n = 38), and pebbles in 5.4% (n = 44). We could not eliminate the possibility of contamination at the collection site for pebbles. Therefore, we did not treat them as 'food' in the current analysis. However, the presence of pebbles in feces might also indicate geophagy, as reported in other primate populations, including chimpanzees (Krishnamani & Mahaney 2000). Therefore, it is necessary to consider this point in future research carefully.

Leaf remains in fecal samples were half-digested or fragmented, making it difficult to identify species. We recorded only two species from leaves: *Dialium eurysepalum* and another species of *Dialium* that we could only identify to the genus in the field. Other leaf remains are qualified simply as 'leaf'.

II. Fruit foods

DS1 and DS2 show similar trends in detection rates and relative volume of each food category, i.e., almost all fecal samples contain fruit, with fruit accounting for the largest volume. The number of fruit species per feces seems higher in DS1 than in DS2 (Table 2). However, direct statistical comparisons between two datasets are difficult due to differences in the length of sampling periods and the number of samples per season.

Table 1   List of plants eaten by chimpanzee at Moukalaba. "+" indicates the method used for confirmation

Family	Species	Fecal data			Direct observation data		
		pulp	seed	leaf	pulp	seed	leaf
Anacardiaceae	*Antrocaryon klaineanum*	+	+				
	Lannea welwitschii	+			+		
	Pseudopondias longifolia	+					
Annonaceae	*Cleistopholia glauca*	+					
	Meiocarpidium lepidotum	+					
	Pachypodanthium staudtii	+					
	Polyalthia suaveolens	+					
	Uvaria klaineana	+					
	Uvaria versicolor	+					
	Uvaria sp.1	+					
	Uvaria sp.2	+					
	Xylopia le-testui	+	+				
Apocynaceae	*Aphanostylis mannii*	+	+				
	Landolphia mannii	+	+				
	Picralima nitida	+	+				
Bombacaceae	*Ceiba pentandra*	+					
Burseraceae	*Canarium schweinfurthii*	+					
	Dacryodes buttneri	+					
	Dacryodes igaganga	+	+				
	Dacryodes klaineana	+					
	Dacryodes le-testui	+	+		+		
Burceraceae	*Pachylobus ferruginea?*				+		
	Santiria trimera	+	+		+		
Cannabaceae	*Celtis tessmanii*	+					
Celastraceae	*Salacia* sp.	+					
Clusiaceae	*Garcinia* sp.	+					
	Mammea africana	+					
Cucurbitaceae	(genus unidentified)	+					
Cyperaceae	*Scleria verrucosa*	+					
Dichapetalaceae	*Dichapetalum* sp.						
Ebenaceae	*Diospyros mannii*	+	+				
	Diospyros sp.	+			+		
	Diospyros sp.1	+					
	Diospyros sp.2	+					
Flacourtiaceae	*Caloncoba welwitschii*	+					
Humiriaceae	*Sacoglottis gabonensis*	+					
Irvingiaceae	*Irvingia gabonensis*	+	+				
	Klainedoxa gabonensis	+					
Lamiaceae	*Pterotaberna inconspicua*	+					
	Vitex doniana	+					
Lauraceae	*Belschmiedia* sp.	+					
Lecythidaceae	*Scytopetalum brevipes*	+					

Table 1 Continued.

Family	Species	Fecal data			Direct observation data		
		pulp	seed	leaf	pulp	seed	leaf
Loganiaceae	*Strychnos* sp.	+					
Sterculiaceae	*Cola* spp. (≥2 species)	+			+		
	Sterculia tragacantha	+					
Malvaceae	*Desplatsia* sp.	+	+				
	Duboscia macrocarpa	+					
	Grewia coriacea	+					
Mimosaceae	*Piptadiniastrum africanum*				+		
Moraceae	*Ficus* spp. (≥2 species)	+			+		
	Parinari excelsa	+					
	Treculia africana	+	+				
Myltaceae	*Psidium guineensis*	+					
Myristicaceae	*Pycnanthus angolensis*	+			+		
	Staudtia gabonensis	+	+		+		
Olacaceae	*Coula edulis*	+					
	Strombosiopsis tetrandra	+					
Putranjivaceae	*Drypetes* sp.	+	+				
Rubiaceae	*Nauclea didderichii*				+		
	Nauclea latifolia				+		
	Porterandia cladantha	+					
	Tricalysia sp.	+					
Sapotaceae	*Chrysophyllum africanum*	+	+		+		
	Manilkara fouilloyara	+					
	Mimusops africana				+		
	Synsepalum dulcificum	+			+		
	#78 (genus unidentified)	+					
Urticaceae	*Musanga cecropioides*	+			+		
	Myrianthus arboreus	+					
Vitaceae	*Cissus dinklagei*	+			+		
Zingiberaceae	*Aframomum giganteum*	+			+		

Species numbered like sp.1, sp.2, etc., indicate that the species was distinguished correctly but could not be identified to the species level. On the other hand, those with spp. (≥2 species) indicate those that contain multiple species but cannot be distinguished each species from the seeds.

III. Seasonality in fruit consumption

In both DS1 and DS2, fruits were detected in most fecal samples regardless of the rainy or dry season (Table 2). However, there were seasonal differences in the relative volume of fruit remains and the number of fruit species per fecal sample. Overall, the relative volume of fruit remains was significantly larger in the rainy than in the dry season (Wilcoxon rank-sum test, DS1: $W = 16400$, $p < 0.001$; DS2: $W = 6501$, $p < 0.001$). Also, the number of fruit species per sample was larger in the rainy than in the dry season (DS1: $W = 17198$, $p < 0.001$; DS2: $W = 11434$, $p < 0.001$).

Table 2 Number of fecal samples, mean number of fruit species per samples with each food categories. a) DS1 (BTS only), b) DS2 (from April 2013 to June 2014)

a)

Season	Year[1]	Number of feces	Fruit				Leaf				Fiber				Insect				Vertebrate				No. spp.[2]	
			n	%	MRV	sd	n	%	MRV	sd	n	%	MRV	sd	n	%	MRV	sd	n	%	MRV	sd	mean	sd
Dry	Overall	281	278	98.9	72.1	25.3	255	90.7	19.6	19.6	144	51.2	7.0	11.8	12	4.3	0.1	0.7	17	6.0	0.1	1.4	3.3	1.4
	2003	75	73	97.3	72.6	25.1	60	80.0	14.3	15.6	49	65.3	9.9	12.8	1	1.3	0.1	0.6	1	1.3	0.0	0.0	3.2	1.5
	2004	83	83	100.0	73.1	25.5	78	94.0	19.2	20.4	44	53.0	7.0	11.9	6	7.2	0.0	0.0	5	6.0	0.4	2.5	3.3	1.1
	2005	96	95	99.0	67.2	26.5	93	96.9	25.9	21.7	45	46.9	6.5	11.9	1	1.0	0.0	0.0	9	9.4	0.0	0.0	3.3	1.5
	2006	27	27	100.0	84.8	15.0	24	88.9	13.5	12.6	6	22.2	0.9	2.4	4	14.8	0.4	1.9	2	7.4	0.0	0.0	3.1	1.8
Rainy	Overall	167	167	100.0	83.7	21.1	144	86.2	13.2	19.2	60	35.9	2.6	7.2	5	3.0	0.0	0.0	9	5.4	0.0	0.4	4.1	1.8
	2003	30	30	100.0	81.8	19.5	21	70.0	8.8	10.2	15	50.0	6.8	9.8	1	3.3	0.0	0.0	1	3.3	0.2	0.9	3.7	1.8
	2004	48	48	100.0	70.8	28.8	45	93.8	26.0	28.1	15	31.3	2.9	9.8	2	4.2	0.0	0.0	2	4.2	0.0	0.0	3.5	1.6
	2005	44	44	100.0	93.5	7.2	34	77.3	5.2	5.5	17	38.6	1.0	2.8	1	2.3	0.0	0.0	1	2.3	0.0	0.0	4.7	1.8
	2006	45	45	100.0	88.9	13.5	44	97.8	10.2	13.4	13	28.9	0.9	2.5	1	2.2	0.0	0.0	5	11.1	0.0	0.0	4.5	1.9

[1] The year 2003 refers to the period from May 2003 to April 2004. The same applies to other years. [2] Number of fruit species per samples with each food category, the number of feces that contained (n) and its percentage (%), relative volume in percentage (MRV) and its standard deviation (sd) are indicated.

b)

Season	Sector	Number of feces	Fruit				Leaf				Fiber				Insect				Vertebrate				No. spp.[*]	
			n	%	MRV	sd	n	%	MRV	sd	n	%	MRV	sd	n	%	MRV	sd	n	%	MRV	sd	mean	sd
Dry	Overall	134	134	100.0	64.4	31.0	115	85.8	34.4	30.8	20	14.9	0.7	2.3	32	23.9	0.4	2.2	8	6.0	0.2	1.1	2.3	1.2
	BTS	67	67	100.0	60.6	33.6	58	86.6	38.1	33.7	3	4.5	0.4	1.8	12	17.9	0.7	3.0	6	9.0	0.4	1.6	2.1	1.4
	MDD	67	67	100.0	68.1	27.9	57	85.1	30.8	27.3	17	25.4	1.1	2.7	20	29.9	0.1	0.6	2	3.0	0.0	0.0	2.4	0.9
Rainy	Overall	227	227	100.0	90.0	18.4	90	39.6	9.5	18.0	6	2.6	0.3	2.5	10	4.4	0.1	0.7	4	1.8	0.1	1.3	2.8	1.5
	BTS	147	147	100.0	93.9	14.7	43	29.3	6.0	14.5	2	1.4	0.0	0.4	7	4.8	0.1	0.9	1	0.7	0.0	0.0	3.1	1.6
	MDD	80	80	100.0	82.9	22.2	47	58.8	16.1	21.7	4	5.0	0.8	4.1	3	3.8	0.0	0.0	3	3.8	0.3	2.2	2.3	0.9

[*] Number of fruit species per sample; For each food category, the number of feces that contained (n) and its percentage (%), relative volume in percentage (MRV) and its standard deviation (sd) are indicated.

However, in DS1, when multiple comparisons were made for each season rather than the entire rainy and dry seasons, it was shown that the relative volume of fruit remains and the number of fruit species per sample did not necessarily increase in the rainy season compared to the dry season. For example, the relative volume of fruit remains in the rainy seasons of years 2003 and 2004 did not significantly larger compared to the surrounding dry seasons. Similar results were found for the number of fruit species per sample (Table 2a, Figure 2).

For DS2, relative volume of fruit remains was significantly larger during the rainy season than in the dry season in both sectors (Wilcoxon rank-sum test, BTS: W = 1385, $p < 0.05$; MDD: W = 1770, $p < 0.05$). In the rainy season, the relative volume of fruit remains was significantly larger in the BTS area than MDD area (W = 7773.5, $p < 0.05$). However, in the dry season, the difference was insignificant (W = 1954.5, $p = 0.195$) (Figure 3a). The number of fruit species per sample was larger in the rainy season than in the dry season in BTS (W = 2992, $p < 0.05$), but did not significantly differ between seasons in MDD (W = 2737.5, $p = 0.811$). In the rainy season, the number of fruit species per sample was significantly larger in the BTS area than in the MDD area (W = 7521.5, $p < 0.05$). However, in the dry season, it was significantly larger in the MDD area than in the BTS area (W = 1708, $p < 0.05$), but the absolute value of the difference was very small (Figure 3b).
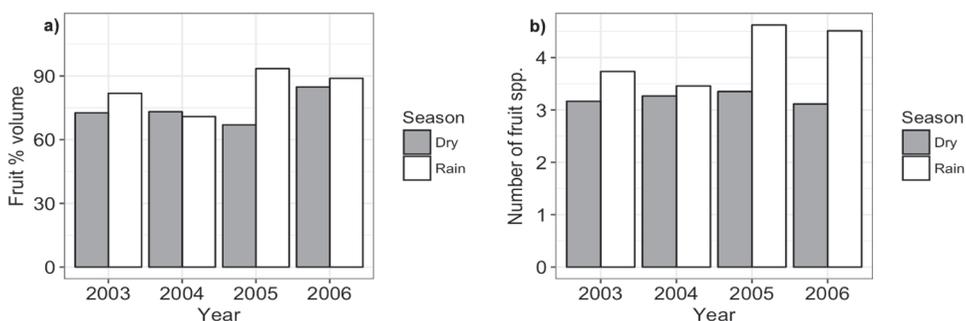
Figure 2 Seasonal and inter-annual fluctuation in a) relative fruit volume and b) number of fruit species in DS1.
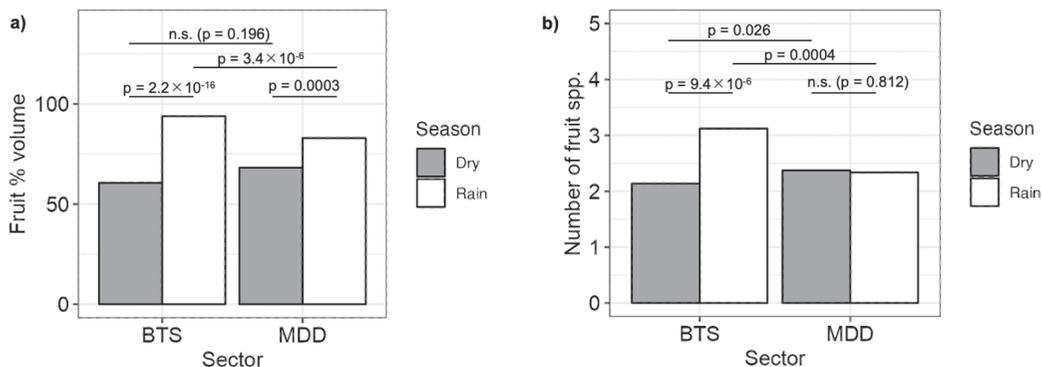

Figure 3 Seasonal variation in a) relative fruit volume and b) number of fruit species in DS2. The *p* values above the horizontal lines are obtained by the Wilcoxon rank-sum test.

IV. Major fruit species

For DS1, three species, *Manilkara fouilloyara*, *Ficus* spp., and *Cissus dinklagei*, were appeared as Type 1, i.e., major in both the dry and the rainy seasons. Seventeen species appeared as Type 2: 7 species were major in the dry seasons, and 10 species were major in the rainy seasons (Table 3).

For DS2, two species appeared as Type 1 major species: *Ficus* spp. and *Dacryodes igaganga*. Eleven species appeared as Type 2: 3 species (*Treculia africana*, *Musanga cecropioïdes*, and *Cissus dinklagei*) were major in the dry season and 8 species were major in the rainy seasons (Table 4).

Ficus spp. was the most common and the Type 1 major species in terms of relative volume from fecal samples. It was detected in 130 samples (29%) of DS1 and 85 samples (26%) of DS2, i.e., throughout the study period and seasons.

V. Non-fruit plant food

Young leaves, stems, and pith of two tree species, *Dialium eurysepalum* and an unidentified *Dialium* sp., were consumed in the rainy season. Leaf remains were detected

Table 3 Seasonal and annual major fruit species of DS1

Species	2003 Dry	2003 Rain	2004 Dry	2004 Rain	2005 Dry	2005 Rain	2006 Dry	2006 Rain	Total Dry	Total Rain
Cissus dinklagei	+++	+	+++		+	+	++	+	4	3
Manilkara fouilloyara	+++	+	+++	+	+++	++			3	3
Ficus spp.	++			++	+	+++	+++	+++	3	3
Pycnanthus angolensis	++		++				+++		3	
Diospyros spp.		+++		++		++				3
Desplatsia dewevrei				+++		+		++		3
Landolphia spp.		+				+++		+++		3
Pseudospondias longifolia					++		+		2	
Aframomum spp.		+++						+		2
Lannea welwitschii				+++				+		2
Myrianthus arboreus				+++				++		2
Uapaca guineensis	+								1	
Staudtia gabonensis			+						1	
Polyarthia sauveolens					+				1	
Porterandia cladantha					+				1	
Musanga cecropiondes							+++		1	
Cola spp.		+								1
Uvaria versicolor								+		1
Dialium spp.						+++				1
Synsephalum longecuneatum								+		1
Total	5	6	4	6	6	7	5	9	10	13

+++, ++, and + indicate that the species are detected >40%, >30%, and >20% of fecal samples, respectively.

Table 4   Seasonal major fruit species of DS2

Species	Seasons	Dry		Rain	
	Total No. of feces	n	(%)	n	(%)
Ficus spp.	85	**53**	**48.6**	**32**	**12.7**
Dacryodes igaganga	57	**20**	**18.3**	**37**	**14.7**
Treculia africana	56	**56**	**51.4**	0	0.0
Uvaria klaineana	48	0	0.0	**48**	**19.0**
Cola spp.	48	0	0.0	**48**	**19.0**
Santiria trimera	47	0	0.0	**47**	**18.7**
Chrysostylis africanum	46	0	0.0	**46**	**18.3**
Aphanostylis mannii	43	0	0.0	**43**	**17.0**
Dialum spp.	35	0	0.0	**35**	**13.9**
Diospyros sp.1	34	0	0.0	**34**	**13.5**
Antrocaryon klaineanum	28	1	0.9	**27**	**10.7**
Polyalthia suaveolens	25	2	1.8	23	9.1
Myrianthus arboreus	25	2	1.8	23	9.1
Drypetes sp.	24	2	1.8	22	8.7
Musanga cecropioides	22	**21**	**19.4**	1	0.4
Cissus dinklagei	20	**17**	**15.6**	3	1.2
Xylopia le-testui	19	0	0.0	19	7.5
Caloncoba welwitschii	19	0	0.0	19	7.5
Staudtia gabonensis	15	0	0.0	15	6.0
Uapaca guineensis	14	0	0.0	14	5.6
Dacryodes le-testui	12	0	0.0	12	4.8

n = number of fecal samples containing the species; Bold text indicates the species detected in >10% of fecal samples.

from 89.1% of fecal samples of DS1 but only 56.8% of DS2 samples. Overall, the relative volume of the leaf remains was larger during the dry season than the rainy season (Wilcoxon rank-sum test, DS1: W = 16400, $p < 0.05$; DS2: W = 23859, $p < 0.05$).

Fiber remains were detected from 45.5% of DS1 samples and 7.2% of DS2 samples. Overall, the relative volume of fiber remains was larger in the dry season than in the rainy season (Wilcoxon rank-sum test, DS1: W = 16400, $p < 0.05$; DS2: W = 17064, $p < 0.05$).

As seen in fruit food, however, in DS1, when multiple comparisons were made for each season, it was shown that the relative volume of leaf and fiber remains did not necessarily increase in the rainy season compared to the dry season (Table 2a).

VI. Non-plant foods

Insect remains were detected in only 3.8% of DS1 samples and 11.6% of DS2 samples, respectively (Table 2). For DS1, insects' detection rate and relative volume were larger in the dry season than in the rainy season, but no significant seasonal differences were detected, possibly due to the low detection rate. For DS2 samples, the rate of feces containing insects was significantly larger in the dry season than in the rainy season (Chi-square test, $\chi^2 = 29.22$, df = 1, $p < 0.05$), and the relative volume of insect remains was significantly larger in the dry season than in the rainy season (Wilcoxon rank-sum test, W =
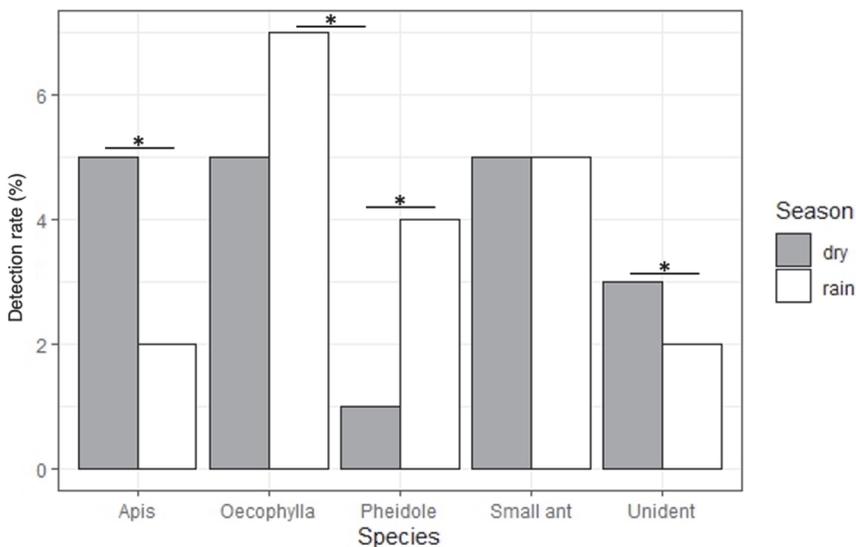
Figure 4 Seasonal variation of insect species consumed in DS2. The horizontal lines with asterisks indicate a significant difference ($p < 0.05$) by Fisher's exact probability test.

18165, $p < 0.05$).

Interestingly, we found neither remains of termites nor driver ants in the chimpanzee feces. Moreover, we did not observe chimpanzees feeding on these insects in Moukalaba. In contrast, chimpanzees consumed *Apis* spp., *Oecophylla longinoda*, small ants, 'unidentified', and *Pheidole* spp. in both the dry and rainy seasons. *Apis* spp. and 'unidentified' were consumed more in the dry than in the rainy season (Fisher's exact probability test, $p < 0.05$). *Oecophylla longinoda* and *Pheidole* spp. were consumed significantly more in the rainy season than in the dry season (Fisher's exact probability test, $p < 0.05$). Small ants are detected at similar rates in both the dry and the rainy seasons (Figure 4).

Vertebrate remains were detected from 5.8% of DS1 samples and 3.3% of DS2 samples. For DS1, both the detection rate and relative volume of vertebrate remains were larger during the dry season than during the rainy season, but no significant seasonal differences were detected, possibly due to the low detection rate. For DS2 samples, the rate of feces containing vertebrates was significantly larger in the dry season than in the rainy season (Chi-square test, $\chi^2 = 4.806$, df = 1, $p < 0.05$), and the relative volume of vertebrate remains was significantly larger in the dry season than in the rainy season (Wilcoxon rank-sum test, W = 15851, $p < 0.05$).

Discussion

I. General description of the diet

Overall, the diet of Moukalaba chimpanzees resembled those of other chimpanzee populations studied, being dominated by succulent fruit pulp, supplemented by a regular intake of vegetative foods and animal prey (Tutin & Fernandez 1992, 1993b; Newton-

Fisher 1999; Basabose 2002; Yamagiwa & Basabose 2006; Moscovice et al. 2007; Head et al. 2011; Watts et al. 2012a, 2012b). The fruit species diversity in fecal samples of Moukalaba chimpanzees was similar to that described in other rainforest sites. The mean number of fruit species per fecal sample of chimpanzees was 2.7 species at Lopé (Tutin & Fernandez 1993a), 2.1 species at Bwindi (Stanford & Nkurunungi 2003), 2.7 species at Kahuzi (Yamagiwa & Basabose 2006), and 3.1 species at Moukalaba (this study, overall mean). It suggests that chimpanzees of these sites consume a similar number of fruit species and digest at similar rates. Among these habitats, Lopé and Moukalaba are in the lowland tropical seasonal forests of Central Africa, while Kafuzi and Bwindi are in the montane forests of East Africa, suggesting differences in the diversity of available fruits for chimpanzees based on their vegetation types. The number of fruit species in a single fecal sample remained constant with little difference among these varying sites suggesting that chimpanzees from all regions tend to use a similar number of fruit species daily, despite differences in fruit diversity within their habitats. In other words, as Kuroda et al. (1996) mentioned, chimpanzees are 'ripe fruit pursuers' who strongly prefer a limited number of fruit species in their habitat.

In this study, we used fecal analysis to reveal the diet of chimpanzees. Some limitations of this method are well established (McGrew et al. 2009; Phillips & McGrew 2013; Moore et al. 2017), with vegetative foods (pith, leaf, stem) and flowers typically not identifiable and thus not accurately represented in comprehensive food lists (Tutin & Fernandez 1993b). Consequently, our results are likely to have underestimated plant food diversity. We also acknowledge that macroscopic analyses of species consumption may not correspond well to the proportion of the ingested volume of fruits nor the amount of time spent eating fruit, which may be more accurate measures of dependence on frugivory.

II. Fruit consumption

Across all years studied, there was no significant seasonal difference in the relative volume of fruit remains or the number of fruit species found in fecal samples, showing that overall, Moukalaba chimpanzees seemed able to sustain their highly frugivorous diet throughout the year. They may have done this by using multiple feeding tactics in response to seasonal/annual fluctuations, as chimpanzees do in other sites, including change in habitat use, greater dietary diversification (Chaves et al. 2012), reducing frugivory (Tutin 1999) and increasing reliance on low-quality items (Donati et al. 2011) or reducing group size (Tutin & Fernandez 1993a; Tutin 1994) and using fallback resources (Irwin 2008).

From the results of datasets DS1 and DS2, the relative volume of fruit remains and the number of fruit species found in fecal samples fluctuated seasonally. Despite the lack of any measure of vegetation sampling or phenology in this study, our results showed that at Moukalaba, within years and sites, seasonal differences in the chimpanzee diet could be pronounced. However, in DS2, the MDD sector showed no seasonality in the number of fruit species found in fecal samples and only a smaller (though still significant) difference in the relative volume of fruit remains. The difference between sites was significant for both parameters in the rainy season but only for the number of fruit species found in fecal samples in the dry season. It suggests that the two chimpanzee populations used different feeding tactics or had access to different resources. BTS groups seemed to consume a small number of fruit species in the dry season, as do Lopé chimpanzees (Tutin 1999). MDD groups seemed able to sustain the diversity of their seasonal fruit intake, maybe because the patterns of seasonal difference in fruit availability differed.

III. The use of figs

Figs have been classified as a primary fallback food for chimpanzees in some populations (Harrison & Marshall 2011). In East African habitats, figs were important fruits in all months but were not preferred because chimpanzees did not eat more figs with increasing availability (Bwindhi: McLennan 2013; Kibale: Wrangham et al. 1993, 1996). In central African habitats, chimpanzees did not prefer figs and used them only when other fruits were scarce (Lopé: Tutin & Fernandez 1993a; Ndoki: Kuroda et al. 1996).

On the other hand, figs are also suggested to be crucial throughout the year in many chimpanzee habitats, with their asynchronous fruiting promoting year-round availability (Tweheyo & Lye 2003; Harrison & Marshall 2011). Some authors have argued that figs could be used as a 'staple' (Conklin & Wrangham 1994; Newton-Fisher 1999; Pruetz 2006; Watts et al. 2012b) or 'preferred' (Yamagiwa & Basabose 2009) food, that is, in these habitats, figs are eaten at high frequencies in both high- and low-fruit seasons.

In this study, figs were classified as a Type 1 major fruit. It indicates that, like in other regions, figs provide staple food resources for chimpanzees in Moukalaba rather than fallback food. We may say that figs are an important food for chimpanzees across habitats, but how they are used is likely to vary between habitats due to differences in the density and distribution of figs and other fruits and their phenology.

IV. Use of non-fruit

In some habitats, fibrous plant matter such as pith from terrestrial herbaceous vegetation, leaves, and bark assumed greater importance in chimpanzee diets during seasonal fruit shortages (Wrangham et al. 1991, 1998; Kuroda et al. 1996; Doran 1997; Yamagiwa & Basabose 2009; Chancellor et al. 2012), constituting 'filler' fallback foods (Marshall & Wrangham 2007). The importance of fibrous plant matter in the diet of Moukalaba chimpanzees is still unclear. However, our results show that the relative volume of leaf presence in feces was significantly higher in the dry season than in the rainy season, perhaps because the chimpanzees replace fruit with leaves during fruit scarcity. The young leaves of two tree species, *Dialium eurysepalum* and *Dialium* sp. were consumed, indicating that chimpanzees may tend to select young leaves high in protein but low in tannins (Takemoto 2003).

In contrast to vegetative foods, animal consumption by Moukalaba chimpanzees seem distinct from that reported in other sites in central Africa, i.e., chimpanzees in Moukalaba seem to consume fewer insects and more vertebrates than in the other sites. For example, insects were found in an average of 31% of fecal samples from Lopé chimpanzees (Tutin & Fernandez 1992, 1993a), while in Moukalaba, the detection rate of insect fluctuated from only 3% to 12%. The variation in the consumption of insects among study sites may reflect differences in the species composition, abundance, and seasonal fluctuations of insect availability at each site. However, it may also be influenced by cultural differences in the techniques used to capture insects and variations in the relative dependence on insects as a food source among chimpanzee populations (Bogart & Pruetz 2008, 2011). Although bees were present in the fecal samples, it was impossible to tell whether their consumption was voluntary. We presume that the target food was honey and that the small number of bees consumed was perhaps involuntary.

At Kahuzi, driver ants synchronize their life cycle to rainfall, and there are abundant adults during the rainy season, which are eaten by chimpanzees (Basabose 2002). However, in Moukalaba, we did not find feces containing driver ants or termites in either the dry or

rainy seasons. It suggests that chimpanzees in Moukalaba did not consume them or did not know how to catch these insects. In contrast, the most frequently eaten insect species was the weaver ant, *Oecophylla longinoda*. This species was also found to be eaten frequently by Lopé chimpanzees (Tutin et al. 1991) and by Bulindi chimpanzees (McLennan 2013). Could this be a cultural pattern observed for chimpanzees in Gabon? Chimpanzees might be simply consuming weaver ants opportunistically when encountered, but at some sites, these ants are more prevalent.

Further research is needed to clarify insect species' availability and cultural importance as food for chimpanzees living in the Moukalaba mosaic ecosystem. However, there were at least two hypotheses about why Moukalaba chimpanzees showed lower insectivory than other study sites. One is that potential insect prey may have been present at much lower densities, and some favorite prey species could have been absent or very low density at Moukalaba sites. The other hypothesis is that the Moukalaba chimpanzees' diet may already have provided access to sufficient calories, fat, or other nutrients, and insects were not needed (Webster et al. 2014).

A higher level of vertebrate consumption was observed in Moukalaba (6%) than at other sites where hunting by chimpanzees is rare or absent (Ndoki: 3.7%, Kuroda et al. 1996; Lopé: 1.7%, Tutin & Fernandez 1992; 1993a). Although observing hunting behavior in unhabituated chimpanzee populations is usually rare, attempts at tool-assisted hunting have been directly observed in Moukalaba (Ebang Ella & Yamagiwa 2014). This suggests that the chimpanzees in Moukalaba may engage in hunting more frequently than those in other sites. Alternatively, it is possible that they may be targeting larger prey species, even if the hunting opportunity is fewer, as Bogert et al. (2008) reported for the chimpanzees at Fongoli, Senegal. In addition, our results show that Moukalaba chimpanzees consumed more vertebrates in the dry season than in the rainy season. Seasonality of hunting may be related to the availability of prey or the lower abundance of fruits. However, our data on chimpanzee vertebrate consumption and information on vertebrate abundance were insufficient for reliable arguments. Our future goal is to assess the ecological and cultural aspects of insectivory and hunting in the chimpanzees' diet in Moukalaba.

To better understand animal (insect and vertebrate) consumption by Moukalaba chimpanzees, we propose to 1) quantify the seasonal availability and accessibility of both the major fruits and the animal prey species, 2) quantify the daily intake of animal by chimpanzees (for example through more intensive fecal sampling and additional observations), and 3) perform nutritional analyses on all dietary items, to investigate the balance between nutritional needs and use of different foods.

Conclusions

Our study shows that chimpanzees in Moukalaba were primarily frugivorous, with similar dietary breadth as those in other rainforest sites. Diet composition was distinct from that recorded at other Central African sites in terms of animal consumption: fewer insects and more vertebrates were consumed. *Ficus* fruit was a major food that supported chimpanzees in Moukalaba throughout the year. In Moukalaba, chimpanzees flexibly adopted a relatively opportunistic feeding strategy switching their diet to temporally abundant fruit species and a more diverse fruit intake, supplemented by other food types, during periods of overall fruit scarcity.

Determining the distribution and abundance of all food resources remain essential next steps to investigate the foraging tactics of the Moukalaba chimpanzees. Future research will

focus on determining seasonal resource availability and evaluating whether fruit availability directly affects the rate and quantity of animals in the chimpanzee diet in Moukalaba or vice versa. In addition, a study of the nutritional quality of preferred food items is essential to investigate why the Moukalaba chimpanzee selects or concentrates on dietary items in the face of diverse resources.

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