Diet of Grauer's Gorillas (*Gorilla beringei graueri*) in a Low-Elevation Forest

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Keywords

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Abstract

Although the vast majority of critically endangered Grauer's gorillas (*Gorilla beringei graueri*) inhabit low-elevation rain forests, current insights into this ape's life history and ecology stem predominantly from 2 small populations ranging in highland habitats. Here, we provide an initial and non-exhaustive overview of food items of Grauer's gorillas in the Nkuba Conservation Area (NCA), a lower-elevation (500–1,500 m) forest located between Kahuzi-Biega National Park and Maiko National Park in the Democratic Republic of the Congo. Community-based conservation efforts at the NCA aim to protect a population of unhabituated Grauer's gorillas, which we have studied since 2014. Between 2014 and 2020, we simultaneously tracked 1–3 gorilla groups and recorded a total of 10,514 feeding signs on at least 100 plant species, ants, termites, and fungi. Vegetative plant parts (plant stems, leaves, pith, bark, and roots), especially of Marantaceae and Fabaceae, made up close to 90% of recorded feeding signs, with fruit accounting for most of the remain-

der and a small (<1%) number of feeding signs on invertebrates and fungi. We found that the most frequently recorded food items were consumed year-round, though fruit intake seems to peak in the September–December wet season, possibly reflecting patterns in fruit phenology. The diet of Grauer's gorillas in the NCA differed from that of Grauer's gorillas in highland habitat and instead showed similarities with Grauer's gorillas at the lowland forest of Itebero and with western lowland gorillas (*G. gorilla*), which live under ecologically comparable conditions.

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Introduction

We know little of the life history and ecology of Grauer's gorilla (*Gorilla beringei graueri*; hereafter GG), a critically endangered ape subspecies found only in the eastern Democratic Republic of the Congo (DRC) [Plumptre, 2016]. Field research across the geographic range of this great ape has been limited by security issues and logistical challenges. Most ecological research on GG is restricted to small populations found at relatively high elevations (> 2,000 m), one in Kahuzi-Biega National Park (KBNP)

[Yamagiwa et al., 2012] and another on Mt. Tshiaberimu [Kyungu Kasolene and Sikubwabo, 2020]. The montane habitats at these latter 2 locations are unrepresentative of the lowland evergreen tropical rain forests that make up the majority of the GG geographic range. The only notable studies at lower (approx. 500–1,500 m) elevations are population surveys in and around low-elevation sections of KBNP [Hall et al., 1998], genetic work including samples from low-elevation forests at Walikale and Nkuba [Baas et al., 2018], intermittent research efforts on GG in lowland sections of Itebero [Yamagiwa et al., 1994], and older short-term studies on populations at lowland sections of Nord Kivu province (“Utu”) and highland Itombwe Mountains [Schaller, 1963]. This lack of knowledge on GG living at lower elevations is concerning and indicates an urgent need for effectively planned and science-based conservation actions, as GG that range across lower elevations experience a rapid decrease in habitat availability and population size [Plumptre et al., 2016a, b].

One factor that determines the long-term persistence and abundance of GG populations is food availability, of which the continuous and year-round supply is under threat from anthropogenic pressures such as forest loss and degradation [Haurez et al., 2016]. To understand how human-induced changes in forest ecosystems may affect the food availability for GG, we first need to obtain baseline data on food resources for GG under “pristine” conditions. An overview of the food resources for GG could then be used as a starting point for the development of targets for forest restoration (“replant important great ape food trees” [Strindberg et al., 2018]) or other conservation and management strategies. Similarly, such data could feed into more in-depth research on patterns of food availability, the processes that influence food availability, and the links between food availability and various aspects of gorilla behaviour such as dietary flexibility [Fossey, 1977; Vedder, 1984; Kaleme et al., 1996; Plumptre, 1996; Yamagiwa et al., 1996; Grueter et al., 2013; Akayezu et al., 2019] and ranging patterns [Vedder, 1984; Kaleme et al., 1996; van der Hoek et al., 2021].

In general, although proportional nutrient and energetic intake may be relatively similar across gorilla populations [Rothman et al., 2007; Wright et al., 2015], dietary composition varies substantially across gorilla groups, populations, subspecies, and species [Ganas et al., 2004]. Moreover, gorillas from different localities show varied temporal patterns in food intake related to the phenology and availability of fruit, ants, bamboo, leaves, flowers, seeds, stem, bark, and pith [Watts, 1984; Yamagiwa et al.,

1994; Rogers et al., 2004; Yamagiwa et al., 2005; Etiendem and Tagg, 2013; Wright et al., 2015]. For example, gorilla populations ranging at lower elevations tend to have a relatively high intake of fruit, following high fruit availability in their environments, and fluctuation in fruit availability thus seems to be a particular cause of seasonality in the diets of these lowland gorillas [Yamagiwa et al., 1994; Rogers et al., 2004; Etiendem and Tagg, 2013; Wright et al., 2015].

Among eastern gorillas, we see that mountain gorillas (*G. beringei beringei*; hereafter MG) from montane habitats in the Virungas (approx. 2,500–4,000 m) consume relatively high amounts of fibrous foods, such as terrestrial herbaceous vegetation as well as leaves, pith, and bark of woody species [Watts, 1984; McNeilage, 2001], a diet that reflects relatively low fruit availability at these high elevations [Grueter et al., 2013]. In contrast, MG from lower elevations in Bwindi Impenetrable National Park incorporate much higher percentages of fruit in their diet. Yet, even within this relatively small geographic region, we see substantial differences in the diets of groups ranging in lower (1,450–1,800 m) and higher (2,100–2,500 m) elevations [Ganas et al., 2004] – groups from lower elevations consume more fruit and a larger number of plant species than those ranging at higher elevations, and groups with adjacent or partially overlapping home ranges share < 50% of food items. Similar patterns are seen for GG, where gorillas at lower elevations (Itebero; approx. 600–1,300 m) incorporate relatively more fruit than those ranging at higher elevations in KBNP (approx. 1,800–2,600 m) [Yamagiwa et al., 2005]. Grauer’s gorillas at Itebero have a diet comparable to that of western lowland (*G. gorilla gorilla*; hereafter WG) and Cross River gorillas (*G. gorilla diehli*; hereafter CRG) in terms of composition (at least at plant generic level), high numbers of food items, high levels of frugivory, and strong seasonality in the consumption of fruit resources [Rogers et al., 2004; Etiendem and Tagg, 2013].

Here, we provide a non-exhaustive overview of food items for GG in a lowland rain forest habitat (500–1,000 m a.s.l.) at the Nkuba Conservation Area (NCA). This list is based on feeding signs and does not reflect the quantity of each food item consumed as we did not observe direct feeding behaviour and made no attempts to quantify consumption. Moreover, we note that indirect observation of feeding signs along trails is likely to underestimate food items (e.g., fruit and leaves) and may fail to record the consumption of leaves, bark, and other vegetative parts of certain plant species [Rogers et al., 2004]. Nevertheless, we predicted to find that certain plant spe-

Fig. 1. The southern-central section of the NCA, a forest located between Maiko National Park and Kahuzi-Biega National Park.

cies would stand out as key food resources for GG in lowland habitat due to the particularly high frequency at which they are recorded (similar to Yamagiwa et al. [2005]). Moreover, we expected these key food resources to differ from those food items that constitute the diet of GG that range in highland KBNP [Goodall, 1977; Yamagiwa et al., 2005, 2012] and Mt. Tshiaberimu [Koto-te-Nyiwa et al. 2014; Kambale, 2018], given the notable absence of certain food plants frequently consumed by highland populations such as bamboo. Rather than being dominated by a relatively small number of fibrous plant parts (e.g., terrestrial herbaceous vegetation) like their high elevation counterparts, we predicted that the diet of lowland GG would resemble the diets of GG in lowland sections of Itebero [Yamagiwa et al., 1994] and WG (*G. gorilla*) [Blake et al., 1995; Rogers et al., 2004; Etiendem and Tagg, 2013] in its high fruit intake, diversity of plant species and parts, as well as the composition of consumed plant taxa.

Materials and Methods

Between March 2014 and April 2020, we continuously tracked between 1 and 3 unhabituated GG groups in the southern-central section of the NCA, a forest located between Maiko National Park and Kahuzi-Biega National Park (between 1°31' and 1°10' S and 27°13' and 27°42' E in Walikale District, Nord Kivu, DRC; Fig. 1). The NCA currently covers approximately 1,300 km² of primary

forest with little human disturbance, at an elevation ranging between 500 and 1,000 m a.s.l., and is managed, studied, and protected through a collaboration with the local community and the Dian Fossey Gorilla Fund. Detailed local climatic records do not exist, but estimates extrapolated from regional sources put mean annual temperatures at between 20 and 27 °C and annual precipitation at 2,100–2,500 mm [Karger et al., 2017a, b]. Although precipitation is high throughout the year, there are 2 rainy seasons (March–May and September–December) and 2 dry seasons (January–March and June–August), with average monthly rainfall ranging between 50 and 600 mm.

We started tracking gorillas in March 2014 at a single site (tracking site A) and added tracking at “tracking site B” and “C” in January 2017 and April 2018, respectively. Although we aimed to track a single group of gorillas at each site, we acknowledge that we were unable to confirm that we were always tracking the same group. For that reason, we refer to these gorillas as those belonging to tracking areas, rather than any particular group. Nevertheless, we recognize that there are at least 3 groups included in this study, each with a probable group size of 14–18 individuals (average nest counts).

Every day, tracking teams followed the trail of their assigned gorilla group until they found the most recent nest site. In general, the nest site was reached after mid-day, hours after the gorilla group had left the area, though on occasion nest sites were reached with a few days' delay. Feeding signs found along the trail of the tracked group and associated with gorilla bite marks or footprints were assigned to gorillas. An effort was made to exclude possible chimpanzee signs, which were recorded separately if these crossed gorilla paths. All records were checked, and local names were translated into scientific names by expert botanist and co-author W.D.P.

We were not always able to identify plants with feeding signs at the species level. For that reason, we classified certain records to

Table 1. List of plant and other food items with feeding signs of Grauer's gorilla between 2014 and 2020, with indications of plant parts consumed

Rank	Food item	Family	Count (%)	Percent of days	Bark	Root	Leaves	Pith	Stem	Fruit
1	<i>Pycnanthus angolensis</i> (Welw.) Warb. ¹	Myristicaceae	5,521 (9.7)	75	10		1,199	3	16	
2	Marantaceae sp.	Marantaceae	5,212 (9.1)	33						x
3	Palisota sp.	Commelinaceae	4,873 (8.5)	36					x	
4	<i>Megaphrynium macrostachyum</i> (Benth.) Milne-Redh. ¹	Marantaceae	3,522 (6.2)	48			280	39	879	
5	<i>Aframomum</i> sp.	Zingiberaceae	3,169 (5.6)	32				x		x
6	<i>Aframomum laurentii</i> (De Wild. & T. Durand) K. Schum. ^{1,2}	Zingiberaceae	2,772 (4.9)	46	2		6	839	52	10
7	<i>Palisota ambigua</i> (P. Beauv.) C.B. Clarke ¹	Commelinaceae	2,231 (3.9)	39			3	4	761	
8	<i>Palisota hirsuta</i> (Thunb.) K. Schum. ¹	Commelinaceae	1,940 (3.4)	36			1	5	707	
9	<i>Cissus dinklagei</i> Gilg & M. Brandt ¹	Vitaceae	1,883 (3.3)	31			3	1		361
10	<i>Uapaca kirkiana</i> var. <i>benguelensis</i> (Müll. Arg.) Meerts	Phyllanthaceae	1,816 (3.2)	34	1	1	5	691	7	13
11	<i>Marantochloa congensis</i> (K. Schum.) J. Léonard & Mullend.	Marantaceae	1,622 (2.8)	21			10	38	327	
12	<i>Musanga cecropioides</i> R. Br. ¹	Urticaceae	1,618 (2.8)	37	12		382	4	9	1
13	<i>Uapaca</i> sp.	Phyllanthaceae	1,470 (2.6)	23	x			x	x	x
14	<i>Marantochloa</i> sp.	Marantaceae	1,407 (2.5)	21					x	
15	<i>Drypetes dinklagei</i> (Pax) Hutch.	Euphorbiaceae	1,323 (2.3)	17	3		326	1	3	2
16	<i>Ataenidia conferta</i> (Benth.) Milne-Redh. ¹	Marantaceae	1,196 (2.1)	20			52	16	219	7
17	<i>Marantochloa leucantha</i> (K. Schum.) Milne-Redh. ¹	Marantaceae	1,034 (1.8)	25			35	26	322	
18	<i>Manniophyton fulvum</i> Müll. Arg.	Euphorbiaceae	976 (1.7)	25	x	1		249	4	1
19	<i>Raphia farinifera</i> (Gaertn.) Hyl.	Arecaceae	931 (1.6)	23	1	2		6	154	4
20	<i>Entada mannii</i> (Oliv.) Tisser.	Fabaceae	810 (1.4)	15				x	x	x
21	<i>Sarcophrynium brachystachyum</i> (Benth.) K. Schum.	Marantaceae	753 (1.3)	15			44	55	114	
22	<i>Eremospatha haullevilleana</i> De Wild. ¹	Arecaceae	699 (1.2)	18		x	6	47	195	2
23	<i>Ficus sur</i> Forssk. ¹	Moraceae	541 (0.9)	11	4	1	77	2	16	12
24	<i>Milicia excelsa</i> (Welw.) C. C. Berg	Moraceae	532 (0.9)	15	104		26	x	17	2
25	<i>Celtis briei</i> De Wild. ¹	Ulmaceae	497 (0.9)	10			115	1	4	2
26	<i>Treculia africana</i> Decne. ¹	Moraceae	487 (0.9)	13	1		29	2	1	88
27	<i>Landolphia buehneri</i> (Hallier f.) Stapf	Apocynaceae	454 (0.8)	8	1		2			56
28	<i>Anonidium mannii</i> (Oliv.) Engl. & Diels ¹	Annonaceae	440 (0.8)	9			1			86
29	<i>Garcinia volkensii</i> Engl.	Clusiaceae	427 (0.7)	7	1		82	x		4
30	<i>Chrysophyllum lacourtianum</i> De Wild. ¹	Sapotaceae	418 (0.7)	6						8
31	<i>Alchornea floribunda</i> Müll. Arg. ¹	Euphorbiaceae	380 (0.7)	8	3			124		2
32	<i>Ficus</i> sp.	Moraceae	347 (0.6)	7	x	1	16			x
33	Unidentified ant sp.		334 (0.6)	9						
34	<i>Aframomum angustifolium</i> (Sonn.) K. Schum. ^{1,2}	Zingiberaceae	272 (0.5)	5				34	9	
35	<i>Uapaca guineensis</i> Müll. Arg. ¹	Phyllanthaceae	254 (0.4)	5				54		
36	<i>Megaphrynium</i> sp.	Marantaceae	209 (0.4)	4						
37	<i>Landolphia</i> sp.	Apocynaceae	196 (0.3)	4	x		x	x		x
38	<i>Cynometra alexandri</i> C.H. Wright	Fabaceae	179 (0.3)	5	56		4		3	2
39	<i>Grewia mildbraedii</i> Burret ¹	Malvaceae	178 (0.3)	4		1	6		2	23
40	<i>Gilbertiodendron dewevrei</i> (De Wild.) J. Léonard ¹	Fabaceae	175 (0.3)	4			x	2	1	12
41	<i>Sarcophrynium</i> sp.	Marantaceae	175 (0.3)	4	x					
42	<i>Myrianthus arboreus</i> P. Beauv. ^{1,2}	Urticaceae	174 (0.3)	5	1		3		2	81
43	<i>Pseuderanthemum ludovicianum</i> (Büttner) Lindau ¹	Acanthaceae	168 (0.3)	2			x	x		
44	<i>Saba comorensis</i> (Bojer ex A. DC.) Pichon	Apocynaceae	160 (0.3)	4						78
45	<i>Julbernardia</i> sp.	Fabaceae	150 (0.3)	3	1		1			14
46	<i>Dialium corbisieri</i> Staner	Fabaceae	145 (0.3)	4	5		9			50
47	<i>Ptisana fraxinea</i> (Sm.) Murdock ^{1,2}	Marattiaceae	143 (0.3)	4			6	x	8	
48	<i>Rhaphidophora africana</i> N.E. Br. ¹	Araceae	139 (0.2)	3			21		x	
49	<i>Landolphia mannii</i> R. A. Dyer	Apocynaceae	137 (0.2)	4			3			63
50	<i>Mitragyna stipulosa</i> (DC.) Kuntze	Rubiaceae	137 (0.2)	4	6	24	4		1	4
51	<i>Myrianthus</i> sp.	Urticaceae	132 (0.2)	4						x
52	<i>Salacia erecta</i> (G. Don) Walp. ²	Celastraceae	117 (0.2)	3	1		23	2	2	
53	<i>Marantochloa monophylla</i> (K. Schum.) D'Orey ¹	Marantaceae	110 (0.2)	3			4		20	
54	<i>Klainedoxa gabonensis</i> Pierre ¹	Irvingiaceae	109 (0.2)	<1		x	1			2
55	<i>Cynometra</i> sp.	Fabaceae	105 (0.2)	2	x					x
56	<i>Cynometra hankei</i> Harms	Fabaceae	103 (0.2)	3	24		9		1	2
57	<i>Costus lucanusianus</i> J. Braun & K. Schum.	Zingiberaceae	99 (0.2)	3	1			3	17	
58	Passifloraceae sp.	Passifloraceae	97 (0.2)	1						
59	<i>Urera hypselodendron</i> (Hochst. ex A. Rich.) Wedd. ^{1,2,3,4}	Urticaceae	96 (0.2)	3	6	1	5	10		
60	<i>Raphia</i> sp.	Arecaceae	91 (0.2)	2		x				

Table 1 (continued)

Rank	Food item	Family	Count (%)	Percent of days	Bark	Root	Leaves	Pith	Stem	Fruit
61	<i>Landolphia owariensis</i> P. Beauv. ^{1,2}	Apocynaceae	89 (0.2)	2						31
62	<i>Mitragyna</i> sp.	Rubiaceae	82 (0.1)	2		x				
63	Unidentified plant sp.		78 (0.1)	2	7		35	5	7	17
64	Unidentified liana sp.		78 (0.1)	2			2		1	
65	<i>Manniophyton</i> sp.	Euphorbiaceae	73 (0.1)	2	x			x		
66	<i>Mammea africana</i> Sabine	Clusiaceae	64 (0.1)	1			1			11
67	<i>Garcinia punctata</i> Oliv. ¹	Clusiaceae	61 (0.1)	1						
68	<i>Begonia ampla</i> Hook. f.	Begoniaceae	59 (0.1)	2			14		1	1
69	<i>Amorphophallus abyssinicus</i> (A. Rich.) N.E. Br.	Araceae	56 (0.1)	2				2	28	
70	<i>Scaphopetalum thonneri</i> De Wild. & T. Durand	Malvaceae	52 (0.1)	2			4			x
71	<i>Dorstenia kameruniana</i> Engl.	Moraceae	48 (0.1)	1	x		9		1	
72	<i>Albizia gummifera</i> (J.F. Gmel.) C.A. Sm.	Fabaceae	41 (0.1)	1	2		2			
73	<i>Treculia</i> sp.	Moraceae	41 (0.1)	1			x			
74	<i>Brazzeia longipedicellata</i> Verdc.	Lecythidaceae	37 (0.1)	1				x		28
75	<i>Urera</i> sp.	Urticaceae	35 (0.1)	1	x					
76	<i>Nauclea vanderghuchtii</i> (De Wild.) E.M.A. Petit	Rubiaceae	32 (0.1)	1		x				13
77	<i>Sclerosperma mannii</i> H. Wendl.	Arecaceae	32 (0.1)	1					8	
78	<i>Ekebergia benguelensis</i> Welw. ex C.DC.	Meliaceae	31 (0.1)	1						x
79	<i>Pycnanthus</i> sp.	Myristicaceae	30 (0.1)	1			x	x		
80	<i>Neoboutonia macrocalyx</i> Pax ³	Euphorbiaceae	29 (0.1)	1	1	1				
81	<i>Pseudospondias microcarpa</i> (A. Rich.) Engl.	Anacardiaceae	27 (<0.1)	1			x	x		x
82	<i>Macaranga monandra</i> Müll. Arg.	Euphorbiaceae	24 (<0.1)	1		x	1			
83	<i>Milicia</i> sp.	Moraceae	18 (<0.1)	1						
84	<i>Ficus asperifolia</i> Miq.	Moraceae	18 (<0.1)	<1	1		3		1	
85	<i>Canarium schweinfurthii</i> Engl. ¹	Burseraceae	16 (<0.1)	1	1		1			1
86	<i>Staudtia kamerunensis</i> Warb.	Myristicaceae	14 (<0.1)	<1			1			
87	<i>Polypodiopsida</i> sp.		14 (<0.1)	<1			x			
88	<i>Thaumatococcus daniellii</i> (Benn.) Benth. ¹	Marantaceae	12 (<0.1)	<1						
89	<i>Trachypyrnum braunianum</i> (K. Schum.) Baker	Marantaceae	12 (<0.1)	<1						
90	<i>Garcinia smeathmanii</i> (Planch. & Triana) Oliv.	Clusiaceae	10 (<0.1)	<1						
91	Unknown termite		10 (<0.1)	<1						
92	<i>Calamus deerratus</i> G. Mann & H. Wendl. ¹	Arecaceae	9 (<0.1)	<1					3	
93	<i>Gambeya gabonensis</i>	Sapotaceae	9 (<0.1)	<1						
94	<i>Greenwayodendron suaveolens</i> (Engl. & Diels) Verdc.	Annonaceae	9 (<0.1)	<1						
95	<i>Paropsia brazzeana</i> Baill.	Passifloraceae	9 (<0.1)	<1						x
96	<i>Tacazzea</i> sp.	Apocynaceae	9 (<0.1)	<1			x			
97	<i>Acacia montigena</i> Brenan	Fabaceae	8 (<0.1)	<1	x		1	1		
98	<i>Musa</i> sp.	Musaceae	8 (<0.1)	<1						
99	<i>Vernonia conferta</i> Benth.	Asteraceae	7 (<0.1)	<1			x			
100	<i>Myrianthus holstii</i> Engl. ²	Urticaceae	6 (<0.1)	<1	x		1			2
101	<i>Julbernardia seretii</i> (De Wild.) Troupin	Fabaceae	6 (<0.1)	<1						
102	Unidentified insect		6 (<0.1)	<1						
103	<i>Elaeis guineensis</i> Jacq. ¹	Arecaceae	5 (<0.1)	<1					1	
104	<i>Dacryodes edulis</i> (G.Don) H.J.Lam ¹	Burseraceae	5 (<0.1)	<1						x
105	<i>Marantochloa purpurea</i> (Ridl.) Milne-Redh.	Marantaceae	4 (<0.1)	<1						
106	<i>Haumania liebrechtsiana</i> (De Wild. & T.Durand) J.Leonard ¹	Marantaceae	3 (<0.1)	<1					2	
107	<i>Autranella congolensis</i> (De Wild.) A.Chev.	Sapotaceae	3 (<0.1)	<1			x			1
108	<i>Aracea</i> sp.	Araceae	3 (<0.1)	<1						
109	<i>Costus</i> sp.	Zingiberaceae	3 (<0.1)	<1					x	
110	<i>Entandrophragma excelsum</i> (Dawe & Sprague) Sprague	Meliaceae	3 (<0.1)	<1						
111	<i>Garcinia</i> sp.	Clusiaceae	3 (<0.1)	<1						
112	<i>Palisota schweinfurthii</i> C.B. Clarke ¹	Commelinaceae	3 (<0.1)	<1						
113	<i>Sarcophrynium prionogonium</i> (K.Schum.)	Marantaceae	3 (<0.1)	<1						
114	<i>Symphonia globulifera</i> L.f. ¹	Clusiaceae	3 (<0.1)	<1						
115	<i>Alstonia boonei</i> De Wild.	Apocynaceae	2 (<0.1)	<1						
116	<i>Antiaris toxicaria</i> Lesch. ¹	Moraceae	2 (<0.1)	<1						
117	<i>Rauvolfia mannii</i> Stapf.	Apocynaceae	2 (<0.1)	<1						
118	<i>Rourea solanderi</i> Baker	Conneraceae	2 (<0.1)	<1	x			x		
119	<i>Zanthoxylum gillettii</i> (De Wild.) P.G.Waterman	Rutaceae	2 (<0.1)	<1						
120	<i>Begonia meyeri-johannis</i> Engl. ^{2, 3, 4}	Begoniaceae	1 (<0.1)	<1						
121	<i>Costus phyllocephalus</i> K. Schum.	Zingiberaceae	1 (<0.1)	<1						

Table 1 (continued)

Rank	Food item	Family	Count (%)	Percent of days	Bark	Root	Leaves	Pith	Stem	Fruit
122	<i>Funtumia elastica</i> (Preuss) Stapf	Apocynaceae	1 (<0.1)	<1				x		
123	<i>Harungana madagascariensis</i> Lam. ex Poir.	Hypericaceae	1 (<0.1)	<1						
124	<i>Ipomoea batatas</i> (L.) Lam.	Convolvulaceae	1 (<0.1)	<1						
125	<i>Jaundea</i> sp.	Conneraceae	1 (<0.1)	<1				x		
126	<i>Myrianthus preussii</i> Engl.	Urticaceae	1 (<0.1)	<1						
127	<i>Penianthus longifolius</i> Miers	Menispermaceae	1 (<0.1)	<1						
128	<i>Rourea thomsonii</i> (Baker) Jongkind	Connaceae	1 (<0.1)	<1						
129	<i>Strychnos usambarensis</i> Gilg	Loganiaceae	1 (<0.1)	<1			x			
130	<i>Tessmannia anomala</i> (Micheli) Harms var. <i>anomala</i>	Fabaceae	1 (<0.1)	<1						x
131	<i>Tetrapleura tetraptera</i> (Schumach. & Thonn.) Taub.	Fabaceae	1 (<0.1)	<1						
132	<i>Trachypphrynium liebrechtsianum</i> (De Wild. & T. Durand) J. Léonard	Marantaceae	1 (<0.1)	<1						
133	Unidentified fungi sp.		1 (<0.1)	<1						

Species are ranked by the count of feeding signs (and % over all items), and percent of days refers to the percentage of all tracking days across 3 tracking areas at which a food item was recorded at least once. Counts of plant parts represent the sum of records between January 2019 and April 2020, and plant parts not recorded over those months, but recorded at least once between 2014 and 2018, are indicated by an “x”. Note that counts of plant parts do not necessarily sum up to the total counts, as not all records of feeding signs included a description of parts. Plant species in bold are also found on the list of food items for Grauer’s gorillas in lowland forests of Itebero¹ or highland Kahuzi-Biega National Park² or Mt. Tshiaberimu^{3,4}. ¹ Yamagiwa et al., 1994. ² Yamagiwa et al., 2005. ³ Koto-te-Nyiwa et al., 2014. ⁴ Kambale, 2018.

genus or higher-level groups of plant species and retained a vast number of common species names that require further clarification via additional studies. Similarly, the identification of plant parts (bark, roots, leaves, pith, stem, flowers, and fruits) was not an initial objective of this study but was gradually included in field protocols and became a standard procedure by January 2019. As such, we were unable to quantify the consumption of plant parts between 2014 and 2018 and restrict analyses of plant parts to data collected from January 2019 to April 2020. Finally, we note that we also made an effort to record feeding signs on fungi and invertebrates. For the latter, we considered ant or termite tracks with clear digging signs as tentative evidence of consumption by gorillas.

We first summarized the total number of feeding records per food item (plant species, higher-level plant taxa, fungi, or invertebrates) over the study period. We then estimated which food items were recorded most often (percentage of feeding signs) and which percentage of tracking days a given food item was recorded at least once. For the latter, we considered fibrous items that occur on > 1% and fruit that occur on > 5% of daily trails as potential key food resources [Doran et al., 2002; Ganas et al., 2004; Yamagiwa et al., 2005]. We state this with caution, as we acknowledge that our field efforts did not allow us to determine relative importance concerning volume of intake or nutrient composition, data for which additional faecal analyses will be required. Moreover, our data on plant parts cover one single year of study, and we were unable to detect consumption of certain parts, for example when the consumption took place up in the trees and there were no clear leftovers on or along gorilla tracks.

Next, we reported whether feeding signs on different plant parts varied across months. For this, we summarized monthly counts of feeding signs and corrected them for variation in overall sampling effort (i.e., tracking days) per month. We divided the number of feeding signs for a particular plant part in a given month by the total number of tracking days that month, and then expressed that number as a percentage of the sum of items consumed

per month. We note that seeds were included as fruit in this study. We also looked in more detail at seasonal patterns in fruit consumption, for which we listed the 20 most frequently recorded fruits in this study and calculated the relative percentage of fruit consumption per month. For the latter, we divided the total number of feeding records on a fruit per month by the number of gorilla tracking days for that month and subsequently expressed that number as a percentage of all fruits consumed over the period January 2019 to April 2020.

We acknowledge that taxonomic issues may influence the list of food plants as well as comparisons with other literature. We aimed to resolve this issue by adopting one single taxonomy for plant families (APG III [Angiosperm Phylogeny Group, 2009]), by basing all species names on the African Plant Database (version 3.4.0 [African Plant Database, 2020]), and by making an effort to search comparative literature on gorilla diets for both currently accepted names and current or historic synonyms.

Results

We recorded 57,059 feeding signs on plants, ants, termites, and fungi (Table 1). In total, we recorded at least 238 different food items and identified 100 food plant species to their scientific species name. These are minimum numbers of food items, as we were unable to identify approximately 34% of food items to species-level – though approximately 97% of items were identified to genus level. Items not identified to their scientific species name were instead classified at higher-level (genus or family) groups of plants (28 such groups, Table 1), recorded by their common name only (62 items;

Table 2. Overview of seasonality among recorded feeding signs on different plant parts by Grauer's gorillas in the Nkuba Conservation Area between January 2019 and April 2020

Plant part	Dry season		Wet season			Dry season			Wet season			
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Fruit	8.4	6.8	5.0	3.7	5.2	3.0	6.2	13.9	21.2	29.6	18.9	20.1
Bark	2.5	3.0	1.9	1.8	3.7	2.1	5.3	3.0	2.9	2.5	0.7	1.5
Leaf	33.3	36.9	35.0	26.4	20.6	30.1	26.2	26.0	20.5	20.0	17.8	22.4
Pith	20.6	20.4	21.3	27.0	27.7	21.7	20.0	23.9	18.5	15.0	20.2	20.8
Root	0.2	0.1	0.2	0.4	0.2	0.5	0.7	0.4	0.4	0.7	0.1	0.0
Stem	35.0	32.9	36.6	40.7	42.7	42.6	41.6	32.9	36.5	32.2	42.4	35.2

The monthly numbers are relative percentages of feeding signs per month, calculated in 2 steps: (1) total number of records per plant part per month/number of gorilla tracking days for that month; (2) express the number calculated under 1 as a percentage of all feeding signs on plants for that month. Numbers shaded grey are the highest monthly percentages for a given plant part.

online suppl. Table S1; for all online suppl. material, see www.karger.com/doi/10.1159/000515377, or classified as “unidentified plant,” “unidentified liana,” “termite,” “black ant,” “fungi,” or “other insect” (Table 1; the latter 4 categories together making up < 1% of feeding signs). Identified food plants belonged to at least 38 families, of which Marantaceae was the most represented (at least 12 species), followed by Fabaceae (10 species).

We were unable to quantify the volume or mass of intake of different food items but calculated that only 22 of the plant food items identified to scientific names made up > 1% of recorded feeding signs, with *Pycnanthus angolensis* (Welw.) Warb., *Megaphrynium macrostachyum* (Benth.) Milne-Redh., *Aframomum laurentii* (De Wild. & T. Durand) K. Schum., *Palisota ambigua* (P. Beauv.) C.B. Clarke, *Palisota hirsuta* (Thunb.) K. Schum., *Cissus dinklagei* Gilg & M. Brandt, and *Uapaca kirkiana* var. *benguelensis* (Müll. Arg.) Meerts all counting for > 3% of feeding signs. These items together totaled approximately 82% of all recorded food items and all other items were recorded only in small numbers. It is not clear how many species are among these 22 plant food items as records identified at higher levels (e.g., Marantaceae sp. and *Palisota* sp.) could refer to one or multiple species and could include plants that were also recognized at the species level. For example, it is not known whether *Palisota* sp. refers to *P. ambigua*, *P. hirsuta*, both these species, or additional *Palisota* species. Finally, we mention that 81 food items were found on at least 1% (fibrous items or other non-fruit resources) or 5% (fruit) of daily paths and may thus tentatively be considered key foods in the diet

of GG (Table 1). Ranking these food items, we find the same food items mentioned above while we note that *Musanga cecropioides* R. Br., *Marantochloa leucantha* (K. Schum.) Milne-Redh., and *Manniophyton fulvum* Müll. Arg. were also found on a high percentage (> 25%) of trails.

We recorded 10,514 plant parts between January 2019 and April 2020. We found plant stems (3,942 records, 37.5% of plant parts), leaves (2,906, 27.6%), and pith (2,268, 21.6%) to be the most frequently recorded plant parts but also note the inclusion of bark (261, 2.5%), roots (33, 0.3%) and fruit of at least 46 plant species (1,103, 10.5%; Table 1). We did not record feeding signs on flowers, though this could be an issue of identification or detection of feeding signs, given the prevalence of flowers in the diet of most other gorillas [e.g., Rogers et al., 2004]. Often, we recorded signs of feeding on different parts of the same plant species. For example, for the frequently consumed *Pycnanthus angolensis*, we recorded feeding signs on bark, leaves, pith, and stems (Table 1).

The various plant parts were all consumed year-round, though with seasonal and monthly fluctuations in relative rates (Table 2). For example, the relative consumption of fruit seemed to peak during the long wet season from September to December, in particular in October (Table 3). These patterns are especially noticeable for frequently consumed species such as *Cissus discolor* and *Annonidium mannii* (Oliv.) Engl. & Diels. A few species, such as *Uapaca kirkiana* var. *benguelensis*, show exceptions to the general pattern with peaks in consumption during one of the dry seasons.

Table 3. Seasonality in records of fruit consumption by Grauer's gorillas in the Nkuba Conservation Area between January 2019 and April 2020

Species	Dry season		Wet season			Dry season			Wet season				Total
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Total, n (%)	51 (4.6)	94 (8.6)	78 (7.1)	51 (4.6)	27 (2.5)	19 (1.7)	54 (4.9)	112 (10.2)	102 (9.3)	238 (21.7)	195 (17.7)	78 (7.1)	1,099
Relative total ¹ , %	4.7	4.2	3.6	3.0	3.0	2.1	4.9	11.0	10.0	23.3	18.4	11.9	
<i>Cissus dinklagei</i>	6	14	15	1	3	5	19	52	53	64	102	28	362
<i>Treculia africana</i>	9	14	4	2	4	6	6	11	4	12	7	8	87
<i>Annonidium mannii</i>	2	2	5				2	2	9	54	10		86
<i>Myrianthus arboreus</i>	6	17	5		4	4	8	10	3	11	6	5	79
<i>Saba comorensis</i>	2	2		1			1	19	8	18	16	11	78
<i>Landolphia manii</i>	2	3	12			1	2	8	7	8	13	7	63
<i>Landolphia buchananii</i>	6	10	2					3	5	11	14	5	56
<i>Dialium corbisieri</i>	1	1	13	13	15		1			1	4	1	50
<i>Landolphia oweriensis</i>							1	1	5	10	12	2	31
<i>Brazzeia longipedicellata</i>									1	27			28
<i>Grewia mildbraedii</i>	4	11	3				2		2			1	23
Unidentified plant species			4	4			4	4	1				17
<i>Julbernardia</i> sp.	1			13									14
<i>Nauclea vanderghuchtii</i>									2	5	3	3	13
<i>Ficus sur</i>		1	4	4		1	1				1		12
<i>Gilbertiodendron deiveirei</i>	1	5	4	2									12
<i>Uapaca kirkiana</i> var. <i>benguelensis</i>	7	4					1						12
<i>Mammea africana</i>		1	1	1					2	6			11
<i>Aframomum laurentii</i>		2	1	2				1		1	1	2	10
<i>Chrysophyllum lacourianum</i>				4			1	1		2			8

Shown are the number of feeding signs on the 20 most frequently recorded fruits out of a total of approximately 43 fruits recorded in this study. ¹ The percentage of fruits consumed in each month after correcting for the number of days that gorillas were tracked per month, calculated in 2 steps: (1) total number of feeding records on fruits per month/number of gorilla tracking days for that month; (2) express the number calculated under 1 as a percentage of all fruits consumed over the time period from January 2019 to April 2020.

Discussion/Conclusion

We estimate that GG ranging at lower elevation forests feed on a large variety of plant species and parts, as well as the occasional invertebrate or fungi. Gorillas in the NCA feed on both vegetative plant parts and fruits year-round. There seems to be seasonal fluctuation in the relative consumption of plant parts, notably with increased fruit consumption during the wet season from September to December. This diet differs substantially in diversity and plant species composition from that of GG in highland and montane habitats and instead shows similarities with the diet of GG in the lower-elevation forests of Itebero [Yamagiwa et al., 1994] and that of WG, which live in lowland forests that are largely similar in structure, diversity, composition, and climatic conditions to the forests of the NCA (see e.g., Goldsmith [2003] for a synthesis of aspects of WG ecology).

At least 38 plant species in the diet of GG at Nkuba are also found in the diet of GG at the lowland forests of Itebero (Table 1). Species such as *Aframomum laurentii*, *Megaphrynium macrostachyum*, and especially *Pycnanthus angolensis*, were found to be frequently consumed at both study locations. Moreover, the overall diversity (238 food items of at least 100 plant species and an undefined number of insects and fungi) and the number of fruit spe-

cies (43) recorded as food items in this study are in line with findings at Itebero (194 foods, at least 121 food plant species, 48 fruits [Yamagiwa et al., 1994]) – we refrain from further comparisons of the diet of GG at Utu [Schaller, 1963] as data for these GG are not exhaustive (only 20 food items recorded). In contrast, only 3 of the food plants listed in this study, *Urera hypselodendron* (Hochst. ex A. Rich.) Wedd., *Neoboutonia macrocalyx* Pax., and *Begonia meyeri-johannis* Engl. were also recorded as gorilla food plants at Mt. Tshiaberimu, and 9 food plants are also consumed by GG in highland KBNP [Yamagiwa et al., 2005; Koto-te-Nyiwa et al., 2014; Kambale, 2018]. Of these latter 9 species, only *Aframomum laurentii*, *Urera hypselodendron*, and *Myrianthus holstii* Engl. were considered important food plants for GG in KBNP, ranking in the top 3 of monthly food items at least once [Yamagiwa et al., 2005] – no quantitative data on relative food intake exist for Mt. Tshiaberimu. We note that we also recorded *Taccazea* sp., though it is unclear whether this refers to *Taccazea apiculata* Oliv., an important food plant in KBNP. Finally, we point out that the plant genera recorded in this study also differed substantially from those listed for the diet of GG at higher elevations, with none of the 20 most frequently recorded plant genera in our study (online suppl. Table S2) also listed for Mt. Tshiaberimu and only *Ficus* represented among the top

20 most consumed plant genera at KBNP. This near-complete lack of overlap in food items in the diets of GG at lower and higher elevations confirms the large variability of the diet of GG, and is a reflection of the high turnover in vegetation characteristics and ecological conditions across the vast gradient of elevations that this gorilla ranges.

In contrast, we found that at least 15 out of the 20 most frequently recorded food plant genera for GG in the NCA were also recognized as important food plant genera for WG and CRG (online suppl. Table S2). The only genera that were among the top 20 in our study but not listed by the consulted literature on WG were *Ataenidia*, *Entada*, *Manniophyton*, *Sarcophrynium*, and *Eremospatha*, which together accounted for about 8.5% of recorded food signs. This pattern even extends to individual plant species. For example, frequently recorded species in this study such as *Pycnanthus angolensis*, *Megaphrynium macrostachyum*, *Palisota hirsuta*, *Musanga cecropioides*, and *Marantochloa leucantha* (K. Schum.) Milne-Redh. are also found to be important food plants for CRG in Cameroon [Etien-dem and Tagg, 2013].

Without quantitative data on consumption, it is impossible to determine how the relative intake of different food items and plant parts differs from the intake estimated for other gorilla populations. Nevertheless, we may draw a few tentative hypotheses that require confirmation in follow-up studies. One, GG inhabiting forests of low to moderate elevations (500–1,500 m; this study and Yamagiwa et al. [1994]) likely show seasonal patterns in fruit consumption; with peaks during the September–December rainy season. *Cissus dinklagei* seems to be at least one fruit species with clear seasonal consumption patterns in the NCA (Table 3). Data for other fruit species were too scarce in this study to draw further conclusions. For example, we infrequently recorded *Gilbertiodendron dewevrei* (De Wild.) J. Léonard and *Klainedoxa gabonensis* Pierre and did not record *Dalium pachyphyllum* Harms, all fruits which were common in faecal samples at Itebero [Yamagiwa et al., 1994]. As we stated previously, the reason for the low number of recorded feeding signs on these food items is likely to stem from methodological biases, which is especially clear if we realize that fruits such as *Dalium corbisieri*, *Ficus sur* Forssk., *Chrysophyllum lacourtianum* De Wild., *Canarium schweinfurthii* Engl., and *Uapaca guineensis* Müll. Arg are all predominantly consumed high up in the trees [Yamagiwa et al., 1994]. These biases also extend to certain fibrous food parts, such as leaves and bark of *Landolphia owariensis* P. Beauv., *Urera hypselodendron* (Hochst. ex A. Rich.)

Wedd., *Celtis briei* De Wild., and *Myrianthus arboreus* P. Beauv. which are predominantly eaten arboreally.

A brief comparison between the relative percentage of feeding signs and the percentage of days at which we recorded a given food item (Table 1) does not convey that any food items are recorded in large frequencies over only few days of the year, which would hint at seasonal patterns of consumption. These data are also not accurate enough, given methodological biases explained in previous paragraphs, to determine whether any food items are only consumed in periods of low fruit availability (fall-back foods; as are found for WG [Rogers et al., 2004] and CRG [Etien-dem and Tagg, 2013] living at comparable elevations). Instead, we may draw a second tentative hypothesis that fibrous foods from plant families such as Marantaceae and Zingiberaceae are important staple foods that are consumed year-round, though they may become relatively more important in months when fruit intake is particularly low (approx. from February to June [Yamagiwa et al., 1994; Rogers et al., 2004; Yamagiwa and Basabose, 2006]). Yet, though we did not find evidence for this, we cannot rule out the possibility that certain non-fruit resources are consumed as seasonal foods, given that both GG in highland KBNP (e.g., bamboo [Yamagiwa and Basabose, 2006]) and WG (e.g., leaves, flowers, and seeds [Rogers et al., 2004]) include seasonal non-fruit resources in their diet.

Similar to our data on plant food items, we do not have quantitative data on non-plant foods such as fungi and invertebrates. For the latter in particular, we note that we might have failed to adequately detect insect consumption by GG as we summarized feeding signs along tracks of unhabituated gorillas. Whereas foraging on plants and fruits often leaves signs that may be detected hours or even days later, signs of invertebrate consumption may be less obvious and easily erased by rain or other factors. Although we found relatively few feeding signs on ants, termites, and other invertebrate species, these food items are found in up to 38% of faecal samples of GG at Itebero [Yamagiwa et al., 1991, 1994], and we can thus not rule out the importance of invertebrates for GG in the NCA.

Data on consumed food items reflect the ecological conditions of the habitat in which gorillas range. For example, we found a high number of feeding signs on leaves of *Pycnanthus angolensis*, which at Itebero was related to gorilla ranging in primary and ancient secondary forests [Yamagiwa et al., 1994]. Similarly, of the fruits consumed by GG at Itebero, some grow predominantly in primary or ancient secondary forest (e.g., *Anonidium mannii* [Oliv.] Engl. & Diels), others in secondary forests (*Mu-*

sanga cecropioides) or across forest types (*Cissus dinklagei*). The presence of all these species in the diet of GG in the NCA, as well as that of several species associated with swamps (e.g., *Raphia farinifera* [Gaertn.] Hyl. [Blake et al., 1995]) and monodominant forests (e.g., *Gilbertiodendron* sp. [Rogers et al., 2004]), thus reflects that GG in the NCA range across a diversity of forest and vegetation types. Future studies will be needed to associate these vegetation types to food availability, and subsequently to foraging and related behaviours (e.g., ranging patterns [van der Hoek et al., 2021]).

This list of food items is a key first step in understanding the ecology of this highly threatened ape and its requirements for long-term persistence. Yet, the methodological limitations of our indirect observations of feeding signs are well known. For example, trail data are likely to substantially underestimate the diversity of leaves of trees and lianas consumed arboreally [Rogers et al., 2004]. As direct observations of foraging behaviour will not be possible in the short term, the next steps for studies of GG at Nkuba will need to focus on analyses of faecal matter to provide quantitative data that allow for more advanced ecological questions. Analyses of faecal samples are well known to complement indirect observations of feeding signs of gorilla and are often conducted in parallel [Yamagiwa et al., 2005; Entiendem and Tagg, 2013], with microscopic examination of faeces providing relatively more adequate detection of fruits and arboreally obtained food items. We may also look at more novel genetic approaches to faecal analyses, such as DNA metabarcoding, which has been proven to be effective in providing fully comprehensive estimations of the diets of primates from faeces alone [Bradley et al., 2007; Quéméré et al., 2013; Srivathsan et al., 2016].

Although our study is preliminary, we propose that these baseline data provide additional evidence to the hypothesis that GG, and eastern gorillas in general [Robbins et al., 2006], exhibit high dietary variability. This variation across elevations and associated ecological conditions also suggests that differences in gorilla diets across localities are the result of local food availability, rather than adaptive traits of specific (sub)species. Gorillas can, for example, switch in diets when certain preferred foods are locally unavailable, which suggests that food availability is a stronger determinant of diets than preferences or selectivity [Yamagiwa et al., 1996; Remis, 2003]. Similarly, habitat characteristics across home-ranges, such as the percentage of area dominated by swamps or the local availability of fruiting trees, may lead to substantial differences in diets even across neighbouring gorilla groups

[Doran et al., 2002; Rogers et al., 2004; Ganas et al., 2004]. That gorilla diets are largely determined by food availability and local environments is also evident when comparing diets across eastern gorillas (GG and MG), where MG at Bwindi show more dietary similarity with GG at comparable elevations [Yamagiwa et al., 2005] than with MG at higher elevations in the Virungas [Robbins et al., 2006]. New lines of research on gorilla dietary flexibility and adaptations may be guided by our initial analyses of food items of GG at lower elevation forests. More immediately, our data may guide the management and conservation efforts of GG, for example by highlighting focal plant species for initial phenological studies (e.g., *Cissus dinklagei*) or efforts of forest restoration.

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Statement of Ethics

No human or animal samples were obtained during this study, and all field efforts took place under permission from L'Institut Congolais pour la Conservation de la Nature (ICCN) and consent by local landowners and community members.

Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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Author Contributions

W.D.P., D.C., U.N., and E.B.: study design and fieldwork; Y.H., W.D.B., D.C., U.N., and T.S.S.: data analysis and writing the article. All authors approved the final paper.

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