High Altitude Diets: Implications for the Feeding and Nutritional Ecology of Mountain Gorillas

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Introduction

Though the majority of primates live in tropical habitats, several species partially or exclusively range in high altitude regions of Africa, Asia, and Madagascar (Blanco and Rahalinarivo 2010; Iwamoto and Dunbar 1983; Kirkpatrick and Grueter 2010; Mendiratta et al. 2009; Watts 1998; Whiten et al. 1987). The differences among the diets of high and low altitude primates are likely due to characteristics in their environment. It has been generally accepted that plant species diversity and density decreases with increasing altitude (Aiba and Kitayama 1999; Hamilton 1975; Pellissier et al. 2012; Proctor et al. 2007; Rahbek 1995; Sharma et al. 2009; Vázquez and Givnish 1998; Zhuang et al. 2012). The number of species of understory herbs, shrubs, and vines decreased as altitude increased along the altitudinal gradient from Mexican seasonal dry forest to cloud forest (Vázquez and Givnish 1998). African forests at higher altitudes have fewer fruiting trees, fewer large buttressed trees and lianas, and lower fruit availability, compared to lower altitude forests (Hamilton 1975; Proctor et al. 2007; Schmitt et al. 2010). A similar pattern is seen in Asia, where lower altitudes are characterized by larger numbers of fruiting trees, and higher altitudes are more likely to be composed of herbs and shrubs (Zhuang et al. 2012).

Primates in these high altitude habitats show dietary flexibility in response to fluctuations in the availability of food in different altitudes. For example, the diet

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of the snub-nosed monkey varies dramatically among subspecies at different altitudes. Black-and-white snub-nosed monkey (*Rhinopithecus bieti*, 3,500–4,250 m) fallback foods in winter include bark and nuts (Xiang et al. 2007), while those of the lower altitude gray snub-nosed monkeys (*Rhinopithecus brelichi*, 800–2,570 m) and golden snub-nosed monkeys (*Rhinopithecus roxellana*, 1,700–2,630 m) include leaf buds (Xiang et al. 2012) and lichen (Yiming 2006), respectively. Multiple macaque species at high altitudes also demonstrate dietary plasticity, relying on lower quality foods at higher altitude (Mehlman 1988; Ménard 2002). Japanese macaques (*Macaca fuscata*) in low altitude areas (0–399 m) of Yakushima Island ate more seeds, fruits and animal matter, and less fungi and fibrous foods than those at high altitude (800–1,199 m) (Hanya et al. 2003). Mouse (*Microcebus* spp.) and dwarf (*Cheirogaleus spp.*) lemurs practice hibernation in low temperature months when food at high altitude is especially scarce (Blanco and Rahalinarivo 2010; Schmid and Ganzhorn 2009). While some species become generalists, or even hibernate, when faced with high altitude challenges, others make subtler adjustments. Chimpanzees in higher altitude Kahuzi (as high as 2,600 m) eat and have availability of fewer fruiting tree species than chimpanzees at lower altitude Lopé (200–500 m) (Basabose 2002).

The nutritional quality of potential primate foods also varies according to altitude. In general, the increased availability of fruit provides a rich energy source at lower altitudes, but the quality of these food sources may vary in relation to altitude. The protein content per leaf area increases with altitude due to increased nitrogen as a result of increased precipitation and cooler temperatures (Friend et al. 1989; Hikosaka et al. 2002; Hodkinson 2005; Kitayama and Aiba 2002; Körner 1989). In addition, higher altitude plants typically have lower levels of lignification because of cooler temperatures and carbon limitation (Guo et al. 2012; Richardson 2004). Herbaceous leaves and stems from a montane forest in the Virunga mountain range contained less fiber and tannins than herbaceous leaves and stems from lower altitude tropical rainforests in Cameroon, Uganda and southern India (Waterman et al. 1983). Near absence of condensed tannins in the afro-montane samples also suggests that montane vegetation is more digestible than lowland evergreen vegetation (Waterman et al. 1983).

However, it is not always the case that higher altitudes have more nutritious plants; in cloud forests on large mountains (1,500–3,300 m), there is typically a decrease in nitrogen and an increase in lignin because leaves tend to become more xeromorphic, or thicker, smaller, and harder, in order to adapt to the harsh windy conditions (Bruijnzeel and Veneklaas 1998; Tanner et al. 1998).

A study of colobus monkeys (*Colobus angolensis*) in the high altitude Nyungwe forest, Rwanda, suggests that large group sizes persist in this location because the leaves are higher quality (protein-to-fiber ratio) than those at lower altitude sites where colobus groups are smaller (Fimbel et al. 2001). Gramnivorous geladas are restricted to high altitude areas (1,500–4,000 m) in Ethiopia that correspond to where grasses are higher in protein (Dunbar 1998; Mau et al. 2009). Protein content of grasses in lower altitude grasslands in East Africa are low (2.2–6.9 % CP) compared to that of the gelada's range (Bole, 2,100 m) where protein is 12.5 %. At altitudes close to the limit of the gelada upper range (3,250–3,900 m), protein content was 7 %, indicating that protein content may relate to gelada distribution and survival (Dunbar 1992). Protein concentrations of 7 % or less are unlikely to meet the protein requirements of primates (Oftedal 1992).

Gorillas (*Gorilla* spp.) are folivore-frugivores that live at a variety of altitudes across Africa. The well-studied mountain gorillas (*Gorilla beringei beringei*) in the Virungas live at altitudes of 2,000–3,600 m, while the mountain gorillas of Bwindi live at altitudes of 1,160–2,607 m. The eastern lowland gorillas (*Gorilla beringei graueri*) in the Democratic Republic of Congo live at 600–2,500 m, and the western lowland gorillas (*Gorilla gorilla gorilla*) live in west Africa at 100–700 m (Yamagiwa et al. 2003). The Cross River gorillas (*Gorilla gorilla diehli*) are found at 80–2,000 m in Nigeria and Cameroon but are the most endangered of all apes (Oates et al. 2007). All gorillas consume fruit when it is seasonally available in their habitats (Doran and McNeilage 1998; McNeilage et al. 2001; Remis 1997; Stanford and Nkurunungi 2003). Western gorillas are generally more frugivorous than eastern gorillas (Doran and McNeilage 1998; Goldsmith et al. 2003), and some mountain gorillas eat little or no fruit because it is not available in their high altitude habitat (McNeilage et al. 2001; Watts 1984).

Mountain gorillas in the Bwindi Impenetrable National Park, Uganda are opportunistic frugivores that eat fruit when it is seasonally available (Goldsmith et al. 2003; Robbins and McNeilage 2003; Rothman et al. 2006b, 2011; Stanford and Nkurunungi 2003). Even when fruit is available, they consume a diverse daily diet of leaves, supplemented with bark, pith, and stems (Stanford and Nkurunungi 2003). Nutritionally, Bwindi gorillas consume a diet that is rich in protein (crude protein (CP): 18 %; available protein (AP): 14 %), high in fiber (neutral detergent fiber (NDF): 43 %), low in fat (2 %), and moderate in nonstructural carbohydrates (19 %) (Reiner et al., in review; Rothman et al. 2007, 2008a). The Bwindi gorilla diet varies seasonally (Rothman et al. 2008b), whereby they prioritize the consumption of nonprotein energy (carbohydrates and fats), and consume a diet high in protein (Rothman et al. 2011).

Here, as an example of a high altitude primate, we describe the diversity of the diet of the Bwindi gorillas over 1 year in terms of its botanical composition. We then determine the plant parts from which the Bwindi gorillas obtain their macronutrients. We test the hypothesis that leaves provide the most protein and fiber in the gorilla diet annually, while fruits provide the most nonstructural carbohydrates in the overall diet on a weight basis. We describe the intraspecific variability in nutritional components in the herbaceous leaves that gorillas eat. Finally, we compare the nutrients within gorilla foods to those at other eastern, mountain, and western sites, and predict that generally the foods of Bwindi gorillas will be higher in protein and lower in fiber than gorillas living in lowland areas.

Methods

Study Site

Bwindi Impenetrable National Park is a rugged, mountainous rain forest that was initially designated as a Forest Reserve in 1932 but was upgraded to a national park in 1991 (Butynski and Kalina 1993). BINP is located in the south-western Kigezi region of Uganda, 0°53′−1°08′S, 29°35′−29°50′E, and contains both medium altitude and montane forest.

We collected data during August 2002–July 2003 in Ruhija which is in a high-altitude region of the park, between 2,100 and 2,500 m. Annually, there are bimodal rains in Uganda; the dry months are December to February and June to August, while the wet months are September to November and March to May. Annual rainfall at Bwindi typically ranges from 1,130 to 2,390 mm. The annual rainfall for the study period was 1,436 mm. The daily mean minimum temperature at Ruhija was 13.6 ± 0.41 °C SD (range: 12.8–14.1 °C), and the mean maximum temperature was 16.7 ± 0.65 °C (range: 15.5–17.7 °C).

The behavioral data sampling regime is outlined in other reports (Rothman et al. 2007, 2008b). Briefly, we followed the Kyagurilo group of gorillas for 4 h per day for 319 days. These 4 h periods ranged from 8:00 to 18:00 h, but on most days, we observed the animals between 09:00 and 14:00 h due to the logistics of traveling in the field. We could not follow the gorillas for longer periods due to regulations of the Uganda Wildlife Authority. At the beginning of the study, there were 14 group members: two silverbacks, six females, four juveniles and two infants. During the study an infant was born, bringing group membership to 15.

As described in Rothman et al. (2007), we used a similar method to that of Watts (1984) to calculate food intake on a wet weight basis for each individual using 30 min focal animal sampling. We calculated the proportional wet-weight intake of each diet item for each independent individual (N = 12). Each individual was observed for as long as possible while feeding until it was out of view. Similar to Watts (1984), the time when the animal started and ended feeding represented a timed feeding bout; however, instead of using feeding rates and times, we counted the actual number of diet items and the amounts eaten during these bouts. Each animal was observed at least 6 days per month and observer biases were minimized by having JMR and the two field assistants observe the same animal on 3 days per month. JMR and field assistants collected these focal observations on 319 days and totalled 1,318 h (Rothman et al. 2008b). The gorillas spent approximately 55 % of their time feeding (Rothman et al. 2007). On a monthly basis, plant collections of each individual diet item (i.e., a single leaf) in the gorilla feeding area were weighed (N = 50) and an average was calculated for each month (Watts 1984). To obtain an estimate of diet quality over the year, these monthly unit weights were averaged for the year (Rothman et al. 2007, 2008b). We used the unit weight to estimate the wet weight contribution of each ingredient to the total daily diet, and then we converted this to dry weight (Rothman et al. 2012).

We collected foods eaten by gorillas in the same locations where they were seen feeding in the same months to account for intraspecific variability in nutritional composition (Chapman et al. 2003; Rothman et al. 2009, 2012). Furthermore, we processed foods similarly to the way the gorillas processed them before feeding. For example, if the gorilla ate the pith and removed the outer peel or bark, we also discarded the outer peel/bark. We identified all foods with the assistance of Robert Baryigya and the herbarium at the Institute of Tropical Forest Conservation (ITFC). When a sample could not be identified at ITFC, we took the sample to Makerere University, Uganda where it was identified by herbarium manager Tony Katende. We left voucher specimens at ITFC and also have voucher specimens that are held at Hunter College. We collected 327 plants for nutritional analysis from 82 species. As described in other reports (Rothman et al. 2007, 2008a, b), we dried samples in the field at <22 °C in darkness, and we ground them in a Wiley Mill through a 1 mm screen. Details on the protocols for nutritional analysis are presented in previous reports (Rothman et al. 2007, 2008a, b). Briefly, JMR analyzed samples in the Department of Animal Science at Cornell University, USA and at Hunter College, USA. We analyzed samples for CP, AP, NDF, acid detergent fiber (ADF), acid detergent lignin (ADL), total nonstructural carbohydrates (TNC), and fat (CF). For some nutritional analyses, we use near infrared spectroscopy (Rothman et al. 2009).

Results

Description of the Bwindi Gorilla Diet

Over the 1 year study, this Bwindi gorilla group ate a diverse diet of over 148 plant parts from 103 species (Table 1). We could not identify two species of herbs where the leaves were eaten. The gorillas ate food items from 23 herbaceous species including a thistle, 21 lianas, 9 shrub species, 31 trees including a tree fern, 5 species of epiphytes including an epiphytic cactus and fern, 2 fungi and 3 species of plant parasites. We estimated that 10 different species of decaying wood were consumed, but we could not confirm their taxonomic identity. The gorillas ate tree bark or herbaceous peel from 17 species, fruit from 30 species, 4 species of flowers, leaves from 57 species, and pith from 6 species. They did not eat any insects and two individuals engaged in coprophagy once during the study. We observed soil eating on two occasions. Although the gorillas ate over 148 plant parts from over 103 species, only 17 plant parts comprised more than 1 % of the wet weight mass of the diet over the year (Table 1). These 17 plant parts (8 species of herbaceous leaves, one species of tree leaves, two species of pith, one species of herbaceous stem or peel, three species of fruit and decaying wood pieces) comprised 96.1 % of the diet (Rothman et al. 2007), with the other 132 remaining plants together composing less than 4 % of the annual diet. On a mass basis,

Table 1 Foods eaten by Bwindi gorillas

Food	Family	Life form	Plant part
Acalypha ornata	Euphorbiaceae	Herb	B, L
Achyranthes aspera	Amaranthaceae	Herb	L
Adenia gummifera	Passifloraceae	Liana	L
Alchornea hirtella	Euphorbiaceae	Shrub	L,F
Allophylus abyssinicus	Sapindaceae	Tree	F, L
Allophylus macrobotrys	Sapindaceae	Tree	L
Allophylus sp.	Sapindaceae	Tree	F
Ancistrorhynchus clandestinus	Orchidaceae	Epiphyte	L
Angraecum infundibulare	Orchidaceae	Epiphyte	L, R
Arundinaria alpina	Poaceae	Grass	YS
Baissea sp.	Apocynaceae	Liana	L
Basella alba	Basellaceae	Liana	L
Carpodinus glabra	Apocynaceae	Liana	B, L
Carduus kikuyorua	Asteraceae	Thistle	L
Cassipourea ruwenzoriensis	Rhizophoraceae	Tree	F
Chrysophyllum albidum	Sapotaceae	Tree	F
Chrysophyllum gorungosanum	Sapotaceae	Tree	F
Clematis sp.	Renunculaceae	Liana	L
Combretum fuscum	Combretaceae	Liana	L
Crassocephalum sp.	Asteraceae	Herb	P
Cyathea manniana	Cyatheaceae	Tree Fern	P
Cyperus renschii	Cyperaceae	Grass	YS
Desmodium repandum	Fabaceae	Liana	L
Diaphanathe subsimplex	Orchidaceae	Epiphyte	L
Dicliptera sp.	Acanthaceae	Herb	L
Dolichos sericeus	Phaseoleae	Liana	L
Dombeya goetzenii	Sterculiaceae	Tree	B, L
Droguetia iners	Urticaceae	Herb	L
Drypetes sp.	Euphorbiaceae	Tree	F
Englerina woodfordioides	Loranthaceae	Parasitic Plant	B, L, S
Ficus asperifolia	Moraceae	Tree	B, L, F
Ficus densistipulata	Moraceae	Tree	L
Ficus exasperata	Moraceae	Tree	B, L, F
Ficus ingens	Moraceae	Tree	B, L, F
Ficus natalensis	Moraceae	Tree	B, L, F
Ficus spp. (Unidentified *Ficus*)	Moraceae	Tree	L, F, B
Ficus conraui	Moraceae	Tree	L, F
Laportea ovalifolia	Urticaceae	Herb	L
Galiniera coffeoides	Rubiaceae	Shrub	F, L
Galium thunbergianum	Rubiaceae	Herb	L
Gandoderma australe	Ganodermataceae	Fungus	Whole
Ganoderma sp.	Ganodermataceae	Fungus	Whole
Gouania longispicata	Rhamnaceae	Liana	L
Helichrysum nudifolium	Compositae	Herb	L
Helichrysum schimperi	Compositae	Herb	L

(continued)

Table 1 (continued)

Food	Family	Life form	Plant part
Ilex mitis	Aquifoliaceae	Tree	B
Ipomoea involcrata	Convolvulaceae	Liana	B, L, S, Fl
Isoglossa sp.	Acanthaceae	Herb	L, Fl
Jasminum abyssinicum	Oleaceae	Liana	L
Jasminum schimperi	Oleaceae	Liana	L
Justicia glabra	Acanthaceae	Herb	L, Fl
Kosteletzkya grantii	Malvaceae	Herb	L
Landolphia buchananii	Apocynaceae	Liana	L
Lasanthus sersecusis	Gentianaceae	Tree	L
Maesa lanceolata	Primulaceae	Tree	L,F
Mimulopsis arborescens	Acanthaceae	Herb	L, P
Mimulopsis solmsii	Acanthaceae	Liana/Shrub	L, B
Momordica foetida	Cucurbitaceae	Liana	L, F
Momordica pterocarpa	Cucurbitaceae	Liana	L, F
Myrianthus holstii	Moraceae	Tree	L, F, B
Mystroxylon aethiopicum	Celastraceae	Tree	B
Mystroxylon aethiopicum	Celastraceae	Tree	F
Olea capensis	Oleaceae	Tree	F
Olea capensis	Oleaceae	Tree	L
Olinia rochetiana	Oliniaceae	Tree	F
Oncinotis sp.	Apocynaceae	Liana	W
Periploca linearifolia	Asclepiadaceae	Liana	L
Pilea holstii	Urticaceae	Herb	L, S
Pilea holstii	Urticaceae	Herb	S
Piper capense	Piperaceae	Herb	P
Pleopeltis macrocarpa	Polypodiaceae	Epiphyte	L
Podocarpus milanjianus	Podocarpaceae	Tree	F
Polystachya adansoniae	Orchidaceae	Epiphyte	L
Polystachya cultriformis	Orchidaceae	Epiphyte	L
Polystachya spatella	Orchidaceae	Epiphyte	L
Pseudodrynaria coronans	Polypodiaceae	Epiphytic Fern	P
Rapanea rhododendroides	Myrsinaceae	Tree	L
Rawnsonia lucida	Lepidoptera	Tree	F
Rhipsalis baccifera	Cactaceae	Epiphytic Cactus	W
Rubus sp.	Rosaceae	Shrub	L, F, S
Rubus steudneri	Rosaceae	Shrub	L, F, S
Rytigynia bugoyensis	Rubiaceae	Shrub	L
Rytigynia kigeziensis	Rubiaceae	Shrub	L, F, Fl
Rytigynia ruwenzoriensis	Rubiaceae	Shrub	L
Salacia elegans	Celastraceae	Liana	L
Sarcorhynchus bilobatus	Orchidaceae	Epiphyte	L, R
Schefflera sp.	Araliaceae	Herb	L
Smilax anceps	Smilacaceae	Liana	L, F
Solanum welwitschii	Liliaceae	Liana	L
Strombosia scheffleri	Olacaceae	Tree	F

(continued)

Table 1 (continued)

Food	Family	Life form	Plant part
Symphonia sp.	Clusiaceae	Tree	F
Syzygium guineense	Myrtaceae	Tree	F
Tapinanthus sp.	Loranthaceae	Parasite	L, S
Teclea nobilis	Rutaceae	Tree	F
Triumfetta tomentosa	Tiliaceae	Shrub	L
Urera cameroonensis	Urticaceae	Liana	B
Urera hypselodendron	Urticaceae	Liana	L,B
Vernonia iodocalyx	Compositae	Herb	P
Vernonia lasiopus	Compositae	Herb	L
Vernonia pteropoda	Compositae	Herb	B
Vernonia tufnelliae	Compositae	Herb	B
Vigna parkeri	Leguminosea	Liana	L
Xymalos monospora	Monimiaceae	Tree	L, B, F

nonwood vegetative foods comprised 80.8 % and fruits comprised 15.3 % annually. Seasonally, the diet varied from 0 to 60 % fruit on a mass basis (Rothman et al. 2008b, 2011).

Nutritional Contributions of Different Plant Parts

Herbaceous leaves composed the bulk of the Bwindi gorilla diet and they also contributed the majority of the protein, fiber, and nonstructural carbohydrates in the diet (Table 2). Surprisingly, fruit contributed a large portion of the fiber in the diet; even though fruit comprised just 15 % of the diet annually, fruits contributed 20–21 % of all fiber (NDF, ADF, ADL) in the diet. Wood also contributed a substantial portion of the fiber in Bwindi diets, though it is likely eaten for its sodium content (Rothman et al. 2006c). Herbaceous leaves, not fruit, contributed the most sugars and other easily digestible carbohydrates to the diet (65 %). Pith contributed few macronutrients to the diet, probably because it is so high in moisture (Rothman et al. 2006a). Fruits contributed the most fat, but fat in the

Table 2 Contributions of different foods eaten by Bwindi gorillas to their overall macronutrient consumption (% dry matter basis)

	Avail P	NDF	ADF	ADL	TNC	CF
Herb leaves	74.5	37.4	32.2	42.9	65.1	16.5
Tree leaves	13.0	14.4	14.3	10.9	3.9	0.6
Fruit	5.8	20.8	21.8	20.3	12.5	80.2
Peel	5.3	5.6	6.7	3.2	1.0	2.0
Pith	0.4	2.6	2.9	2.0	3.1	0.7
Wood	0.9	19.1	22.1	20.8	14.3	0.0

overall Bwindi diet is low (Reiner et al., in review). The results of our nutritional analyses by plant part are presented in Table 3 in comparison to gorilla foods at other sites.

Intraspecific Variability in Nutritional Composition of Staple Foods

Over 7 months of the study we collected and subsequently analyzed five of the herbaceous leaf species from the same site to investigate monthly intraspecific variability in the vegetative portion of the gorilla diet. The nutrients in these foods were variable in different months from the same site (Fig. 1), for example, TNC varied from 15 to 35 % in *Basella alba* leaves, and CP varied from 23 to 37 % in *Urera hypseledendron* leaves. There were no apparent monthly trends that applied to all species.

Discussion

Gorillas have a diverse diet that incorporates a wide range of plant species and parts. Although there are differing sampling methods, Bwindi gorillas appear to eat a lower diversity of foods compared to some western sites (mean diversity is 148 species; Rogers et al. 2004), and a higher number of species than mountain gorillas in the Virungas (Rogers et al. 2004; Watts 1984) as would be expected at a higher altitude. However, only about 11 % of the species that they ate actually contributed more than 1 % of the overall mass of their diet annually. This indicates that although the gorillas eat a wide variety of plant parts and species in their diets, the major macronutrients are gained from just a few food parts and species. The other sparsely eaten dietary components probably provide important micronutrients, fatty acids, amino acids or other important compounds, or serve to help detoxify the toxins in the diet (Dearing et al. 2000; Milton 1999). For example, decaying wood contributes 4 % of the diet, but contributes >95 % of sodium (Rothman et al. 2006c). It is also possible that some of these plants are simply not widely available otherwise they would be eaten more often; we suggest this is the case because many of the herbaceous leaves were higher in TNC than staple foods and gorillas prioritize energy (Table 3; Rothman et al. 2007, 2011). The types of staple foods in their diets during this study were consistent with other studies of Bwindi gorillas at the same site, suggesting that there is stability in these particular food items (Ganas et al. 2004; Robbins et al. 2006; Stanford and Nkurunungi 2003). The Bwindi gorillas also tend to incorporate staple herbaceous foods in their diet regardless of whether fruit is eaten (Robbins et al. 2006), though the amounts of fruit and leaves are quite variable seasonally (Rothman et al. 2008b, 2011).

Table 3 Nutritional composition of foods eaten by gorillas at study sites across Africa

Subspecies	*Gorilla g.gorilla*				*Gorilla b.graueri*		*Gorilla b.beringei*				
Site[1]	Campo, Cameroon[3]	Lope, Gabon[4]	Bai Hokou, CAR[5]	Bai Hokou, CAR[6]	Mondika, CAR/Congo[7]	Kahuzi, DRC[8]	Tshibinda, DRC[9]	Karisoke, Rwanda[10]	Karisoke, Rwanda[11]	Bwindi, Uganda (Ruhija)[12]	Bwindi, Uganda (Buhoma)[13]
No of species in the diet[2]	50	134	>200	138	25	121[14]	>104	75[15]	9	82	140[16]
No. parts analyzed	36	95	31	68	25	14	39	33	9	327	25
Altitude (m)	200	200–500	400	400	400	2,050–2,350	2,000–2,500	2,680–3,710	2,700–4,500	1,190–2,607	1,450–1,800
Forest type	Lowland evergreen	Lowland rain forest	Semideciduous rain forest	Semideciduous rain forest	Semi-evergreen forest	Montane forest	Montane forest	Montane rainforest	Tropical montane forest	Rugged montane rainforest	Rugged montane rainforest
Herb density	1.1 shrubs or herbs/100 m[17]	7.7 stems/m^2 [18]	1.1 stems/m^2 [19]	1.1 stems/m^2 [19]	0.78 stems/m^2 [20]	1.03 stems/m^2 [21]	1.0 stems/m^2 [21]	8.8 stems/m^2 [15]	8.8 stems/m^2 [15]	10.6 stems/m^2 [16]	4.36 stems/m^2 [16]
Herb leaves											
TNC	26.9	NA	10.9	NA	NA	NA	NA	NA	21.1	38.1	NA
NDF	41.6	NA	63.3	67.2	NA	NA	NA	NA	45.5	35.9	35.3
ADF	37.6	29.9	44.8	49.5	NA	NA	NA	35.5	NA	23.9	17.3
ADL	15.0	NA	NA	18.3	NA	NA	NA	NA	NA	9.5	4.4
Fat	5.5	2.1	0.5	NA	NA	NA	NA	NA	NA	1.0	1.9
Protein	19.4	19.5	16.4	17.2	NA	26.1	24.2	15.5	20.2	19.2	26.6
Tree leaves											
TNC	34.3	NA	14.3	NA	14.5	NA	NA	NA	NA	33.0	NA
NDF	43.2	NA	58.2	69.3	55.8	NA	NA	NA	NA	42.1	NA
ADF	44.1	30.5	44.6	54.7	NA	NA	NA	NA	NA	29.7	NA
ADL	23.0	NA	NA	31.8	17.6	NA	NA	NA	NA	11.5	NA
Fat	4.2	2.6	0.6	NA	2.8	NA	NA	NA	NA	1.0	NA
Protein	13.5	16.5	20.2	17.0	18.7	6.2	36.4	NA	NA	16.7	NA
Herb stems/herb peel											
TNC	24.9	NA	11.2	NA	0.6	NA	NA	NA	19.8	30.5	NA
NDF	54.4	NA	80.4	67.4	62.4	NA	NA	NA	58.5	58.2	61.6
ADF	41.6	44.6	54.5	49.2	NA	NA	NA	49.3	NA	45.6	52.3
ADL	9.4	NA	NA	26.0	11.0	NA	NA	NA	NA	9.0	8.1
Fat	3.3	1.3	0.3	NA	3.0	NA	NA	NA	NA	1.0	0.6
Protein	7.2	5.1	3.4	16.9	16.4	NA	NA	6.2	9.2	7.8	13.0

(continued)

Table 3 (continued)

Subspecies	*Gorilla g.gorilla*				*Gorilla b.graueri*		*Gorilla b.beringei*				
Site[1]	Campo, Cameroon[3]	Lope, Gabon[4]	Bai Hokou, CAR[5]	Bai Hokou, CAR[6]	Mondika, CAR/ Congo[7]	Kahuzi, DRC[8]	Tshibinda, DRC[9]	Karisoke, Rwanda[10]	Karisoke, Rwanda[11]	Bwindi, Uganda (Ruhija)[12]	Bwindi, Uganda (Buhoma)[13]
Fruits											
TNC	20.1	NA	10.7	NA	42.9	NA	NA	NA	NA	45.0	NA
NDF	64.6	NA	78.7	59.3	44.5	NA	NA	NA	NA	37.3	32.7
ADF	44.8	23.9	65.4	45.3	NA	NA	NA	NA	NA	26.8	20.1
ADL	26.9	NA	NA	24.9	13.4	NA	NA	NA	NA	12.2	7.5
Fat	6.2	4.0	0.8	NA	1.3	NA	NA	NA	NA	5.0	6.1
Protein	6.2	6.1	5.7	8.4	7.4	7.5	17.3	NA	NA	10.9	8.1

[1] All data are presented as a percentage of dry matter aside from the Mondika site where data are presented on an organic matter basis
[2] Items in the total diet aside from Mondika where the important preferred foods and fallback foods are considered by Doran- Sheehy et al. (2009), and in the Virungas where only staple foods are considered by Rothman et al. (2007)
[3] Calvert (1985)
[4] Rogers et al. (1990)
[5] Popovich et al. (1997)
[6] Remis et al. (2001)
[7] Doran-Sheehy et al. 2009 (number of important foods)
[8] Casimir (1975)
[9] Goodall (1977)
[10] Waterman et al. (1983)
[11] Rothman et al. (2007)
[12] this study
[13] Ganas et al. (2008)
[14] Yamagiwa and Mwanza (1994)
[15] Watts (1984)
[16] Ganas et al. (2004)
[17] Tchouto et al. (2006)
[18] Rogers and Williamson (1987)
[19] Goldsmith et al. (2003)
[20] Rogers et al. (2004)
[21] Basabose (2002)

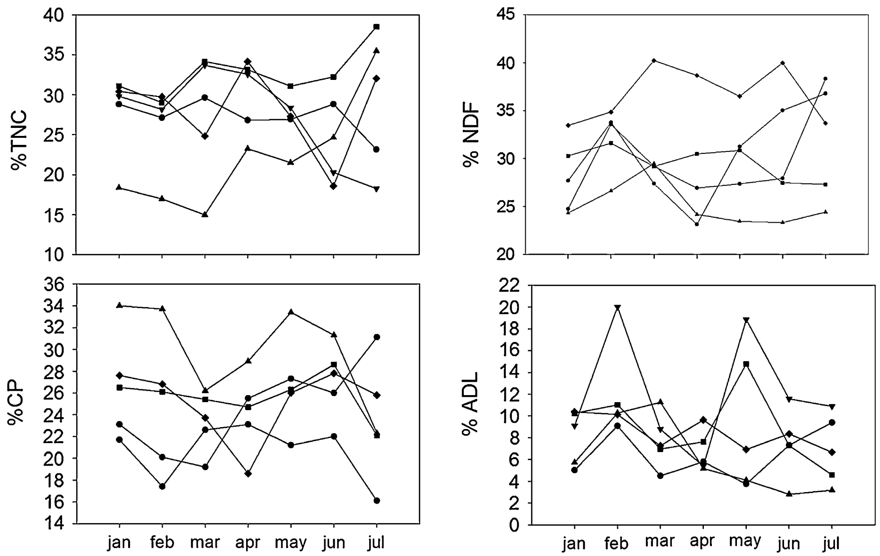

Fig. 1 Intraspecific variability in the nutritional components of five staple herbaceous leaf species over 6 months (●—*Carduus* sp. ■—*Ipomea* spp. ◆—*Triumfetta tomentosa* ▲—*Basella alba* ▼—*Urera hypseledendron*)

Gorillas receive most of their available protein, sugar, and fiber from the herbaceous component of their diets. They also receive a substantial portion of their fiber from wood and fruit; fruits in the Bwindi gorilla diet are similar in their fiber content to leaves, suggesting that 'fibrous' foods are not always leaves and pith as sometimes indicated in the ape literature (Ganas et al. 2004; Rogers et al. 2004; Stanford and Nkurunungi 2003). In addition, the herbaceous leaves provided most of the sugar in the annual diet. These findings are similar to a study on folivorous colobus monkeys in Kibale in which fruits and leaves were similar in their sugar contents (Danish et al. 2006). Western gorillas in the Central African Republic also eat fibrous fruits, particularly during seasons of low food availability (Remis et al. 2001), and fruits eaten by gorillas in Campo, Cameroon were also similar in TNC to leaves (Calvert 1985). The large body size of gorillas is a dietary adaptation that offers an opportunity to eat fibrous foods, especially in periods of food scarcity (Remis 2000; Remis et al. 2003; Doran et al. 2009).

Our hypothesis that gorilla herbaceous leaves in higher altitudes would be of higher quality (higher in TNC and CP, and lower in NDF, ADF, ADL) was partially supported (Table 3). Foods eaten by gorillas in Bwindi were higher in TNC and similar in CP to those in CAR and Campo, Cameroon, and, similar to those in the Virungas (Rothman et al. 2007) which are also higher in altitude. Bwindi fruits were also higher in TNC than those at other sites. However, fiber contents were similar among the different gorilla sites. Bwindi gorillas prioritize energy and consume a surplus of protein (Rothman et al. 2011), so they may be selecting high TNC leaves. In a study of mountain baboons (*Papio ursinus*) where two groups were separated by 400 m in altitude, baboons were similarly constrained because of seasonal differences in food supply and ate diets composed of different plant parts; however, individuals obtained the same nutrient yield (Byrne et al. 1993). The staple foods of the gorilla diet in the Virungas and Bwindi are similar in nutritional composition, even though their diets are different compositionally (Rothman et al. 2007). Other studies have also found that primate diets can vary compositionally but not nutritionally (Conklin-Brittain et al. 1998; Ryan et al. 2013; Twinomugisha et al. 2006). We hope that upcoming new nutritional data from western gorilla sites will be informative for interspecific comparisons of nutrient intake (Jessica Lodwick, personal communication, Shelly Masi, personal communication).

Our results demonstrate that there is considerable intraspecific variability in the nutritional composition of herbaceous leaves eaten by Bwindi gorillas (Rothman et al. 2009, 2012). Thus, a particular food item could be high quality (high TNC, high CP and low NDF, ADL) in some months and low quality in another. It is well known that the nutrient content of a single plant species can vary over different spatial and temporal scales in primate studies (Barton et al. 1993; Rothman et al. 2012). For example, young leaves of the same species eaten by colobines in Kibale National Park, Uganda varied in protein content from 22 to 47 % (Chapman et al. 2003), and the fat content of a single species of ripe fruit in this forest varied seasonally from 0.3 to 30.0 % (Worman and Chapman 2005). Sun-exposed leaves had more protein than shaded leaves in Madagascar (Ganzhorn 1995), and the nutritional value of tamarind leaves and fruits eaten by ring-tailed lemurs (*Lemur catta*) varied according to forest type (Mertl-Millhollen et al. 2003).

This variability has important implications for sampling biases. If samples are not collected from the same site where a primate is feeding at the same time then it may not be representative of the nutrients in the food item ingested at that time (Rothman et al. 2012). Furthermore, it has been demonstrated that the nutrients in primate foods vary diurnally in relation to time of day (Ganzhorn and Wright 1994). For example, chimpanzees (*Pan troglodytes*) feed on leaves later in the day when they are higher in nonstructural carbohydrates and sugar (Carlson et al. 2013). Here, we collected foods from the exact site where the gorillas were feeding, thus all of these leaves were acceptable and eaten by them. It would be interesting to investigate whether the gorillas avoid eating the same species of food because it differs in nutritional composition. Studies of captive western gorillas demonstrate that they are able to discern solutions that have sugars and tannins, and that they use sweetness as a criteria for food selection (Remis and Kerr 2002).

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