Nutritional composition of the diet of the gorilla (Gorilla beringei): a comparison between two montane habitats

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Abstract: The mountain gorilla (Gorilla beringei beringei) lives in two geographically separated populations, Bwindi Impenetrable National Park, Uganda and in three national parks spanning the Virunga mountain region in Rwanda, Democratic Republic of Congo, and Uganda. The altitude, climate and plant composition of these habitats differ. Our goal was to compare the diets of gorillas living in each of these habitats. The nutrients in staple foods and in the diets of individuals in a group of gorillas in Bwindi (N = 12 individuals) and a group in the Virungas (N = 7 individuals) were compared to determine if differences in dietary composition affected concentrations of nutrients in their diets. At both sites gorilla diets consisted primarily of herbaceous leaves, but the diet of Bwindi gorillas contained more tree leaves, fruit, pith and dry wood, and fewer stems. Despite differences in habitat and dietary composition, the nutrient concentrations in both gorilla diets were remarkably similar. On a dry matter basis, the diets and staple foods of Bwindi and Virunga gorillas contained similar concentrations of crude protein (CP), fibre (NDF) and non-structural carbohydrates (TNC). Bwindi gorillas ate diets containing 18% CP, 43% NDF and 19% TNC on a dry-matter basis, while the diets of the Virunga gorillas contained 17% CP, 41% NDF and 18% TNC. Our results demonstrate that gorillas consume diets that differ by plant species and part, but contain similar concentrations of nutrients. This suggests that classifying animals by broad dietary strategy (e.g. frugivory and folivory) does not provide a reliable indicator of the nutritional quality of their diet, and that our previous assumptions about these categories should be re-evaluated.

Key Words: apes, dietary variability, food chemistry, nutritional ecology, primates, tropical forests

INTRODUCTION

Although the remaining two populations of mountain gorilla (Gorilla beringei beringei) are geographically separated by just 30 km, their habitats differ markedly. At an elevation of 1160–2607 m, the 331-km² Bwindi Impenetrable National Park (BINP) in Uganda contains a continuum of lowland and montane forest with fruiting trees (Butynski & Kalina 1993, Howard 1991). The Parc National des Volcans (PNV) in Rwanda is within the Virunga mountain region, a chain of volcanoes which spans three countries, Rwanda, Democratic Republic of Congo and Uganda. The altitude of this 440-km² area varies from 2000 to 4507 m, and much of the vegetation occurs above 2500 m. As a result, a wide range of high-altitude vegetation zones occur, including Afroalpine vegetation, Hagenia–Hypericum forest and bamboo dominating the vegetation types (Fossey & Harcourt 1977, Watts 1984). This difference in the altitude ranges of BINP and PNV means that the vegetation types found within each site differ greatly. Mountain gorillas therefore subsist on different plants in the two forests.

The variability in diet items chosen by Gorilla spp. in different habitats has been documented through a number of studies (Doran & McNeilage 1998, Rogers et al. 2004, Stanford & Nkurunungi 2003, Watts 1984, Yamagiwa et al. 2003). Mountain gorillas in both PNV and BINP consume parts of many different plant species, but concentrate on a few foods that are generally abundant in their

Although the variability of plant species and parts consumed by gorillas across sites is well documented, to better understand their feeding ecology, it is not only important to consider the types of dietary items consumed but also to evaluate the types and amounts of nutrients these items provide. Using data on food intake (wet weight basis) of the Virunga (Watts 1984) and Bwindi gorillas (determined during this study), and a nutritional analysis of the diet items of gorillas in PNV and BINP, the objective of our study was to determine whether dietary variability affected the nutrient concentrations in gorilla diets.

METHODS

Study sites

Bwindi Impenetrable National Park, Uganda. 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 & Kalina 1993). It 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 (Figure 1). As there is micro-scale variation in the composition and density of the vegetation within the forest at different elevations (Nkurunjungi et al. 2004), the food available to and chosen by the gorillas differ in different locations within BINP (Ganas et al. 2004, Nkurunjungi et al. 2004).

The Bwindi study was conducted during August 2002–July 2003 in Ruhija which is in a high-altitude region of the park, between 2100–2500 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 1130–2390 mm (Howard 1991). The annual rainfall for the study period was 1436 mm. The daily mean minimum temperature at Ruhija was 13.6 °C ± 0.41 °C SD (range: 12.8–14.1 °C), and the mean maximum temperature was 16.7 °C ± 0.65 °C (range: 15.5–17.7 °C).

Parc National des Volcans, Rwanda. Located at 1° 50′S, 29° 30′E, PNV lies in the Rwandan portion of the Virunga Volcanoes (Figure 1). The plant material collected from the PNV for chemical analysis was obtained in the study area around the Karisoke Research Station, and details of the study site were outlined in other reports (Plumptre 1991, 1995). The Karisoke study area was south of the Volcano Visoke, but included its summit and southern flanks, south to the flanks of the volcano Karisimbi to an altitude of 3500 m (Plumptre 1991, 1996). This region ranges from 2900–3700 m and included habitat from bamboo at the lowest altitude to afroalpine vegetation at the highest altitude. Observational data on gorilla food plant intake were collected by David Watts on one habituated gorilla group, Group 4 (Watts 1984), which ranged in part of the Karisoke study area and up to 2 km further west into the Democratic Republic of Congo. Another gorilla group (Group 5) used the eastern portion of the Karisoke study area but had a similar plant species intake in their diet compared with Group 4 (Watts 1984).

Study animals and field methods

The Kyagurilo research group of Bwindi gorillas has been habituated to humans for research by the Uganda Wildlife Authority and the Institute of Tropical Forest Conservation. At the beginning of the study, there were 14 group members: two silverbacks (mature males), six females, four juveniles and two infants. During the study, an infant was born, bringing group membership to 15. The Bwindi gorillas were observed for at least 4 h daily by JMR and field assistants for 319 d. These 4-h periods ranged from 8h00 to 18h00, but on most days, the animals were observed between 09h00 and 14h00 due to the logistics of travelling in the field. We could not follow the gorillas for longer time periods due to regulations of the Uganda Wildlife Authority.

We used a similar method to that of Watts (1984) to calculate food intake on a wet weight basis for each individual. Using focal animal sampling, the proportional wet-weight intake of each diet item was calculated for each independent individual animal (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 field assistants observe the same animal on 3 days per month. These focal observations were collected on 319 days by JMR and/or field assistants and totalled 1318 h (Rothman 2006). The gorillas spent approximately 55% of their time feeding. 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. We used the unit weight to estimate the wet weight contribution of each ingredient to the total daily diet. For some food items, e.g. *Momordica* spp., it was impossible to tell which of the *Momordica* species was being eaten during observations. However, the gorillas were either eating one of two species, *Momordica foetida* or *M. pterocarpa* during the study. Similarly, it was impossible to identify the species or genus of the pieces of wood eaten, so we grouped all dry wood eaten into one category to estimate wet-weight intake.

We used published estimates of food intake from Group 4 for estimating the diets of gorillas in PNV (Watts 1984).

**Plant collections**

Approximately 0.5–1 kg of each plant part consumed was collected over different seasons and from different environments in areas where the gorillas fed in both BINP (by JMR and field assistants) and PNV (by AJP and Aimable Nsanzurwimo, Karisoke Research Center). The samples were collected to ensure that they were similar to what was consumed by the gorillas. For most foods, we collected between 4 and 12 samples in different seasons and environments at each study site. After collection, food items were dried in a cool, dark area (≤ 22 °C), and were ground in a Wiley Mill® through a 1-mm screen. Dry matter was calculated by a two-step process involving both field and oven-drying. In the field, samples were weighed shortly after collection and then were dried at ambient temperature in the dark. Initial moisture was calculated by subtracting the constant dry
weight of the plant part from the weight obtained shortly after collection. Immediately before chemical analysis, an accurately weighed small portion of the previously dried samples were dried again at 105 °C to remove any adsorbed atmospheric water to calculate the true dry matter of each sample.

Nutritional and statistical analyses

Food samples were analysed either in the Animal Nutrition laboratory at Cornell University, New York, USA (BINP samples), or at the Wildlife Health Center at the Wildlife Conservation Society, New York, USA (PNV samples). A subset of Bwindi plants from an earlier study (Rothman et al. 2006a) was analysed in both laboratories to check the accuracy of chemical protocols and all samples were found to be within 2% error. The samples were first analysed for neutral detergent fibre with residual ash (NDF), and then for acid detergent fibre with residual ash (ADF) (Van Soest et al. 1991) using filter bags in an A200 fibre analyser (ANKOM, Macedon, NY, USA). Sodium sulphite was added to the neutral detergent solution of the Bwindi, but not the Virunga samples. Most of the staple Bwindi foods contain condensed tannins (Rothman et al. 2006a), while Virunga foods do not (Waterman et al. 1983). The addition of sodium sulphite reduces the amount of insoluble proanthocyanidin complexes bound to fibre (Krueger et al. 1999). Analysis of the foods that do not contain condensed tannins (n = 5) with and without sodium sulphite added to the neutral detergent solution did not result in a significant difference in fibre fractions (paired t-test, t = 1.59, P = 0.19). Since the Bwindi foods have tannins, we quantified them (%DM) by using the acid butanol assay (Porter et al. 1986) and internal standards were generated for each plant species. We determined the ether extract of the Bwindi foods by standard methods. We did not determine ether extract on the Virunga food samples but since the ether extract of leaf and stems was low for the Bwindi samples (mean: 1.8 ± 0.55 %DM), and is generally low in tropical leaves and stems (Conklin-Brittain et al. 1998), we used this Bwindi average to estimate the ether extract in leaves and stems of the Virunga samples. The amount of hemicellulose (HC) in the diet was assessed by subtracting ADF from NDF, and the amount of cellulose (CS) in the diet was estimated by subtracting lignin from ADF. For the Virunga samples, total nitrogen (N) was determined using the macro-Kjeldahl method with a copper catalyst (AOAC 1990). For the Bwindi samples, N was determined by a Leco FP-528 Combustion analyser (AOAC 1990), which is faster and uses less-hazardous materials. The combustion procedure gives N values that are comparable to the Kjeldahl procedure (Etheridge et al. 1998). Crude protein was estimated by multiplying N by 6.25.

To calculate the DM contribution of each nutrient to each individual’s diet, we used a process that included three calculations:

First, we estimated the total dry matter content of the diet using the following formula:

\[ DM_{\text{diet}} = \Sigma [(DM_i)(P_i)] \]

where: \( i = \) the \( i \) th food item in the diet, \( P = \) proportion of wet weight intake, \( DM = \) dry matter.

Second, we estimated the weighted (w) dry matter contribution of each food item to the diet:

\[ wDM_i = \frac{P_i}{DM_{\text{diet}}} \]

Lastly, we estimated the DM contribution of CP and ADF to each individual’s diet:

\[ N_{\text{diet}} = \Sigma (N_i \times wDM_i) \]

where \( N = \) nutrient on a DM basis.

This process was used to calculate the nutritional contributions of each diet item for each individual. Then the diets of individuals were pooled to provide ranked proportional intake values of each food item for the group (Watts 1984). Only foods that formed > 1% of the total diet were included in the pooled data set for nutritional analysis; these were considered ‘staple’ foods. There are seasonal differences in dietary composition and nutrient intake of the Kyagurilo group (Rothman 2006), but we pooled the data on wet-weight proportional intake over the year to permit uniform comparisons to the Virunga data set (Watts 1984). Dr Peter Waterman and colleagues analysed plant species from the Virunga region in earlier years but the analytical methods used were different from those used for the Bwindi sample set and were not comparable. For example, Waterman et al. (1983) did not collect multiple samples from different seasons and environments, plants were sun-dried and the fibre analyses were not sequential.

While it would have been preferable to sample more than one group in each habitat, mountain gorillas are critically endangered and research access to study groups is limited. Because there is only one group of habituated mountain gorillas where observations are permitted by the Uganda Wildlife Authority, our data collection was limited to one group of gorillas in Bwindi. Groups within Bwindi may have different diets (Ganas et al. 2004), and it is not yet known whether their diets are nutritionally comparable. Detailed information on food intake of the Virunga population was limited to a single group (Watts 1984). Individuals within each gorilla group cannot be considered independent samples (i.e. a group member is influenced in what they eat by the rest of the group) therefore we provide descriptive statistics of the mean
A comparison of mountain gorilla diets

(±SD) intake of individuals in each of the groups for each nutrient. To statistically compare the differences between the staple foods of the two gorilla groups, we used t-tests (all the assumptions of normality and variance were met).

RESULTS

On a wet-weight intake basis, the diet composition of the Bwindi and Virunga gorillas varied with respect to plant part (Table 1). Although both groups of gorillas ate diets composed primarily of leaves from THV, the Bwindi gorillas ate more fruit, tree leaves, pith and peel than the Virunga gorillas, while the Virunga gorillas ate more herbaceous stems. The staple diet of the Bwindi gorillas was more diverse than the diet of the Virunga gorillas and they ate different plant species and parts. The Bwindi gorillas ate 15 foods that each comprised >1% of their diet, while the Virunga gorillas ate nine staple foods. In both cases over 90% of the diet was comprised of these staple foods.

Despite differences in their habitats and availability of diet items, the nutrients in both gorilla diets were remarkably similar. The mean percentage of CP in the staple foods eaten by the Virunga gorillas (15.3 ± 9.0% DM) was not significantly different from the mean amount of CP in the Bwindi staple foods (17.0 ± 9.2% DM) (t = -0.43, df = 17, P = 0.67). The NDF in the staple foods eaten by the Virunga gorillas (51.3 ± 12.3% DM) was similar to the NDF content of the Bwindi staple foods (41.3 ± 14.3% DM) (t = 1.81, df = 19, P = 0.11). Similarly, the HC contents of the gorilla staple foods were similar (Bwindi: 13.3 ± 3.8% DM; Virunga: 10.6 ± 2.8, t = 1.88, df = 12, P = 0.10), as were the CS contents (Bwindi: 25.8 ± 11.7; Virunga 25.8 ± 10.4, t = 1.53, df = 15, P = 0.15) and the TNC contents (Bwindi: 20.5 ± 9.2% DM; Virunga: 20.7 ± 8.8, t = -0.06, P = 0.95) (Table 2).

Table 1. Proportion of different gorilla foods (wet-weight basis) eaten by Bwindi and Virunga gorillas.

<table>
<thead>
<tr>
<th>Category</th>
<th>% Bwindi intake</th>
<th>% Virunga intake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herb/shrub leaves</td>
<td>61.1</td>
<td>67.7</td>
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<tr>
<td>Fruit</td>
<td>15.3</td>
<td>&lt; 0.1</td>
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<td>Tree leaves</td>
<td>7.3</td>
<td>&lt; 0.1</td>
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<tr>
<td>Inner stem cortex/pith</td>
<td>6.4</td>
<td>2.4</td>
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<tr>
<td>Peel</td>
<td>5.5</td>
<td>&lt; 0.1</td>
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<tr>
<td>Decaying wood</td>
<td>3.9</td>
<td>0.3</td>
</tr>
<tr>
<td>Tree bark/twigs</td>
<td>0.5</td>
<td>0.9</td>
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<tr>
<td>Herbaceous stems</td>
<td>0.1</td>
<td>25.0</td>
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<tr>
<td>Root/ root epidermis</td>
<td>&lt; 0.1</td>
<td>1.7</td>
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<tr>
<td>Flowers</td>
<td>&lt; 0.1</td>
<td>1.1</td>
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<td>Fungus</td>
<td>&lt; 0.1</td>
<td>0.2</td>
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<tr>
<td>Dead leaves</td>
<td>&lt; 0.1</td>
<td>0.2</td>
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*aData adapted from Group 4 in the Virungas (Watts 1984).*

Similarly, when we considered the weighted nutritional contribution of each food to the diet, the Bwindi and Virunga gorillas ate diets that were nearly identical nutritionally (Table 3). The mean (±SD) individual diets within each group for protein: Bwindi 18.2 ± 2.4; Virunga 17.2 ± 0.5, NDF: Bwindi 42.9 ± 3.7; Virunga 41.1 ± 1.6, HC: Bwindi 10.8 ± 0.35; Virunga 12.5 ± 0.3, CS: Bwindi 17.5 ± 1.9; Virunga 19.8 ± 1.2, TNC: Bwindi 18.8 ± 1.7; 18.2 ± 0.64 (Table 3).

DISCUSSION

We found that mountain gorillas living in two geographically separated habitats consumed different plant species and plant parts, yet their diets and staple foods contained similar concentrations of nutrients. Virunga gorillas in PNV consumed fewer staple foods from different plant species than did gorillas in BNP. Similarly, fewer foods and less fruit formed the staple diet of cercopithecine monkeys (Cercopithecus mitis kandti) living in the Virunga Region compared with those in Kibale National Park, Uganda (Cercopithecus mitis stuhlmanni) (a middle-elevation forest with a diverse community of fruiting trees), yet their diets were nutritionally similar (Twinomugisha et al. 2006). That the diet of a single species can vary between geographically separated areas, and on spatial and temporal scales within the same area has been documented for many taxa, including primates (Chapman et al. 2002a, b; Hill & Dunbar 2002, Russo et al. 2005), and gorillas specifically (Doran & McNeilage 1998, Ganas et al. 2004, McNeilage 2001, Rogers et al. 2004). However, it is possible that groups or populations of the same species living in different habitats that eat different foods consume diets containing similar proportions of nutrients. Therefore, while gorillas may consume diets that differ by plant species and part, the nutritional quality of their diets may be quite similar (Conklin-Brittain et al. 1998, Dierenfeld & McCann 1999). Our study provides further evidence that broad food classes and dietary categories such as frugivory and folivory are not necessarily useful in predicting diet nutritional quality (Barton et al. 1993, Ofedal 1991).

Like many other primates, both of these gorilla groups ate a diverse diet. The Virunga gorilla group ate 75 foods from 38 plant species (Watts 1984) and the Bwindi group ate 158 parts from 107 plant species (Rothman 2006). However, we found that in both groups the bulk of gorilla diets were comprised of only a few species, suggesting that dietary diversity and composition tells us little about nutritional quality. Bwindi gorillas are more frugivorous than Virunga gorillas (Stanford & Nkurunungi 2003). Our wet-weight estimates suggest that the annual diet of the Bwindi gorillas contains 15.3% fruit. Myrianthus holstii contains more sugar than other fruits in the Bwindi
Table 2. Mean concentrations of nutrients (percentage of dry matter) in the staple foods eaten by Virunga and Bwindi mountain gorillas. Key: CP = crude protein; NDF = neutral detergent fibre; HC = hemicellulose; CS = cellulose; TNC = total non-structural carbohydrates; HL = herbaceous leaves; HS = herbaceous stems; F = fruit; TL = tree leaves; PL = peel; DW = decaying wood; P = pith.

<table>
<thead>
<tr>
<th>Part</th>
<th>% Intake</th>
<th>CP</th>
<th>NDF</th>
<th>HC</th>
<th>CS</th>
<th>TNC</th>
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<td>Virunga gorillas</td>
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<td>C. ruvunzorensis (Cortesi) Chiov.</td>
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<td>C. nyasanthus (S. Moore) R. E. Fr.</td>
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<td>L. alataipes Hook. f.</td>
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<td>U. massaica Mildbr.</td>
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<td>H. formosissimum Sch.Bip.</td>
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<td>U. hygrosedron (Hochst. ex A. Rich.) Wedd.</td>
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<td>M. foetida Schumach./M.pterocarpa A. Rich.</td>
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<td>Decaying wood pieces</td>
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*Intake data for the Virunga gorillas adapted from Group 4 in the Virungas (Watts 1984).

gorilla diet (Rothman et al. 2006a), and comprises over half of wet-weight fruit intake. In an earlier study, M. holstii seeds were found in 13.9% of faecal samples (Nkurunungi 2005). Although fruits are usually less fibrous than leaves, the three fruits included in the staple diet of the gorillas were similar in fibre to staple herbaceous leaves. In the Bwindi gorilla diet, fruits also contained the same amounts of protein as tree leaves (Rothman et al. 2006a) and in a neighbouring forest red colobus and red-tailed monkey consumed leaves that had similar sugar contents to fruit (Danish et al. 2006). These results suggest that categorizing gorilla non-fruit food items as ‘fibrous’ (Doran et al. 2002, Ganas et al. 2004, Remis 1997, Robbins et al. 2006) makes an implicit assumption that non-fruit foods have more fibre than fruit, and that fruit-dominated diets vary nutritionally from leaf-dominated diets, which was not the case here. Additionally, the considerable inter- and intraspecific

Table 3. Nutrient concentrations (percentage of dry matter intake) in the diets of mountain gorillas and other hindgut-fermenting primates. Key: CP = crude protein; NDF = neutral detergent fibre; HC = hemicellulose; CS = cellulose; TNC = total non-structural carbohydrates.

<table>
<thead>
<tr>
<th>Gorilla species</th>
<th>CP</th>
<th>NDF</th>
<th>HC</th>
<th>CS</th>
<th>TNC</th>
</tr>
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<tbody>
<tr>
<td>Virunga gorilla</td>
<td>18.2</td>
<td>42.9</td>
<td>10.8</td>
<td>17.5</td>
<td>18.8</td>
</tr>
<tr>
<td>Bwindi gorilla</td>
<td>17.2</td>
<td>41.2</td>
<td>12.5</td>
<td>19.8</td>
<td>18.2</td>
</tr>
<tr>
<td>Howler monkey (A. pallia Gray 1849)</td>
<td>12.4</td>
<td>27.5</td>
<td>11.8</td>
<td>12.3</td>
<td>35.3</td>
</tr>
<tr>
<td>Blue monkey (Cercopithecus mitis stuhlmanni Matschie 1893)</td>
<td>17.6</td>
<td>32.3</td>
<td>12.0</td>
<td>11.9</td>
<td>34.0</td>
</tr>
<tr>
<td>Mangabey (Lophocebus albigena Johnstoni Gray 1850)</td>
<td>16.3</td>
<td>32.0</td>
<td>11.8</td>
<td>12.3</td>
<td>35.3</td>
</tr>
<tr>
<td>Bonobo (P. paniscus Schwarz 1934)</td>
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<td>26.8</td>
<td>10.1</td>
<td>11.5</td>
<td>36.5</td>
</tr>
<tr>
<td>Red-tailed monkey (Cercopithecus ascanius schm siti Matschie 1892)</td>
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<td>31.3</td>
<td>11.4</td>
<td>11.6</td>
<td>36.5</td>
</tr>
<tr>
<td>Chimpanzee (P. troglodytes schweinfurthii Giglioli 1872)</td>
<td>9.5</td>
<td>33.6</td>
<td>13.7</td>
<td>11.8</td>
<td>38.8</td>
</tr>
</tbody>
</table>

*From this study.
[b]Milton (1979a)*[mean value of commonly eaten leaves that comprise 48% of the diet).
[c]Mean value of commonly eaten foods.
[d]Dorakin-Brittain et al. (1998), values are room temperature DM (20 °C).
variability in the nutritional content of primate foods that has been demonstrated at different spatial and temporal scales (Chapman et al. 2003, Worman & Chapman 2005) needs to be considered. Despite the fact that gorillas in PNV are more folivorous than those in BINP, they did not consume more fibre.

Of the staple foods eaten by gorillas in both habitats, herbaceous leaves contributed the most wet weight mass and CP to the diet. Milton (1979) proposed that the protein:fibre ratio was the single most important factor for food selection of primates and building on this work, several studies have emphasized the importance of protein and fibre in the diets and habitats of primates (Chapman et al. 2004, Davies et al. 1988, Ganzhorn 1992, Oates et al. 1990). Across study sites there is evidence that gorillas eat foods higher in CP than non-plant foods, suggesting that high-protein foods, and herbs in particular, are important for gorillas and other apes (Calvert 1985, Malenky & Stiles 1991, Rogers et al. 1990, Wrangham et al. 1991). In Cameroon, lowland gorillas selected foods that had the most CP, were most digestible (determined from in vitro digestibility analysis) and had less lignin than foods avoided (Calvert 1985). Similarly, gorilla foods in Lopé, Gabon, contained more CP and less fibre than non-foods (Rogers et al. 1990).

Foods frequently eaten by Bwindi gorillas have more CP than other diet items (Rothman et al. 2006b) but in PNV, availability and digestibility (determined from in vitro digestibility analysis of gorilla foods) are important selection criteria for gorillas (Plumptre 1995), and CP is not as important when non-foods and foods are compared, likely because most of the available plants in PNV are also high in CP. It may be that the high protein concentrations in ape diets is simply a consequence of the availability of high-protein foods in their habitats, while other nutrients might be limiting and apes are eating high-protein foods to meet other nutritional needs. Just because a high-protein diet is consumed does not necessarily mean that it is required; animals such as gorillas that have a long life span and slow growth require a relatively low CP diet (Oftedal 1991). Wild chimpanzees consumed diets containing 9.5% CP and the average leaf consumed by orang-utans is 11.9% CP. Further studies are needed to investigate protein quality and amino acid composition (Milton & Dintzis 1981). For example, in Kibale National Park forest elephants ate a diet of 22% CP (Rode et al. 2006), which is quite high compared to their estimated requirements, while another nearby population of elephants ate a diet of 13% CP (Jachmann 1989). It is likely that elephants in Kibale were ingesting high-protein foods because these foods met other nutritional requirements, particularly minerals (Rode et al. 2006). Several other nutritional factors need to be considered in assessing what might be limiting in gorilla diets, such as energy, as seen with orang-utans (Knott 1998) and micronutrients such as sodium (Rode et al. 2003). The Bwindi gorilla group we studied ate decaying wood, which provided 95% of their sodium intake, a micronutrient that was limited in their diet (Rothman et al. 2006c).

The nutrient concentrations in the diets of other hindgut-fermenting primates were compared with those of gorillas (Table 3). Due to its high concentration of hemicellulose (18.7% DM) and cellulose (28.1% DM), the consumption of pith probably provides energy to chimpanzees when fruits are not available (Wrangham et al. 1991). Piths eaten by the Virunga gorillas were also high in hemicellulose and cellulose and may be a valuable energy source for this group of mountain gorillas. Pith, decaying wood and the frequently eaten outer peel of the herb *Urera* had high concentrations of hemicellulose (Table 3), similar to the piths in the Virunga gorilla diet and chimpanzee diet (Wrangham et al. 1991). Our study suggests that hemicellulose concentrations in the diets of mountain gorillas are similar to that of chimpanzees and cercopithecines, but that cellulose concentrations in the diets of gorillas are higher and TNC concentrations are lower than other primates. Based on captive studies, chimpanzees can digest about 60% of the hemicellulose and 38% of the cellulose in their diets on a high-fibre diet (34% NDF) (Milton & Demment 1988), indicating that hemicellulose and cellulose are important energy sources for chimpanzees. Like chimpanzees, gorillas have a large colon relative to other segments of their gastrointestinal tract (Milton 1985), harbour fibre-digesting bacteria (Frey et al. 2006) and have a relatively slow passage rate (∼50 h) to facilitate fibre digestion (Remis 2000, Remis & Dierenfeld 2004). In general, the fibre concentrations of wild chimpanzee diets were lower than gorilla diets (Table 3), and the diets of gorillas were lower in TNC than those of chimpanzees and other more frugivorous primates. Although the large body size of gorillas is likely important for fibre digestion, small-sized cercopithecines, such as red-tailed and blue monkeys may also have an increased capacity for digesting fibrous foods based on their long retention times (Lambert 2002), and howler monkeys have considerable fermentation returns (Milton 1983, Milton & McBee 1983, Milton et al. 1980). No generalizations can be made regarding digestive strategies and body size without more data on fibre digestibility across the Primate Order (Lambert 1998, Milton 1981, 1998).

Our study provides further evidence that understanding the dietary diversity alone is insufficient to assess the quality of food species and evaluate habitat suitability (Twinomugisha et al. 2006). In both BINP and PNV, gorilla diets contained similar concentrations of protein, fibre and non-structural carbohydrates. While the diets of gorillas and nutrients in dietary items differ across study sites (Rothman et al. 2006b), we do not know if the nutritional proportions of their diets vary as well, and
whether a variation might change seasonally or spatially within habitats. Unfortunately, it will be increasingly important to understand the adaptability of gorillas in a range of habitats, as tropical forests are progressively being anthropogenically modified. Presently both the BINP and PNV are well protected, but the same cannot be said for other gorilla habitats: habitat loss, civil unrest, encroachment and disease have seriously affected mountain gorilla populations in the past (Plumptre & Williamson 2001). The capacity for gorillas and other primates to survive in marginal habitats is likely dependent on their ability to avoid nutritional stress.

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