

CHAPTER NINE

Nutritional Aspects of the Diet of Wild Gorillas

How Do Bwindi Gorillas Compare?

*Jessica M. Rothman, Alice N. Pell,
J. Bosco Nkurunungi, and
Ellen S. Dierenfeld*

INTRODUCTION

The foraging behaviors and diet selection of animals in their natural habitats have been the focus of ecological field studies for decades. Diet affects the lifetime fitness of primates and reproductive performance, an essential consideration for highly endangered species (Altmann, 1991, 1998).

The abundance of tropical arboreal folivores is positively correlated with the protein content of leaves and negatively correlated with fiber (Waterman *et al.*, 1988; Oates *et al.*, 1990; Ganzhorn, 1992; Chapman *et al.*, 2002; Chapman *et al.*, 2004). Mountain gorillas in Rwanda prefer foods that are high in protein and their movement patterns are related to the quality and availability of foods (Vedder, 1984). There is evidence that some primates in tropical forests

Jessica M. Rothman and Alice N. Pell • Department of Animal Science, Cornell University, Ithaca, NY 14853, USA **J. Bosco Nkurunungi** • Department of Zoology, Makerere University, Kampala, Uganda **Ellen S. Dierenfeld** • Department of Animal Science, Cornell University, Ithaca, NY 14853 and St. Louis Zoo, 1 Government Drive, St. Louis, MO 63110, USA.

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have difficulty obtaining required amounts of certain minerals such as sodium (Rode *et al.*, 2003). In western forest clearings, gorillas groups congregate with other animals to seek out water plants that are high in minerals (Magliocca and Gautier-Hion, 2002). Understanding of nutrient requirements and which plants are preferentially consumed can be used to establish priorities for habitat conservation.

Approximately 320 gorillas live in Bwindi Impenetrable National Park (BINP), a 360-km² forest “fragment” in southwestern Uganda (McNeilage *et al.*, 1998, 2001). Bwindi gorillas are currently classified as mountain gorillas (*Gorilla beringei*) (Groves, 2001). They are genetically similar to populations of mountain gorillas in the Virunga Volcanoes area in Rwanda (Garner & Ryder, 1996; Jensen-Seaman & Kidd, 2001), although some have questioned their taxonomic classification at the subspecies level (Sarmiento *et al.*, 1996).

Here, we review the nutritional ecology of gorillas through a discussion of diet, food choice, and digestive anatomy. We compare the nutritional content of foods eaten by gorillas living in different habitats to those consumed by the Bwindi gorillas and discuss the nutritional factors that may influence food selection. The effects of the physical environment on the nutritive value of gorilla foods and some of the analytical challenges that arise on cross-study comparisons are also considered.

DIET AND FORAGING STRATEGY OF GORILLAS

The composition of the diet of wild gorillas has been studied at several sites across central Africa. An initial understanding of gorilla feeding ecology was obtained from the mountain gorillas (*Gorilla beringei beringei*) in the Virunga region on the borders of Rwanda, Democratic Republic of Congo, and Uganda, an area characterized by afro-alpine vegetation with few or no fruiting trees. These gorillas are folivores whose diet consists primarily of a few species of herbaceous leaves, vines, stems, and shoots (Schaller, 1963; Fossey & Harcourt, 1977; Vedder, 1984; Watts, 1984, 1990, 1996; McNeilage, 1995, 2001). Thistle, wild celery, and *Galium* spp. are primary components of the diets of these gorillas (Watts, 1984). Diet remains relatively constant throughout the year, except for the seasonal consumption of bamboo shoots. Groups of mountain

gorillas at lower elevations in the Virungas eat different, more varied foods and more fruit than those at higher altitudes (McNeilage, 2001).

In the Kahuzi-Biega National Park of the Democratic Republic of Congo, eastern lowland gorillas (*Gorilla beringei graueri*) eat more fruit than the Virunga population, reflecting the greater distribution and availability of fruit in the Kahuzi-Biega habitat (Yamagiwa *et al.* 1994, 2003). When fruits are unavailable, these gorillas supplement their diet with herbaceous vegetation and the bark of trees and woody lianas (Casimir, 1975; Yamagiwa *et al.*, 1994).

Overall, the western gorilla (*Gorilla gorilla gorilla*) diets are more diverse than those of the mountain gorillas; as many as 230 different plant parts of 180 species are consumed at some locales (e.g. Williamson *et al.*, 1990; Tutin & Fernandez, 1993; Nishihara, 1995; reviewed in Doran & McNeilage, 1998; Doran *et al.*, 2002; Rogers *et al.*, 2004). If fruits are available, they are consumed regularly. Sweet fruits are preferred, but astringent fruit is eaten when sugary fruits are scarce (Tutin & Fernandez, 1985; Rogers *et al.*, 1990; Williamson *et al.*, 1990; Nishihara, 1995; Remis, 1997; Remis *et al.*, 2001; Goldsmith, 1999; reviewed in Doran & McNeilage, 1998, Doran *et al.*, 2002, Rogers *et al.*, 2004). Along with fruit, western gorillas also eat large quantities of terrestrial vegetation throughout the year (Doran & McNeilage, 1998; Rogers *et al.*, 2004). In some areas, gorillas forage in swampy open forest clearings regularly to consume the readily available ripe fruits (Doran-Sheehy *et al.*, 2004), and/or mineral-rich water plants (Kuroda *et al.*, 1996; Magliocca & Gautier-Hion, 2002).

The altitude of the range of the Bwindi gorillas, between 1160 and 2600 m above sea level is similar to that of the gorillas living in the lower ranges of the Virungas and the higher ranges of the eastern lowland populations. Bwindi gorillas eat more diverse diets than do the gorillas in the Virungas. Between August 2002 and 2003, a single Bwindi group (Kyagurilo) consumed at least 160 parts (leaves, stems, fruits, etc.) of 105 different plant species (J. M. Rothman, unpublished data), and, in earlier years, the same group consumed at least 133 parts of 96 species, some of which differed from those eaten in the later study (Stanford & Nkurunungi, 2003). Gorilla groups at different sites within Bwindi consumed a more varied diet than the Kyagurilo group (Ganas *et al.*, 2004).

The Bwindi gorillas consume more fruit than the Virunga gorillas, but less fruit than the eastern and western lowland gorillas (Goldsmith, 2003;

Robbins & McNeilage, 2003), an observation based on the presence of seeds in fecal samples. Greater fruit consumption is likely a result of fruit availability (Goldsmith, 2003; Robbins & McNeilage, 2003; Stanford & Nkurunungi, 2003; Nkurunungi, 2005). Bwindi gorillas depend heavily on terrestrial herbaceous vegetation (Goldsmith, 2003) and consume it daily, even when fruit is in abundance.

In addition to herbaceous vegetation and fruits, Bwindi gorillas also consume mature and young true leaves, woody lianas, bark, epiphytes, moss, and a fungus. Bwindi gorillas spend some of their foraging time eating dry, decaying wood and bark (Goldsmith, 2003; Stanford & Nkurunungi, 2003), which has little obvious nutritional value (J. M. Rothman *et al.*, in press).

Insectivory and geophagy have been recorded at most study sites (Insectivory: Tutin & Fernandez, 1983, 1992; Harcourt & Harcourt, 1984; Carroll, 1986; Watts, 1989; Nishihara & Kuroda, 1991; Yamagiwa *et al.*, 1991; Kuroda, 1992; Nishihara, 1992; Kuroda *et al.*, 1996; Remis, 1997; Deblauwe *et al.*, 2003; Geophagy: Schaller, 1963; Fossey & Harcourt 1977; Watts, 1984, 1989; Mahaney *et al.*, 1990, 1995a,b; Williamson *et al.*, 1990). Insect consumption has been observed rarely, among both Bwindi and Virunga gorillas (Fossey & Harcourt, 1977; Harcourt & Harcourt, 1984; Watts, 1984, 1989; Stanford & Nkurunungi, 2003; Ganas & Robbins, 2004). In Bwindi, groups at lower elevations in Bwindi seasonally ate ants more frequently than did a group living at a higher elevation (Ganas & Robbins, 2004). Western gorillas eat insects more frequently than do mountain gorillas. In Cameroon, 74% of 34 fecal samples contained insect remains (Deblauwe *et al.*, 2003). Geophagy may be a means to adsorb plant toxins in the diet or relieve stomach discomfort (Krishnamani & Mahaney, 2000). Occasionally, gorillas consumed rocks and soil in Bwindi, either deliberately or accidentally (Stanford & Nkurunungi, 2003; J. M. Rothman, unpublished data).

Coprophyagy by wild gorillas is rare. In the Virungas, only 25 instances of coprophagy occurred over thousands of hours of observation (Harcourt & Stewart, 1978). Similarly, the Bwindi gorillas were observed reingesting their own feces only twice during a year of regular observations and a juvenile ate the feces of another individual once (J. M. Rothman, unpublished data). Because this behavior is so uncommon, its nutritional significance is limited. Proposed reasons for gorilla coprophagy include boredom or the craving for warm food on cold days (Harcourt & Stewart, 1978). The rare instances of coprophagy in Bwindi occurred when the gorillas were eating fruit, and the ingested feces

contained large amounts of seeds. It is possible that the gorillas were reingesting the feces to gain nutrients from the seeds (Krief *et al.*, 2004).

DIGESTIVE ANATOMY AND PHYSIOLOGY

Gorillas are the largest extant nonhuman primate. Male gorillas weigh between 139 and 278 kg, and mature females weigh between 72 and 98 kg (National Research Council, 2003). Mountain gorillas are larger in size and mass compared to lowland gorillas. Captive gorillas weigh more than wild gorillas, but the weight of the latter tends to be estimated (Leigh, 1994).

The anatomy of the gorilla provides a large capacity for microbial fermentation and subsequent energy gain through the absorption of volatile fatty acids and microbial protein (Stevens & Hume, 1995). Gorillas have a large, pouched colon, which, based on a male specimen, is about 200 cm long and has a maximum width of approximately 30 cm in the lower ascending colon (Steiner, 1954). While gorillas are frequently considered to be ceco-colonic fermenters, their cecum is relatively small: cecal volume is only about 14% that of the colon, typical of animals that are folivorous and frugivorous (Chivers & Hladik, 1980).

On a captive zoo diet of cultivated fruits, commercially prepared primate biscuits, mixed greens, and hay, captive lowland gorillas had a mean retention time of 50 h, with a range of 16.5–136 h measured with a chromium marker (Remis, 2000). Particulate material is retained longer than liquid material (Remis & Dierenfeld, 2004). When gorillas were fed a diet of 30% neutral detergent fiber (NDF) and 7% acid detergent fiber (ADF), NDF digestibility was 70% but, when the diet contained 30% NDF and 19% ADF, the apparent digestibility of the diet decreased to 45% (Remis & Dierenfeld, 2004). Energy derived from microbial fermentation in the form of short-chain fatty acids may provide between 30 and 60% of the maintenance energy requirements of gorillas (Popovich *et al.*, 1997). Most fiber digestion in the gorilla probably occurs in the colon, but there is no research on sites of fermentation in the gorilla. Although gorillas preferentially consume nutritious, readily digestible fruits and herbaceous leaves, they can subsist on fibrous fruit and vegetation when succulent fruits are not in season or available in a habitat. Mobilization and repletion of body reserves provide nutritional safety nets to many species of animals faced with recurring feast or famine conditions. The extent to which

gorillas lose weight during lean times and regain it during times of abundance has not been established.

CROSS-SITE COMPARISONS

Environmental Effects on Nutritional Composition

The nutritional composition of plants is affected greatly by external factors in the environment. Soil, water, carbon dioxide, soil nutrients, stress, disease, predation, and weather all influence plant metabolism and the production of resistant structures (Van Soest, 1994). For example, plants that grow at higher temperatures accumulate structural cell wall more quickly than those that grow at lower temperatures. In cooler eastern afro-alpine gorilla habitat, leaves contained more protein and less fiber, were more digestible and richer in phosphorous than foliage from western rain forest trees (Waterman *et al.*, 1983).

Considerable between- and within-plant variation in chemical composition has been observed in Kibale forest trees (Chapman *et al.*, 2003). Canopy leaves eaten by lemurs in Madagascar contained more protein than leaves from undisturbed areas in the same forest (Ganzhorn *et al.*, 1995). The nutrients in the leaves eaten by colobus monkeys changed seasonally, which influenced the monkeys' food choices (Baranga, 1983). Therefore, a chemical analysis provides only a snapshot of the nutrient content of a particular plant at a single point in time. Careful sampling protocols are needed to ensure that the samples collected reflect what the target animal actually consumed, and that seasonal and spatial variation in food composition are accounted for (Chapman *et al.*, 2003).

Standardizing Analytical Techniques

Standardization of the techniques used to measure the nutrient content of primate foods and nonfoods in habitats is necessary to ensure that cross-site comparisons are valid (Chapman *et al.*, 2003). Freeze-drying, a very effective means of preserving plants, frequently is not an option at field stations, but drying at temperatures less than 45°C in low light minimizes the effects of temperature and oxidation (Palmer *et al.*, 2000). Physical processing, including the type of mill and size of the screen used, also is an important consideration because particle size affects many chemical analyses (Mullin & Wolynetz, 1995).

Choosing an appropriate analytical technique is essential. While a comprehensive analysis of appropriate techniques for measuring the nutrient content of

primate foodstuffs is beyond the scope of this review, there are a few problems with commonly used analytical techniques that merit consideration.

Condensed Tannins

Many different methods are used to estimate the condensed tannin content in animal diets (Waterman & Mole, 1994), each of which has its strengths and limitations. The butanol-HCl assay to measure condensed tannins has been the most commonly used for the tannin analysis of primate foods (Porter *et al.*, 1986). In this spectrophotometric assay based on oxidative depolymerization of the condensed tannin and measurement of red anthocyanidins, the tannin usually is extracted with acetone or methanol. The quantity of tannin is estimated using a standard curve (absorbance vs. tannin concentration) of a known compound, usually quebracho. However, reliance on external standards may pose analytical problems because of the great variation in the structure and biological activity of tannins. When external standards are used, it is implicitly assumed that all tannins have the same absorbance per unit mass as the standard. In some plants with high levels of biologically active tannins such as *Desmodium ovalifolium*, the estimates of tannin content may be off by a factor of 5 if a quebracho standard is used instead of relying on an internal standard (Giner-Chavez *et al.*, 1997). The case for extracting tannins from each plant species to develop internal standard curves has been forcefully made by Giner-Chavez *et al.* (1997) and Schofield *et al.* (2001). Controlling for color interference in samples is also necessary because many fruits and flowers contain red pigments that interfere with condensed tannin measurements (Watterson & Butler, 1983).

In Vitro Dry Matter Digestibility

Choo *et al.*'s (1981) *in vitro* digestibility method using a fungal cellulase is often used to estimate the digestibility of primate foods. Although fungal cellulase assays permit easy comparisons of foods and minimize interlaboratory variation, fibrolytic enzymes of fungi differ from those in bacteria, resulting in different estimates of digestibility. The various fungal and bacterial enzymes in an animal's gut act synergistically to digest a mixed diet (Béguin & Aubert, 1994). *In vitro* assays that use digestive fluids from domesticated ruminants have the advantage of using live microbial cultures to simulate digestion, but

microbial populations and their activities are affected by the physiological status and diet of individual animals (Palmer *et al.*, 1976; Pehrson & Faber, 1994). It has not been established that the species, and activities, of ruminal microbes are similar to those from the ceco-colon, which is likely the primary fermentation site in the gorillas.

Digestibility also can be estimated on the basis of plant lignin content. Lignin is largely indigestible by both mammals and microbes, so high lignin foods are poorly digested (van Soest, 1994). In vitro methods may provide a means of ranking feed ingredients by digestibility, but the actual data may differ from in vivo observations. Animals eat mixed diets and the associative effects of one ingredient often affects the digestibility of another. Therefore, the application of these digestibility numbers to estimate intake or other parameters of interest should be performed cautiously.

Lipids

In the few studies with measurements of the fat content of primate diets, the ether extract method has usually been used (Horwitz, 2000). While this method is appropriate for the measurement of triglycerides, plants have non-fat components that are extracted by ether, such as wax, cutin, galactose, chlorophyll, glycerol, and other compounds that cannot be saponified and that are frequently indigestible (Palmquist & Jenkins, 2003). In a study by Palmquist and Jenkins (1980), forage leaves contained 5.3% fat as determined by ether extract, but 57% of the ether extract comprised nonnutritive substances. In the gorilla literature, clarification of how much of the ether extract consists of fatty acids is important to resolution of the ongoing debate about whether gorillas choose fatty fruits (Calvert, 1985) or avoid them (Rogers *et al.*, 1990). The fatty acid protocol suggested by Sukhija and Palmquist (1988) (protocol described in Palmquist & Jenkins, 2003) circumvents this problem.

NUTRITIONAL COMPOSITION OF FOODS EATEN BY GORILLAS

The nutritional composition of foods eaten by gorillas in different habitats has been studied in some detail across study sites. Remis (2003) summarized

the roles of habitat, body size, and preference on gorilla nutrition, with an emphasis on captive and wild western gorillas. In this section, we provide general comments on the nutritional characteristics of leaves, fruits, and stems eaten by gorillas and review the nutritional composition of foods and aspects of food selection in different habitats across Africa. The mean values for nutrients at each site for leaves, fruit, and stem are compared in Table 1.

Nutritional Characteristics of Gorilla Foods

Across gorilla habitats, leaves contained more crude protein (16–26% on a dry matter [DM] basis) than stems (3–17% DM) and fruits (6–11% DM) (Casimir, 1975; Goodall, 1977; Waterman *et al.*, 1983; Calvert, 1985; Rogers *et al.*, 1990; Plumptre, 1995; Popovich *et al.*, 1997; Remis *et al.*, 2001; Rothman *et al.*, in press) (Table 1). This is not surprising, since leaves contain appreciable amounts of rubisco, the most common protein in the world that is involved in photosynthesis.

Fruits are high in energy because they usually contain large amounts of easily digested nonstructural, water-soluble carbohydrates in the form of sugars. Fruits eaten by gorillas across sites varied in their sugar content (<70% DM), but fruits contained more sugars than leaves (<12% DM), stems (<31% DM), and bark (<10% DM) across sites (Calvert, 1985; Rogers *et al.*, 1990; Remis *et al.*, 2001; Rothman *et al.*, in press).

All populations of gorillas select some stems in their diet and eat the whole stem or inner core (pith) after removing the bark. Usually, whole stems are fibrous, with a succulent inner core. Young bark may be protein-rich and contains soluble carbohydrates, but, as the bark ages, it becomes less digestible because of the synthesis of complex structural carbohydrates.

Western Gorillas

The available data on the chemical constituents of western lowland gorilla foods highlight the nutritional variability in foods eaten by gorillas living in lowland rain forests (Rogers *et al.*, 1990; Popovich *et al.*, 1997; Remis *et al.*, 2001) and logged/disturbed forests (Calvert, 1985) in West Africa.

In coastal Cameroon, gorillas forage for foods that are higher in protein, more digestible, and lower in lignin compared to foods not chosen. Shoots

Table 1. Mean nutrient content of foods eaten by gorillas across sites

| Subspecies | <i>Gorilla g. gorilla</i> | | <i>Gorilla b. graueri</i> | | <i>Gorilla b. beringei</i> | | | | |
|--|------------------------------|--------------------------|-----------------------------|-----------------------------|----------------------------|-----------------------------|-------------------------------|-------------------------------|-----------------------------|
| | Campo, Cameroon ¹ | Lopé, Gabon ² | Bai Hakou, CAR ³ | Bai Hakou, CAR ⁴ | Kahuzi, DRC ⁵ | Tshibinda, DRC ⁶ | Karisoke, Rwanda ⁷ | Karisoke, Rwanda ⁸ | Bwindi, Uganda ⁹ |
| No. of species in diet/No. of parts in diet† | 50/69 | 134/144 | >200/>300 | 138/239 ¹⁰ | 121/194 ¹¹ | >104/>160 | 75/38 ¹² | NA** | >133/>96 ¹³ |
| No. of parts analyzed† | 36 | 95 | 31 | 68 | 14 | 39 | 33 | 18 | 125 |
| Leaves | | | | | | | | | |
| DM digestibility | 45.0 | — | — | — | — | 66.4 | 56.5 ^b | 56.7 ^b | — |
| Protein | 16.6 ^{a,b} | 17.8 ^a | 17.3 ^a | 18.9 ^a | 20.4 ^{a,b} | 25.3 ^b | 15.5 ^a | 25.6 ^b | 16.9 ^a |
| Fiber: | | | | | | | | | |
| NDF | 46.1 ^a | — | 64.2 ^b | 64.0 ^b | — | — | — | — | 40.2 ^a |
| ADF | 42.6 ^{a,b} | 30.1 ^{b,c} | 47.7 ^a | 47.5 ^a | — | — | 35.5 ^b | — | 25.5 ^c |
| Lignin | 19.4 ^a | — | — | 25.2 ^a | — | — | — | — | 9.1 ^b |
| Condensed tannin† | 50% | 68% | — | 13%*** | — | — | 14.3% | — | 38% |
| Fruits | | | | | | | | | |
| DM digestibility | 28.4 ^a | — | — | — | — | 70.7 ^b | — | — | — |
| Protein | 6.2 ^{a,b} | 6.11 ^a | 5.7 ^{a,b} | 8.4 ^{b,c} | 7.5 ^{a,b,c} | 13.1 ^{b,c} | — | — | 9.8 ^c |
| Fiber: | | | | | | | | | |
| NDF | 64.6 ^{a,b} | — | 78.7 ^a | 59.3 ^b | — | — | — | — | 42.9 ^c |
| ADF | 44.8 ^{a,b} | 23.9 ^c | 65.4 ^a | 45.3 ^b | — | — | — | — | 28.0 ^c |
| Lignin | 26.9 ^a | — | — | 24.9 ^a | — | — | — | — | 13.3 ^b |
| Condensed tannin† | 38% | 93% | — | 41%*** | — | — | — | — | 38% |

| | | | | | | | | |
|-------------------------------------|---------------------|---------------------|-------------------|---------------------|---|---|---------------------|--------------------|
| Stems | | | | | | | | |
| DM Digestibility | 41.1 ^a | — | — | — | — | — | 41.1 ^a | — |
| Protein | 7.2 ^a | 5.1 ^{a,b} | 3.4 ^b | 16.9 ^c | — | — | 6.2 ^{a,b} | 6.4 ^{a,b} |
| Fiber: | | | | | | | | |
| NDF | 54.4 ^a | — | 80.4 ^b | 67.4 ^b | — | — | — | 53.3 ^a |
| ADF | 41.6 ^{a,b} | 44.6 ^{a,b} | 54.5 ^a | 49.2 ^{a,b} | — | — | 49.3 ^{a,b} | 34.3 ^b |
| Lignin | 9.4 ^a | — | — | 26.0 ^b | — | — | — | 5.5 ^a |
| Condensed tannin[†] | 10% | 100% | — | 0%*** | — | — | 9% | 25% |

* Mean nutrient and dry matter (DM) digestibility values are reported on a DM basis (% DM of the diet) and were recalculated to permit uniform comparisons (Casimir, 1975; Goodall, 1977; Waterman *et al.*, 1983; Calvert, 1985; Rogers *et al.*, 1990; Plumptre, 1995a,b; Popovich *et al.*, 1997; Remis *et al.*, 2001; Rothman *et al.*, in review).

** Study based on food intake of large mammalian herbivores, based on foods identified from gorilla dung.

*** Based on Remis *et al.*, 2001, results of radial diffusion assay.

† As reported by the study unless otherwise noted.

‡ Percent of species analyzed that contain condensed tannins.

^{a,b,c} Denotes statistical significance, using Student Neuman-Keul's multiple range and Mann-Whitney *U* test at $P < 0.05$.

¹ Calvert, 1985; ² Rogers *et al.*, 1990; ³ Popovich *et al.*, 1997; ⁴ Remis *et al.*, 2001; ⁵ Casimir, 1975; ⁶ Goodall, 1977; ⁷ Waterman *et al.*, 1983; ⁸ Plumptre, 1995;

⁹ Rothman *et al.*, in review; ¹⁰ Remis, 1997; ¹¹ Yamagiwa *et al.*, 1994; ¹² Watts, 1984; ¹³ Stanford & Nkurunungi, 2003.

and stems eaten frequently, were lower in lignin (shoots: 11.3%; stems: 11.3%) and higher in moisture (shoots: 89.0%; stems: 86.6%) compared to the rest of the diet, and both rarely contain phenolic compounds (Calvert, 1985). Gorillas preferentially ate mature *Aframomum* fruits that did not contain tannins over immature fruits with tannins (Calvert, 1985). The gorillas also eat the pith of wild and cultivated banana trees, which were higher in protein and gross energy than the discarded outer stem/bark.

In Lopé, Gabon, Rogers *et al.* (1990) determined the nutritional composition of foods eaten by gorillas in lowland rainforest. Gorillas in Lopé typically ate sugary fruits; protein-rich leaves; and succulent, fibrous inner stems. Leaves eaten were lower in fiber and higher in protein than those that were not eaten. Like the gorillas in Cameroon, the Lopé gorillas ate large quantities of pith, which were high in water-soluble carbohydrates (<20.3%) (Rogers *et al.*, 1990). Bark, which contains up to 17% crude protein, is a source of protein for Lopé gorillas, particularly when young leaves are not available (Rogers *et al.*, 1990). Lopé gorillas ate some foods with high levels of ADF (~50%), especially when succulent, sweet fruits were not available, but the most fibrous parts of the plants were discarded. The fruits that Lopé gorillas ate do not have significantly higher sugar content than those eaten less frequently. Unripe fruits that were avoided did not have significantly lower sugar content, but were tougher and more astringent, which may have contributed to their unpalatability. The parts of eaten fruits that were discarded, such as the outer skin of some fruits whose flesh was eaten, contained less sugar and had higher levels of fiber and secondary compounds (Rogers *et al.*, 1990).

Foods eaten by gorillas in the lowland rainforests of Dzangha-Sangha Reserve, Central African Republic, were collected when preferred fruits were not available and analyzed for their nutrient content by Remis *et al.* (2001). The most frequently eaten fruits in the diet of Bai Hakou gorillas were higher in sugar and lower in protein than other eaten fruits. Although the most succulent, sweet fruits were not available during seasons of fruit scarcity, the Bai Hakou gorillas tolerated fruits that contained relatively high amounts of fiber and tannins (Remis *et al.*, 2001).

Tannins are present in the diets of the western gorilla population, but, because of the difficulties in interpreting data from assays standardized with quebracho, whether they affect food selection, whether they are present in large quantities, or whether they have high levels of biological activity is not known.

Eastern Gorillas

Casimir (1975) completed a study of the feeding ecology of eastern lowland gorillas living in the Mt. Kahuzi region in the Democratic Republic of Congo in 1971–1972. The crude protein content of nine frequently eaten leaves was 19.7%. According to the micromineral (Na, K, Ca, Mg) analyses of eight foods, the sodium requirement (generally 0.25% of the diet) was not met, so gorillas may seek mineral supplements and/or consume mineral rich soil (Casimir, 1975).

Goodall (1977) analyzed foods eaten by the eastern lowland gorillas. Bamboo shoots eaten seasonally contained 47% crude protein. The percentage of crude fiber in the samples was relatively low (range: 7.3–43.1%), with the highest fiber found in bark (Goodall, 1977).

In terms of diet composition and variability in feeding habits of study groups, and individuals within those groups, the Virunga gorillas are well-studied compared to other populations (Vedder, 1984; Watts, 1984; McNeilage, 2001). Nutritional analyses of frequently consumed gorilla leaves and stems were completed by Waterman *et al.* (1983): leaves contained more protein (leaves: 15.5%, stems: 6.2%) and were more digestible (leaves: 56.5%, stems: 41.1%) (digestibility estimated using fungal cellulases) than stems. Digestibility was negatively correlated with ADF. Minerals in the mountain gorilla diet (P, K, Ca, Mg) were more concentrated in leaves than in stems (Waterman *et al.*, 1983). The protein content, digestibility, and the ratio of protein to digestion inhibitors were higher in preferentially consumed foods than in foods that were not favored (Watts 1984, 1990). Most of the plants consumed were low in phenolics, and few plants contained condensed tannins (Waterman *et al.*, 1983). Plumptre (1995), who analyzed foods eaten by large mammalian herbivores and related these data to their consumption and proportion in the diet, found that gorillas selected the most digestible foods in the habitat.

Bwindi Gorillas

When compared to gorillas at other sites, the Bwindi gorillas ate leaves that have similar levels of protein (16.9%) and lignin (9.1%) (Table 1). Bwindi gorillas consumed fruits that were higher in crude protein than the fruits eaten by the western gorillas. In the Bwindi gorilla diet, fruits (15.3%) and pith (8.4%)

have the most water-soluble carbohydrates compared to other plant parts, and the most frequently eaten fruit (Robbins & McNeilage, 2003) is the sweetest (*Myrianthus holstii*: ~50% sugar). Bwindi fruits were significantly less fibrous than those eaten by western gorillas in Campo and at Bai Hakou (Table 1). Both the leaves and fruits eaten by Bwindi gorillas have less lignin than those eaten by other groups across sites and are more digestible: cooler temperatures in Bwindi may contribute to these differences. Thirty-eight percent of the leaves consumed in Bwindi contained condensed tannins compared to 14% of the leaves eaten by gorillas in the Virungas. The occurrence of condensed tannins was not as widespread in the Bwindi gorilla diet as in the diets of western gorillas (Table 1).

Bwindi gorillas frequently consumed dry, decaying wood stumps, an interesting phenomenon that is difficult to explain. During 1 year of observations, a group of gorillas ate wood from up to 12 species of trees (J. M. Rothman, unpublished data). Often individuals carried the wood for several meters, and one juvenile carried wood for 100 m before eating it. The wood is high in lignin (~40%) and low in protein (~3%) and water-soluble carbohydrates (<1%) (Rothman *et al.*, in press). It is possible that wood is eaten for nonnutritional reasons, possibly serving a prophylactic medicinal purpose (Cousins & Huffman, 2002). The wood could also be used to aid digestion by altering passage rate or filling the gut. Nevertheless, why Bwindi gorillas eat wood is not obvious and is of interest for future research.

Some groups of Bwindi gorillas range outside of the park and raid crops in nearby villages. They eat the pith of banana stems (*Musa* spp.) and the midrib of banana leaves (J. M. Rothman, unpublished observation). Both of these food items are high in water; banana pith is 96% water and the midrib of the leaves is 90% water (Rothman *et al.*, in press). Otherwise they were lower in protein compared to the rest of the diet (pith: 8.6%, midrib: 4.2%) and similar in NDF and ADF content (pith: NDF = 50.0%; ADF = 30.9%), but lower in lignin (pith: 2.0%; midrib: 2.6%). The pith of *Musa* sp. has 5.0% water-soluble carbohydrates (Rothman *et al.*, in press). The gorillas may be raiding crops to eat the pith for its water content, but minerals and other compounds were not analyzed.

Nkurunungi (2005) examined the habitat use patterns of the Bwindi mountain gorillas and assessed the availability of food plants through study of one group. According to the analysis of feeding sites using an indirect method and calculations of Ivlev's electivity index, Bwindi gorillas are selective feeders that consume some herbs, shrubs, and fruits at a higher frequency than their

availability in the environment would predict. Nkurunungi (2005) identified the foods that the gorillas preferred, on the basis of frequency of consumption, and the foods selected, the basis of the availability of these plants in their range. These estimates were not based on intake, and so the results are biased toward food items that were eaten in small quantities on a regular basis.

To better understand food selection, we sought to determine whether the preferred nonfruit foods that were frequently consumed were higher in protein, fiber (NDF, ADF, and lignin), and/or water-soluble carbohydrates than other foods. We used the chemical analyses of gorilla plants (Rothman *et al.*, in review) and compared the mean values of nutrient content between preferred foods and other foods using the Mann–Whitney test. The 10 most frequently eaten nonfruit foods (preferred foods) were significantly higher in crude protein (21.8%) compared to the other nonfruit foods (14.1%) in the diet ($P < 0.05$) (Table 2). There was no difference between the frequently eaten nonfruit foods compared to other nonfruit foods with respect to fiber (NDF, ADF, and lignin). Water-soluble carbohydrates in the preferred foods compared to others were similar.

Selected nonfruit foods (those that were eaten at a higher frequency compared to their availability in the environment) and selected fruits were similar in their contents of protein, NDF, ADF, lignin, and water-soluble carbohydrates (Table 2). Additional studies are underway in our nutritional ecology laboratory (Cornell University) to provide more complete understanding of the nutritional aspects of food preference and selection with respect to estimates of food intake.

Table 2. Nutritional aspects of preference and selection of foods eaten by Bwindi gorillas

| | N | Protein | NDF | ADF | Lignin | WSC |
|-------------------------------|----|-------------|------|------|--------|------|
| <i>Nonfruit foods</i> | | | | | | |
| Frequently consumed | 10 | 21.8 | 41.3 | 28.2 | 7.4 | 3.4 |
| Other diet items ^a | 69 | 14.1 | 44.4 | 29.0 | 9.2 | 3.9 |
| Selected | 12 | 16.6 | 44.3 | 30.1 | 9.0 | 3.6 |
| Not selected ^b | 16 | 14.1 | 42.6 | 27.2 | 9.2 | 4.8 |
| <i>Fruit foods</i> | | | | | | |
| Selected | 5 | 8.3 | 46.3 | 26.8 | 10.1 | 26.4 |
| Not Selected | 5 | 10.0 | 44.9 | 28.6 | 14.1 | 15.3 |

Bold values are significantly different as determined by the Mann–Whitney test ($P < 0.05$), nutrient values are from Rothman *et al.* (in press); all data is presented as percent dry matter.

^a Dry wood diet items omitted.

^b Only items sampled by Nkurunungi (2005) were used in the analysis.

NUTRITION OF GORILLAS: HOW DO BWINDI GORILLAS COMPARE?

Bwindi gorillas feed heavily on terrestrial herbaceous plant material, which constitutes the bulk of their diet, but they also eat ripe fruit when it is available. Aside from the common, most frequently eaten foods in their diet, the Bwindi gorillas eat a range of tree barks, leaves, orchids, and the bark and stems of uncommon herbs that they come across on their daily paths.

The preferred foods eaten almost daily by the Bwindi gorillas are leaves, bark, and stems from lianas and shrubs that grow mainly in the large open forest gaps that are common throughout the rugged terrain of the forest. These have more protein than other items in their diet, but similar amounts of fiber. Because of their digestive strategy and large body size, the gorillas probably have the ability to use the lower quality items in their diet to a larger extent than other primates. Fiber estimates in Bwindi gorilla foods were generally lower compared to foods at other sites (Table 1). All gorillas, including those in Bwindi, appear to tolerate foods that contain condensed tannins. The function of dry wood and bark in the diet of Bwindi gorillas is puzzling and studies are ongoing to try to understand its role in the gorilla diet (J. M. Rothman, in preparation).

NUTRITIONAL ECOLOGY: FUTURE DIRECTIONS FOR GORILLA CONSERVATION

All subspecies of gorillas are endangered, with population estimates for *Gorilla gorilla* of ~90,000), and for *Gorilla beringei* of ~3700. For some subspecies, the numbers are even more daunting, *Gorilla beringei beringei*: ~700; *Gorilla gorilla diehli*: ~150. The management of gorilla habitats is more likely to be successful if we know which plants are most important to protect and how many gorillas can be sustained in a specific area (McNeilage, 1995). Baseline studies should address nutrient intake and selection along with assessments of food distribution so that models of carrying capacity and habitat use can be developed to establish management guidelines and to determine which areas are essential for gorillas' survival.

In the Virungas, food distribution and density are important factors for mountain gorillas with respect to habitat selection (Vedder, 1984; Watts, 1991, 1998a). Whether the nutrient content of food has an impact on their density and range has not yet been determined, but these gorillas favor parts of the

habitat where they find the most nutritious plants (Vedder, 1984; Watts, 1991) and they revisit areas that have a greater density of high quality food species (Watts, 1998b).

Future studies of nutritional ecology should emphasize the relationship between nutrient requirements and nutrient supply across different habitats with consideration of seasonal and spatial variation. Presently, the entire habitat of the Bwindi gorillas is well protected, but recommendations from nutrition studies could be used to develop habitat management and protection strategies. Although logging and overharvesting are not currently problems for Bwindi gorillas, the same cannot be said of other gorilla populations. Changes in habitat structure and food availability may have serious implications for diet adequacy, gorilla health, and, ultimately, their continued existence. By understanding the nutritional demands imposed by gorillas on their habitat, we will be better able to ensure their continued survival.

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