Variability of the Feeding Ecology of Eastern Gorillas

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Dietary Variability of Mountain Gorillas in Bwindi Impenetrable National Park, Uganda

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*Data on intraspecific dietary variability has important implications for understanding flexibility in foraging behavior, habitat utilization, population dynamics, and social behavior and may also assist in conservation efforts. We compared food availability and diet of a group of mountain gorillas (*Gorilla beringei beringei*) at a high altitude site and 2 groups at a low altitude site in Bwindi Impenetrable National Park, Uganda, from September 2001 to August 2002. Plant species diversity was greater at the low altitude site than at the high altitude site. The two groups at the low elevation consumed more plant species (140 species vs. 62 species), and a greater number of fruit species per mo (7 vs. 3 species) and per yr (36 vs. 11 species) than the high altitude group did. Furthermore, each group shared <51% of important fibrous food items in their diet with the 2 other groups. There is no significant difference in the proportion of days fruit remains were found in the dung among groups. Finally, according to Ivlev's electivity index, all groups positively selected the majority of food items in their diets. We attribute a large proportion of dietary variation between locations to differences in fruit availability and plant species composition between sites. Differences between groups at the low altitude site may be due to variation in food profitability—more profitable foods available to choose in the same area—within their overlapping home range, or*

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group traditions. A comparison of our results with the diets of gorillas of the Virunga Volcanoes in Rwanda and Kahuzi-Biega, DRC shows that eastern gorilla populations have highly variable dietary patterns with limited overlap in species consumed among groups and populations.

INTRODUCTION

Interspecific and intraspecific dietary variability in primates has implications for predicting patterns of sociality, habitat utilization, and population dynamics (Doran and McNeilage, 1998; Dunbar, 1988; Oates, 1987; Sterck *et al.*, 1997; van Schaik, 1989; Wrangham, 1980). Within the restrictions imposed by body size and morphology, a key factor leading to intraspecific dietary flexibility is the spatial and temporal variability of food resources (Clutton-Brock, 1977; Oates, 1987). However, variation may be due not only to the availability of a particular food but also whether there are more profitable foods available to choose in the same area: food profitability hypothesis based on optimal foraging theory (Chapman and Fedigan, 1990). Variation in diet within populations may also be due to local traditions based on learning (Chapman and Fedigan, 1990; Nishida *et al.*, 1983; Schoener, 1971).

Studies of dietary variability have demonstrated that portraying the diet of a species from research of one or two groups can lead to overgeneralizations that may provide too limited a view of dietary flexibility (chimpanzees: Basabose, 2002; Ghiglieri, 1984; McGrew *et al.*, 1988; black-and-white colobus: Clutton-Brock, 1975, Dasilva, 1994; Fashing, 2001; Oates, 1977; white-faced capuchins: Chapman and Fedigan, 1990; red colobus: Chapman *et al.*, 2002; Chapman and Chapman, 1999; blue monkeys: Butynski, 1990; Fairgrieve and Muhumuza, 2003; Kaplin *et al.*, 1998; yellow baboons: Norton *et al.*, 1987; Pochron, 2000; Post, 1982; chacma baboons: Byrne *et al.*, 1993). Such overgeneralizations of dietary patterns in relation to food distribution within a species may limit their validity in comparative models of socioecology and may lead to the incorporation of incorrect assumptions into conservation plans. In particular, species that live in highly variable ecological conditions, eg., across large altitudinal ranges, are predicted to exhibit a high degree of dietary variability and should be the focus of comparative dietary studies.

Gorillas live in a diversity of habitats across central Africa and correspondingly show significant variation in feeding ecology and ranging patterns (Doran and McNeilage, 1998, 2001; McNeilage, 2001; Watts, 1996; Yamagiwa *et al.*, 1994, 1996). The pioneering studies of mountain gorillas (*Gorilla beringei beringei*) at the Karisoke Research Center led to a long-standing

generalization that all gorillas were generally folivorous (McNeilage, 1995; Vedder, 1984; Watts, 1984). Studies of western gorillas (*Gorilla gorilla gorilla*) and Grauer's gorillas (*Gorilla beringei graueri*) have shown that fruit is an integral part of their diet and that there are broad scale differences between western and eastern gorilla diets (Doran *et al*., 2002; Goldsmith, 1999; Nishihara, 1995; Remis, 1997; Rogers *et al*., 1988; Sabater Pi, 1977; Tutin and Fernandez, 1985; Williamson *et al*., 1990; Yamagiwa *et al*., 1996). In addition to food availability, gorillas may preferentially select foods based on particular characteristics of the food items. Mountain gorillas select foods based on availability, protein, and digestibility (Plumptre, 1995; Vedder, 1984, 1990; Waterman *et al*., 1983), while western gorillas select foods based on availability, secondary compounds such as tannins, and nutrient content including sugars, protein, fiber, and minerals (Calvert, 1985; Magliocca and Gautier-Hion, 2002; Remis *et al*., 2001; Rogers *et al*., 1990).

The dietary differences among gorilla species and subspecies are due mainly to the availability of fruit and fibrous foods (Doran and McNeilage, 1998, 2001). With decreasing elevation, forests have higher mean annual temperatures, changes in vegetation structure and distribution, and an increase in species diversity (Hamilton, 1975; Richards, 1996). Thus the number, density, and availability of fruit and fibrous food species varies with altitude.

Eastern gorillas live at a particularly wide range of altitudes and habitat types (Fig. 1a). Mountain gorillas occur in the Virunga Conservation Area in Rwanda, Democratic Republic of Congo (DRC), and Uganda (elevation 2300–4507 m), and in Bwindi Impenetrable National Park in Uganda (elevation 1160–2600 m). Grauer's gorillas occur in eastern DRC and have been the focus of study in Kahuzi-Biega National Park and other forests of eastern DRC (elevation 600–2600 m). Dietary variability correlated to altitudinal variation occurs among mountain gorillas in the Virunga Volcanoes (Goodall, 1977; McNeilage, 1995, 2001; Watts, 1984) and Grauer's gorillas in Kahuzi-Biega National Park (Yamagiwa *et al*., 1994, 1996; Yumoto *et al*., 1994). These studies highlight that the well-studied mountain gorillas of Karisoke Research Center in the Virunga Volcanoes live at the ecological extreme of mountain gorilla range (>2700 m), and their feeding ecology is not necessarily representative of the subspecies.

Recently the feeding ecology of half of the world's population of mountain gorillas, living in Bwindi Impenetrable National Park has become the focus of attention (Goldsmith, 2003; Nkurunungi, 2004; Nkurunungi *et al*., in press; Robbins and McNeilage, 2003; Stanford and Nkurunungi, 2003). Bwindi has a higher mean annual temperature, greater plant diversity (Butynski, 1984) and is floristically unlike the habitats of the areas around the Karisoke Research Center. Most notably, fruit availability is much greater in Bwindi (Butynski, 1984; Goldsmith, 2003; Nkurunungi *et al*., in press; Robbins and McNeilage, 2003; Sarmiento *et al*., 1996). Within Bwindi itself,
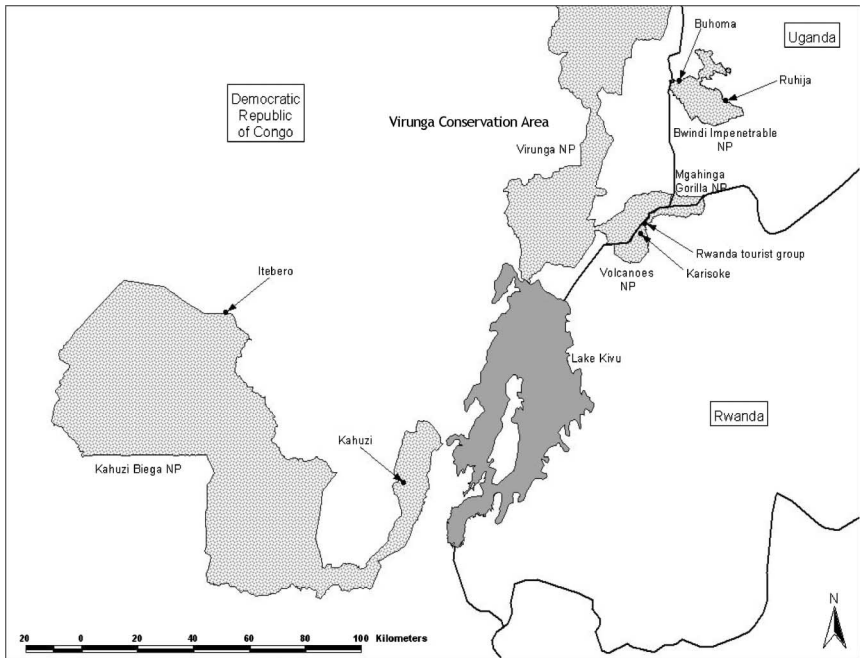
Fig. 1a. Map of 6 eastern gorilla study sites: Bwindi Impenetrable National Park (Ruhija and Buhoma), Virunga Conservation Area (Karisoke Research Center and Rwanda tourist group) and Kahuzi-Biega National Park (Itebero and Kahuzi). Grauer's gorillas also occur in other areas of eastern Democratic Republic of Congo that are not indicated on the map.

there is variation in climate, altitude, and forest composition with significant differences in plant species composition, density, and fruit availability related to altitude (Butynski, 1984; Nkurunungi *et al.*, in press). Therefore, to describe the dietary patterns of Bwindi mountain gorillas and to compare them to other eastern gorilla populations we need to consider a cross-section of different sites within the park.

Our goals were threefold: first, to compare the spatial and temporal dietary variability of mountain gorilla groups at a high altitude site (2100–2500 m) and a low altitude site (1450–1800 m) in Bwindi and to test the food availability hypothesis to examine how differences in availability of gorilla foods may lead to differences in dietary composition. We predicted that there would be differences in dietary diversity between groups at the 2 sites and that fruit consumption would be greater at the low altitude site. Furthermore, we predicted that there would be no difference in the variables between neighboring groups with overlapping home ranges at the low altitude site. We were not able to test the alternative hypotheses of group traditions or food profitability because data on the ontogeny of feeding behavior is
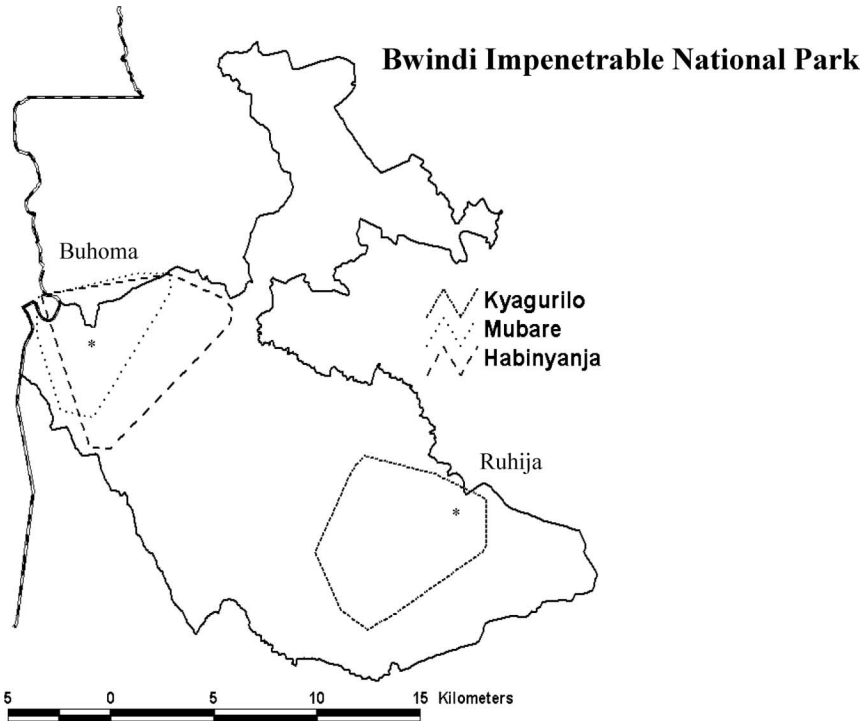
Fig. 1b. Map of Bwindi Impenetrable National Park, Uganda and the 2 study sites, Buhoma (1450–1800 m) and Ruhija (2100–2500 m). The home range size of each group was calculated using the minimum convex polygon method.

necessary to test the former and data on the nutritional content of all potential food items is required for the latter. Moreover, variation may be caused by sampling error, especially when relying on the indirect methods that we used. Our second goal was to examine food selection within and between groups. We predicted that the particular foods selected would vary among groups depending on food availability. Thirdly, we compare our results with those from gorilla populations in the Virunga Volcanoes and Kahuzi-Biega to examine dietary variability across eastern gorilla populations.

METHODS

Study Site and Study Groups

We collected dietary data on 3 habituated mountain gorilla groups in Bwindi Impenetrable National Park (331 km^2) in southwestern Uganda

(0°53′–10°8′N; 29°35′–29⁰50′E) for one year between September 2001 and August 2002 (Fig. 1b, Table I).

The 2 groups at the low altitude site—Mubare and Habinyanja—range around Buhoma, in the western section of the park (1450–1800 m) and have overlapping home ranges. Halfway through the study (Feb 2002), the Habinyanja group fissioned and 8 gorillas jointly emigrated to form a new group. Both the Mubare and Habinyanja groups are part of a tourist program, but to minimize human contact with the gorillas, observations are allowed only during a 1 h tourist visit each day (Homsy, 1999). Therefore, we were unable to make direct observations and used only indirect data collection methods. At the higher altitude, the Kyagurilo group ranges near Ruhija, in the eastern section of the park (2100 m–2500 m). The group is habituated for research purposes, and we used both indirect, and direct observation methods. The Buhoma and Ruhija sites are at opposite ends of the park and separated by 18 km (Fig. 1b).

Both areas experienced 2 wet seasons (Sept.–Nov. 2001 and March–May 2002) and 2 dry seasons (Dec. 2001–Feb. 2002 and June–Aug. 2002). We collected data on rainfall and maximum and minimum mean temperatures daily from stations in Buhoma and Ruhija that are monitored by the Uganda Wildlife Authority and the Institute of Tropical Forest Conservation (Table II). Habitat types and how much area they cover at each location vary. Between Buhoma and Ruhija there is a total of 7 habitat types but the sites share only 2 in common, mixed forest (Buhoma = 58.4%, Ruhija = 28.8%) and open forest (Buhoma = 20.6%, Ruhija = 67.3%: Nkurunungi *et al.*, in press).

Diet

Fibrous Foods

Fibrous foods are nonreproductive plant parts from herbs, shrubs, and trees. To quantify fibrous foods eaten by the Mubare and Habinyanja groups, we used the indirect method of following gorilla trails and recording the first observation of food remains left behind, and the part of the plant that had been consumed, which on a daily basis indicated the plants present or absent in the diet (Doran *et al.*, 2002; Williamson *et al.*, 1990). For the Kyagurilo group, field assistants conducted direct observations for an average of 4 h per day and recorded only the first observation of plants and parts eaten by the gorillas (in order to make the 2 methods comparable). The method is likely to underestimate the number of plants eaten in a day, and it is biased towards excluding rarely eaten foods. Due to differences in data collection

Table I. Composition and location of study groups. Classifications follow Watts (1990)

Group	Location	No. of individuals	Silverback	Blackback	Adult female	Subadult	Juvenile	Infant
Mubare	Buhoma (low alt)	11–13	1	0	5–6	0	4	1–2
Habinyanja[a]	Buhoma (low alt)	22–32	1–2	1	10–15	2–3	1–2	9
Kyagurilo	Ruhija (high alt)	14	2	0	5	3	2	2

[a]The Habinyanja Group fissioned in February 2002. Data analysis continued for the larger subgroup for the remainder of the study period.

Table II. Intersite comparisons of climate, altitude, and vegetation density

	Buhoma	Ruhija
Rainfall	1928 mm	1278 mm
Ave. temperature	Max: 25.4°C	Max: 16.6°C
	Min: 14.8°C	Min: 13.4°C
Altitude	1450–1800 m	2100–2500 m
Gorilla herb density[a]	4.36/m^2	10.6/m^2
Gorilla shrub density[a]	4.05/m^2	0.11/m^2
Gorilla tree density[a]	95/ha	48/ha

[a]Nkurunungi *et al.* (in press).

between the sites, fungus and some plant parts—wood, flowers, shoots—that are on the Kyagurilo plant list (direct observation) as plant parts eaten but were not recorded from the trail remains sampling for the 2 Buhoma groups. Categories of plant types include trees, shrubs, vines/lianas, herbs, including grasses, sedges, and orchids, epiphytes, including both parasitic and non-parasitic, ferns, including tree ferns, and an agricultural crop. Due to the difficulty of identifying ferns and epiphytes to species level, we collapsed them into 2 categories—ferns and epiphytes—their diversity in the diet is underestimated and we only note them in the overall dietary lists.

We compared species of fibrous foods eaten by the groups by calculating the number of plant species eaten overall, the number of important plant species eaten, and the degree of overlap in consumption among groups. Important fibrous food species occur on $\geq 5\%$ of daily food trails or daily observations (Doran *et al.*, 2002). Because there are only 7 mo of data for the Habinyanja group (Feb–Aug), when comparing them with the Mubare and Kyagurilo groups, we only used data from February through August for all groups. On average, we analyzed data for 22 days per mo per group (Mubare range = 14–23, $SD = 2.701$; Habinyanja range = 16–22, $SD = 1.90$; Kyagurilo range = 9–31, $SD = 6.052$).

Fruit

To determine the species and estimate the amount of fruit eaten by the gorillas, we collected fecal samples from night nests (<48 h old) of all groups, and assigned each a sex and age class based on bolus size (Schaller, 1963). We collected samples from nests of a silverback, an adult female/blackback (indistinguishable based on size), and a juvenile (defined as sleeps in his/her own nest, sexually immature) nest each day. Samples weighed *ca.* 250 g for silverbacks and adult females and 150 g for juveniles. We excluded months with <10 sampling days from the analysis (October and April for the Kyagurilo group). For analysis we had an average of 23 ($SD = 4.26$) sample days per mo

(Mubare mean = 23.7, range = 20–30, SD = 2.96; Habinyanja mean = 22.4, range 13–26, SD = 3.4; Kyagurilo mean = 23.8, range = 14–31, SD = 5.47).

We weighed fecal samples and washed them through a 1-mm sieve. We identified seed species and quantified them (Williamson *et al.*, 1990). Although at least fruit of 7 species of *Ficus* were consumed by the low altitude groups (Mubare and Habinyanja), only 3 species distinctions were possible (*Ficus spp.* #1, #2, #3). Further, the groups at the low altitude site ate 2 species of fruit that had seeds too large to be swallowed—*Leplaea mayombensis* and *Carapa grandiflora*—and one species with seeds that were tiny and not easily visible in feces: *Solanum anguvi*. We quantified them from trail remains. We analyzed samples for sex/age class differences, and seasonal and overall variability within and among groups. Neither the Mubare nor the Kyagurilo group contained a blackback, so all adult dung samples could be assigned to a sex. Therefore, we used them for comparisons of sex differences.

We calculated the number of fruit species eaten per sample and per mo, measures of selectivity, and the proportion of days that feces contained seeds. We also compared the fruit diet among groups by calculating important fruit species, which occur in ≥1% of samples per group (Remis, 1997). Six seed species could not be identified and were counted only once; therefore, the highest number of species consumed per mo is likely to be a conservative estimate.

To quantify the relative amount of fruit eaten, we used a scoring system as follows. Seeds <2 mm, e.g. *Ficus spp*, had scores of 1 = few (1–50 seeds), or 2 = many (>50). For seeds >2 mm, we counted the seeds and calculated the mean number of each seed species per 50 g of dung and then averaged the mean number of each species across groups for the study period. For each seed species, a number below the mean is 1 for few and a number above the mean is 2 for many. Then for each fecal sample, we added the individual species fruit scores to get a total fruit score based on quantity and number of species.

Resource Availability

We cut transects within the gorillas' current home ranges via the stratified random technique (Grieg-Smith, 1983) to determine resource availability. In Buhoma, we cut 50 200-m transects and in Ruhija we cut 4 2-km transects. We measured herbs, vines, ferns, seedlings and saplings <2 m in height in 1-m^2 plots, lianas and young trees of <10 cm dbh and >2 m in height 5-m^2 plots, and trees >10 cm dbh in 10-m^2 (Buhoma) and 10 m × 20 m (Ruhija) plots. In both locations, we did not record epiphytes and fungus. We measured a total of 500 plots in Buhoma and 400 plots in Ruhija.

We calculated species richness, stem density, and species density for all plant species and measured the dbh of trees >10 cm dbh. We measured 6.3 ha in Buhoma and 9.04 ha in Ruhija. Although the number of transects differed, we used the same procedure to quantify the plant resources; therefore, we could make comparisons between sites (Nkurunungi *et al.*, in press).

We monitored a total of 328 trees (190 [mean # per species = 16] and 138 [mean # per species = 6.68] trees at Ruhija and Buhoma, respectively) from 25 species known to provide gorilla food fruits, of which 11 species were in both sites. At approximately the same time each month, for each tree we recorded the percent abundance of fruit and flowers in the crown using an independent score for each category between 0 and 4 (0 = 0%, 1 = 1–25%, 2 = 26–55%, 3 = 51–75% and 4 = 76–100%) based on Sun *et al.* (1996). We used a fruit availability index (that multiplied mean dbh, density, and mean monthly fruit score per species) to represent monthly fruit abundance for species and sites (Nkurunungi *et al.*, in press).

Selection Categories

Following Chapman and Fedigan (1990), we placed gorilla fibrous foods and fruits into one of 4 categories to distinguish whether their consumption could be correlated with availability or could be attributed to food profitability or local traditions or both. Because we had no data on nutritional content or local traditions, we did not attempt to test the 2 hypotheses. Category 1 represents food species that were found only in the home range of the high or the combined low altitude groups, and only eaten by the respective group; We attribute selection of these species to food availability. Category 2 represents plants used by all 3 groups and the level of use was proportional to availability; [again we attribute selection to food availability]. Category 3 represents plants present in all group ranges, but were not eaten by all gorilla groups; here we attribute selection to food profitability or local traditions or both factors. Category 4 included plants that were used by all groups but the frequency in the diet per group is not directly proportional to availability at each locality; we attribute selection to food profitability. While not as strong as category 3, category 4 demonstrates that the differences can be a result of learned differences or food profitability (Chapman and Fedigan, 1990).

Measure of Selectivity

To obtain a more detailed measure of selectivity in choice of food items, we used Ivlev's electivity index (Malenky and Stiles, 1991; McNeilage, 2001;

Milton, 1980). We calculated selectivity for particular food items via the formula:

$$\text{Ivlev's electivity index} = (r_1 - n_1)/(r_1 + n_1)$$
$$\text{where in } r_1 = \text{proportion of food item in diet}$$
$$n_1 = \text{proportion of food item in the home range}$$

We calculated the proportion of fibrous food in the home range as the percent frequency of it along transects. We calculated the proportion of the fibrous food item in each group's diet as the percent frequency of the species on daily trails. We calculated fruit availability (from trees only) for the year and per mo by dividing the fruit availability index per species by the overall gorilla tree fruit availability index per study site. We calculated the proportion of fruit in each group's diet as the percent frequency of seed species in dung samples. We excluded *Ficus spp*. from the analysis due to the difficulty of identifying them to species in the dung samples. We calculated no index for fruit species absent from our phenological study (*Carapa grandiflora*). We also could not determine selectivity of fruit and fibrous food species that were eaten, but not recorded along transects. Values for Ivlev's electivity index range between -1 and 1; >0 indicates positive selection of a food item, and <0 indicates selection against, or avoidance of, a food item. Fibrous and fruit foods were considered to be highly selected when values are ≥ 0.50.

Statistics

We used a Freidmann ANOVA to determine if the gorilla groups differ significantly in the percentage of days per mo that feces contained seeds. We used a Kruskal-Wallis test in comparisons within the 3 groups in sex/age class differences and between groups in the monthly percentage of days that feces contained seeds, differences in monthly means for the number of fruit species per sample and mo, and fruit consumption. Following a significant result, we performed a test post hoc via a Mann Whitney U test. All results are two-tailed and significant when $p < 0.05$.

RESULTS

Altitudinal Differences in Vegetation

More species of plants were at the low altitude site, Buhoma ($n = 218$), than the high altitude site, Ruhija ($n = 179$). Buhoma had a higher density of shrubs and trees, while Ruhija had a higher density of herbs (Table II).

Table III. Plant species and plant parts consumed by the gorilla groups

Group	No. of species	No. of plant parts	No. of families	No. of important fibrous food spp.	No. of fruit species	No. of important fruit species
Mubare	113	205	56	41	36	13
Habinyanja[a]	104	187	56	33	31	13
Kyagurilo	62	106	39[b]	16	11	9

[a]7 mo of data (Feb 2002–Aug 2002).
[b]Two plant species were not identified to family; therefore 39 is the minimum number of families.
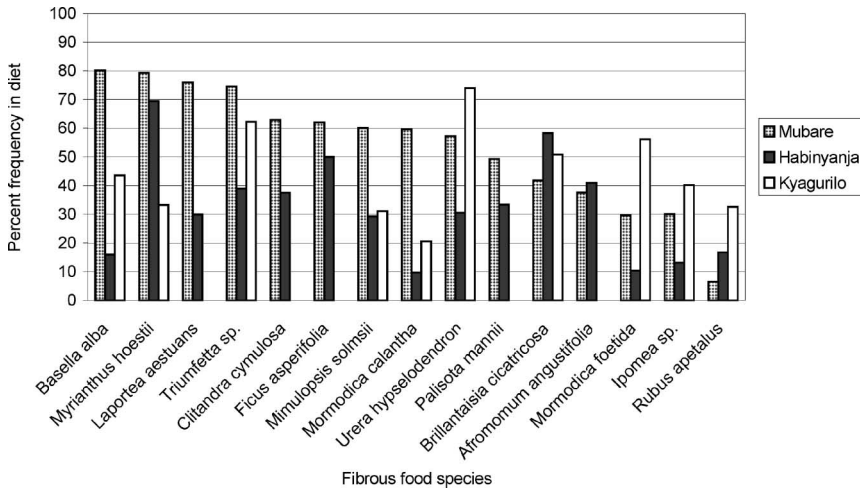
Fibrous Food Diet

The Mubare group consumed 205 plant parts from 113 species, the Habinyanja group consumed 187 plant parts from 104 species, and the Kyagurilo group consumed 106 plant parts from 62 species (Table III).

The Mubare group diet included 41 species, the Habinyanja group 33 species and the high altitude Kyagurilo group 16 species of important food (those occuring on ≥5, of daily trails) respectively. The lower altitude groups—Mubare and Habinyanja—shared 43.6% of them in common, while the Mubare and Kyagurilo groups had 24.4% in common and the Habinyanja and Kyagurilo groups shared only 12.7% of important food items. Of the 10 most commonly eaten foods per group, both the Mubare and Habinyanja groups shared 66.7% each with Kyagurilo, and the Mubare and Habinyanja groups shared 100%, though the percent frequency in trail remains/observations varied between all groups (Fig. 2). Of the 55 important plant species in the diets of all 3 groups, excluding epiphytes and ferns, 6 were not at Buhoma, and 24 were not at Ruhija.

Of all plant species eaten by the gorillas, 58.9% were only in the home range of either the high altitude group or the low altitude groups, and were eaten by only them which, places them in category 1: choice limited by presence of food item in habitat. Category 2—plants eaten in proportion to availability by all 3 groups and choice attributed to food availability—were 12.2% of samples. Category 3—plants present in all group ranges, but not eaten by all of them—included 24.4% of the plants. Category 4—plants that used by all groups but not in proportion to availability per locality—were 4.4% of samples.

Therefore, selection of 71.1% of plants in the gorilla diet could be explained by availability (categories 1 and 2), while 28.8% of plants were eaten according to either food profitability or local traditions (Categories 3 and 4). For important species only, 50% of plants are in category 1, 12% are in category 2, 34% are in category 3, and 4% are in category 4. Therefore, for important foods only, 62% of the differences in gorilla fibrous food diets

Fig. 2b. Percent frequency of the 10 most commonly eaten fibrous foods in the diet of each group.

could be attributed to differences in availability and 38% is due to either food profitability or local traditions.

Per Ivlev's electivity index, the degree of selection by the 3 groups varied by plant species with the majority of them positively selected (Table IV). Overall, Bwindi gorillas are highly selective (index >0.50) of important fibrous foods. For the Mubare group, the Habinyanja group, and the Kyagurilo group 74.3% ($n = 35$), 45.8% ($n = 35$), and 66.6% ($n = 12$), respectively, of important fibrous foods were highly selected. Of the 10 fibrous foods most commonly eaten by each group, both the Mubare group and the Habinyanja group highly selected 80% and the Kyagurilo group highly selected 100%. *Momordica calantha, Urera hypselodendron, Basella alba*, and *Rubus apetalus* were highly selected by all 3 groups (Table IV).

Fruit Diets

The Mubare group consumed 36 species of fruit and the Habinyanja group consumed 31 species of fruit, whereas the Kyagurilo group consumed only 11 species of fruit (Tables III and IV).

Of important fruit species eaten by the gorillas ($\geq$1% occurrence in dung samples), 50% were only in the home range of either the high altitude group or the low altitude groups, and were eaten by only them, placing them in category 1. Category 2 included 43.8% of the fruits sampled. None of the

Table IV. The percentage of important species occurring in trail remains (>1% occurrence for fruit, >% 5 occurrence for fibrous foods), herb, shrub, and adult tree densities at each site, and electivity indices

Species	%M	Density Buhoma	FAI Buhoma	Electivity index	%H	Electivity index	%K	Density Ruhija	FAI Ruhija	Electivity index
FRUIT										
Herbs										
Aframomum angustifolium	3.2	0.05	—	—	3.7	—	0	Not found	—	—
Aframomum sanguinum	4.2	0.06	—	—	1.9	—	0	Not found	—	—
Piper guineense	0	24	—	—	1.1	—	0	Not found	—	—
Smilax anceps	2.5	6	—	—	<1	—	0	0[a]	—	—
Shrubs										
Allophyllus sp.	<1	24	—	—	<1	—	5.6	9	—	—
Ficus asperifolia	4.2	8	—	—	2.6	—	0	Not found	—	—
Rubus apetalus	1.8	1.6	—	—	0	—	1.6	16	—	—
Solanum anguvi	30	0.4	—	—	4.4	—	0	Not found	—	—
Trees										
Bridelia micrantha	0	4	772.7	—	2.6	—	0	0.13	—	—
Carapa grandiflora	<1	17	—	—	2.9	—	0	Not found	—	—
Cassine aethiopica	10.9	29	31957.7	-0.730	23.9	-0.490	0	Not found	—	—
Chrysophyllum sp.	0	1	242.2	—	4.1	0.078	16.5	5.6	5962.3	-0.580
Ficus sp. #1	15.8	0[a]	—	—	15.3	—	0	0[a]	—	—
Ficus sp. #2	8.1	0[a]	—	—	3	—	0	Not found	—	—
Ficus sp. #3	7	1.2	40.2	0.75	5.6	0.697	0	Not found	—	—
Harungana madagascariensis	13	2	1266.9	0.646	10.1	0.566	0	0[a]	—	—
Leplaea mayombensis	1.8	6	2224.8	-0.695	8	-0.111	0	Not found	—	—
Maesa lanceolata	1.8	12	2309.9	-0.471	0	—	4.4	2.6	52.4	0.656
Myrianthus holstii	32.4	15	4444.9	0.539	26.1	0.458	12.5	0.9	460.6	0.534
Mystroxylon aethiopicum	0	Not found	—	—	0	—	1.2	0.1	57.3	-0.817
Olea capensis	0	Not found	—	—	0	—	17.3	2	1468.6	0.979
Prunus africana	<1	3.4	1116.9	-0.745	1.1	-0.371	0	1.6	959.5	—
Syzigium guineense	0	6	432.3	—	<1	-0.385	14.9	2.4	1402.3	0.010
Teclea nobilis	0	1	31.1	—	0	—	1.6	0.8	17.2	0.667

FIBROUS FOODS							
Herbs							
Afromomum angustifolia	37.6	0.038	0.918	41	0.925	0	Not found	—
Afromomum sanguinum	25.4	0.064	0.841	7.6	0.551	0	Not found	—
Basella alba	80.3	0.014	0.975	16	0.882	43.5	2.18	0.959
Cardus sp.	0	Not found	—	0	—	9.4	0[a]	—
Clitandra cymulosa	62.9	0.004	0.987	37.5	0.979	0	Not found	—
Commelina capipata	<5%	0.508	−0.692	9.7	−0.640	0	0[a]	—
Grewia pubescens	18.8	0.002	0.98	0	—	0	Not found	—
Ipomea wightii	29.6	0[a]	—	0	—	0	0[b]	—
Ipomea sp.	29.6	0.042	0.947	13.2	0.943	0.2	0.32	0.570
Kostelezkya grantii	0	Not found	—	0	—	5.43	0[a]	—
Landolphia buchananii	17.4	0.014	0.851	0	—	0	Not found	—
Laportea aestuans	76.1	0.082	0.891	29.9	0.743	0	Not found	—
Laportea mooreana	8.9	0[a]	—	0	—	0	Not found	—
Mimulopsis arborescens	0	0	—	0	—	31.1	1.32	0.665
Mimulopsis solmsii	60.1	0.31	0.713	29.2	0.482	0	0	—
Momordica calantha	59.6	0.008	0.987	9.7	0.921	20.4	1.5	0.864
Momordica foetida	29.5	0.032	0.91	10.4	0.763	56.1	0.24	0.745
Musa sp.	10.3	0[a]	—	0	—	0	Not found	—
Palisota mannii	49.3	0.274	0.652	33.3	0.524	0	Not found	—
Pennisetum purpureum	25.4	0.044	0.969	0	—	0	Not found	—
Penntarrhinum gonoloboides	8.5	0.068	0.206	6.9	0.104	0	Not found	—
Piper capense	45.5	0.06	0.876	18.8	0.725	14.5	0.01	0.933
Piper guineense	<5%	0.024	−0.692	6.3	0.482	0	Not found	—
Smilax anceps	8	0.032	0.539	13.2	0.692	0	0[a]	—
Tragia sp.	16.4	0.006	0.976	13.2	0.941	0	Not found	—
Triumfetta sp.	74.6	0.112	0.447	38.9	0.733	62.2	0.08	0.914
Urera hypselodendron	57.3	0.02	0.986	30.6	0.949	74	0.07	0.94
Shrubs							
Acacia brevispica	<5%	14.4	0.867	14.6	0.659	0	Not found	—

Table IV. Continued

Species	%M	Density Buhoma	FAI Buhoma	Electivity index	%H	Electivity index	%K	Density Ruhija	FAI Ruhija	Electivity index
Allophyllus sp.	8.9	1.49		0.092	9	0.098	0	9		—
Brillantasia cisetricosa	41.8	151.2		0.393	58.3	0.524	0	0[b]		—
Brillantasia sp.	13.1	6.97		0.362	0	—	50.7	2.64		0.864
Cissempelos mucronata	7.9	0.4		0.903	0	—	0	Not found		—
Cyathea manniana (tree fern)	20.2	25.6		0.675	12.5	0.534	<1%	5.14		—
Cyphostemma bambusetti	5.5	0[a]		—	0	—	0	2.5		—
Ficus asperifolia	62	8.4		0.931	50	0.916	0	Not found		—
Rhytinginia kigeziensis	6.1	13.6		0.435	0	—	0	0.002		—
Rubus apetalus	6.5	1.6		0.884	16.7	0.953	32.6	16		0.858
Solanum anguvi	26.8	0.4		0.971	<5%	0.907	0	Not found		—
Vernonia calongensis	0	0.4		—	0	—	12.1	12		—
Trees										
Bridelia micrantha	0	4		−0.263	10.4	0.645	0	0.13		—
Chrysophyllum sp.	0	1		—	5.5	0.74	0	5.6		—
Drypetes sp.	0	13		—	6.3	−0.246	0	1.75		—
Eucalyptus sp.	9	0.4		0.835	15.3	0.949	0	Not found		—
Ficus sp. #1	5.1	0[a]		—	5.5	0[a]	0	0		—
Ficus sp. #2	13.1	0[a]		—	23.6	—	0	Not found		—
Ficus sp. #3	8	1.2		—	<5%	0.655	0	Not found		—
Galiniera coffeeoides	0	0.6		—	6.3	0.826	0	0.028[c]		—
Maesa lanceolata	47.9	12		0.726	<5%	−0.486	0	2.6		—
Myrianthus hostii	79.3	15		0.796	69.4	0.770	33.2	0.9		0.725
Omucundura	5.6	0[a]		—	0	—	—	—		—
Psychotria mahonnii	19.2	5.6		0.600	<5%	−0.778	0	Not found		—
Xymalos monospora	21.6	8.8		0.532	21.5	0.530	0	0.2		—

Note. M% = percent found in the Mubare trails; H% = percent found in the Habinyanja trails and K% = percent found in the Kyagurilo trails. FAI = fruit availability index. Presence and density of epiphytes and fungus were not recorded during transects and thus do not appear in the table, and ferns were not identified to species. Density of trees and shrubs in ha, herbs per m². Electivity indices for fruit species are presented only for species in our phenological study.

[a]Found at site, but not recorded in transects.

[b]probably available, but not all *Ipomea* spp. & *Brillantaisia* spp. were identified to species.
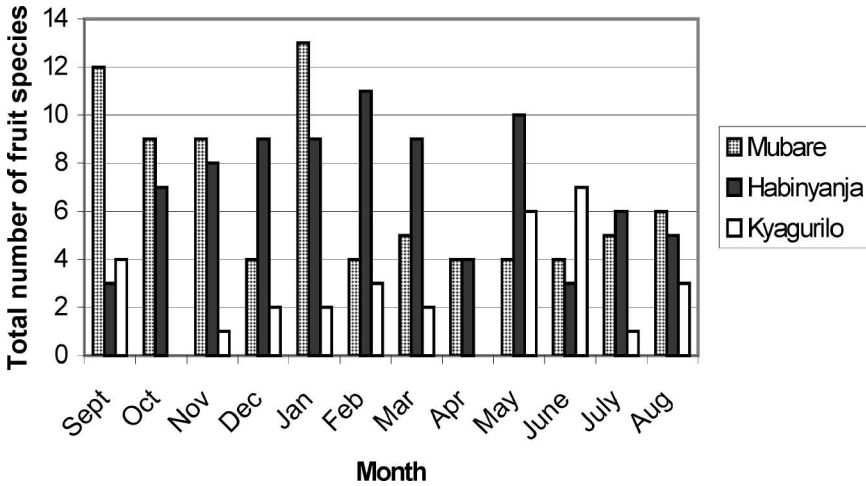
[c]Considered a shrub in Ruhija.

Fig. 3b. The number of fruit species eaten by each group per month.

plants are in category 3, and 6.25% are in category 4. Therefore, over 90% of the fruit diet could be explained by availability of the fruit.

The Mubare and Habinyanja groups ate significantly more species of fruit per mo than the Kyagurilo group (Kruskal-Wallis: $\chi^2 = 11.238$, df $= 2$, $p < 0.004$; Mubare $= 6.58$ [mean monthly range 4–12]; Habinyanja $= 7$ [mean monthly range 4–13]; Kyagurilo $= 3.1$ [mean monthly range 1–7]). There is no difference in the number of fruit species eaten per month between the Mubare group and the Habinyanja group (Mann-Whitney U: $Z = -0.410$, $p = 0.682$, Fig. 3).

There is no significant difference in the monthly mean number of fruit species per daily dung sample for sex/age class within a group. (Kruskal-Wallis: Mubare: $\chi^2 = 1.098$, df $= 2$, $p = 0.577$; Habinyanja: $\chi^2 = 0.155$, df $= 2$, $p = 0.926$; Kyagurilo: $\chi^2 = 0.067$, df $= 2$, $p = 0.967$). Therefore, we only used samples from adult female/blackbacks for intergroup analyses. There is no significant difference between groups in monthly mean number of fruit species per daily dung sample (Kruskal-Wallis: $\chi^2 = 1.323$, df $= 2$, $p = 0.516$): Mubare $= 1.11$ species ($r = 0.31–1.92$), Habinyanja $= 1.04$ species ($r = 0.19–1.84$), and Kyagurilo $= 0.85$ species ($r = 0.03–1.71$).

To compare overall levels of fruit eating between groups, we considered the presence or absence of fruit seeds in fecal samples per day as an indication that the group ate fruit. We first tested for differences among sex and age classes in fruit seed presence and found none within the Habinyanja group (Kruskal-Wallis: $\chi^2 = 1.708$, df $= 2$, $p = 0.426$) or the Kyagurilo group ($\chi^2 = 0.278$, df $= 2$, $p = 0.870$). In the Mubare group, the female and juvenile sam-

ples contained seeds more often than the silverback feces did ($\chi^2 = 11.65$, df $= 2$, $p < .0029$). However, samples within the Mubare group compared by season showed March-May to be the only season in which there are significant differences ($\chi^2 = 16.6$, df $= 2$, $p < .0002$). Because only one season showed differences and fruit remains were in very small amounts at that time, we considered that the sex/age class differences in the Mubare group are negligible across the year for the purposes of the analyses and therefore we used adult female samples for intergroup comparisons.

The Mubare group ate fruit on 69.7% of days ($n = 198$); the Habinyanja group ate fruit on 82.1% of days ($n = 221$); and, the Kyagurilo group ate fruit on 65.6% of days ($n = 163$). There is no significant difference among groups in the percent of days each mo the gorillas ate fruit (Friedmann Test: $\chi^2 = 0.667$, df $= 2$, $p = 0.717$; Fig. 4).

Via the number scoring system based on seed amounts, there is no significant difference in the amount of fruit eaten between sex and age classes within any group (Kruskal Wallis: Mubare: $\chi^2 = 1.146$, df $= 2$, $p = 0.564$; Habinyanja: $\chi^2 = 0.402$, df $= 2$, $p = 0.818$; Kyagurilo: $\chi^2 = 0.188$, df $= 2$, $p = 0.910$). Therefore, we used adult female/blackback samples for intergroup analyses. There is no significant difference among groups in mean monthly fruit consumption based on seed scores (Kruskal-Wallis: $\chi^2 = 2.369$, df $= 2$, $p = 0.306$; Mubare mean monthly fruit seed score $= 1.50$, $r = 0.32–2.76$;
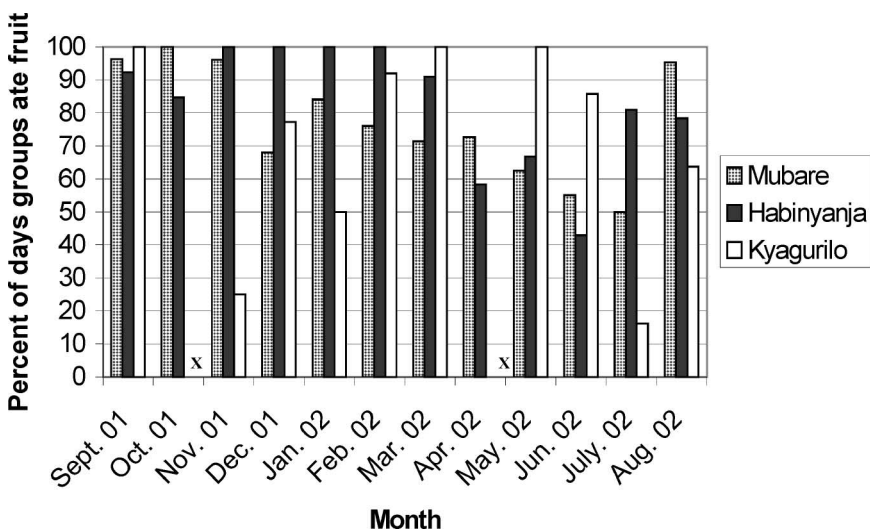

Fig. 4b. The monthly percent of days each group ate fruit. X over October and April on the X-axis indicates there is no datum for the month for the Kyagurilo group.

Habinyanja mean monthly fruit seed score $= 1.42$, $r = 0.24$–2.74; Kyagurilo mean monthly fruit seed score $= 1.00$, $r = 0.18$–2.28).

Of the 16 important fruit species, only one, *Myrianthus holstii*, was important for all 3 groups. Only 3 species were important for groups in Buhoma and Ruhija: *M. holstii; Chrysophyllum sp.* (Habinyanja and Kyagurilo), and *Maesa lanceolata* (Mubare and Kyagurilo). Between the 2 low altitude groups in Buhoma, there are 11 important fruit species in total, 7 of which were shared (Table IV).

Out of the 4 shrub fruit species classified as important, there was none in common among the 3 groups and only one was considered important by groups at in both sites: *Rubus apetalus* (Mubare and Kyagurilo). The Habinyanja and Mubare groups ate only one important shrub fruit species in common: *Solanum anguvi* (Table IV).

The Kyagurilo group did not eat fruit from herb species. There were 3 herb species that produced fruits important in the diets of both groups in Buhoma: *Aframomum angustifolia*, *Aframomum sanguinum*, and *Smilax anceps* (Table IV).

All 3 groups were highly selective of some important fruit species per Ivlev's electivity index (Mubare: 33.3% [$n = 6$], Habinyanja: 14.3% [$n = 8$], Kyagurilo: 16.7% [$n = 7$], Table IV). Although we did not calculate selectivity of *Ficus spp.*, fruits of *Ficus* were consumed throughout the year by the Mubare and Habinyanja groups. They occurred at extremely low densities (most species were not recorded along vegetation transects), which suggests that they may be highly selecting fig fruits. *Myrianthus holstii* was positively selected by all 3 groups and highly selected by the Mubare and Kyagurilo groups. However for each species, selectivity varied across months. There are some species for which the total year electivity index is negative, yet in some months they are positively selected: *Cassine aethiopica, Chrysophyllum sp., Leplaea mayombensis, Maesa lanceolata, Mystroxylon aethiopicum, Prunus africana, Syzigium guineense* (Fig.. 5a–5c).

DISCUSSION

Dietary Variability

We observed striking differences in the fibrous food and fruit diets between the low altitude groups and the high altitude group. The low altitude groups consumed more species of fibrous food ($n = 140$) and fruit ($n = 36$) than the high altitude group did (fibrous foods: 62; fruit: 11). In addition, there is little overlap of both important fibrous foods (Mubare and Kyagurilo groups shared 24.4% and Habinyanja and Kyagurilo groups shared 12.7%) and fruit species (Mubare and Habinyanja groups shared
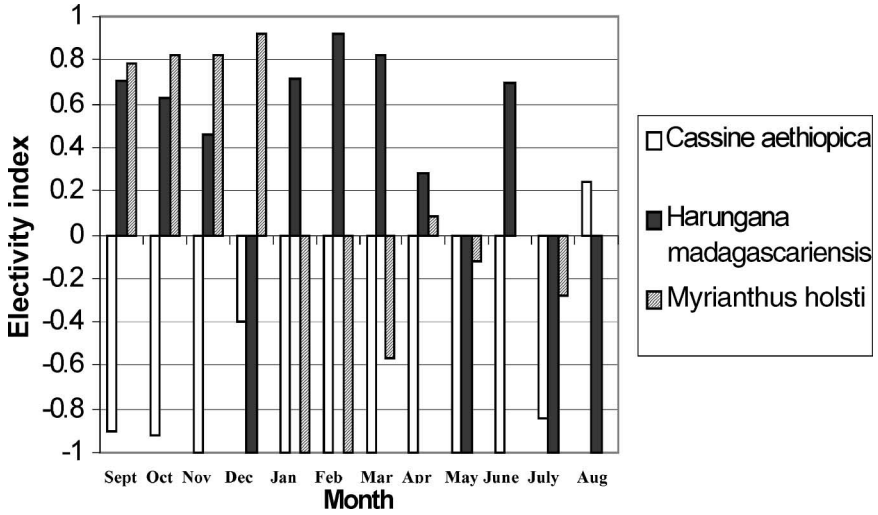
Fig. 5a. Monthly selectivity indices (via Ivlev's electivity index: >0 = positive selection, <0 = selection against) for fruit species >5% (frequently eaten) in the Mubare group's diet.
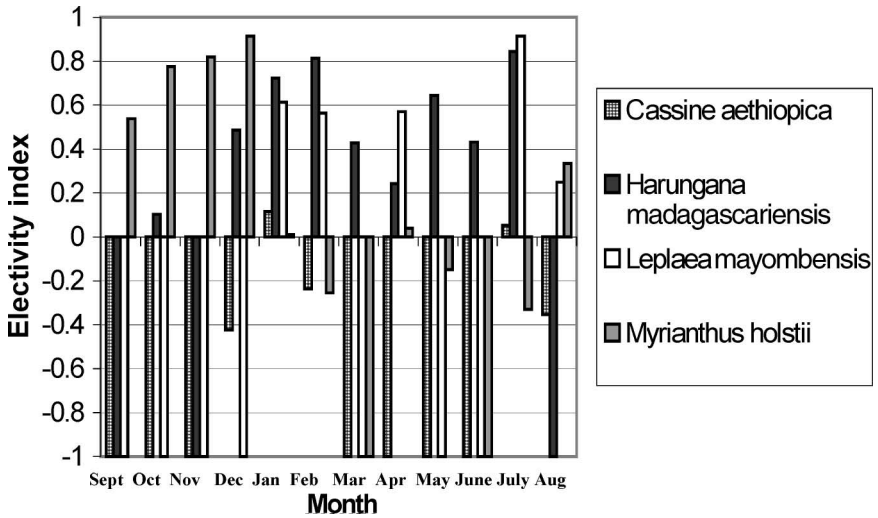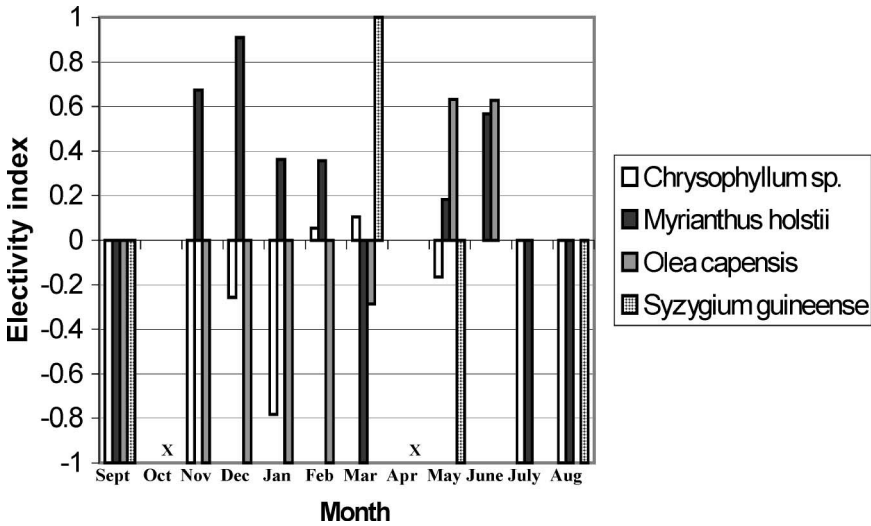

Fig. 5b. Monthly selectivity indices (via Ivlev's electivity index: >0 = positive selection, <0 = selection against) for fruit species >5% (frequently eaten) in the Habinyanja group's diet.

Fig. 5c. Monthly selectivity indices (via Ivlev's electivity index: >0 = positive selection, <0 = selection against) for fruit species >5% (frequently eaten) in the Kyagurilo group's diet. X over October and April on the X-axis indicates there is no datum for this month.

16.7% with Kyagurilo group) eaten between sites. Per Chapman and Fedigan's (1990) categories, most of the intersite differences in species eaten can be attributed to food availability: 71% for fibrous foods and 94% for fruit, (Table IV). Therefore, we suggest that differences in the spatial and temporal availability of food items at each site influenced dietary diversity (Butynski, 1990; Chapman and Chapman, 1999; Richard, 1977). This likely explains why groups at the low altitude site ate significantly more species of fruit per mo than the high atitude group did. Interestingly fruit of *Ficus*, which was previously identified as a negligible part of the diet of Bwindi gorillas (Stanford and Nkurunungi, 2003), are an important fruit for gorillas in another location of the park.

Although we expected the lower altitude groups to consume a greater quantity of fruit than the high altitude group because of the higher fruit availability there, based on the simple measurement of presence/absence of fruit seeds and scoring system for fruit quantity in feces, there is no difference in the number of days fruit was eaten or how much fruit was consumed among the groups. Quantifying fruit eating can be challenging (Doran *et al.*, 2002; Tutin and Fernandez, 1985); researchers who have studied the feeding ecology of gorillas have relied heavily on indirect methods to quantify fruit eating. These methods provide only rough estimates of diet and no measure of absolute quantity of food consumed. Therefore, the lack of difference in

fruit eating among sites may be because of indirect measures in conjunction with our quantification method, which did not detect differences and could simply be attributed to sampling error.

A surprising result is the differences in fruit and fibrous foods eaten between the 2 groups with overlapping home ranges. They shared only 46.3% of important fibrous food items and 62.5% of important fruits. While their home ranges overlapped by 45% (Ganas and Robbins, in review), there are areas exclusively occupied by only one group and these may differ in fruit availability and species composition. However, the differences may not be entirely explained by availability, and other factors such as food profitability or group traditions or both factors may contribute to the divergence in diet, though we could not distinguish between the hypotheses. Furthermore, habitat use varied between groups and may have influenced dietary patterns. For example, the Habinyanja group only ate fruits of *Chrysophyllum sp*. and *Bridelia micrantha* while the Mubare group only ate fruits of *Maesa lanceolata*, *Prunus africana*, and *Smilax anceps*. All of them, except *Maesa lanceolata* occur at low densities and thus may be restricted to certain areas of one group's range. Low density prevented us from calculating whether the species were clumped in their distribution. Furthermore, we observed that during particular time periods, the groups focused on different fruit species. When the Habinyanja group were feeding on fruits of *Chrysophyllum sp.*, the Mubare group ate fruits of *Ficus spp*. (March); when the Mubare group ate fruits of *Prunus africana*, the Habinyanja group ate fruits of *Myrianthus holstii* (August). The fruit species may be comparable in nutrient and energy content (food profitability), or there may be group traditions in fruit-eating behavior.

Group traditions may explain dietary variability within and between populations of Japanese macaques (Azama 1973; Kawai, 1965), white-faced capuchins (Chapman and Fedigan, 1990) and chimpanzees (Goodall, 1986; Nishida *et al.*, 1983). Although anecdotal, there is also evidence of group traditions in mountain gorillas. Watts (1984) noted a silverback at Karisoke that shifted his home range area completely had the most divergent diet among all group members. Byrne (1999) described the case of a young female that transferred from a habitat where nettle species are not found, into a group whose range included nettle species. She never became proficient at folding nettle leaf blades and her son was the only other group member that lacked the skill, though both individuals ate them. Group traditions are perhaps more likely for fibrous food species that require complex processing techniques than fruit species.

Selectivity

Gorillas select foods based upon both availability and nutritional content (Plumptre, 1995; Remis *et al.,* 2001; Rogers *et al.,* 1990). The focal groups

selected the majority of fibrous foods in their diets in greater proportion than their availability in the habitat (Mubare = 92%, Habinyanja = 89% and Kyagurilo = 100%; Table IV). In particular, despite differences in fibrous food availability between the 2 sites, *Momordica calantha*, *Urera hypselodendron*, *Basella alba*, and *Rubus apetalus* were highly selected by all 3 groups.

Although the gorillas positively selected a smaller proportion of fruits (Mubare = 43%, Habinyanja = 50%, Kyagurilo = 75%) than fibrous foods, they positively selected for 75% of fruits they ate frequently (>5% in overall diet; Table IV). All groups positively selected the fruits of *Myrianthus holstii*. However, examining fruit selection at a yearly scale may not accurately portray levels of selectivity because when we examined fruit selection at a finer scale, we found that electivity values differed between months and often species were avoided one month and highly selected another (Figs. 5a–c). Our data suggest that the gorillas avoided certain fruit species when they were available, but this may be due to the rough phenological measures we used. Fruits that were available but avoided may have been unripe, and we did not score ripeness. Additionally, even if small amounts of a particular fruit were available and the gorillas did not eat them, the electivity value would be −1. However, per the optimal foraging model, the gorillas may be judging fruit patches for overall profitability and therefore not eat a fruit when it is available in only small amounts (Stephens and Krebs, 1986).

Comparisons With Other Gorilla Populations

Our findings demonstrate that there are large dietary differences between the mountain gorillas in the Virunga Volcanoes and those in Bwindi Impenetrable National Park (Nkurunungi, 2004). Bwindi gorillas eat a greater quantity of fruit, and they eat more and different species of both fruit and fibrous foods (Table V). Given the ecological extreme (high altitude) of the areas surrounding Karisoke Research Center, they may be the only mountain gorilla groups that rarely eat fruit. The total number of food species eaten and the degree of frugivory are more similar between eastern gorillas at Kahuzi-Biega and Bwindi than between the populations of mountain gorillas at Bwindi and the Virungas (Table V).

However, there is little overlap of the 10 most commonly eaten species among 6 study sites of eastern gorillas (Table V; McNeilage, 1995, 2001; Vedder, 1984; Watts, 1984; Yamagiwa *et al.*, 1992, 1994, 1996; Yumoto *et al.*, 1994). In fact, only one species, *Basella alba*, was one of the 10 most commonly eaten species by gorillas in the Virungas, Bwindi, and Kahuzi-Biega. Likewise, gorillas in Bwindi and Kahuzi-Biega eat only 4 fruit species in common: *Myrianthus holstii, Harungana madagascariensis, Syzigium guineense*, and *Aframomum sanguinum* (Casamir, 1975; Yamagiwa *et al.*, 1994; Yumoto *et al.*, 1994). Gorillas in Bwindi and the Virungas eat only 1 species of fruit

Table V. Eastern gorilla site comparisons of altitude, fruit and fibrous food species consumed, the degree of frugivory, and top ten most commonly eaten fibrous foods (based on frequency of remains on gorilla trails at each site). Top 10 foods are listed alphabetically, and are ranked at all sites except Kahuzi-Biega, where they are denoted with a X. The top 10 species consumed in Buhoma are taken from the Mubare group

Site	Itebero (Kahuzi-Biega)	Kahuzi (Kahuzi-Biega)	Buhoma (Bwindi)	Ruhija (Bwindi)	Rwandan tourist group (Lower altitude Virungas)	Karisoke (High altitude Virungas)
Altitude	600–1300 m[a]	1800–2600 m[a]	1450–1800 m[b]	2100–2500 m[b,c]	2500–2800 m[d]	2680–3710 m[d,e,f]
Length of study	60 months[a]	60 months[a]	12 months[b]	46 months[b,c]	12 months[d]	30 months[d,e,f]
No. of groups studied	10	4	2	1	1	1
No. of species eaten	142	77	140	112	42	36
No of herb spp.	117	60	134	98	42	36
No of fruit spp.	67	24	36	30	2	1
Degree of frugivory	89% of fecal samples contained fruit remains[a]	96.5% of fecal samples contained fruit remains	67.9 & 82.1% of fecal samples contained fruit remains	65.6% of fecal samples contained fruit remains[b]	occurring on <1% trail remains[d]	<1% feeding time spent eating fruit[e]
Combined top ten fibrous foods for all sites						
Aframomum laurentii	X					
Aframomum sanguinum	X					
Arundinaria alpina		X				
Basella alba		X	1		3	
Brillantaisia arborescens				5	2	
Carduus leptocanthus				4		
Carduus nyassanus					7	2
Carex bequaertii						9
Clitandra cymulosa			5			
Cyathula sp.		X				
Cyperus latifolius		X				
Discopodium penninervium					9	
Droguetia iners					4	10
Elastostema welsitschii		X				
Ficus asperifolia			6			
Galium sp.					1	1
Halopegia azuera	X					
Haumania liebrechtsiana	X					

Species	[a]	[b]	[c]	[d]	[e]	[f]
Impatiens niamniamensis		X				
Ipomea sp.				6		
Lactuca attenuata		X				
Laportea aestuans			3			
Laportea alatipes						4
Lobelia stuhlmanii						7
Marantochloa leucantha	X					
Megaphrynium macrostacgyum	X					
Mimulopsis arborescens				9		
Mimulopsis solmsii			7			
Momordica calantha			8	10		
Momordica foetida					3	
Myrianthus holstii			8	7		
Palisota hirsuta	X					
Palisota mannii			10			
Peucedanom linderi				6	3	
Renealmia congolana	X					
Rubus apetalus			8			
Rubus sp.					10	6
Rumex abyssinicus		X				
Sacrophrynium leiogonium	X					
Senecio johnstonii						5
Thaumatocupccus daniellii						
Triumfetta cordifolia		X				
Triumfetta sp.			4	2		
Urera hypselodendron			9	1		
Urtica massaica					8	
Vernonia auriculifera					5	8

[a] Yamagiwa *et al.* 1994; Yumoto *et al.* 1994, 1996; Yamagiwa pers. comm.
[b] This study.
[c] Nkurunungi 2004.
[d] McNeilage 1995.
[e] Watts 1984.
[f] Vedder 1984.

in common, a shrub, *Rubus apetalus*. The differences within *Gorilla beringei* highlight the dietary diversity within the species and provide further evidence that dietary diversity and the degree of frugivory are negatively related to altitude (Table V). Furthermore, eastern gorillas may exhibit high dietary flexibility versus that of western gorillas. Doran *et al*. (2002) found little difference in western gorilla diets across 4 sites and suggested that indirect methods may mask dietary variability. However, indirect methods were used at 4 of 6 eastern gorilla sites with significant variation detected within and between locations.

Western gorillas appear to be more frugivorous than most eastern gorilla populations based on the diversity of fruit in the diet and the percentage of days fruit was consumed, though the actual quantity of fruit eaten by both gorilla species is unknown (Western gorillas: 26–95 fruit species eaten; fruit remains in 98–99% of dung samples; Cippolletta, 2003; Doran *et al.*, 2002; Remis, 1997; Williamson *et al.*, 1990). Differences in frugivory are probably due to the abundance and distribution of food; fruit tree density is higher while the density of herbaceous vegetation is lower in forests inhabited by western gorilla populations (Doran and McNeilage, 1998).

Differences in food distribution have been shown to influence the socioecology of other primate species (baboons: Bartow *et al.*, 1996; grey langurs: Koenig *et al.*, 1998; Koenig and Borries, 2001; squirrel monkeys: Boinski *et al.*, 2002). How differences in food distribution between the *Gorilla* species affects group sizes, habitat use, feeding competitiion, and reproductive strategies is an important avenue for future research (Doean and McNeilage, 1998, 2001; Robbins *et al.*, in press).

ACKNOWLEDGMENTS

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