

Food choices of the mountain gorilla in Bwindi Impenetrable National Park, Uganda: the influence of nutrients, phenolics and availability

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Abstract: The factors that influence food choice have implications for animal survival, reproduction and population growth. We conducted a 1-y study of food choice by four mountain gorilla groups that consumed herbs and fruit at two locations differing spatially and temporally in food availability in Bwindi Impenetrable National Park, Uganda. We collected data on 45 important foods consumed by the gorillas, the availability of those foods in each gorilla group's home range and their corresponding nutrient and phenolic concentrations. Employing a linear multiple regression, we tested three hypotheses regarding the influence of food availability and the nutritional and phenolic concentrations of food on food choice. Regardless of changes in herb availability, the choice of herbs was positively influenced by their abundance and sugar concentrations and negatively influenced by their fibre, condensed tannin and protein concentrations. Furthermore, regardless of changes in fruit availability, the choice of fruit was positively influenced by its abundance and negatively influenced by its condensed tannin concentrations. During periods of low fruit availability, the gorillas did not increase the consumption of herbs high in fibre and sugar. The choice of herbs low in fibre had less of an influence on food choice at the location with lower fruit availability than the other location. Our results underscore the importance of incorporating both availability and nutrient concentrations into studies of food choice; by doing so we found Bwindi gorillas were able to choose abundant, relatively high-quality foods year round.

Key Words: diet, fibre, food availability, *Gorilla beringei beringei*, nutritional ecology, protein, tannin

INTRODUCTION

Food choice, the factors involved in the decision to consume particular foods, is influenced by an animal's physiological and nutritional requirements, the need to avoid anti-feedants (secondary metabolites and fibre), the physical and sensory properties of food, food availability and culture (Boesch *et al.* 2006, Dominy *et al.* 2001, Freeland & Janzen 1974, Lambert 1998, Milton 1981, Westoby 1974). While it is known that many variables impact the choice of foods, very few studies have examined more than one factor influencing food choice in a single analysis. Determining what influences choice will be enhanced if many variables are included together, in particular both nutritional and anti-feedant composition

of foods and food availability (Janson *et al.* 1986, Leighton 1993). Food choice differs from food preference; food choice investigates how the different attributes of each food type may influence the decision of what an animal consumes (i.e. availability and nutrient concentrations), while preference controls for differences in availability and then calculates which food type would be chosen over another (Chesson 1983, Ganas *et al.* 2008, Johnson 1980).

Gorilla species (eastern: *Gorilla beringei* Matschie 1903 and western: *Gorilla gorilla* Savage & Wyman 1847) can be considered generalist herbivores as they consume foliage and fruit (Ganas *et al.* 2004, Rogers *et al.* 2004, Watts 1984).

Previous studies that have examined the nutritional composition of gorilla diets have found that gorillas consume fruits high in sugar or fat with varying levels of phenolics, tannins and fibre and eat foliage high in protein or sugar, with low to intermediate values of fibre and phenolics compared with non-foods (Calvert 1985, Remis

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Table 1. Ecological characteristics of the two study locations in Bwindi. FAI = Fruit availability index: the product of the mean dbh (calculated using the trees in phenology study), density of those species in the gorillas' range and their mean monthly abundance score from the phenology (0–4 score based on per cent fruit coverage in canopy, following Sun *et al.*, 1996). For purposes of analysis the FAI was calculated fortnightly but the average of the fortnightly FAI scores over the 1-y study period is presented here. Herb biomass values here are presented as the yearly average of the monthly herb biomass values. Total annual rainfall is the sum of the daily rainfall over the 1-y study period. Mean temperature represents the daily average of the highest and lowest recorded temperature each day over the 1-y study period. Mean temperatures are a yearly score, based on daily readings.

	Buhoma	Ruhija
Gorilla groups	Mubare Habinyanja Rushegura	Kyagurilo
Altitude (m asl)	1450–1800	2100–2500
Mean temperature low and high (°C)	17.2–27.4	13.5–19.4
Total annual rainfall (mm)	2092 ¹	1176
Mean FAI and range	1541.4 (432.1– 2904)	80.3 (0–328.6)
Mean herb biomass (g m ⁻²) and range	41.6 (33–47.6)	82.9 (66.3–101.1)

¹Data from the month of April are missing; therefore this figure is an underestimate.

et al. 2001, Rogers *et al.* 1990, Waterman *et al.* 1983). In a more detailed study of food choice, Watts (1983) found that protein and digestibility positively influenced the choice of foods by mountain gorillas at a high-altitude site (2700–3700 m) in Rwanda. However, with the exception of Watts' work, none of these studies considered both the nutrient composition and food availability simultaneously (in fact most did not consider availability at all), which limits the interpretation of the results and may lead to misleading conclusions. Furthermore, previous studies of the food choice of gorillas, in particular from western gorillas, have examined only a single gorilla group or pooled data from multiple unhabituated groups (Calvert 1985, Remis *et al.* 2001, Rogers *et al.* 1990).

We studied four mountain gorilla groups at two locations (Buhoma and Ruhija) in Bwindi Impenetrable National Park, Uganda to investigate what nutritional, phenolic and food-availability factors influence food choice (Table 1). These locations differ in altitude, rainfall, temperature, plant species composition, habitat types, fruit availability and the biomass of herbaceous vegetation (Ganas *et al.* in press, Nkurunungi *et al.* 2004). Our study tested three hypotheses concerning how both food availability and nutritional composition of herbs and fruits influence food choice. (1) We predicted that (a) when food availability is higher, nutritional composition of foods will influence choice and (b) when food availability is lower, availability will influence choice. During the period of high food availability, we predicted

that herbs would be chosen for relatively high protein and sugar concentrations while fruit would be chosen for relatively high sugar, fat and/or energy concentrations. For both food groups, gorillas would not choose foods relatively high in fibre and phenolics. (2) Fruit availability influences the choice of herb foods. Assuming the need to maintain a constant intake of energy, we predicted an inverse relationship between the availability of fruit and consumption of herbs high in sugar and/or fibre. (3) Spatial variation in food availability affects which factors influence an animal's choice of food. Because the total herb biomass was greater in Ruhija than at Buhoma, the gorillas at Ruhija could be choosier. Therefore we predicted that (a) nutritional factors would more strongly influence choice of herbs by the gorillas at Ruhija than those in Buhoma. Additionally, because in Ruhija fruit availability was relatively very low compared with Buhoma, we also predicted that (b) gorillas in Ruhija would need to compensate for the lack of easily digested energy in fruit and would chose herbs for their higher sugar and fibre concentrations more so than gorillas in Buhoma.

METHODS

Study groups

Data on diet were collected from four habituated gorilla groups from September 2004 to August 2005. Three groups, Mubare, Habinyanja and Rushegura ranged around Buhoma (1450–1800 m). These gorilla groups contained 8, 22 and 13 individuals respectively and had overlapping home ranges (to various degrees). Because these groups are used for an ecotourism programme, the Uganda Wildlife Authority limits direct contact with them and we were not able to conduct direct observations. The fourth group, Kyagurilo (14 individuals), ranged near Ruhija (2100–2500 m), and is habituated for research. While direct observations are possible with this group, we used indirect methods on all groups for comparative purposes. For details of the study site see McNeilage *et al.* (2006).

Diet

Herbaceous vegetation. All weaned individuals of a group make a nest in close proximity to one another to form a nest site every night. During the day, the gorillas move and feed between each night's nest location creating obvious trails with bent vegetation, discarded food items and dung, which makes it easy to document what the gorillas have been eating. Bwindi gorillas consume foliage from herbs, shrubs and trees. However, herbs comprise the

majority of their diet, and therefore we focused on herbs (Ganas *et al.* 2004, Robbins *et al.* 2006). To quantify the relative frequency of the herbs in the gorillas' diet, we followed each group's main trail on a daily basis and recorded observations of what species and part of the plant were consumed based on feeding remains. These trails are easy to follow with the assistance of experienced trackers. The monthly frequency of each species found on these trails was then calculated to represent relative proportion of foods in diet (Frequency of species A = number of feeding spots of Species A/total number of feeding spots; following Calvert 1985, Doran *et al.* 2002, McNeillage 1995). We defined important species of herb as those occurring in $\geq 1\%$ frequency in any month. This excluded foods that were rarely eaten. On average, we analysed 19 d mo^{-1} per group (Mubare monthly range = 14–26, SD = 3.09; Habinyanja monthly range = 15–23, SD = 3.01; Rushegura range = 17–25, SD = 2.19; Kyagurilo range = 14–19, SD = 1.71). The gorillas occasionally eat leaves from trees, in particular those from the understorey tree *Myrianthus holstii* (Ganas *et al.* 2004, Rothman *et al.* 2007). However, the various plant parts from herbs make up the vast majority of the non-fruit diet of Bwindi gorillas (Rothman *et al.* 2007) and thus while it would be best to include the leaves of trees in the analysis, it was not possible here due to the use of trail signs as a method of quantifying diet (although often discarded parts from trees are found on these trails). Further, we did not have biomass availability measures of tree leaves for the subsequent analyses. Recording diet using these indirect methods, rather than behavioural observations to quantify the actual amount of each food type consumed, has the potential to lead to biases in the data. For example, because this method calculates a frequency for the gorilla group as a whole, it may over- or underestimate individual animal diets and/or fail to capture interindividual variation (Doran *et al.* 2002). Further, these methods are not as precise as recording actual amounts consumed. However, because our research looks at more general changes in the diet in response to changes in food quantity and quality, the biases of these methods were likely minimized.

Fruit. To determine the frequency and species of fruit consumed, we collected faecal samples from each group's night nests (<48 h old), and assigned dung to a sex and age class based on bolus size (Schaller 1963). Samples were collected 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) each day. Faecal samples were washed through a 1-mm sieve and seeds of different species were identified (following Ganas *et al.* 2004). Important fruits of different species were defined as those

occurring in $\geq 1\%$ of samples per group in any month (modified from Ganas *et al.* 2004, Remis 1997). Because gorillas in Bwindi have not been seen to spit seeds out in over 8 y of observation and also because the vast majority of fruits consumed during this study period were relatively small and eaten in their entirety (mean width of fruit = 7.7 mm, Ganas unpubl data, Robbins pers obs) we assumed that if the gorillas ate fruit, the seeds would be detected in the faecal samples. There were no within-group differences between age and sex classes in the frequency of species consumed as fruit (analysed using a χ^2 test) and thus we used only adult female samples in the food choice analysis. We collected faecal samples an average of 25 d mo^{-1} (SD = 3.98 d mo^{-1}) (Mubare mean = 23.3 d mo^{-1} , monthly range = 17–26 d mo^{-1} , SD = 2.46 d mo^{-1} ; Habinyanja mean = 24 d mo^{-1} , monthly range = 17–29 d mo^{-1} , SD = 3.72 d mo^{-1} ; Rushegura mean = 23.8 d mo^{-1} , monthly range = 18–30 d mo^{-1} , SD = 3.33 d mo^{-1} ; Kyagurilo mean = 26.9 d mo^{-1} , monthly range = 12–30 d mo^{-1} , SD = 5.32 d mo^{-1}). Biases associated with indirect methods as discussed above are also relevant to our sampling of fruit in the gorillas' diet.

Food availability

Spatial. To determine the spatial distribution of plants at each study location, we measured plant availability on 102 and 54 transects 200 m in length at Buhoma and Ruhija respectively using a stratified random technique (Greig-Smith 1983). Each transect was placed randomly within a $500 \times 500\text{-m}$ grid square which was placed over a map of each study location, (encompassing where the gorillas ranged during the study period). For every transect there were 10 nested quadrats alternatively placed on each side of the transect in intervals of 20 m. Within each nested quadrat, herbs and their biomass were estimated in 1-m^2 plots, lianas and young trees of less than 10 cm dbh and above 2 m in height were counted in 5-m^2 plots, and trees greater than 10 cm diameter at breast height (dbh) were counted and dbh quantified in 10-m^2 plots (see Ganas *et al.* in press for further details).

Temporal. To calculate the temporal availability of herbs, we established 89 1-m^2 permanent plots (Buhoma = 51, Ruhija = 38) in the forest. At approximately the same time every month, for each permanent plot, we took measurements of particular plant parts. For trailing plants, we counted the number of leaves that were in the plot regardless of whether they were rooted in the plot or not, since the rooted position is often difficult or impossible to locate. For herbs with rooted stems, we measured the length of the plant from the rooted position

to the base of the top leaf. We also harvested 40 individuals of each of these species of varying lengths from outside the permanent plots. For each of these harvested individuals, we measured the length of the plant stem or counted the number of leaves on the individual plant and recorded the wet weight of the part eaten by the gorillas. We then dried the plant parts to obtain a dry weight for each corresponding length. The data on plant part dry weight and length were used to produce regression equations which allowed us to determine the monthly changes in herb biomass per species in the permanent plots. These equations were also used with the spatial measurements of herb biomass availability (quantified in the 1-m² quadrats on the transects during the spatial availability measures) allowing us to calculate the individual species and total herb biomass per month per location. For more detailed information on these methods, see Ganas *et al.* in press.

To calculate the temporal availability of fruit, on a fortnightly basis within each location, we monitored 397 trees and herbs of 40 species, 13 of which were found at both sites (211 (mean number per species = 7.3, SD = 4.6) and 186 (mean number per species = 7.8, SD = 4.1) at Ruhija and Buhoma, respectively) which have been known to be consumed by the gorillas. For each species, we recorded the per cent abundance of ripe fruit in the crown scoring between zero and four (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75% and 4 = 76–100% of crown covered) following Sun *et al.* (1996). To determine fruit availability at each location for each fortnightly period, a score of fruit abundance was calculated using a fruit availability index (FAI, following Nkurunungi *et al.* 2004; calculated as the product of the mean dbh (of phenology trees of each species of fruit eaten by the gorillas), density of each species at each location (recorded during the spatial availability measurements) and their mean fortnightly abundance score value from the phenology study). To get a value for total fruit availability for each location, we summed the individual FAI scores for each fortnightly period.

Three species of fruit were not known at the beginning of the study to be consumed by the gorillas (*Trichilia* sp., *Memecylon jasminoides* and *Galiniera coffeoides*) and we have no phenological data on them and excluded them from the analysis. Additionally, the majority of *Ficus* spp. (excluding *F. capensis*) were strangler figs and a FAI could not be calculated.

Nutritional sampling

We collected a total of 45 important food species consumed by the gorillas between locations. Because we did not directly see which exact plants were consumed by the gorillas or the entire plant was eaten, many times it

was difficult to collect plant parts from which the exact tree or herb the part was consumed. Nonetheless, every attempt was made to sample food items from the specific areas where the gorillas fed. Second, the nutritional composition of a particular plant species has been shown to vary among individual plants, seasons and different areas of a forest (Chapman *et al.* 2003). Thus, we made multiple collections of plant species when possible by collecting them from different areas of the gorillas' home range (where they had been feeding) and collecting them during the two different wet seasons. Due to the difficulty of collecting fruit from tall canopy trees, most fruit samples came from a single tree or location. Due to the short-term availability of fruits in Bwindi, fruit was sampled once when available. Three species produced very small fruit crops and we could not obtain samples for nutritional analysis. All food items collected for nutrient/chemical analyses were processed in a way that mimicked which parts the gorillas consumed. For example, if the gorillas ate pith from a particular species, we processed and collected only pith. We included between 56–67% (Buhoma 5 and 6 spp. (Mubare & Habinyanja)) of the important fruits and 77–83% of important herbs (Buhoma: 19 spp. and Ruhija: 12 spp.). Foods that were not included in the analyses were those that contributed a small amount to the gorillas' diet.

Samples were frozen in liquid nitrogen and freeze dried. Dried samples were kept in a cool, dry place until they were sent to the Institute of Zoo and Wildlife Research in Berlin, Germany for nutritional analysis and the University of Hohenheim in Stuttgart, Germany for phenolic determination.

Phytochemical analysis

All samples were ground prior to analysis. Dry matter content (DM) was determined by drying a portion of the sample at 105 °C overnight. All data are given as % dry matter. Samples were analysed for the following macronutrients using standard techniques: nitrogen was determined by complete combustion (Dumas combustion) at high temperature (approximately 950 °C) in pure oxygen, using a Rapid N III analyser (Elementar Analyser Systeme GmbH, Hanau, Germany) using a factor of 6.25 for conversion into protein (crude protein (%DM) = 6.25 × N (%DM)). Starch, D-glucose, D-fructose and sucrose were determined with commercialized enzymatic tests (UV method; R-Biopharm AG, Darmstadt, Germany). Lipids were extracted with ethyl ether using a fully automatic Soxhlett-system (Soxtherm; Gerhardt Laboratory Systems, Königswinter, Germany), and gross energy was determined by burning a sample of dry matter in pure oxygen atmosphere in a bomb calorimeter (C5003 bomb calorimeter; IKA-Werke GmbH & Co. KG, Staufen,

Germany). The heat produced was measured in kJ g^{-1} DM. Detergent fibre analysis was performed following Van Soest *et al.* (1991) with NDF (neutral detergent fibre), ADF (acid detergent fibre) and ADL (acid detergent lignin) being determined sequentially from each sample using an Ankom Fibre Analyser 220 (Ankom Technology, Macedon, USA). Hemicellulose (NDF-ADF) and cellulose (ADF-ADL) were calculated by weight difference. All samples were analysed in duplicate.

The total phenolics were determined according to Makkar *et al.* (1993). Aliquots of the sample were placed in a test-tube and made up to 500 μl with distilled water, then 250 μl of the Folin Ciocalteu reagent followed by 1.25 ml of the sodium carbonate solution. The total amount of phenolics was then calculated as tannic acid equivalent from a calibration curve prepared with tannic acid. Estimation of total tannins from total phenolic extracts: 100 mg of polyvinylpyrrolidone (PVPP) was weighed into a 100 \times 12-mm test-tube; 1.0 ml distilled water followed by 1.0 ml of the sample phenolics extract was added to the test tube. The tannin concentration of the sample was then calculated as: total phenolics – non-tannin phenolics = tannins (%). Determination of condensed tannins followed Porter *et al.* (1986) and Rothman *et al.* (2007).

Statistical analysis

We used a multiple linear regression to determine how nutrient, phenolic and food availability factors influenced food choice. Two separate models were used, one for fruit and one for herbs because data on frugivory, herbivory and availability were recorded differently.

Data reduction. First, for fruit and herbs separately, we reduced the number of independent variables (protein, starch, fructose, glucose, sucrose, WSC (water-soluble carbohydrates, the sum of fructose, glucose and sucrose), hemicellulose, cellulose, lignin, NDF (sum of hemicellulose, cellulose and lignin), ADF (sum of cellulose and lignin), fat, energy, total phenolics, total tannins and condensed tannins) by inspecting correlations between variables and in the case of two variables being highly correlated to one another (absolute correlation coefficient > 0.75) we removed one of them. The correlations made biological sense (e.g. fructose and water-soluble carbohydrates were highly correlated). The remaining variables were then subjected to two separate Principal Components Analyses (PCA with a varimax rotation; one for fruit, one for herbs). In case of a principal component on which only a single variable had its highest loading, we reran the PCA without that variable and included the variable directly into subsequent analyses.

Multiple regression

Several of our hypotheses represented interactions between continuous predictor variables. To incorporate these into the multiple regressions, we first z-transformed the corresponding variables. We then multiplied the z-scores of a pair of variables and incorporated the result as the term representing the interaction between the two and also the two z-transformed main independent variables into the model (Aiken & West 1991). Second, we also aimed to compare the four gorilla groups. We included group as a categorical independent variable into the model using three dummy coded variables (Field 2005). Interactions between dummy coded and continuous predictors were included by incorporating the product of the dummy coded variable and the z-transformed continuous predictor into the model.

The variables used in each model to test our hypotheses are presented in Appendix 1. After incorporating interactions into the model and excluding cases from the data both data sets (herb and fruit) still fulfilled the requirements of a multiple linear regression with regard to the relation between the number of predictor variables and the number of cases (Field 2005).

After running an initial multiple linear regression, we inspected whether multi-collinearity could invalidate the conclusions (Field 2005). Although near the threshold of what is permissible, multi-collinearity was not completely absent. For herbs, to assess whether the derived final model could be unstable due to multi-collinearity, we bootstrapped the data 1000 times and then determined minimum and maximum model parameters (i.e. mean and SE) as well as average P-values for the individual predictor variables and the overall model (Manly 1997).

For the analysis of herb choice, all groups were included in the model. From the analysis of fruit choice we first removed all data points when availability for a particular species was zero. We excluded the Rushegura group from this analysis since we did not have nutritional data for over 60% of the fruits they consumed, and the Kyagurilo group, since typically they only consumed fruit of one species per fortnightly period. Thus for the fruit choice analysis, only the Mubare and Habinyanja groups were included in the model. From these groups, we were able to include 67% and 63% of the important fruits in the model. Fruits of species not included in the model were of lesser importance (e.g. two species constituted only 1% frequency of the annual diet). Since the dependent variable (frequency of fruit consumed) comprised many zeros, no transformation could normalize it. Hence we assessed the significance of the overall model using a permutation test (which was based on 1000 permutations and included the original data as one permutation; Manly 1997). Significance was assessed by determining the

proportion of permuted data sets revealing an R^2 at least as large as the original data. Since coefficients of individual independent variables were likely to be inaccurate due to non-normality of the response variable we did not focus on the specific values of the coefficients but only present their signs and P-values.

RESULTS

Principal components analysis

Both PCAs were justified (Kaiser–Maier–Olkin measure of sampling adequacy: herbs: 0.48, fruit: 0.64, Bartlett's test of sphericity: herbs: $\chi^2 = 117$, $df = 36$, $P < 0.001$; fruit: $\chi^2 = 23.3$, $df = 15$, $P < 0.08$). The PCAs revealed three (for herbs) and two (for fruit) principal components (with eigenvalues in excess of one) which together explained 71.2% (herb) and 68.2% (fruit) of the total variance (Table 2).

Food availability

The total average herb biomass of important herbs in Ruhija was double that of Buhoma (Figure 1), but there were no strong seasonal changes in herb biomass availability at either location. In contrast, fruit availability was much greater in Buhoma than Ruhija, and showed a seasonal pattern (Figure 2).

Diet

Herb and fruit diet and corresponding nutritional and phenolic concentrations varied between groups and locations (Tables 3 and 4). In Buhoma a mean of 29.3 (SD = 2.5, average of three groups) and in Ruhija 11 important herbaceous species were consumed. Fruits of nine (SD = 1.7, average of three groups)

Table 2. Results of the Principal Components Analyses on the herb and fruit nutrient and phenolic values. WSC = water-soluble carbohydrates (sum of glucose, fructose, sucrose), NDF = neutral detergent fibre (sum of cellulose, hemicellulose, lignin). Indicated are loadings of the variables on the principal components derived. Bold values indicate the largest absolute loading per variable.

Trait	Component 1	Component 2	Component 3
Herbs			
Protein	0.135	0.618	-0.597
WSC	-0.324	0.195	0.773
Sucrose	0.002	-0.067	0.719
NDF	0.837	-0.412	-0.091
Hemicellulose	0.549	0.071	-0.184
Lignin	0.766	0.269	-0.418
Fat	-0.156	0.816	0.299
Total phenolics	0.172	0.857	-0.152
Condensed tannin	0.732	0.139	0.458
Eigenvalue	2.77	2.09	1.55
% variance explained	30.8	23.2	17.2
Fruit			
Sucrose	0.160	-0.755	
WSC	-0.857	-0.157	
Fat	0.441	0.762	
Energy	0.345	0.636	
Lignin	0.596	0.581	
NDF	0.862	0.069	
Eigenvalue	3.03	1.06	
% variance explained	50.5	17.8	

species were consumed in Buhoma and seven in Ruhija. There were no differences in the nutrient composition of herbs consumed by the gorillas in the two locations (tested by comparing the three PCA factor scores of all herbs; Mann–Whitney $U = -6.7$; $P < 0.001$ Buhoma $n = 22$, Ruhija $n = 14$, Table 2). We were unable to sample a few important herbs for nutritional analysis, so the number of species used in this analysis differed than the total number of important herb species recorded. PCA loading number one,

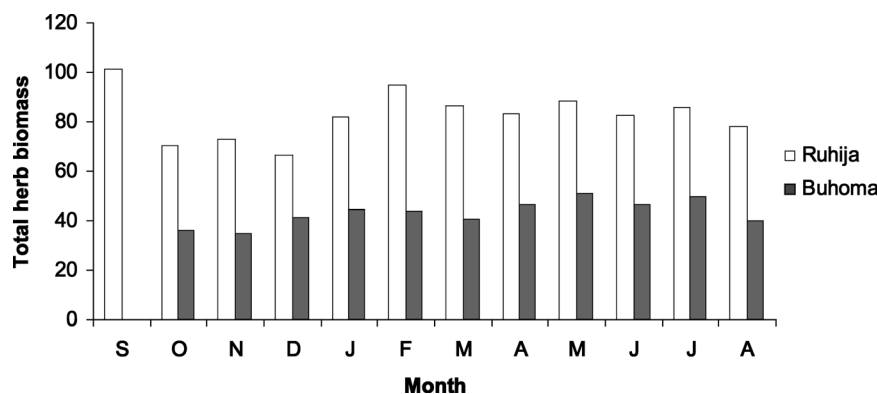


Figure 1. Variability in total biomass (g m^{-2}) of important ($\geq 1\%$ frequency in diet for at least one month) herbs consumed by the gorillas at each location (Buhoma and Ruhija) over the study period.

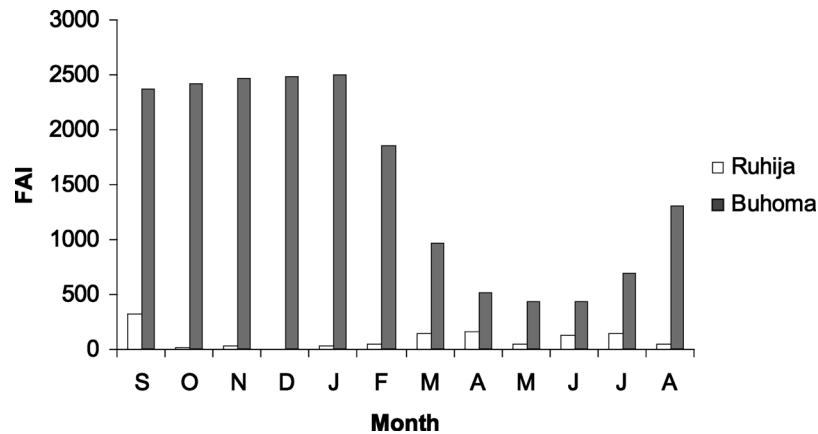


Figure 2. Variability in total fruit availability of important ($\geq 1\%$ frequency in diet for at least one month) fruit consumed by the gorillas at each location over the study period.

NDF, hemicellulose, lignin and condensed tannin: $Z = -0.220$, $P = 0.826$; PCA loading number two, protein, fat, total phenols: $Z = -1.14$, $P = 0.253$; PCA loading number three, WSC (water-soluble carbohydrates, sum of fructose, glucose and sucrose) and sucrose: $Z = -1.63$, $P = 0.104$; Table 2).

The overall multiple regression revealed significant influences of the independent variables on the choice of herbs ($R^2 = 0.41$, $F = 26.4$, $P < 0.001$) and fruit ($R^2 = 0.22$; $F = 10.1$, $P < 0.001$). For the herb model, the bootstrapping analysis showed very little variation in results (by examining the mean, SE and P-values of the 1000 tests) in comparison with our regression test, thus confirming the validity of the overall model.

The hypothesis that when food availability is higher, nutritional composition will influence choice (1a) and when food availability is lower, availability will influence choice (1b) was not supported for both herbs and fruit (all $P > 0.05$, Tables 5 and 6). Furthermore, regardless of changes in overall herb availability, gorillas chose herbs that were more abundant, had a relatively high sugar concentration, and those that had relatively lower fibre, condensed tannin, protein, fat and phenolic concentrations (Table 5). Further, regardless of changes in fruit availability, the gorillas chose fruits that were more abundant, and also those with relatively low condensed tannin concentrations (Table 6).

Second, our prediction (2) that there would be an inverse relationship between the availability of fruit and consumption of herbs high in sugar and/or fibre was also not supported ($P > 0.05$, Table 5).

Third, our results provided support for the third hypothesis (3); spatial variation in food availability affects which factors influence an animal's choice of food. Gorillas in Ruhija chose herbs relatively higher in fibre (predictions a and b) and condensed tannins significantly more than the gorillas in Buhoma (although both groups

consumed foods with relatively low fibre amounts; Table 5). However, they did not choose herbs relatively high in sugar.

DISCUSSION

To date, this is the most comprehensive study of food choice in gorillas; the diets of four groups of habituated gorillas were measured systematically for an entire year. By using a multivariate test, we were able to show a relationship between both the nutrient and phenolic concentrations of foods in the gorillas' diet and food availability and the choice of foods. Regardless of changes in food availability, gorillas in Bwindi chose herbs that were more abundant, with relatively higher sugar concentrations and with lower fibre, condensed tannin, protein, fat and total phenolic concentrations. They also chose fruit relatively high in abundance and relatively low in condensed tannin concentrations. In other words, they chose abundant foods with particular nutritional and phenolic profiles. Second, there was not an inverse relationship between the availability of fruit and consumption of herbs high in sugar and/or fibre. Third, the group at the location with very low fruit availability and higher herb availability chose herbs relatively higher in fibre than the groups at the other location, where fruit was more available. Possible explanations for our results are given below.

There are two possible reasons why shifts in overall herb and fruit availability did not alter the choice of foods, in contrast to our predictions (1a and 1b). First, there appears to be a plentiful supply of protein-rich herbs year round (Figure 1, Table 4). Herb availability varied little over the year so that even during times of lower herb availability there may have been an abundant supply from the perspective of the gorillas and these

Table 3. The yearly frequency of important ($\geq 1\%$ in any month) fruit and herbs consumed by each group and used in the model. ^X indicates that there is no phenology or nutrient/phenolic data and therefore they were not included in the regression model. NA = Not available in this location. NI = consumed during the study period, but not classified as important. — = available but not consumed.

Plant species	Part eaten	Mubare	Habinyanja	Rushegura	Kyagurilo
Herbs					
<i>Aframomum angustifolium</i> K. Schum.	pith	1.7	0.7	1.0	NA
<i>Aframomum sanguineum</i> K. Schum.	pith	1.5	1.2	0.9	NA
<i>Aframomum</i> sp.	pith	0.9	1.1	1.8	NA
<i>Basella alba</i> L.	leaves	13.5	10.7	10.5	7.5
<i>Carduus</i> sp.	stalk	NA	NA	NA	1.6
<i>Desmodium repandum</i> (Vahl) DC.	leaves	0.3	0.4	—	NA
<i>Gouania longispicata</i> Engl.	leaves	0.8	0.7	0.4	—
<i>Ipomoea wightii</i> All.	leaves	4.2	3.7	4.7	—
<i>Ipomoea</i> sp.	leaves	1.8	3.7	0.7	8.9
<i>Ipomoea</i> sp.	bark	N	NI	NI	1.2
<i>Laportea aestuans</i> (L.) Chew	bark	6.6	5.4	7.4	NA
<i>Laportea aestuans</i>	leaves	0.9	0.8	0.5	NA
<i>Mimulopsis arborescens</i> C.B. Clarke	pith	12.4	16.0	22.8	14.6
<i>Momordica calantha</i> Gilg.	leaves	1.7	2.1	2.6	12.6
<i>Momordica foetida</i> K. Schum.	leaves	0.9	1.2	1.0	0.1
<i>Mimulopsis solmsii</i> Schweinf.	leaves	3.0	2.3	1.8	7.0
<i>Mimulopsis solmsii</i>	bark	—	—	—	11.1
<i>Palisota mannii</i> C.B. Clarke	pith	5.1	6.0	4.4	NA
<i>Pennisetum purpureum</i> K. Schum.	pith	0.9	0.3	—	—
<i>Piper capense</i> L.f.	pith	0.7	1.4	0.9	0.8
<i>Rubus</i> sp.	leaves	0.3	0.3	0.2	5.3
<i>Triumfetta</i> sp.	leaves	9.9	5.0	5.8	7.8
<i>Urera</i> sp.	bark	7.4	5.4	7.2	11.2
<i>Urera</i> sp.	leaves	0.8	0.6	0.7	2.3
Fruit					
<i>Aframomum angustifolia</i>	—	—	—	0.7	—
<i>Aframomum</i> sp.	—	1.1	—	—	—
<i>Allophyllus macrobotrys</i> Gled.	—	NA	NA	NA	19.5
<i>Cassine aethiopica</i> Thunb.	—	34.6	33.7	21.5	NA
^X <i>Drypetes gerrardi</i> Hutch.	—	—	—	2.1	—
<i>Ficus capensis</i> Thunb.	—	5.1	2.8	5.3	NA
^X <i>Ficus</i> spp.	—	4.0	6.9	4.2	—
^X <i>Galiniera coffeoides</i> Delile.	—	—	—	4.2	—
<i>Maesa lanceolata</i> G. Don	—	—	1.0	—	16.2
^X <i>Memecylon jasminoides</i> Gilg.	—	—	—	1.4	—
<i>Myrianthus holstii</i> Engl.	—	29.5	31.3	28.2	12.3
<i>Olinia usambarensis</i> Gilg ex Engl.	—	NA	NA	NA	16.2
<i>Podocarpus milanjiana</i> Rendle	—	—	—	—	1.3
^X <i>Prunus africana</i> (Hook.f.) Kalkman	—	1.8	12.5	3.2	—
<i>Syzygium guineense</i> Guill. & Perr.	—	19.6	19.1	10.6	2.6
^X <i>Teclea nobilis</i> Delile	—	—	—	—	2.0
<i>Trichilia</i> sp.	—	2.2	9.4	5.3	—

relatively small differences in availability were not enough to change what influenced the choice of herbs by the gorillas during different seasons. In contrast, although fruit availability varied significantly over time (Figure 2), the gorillas generally did not switch to lower-quality fruit when overall fruit availability declined. This could be because they do not need to consume poor-quality fruits if there is an abundant year-round supply of herbs (Figure 1). Furthermore, considering optimal foraging, it would likely be better to consume more readily available herbs rather than increase their daily travel distance to seek out more dispersed poor-quality fruit.

Interestingly, a relatively high concentration of sugar positively influenced the choice of herbs, which has not been observed in previous studies of gorilla nutritional ecology. Sugary pith may serve as a good, year-round energy source for Buhoma gorillas (pith in Ruhija had significantly lower sugar amounts than pith in Buhoma; Ganas *et al.* in prep) as it was consumed steadily throughout the year. The availability of high-quality pith may be a reason why gorillas can subsist without fruit and allow the gorillas to reduce their fibre consumption, as sugar is a better source of energy (easily digested) than fibre. Pith is also eaten by chimpanzees (*Pan troglodytes*

Table 4. The mean (\pm SD) of the nutritional and phenolic concentrations (%DM) of important foods tested in our model. PT = protein, ST = starch, FC = fructose, GC = glucose, SC = sucrose, NDF = neutral detergent fibre, ADF = acid detergent fibre, LN = lignin, CL = cellulose, HC = hemicellulose, FT = fat, EN = energy, TP = total phenolics, CT = condensed tannins. Buhoma and Ruhija are the two study locations.

	Buhoma		Ruhija	
	Herbs (n = 20)	Fruit (n = 9)	Herbs (n = 12)	Fruit (n = 4)
PT	20.5 \pm 8.7	8.1 \pm 2.8	19.8 \pm 8.0	9.4 \pm 3.4
ST	2.0 \pm 2.2	6.3 \pm 12.3	3.0 \pm 2.5	3.0 \pm 5.6
FC	3.6 \pm 5.1	7.5 \pm 8.6	1.2 \pm 1.1	10.2 \pm 5.7
GC	3.3 \pm 4.5	7.1 \pm 7.9	1.3 \pm 1.3	6.3 \pm 2.7
SC	0.4 \pm 0.4	1.5 \pm 2.5	0.2 \pm 0.3	0.05 \pm 0.1
NDF	39.4 \pm 10.7	32.7 \pm 13.0	43.0 \pm 11.9	25.1 \pm 9.2
ADF	22.5 \pm 11.3	20.1 \pm 8.3	22.2 \pm 10.6	16.8 \pm 7.8
LN	4.0 \pm 3.5	7.5 \pm 4.8	4.5 \pm 3.3	7.0 \pm 3.4
CL	18.5 \pm 10.1	12.7 \pm 4.4	17.6 \pm 9.0	9.8 \pm 5.1
HC	16.9 \pm 5.9	12.6 \pm 8.9	20.9 \pm 9.1	8.3 \pm 2.5
FT	1.4 \pm 0.8	6.1 \pm 7.2	1.3 \pm 1.7	7.5 \pm 11.0
EN	17.7 \pm 2.4	18.8 \pm 2.1	17.3 \pm 2.6	20.2 \pm 2.1
TP	2.7 \pm 3.0	4.2 \pm 3.6	2.8 \pm 3.6	4.0 \pm 4.7
TT	2.0 \pm 2.6	3.6 \pm 3.7	2.1 \pm 3.3	2.7 \pm 2.9
CT	0.8 \pm 1.5	4.4 \pm 4.5	0.3 \pm 0.6	5.1 \pm 7.2

Table 5. Results of the linear regression of the influence of nutritional compounds and food availability factors on herb choice (dependent variable: diet frequency). The overall model was significant ($F = 26.4$, $df = 20$, df residual = 716, Adjusted $R^2 = 0.41$). When testing for group differences, the Kyagurilo group was entered into the model as a dummy coded variable.

Independent variable	Unst. β	t value	P value
Fibre and condensed tannins	-0.455	-11.2	< 0.001
Biomass of herbs	0.382	9.09	< 0.001
Sugars	0.293	4.29	< 0.001
Protein, fat and total phenols	-0.237	-4.27	< 0.001
Kyagurilo group and fibre and condensed tannins interaction	0.113	2.56	0.01
Kyagurilo group and sugar interaction	-0.072	-1.64	0.102
Total herb biomass and fibre interaction	-0.047	-1.45	0.148
Total herb biomass and sugar interaction	0.053	1.31	0.191
Total herb biomass and individual herb biomass interaction	0.025	0.63	0.531
Total herb biomass and protein interaction	0.20	0.55	0.582
Total fruit availability and sugar interaction	-0.19	-0.50	0.616
Kyagurilo and protein interaction	-0.13	-0.37	0.712
Total fruit availability and fibre interaction	0.006	0.14	0.885

schweinfurthii) in the Kibale forest, Uganda during times of low fruit availability, suggesting that pith also serves as an alternative energy source for other species (Wrangham *et al.* 1991).

Consistent with other studies of the nutritional concentrations of gorilla foods, consuming herbs and fruit

Table 6. Results of the linear regression of the nutritional and food availability factors influencing fruit choice (dependent variable: diet frequency). The overall model was significant ($F = 10.1$, $df = 11$, df residual = 236, Adjusted $R^2 = 0.29$). Because data were permuted, analysing the unstandardized β is not valid and thus only a positive or negative effect is indicated.

Independent variable	Effect	P value
Fruit availability	+	< 0.001
Condensed tannin	-	0.001
Total fruit availability and condensed tannin interaction	-	0.01
Fibre:sugar ratio	+	0.09
Total fruit availability and individual fruit availability interaction	+	0.15
Energy, sucrose and fat concentration	-	0.60
Total fruit availability and energy, sucrose and fat concentration interaction	-	0.69
Total fruit availability and fibre:sugar concentration interaction	-	0.86
Total fruit availability	-	0.93

relatively low in anti-feedants (fibre and phenolics) is one of the main determinants of food choice for Bwindi gorillas (Calvert 1985, Rogers *et al.* 1990, Waterman *et al.* 1983, Watts 1983). Despite adaptations for digesting some fibre to assimilate as energy, when possible, the gorillas likely aim to minimize fibre intake because it can be associated with reduced protein uptake. Since gorillas in Bwindi have access to good sources of energy from easily digested sugar in pith and fruit, consuming relatively high levels of fibre is likely not obligatory to meet energy needs.

Surprisingly, our data showed a negative relationship between herb choice and protein concentrations (although the strength of this effect was small). In Bwindi, herbs are high in protein, particularly leaves (mean = 22.5–25.4% DM; although the degree of assimilation is dependent on concomitant fibre and tannin intake). This, coupled with high herb availability, suggests that protein is not a limiting nutrient for Bwindi gorillas and that they do not need to seek out foods high in protein. This explanation has also been suggested for other species that do not seek out high-protein foods (various ruminants; Cooper & Owen Smith 1985, silver leaf monkey (*Trachypithecus auratus sondaicus*), Kool 1992). The concentration of protein in the diets of the Kyagurilo group in a previous study exceeded the protein requirements of humans, further suggesting that Bwindi gorilla protein intake is sufficient (Rothman *et al.* 2008). In a concurrent study on Bwindi gorilla food preference (which quantified diet choices based on relative equal availability of food items in the diet), we found that protein was a preferred nutrient in leaves and for one gorilla group, protein was preferred in pith, demonstrating that while protein is still an important component of the Bwindi gorilla diets, due to the year-round high availability of protein-rich herbs, it does not influence the choice of herbs (Ganas *et al.* 2008).

We did not find a significant result for the second hypothesis; that there would be an inverse relationship between the availability of fruit and consumption of herbs high in sugar and/or fibre. For gorillas in Buhoma, it could be that since sugary herbs, in particular pith, are consumed year-round, these herbs could be fulfilling the gorillas' necessary energy requirements, and that when fruit is available, it is an added bonus for energy intake. In Ruhija, since fruit availability was very low and often unavailable, fibre and sugar in herbs may be fulfilling the gorillas' energy requirements. An alternative explanation could be that the biases associated with our indirect measures of frugivory were strong enough to influence our results and that perhaps Bwindi gorillas do increase their consumption of sugary herbs when fruit is relatively low in availability. Similar studies in the future should strive to use behavioural observations when possible.

As predicted by hypothesis 3, nutritional factors played a stronger role in the choice of herbs for gorillas in Ruhija than gorillas in Buhoma; fibre was avoided significantly less by gorillas in Ruhija than in Buhoma (but fibre was still avoided by all groups). Although some fibre can be converted to energy by gorillas, because fibre can decrease protein uptake, a diet higher in fibre may indicate that the diet of the Kyagurilo group is of a lesser quality (but not of poor quality) than the diet of the Buhoma groups. Interestingly, Rothman *et al.* (2007) found that while the diet composition of mountain gorillas at Karisoke in the Virunga Volcanoes, Rwanda, and those of the Kyagurilo group in Bwindi differed, nutritionally they were comparable. Data on actual intake rates of the four study groups in Bwindi would allow us to understand if this is the case among the Bwindi groups as well.

Comparisons with western gorillas

Comparisons among studies of food choice in different populations of gorillas can be made, but differences in definitions and methodologies (data collection, statistical analyses, variables analysed) need to be taken into account. However, one difference emerges: whereas protein was not a positive factor influencing foliage food choice in Bwindi, it was important at three western gorilla study sites, but none of these studies included food availability in a multivariate analysis (Calvert 1985, Remis *et al.* 2001, Rogers *et al.* 1990). However, protein is still important to Bwindi gorillas, as evidenced by their preference for protein in leaves (Ganas *et al.* 2008). But because availability was not included in the analyses of western gorilla food choice, it may be that protein would not influence the choice of foliage in western gorillas if using the same definition for food choice as we did and tested in a multivariate analysis. Further studies of food choice in western gorillas that include both a food's availability and its nutritional composition together into

a single analysis will allow us to better understand if the differences between Bwindi gorillas and western gorillas in foliage choice are real.

For Bwindi gorillas, sugar was not important in the choice of fruit but it was for western gorillas (Remis *et al.* 2001, Rogers *et al.* 1990). However, studies of western gorillas defined choice differently (they compared frequently consumed fruits with fruits that were readily available, but not consumed). When we used this same method, sugar was also found to be significantly higher in fruits consumed by Bwindi gorillas than those not consumed, but readily available (Ganas *et al.* unpubl. data). Again, this underscores the importance of including availability in food-choice measures as it can aid in understanding if the nutrient selected for is limiting in the environment. Further, this emphasizes that the terms used in studies of foraging behaviour (i.e. choice, preference, selectivity) need to be clearly defined and standardized to facilitate direct comparisons amongst studies.

Usefulness of model

Because the nutritional composition of diets is constrained by food availability, it is important to use models that incorporate both variables. Therefore our results go beyond earlier studies of the nutritional ecology of gorillas, and lend insight into how changes in food availability influenced gorilla diet. By not including availability in food choice analyses, the importance of particular nutrients to an animal may be over- or underestimated. Second, using a multivariate analysis permits an understanding of the contribution of different food items to an animal's diet. For example, currently, we do not fully understand how gorillas nutritionally balance their diets with foliage and fruit. Here, we showed that in Bwindi, fruit is not the only source of energy for the gorillas – sugar and fibre in herbs also appeared to be a good source of energy. This model can be of particular importance for species that experience relatively large fluctuations in food availability such as animals living in tropical forests. Given that western gorillas experience lower herb availability and higher fruit availability than eastern gorillas, and that their food resources are much more seasonal, this model would be useful for western gorillas, and could be compared with our results.

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Appendix 1. Predictor variables used in the two models of herb and fruit choice. Each group (Mubare, Habinyanja, Rushegura, Kyagurilo, the latter two excluded from fruit model) and plant part consumed (leaves, pith, bark) were included in the model as dummy coded variables to control for their influence in food choice. Total fruit availability and total biomass are the sums of the individual species availability (herbs or fruit) during each time period. WSC = water-soluble carbohydrates (sum of fructose, glucose, sucrose).

Predictor Variable	Tests Hypothesis no
Herb model	
Individual species monthly herb biomass	1
PCA 1: Fibre/condensed tannin	1
PCA 2: Protein, fat, total phenolics	1
PCA 3: WSC and sucrose	1
Individual biomass × total biomass	1
Total biomass × PCA 1	1
Total biomass × PCA 2	1
Total biomass × PCA 3	1
Fruit availability × PCA 1	2
Fruit availability × PCA 3	2
Kyagurilo × PCA 1	3
Kyagurilo × PCA 2	3
Kyagurilo × PCA 3	3
Total fruit availability	
Total monthly herb biomass	
Groups	
Food categories	
Fruit model	
Individual species fruit availability	1
PCA 1: NDF and lignin/ (-) WSC	1
PCA 2: Fat and energy/ (-) sucrose	1
Condensed tannins	1
Total fruit availability × fruit availability	1
Total fruit availability × PCA 1	1
Total fruit availability × PCA 2	1
Total fruit availability × condensed tannins	1
Groups	