A comparison of two Mountain gorilla habitats in Bwindi Impenetrable National Park, Uganda

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A comparison of two mountain gorilla habitats in Bwindi Impenetrable National Park, Uganda

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Abstract

Bwindi Impenetrable National Park, Uganda, is a small protected area (331 km^2) within which there is large climatic and altitudinal variation. Therefore we compared habitat types and forest composition between two locations to investigate differences that may influence ecological conditions for large mammals, including endangered mountain gorillas. We demonstrate that there is considerable intersite variation in habitat types and spatial and temporal availability of vegetation resources of which the most apparent are the differences in species composition of plants and fruit availability. Buhoma (the lower altitude site) has a greater diversity of plant species and higher tree and shrub densities, yet has a much lower density of herbaceous vegetation eaten by gorillas compared with Ruhija. Fruit availability is significantly higher throughout the year in Buhoma compared with Ruhija. Both sites exhibit seasonal variation in fruit availability although they do not follow the same seasonal pattern, perhaps because of inherent asynchronous phenological differences amongst individual tree species. The results of this study are important because distribution and abundance of both terrestrial herbaceous vegetation and fruit resources are believed to influence aspects of feeding ecology for large mammals.

Key words: Bwindi, ecology, food availability, mountain gorilla, phenology, vegetation

Résumé

Le Parc National de la Forêt Impénétrable de Bwindi, en Ouganda, est une petite aire protégée (331 km^2) au sein de laquelle existent de grandes variations de climat et d'altitude. C'est pourquoi nous avons comparé les types d'habitats et de compositions forestières à deux endroits pour étudier les différences qui peuvent influencer les conditions écologiques que connaissent les grands mammifères, dont les gorilles de montagne en danger. Nous montrons qu'il y a des variations considérables entre les sites en ce qui concerne le type d'habitat et la disponibilité spatiale et temporelle des ressources végétales, dont les plus évidentes sont les différences de compositions des espèces végétales et la disponibilité des fruits. Buhoma (le site le moins élevé) a une plus grande diversité d'espèces végétales et une plus forte densité d'arbres et d'arbustes, mais une densité beaucoup plus faible, par rapport à Ruhija, de cette végétation herbeuse que mangent les gorilles. La disponibilité des fruits est significativement meilleure à Buhoma qu'à Ruhija, et ce toute l'année. Les deux sites présentent une variation saisonnière de la disponibilité des fruits, mais ils ne suivent pas le même schéma saisonnier, peut-être à cause des différences phénologiques de chronologie inhérentes aux espèces d'arbres elles-mêmes. Les résultats de cette étude sont importants parce qu'on pense que la distribution et l'abondance de la végétation herbacée et des fruits influencent divers aspects de l'écologie alimentaire des grands mammifères.

Introduction

Comparative studies of vegetation resources in tropical forests that are widely separated geographically or with marked differences in climatic patterns show obvious differences in forest structure and composition (Frankie, Baker & Opler, 1974; Whitmore, 1979; Gentry, 1990). However, while comparisons of forest composition of sites within a small geographical area of particular protected

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areas have received less attention, there may be significant variation at a smaller scale especially in areas with known variation in climatic patterns, altitude, and/or degree of human disturbance (Butynski, 1990; Chapman *et al.*, 1997). Understanding the variation in habitat characteristics on a small scale is useful when considering resource availability and utilization, spatial requirements, population dynamics, and adaptations of animals to their environment (Butynski, 1990).

Gorillas occupy a wide range of altitudinal and ecological zones across Africa extending from lowland to montane forest habitats. Correspondingly, they exhibit a diversity in their ecological habits which is partially dependent on the distribution and abundance of food resources available within their habitats (Doran & McNeilage, 2001; McNeilage, 2001; Doran *et al.*, 2002; J. Ganas *et al.*, in press). Studies of eastern lowland gorillas (*Gorilla beringei graueri*) in Kahuzi-Biega National Park and mountain gorillas (*G. b. beringei*) of the Virunga Volcanoes have demonstrated that there is large variation in the vegetation composition and fruit availability within the gorillas' habitats that largely corresponds to altitudinal changes (Yamagiwa *et al.*, 1994, 2003; McNeilage, 2001). These studies emphasize the limitations of making generalizations about patterns of dietary and habitat requirements of gorillas from studies conducted in only one small area of their habitat.

The forest types of Bwindi Impenetrable National Park (BINP) range from lower altitude tropical moist forest to high altitude afro-montane forest (Sarmiento, Butynski & Kalina, 1990). The primate community of Bwindi includes chimpanzees (*Pan troglodytes schweinfurthii*), monkeys (*Cercopithecus mitis*, *C. ascanius*, *C. abyssinicus*, *C. l'hoesti*, *Papio anubis*), pottos (*Perodicticus potto*), galagos (*Galago demidivii* and *G. inustus*) and half of the world's remaining population of mountain gorillas (Butynski, 1984; Mc Neilage, 2001). Studies of Bwindi mountain gorillas are revealing that not only do they differ greatly in their feeding ecology and ranging patterns from the mountain gorillas of the Virunga Volcanoes and eastern lowland gorillas of Kahuzi-Biega (Sarmiento *et al.*, 1990; Nkurunungi, 2003; Robbins & McNeilage, 2003), but that there is significant variability in their feeding ecology within Bwindi (Ganas *et al.*, in press). Therefore a comparison of habitats in two locations within Bwindi can provide useful information of variation in forest composition, distribution and abundance of plants, and availability of gorilla food resources.

In this study, we describe the forest composition of two sites in Bwindi that differ in altitude and climatic patterns, Ruhija and Buhoma (approximately 20 km apart; Fig. 1) to quantify the spatial and temporal variability of vegetation found in each site. This was accomplished through vegetation sampling for herbs, shrubs, and trees; phenological data were analysed to quantify fruit availability. We also analysed separately the spatial and temporal availability of plant species at the two sites that are known as foods consumed by mountain gorillas (see Nkurunungi, 2003; Ganas *et al.*, unpublished data). Based on our findings, we briefly discuss how considerable variability in food resources has implications on the ecology and behaviour of mountain gorillas living within the same forest.

Methods

Bwindi Impenetrable National Park is located in southwestern Uganda (0°53′–1°08′N and 29°35′–29°50′E). It covers approximately 331 km^2, characterized by steep hills and narrow valleys with continuous forest vegetation throughout. The elevation of Bwindi ranges from 1160 to 2607 m and encompasses a rare ecological continuum of medium altitude and afromontane forest. Although classified as moist lower montane forest, the vegetation composition is complex and greatly affected by altitude, topography and soil depth (Hamilton, 1982).

Two research sites were chosen for this study based on the home ranges of habituated gorilla groups whose feed-

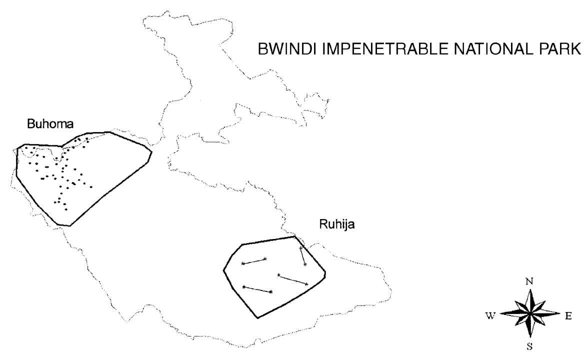

Fig 1 Map of Bwindi Impenetrable National Park with the two study sites, Buhoma (1450–1800 m) and Ruhija (2100–2500 m). The placement of transects at Buhoma is represented by individual points. Transects at Ruhija are represented by two points with a connecting line. During the final month of research in Buhoma, one gorilla group greatly expanded their home range to the east after the vegetation sampling was completed

ing ecology is under investigation (Fig. 1). Ruhija, the high elevation site, is located near the Institute of Tropical Forest Conservation field station and around Mubwindi swamp between 2100 and 2500 m; feeding ecology research has taken place here since 1997. The low elevation site, Buhoma, is found at the edge of the forest between elevation 1450 and 1800 m where research was conducted from September 2001 to August 2002.

The climate is tropical with two rainy seasons from March to May, and September to November and two dry seasons from December to February and June to August. The annual precipitation lies in the range 1130–2390 mm (Howard, 1991). During this study, rainfall varied between sites with a total of 1924 mm (monthly median = 139, range = 28–365, n = 12 months) recorded at Buhoma and 1278 mm (monthly median = 107, range = 6–277, n = 12) at Ruhija (Fig. 2). Rainfall was higher in all months at Buhoma with September 2001 being the wettest month for both sites. The annual mean temperature range in Bwindi is 7–15°C minimum to 20–27°C maximum. Buhoma had a monthly median temperature of 20.1°C (range = 19.4–21.1) that was warmer than Ruhija with a monthly median temperature of 15.1°C (range = 14.2–15.6; see Fig. 2).

Spatial variation measurements

Vegetation sampling was conducted between May and June 2000 and February and July 2002 at Ruhija and Buhoma, respectively. We used methods that combined

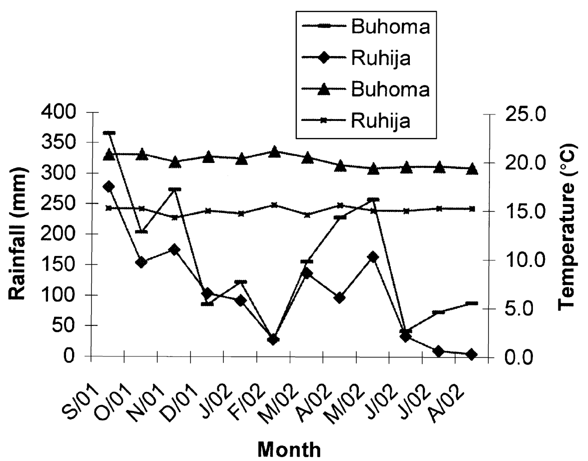

Fig 2 Monthly variation in rainfall and temperature for Buhoma and Ruhija sites

transects and quadrats to study the vegetation resources but with slight variation in methodology between sites. At the Ruhija study site, the transects were chosen by starting from a random point and aimed to pass through a drainage system and followed a compass direction so as to traverse most of the habitats present in the gorillas' home range (following Williamson, 1988; White, 1992; Goldsmith, 1996). Four transects of 2 km, each narrow enough for an individual to pass through, were cut. In the Buhoma area, a 500-m^2 grid was overlaid onto a map of the gorillas' home range and within each grid cell, a random point was assigned. At each point, a randomly chosen direction was taken for a 200-m transect for a total of 50 transects. At both sites, nested quadrats were placed alternately at regular intervals of 20 m along each transect. In each quadrat, all plant species were identified by their vernacular or botanical names and their stems counted.

Each quadrat was assigned to a habitat type according to forest structure into one of the following categories:

Open forest. A colonizing forest with noncontinuous canopy and characterized by mixed herbaceous ground cover of herbs and vines. In some valleys and lower slopes, a woody herb, *Mimulopsis arborescens*, that grows into large woody trees is the dominant vegetation. When these plants die synchronously, it opens the understory with more light to create wide areas of herbaceous plants and vines. Trees are few and form a noncontinuous canopy cover; gap specialists such as *Neoboutonia macrocalyx*, *Allophyllus albisinicus* (Ruhija), *Milletia dura* and *Albizia gummifera* (Buhoma) may be present. In some places, it is characterized by gaps dominated by herbaceous vines, such as *Serioitachys scandens* and *Mimulopsis* spp. When on slopes there might be a mixture of bracken ferns, herbs, and trailing vines or gaps dominated with bracken fern. Areas that result from clearings made by elephants, tree falls, and/or landslides also fall into this category (Babaasa, Eilu & Bitariho, 2001).

Mixed forest. A habitat dominated by both understory and canopy trees and shrubs, usually interspersed with lianas and woody vines, especially *Mimulopsis* spp. The canopy is discontinuous, open, or partially closed. When on slopes in the Ruhija area, this forest type usually forms a transition between open forest and mature forest and is often dominated with a terrestrial woody shrub, *Alchornea hirtella*. In the Buhoma area, the ground layer is dominated by *Asplenium* and *Pteris* fern species or herbs.

Mature forest. A habitat with large, tall canopy trees which often bear lianas. The trees form a continuous canopy and the undergrowth usually contains leaf litter and very scanty small herbs. In some places, the forest is stratified into tall canopy trees, a shrub layer with young trees whose d.b.h. is <10 cm, and a herb layer with seedlings and saplings.

Swamp forest. A habitat with temporary or permanent streams found on lower slopes or valleys. In a few places there may be some water-logged open areas dominated by sedges. However, in most cases it is composed of a mixture of herbs, vines, shrubs and short trees usually found on the periphery of water logged swamp habitats. *Brillantaisia* spp. and *Mimulopsis arborescens* are often present.

Riverine forest. A habitat with permanent or temporal streams or rivers and a continuous or open canopy. Dominant herbs include *Palisota mannii* and *Aframomum* spp.; dominant shrubs include *Brillantaisia* spp. The tree fern, *Cyathea manniana* is often found here as well.

Regenerating forest. A previously anthropogenically disturbed (logged) habitat that may have been burned. Dominant vegetation includes grasses such as *Pennisetum purpureum*, sedges such as *Cyperus* spp., and the ferns of *Pteridium* spp. There are also herbs, vines, shrubs, and a few colonizing tree species such as *Maesa lanceolata* and *Xymalos monospora*.

Different sizes of quadrats were used to determine species diversity, density and spatial patterns of plants. Herbaceous plants (herbs, vines, ferns, seedlings and saplings of <2 m in height) were measured in 1 m^2 quadrats. Shrubs (lianas and young trees of <10 cm d.b.h. and above 2 m in height) were measured in 5 m^2 quadrats. Trees (>10 cm d.b.h.) were measured in 10 m × 20 m and 10 m^2 quadrats respectively for Ruhija and Buhoma sites. At Ruhija, a total of 400 nested quadrats covering approximately 8 ha for trees, 1 ha for shrubs, and 0.04 ha for nonfruit herbaceous vegetation were examined. At the Buhoma site, 500 quadrats covering 5 ha for trees, 1.25 ha for shrubs, and 0.05 for nonfruit herbaceous plants were examined. Overall, transects were cut over approximately 25 km^2 of each study site.

Different methods were employed for counting individual plants in quadrats due to variation in the floristic structure of plant forms. For herbs, ferns, seedlings, saplings, trees and shrubs that were always rooted in the quadrats, they were recorded by root frequency. In Ruhija, for some vines and small woody lianas such as *Mimulopsis solmsii* and *Urera* sp., it was often difficult to locate their rooting positions and their densities were recorded by their shoot frequency. Trailing vines (e.g. Cucurbitaceae and Convulvulaceae vines) that twined on other plants and formed huge masses of shoots were counted indirectly by the number of other plants on which they twined or touched. In Buhoma, we were able to locate rooting positions for these plant types. However, we used both methods of counting vines for approximately 50% of the transects in Buhoma. We made a quantitative comparison between the two methods employed in Buhoma and calculated a correction factor (0.896) to adjust the number of plants in the herbaceous plots that were not quantified using the touching method.

Temporal variation measurements

From September 2001 to August 2002, a total of 328 trees (190 and 138 trees for Ruhija and Buhoma, respectively) were monitored from 25 species known to be gorilla fruit foods of which eleven species were shared between the two sites. Buhoma had more tree species monitored (21) compared with Ruhija (fourteen). At approximately the same time each month, for each tree we recorded the presence of fruit and an abundance score using categories between zero and four (0 = 0%, 1 = 1–25%, 2 = 26–55%, 3 = 51–75% and 4 = 76–100%) based on Sun *et al.* (1996). Given that not all fruits could be easily differentiated as ripe or unripe from observing the canopy, ripeness was not measured in our analysis.

Data analysis

Species richness (total number of species) was determined from all 400 and 500 quadrats for Ruhija and Buhoma sites respectively. Mean species density, mean stem density, and spatial patterns of all plants and gorilla food plants were compared using data from 80 randomly selected quadrats from each site based on the species area curves and were then compared statistically using a *t*-test. The distribution of plants within each site was estimated using the ratio of the variance to mean [coefficient of dispersion (CD): Blackman, 1942 cited in Malenky *et al.*, 1993]. This ratio describes the degree of clumping with values >1 indicating clumping, those <1 indicating a regular or even distribution, and 1 indicating random distribution, such that the higher the CD value, the greater the degree of clumping.

Monthly variation of fruit abundance was represented by a fruit availability index (FAI) calculated as the product of the mean d.b.h., density, and mean monthly abundance score value for each species. We excluded strangling figs because it was not possible to measure d.b.h.; this is unlikely to affect the overall results because they occurred at low densities at both sites. The sum of FAI for all species at each site produced a total FAI per month and for the year. Comparisons between sites were made using a paired *t*-test. All data sets were tested and had a normal distribution.

Results

Proportion of various habitat types between sites

The two study sites varied considerably in the proportion of each forest type (Table 1). The relative sizes of habitats according to forest types showed that in Ruhija, open forest covered the majority of the area (67.25%) followed by mixed forest (28.75%). This was different from Buhoma where mixed forest dominated (58.4%) followed by open forest (20.6%), riverine (10.4%), regenerating (10.2%) and cultivated fields (0.4%).

Variability of plant resources between sites

Overall, a total of 297 plants belonging to at least 95 families were identified at both sites of which 256 were identified to genera. Buhoma was more diverse (218 plants) than Ruhija (179 plants), of which 97 plants in 58 families were shared. In addition, a total of 116 different gorilla plant foods from at least 56 families were identified. The two sites had comparable numbers of gorilla plant foods recorded (Buhoma, 85 foods from 59 families; Ruhija, 89 from 62 families) with most foods shared between habitats (58 in 39 families).

Table 1 Proportions of various habitat types in the two study sites

	Percentage of area	
Habitat types	Ruhija (N = 400)	Buhoma (N = 500)
Open forest (gaps)	67.3	20.6
Mixed forest	28.8	58.4
Mature forest	1.8	0
Swamp	2.3	0
Regenerating forest	0	10.2
Cultivated fields	0	0.4
Riverine forest	0	10.4

See text for description of habitat types.

While the Buhoma site had a greater overall number of both herbaceous species and gorilla food herb species, the species density and stem density of both were significantly higher at Ruhija compared with Buhoma (Table 2). The high density of herbs at Ruhija was probably largely due to two *Mimulopsis* species that were newly sprouting following a large-scale die off within the previous year. Herbaceous plants including gorilla food stems were spatially clumped at both sites with more clumping within the Buhoma site.

The number of shrub species and gorilla food shrubs was greater at Buhoma compared with Ruhija (Table 2). In addition, both species density and stem density of shrubs including gorilla foods were higher at Buhoma. Although shrub stems showed greater clumping at Ruhija compared with Buhoma, gorilla shrub food stems were more clumped at Buhoma.

While more tree species were recorded at Buhoma, both sites had a comparable number of species providing fruits for gorillas (26 versus 21; Table 2). Tree density was significantly higher at Buhoma than at Ruhija. Although trees were randomly distributed at Ruhija, and evenly distributed at Buhoma, gorilla tree foods were more clumped in the Buhoma site.

Fruiting patterns

The production of fruits fluctuated during the study period with 12.6 ± 2.1(range: 10–16) and 11.4 ± 1.1 (range: 10–13) tree species fruiting each month on average for Buhoma and Ruhija respectively. The percentage of fruiting trees each month varied on a monthly basis with a similar percentage of trees fruiting at each site (Ruhija, mean = 39.9 ± 2.6, range: 35.8–44.2; Buhoma, mean = 38.8 ± 5.4, range: 33.3–52.2).

Individual tree species varied in size, density, duration, timing and relative amounts of fruit available (Table 3). Most species were asynchronous in their fruiting seasonality. At Ruhija, *Chrysophyllum* sp. produced more fruit annually than any other tree species, whereas at Buhoma the greatest amount of fruit was produced from *Cassine aethiopica*.

Total fruit availability, as measured by the FAI index, which incorporates phenology, tree density, and tree d.b.h., was significantly greater at Buhoma than Ruhija (t-test = 2.2, $P < 0.001$), with an approximately fourfold

Table 2 Variation of number, density, and the coefficient of dispersion of all plant and gorilla foods types at Ruhija and Buhoma. *t*-Test *P* values indicate comparisons made. Some species are counted in more than one category

Measure	Ruhija	Buhoma	*P*
Nonfruit herbaceous plants			
No. of species	103	215	
No. of gorilla food species	59	91	
No. of species/m^2	4.71 ± 0.32	2.68 ± 0.06	<0.001
No. of gorilla food species/m^2	4.48 ± 0.33	1.73 ± 0.05	<0.001
No. of stems/m^2	24.2 ± 3.4	6.50 ± 0.19	<0.001
No. of gorilla food stems/m^2	10.6 ± 1.9	4.33 ± 0.16	<0.001
Coefficient of dispersion of stems	2.1	2.81	
Coefficient of dispersion of food stems	2.0	3.03	
Shrub plants			
No. of shrub species	69	124	
No. of gorilla shrub food species	4	31	
No. of shrub species/5 m^2	1.26 ± 0.11	2.71 ± 0.79	0.03
No. of gorilla shrub food species/5 m^2	0.09 ± 0.03	1.25 ± 0.44	<0.001
No. of shrub stems/5 m^2	4.10 ± 0.82	6.72 ± 0.22	<0.001
No. of shrub gorilla food stems/5 m^2	0.11 ± 0.05	4.05 ± 0.20	<0.001
Coefficient of dispersion of shrub stems	13.24	3.68	
Coefficient of dispersion of gorilla food stems	1.57	4.91	
Trees			
No. of tree species	50	77	
No. of gorilla fruit tree species	26	21	
No. of tree species/quadrat	2.3 ± 1.5	2.01 ± 0.74	0.08
No. of tree gorilla food species/quadrat	1.0 ± 0.01	0.75 ± 0.04	0.79
No. of trees/hectare	165 ± 15.3	253.75	0.07
No. of gorilla fruit trees/hectare	25 ± 7.0	106 ± 6.8	0.95
Coefficient of dispersion of trees	1.0	0.82	
Coefficient of dispersion of gorilla fruit trees	1.2	1.43	

Coefficient of dispersion (the ratio of variance to mean) represents the degree of clumping of each plant type; >1 indicates clumping, <1 indicates a regular or even distribution, and 1 indicates a random distribution.

variation in fruit availability across the months (Fig. 3). The total fruit availability for Ruhija was less than half of Buhoma's total fruit availability. The lowest month of fruit availability in Buhoma was greater than the highest month of fruit availability in Ruhija. There was a more pronounced seasonality of fruit availability in Buhoma than Ruhija, but both sites had approximately double the amount of fruit available in the months of highest availability compared with that of the lowest.

Monthly fruiting patterns between sites were not similar as the highest FAI at Ruhija was in December 2001 (dry month), but September 2001 (wet month) for Buhoma. The lowest FAI for both sites was in dry months, but they were not during the same dry season (Buhoma June 2002 but February 2002 for Ruhija). Notably, monthly variation of fruiting patterns was not directly associated with monthly rainfall patterns as monthly rainfall and monthly average phenology scores at each site were not significantly correlated (Spearman rank correlation, $r = 0.186$, $P = 0.56$ for Buhoma and $r = 3.95$, $P = 0.20$ for Ruhija).

Discussion

By comparing vegetation resources at two sites in BINP we were able to demonstrate that there can be substantial variation even within a small protected area. The differences in the proportions of major habitat types and consequently on the composition, abundance and distribution of plant resources (Tables 1 and 2) were not surprising considering that there are obvious differences in elevation, climate, past and present land use practices, physical features, and resident fauna. Accordingly, the most significant differences were plant species composition and fruit availability. While the goal of this study was not to examine inter-annual variability, observations suggest that the yearly phenology patterns and possibly abun-

Table 3 Fruit tree characteristics, phenology, and fruit availability between Ruhija (R) and Buhoma (B). Trees are listed only for the sites where they occurred

Site	Species	d.b.h.	Trees/ha	N	S-01	O-01	N-01	D-01	J-02	F-02	M-02	A-02	M-02	J-02	J-02	A-02	Total FAI
R	*Chrysophyllum* sp.	84.5	5.6	20	1.10	1.55	2.40	2.60	1.80	1.35	1.05	0.30	0.10	0	0.10	0.25	5962.3
B	*Chrysophyllum* sp.	69.2	1	4	0.50	0	0	1.50	0.25	0.25	0	0	0.25	0	0	0.75	242.2
R	*Drypetes gerrardii*	38.82	1.75	4	0.75	0.25	0.25	0	0	0	0	0	0	0	0	0	84.9
B	*Drypetes gerrardii*	29.5	0	2	0	0	0	0	0	0.50	0	0.50	0.50	0.50	0	0.50	0.00
R	*Ficus* sp. (strangler)	–	–	8	1.38	1.13	1.13	0.88	1.00	0.63	0.75	1.13	1.50	1.25	1.38	1.63	0.00
B	*Ficus* sp. (strangler)	–	–	7	0.29	0.43	0.29	0.29	0.57	0.86	0.43	1.57	1.43	0.57	0.57	0	0.00
R	*Maesa lanceolata*	29.6	2.6	18	0.33	0.06	0	0	0.06	0	0.06	0.06	0	0	0	0.11	52.4
B	*Maesa lanceolata*	21.8	12	13	0.92	0.54	0.38	0.15	0.23	0.31	0.23	0.23	0.31	1.69	2.15	1.69	2309.9
R	*Myrianthus holstii*	47	0.9	18	1.11	1.11	1.28	1.17	1.17	0.94	0.83	0.83	0.56	0.50	0.56	0.83	460.6
B	*Myrianthus holstii*	34.1	15	15	1.13	0.87	0.67	0.20	0.27	0.60	0.80	0.67	0.67	0.87	0.87	1.07	4444.9
R	*Podocarpus milanjianus*	33.3	0.9	22	0.18	0.14	0.09	0.09	0.36	0.55	0.41	0.41	0.32	0.32	0.32	0.55	112.1
B	*Podocarpus milanjianus*	25.1	1	7	0.29	0	0.43	0	0	0	0	0	0	0	0	0	18.1
R	*Prunus africana*	69.25	1.63	2	0	0	0	0	0	0.50	1.50	1.00	0.50	1.00	1.00	3.00	959.5
B	*Prunus africana*	73	3.4	2	0.50	0	0	0	0	0	0	0	0	0	2.00	2.00	1116.9
R	*Syzigium* sp.	71.6	2.4	25	0.44	0.36	0.32	0.48	0.64	0.84	1.08	1.08	1.12	0.76	0.64	0.40	1402.3
B	*Syzigium* sp.	66.1	6	11	0.09	0	0	0	0	0	0	0	0.09	0	0	0.91	432.3
R	*Teclea nobilis*	31.8	0.8	15	0.27	0.13	0.07	0.07	0	0	0.07	0.20	0.20	0.07	0.07	0.07	30.8
B	*Teclea nobilis*	25.6	1	6	0	0	0	0	0	0	0	0	0	0.17	0	0.50	17.2
R	*Xymalos monospora*	21	0.2	10	1.60	1.40	1.30	1.10	1.10	1.00	0.90	1.00	1.00	1.00	1.00	1.10	52.7
B	*Xymalos monospora*	19.7	8.8	8	0	0	0	0	0.38	0.13	0.50	0.50	0.38	0.38	0.63	0.38	568.6
R	*Mystroxylon* sp.	61	0.1	8	0.50	0.38	0.13	0.13	0.50	0.13	0.50	1.00	1.38	1.50	1.50	1.75	57.3
R	*Olea capensis*	61.2	2	17	1.35	1.76	1.65	1.47	1.41	1.00	1.12	1.00	0.88	0.24	0.12	0	1468.8
R	*Olinia usambarensis*	51.7	1.3	22	0.45	0.68	0.77	0.68	0.55	0.32	0.27	0.23	0.32	0.55	0.77	0.86	433.5
R	*Symphonia globulifera*	–	–	1	1.00	1.00	0	0	0	0	0	0	0	1.00	1.00	2.00	0.00
B	*Bridelia micrantha*	15.9	4	7	0.29	1.00	1.29	1.43	1.43	1.71	1.29	1.57	1.00	0.57	0.43	0.14	772.7
B	*Cassine aethiopica*	55.6	29	11	2.36	2.36	2.00	2.64	1.55	0.82	1.00	0.91	1.36	1.36	1.73	1.73	31958.0
B	*Dichaentathera corymbosa*	17.2	0	4	0.25	0	0.50	0.75	3.75	3.25	2.25	1.50	0.25	0	0	1.50	192.6
B	*Dasylepsis eggelingii*	19.9	0.4	8	0.50	0.75	0.75	0.13	0.13	0.88	0.50	0.38	0.63	0.88	1.13	1.88	67.9
B	*Ficus* sp. No. 2	25.7	0	1	2.00	2.00	2.00	0	1.00	0	0	1.00	0	0	1.00	1.00	0.00
B	*Ficus* sp. No. 3	20.1	1	3	1.00	1.00	0	0	0	0	0	0	0	0	0	0	40.1
B	*Harunana madagascarensis*	36.3	2	13	2.00	2.15	2.69	3.15	1.77	1.15	0.62	0.77	0.77	0.92	0.77	0.69	1266.9
B	*Leplea mayombensis*	51.5	6	10	1.00	1.20	1.00	0.90	0.30	0.30	0.10	0.20	0.60	0.50	0.50	0.60	2224.8
B	*Rawnsonia lucida*	14.1	3	6	0.17	0	0	0	0.17	0	0.17	0.33	0	0.17	0	0.33	56.7
R	Total fruit availability																22154.2
B	Total fruit availability																45729.8

d.b.h., Mean diameter at breast height per species; N, number of trees in phenology at each site, values per month represent the mean fruit ripeness scores from the phenology. See Methods for explanation of FAI. FAI was not calculated for strangler *Ficus* sp. because its d.b.h. was not possible to measure. FAI was also not calculated for *Ficus* sp. No. 2 and *Drypetes gerrardii* in Buhoma because they were not recorded during vegetation sampling and no d.b.h. and density measurements were available.

dance of herbaceous vegetation vary over time at each site and warrants further investigation (J.B. Nkurunungi & M.M. Robbins, personal observation).

While the variation in habitat types and vegetation distribution and abundance may not be unexpected, it is likely to have an impact on the feeding ecology and perhaps the distribution and abundance of large mammals including mountain gorillas. Buhoma has a much lower density of herbaceous vegetation eaten by gorillas yet the fruit availability is significantly higher throughout the year than in Ruhija. Both sites exhibited seasonal variation in fruit availability but did not follow the same seasonal

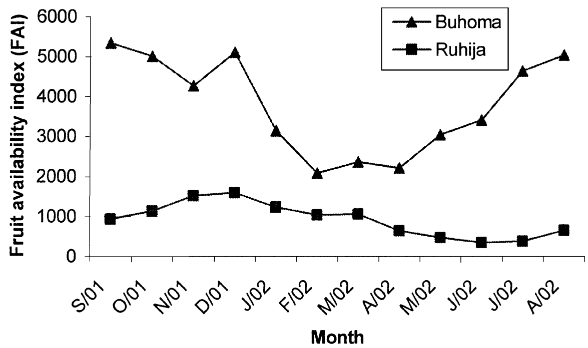

Fig 3 Monthly variation of fruit availability index (FAI) for Buhoma and Ruhija sites. See text for calculation of FAI values

pattern; such differences are probably due to variation in species found in each location. The implications of these differences in food availability within Bwindi on gorilla dietary and ranging patterns are currently under investigation (J. Ganas, J. B. Kurunungi & M. M. Robbins, unpublished data)

Concurrently, large mammals may in turn have an impact on the vegetation composition in Bwindi. The elephants of Bwindi spend a significant amount of time at the Ruhjia site and they play a role in creating gaps and opening the forest (Babaasa *et al.*, 2001). The role that gorillas and other large mammals play in encouraging regrowth of herbaceous vegetation has been studied in the Virunga Volcanoes (Watts, 1987; Plumptre, 1994, 1996) but not yet in Bwindi.

The results of this study further emphasize that information concerning mountain gorilla behavioural ecology from the Virunga Volcanoes cannot be extrapolated to BINP. There are comparable densities of terrestrial herbaceous vegetation in Bwindi and the Virunga Volcanoes, but much greater densities than for lowland gorilla habitats. Fruit availability in Bwindi is intermediate between the Virunga Volcanoes (very little fruit) and eastern lowland gorilla and western lowland gorilla habitats (Doran *et al.*, 2002; Yamagiwa *et al.*, 2003). The distribution and abundance of both terrestrial herbaceous vegetation and fruit resources are believed to influence aspects of gorilla sociality and ranging patterns (Doran & McNeilage, 2001), and indeed there are noticeable differences in the feeding ecology and ranging patterns between the Virunga and Bwindi mountain gorillas (Nkurunungi, 2003; Robbins & McNeilage, 2003; Ganas *et al.*, unpublished data; Ganas & Robbins, unpublished data).

The relationship between the food availability and population dynamics including carrying capacity, for Bwindi mountain gorillas is not yet known, but the variability of food resources should be taken into account when any such estimates are made. Finally, the variability of mountain gorilla habitat across Bwindi should be considered when making conservation strategies for all large mammals, including mountain gorillas.

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