



A Preliminary Study of the Temporal and Spatial Biomass Patterns of Herbaceous Vegetation Consumed by Mountain Gorillas in an Afromontane Rain Forest

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ABSTRACT

Although many animal species consume herbaceous vegetation found in African tropical forests, little is known of the temporal and spatial availability of these plants. From September 2004 to August 2005 we conducted a study that quantified the temporal and spatial biomass availability of 20 species of herbs frequently consumed by endangered mountain gorillas at two locations (Buhoma and Ruhija) in Bwindi Impenetrable National Park, Uganda. In general, the biomass of herbs varied over the study period, but these changes were relatively small. For 12 of 18 and nine of 11 species in Buhoma and Ruhija, respectively, herb biomass differed significantly among habitat types. Of the nine species found in both locations, seven species had a higher biomass at Ruhija, one species had a higher biomass at Buhoma, and one species showed no difference. These results demonstrate that herb biomass varied little temporally but spatial differences in herb biomass were more pronounced. Future studies should investigate the variables that may influence herb phenological patterns such as rainfall, light, soil quality, previous disturbance regimes, and animal foraging and trampling damage.

Key words: Bwindi Impenetrable National Park; *Gorilla beringei beringei*; habitat type; phenology; Uganda.

FOOD AVAILABILITY INFLUENCES MANY ASPECTS OF AN ANIMALS' LIFE including diet, habitat utilization, sociality, and population dynamics (McDonald 1983, Terbough & van Schaik 1987, Janson & Chapman 1999). Phenological research (the study of a plant's response to environmental variables such as rainfall and sunlight) has focused primarily on temporal patterns of leaf, flower, and fruit availability from trees since these items are a major food source for many animal communities (Gautier-Hion *et al.* 1985, Moermond & Denslow 1985, Terborgh 1986, Kinnaird 1992, White *et al.* 1993). These phenological events are influenced by numerous factors including herbivory, pollination, seed dispersal, rainfall, temperature, irradiance, and photoperiod (Opler *et al.* 1976, Rathcke & Lacey 1985, Aide 1992, Wright & van Schaik 1994). For example, the timing of flowering in trees has been shown to be influenced by rainfall and/or maximal irradiance, while fruit production may be influenced by an increase in moisture, minimum temperature during a dry season, optimal seed dispersal conditions, or internal factors that control the rate of fruit development (Howe & Smallwood 1982, Borchert 1983, Wheelwright 1985, Chapman *et al.* 1999). Additionally, peaks in leaf flushing have been shown to be influenced by the period of maximum irradiance and/or minimal insect herbivore activity (Clark & Clark 1991, Aide 1992, van Schaik *et al.* 1993, Wright & van Schaik 1994).

Herbaceous vegetation (more generally known as herbs; defined as nonwoody and subwoody plants) is also a food source for many animals in tropical forests (Watts 1984, Gentry & Emmons 1987, White *et al.* 1993, Wrangham *et al.* 1993, Kaplin & Moermond 2000, Hofmann & Roth 2003). However, in contrast to detailed studies that have shown variability in the phenological

patterns of trees as well as the spatial and temporal availability of herbs in woodland and savannah ecosystems in Africa and the effects of such seasonality on animal foraging behavior (McNaughton 1985, Dunham 1990, Illius & O'Conner 2000), little research has been conducted on herb phenology in African tropical forests (but see White *et al.* 1995). Like tree phenology, the temporal availability of herbs may be influenced by rain and light, but also by animal foraging and/or trampling, or resource competition with other plant species (Crawley 1983, Rathke & Lacey 1985). Spatial variability may be due to differences in canopy cover, soil type, amount of water in soil, altitude, slope, and level of disturbance (Lieberman *et al.* 1985, Gentry 1988, Poulsen & Balslev 1991, Poulsen 1996, Costa 2006).

Herbs are a major component of the diet of gorillas (*Gorilla gorilla* and *Gorilla beringei*) throughout their range in a wide variety of habitats in Africa (Watts 1984, Ganas *et al.* 2004, Rogers *et al.* 2004, Yamagiwa *et al.* 2005). It has been suggested that herbs are a staple food resource for gorillas and the amount available in their habitats strongly influences group size and population density (White *et al.* 1995, Doran & McNeillage 1998, Rogers *et al.* 2004). Despite its importance in the gorilla diet, our knowledge of herb biomass within their habitats is poor (but see Watts 1984).

Bwindi Impenetrable National Park, Uganda, is an afromontane rain forest with a large altitudinal gradient (1160–2607 m) and is characterized in many areas by a dense understory of herbs. It is also home to approximately half (320 individuals) of the world's remaining endangered mountain gorillas (*Gorilla beringei beringei*; McNeillage *et al.* 2006). Herbs in Bwindi are known to provide food for mountain gorillas (Ganas *et al.* 2004), elephants (*Loxodonta africana*; Babaasa 2000), red-tail monkeys (*Cercopithecus ascanias*; F. Natakunda & A. McNeillage, pers. comm.), L'hoesti monkeys (*Cercopithecus lhoesti*; T. Ukizintambara & B. A. Kaplin, pers. comm.), blue monkeys (*Cercopithecus mitis*, B. A. Kaplin, pers.

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TABLE 1. *Ecological characteristics of the two study locations, Buhoma and Ruhija in Bwindi Impenetrable National Park, Uganda. Habitat type percentages represent the proportion of each type at each study sites. “—” indicates habitat type not found at this location. ¹Data are missing for April, so this figure under-represents yearly rainfall amount in Buhoma for the study period.*

	Buhoma	Ruhija
Altitude (m asl)	1450–1800	2100–2500
Average temp range (°C)	17.2–27.4	13.5–19.4
Rainfall ¹ (mm)	2092	1176
<i>Habitat types</i>		
Open	22%	55.6%
Mixed	54.1%	36.3%
Mature	0.8%	1.1%
Regenerating	8.7%	—
Riverine	11.1%	—
Swamp	—	7.0%
Fire disturbed	3.1%	—
No. of permanent plots:	51	38
No. of species monitored:	18	11
No. of species shared:	9	9
No. of 1-m ² quadrats measured:	1020	540
Total area surveyed (ha):	10.2	5.4

comm.) and chimpanzees (*Pan troglodytes schweinfurthii*; Stanford & Nkurunungi 2003). Bwindi mountain gorillas consume herbs daily. In one group, 73 percent of food intake consisted of herbs (Rothman *et al.* 2007). Herbs are clearly an integral part of gorillas' diet.

Past research using stem density as a measure of food availability for gorillas in Bwindi found that the density and spatial availability of herbs varied at two locations at different altitudes, however, biomass was not recorded (Nkurunungi *et al.* 2004). We lack data that would allow us to calculate if herbs are a limiting resource for Bwindi gorillas, but recent research suggests that they may not be (Ganas 2008).

The objective of this study was to better understand herb availability for the gorillas in Bwindi by measuring: (1) temporal changes in the biomass of individual herb species; (2) differences in herb biomass among habitat types; and (3) differences in herb biomass between two locations (Buhoma and Ruhija). We recorded the biomass of herbs considered to be important to the gorillas (see Methods). Although we recorded rainfall in one location at each study site, and the presence or absence of animal foraging and trampling damage within each plot, these data were not specific enough (*i.e.*, presence or absence of foraging rather than actual amounts foraged) to be included in the present analyses. The absence of ecological variables in our analyses limits the conclusions we can draw. Nonetheless, our study is useful for understanding the influence of herb availability on gorilla diet and habitat use.

METHODS

STUDY SITE.—This study was conducted at two locations (Buhoma and Ruhija) in Bwindi Impenetrable National Park, Uganda (331 km²). These sites are separated by approximately 17 km and differ in altitude, temperature, rainfall, and plant temporal and spatial availability (Nkurunungi *et al.* 2004; Table 1). Buhoma is located at the far western part of the park; and Ruhija is found in the northeastern section (Fig. 1A, B). These two locations were

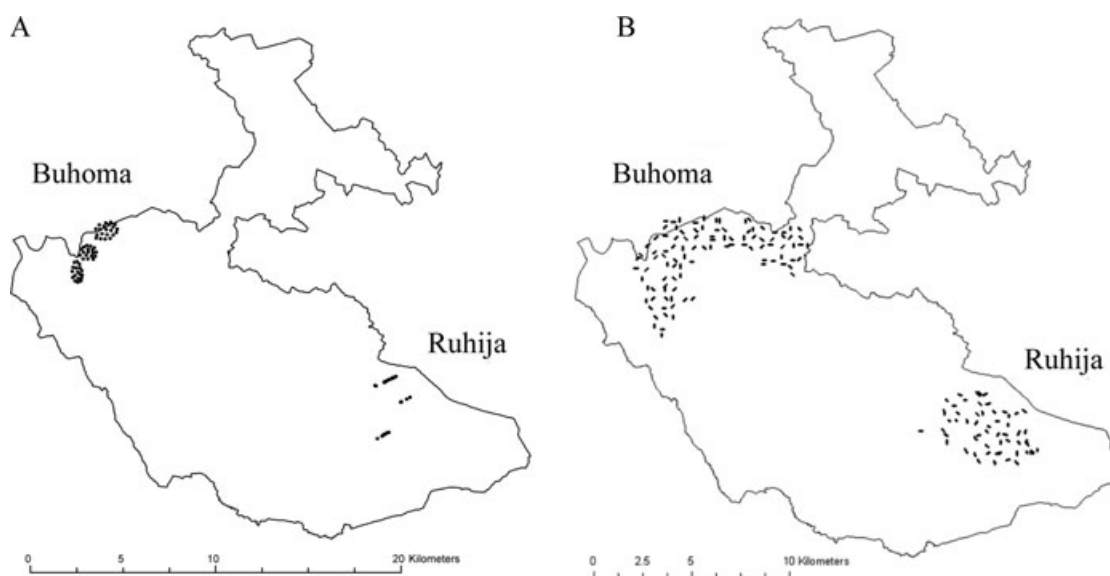


FIGURE 1. Location of (A) permanent plots and (B) transects at Buhoma and Ruhija.

selected because they fall within the home ranges of habituated gorilla groups under observation in a related study of feeding ecology. At the two locations, there were seven habitat types, three of which were shared. The number of habitat types is greater than that of an earlier study (Nkurunungi *et al.* 2004) due to the expanded vegetation sampling we conducted in Buhoma.

CLIMATE.—Rainfall and temperature data were collected daily from stations in Buhoma and Ruhija. Each location was characterized by two wet seasons (Sep–Nov 2004 and Mar–May 2005) and two dry seasons (Dec 2004–Feb 2005 and Jun–Aug 2005). In total, Buhoma received 2092 mm of rainfall and Ruhija received 1176 mm (Table 1).

TEMPORAL AVAILABILITY.—From September 2004 to August 2005 we measured the phenological patterns of the biomass of herbs in 89 1-m² permanent plots (Buhoma = 51, Ruhija = 38; Fig. 1A). In Buhoma, with the exception of three species within six plots (*Aframomum* spp.), monitoring did not begin until October 2004. We chose species considered important in the gorillas' diets at each location based on previous and ongoing research ($\geq 1\%$ frequency in daily diet according to Ganas *et al.* 2004, although not all important species could be monitored for logistical reasons). These represented 25 and 15 percent of species making up the herb community in

Buhoma and Ruhija, respectively. The number of herb species monitored within each habitat type represented 17–47 percent of the herb community in Buhoma and 15–34 percent in Ruhija (based on the number of species eaten by gorillas included in the plots of each habitat divided by the total number of species encountered per habitat).

Twenty plant species were monitored (Buhoma = 18, Ruhija = 11, nine species in common; Table 2). *Piper capense* is consumed by gorillas at both locations, however, in Buhoma we were only able to monitor one plant and therefore this species was excluded from the analyses at this location. Plots (1-m²) were established in areas of high herb density within three different areas of the gorillas' range per location (Fig. 1A). The number of plots established was driven by both the need to ensure an appropriate sample size but also imposed by the amount of time we had for data collection, as this study was part of a larger one on the foraging strategies of the gorillas (Ganas 2008). In these areas, transects were laid out and plots were marked on transects with a minimum of 50 m between each plot, with transects crossing different habitat types. Plots were marked with wooden poles in each corner and tagged with an identification number. An average of 16.8 individual plants/species/mo (range 2.8–37.9, SD = 11.5) were monitored in Buhoma, and 24.2 individual plants/species/mo (range 8.5–60.1, SD = 15.3) in Ruhija. The variation in number of individual plant species

TABLE 2. Biomass estimate and regression relationship for each herb species investigated. For all species $n = 40$. For *Cardus* sp., we used the number of leaves as an estimate of biomass, however, in some instances the leaves were stripped off (presumably consumed by animals) and therefore we used length as a biomass estimate during these months. Both equations are listed below. 'Peel' refers to the outer layer of a plant's stem. LN = Natural logarithm; in a few species the data were log transformed for a better fit in the linear regression. All p -values were < 0.001 .

Plant species and part consumed by gorillas	Plant family	Location	Type of biomass estimate	Regression equation	R^2
<i>Mimulopsis arborescens</i> –PITH	Acanthaceae	Both	Stem mass/stem length	$y = 8.19 \times x$	0.72
<i>Mimulopsis solmsii</i> –LEAVES AND PEEL	Acanthaceae	Both	Leaf mass/stem length	$y = 0.02 \times x$	0.83
<i>Basella alba</i> –LEAVES	Basellaceae	Both	Leaf mass/#leaves	$y = 0.20 \times x$	0.74
<i>Palisota mannii</i> –PITH	Commelinaceae	Buhoma	Pith mass/stem length	$y = 5.11 \times x$	0.8
<i>Cardus</i> sp.–STEM AND PITH	Compositae	Ruhija	Stem and pith mass/LN stem length	$y = 0.98 \times x$	0.96
<i>Cardus</i> sp.–LEAVES	Compositae	Ruhija	Leaf mass/#leaves	$y = 1.06 \times x$	0.8
<i>Ipomea</i> sp.–LEAVES AND PEEL	Convulvulaceae	Both	Leaf mass/#leaves	$y = 0.26 \times x$	0.34
<i>Ipomea wightii</i> –LEAVES	Convulvulaceae	Buhoma	Leaf mass/#leaves	$y = 0.26 \times x$	0.34
<i>Mormodica calantha</i> –LEAVES	Curcubitaceae	Both	Leaf mass/#leaves	$y = 0.11 \times x$	0.67
<i>Mormodica foetida</i> –LEAVES	Curcubitaceae	Both	LN leaf mass/ LN #leaves	$y = 0.41 \times x$	0.75
<i>Desmodium repandum</i> –LEAVES	Fabaceae	Buhoma	Leaf mass/#leaves	$y = 2.16 \times x$	0.8
<i>Piper capense</i> –PITH	Piperaceae	Ruhija	Stem mass/stem length	$y = 0.21 \times x$	0.77
<i>Pennisetum purpureum</i> –PITH	Poaceae	Buhoma	Pith mass/stem length	$y = 4.72 \times x$	0.82
<i>Gouania longispicata</i> –LEAVES	Rhaminaceae	Buhoma	Leaf mass/#leaves	$y = 0.19 \times x$	0.97
<i>Rubus</i> sp.–LEAVES	Rosaceae	Both	Leaf mass/#leaves	$y = 0.53 \times x$	0.76
<i>Triumfetta</i> sp.–APICAL SHOOT	Tiliaceae	Both	Shoot and stem mass/stem length	$y = 0.07 \times x$	0.58
<i>Laportea aestuans</i> –LEAVES AND PEEL	Urticaceae	Buhoma	Leaf and peel mass/#leaves and peel length	$y = 9.57 \times x$	0.89
<i>Urera</i> sp.–LEAVES AND PEEL	Urticaceae	Both	Shoot mass/stem length	$y = 2.76 \times x$	0.44
<i>Aframomum angustifolia</i> –PITH	Zingiberaceae	Buhoma	Pith mass/stem length	$y = 1.38 \times x$	0.91
<i>Aframomum sanguinum</i> –PITH	Zingiberaceae	Buhoma	Pith mass/stem length	$y = 3.25 \times x$	0.85
<i>Aframomum</i> sp.–PITH	Zingiberaceae	Buhoma	Pith mass/stem length	$y = 1.83 \times x$	0.91

monitored monthly was likely due to die-off, new growth of plants, and trampling and foraging damage.

To estimate the biomass of herbs, at approximately the same time each month, for each permanent plot, we took measurements of particular plant parts (modified from Watts 1987, Plumptre 1996). For vines, defined as a climbing or trailing plant with long flexible stems, we counted the number of leaves that were in the plot regardless of whether or not they were rooted in the plot, since the rooted position is often difficult to locate (Rogers & Williamson 1987). Because vines are often intertwined with many other vines, measuring vine length would be subject to errors. For herbs, because it was not difficult to locate the rooted position, we measured the length of the plant from the rooted position to the base of the top leaf. In addition, we recorded the presence or absence of foraging and/or trampling damage to the plots by gorillas or other animals (*e.g.*, duiker and elephant).

For some species we were only able to monitor < 10 individuals in some months. Nonetheless, our data indicate that the biomass of a particular species in all plots never reduced to zero due to foraging or trampling damage. In total, an average of only 17 percent of stems over the study period (based on monthly averages of presence of damage per plant species; SD = 13.4%) suffered from foraging or trampling damage (but not complete removal).

To estimate the biomass from the plant measurements, we harvested forty individuals of each species of varying lengths from outside the permanent plots. For each plant, 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 since they, like many other animal species, selectively consume particular plant parts rather than the entire plant (Crawley 1983, Cork & Foley 1991, Rogers *et al.* 2004). For example, for *Aframomum* spp., we measured stem length and then recorded the weight of the pith (the part consumed by the gorillas). Although gorillas often selectively eat a particular portion of a plant part, the amount consumed from each individual plant may differ. Therefore we included the entire part in the biomass estimates. We dried the plant parts in sheds using charcoal stoves and then recorded the weight of each individual plant. Harvesting and weighing were not done over the year study period but rather within a 4-mo time period. Therefore, there may be slight differences in the estimates for weight, but we do not expect these differences to be large enough to significantly alter our results since differences in weights would be miniscule. Dry rather than wet weights were used to control for variation in water content that may have occurred during different seasons, which could bias phenological measures.

SPATIAL AVAILABILITY.—To determine the spatial distribution of individual herb species and overall biomass at each site, we cut and measured 102 and 54 200-m transects at Buhoma and Ruhija, respectively, placing one transect each within a 500-m² grid overlaid onto a map of each site (Fig. 1B; Grieg-Smith 1983). There are potential biases associated with this method, *e.g.*, rare habitat types may be undersampled or common habitat types oversampled (Barbour *et al.* 1999, Krebs 1999). However, because the area is subdivided systematically, the majority of the habitat types will be

represented, and this is one of the best methods to sample heterogeneous areas (Barbour *et al.* 1999, Krebs 1999). Because one transect was placed randomly within a grid, transects were not stratified by habitat type but rather by grid. For each transect, we placed 1-m² quadrats on alternate sides in intervals of 20 m for a total of 10 quadrats per transect. We quantified the spatial availability of herbs in the quadrats using the same method that was used to document herb biomass in the permanent plots (*i.e.*, counted leaves/measured stem). Additionally each quadrat was assigned a habitat type (see below).

Due to the extensive areas surveyed for spatial availability, we were unable to measure the entire area at each site during the same month, which would have permitted analysis of the temporal changes in monthly biomass of herbs among habitat types and locations (but temporal changes in biomass were recorded from the permanent plots at each site every month). Instead, we recorded data from a transect once within each 500-m² grid, but data collection between lasted *ca* 5 mo. Transects recorded during a particular month were called sublocations and were defined as *n* number of 500-m² grids during month *x*. For example, there were 102 grids (and thus 102 transects, measuring 10.2 ha) that encompassed the gorillas' home ranges in Buhoma. If we measured 20 transects (2.0 ha) in Buhoma in July then these transects were considered a 'sublocation'. Buhoma had five sublocations (1.4 ha + 1.9 ha + 4.2 ha + 0.5 ha + 2.2 ha = 10.2 ha, or 102 grids and the entire study location); Ruhija had three (0.6 ha + 1.6 ha + 3.2 ha = 5.4 ha, or 54 grids and the entire study location).

To calculate the spatial biomass availability of herbs in the entire study location per month (*i.e.*, to account for temporal variability), we standardized the biomass of herbs measured in each of these sublocations during a different month to the same month. First, we applied the biomass estimates (regression equations) recorded from the permanent plots to the transects (quadrats) to determine the biomass of herbs in each sublocation. Second, we applied the monthly changes in biomass (%) (recorded from the permanent plots) to the sublocations. Last, we added the sublocation data together to get a total per month per location (both per species and in total). To determine the average herb biomass grams per meter square at each location, we divided the sum of all species biomass by the number of quadrats sampled.

Because transects were placed in a stratified random fashion, we assume that this sampling method is a good estimator of how much of each habitat type covers each study location. Therefore, to calculate the biomass of herbs (per species and in total) in each habitat type within each study location, we divided either the sum of a particular species or all species biomass by the number of quadrats assigned to a particular habitat type.

HABITAT TYPES.—Habitat types were classified according to forest structure and species composition (modified from Nkurunungi *et al.* 2004):

'Open forest': A colonizing forest with noncontinuous canopy characterized by a thick ground cover of herbs. In some valleys and lower slopes, a woody herb, *Mimulopsis arborescens* is

the dominant species. Trees are few and gap specialists such as *Neoboutonia macrocalyx* and *Allophylus albisinicus* or *Milletia dura* and *Albizia gummifera* are often present. Clearings made by elephants, treefalls, and/or landslides (*i.e.*, gaps) also fall into this category.

‘Mixed forest’: A forest dominated by both understory and canopy trees and shrubs, commonly interspersed with lianas and subwoody vines. Canopy height is 20–30 m. This forest type can form a transition between open forest and mature forest and is often dominated with a terrestrial woody shrub, *Alchornea hirtella*. In some areas, the ground layer is dominated by *Asplenium* and *Pteris* ferns or herbs.

‘Mature forest’: A forest with large, tall canopy trees often bearing lianas. Trees form a continuous canopy and the undergrowth usually contains very sparse small herbs. In some places, the forest is stratified into tall canopy trees, a shrub layer with young trees whose dbh is < 10 cm, and a herb layer with seedlings and saplings, with a few areas dominated by the subwoody herb *Mimulopsis solmsii*. Canopy trees can reach over 30 m in height.

‘Swamp forest’: A very flat forest area found on lower slopes or valleys with temporary or permanent streams. In a few places there may be some waterlogged 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 waterlogged swamp habitats. *Mimulopsis arborescens* is often present.

‘Riverine forest’: A forest with permanent or temporal streams or rivers and a continuous canopy with moist or wet soil usually found on lower to bottom slopes. Trees are often covered in moss. Dominant herbs include *Palisota mannii* and *Aframomum* spp.; dominant shrubs include *Mimulopsis* spp. The tree fern, *Cyathea manniana* is common.

‘Regenerating forest’: A recently disturbed (logged) forest that may have also been burned. Vegetation is dominated by herbs, vines, shrubs, and a few colonizing tree species such as *Maesa lanceolata* and *Xymalos monospora*. Many areas are dominated by ferns of *Pteridium* spp.

‘Fire disturbed forest’: A forest type that was previously afflicted by fire (near the edge of the park) in the mid 1980s and is recovering. It is dominated by the colonizing tree species *Macaranga kilimandsherica* and *Aguaria salicifolia*. The understory has some herbs but is thick with saplings.

STATISTICS.—To determine whether there was a significant relationship between the length of stem or number of leaves and weight we plotted each independent variable against the weight (one test each for wet and dry weight; following Watts 1987, Plumptre 1996) and calculated a linear regression that was forced through the origin (Zar 1999). To assess the accuracy of the biomass estimate, we bootstrapped confidence limits of the slope of the regression using ‘accelerated bias-corrected confidence limits’ (Manly 1997). All results are presented in dry weight.

To test for temporal differences in the biomass of individual species, we used a linear autocorrelation coefficient using a Spearman’s rank correlation with a 1-mo lag. This tested whether there was a change in biomass from the previous month for every month except the first. Because we tested the null hypothesis of no temporal autocorrelation in biomass many times, (*i.e.*, for each species separately), we controlled for multiple testing by using Fisher’s Omnibus test, a meta analysis tool that combines the number of *P*-values into a single chi square distributed value, with its degrees of freedom equaling twice the number of *P*-values (Haccou & Meelis 1994). In this way, the Fisher’s Omnibus test also verifies the overall significance of the autocorrelation.

To investigate spatial differences as measured by the biomass of individual species among habitat types, we first tested for spatial autocorrelation in biomass within each location using a Mantel test to verify that differences between quadrats were not solely related to the distance between them (Sokal & Rohlf 1995). To do so, we correlated the spatial distance between two quadrats (derived from their respective GPS positions) with the difference between their biomass estimates separately for each species. Differences between biomass estimates were calculated as the absolute biomass difference between two quadrats divided by the corresponding sum of the two biomass estimates. When both plots had a value of zero, the differences were set to zero. We controlled for multiple tests using two approaches. First, we used a Fisher’s Omnibus test (see above). Second, we used one-sample *t*-tests to determine whether the derived correlation coefficients were on average equaling zero. A significant *P*-value indicated overall significance.

To test for biomass differences among habitat types, we used a Monte-Carlo based Kruskal–Wallis *H*-test, applied separately for each species, with the biomass of each species standardized to the month of April. Because it would be overly complicated to compare differences in the biomass of each herb species in each habitat type for each of the 12 mo, we randomly chose April to test for differences. The Monte Carlo test is a permutation test that controls for the potential effect of the majority of biomass measures in the plots equaling zero. Thus the *P*-values are not derived from a chi square approximation but from a permutation test.

To test for differences in biomass for the herb species found in both locations, we again standardized the biomass of each species to April. Then, using a Mann–Whitney *U*-test, we compared the biomass of all plots for that mo for each species between locations. Fisher’s Omnibus was used to control for multiple testing and to test for overall significance. Sampling units in tests for differences between habitat types and the two locations were individual plots. This was justified due to the almost complete absence of spatial autocorrelation.

To calculate the absolute biomass of individual herb species g/m² in each habitat and location, we summed each species’ biomass among all quadrats and then divided it by the number of quadrats sampled in each habitat and location, respectively (as the sum of the differently classified quadrats equals the total number of quadrats recorded). For total herb biomass, we summed all herb species together and also divided it by the total number of quadrats sampled. To calculate the relative biomass of herbs grams per meter square

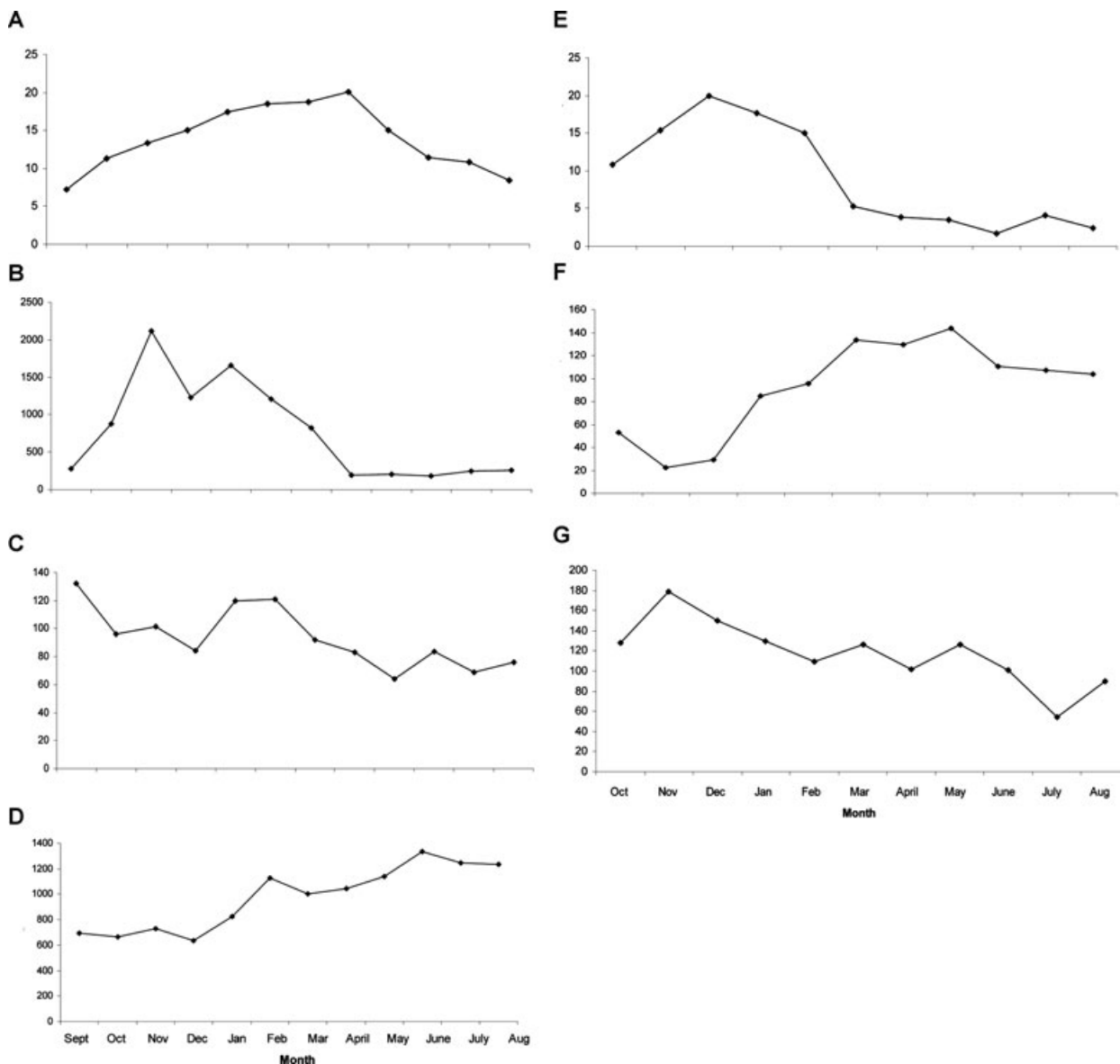


FIGURE 2. The temporal availability of those species in which there was a significant ($P < 0.05$) change in biomass. (A) *Aframomum* sp., (B) *Laportea aestuans*, (C) *Mimulopsis solmsii* (Buhoma only), (D) *Rubus* sp. (Buhoma only), (E) *Mormodica foetida* (Ruhija only), (F) *Cardus* sp., (G). *Piper capense* (Ruhija only). ‘Only’ signifies that while the species occurred at both sites, a significant result only occurred at the location indicated. Figures 2A, B, and F correspond to the only location they were found in. Results are presented in absolute values.

in each habitat, we multiplied the herb biomass grams per meter square in a particular habitat with the proportion of that habitat type at each location.

RESULTS

BIOMASS REGRESSIONS.—Due to the highly significant relationship between stem length or number of leaves and their corresponding dry weights, our measures can be considered accurate predictors of biomass. Regression equations were used to calculate the biomass of

each herb species (Table 2). Biomass for each species is represented in dry grams of the part(s) consumed by the gorillas.

TEMPORAL DIFFERENCES.—Overall there was temporal variation in the biomass of herbs at each location (nonparametric linear autocorrelation, applied separately to each species at each site; $\chi^2 = 121.4$, $df = 58$, $P < 0.001$). There was significant ($P < 0.05$) seasonal variation in the biomass of eight herb species (Buhoma = 5, Ruhija = 3; Fig. 2A–G). For one species (*Aframomum sanguineum*), the biomass in every month was similar, except for one month when there was a large drop (55%), which then increased to approximately

the same biomass as in the previous month. This suggested an error in data collection for this month, and there were no significant differences in biomass during the study for this species. We removed this particular month for this herb species from further analyses. Of 29 species in the two locations, 26 had positive correlation coefficients (positive coefficient range 0.04–0.79) with a total average coefficient of 0.42 (SD = 0.29, $t = 7.82$, $df = 28$, $P = < 0.001$). This suggests that some temporal variation in biomass was also present in species other than the ones revealing significance. The Fisher's Omnibus test found that when all species were combined, they showed temporal variation. The one sample t -test also demonstrated that in total, the correlation coefficients were significantly different from 0, further verifying an overall significance. Temporal biomass results are presented as absolute values (Fig. 2A–G).

DIFFERENCES AMONG HABITAT TYPES.—There was a significant autocorrelation among quadrats in Buhoma ($\chi^2 = 93.9$, $df = 38$, $P < 0.001$). However, the overall correlation coefficient was not significant (average rho = -0.008 , SD = 0.03, $t = -1.27$, $df = 18$, $P = 0.22$). In addition, of the 18 species, only six were significantly autocorrelated and of those, four were actually negatively correlated while the other two had very small correlation coefficients (< 0.07). Therefore we can conclude there is no obvious spatial autocorrelation.

Herb biomass differed among the five habitat types in Buhoma for 12 of 18 species (all $\chi^2 > 18.9$, $df = 6$, $P < 0.05$). For those that did not show significant differences, five of the six had a small biomass in any one habitat (> 0.3 g/m²). The greatest biomass of herbs (in total) here was in open forest, followed by regenerating, fire-disturbed, riverine, mixed, and mature (Table S1).

There was no significant spatial autocorrelation among quadrats in Ruhija (average rho = -0.03 , SD = 0.02, $t = -4.79$, $df = 10$, $P = 0.10$, $\chi^2 = 27.1$, $df = 22$, $P = 0.20$).

Nine of the 11 species differed significantly in biomass among the four habitat types in Ruhija (all $\chi^2 > 10.8$, $df = 3$, $P < 0.05$). The greatest biomass of herbs (in total) here was in swamp forest, followed by mixed, open, and mature (Table S1).

DIFFERENCES IN HERB BIOMASS BETWEEN LOCATIONS.—Of the nine shared species, seven had a higher biomass at Ruhija than Buhoma, one had a higher biomass in Buhoma, and one showed no difference ($\chi^2 = 108$, $df = 18$, $P < 0.001$; Table 3).

Comparing total herb biomass (sum of species monitored) between locations, Ruhija had over double the biomass of herbs than Buhoma (Buhoma average = 5.8 g/m², monthly range = 4.7–6.9 g, SD = 0.7; Ruhija average = 13.6 g/m², monthly range = 11.2–16.1 g, SD = 1.5). All habitat biomass results are presented as g/m².

TOTAL HERB BIOMASS WITH HABITAT TYPES TAKEN INTO CONSIDERATION.—When accounting for the proportion of each habitat type at each location, the relative herb biomass grams per meter square was greater in Ruhija than Buhoma. For the three habitat types in common between locations, total herb biomass grams per meter square was also greater in Ruhija than Buhoma (Fig. 3).

TABLE 3. Statistical results (\pm SD) of the interlocation comparisons in Bwindi. Bold figures depict a significantly greater biomass at this location.

Species	Mean biomass (g/m ²)		Z	P
	Ruhija	Buhoma		
<i>Basella alba</i>	0.2 (0.07)	0.05 (0.03)	-4.26	< 0.001
<i>Mimulopsis arborescens</i>	1.2 (0.2)	2.2 (0.5)	-4.6	< 0.001
<i>Triumfetta</i> sp.	2.1 (0.5)	0.6 (0.1)	-1.18	0.24
<i>Urera</i> sp.	0.2 (0.03)	0.1 (0.01)	-2.31	0.02
<i>Ipomea</i> sp.	0.8 (0.2)	0.1 (0.04)	-12.3	< 0.001
<i>Mimulopsis solmsii</i>	6.2 (1.0)	2.2 (0.7)	-9.4	< 0.001
<i>Mormodica calantha</i>	0.2 (0.05)	0.01 (0.001)	-6.7	< 0.001
<i>Mormodica foetida</i>	0.8 (0.2)	0.1 (0.1)	-8.36	< 0.001
<i>Rubus</i> sp.	1.0 (0.2)	0.07 (0.02)	-9.31	< 0.001

DISCUSSION

This is one of the first systematic studies to report on the phenological and spatial patterns of herbs (particular plant parts) consumed by mountain gorillas in an African montane tropical rain forest. We found temporal differences in herb biomass of individual species and spatial differences in herb biomass among habitat types and between locations. Our results demonstrate that herbs consumed by mountain gorillas in Bwindi are not evenly distributed in their habitats but instead differ in temporal and spatial availability. Although we lack environmental data that would enable us to draw conclusions about the causes of these patterns, we discuss how different variables may have influenced the patterns we encountered and how our results may impact gorilla ecology.

Temporally, we found differences between months in the biomass of herbs at each location. Although there was temporal variation, only a few species (*Laportea aestuans*, *Mimulopsis solmsii*, *Cardus* sp.) showed strong changes in biomass over the study period. In fact, these species appeared to have a 'die-off' at some

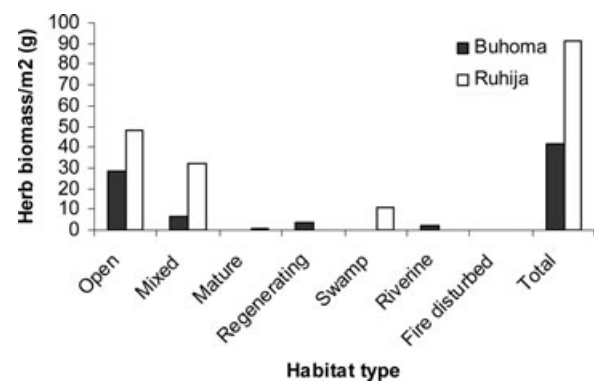


FIGURE 3. Relative average biomass of herbs g/m² in each habitat type, calculated by using the proportion of each habitat type at each location.

point during the study. Because gorillas eat a variety of herb species, consuming different herbs when these particular species were low in availability would be unlikely to negatively impact the gorillas' diet, especially since the majority of herbs consumed by gorillas are of high quality (Ganas 2008). Furthermore, the small scale temporal variation in herb availability suggests a constant supply of staple food available to the gorillas. Data are needed on the total biomass of herbs consumed by gorillas at several locations in Bwindi to determine whether the amount of herbs available in Bwindi is adequate for the growth of the gorilla population.

The influence of rainfall on herb biomass has been shown in both tree and understory/herb phenology studies and satellite imagery (Opler *et al.* 1976, Rathcke & Lacey 1985, Gentry & Emmons 1987, Davenport & Nicholson 1993). Although peaks in leaf flushing during periods of high irradiance (*i.e.*, dry season) are predicted for trees in tropical forests, the temporal availability of herb biomass in Bwindi showed no clear pattern with an increase in biomass and dry season (December–February and June–August) or rainfall (September–November and March–May). While taking advantage of peak photosynthetic activity and rainfall is likely important for herbs, additional factors such as soil quality and animal foraging and trampling damage are likely to play a simultaneous role which may obscure any obvious relationships. To determine the influence of sunlight and rainfall on herb biomass, enclosure plots should be created, which control for animal damage, and both rainfall and insolation amount should be recorded.

Patterns of temporal availability for *Ipomea* spp., *Mimulopsis solmsii*, *M. arborescens*, *Cardus* sp., *Mormodica calantha*, *M. foetida*, *Triumfetta* sp., *Urera* sp., *Basella alba*, *Piper capense*, *Gouania longispicata*, *Laportea aestuans*, and *Rubus* sp. were likely influenced by foraging and trampling by gorillas and other medium and large sized mammals such as elephants and duiker, which was documented on a presence/absence basis in the plots in this study and has also been found to influence herb availability in other studies (Watts 1987, Plumptre 1993, Gomez 2005). Future studies in Bwindi and elsewhere would benefit from more quantified measurements of these occurrences to understand how they influence herb phenological patterns. Second, longer studies (2 yr +) would reveal if the temporal patterns in herb biomass we found are typical.

The biomass of herbs differed significantly among habitat types for the majority of herb species at each location. This is not surprising given that habitat types are usually defined by factors such as canopy cover, level of disturbance, soil type, amount of water in soil, and plant species composition. Thus, we would expect most plant species to have habitat specific requirements and to occur in particular habitat types (Harms *et al.* 2001). The greatest total biomass of herbs occurred in open forest in Buhoma and swamp forest in Ruhija. Swamp forest, however, comprises a very small proportion of the total habitat in Ruhija and its high biomass is due to one species *Mimulopsis arborescens*, a large (up to 5 m) subwoody herb. Considering the amount of area covered by and herbs contained within each habitat type, open forest contributes the greatest proportion of herb biomass in both locations.

Open forest can be considered vital habitat for gorillas because it contained a relatively high biomass of herbs considered important in the gorillas' diet and it covers a relatively large area in Buhoma and Ruhija. Based on these criteria, regenerating forest can also be considered important. Additionally, indices of habitat selection for four gorilla groups in these two locations indicated that the number of feeding remains (places on the gorillas' trail where they have discarded uneaten plant parts) in open forest for all groups were almost always of higher proportion than availability, suggesting that gorillas favored this habitat (J. Ganas, pers. obs.). The same was found for regenerating forest on a seasonal basis. According to these criteria, mixed, swamp, mature and riverine forests are less important for gorillas. However, mixed forests contain the majority of trees that provide fruit for gorillas and could be considered important during times of high fruit availability. Due to the importance of open and regenerating habitats to gorilla survival, increasing protection efforts (*e.g.*, additional ranger patrols) in these areas may aid mountain gorilla conservation efforts.

Several factors may have contributed to a higher herb biomass at Ruhija. Areas in both locations were intensively pit-sawed in the past, altering the vegetation structure of the forest by creating forest gaps. Logging could have been more intense in Ruhija than Buhoma, creating more gaps, and thus a higher biomass of herbs (although we do not have data on how much pit-sawing occurred; Babaasa *et al.* 2004). Second, elephants are thought to range primarily in the Ruhija area (based on 1997 large animal census in Bwindi, A. McNeilage, A. Plumptre, A. Brock-Doyle, and A. Vedder, pers. comm.). Elephants in Bwindi prefer these gaps and forage within them, creating a feedback system in which herbs persist or even increase, creating elephant 'gardens' (Struhsaker *et al.* 1996, Babaasa 2000, Babaasa *et al.* 2004). Third, the topography in Ruhija is much steeper than in Buhoma, so landslides may be more likely here which could create more gaps (Butynski 1984; D. Babaasa, pers. comm.). Although we have no measures of the effects of gorilla foraging on herb biomass, they may also contribute to gaps/open forest, as has been documented in the Virunga Volcanoes (Watts 1987).

Although Ruhija has a higher biomass of herbs, this does not confirm that there is less food for gorillas in Buhoma than in Ruhija. There are other foliage foods that are eaten by gorillas in Buhoma for which biomass was not measured (*i.e.*, leaves and pith from trees, shrubs and a few rarely eaten herbs). Second, fruit availability is greater in Buhoma than Ruhija, thus, the gorillas in Buhoma may consume more fruit than those in Ruhija (Nkurunungi *et al.* 2004). Third, despite differences in herb biomass between locations, alternative foods sources at each location may allow gorillas in Bwindi to consume a nutritionally similar diet (Ganas 2008). Finally, although herb availability influences the density of gorillas, other factors such as fruit availability, interspecies competition, and human disturbance may also play a role, obscuring any clear relationships between herb biomass and gorilla densities (White *et al.* 1995, McNeilage *et al.* 2006; A. Todd, pers. comm.).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Herb species monitored and their corresponding median biomass in each habitat type.*

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