UNIVERSITY *of* RWANDA

EFFECT OF MOUNTAIN GORILLA (*Gorilla beringei beringei*) POPULATION GROWTH ON THEIR KEY FOOD PLANT SPECIES BIOMASS IN VOLCANOES NATIONAL PARK, RWANDA

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DECLARATION

This thesis is my original work and has not been presented for a degree in any other university

Signed………………………   Date…………………

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The thesis has been submitted for examination with my approval as the university supervisor

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Abstract

High densities of large herbivores can have detrimental effects on plant biomass. Understanding the relationship between animal densities and plant distribution and abundance is essential for the conservation of endangered species and ecosystems. Mountain gorilla censuses conducted for different periods in the last three decades have revealed a steady increase of gorilla population in Virunga Massif whereby the recent number of gorillas has doubled compared to their number in the 1980s. It is unclear whether the continuous population growth of the herbivorous Virunga gorilla within an isolated forest 'island' has been affecting gorilla food plant biomass. This study investigated the effect of varying mountain gorilla densities on the biomass of the five key food plant species (*Galium spp.*, *Carduus nyassanus*, *Peucedanum linderi*, *Rubus spp.*, *Laportea alatipes*) that make up >70% of the mountain gorilla diet. We used plant biomass data collected in a central part of the Virunga massif, commonly known as Karisoke sector from 2009 to 2011, and GPS records of gorilla groups ranging in the same area nine months prior biomass assessment. Gorilla densities were estimated using the Kernel Utilization Distribution (KDE) analysis (functions: 'kernelUD' and 'getvolumeUD') from the Adehabitat package in R software, which provides the probability density of gorilla occurrence at each coordinate (x, y) of the study area. Analyses using GLMs suggest that gorilla densities (a proxy of previous gorilla utilization intensity) did neither affect the total biomass of key food plant species nor the biomass of each key food plant species (p>0.05). These results may indicate that current revisit rates of feeding sites by gorillas allow for complete plant regeneration, and no signs of overharvesting. Alternatively, feeding sites characterized by very high biomass may be preferred by gorillas and remain sites with the highest biomass even after being frequently used by gorillas. Findings also suggest that carrying capacity of the gorilla population in the study areas may not yet be reached if food is the driving constraint. However, monitoring of the relationship between gorilla densities and food plant biomass must continue while the Virunga population continues growing. Future studies also need to incorporate other sympatric large herbivores in the Virungas who share food plants with mountain gorillas.

Keywords: habitat use, *Gorilla beringei beringei,* herbaceous plants food biomass, Volcanoes National Park.

List of symbols and acronyms

DFGFI	The Dian Fossey Gorilla Fund International
DRC	Democratic Republic of Congo
GIS	Geographic Information System
GPS	Global Position System
GVTC	Greater Virunga Transboundary Collaboration
KDE	Kernel Utilization Distribution
KRC	Karisoke Research Center
RDB	Rwanda Development Board
VNP	Volcanoes National Park

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CHAPTER 1. INTRODUCTION

1.1. Background

Investigating changes in the relationship between animals and their environment is one of the most relevant subjects in ecology (Calenge, 2006; Barton and Hanley, 2013). The environment determines the diet, movement patterns and in some cases, breeding cycles of a species, and is thus of great importance in wildlife management (Johnson, 1980; McNeilage, 1995). The population density of a species can be a fundamental driver of many ecological processes, including habitat selection (Beest *et al.*, 2013). Therefore, monitoring of population density is important in the conservation of endangered species as it can be used to predict changes in a species ecology. This knowledge can eventually help design mitigation measures to ease the impact of changes in population density on the available habitat of endangered species (Norris, 2004). Plants are producers in food webs and are therefore an essential ecosystem element that all animal communities are built on (Maron and Crone, 2006). Herbivores play a large role in shaping plant community compositions in their habitat by influencing species abundance and distribution through trampling and plant consumption (Watts, 1987; Plumptre, 1991; Maron and Crone, 2006; Barton and Hanley, 2013; Lefebvre and Gallet, 2017). However, the effects of herbivores on the abundance and distribution of plant species can be complex and exhibit extensive variability (Bigger and Marvier, 1998; Vesk and Mark, 2001; Maron and Crone, 2006). Effects can be detrimental on the fitness and productivity of plant species, which subsequently affects plant growth and distribution (Crawley, 1997; Bigger & Marvier, 1998; Gomez, 2005; Tiffany, 2004). However, damage from herbivores can also result in higher plant productivity and biomass (Hawkes and Sullivan, 2001). On the other hand, some plants have evolved mechanisms and traits towards a high tolerance to herbivory, often leading to negligible effects of herbivores on plant distribution and abundance (Strauss and Agrawal, 1999; Stowe *et al.*, 2000).

Mountain gorillas remain in only two isolated populations, one is found in Virunga massif (shared between Rwanda, Uganda and the Democratic Republic of Congo) and the other is found in Bwindi Impenetrable Forest (Uganda). Censuses conducted previously on mountain gorilla in

Virunga Massif have demonstrated a continuous increase in the gorilla number where the number nearly double from 250 individuals in 1981 to 480 individuals in 2010 (Gray *et al.*, 2013). Moreover, the most recent census in 2016 revealed that the number of gorillas inhabiting Virunga massif has reached 604 individuals with 3.8 percent annual rate increase (Hickey *et al*., 2018). Until 2010, this steady population increase was exclusively observed in groups of habituated gorillas that are subject to integrated conservation activities, including daily protection, monitoring, patrolling for illegal activities, tourism, veterinary care, and educational programs (Robbins *et al.*, 2011). Census results have also shown an uneven distribution of gorilla groups throughout the Virunga habitat. Specifically, the southeastern-central region of the Virunga massif, known as the Karisoke sector, in the Volcanoes National Park (VNP) in Rwanda, has some of the highest observed gorilla density (Robbins *et al.*, 2011; Gray *et al.*, 2013). Increases in the population density in the Karisoke area have been associated with significant home range overlap of gorilla groups while home range size has remained relatively consistent, despite the increase in the number of gorilla groups that occurred due to multiple group fission events and groups being newly formed since 2007 (Caillaud *et al*., 2014).

Mountain gorillas live primarily in stable, cohesive social units, although adult males may be solitary (Robbins, 2007). Mountain gorillas are large herbivores that feed mainly on leaves, stems, and roots of different plant species (McNeilage, 2001). In the Karisoke area, more than 80% of the gorilla's diet is composed of only six key plant species, namely *Galium spp*., thistles (*Carduus nyassanus*), wild celery (*Peucedanum linderi*), bamboo (*Yushania alpina*), blackberries (*Rubus spp*.) and nettles (*Laportea alatipes*) (Grueter *et al.*, 2013). These key gorilla food species are available all year-round, except for bamboo shoots which are only available for four months per year coinciding with the two rain seasons (Vedder, 1984; Watts, 1991). The habitat of mountain gorillas is broadly classified into different vegetation zones following altitudinal succession (McNeilage, 1995). The vegetation of the Karisoke study area consists mostly of open canopy *Hagenia–Hypericum* woodland with a dense herbaceous understory, bamboo forest, and subalpine areas. The large proportion of open herbaceous vegetation in the area is known to provide the highest gorilla food biomass and nutritional quality (Plumptre, 1993; Watts, 1998), which may explain the highest population increases in this area within the Virunga massif. Although food plant species frequently consumed by gorillas are found in almost every vegetation zone, the density and distribution of plant species can vary within vegetation zones

(Vedder, 1984; McNeilage, 1995). Variation in the spatial distribution, abundance and nutritional quality of gorilla food species can, therefore, influence the frequency and duration of visits by gorilla groups in specific areas of the habitat (Vedder, 1984; McNeilage, 1995; Watts, 1998). Previous research suggests that when a herbivorous species consumes vegetation faster than the plants can regenerate, there can be considerable decreases in the availability of food resources for animals in the area (Watts, 1998). Thus, differences in the usage of certain areas of the habitat in the light of growing gorilla densities can, therefore, result in over-harvesting of key gorilla food species. In addition, as the total population size increases, so does competition among gorilla groups for space in good quality areas. This may result in less competitive groups using poorer quality sites, and since access to high-quality food resources can affect female reproductive success, over-harvesting of food species by gorillas due to rapid increases in population growth may finally affect individual fitness (Norris, 2004; Robbins *et al.*, 2007).

Because food resources are a key factor limiting population density, the correlation between food availability and population size need to be studied and understood for better wildlife conservation (Chapman and Rode, 2003). Understanding the relationship between the population density of an herbivorous species and food distribution and abundance is essential for understanding the dynamics of the ecosystem they inhabit. For example, the relationship between an animal and its environment can help estimate the approximate carrying capacity of a particular area (McNeilage, 1995), which can, in turn, provide information about the minimum area that has to be protected to guarantee the survival of a population. Grueter et al (2013) revealed changes in biomass in the top five most consumed gorilla food species in the Karisoke area; two of them (*Galium spp*. and *Laportea alatipes*) showed a decline in biomass, while the other three (*Carduus nyassanus*, *Peucedanum linderi,* and *Rubus spp*.) showed an increase in biomass as well as a shift in altitudinal distribution compared to that in 1989. However, whether these observed changes in biomass of gorilla key food species are linked to changes in gorilla ranging patterns, habitat use and population density in this south-eastern central forest area remain unknown. Therefore, understanding how gorillas shape their habitat will provide useful information in understanding the dynamics of gorilla habitat and ecology at large. Thus, this study investigates whether gorilla density is associated with variability in the biomass of the five key gorilla food species in the southeastern-central region of the Rwandan component of the Virunga massif.

1.2. Problem Statement

Mountain gorillas live in an isolated small forest fragment surrounded by a high human population density (Weber, 1987). Despite high anthropogenic pressure on the gorilla habitat, the Virunga population has been steadily growing since the 1980s. According to the census of mountain gorillas in 2010 in Virunga Massif, the population of mountain gorillas increased at almost 3.4 percent annually (Robbins *et al.*, 2011; Gray *et al.*, 2013) with the highest concentration of gorillas in the south-central region of the massif which encloses the Karisoke research area (Plumptre, 1991; Robbins *et al.*, 2011; Gray *et al.*, 2013). The high gorilla utilization of the Karisoke area is mainly explained by the high quality and abundance of gorilla food in the area, but may have also resulted from anthropogenic threats (mainly poaching and habitat disturbance) in other areas of Virunga Massif, which limits gorillas from using them (Gray *et al.*, 2013). The fast and continuous increase of the mountain gorilla population, and the highly specific feeding behavior of mountain gorillas (i.e. having preference on few plant species in their diet) may be related to an increase in the frequency and duration of time that gorillas spend in highly profitable areas, which may be influencing the abundance and biomass of plant species (Grueter *et al.*, 2013). Therefore, it is critical that we better understand the extent to which gorilla density affects the biomass of their key food species, specifically, at which gorilla density, gorilla food biomass begin to decline and no longer support the population.

1.3. Objective and hypothesis

This study aims to examine the association between the local gorilla density (Proxy to gorilla visitation intensity) and the biomass of five key gorilla food species in the Karisoke research area in the Volcanoes National Park, Rwanda. The main question to address is "Does gorilla density affect key gorilla food plant biomass?". It is hypothesized that a negative relationship between gorilla food biomass and previous gorilla density probability (i.e. low food biomass related to high population density) is expected.

CHAPTER 2. LITERATURE REVIEW

2.1. Taxonomy and distribution of mountain gorilla

The Mountain Gorilla (*Gorilla beringei beringei*) belongs to the eastern gorilla species, which also includes the Eastern Lowland Gorilla (*Gorilla beringei graueri*). There are two populations of mountain gorillas one among the volcanoes of the Virunga Massif at the border of the DRC, Rwanda and Uganda with currently 604 individuals (Hickey *et al*., 2018), the other in Bwindi Impenetrable National Park in southwest Uganda on the border with DRC with 400 individuals (Roy *et al.*, 2014).

Mountain gorillas live primarily in stable, cohesive social units, although adult males may be solitary (Robbins, 2007). Groups typically contain several adult females, their immature offspring, and always at least one silverback (*ibid*.). Age/sex classifications typically used for gorillas include infants (0-3.5 years), juveniles (>3.5-6 years), subadults (>6-8 years), adult females (>8 years), blackback males (>8-12 years), and silverback males (>12 years). Infants completely depend on their mothers and are unlikely to survive without their mother until they reach the age of 3 years, because of their nutritional dependence as well as their dependence for locomotion (Robbins, 2007). Groups may be one-male, multi-male, or all-male (non-reproductive, containing no adult females) (Stewart and Harcourt 1987; Robbins et al.,1995). Mountain gorillas are not territorial and have overlapping home ranges (Watts 1998b, Ganas and Robbins, 2005).

2.2. Diet

Mountain gorillas are selective in their feeding behavior (Watts, 1984). Their diet is primarily influenced by the availability of food resources, but it is clear that mountain gorillas seek out foods with particular nutritional composition and often forage on rare species, where they select leaves and herbaceous material that are high in protein (Watts, 1991). Mountain gorillas are largely vegetarian, with the only non-vegetative foods in their diet being ants and termites (Watts, 1984). Mountain gorillas eat non-reproductive plant parts (leaves, stems, pith, and bark) as well as flower and fruit. In general, the degree of frugivory decreases as altitude increases, because of reduced fruit availability in higher altitudes (Ganas et al., 2004). The number of herb species consumed by mountain gorillas also decreases with increasing altitude, probably a result

of decreased plant diversity as altitude increases (Robbins, 2007). This makes mountain gorillas in the Virunga massif to be highly folivorous with only a negligible amount of fruit in their diet (Fossey and Harcourt, 1977; Watts, 1984; Vedder, 1984; McNeilage, 1995). Mountain gorilla herbaceous food in Virunga massif is almost available throughout the year, with only seasonal food for Virunga mountain gorillas being bamboo shoots (Vedder, 1984). Despite the fact that bamboo is one of important food in the mountain gorilla diet due to its high content in protein, however not all mountain gorillas consume bamboo shoots because of its scarcity (Watts, 1984; McNeilage, 1995, 2001).

2.3. Ranging pattern

Mountain gorillas are not territorial animal species (Watts 1998b, Ganas and Robbins, 2005; Seiler *et al*., 2018), and they use all nine different vegetation types that is found in Virunga massif (McNeilage, 1995; Table 1; Figure 2), the lack of territoriality increase the home-ranges overlaps where the gorilla density is high (Caillaud *et al*., 2014). The home-ranges overlaps may decrease the predictability of food resources in shared areas (Grant *et al*., 1992). Mountain gorilla have relatively smaller home-range compared to other species of gorillas species mainly due to their low food competition as their herbaceous food is abundant and relatively evenly distributed in their habitat (Watts, 1994a, 1998b; Doran-Sheehy *et al*., 2004; Ganas & Robbins, 2005). Expanding to new areas in mountain gorillas is progressive and takes a relatively long time, approximately going up to seven years (Watts, 1998b). However, sometimes, there is a sudden group home-range change resulting from the avoidance of mates competition (Watts, 1998b).

Table 1. Description (altitude and general characteristics) of the nine vegetation zones of the VNP (McNeilage, 1995).

Vegetation zone	Altitude	General characteristics
Alpine	Above 3600 m	Low grasses, mosses, and lichens, bare rocky areas
Subalpine	3300 m to 3600m	Abundant *Senecio John stonii, Lobelia stuhlmanni* and/or *L. wollostonii, Hypericum*

		revolutum and *Rubus kirungensis.*
Brush ridge	2950 m to 3300 m	Abundant *Hypericum revolutum* and shrubby growth of *Senecio mariettae*, reaching around 10 m high
Herbaceous	2800 m to 3300 m	Open areas with low (1-2 m), dense herbaceous vegetation, with very few *Hagenia abyssinica* and *Hypericum revolutum* trees
Hagenia-Hypericum woodland	2750 m to 3300 m	Dominated by *Hagenia abyssinica* and *Hypericum revolutum* trees, with a dense herbaceous understorey
Bamboo	2550 m to 2950 m	Dominated by monospecific stands of bamboo, mixed with a few trees and vines at lower altitudes.
Mimulopsis	2550 m to 2800 m	Open herbaceous areas dominated by *Mimulopsis excellens.*
Mixed Forest	2000 m to 2550 m	Mixed species montane forest with abundant *Neobutonia macrocalyx* and *Dombeya goetzenii*
Meadow	Variable Altitude	Open grassy areas at a variety of altitudes. These areas are often marshy and contained very little gorilla food
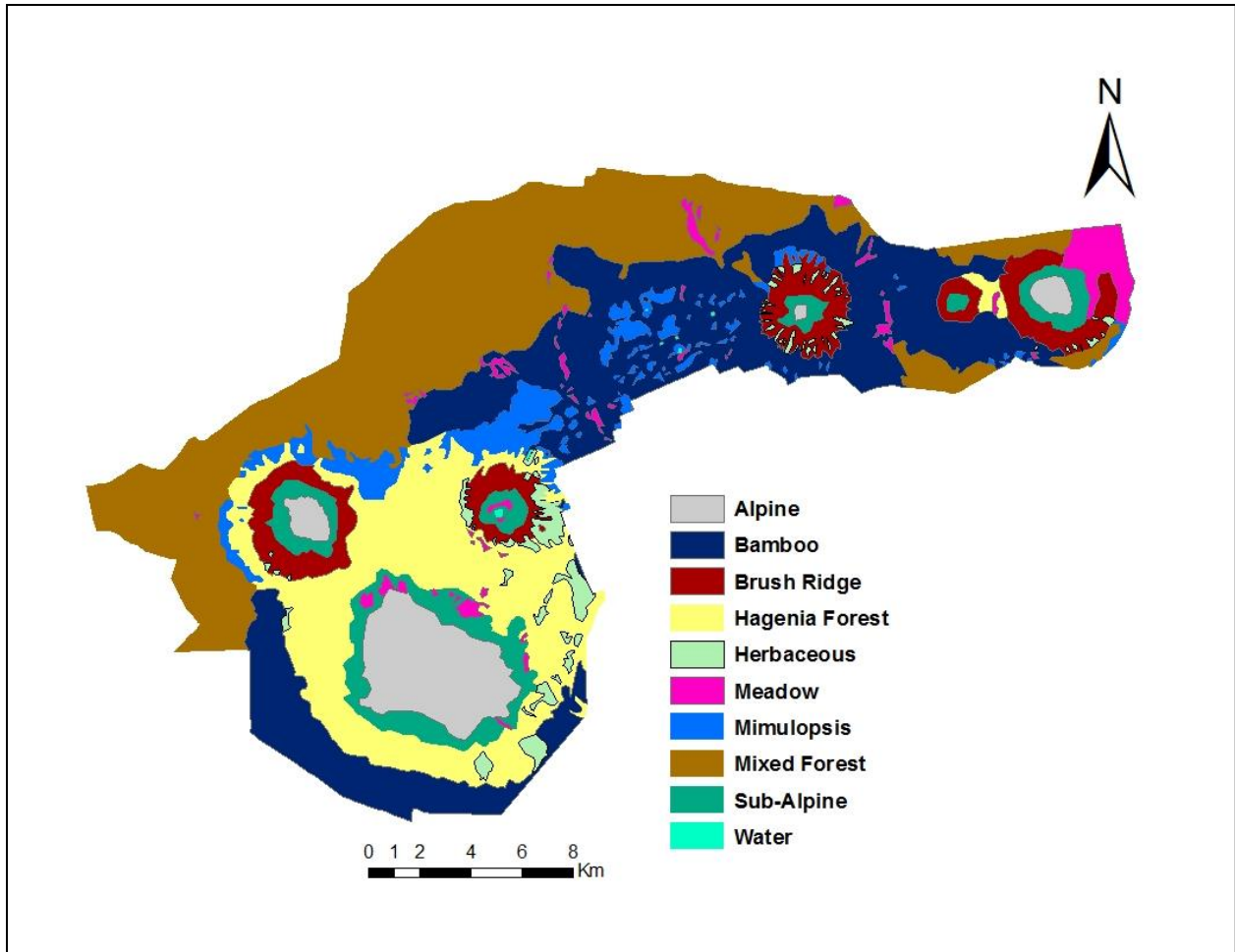
Figure 1. Vegetation types distribution

2.4. Threats

Mountain gorillas face an extremely high risk of extinction in the wild due to their very small population level, habitat loss, poaching, human disease, and war (Plumptre *et al*., 2003). Mountain gorillas are probably having no predators other than humans (Robbins, 2007). Mountain gorillas are categorized as endangered species on the International Union for Conservation of Nature (IUCN) red list (Hickey *et al.,* 2018).

CHAPTER 3. MATERIALS AND METHODS

3.1. Study area

This research was undertaken in the Virunga Massif which stretches out between 1º and 2º of latitude South and 29º to 30º of longitude East at the borders of Democratic Republic of Congo (DRC), Uganda and Rwanda. Virunga Massif comprises three adjacent national parks: Virunga National Park (DRC), Mgahinga Gorilla National Park (Uganda) and Volcanoes National Park (Rwanda). The Virunga massif is an afromantane forest and lies on six extinct volcanoes respectively from East to West Muhabura (4,127 m), Gahinga (3,474 m), Sabyinyo (3,634 m), Bisoke (3,711 m), Karisimbi (4,507 m) and Mikeno (4,380 m) and range from an altitude of 2300 to 4,507 meters above sea level covering of approximately 450 km^2 (Weber, 1987; Figure 2).

This area is rich in biodiversity with several species which are endemic to the area and to the Albertine Rift (Owiounji *et al*, 2005). Along with Bwindi Impenetrable National Park (Uganda), it is the last remaining habitat of the endangered mountain gorillas. According to Plumptre *et al* (2003), Virunga Massif has a total list of 86 species of mammals out of which 34 are large mammals. The larger mammals include six herbivorous larger mammals which are mountain gorilla (*Gorilla beringei beringei*), buffalo (*Syncerus caffer*), bushbuck (*Tragelaphus scriptus*), black-fronted duiker (*Cephalophus nigrifrons*) and elephant (*Loxondata africana*) (Owiounji *et al*, 2005). The area is also a habitat to endangered golden monkey (*Cercophithecus mitis kandti*) which has a diet that overlapping with one of the gorillas.
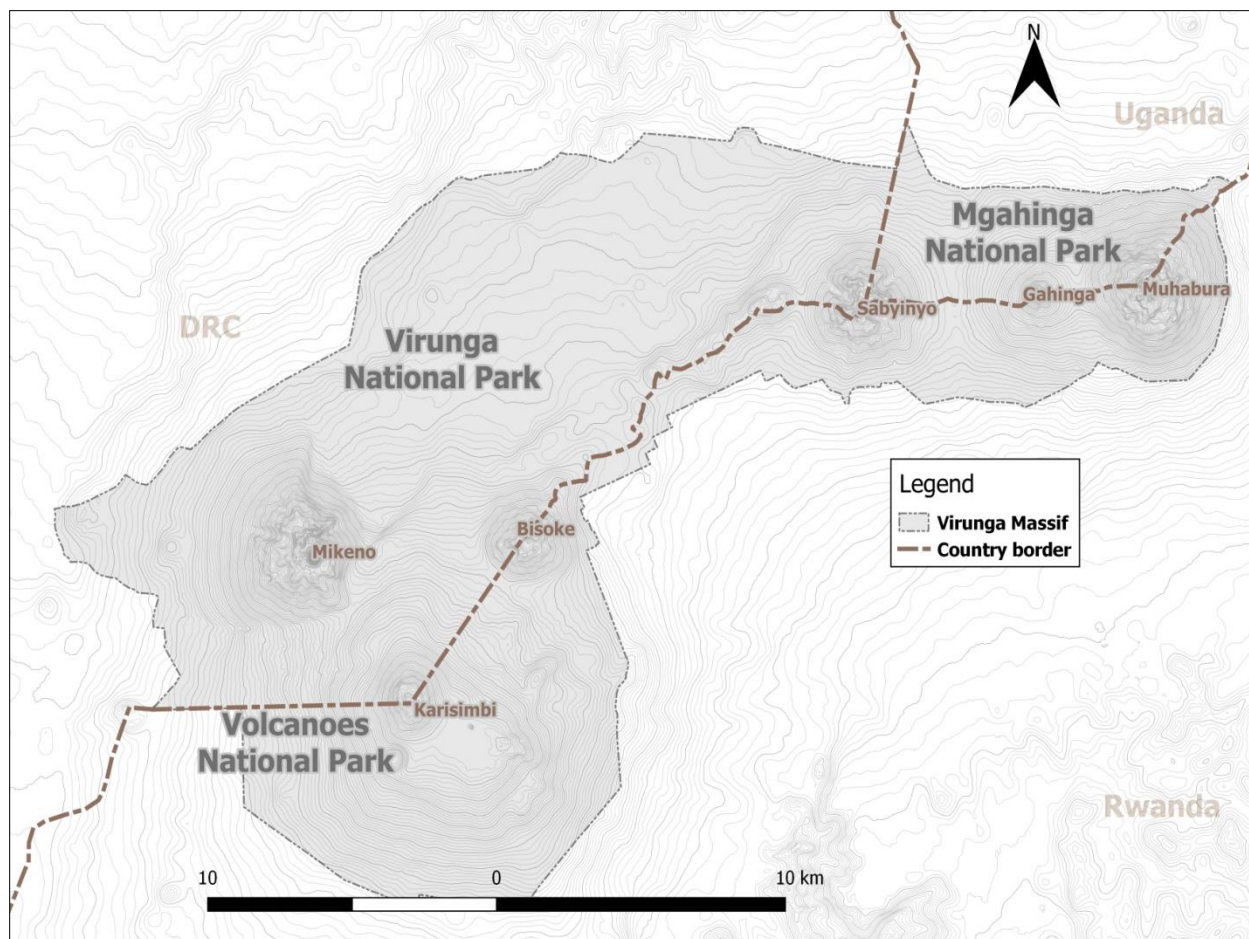
Figure 2. Virunga Massif with its three different parks

3.2. Study Animals

The current research was conducted on habituated gorilla groups that were ranging in the center part of the park of the Volcanoes National Park (VNP) in an area commonly called Karisoke which situated between Karisimbi and Bisoke Volcanoes (Fig. 2). During the study period (from 2009 to 2011), Karisoke research gorilla population mean size was 123 gorillas distributed in 9 social groups (Fig. 3; Table 2).

Table 2. Summary of the study groups mean composition from 2009 to 2011. SB = Silverback (≥12 years male); BB = Blackback (8-12 years male); ADF = Adult female (≥8 years female); SA = Subadult (6-8 years); JUV = Juvenile (3.5-6 years); INF = Infant (0-3.5 years).

Group Name	Mean group size	Mean Age sex class composition
Pablo (PAB)	46	5SB, 14AF , 7BB, 6 SA, 4JUV, 10INF
Kuryama (KUY)	14	3SB, 3 AF, 2BB, 4JUV, 2 INF
Bwenge (BWE)	11	1 SB, 5AF, 2 JUV, 3INF
Isabukuru (ISA)	12	2 SB, 5 AF, 1 JUV, 4INF
Ntambara (NTA)	11	3SB, 5AF, 1, JUV, 2INF
Titus (TIT)	7	2SB, 2BB, 1 SA, 2AF
Ugenda (UGE)	10	2SB, 4AF, 3JUV, 1INF
Urugamba (URU)	6	1SB, 2AF, 1 SA, 1JUV, 1 INF
Inshuti (INS)	6	1SB, 3AF, 2INF

3.3. Data collection

3.3.1. Plant biomass

Plant biomass data of five key gorilla food species (*Galium* spp., *Carduus nyassanus*, *Peucedanum linderi*, *Rubus* spp, and *Laportea alatipes*) and their corresponding GPS coordinates were obtained from a study that was carried out by Grueter between 2009 to 2011 in the southern central part of VNP commonly known as Karisoke area (Grueter *et al.*, 2013). Grueter et al. (2013) sampled vegetation in two phases. The first phase lasted from September 2009 to May 2010 and covered an area of approximately 6 km^2, while the second phase lasted from June 2010 to March 2011 and covered approximately 25 km^2 (for more details see Grueter *et al*. 2013; Figure 3). A stratified random sampling method was used, and the study area was divided into a grid with cells of approximately 100m and 250m length in the first phase and the second phase, respectively. A nested circular plot was located within each cell (Plumptre, 1991; Grueter *et al.*, 2013). Different plot sizes were used for assessing biomass of different plant types: 1m^2 (r = 0.56m) for tall herbs and vines, 5m^2 (r = 1.26m) for shrubs, and 10m^2 (r =

1.79m) for trees (Grueter *et al.*, 2013). A total of 969 plots were established in both phases (Grueter *et al.*, 2013).

Dry biomass of the five key plant species was obtained using different methods. For the tall herbs (*Carduus nyassanus*, *Peucedanum linderi*, and *Laportea alatipes*), their biomass was estimated based on the assumption that one measurable plant trait correlates with the total biomass of the plant individual (Whittaker, 1965). Thus, the measurements of stem and leaf length of these tall herbs were recorded, then their length measurements were entered into existing phytometric regression equations developed by Plumptre and converted into dry biomass (Plumptre, 1991; Appendix. 1). For *Galium sp* which is a vine and grows in tangles on other plants, their biomass was obtained by harvesting all the *Galium sp* found in the plot and then dried them and measured on a high precision balance at Karisoke Research Center laboratory facilities. For *Rubus sp.*, which is a shrub and which the length vegetative parts are not easily measured, 50 leaves (including petioles) were collected and obtained the average weight of the *Rubus sp* leaves, which we subsequently used for biomass estimates by multiplying with the number of the leaves counted on each *Rubus* species found in the plot.
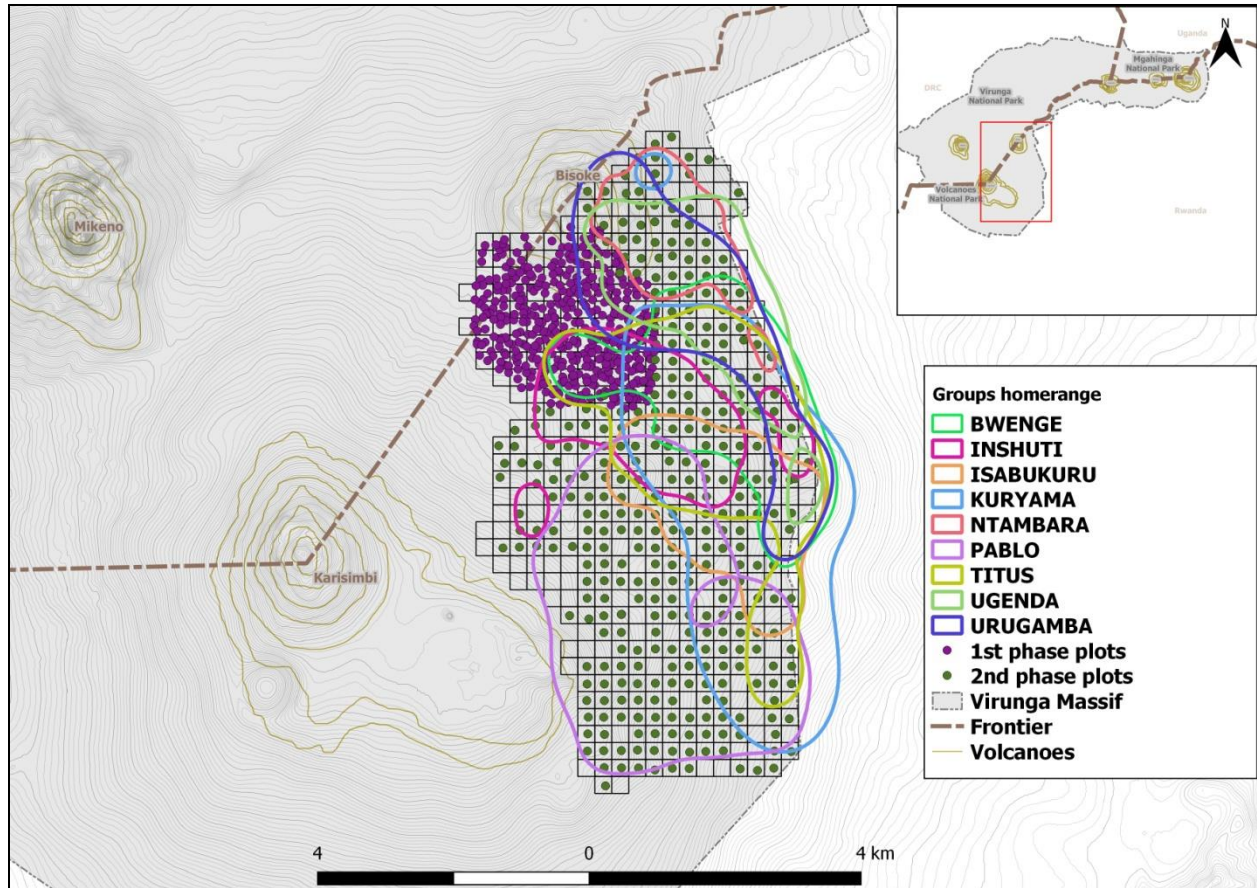
Figure 3. Karisoke research area showing plant biomass plot assessed in two phases and gorilla groups home ranges from January 2009 to March 2011

3.3.2. Gorilla location

GPS coordinates were recorded using handheld GARMIN GPS devices twice a day in each monitored group. The first GPS point corresponded to the location of the night nest site where the group spent the previous night, and the second GPS point corresponded to the location of the group at noon. The GPS points were recorded in UTM projection, which has coordinate-units of 1 meter. We used GPS coordinates collected in nine consecutive months prior to the date of biomass sampling for each sampled plot. The criteria of nine months prior to the plant biomass assessment was chosen because a full regeneration of herbaceous gorilla food typically requires six to eight months after being fed on and/or trampled (Plumptre, 1993; Watts, 1998). In addition, to investigate whether gorilla densities have a shorter or longer term effect on the

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biomass of consumed key food plants, we also calculated gorilla densities derived from GPS data of one month and five years prior the biomass assessment in each plot.

3.4. Data analysis

Gorilla densities were calculated using locations of gorilla groups that were ranging in the study area and monitored by KRC. We controlled for differences in the amount of food consumed and trampling at feeding sites related to group size by replicating each GPS location by the number of weaned individuals in a group in the data set (i.e. over the age of 3 years, Caillaud *et al.*, 2014). The dataset analyzed here includes a total of 13,330 GPS points. These GPS coordinates were then used to calculate the intensity of habitat use by gorillas using the Kernel Utilization Distribution (KDE) analysis (Worton, 1989). This method generates utilization distributions, which represent animal's relative use of space (Van Winkle, 1975). KDE is a weighted probability function which is put over each observations data point and then aggregating them to yield the overall density (Worton, 1989). In this way kernel function estimate high density in the place that has a high concentration of data points than in the place that has few points and it insures that the contribution of each point to the density of an area is inversely proportion to its distance to that area (Worton, 1989). To have a robust estimate of utilization density we need to have a good value for one of the important parameter in Kernel Density Estimation method which is known as the smoothing (or bandwidth) parameter commonly written as h, as the small value of h could lead to underestimate of utilization density and large value of h could lead to overestimate of utilization density (Worton, 1989; Kie *et al.*, 2010). There are many methods to estimates the bandwidth parameter (Worton, 1989) but the most commonly used method to estimate the bandwidth parameter is the least-square cross validation method, however the least square cross validation method has been demonstrated to be sensitive to data size and can lead to an underestimation of the utilization density when the sample size is large (Kie *et al.*, 2010). In this study we choose to use a fixed bandwidth parameter of 200 m as in previous studies of mountain gorillas this fixed bandwidth of 200m showed to produce utilization density which is robust to data size change (Caillaud, *et al.*, 2014; Seiler *et al.*, 2017). All Kernel utilization density calculations were performed using software 3.4.3. (R. Core Team, 2017) and package Adehabitat HR (Calenge, 2006), which provides the density based probability of animal occurrence (in our case gorilla groups) at each coordinate of the study area (Calenge, 2015).

After calculating KDE, the 'raster' function in the raster library (Hijmans, 2017) in R software was used to convert the KDE output into a raster image, where the values in each pixel of the image corresponding to the probability of a gorilla occurring in that particular pixel, which is directly related to the density of gorillas (higher probability of finding a gorilla = higher density). Finally, the raster image was overlaid with the GPS locations of biomass grids and by using the 'extract' function in R, we estimated the density values corresponding to the coordinates of each grid in which plant biomass was sampled.

To assess whether the change in biomass of (1) each of the five key food species and (2) the total key food plant biomass was correlated to gorilla density probability, General Linear models (GLMs) was used, which included food biomass as the dependent variable and gorilla density as the predictor variable. The log-transformation of food biomass and gorilla density data was done before analysis to normalize the data. The plant biomasses from both phases were analyzed together, and a p-value threshold of 0.05 was used to detect statistical significance.

CHAPTER 4. RESULTS

4.1. Distribution of key gorilla food plant biomass and gorilla densities

There was a wide variation in the biomass of gorilla key food within the study area ranging between 0.2 g/m^2 to 755.6 g/m^2 in the plots sampled with a mean (±SD) biomass of 117.5 (±117.3)g/m^2 (Figure 4). Similarly, habitat use by gorillas was highly variable, with the gorilla density probability ranging between 0% and 99.97% and a mean (±SD) of 20.68 (± 26.53)% (Figure 5).
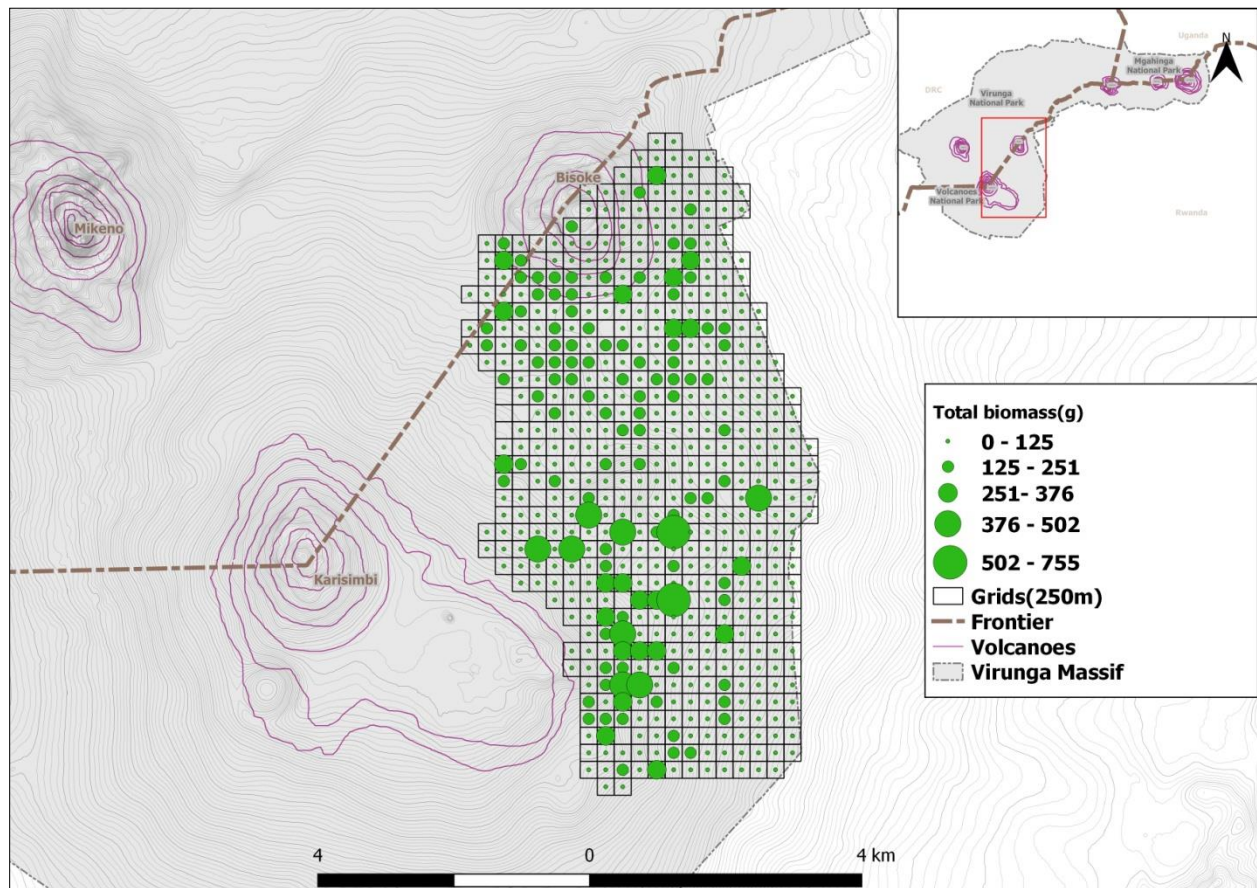
Figure 4. Total biomass (in grams) of the five key gorilla food species in each study plot located in the Karisoke study area (from September 2009 to March 2011).
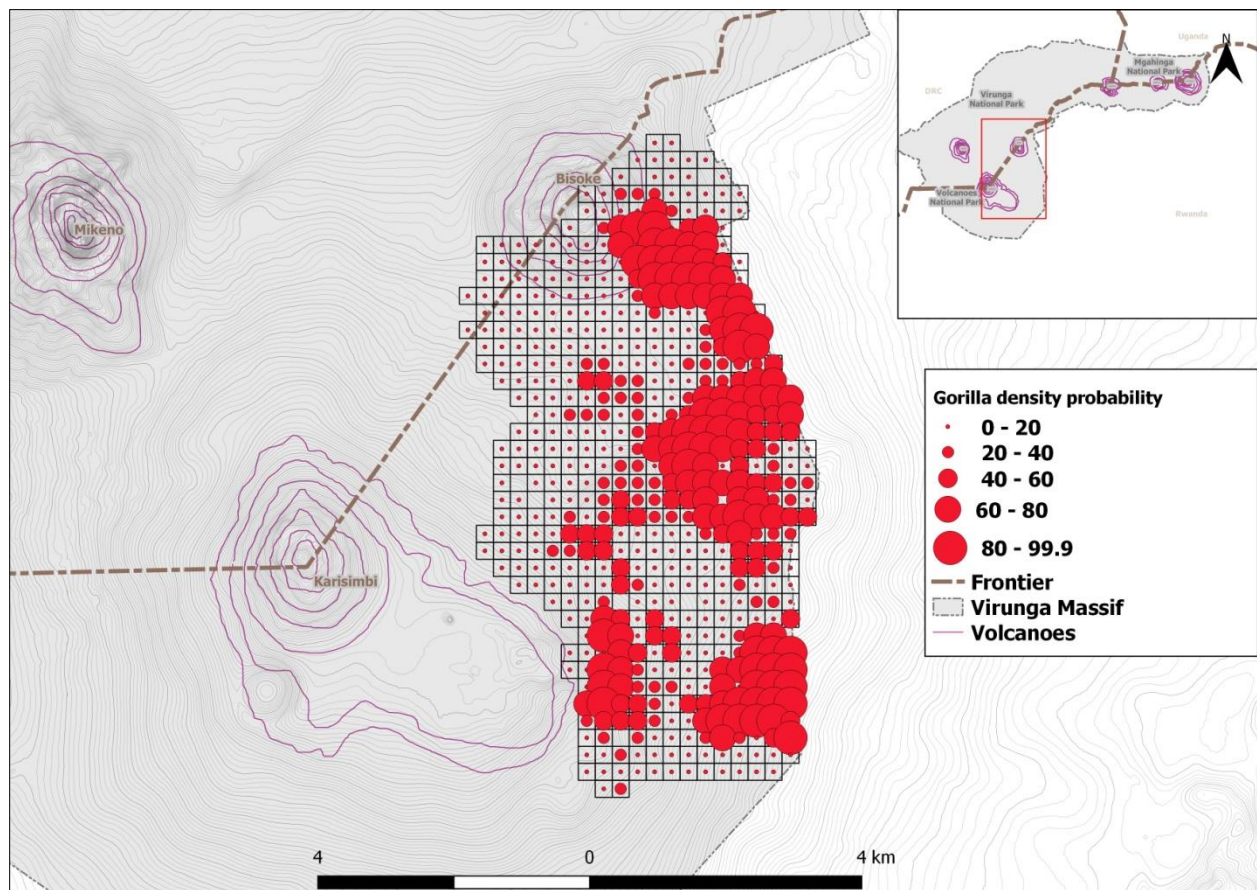
Figure 5. Variation in gorilla density density probability (%) in every grid of 250 m of the side corresponding to where the plant biomass was collected in the study area (from September 2009 to March 2011).

4.2. Relationship between key gorilla food biomass and gorilla density probability

A significant relationship was not found neither between the gorilla density probability and the biomass of any key food species nor between gorilla density probability and the total biomass of these key food species (Table 3 & Fig. 6).

Table 3. Statistical output of model investigating the relationship between key food plant biomass and gorilla density probability.

Species name	Number of plots	Degree of freedom	F-statistic	P-Value
Galium sp	246	(1, 245)	1.44	0.231
Carduus nyassanus	216	(1, 215)	0.02	0.878
Pceudanum linderi	95	(1,94)	1.33	0.251
Laportea alatipes	345	(1,344)	0.52	0.474
Rubus sp	262	(1, 261)	0.02	0.886
All species (Total)	732	(1,731)	1.66	0.197
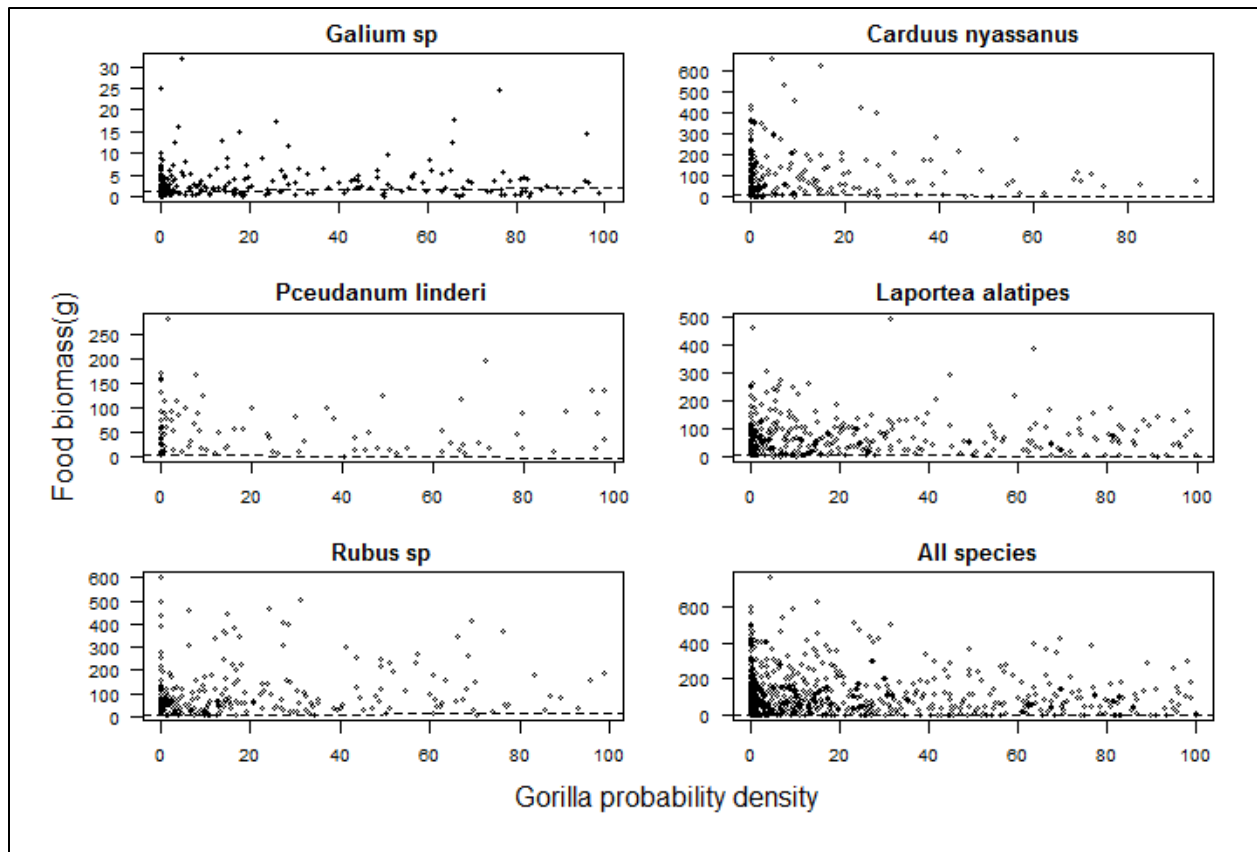
Figure 6. Scatter plots showing the relationship between key food plant biomass (in grams) and gorilla density probability (%).

In terms of the short-term effect of changes in gorilla density (1-month gorilla density probability before biomass assessment) and long-term effect of changes in gorilla density (5-years gorilla density probability before biomass assessment) on plant biomass, we also found no correlation between the gorilla density probability and the biomass of each single key food species and the total biomass (Appendix 2). We also compared the mean biomass of key species in grid cells where we have high density probability of gorilla (over than 70%) and the mean biomass of the grid where we have lower density probability of gorilla (less than 1%) and using t-test we found that the means were not statistically significant neither for each key species nor for total biomass of these key food species , P>0.05 (Figure 7).
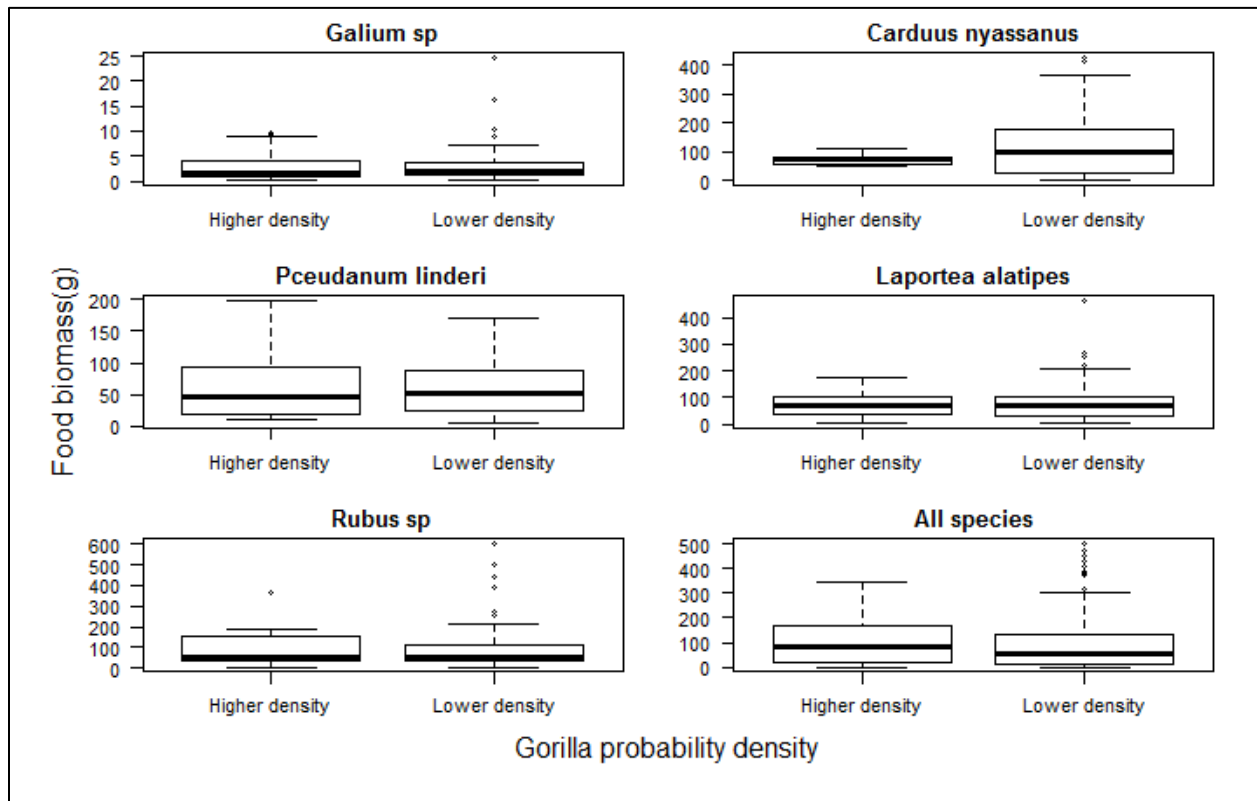
Figure 7. Box-plots plots showing comparisons of plant biomass in areas of higher and lower gorilla density.

CHAPTER 5. DISCUSSION

The goal of this study was to investigate if an increasing number of gorillas has impacted the availability of their key food species. The findings suggest that the biomass of the five most consumed gorilla food species in the Karisoke research area cannot be explained by gorilla habitat use (Fig. 6). Areas characterized by a higher probability of being visited by gorillas did not show lower food availability as expected, and thus there were no signs of overharvesting by the end of this study period in 2010. These results also suggest that the habitat in the study area had a high gorilla food resource availability and therefore had not yet reached its carrying capacity (McNeilage, 1995) if food is limiting factor. This is in line with other studies that have suggested that the Virunga massif can sustain a high number of herbivores due to its high biomass of herbaceous vegetation (Plumptre, 1991; McNeilage, 1995; Robbins *et al.*, 2007). Mountain gorilla groups may therefore not experience food competition over high-quality areas, as the food species are abundant in those areas (Watts, 1998; Robbins *et al.*, 2007), and as a result, mountain gorillas would possibly not exhaust food recourses in more heavily used areas (Fossey & Harcourt, 1977). In addition, mountain gorillas typically only partially defoliate a plant (Fossey & Harcourt, 1977; Watts, 1987), which can allow a faster vegetative regeneration. Partial removal of leaves on a plant accelerate the photosynthetic capacity of the remaining leaves and revitalize the old remaining leaves because partial defoliation reduces the competition among plant organs and increase efficiency in nutrients usage. In addition, newly emerging leaves have higher photosynthetic activities than remaining leaves that have not undergone defoliation as the former assimilate more photosynthetic active radiation which increases the plant photosynthetic activity and consequently increase the plant growth (Aldefer and Eagles, 1976; Khan and Lone, 2005; Guo *et al.*, 2015).

Moreover, the lack of effect of gorilla density on food plant biomass may be related to the potential positive effect of damage by gorillas, where trampling of the plants can stimulate the primary productivity of food species (Watts, 1987), which can outweigh the negative effect caused by feeding.

A population density of gorillas is positively correlated with food availability, thus gorilla density is highest where particular herbaceous, staple foods are found in high abundance (Bermejo, 1999; Rogers et al, 2004). In addition, previous studies showed that mountain gorillas

forage in areas where food resources are abundant and of high quality (Vedder, 1984; Watts, 1991; Watts, 1998). Similarly, a recent study on mountain gorillas in Bwindi showed that high abundance of herbaceous gorilla food is linked to smaller gorilla home range sizes because gorilla can stay longer in the area with high food availability (Seiler *et al.*, 2018). Therefore, findings from this study may also suggest that areas preferred by the study groups had such high food availability that despite frequent gorilla visitation rates food availability remained relatively high compared to other areas, and thus masks effects investigated in this study.

To test the hypothesis of whether ranging pattern of mountain gorillas in VNP follows the resources availability and abundance, future studies should evaluate how ecological and social factors can influence spacing behavior in mountain gorillas in Virunga Massif, in this way, future analysis should focus on how herbaceous food quantity and quality influence mountain gorilla home range sizes. Therefore, in addition to current study, future studies should analyze the dataset using gorilla ranging parameters as response variables and for predictable variables we suggest to use frequency of intergroup interactions, group size, gorilla density (as social factors) and ecological factor being the current food availability (in current study considered as response variable). For gorilla ranging parameters, variables of interest would be gorilla monthly home range size, revisiting frequencies per grid cell and intensity of habitat use by the gorilla in each cell. All these parameters would be determined by group and grid cell and therefore need to be analyzed using generalized linear mixed models by controlling the group and month and year.

Besides gorilla revisitation rates, other environmental factors may have influenced gorilla food plant biomass in study plots; e.g. factors that affect plant abundance and regeneration, such as canopy cover, slope, altitude, soil pH, water retention, temperature, presence of other herbivores (Olff and Ritchie, 1998; Vickers and Palmer, 2000; Auslander, Nevo and Inbar, 2003; Cierjacks *et al.*, 2008; Caldeira *et al.*, 2014; Nishar *et al.*, 2017).

Moreover, ranging patterns of gorillas are not only driven by food availability; social factors, such as the proximity to neighboring groups (Fossey & Harcourt, 1977; Watts, 1991), and anthropogenic disturbances play an important role (Watts, 1991; Gray *et al.*, 2013; Caillaud *et al.*, 2014). Therefore, future studies should integrate the social aspects such as groups encounters frequency, and human disturbances (snares) distribution in the analysis for a better understanding of gorilla space use patterns.

Limitations of data used in the study might be another source of explanation of our findings and should be addressed in future studies. For example, two GPS data, from night nests and noon, used for the estimation the gorilla visitation probability may not be enough representation of gorilla habitat use. Thus, future studies should include more frequent locations of daily group movement. Also, other gorilla groups that are not monitored by KRC use the study area occasionally and thus may have affected our estimation in the gorilla density, tough such visits by other groups are rare, however, follow-up studies should ideally incorporate ranging data from groups neighboring the KRC research population.

CHAPTER 6. CONCLUSIONS AND RECOMMENDATIONS

This study investigated the effect of varying mountain gorilla densities on the biomass of the five key food plant species. Results indicated that gorilla densities did neither affect the total biomass of key food plant species nor the biomass of each key food plant species. Results demonstrate the complex nature of plant-herbivore relationships and the need to consider other potential factors that affect herbivores' ranging patterns and plant biomass, distribution, and regeneration in future investigations, such as social interactions between gorilla groups, habitat canopy cover, slope, altitude, soil pH, water retention, temperature, and ranging patterns of other herbivores that share gorilla diet. I recommend the extension of this study to the whole VNP using marked plots to regularly monitor effects of gorilla visits, human influences, climate, a wide range of habitat conditions, and other herbivores on gorilla food plant biomass across the park. The expansion is necessary because key food plant species of groups in the Karisoke area may not be key food species in other areas of the forest that are dominated by different habitat types such as the mixed forest. In addition, the fact that population growth was not homogeneous throughout the park, thus it is important to include different forest areas for better understanding the relationship between gorilla density and plant biomass.

Future monitoring of gorilla food plant biomass should also address limitations in this study to further improve the quality of outcomes. Firstly, our results showed that the gorilla food plants distribution is clumped (i.e. not following a regular pattern) then biomass resulting from only one plot may not be representative of a 250m^2 and 100m^2 forest quadrant. We, therefore, propose to establish at least five plots in each quadrant; one at the center of the quadrant and one in each corner of the quadrant so that we can capture the variation on topography, aspect, apparent floristic differences and other physical features of the quadrant. Secondly, the fact that some groups that are not monitored by KRC staffs could have used the same area, though not frequently but it could have affected the at some extent the gorilla density calculations and we suggest the incorporation of data of all groups that overlap with the Karisoke research population, for more accurate gorilla density calculations, mainly in the area where we suspect a

home range overlaps. Future studies, also needs to record the cause of the plants damage such as trampling, partial consumption or complete consumption, so that we can understand how different types of plant damage by herbivores are affecting the growth of the plant. We recommend exploring the feasibility of available sophisticated new technology for collecting more regular accurate data, for example, the usage of drones for faster and more frequent plant biomass assessment and the usage of cyber-tracker software for collecting gorilla ranging data in very frequent time intervals while following gorilla trails and groups. As the population of gorilla continues to increase steadily, potential density effect may become severe and more obvious in coming decades, this effect alongside with climate change can change the plant-gorilla dynamics and requires continuous monitoring for better management of gorilla and their habitat.

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APPENDICES

Appendix 1. Phytometric regression equations relating plant height in centimeters to dry mass in grams

The number of samples (n), regression coefficient (r) and the significance of the fit are given below each equation (Plant height was measured from the meristem at the apex of the plant to the ground. Stem diameter was measured at ground level. Leaf length was from the leaf tip to the base of the petiole where it met the stem)

Species:

Crassocephalum ducis-aprutii:

Total mass: mass = 6.63×10^{-3}*(height)$^{1.661}$

(n=44, r=0.97, P<0.001)

Leaf mass: mass = (0.035*height) -0.179

(n=44, r=0.89. P<0.001)

Solenostemon sylvaticum:

Total mass: mass = 0.0145*(height)$^{1.282}$

(n=44, r=0.97, P<0.001)

Leaf mass: mass = (0.017*height) -0.033

(n=45, r=0.88, P< 0.001)

Uritica massaica:

Total mass: mass = 7.11×10^{-3}*(height)$^{1.589}$

(n=53, r=0.98, P< 0.001)

Leaf mass: mass = (0.048*height) -0.471

(n=52, r=0.87, P< 0.001)

Stachys aculeolata:

Total mass: mass = 7.03×10^{-3}*(height)$^{1.216}$

(n=40, r=0.97, P<0.001)

Leaf mass: mass = (0.0068*height)+0.016

(n=40, r=0.94, P<0.001)

Galium spp.:

Total mass: mass = 1.06×10^{-3}*(height)$^{1.483}$

(n=55, r.0.96, P< 0.001)

Carex simensis:

Leaf mass: mass = 6.26×10^{-4}*(leaf length} $^{1.396}$

(n=89, r=0.99, P<0.001)

Carex bequaertii:

Leaf mass: mass = 6.9×10^{4}*(leaf length)$^{1.591}$

(n=38, r=0.95, P< 0.001)

Peucedanurn kerstenii:

Leaf mass: mass = 1.57×10^{-3}*(leaf length)$^{1.710}$

(n=31, r=0.98, P<0.001)

Echinops hoehlenii:

Leaf mass: mass = 4.7×10^{4}*(leaf length)$^{2.262}$

(n=19, r=0.95, P< 0.001)

Helichrysum globosum:

Leaf mass: mass = (0.0148*height) -0.038

(n=33, r=0.82, P<0.001)

Rubus spp:

Leaf mass: mass = (0.2114*stem length) -4.852

(n=26, r=0.94, P<0.001)

Hypericum revolutum:

Leaf mass: mass = (0.0610*stem length) -0.707

(n=40, r=0.79, P<0.001)

Laportea alatipes:

Total mass: 0-76 cm: mass = $0.04128*(height)^{1.149}$

(n=23, r=0.95, P<0.001)

77 cm+ : mass = (0.3396*height) -19.93

(n= 22, r=0.89, P<0.001)

Leaf mass: mass = $0.0571*(height)^{0.845}$

(n=43, r=0.90, P<0.001)

Carduus nyassanus:

Stem mass : mass = $8.86 \times 10^{-3}*(height)^{1.581}$

(n=29, r=0.98, P<0.001)

Leaf mass: 0-36cm mass = $6.06 \times 10^{-3} *(leaf\ length)^{1.618}$

(n=45, r=0.98, P<0.001)

77 cm+ : mass = (0.1021*leaf length) -2.00

(n= 27, r=0.94, P<0.001)

Impatiens spp.:

Total mass: 0-51cm mass = $6.16 \times 10^{-3}*(height)^{1.388}$

(n=50, r=0.96, P<0.001)

52 cm+ : mass = (0.051*height) -1.163

(n= 17, r=0.86, P<0.001)

Leaf mass: mass = (0.009 *height) -0.032

(n=48, r=0.94, P<0.001)

Peucedanum linderi:

Stem mass : 0-234 mass = $0.0606*(height*stem\ diameter)^{1.107}$

(n=29, r=0.95, P<0.001)

235+   mass = (0.147*height*stem diameter) -10.132

(n=13, r=0.95, P<0.001)

Leaf mass: 0-43cm mass = $1.66 \times 10^{-3} *(leaf\ length)^{1.841}$

(n=41, r=0.93, P<0.001)

44 cm+ : mass = (0.121*leaf length) -3.680

(n= 22, r=0.87, P<0.001)

Plectranthus sylvestris:

Total mass : 0-87cm mass = $2.45 \times 10^{-3} *(height)^{1.726}$

(n=31, r=0.98, P<0.001)

88cm+   mass = (0.205*height) -12.478

(n=20, r=0.97, P<0.001)

Leaf mass: 0-89cm mass = $1.66 \times 10^{-3} *(height)^{1.402}$

(n=49, r=0.97, P<0.001)

90cm+ : mass = (0.121*height) -1.420

(n= 21, r=0.86, P<0.001)

In this study, *Rubus spp* and *Galium spp* biomass were calculated differently (not using the phytometric equation). For *Rubus spp*., 50 leaves of *Rubus spp* were collected (including petioles) and obtained the average weight, which were subsequently used for biomass estimates. For *Galium* spp. (which grows in tangles on herbaceous stems and on woody plants): all the vines (leaves and stems) in the plots were harvested, dried at KRC laboratory facilities, and weighed on a high precision balance (Grueter *et al.*, 2013).

Appendix 2. Statistical results of short term and long term effects of gorilla density on key gorilla food plant species

Statistical output of model investigating the relationship between key food plant biomass and short-term (one month) gorilla density probability

Species name	Number of plots	Degree of freedom	F-statistic	P-Value
Galium sp	246	(1, 245)	0.15	0.692
Carduus nyassanus	216	(1, 215)	3.21	0.074
Pceudanum linderi	95	(1,94)	1.58	0.211
Laportea alatipes	345	(1,344)	0.66	0.416
Rubus sp	262	(1, 261)	0.04	0.831
All species (Total)	732	(1,731)	2.16	0.142

Statistical output of model investigating the relationship between key food plant biomass and long-term (five years) gorilla density probability

Species name	Number of plots	Degree of freedom	F-statistic	P-Value
Galium sp	246	(1, 245)	2.43	0.120
Carduus nyassanus	216	(1, 215)	0.01	0.894
Pceudanum linderi	95	(1,94)	3.79	0.054
Laportea alatipes	345	(1,344)	0.32	0.568
Rubus sp	262	(1, 261)	0.42	0.567
All species (Total)	732	(1,731)	1.36	0.242