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RESEARCH ARTICLE

Long-Term Temporal and Spatial Dynamics of Food Availability for Endangered Mountain Gorillas in Volcanoes National Park, Rwanda

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Monitoring temporal and spatial changes in the resource availability of endangered species contributes to their conservation. The number of critically endangered mountain gorillas (*Gorilla beringei beringei*) in the Virunga Volcano population has doubled over the past three decades, but no studies have examined how food availability has changed during that period. First, we assessed if the plant species consumed by the gorillas have changed in abundance and distribution during the past two decades. In 2009–2010, we replicated a study conducted in 1988–1989 by measuring the frequency, density, and biomass of plant species consumed by the gorillas in 496 plots (ca. 6 km^2) in the Karisoke study area in Volcanoes National Park, Rwanda. We expected to observe a decreased presence of major gorilla food plants as a likely result of density-dependent overharvesting by gorillas. Among the five most frequently consumed species (composing approximately 70% of the gorilla's diet, excluding bamboo), two have decreased in availability and abundance, while three have increased. Some species have undergone shifts in their altitudinal distribution, possibly due to regional climatic changes. Second, we made baseline measurements of food availability in a larger area currently utilized by the gorillas. In the extended sampling ($n = 473$ plots) area (ca. 25 km^2), of the five most frequently consumed species, two were not significantly different in frequency from the re-sampled area, while two occurred significantly less frequently, and one occurred significantly more frequently. We discuss the potential impact of gorilla-induced herbivory on changes of vegetation abundance. The changes in the species most commonly consumed by the gorillas could affect their nutrient intake and stresses the importance of monitoring the interrelation among plant population dynamics, species density, and resource use. Am. J. Primatol. 75:267–280, 2013. © 2012 Wiley Periodicals, Inc.

Key words: feeding ecology; *Gorilla beringei*; herbaceous plants; Rwanda; vegetation dynamics

INTRODUCTION

Understanding the ecological and social determinants of animal abundance is of paramount importance when it comes to the design of conservation management plans for endangered species [Morrison et al., 1998]. The density of consumers will determine the quantity of food resources depleted from the environment, and the consumer population dynamics are determined by the density of plants [Altmann et al., 1985; Crawley, 1983]. Plant population dynamics are influenced by various processes including inter- and intraspecific competition, herbivory, and seed limitation [Crawley, 1990]. Herbivore damage can be detrimental by removing available food, but can also have positive effects by increasing plant productivity and standing crop biomass [Crawley, 1983, 1987; McNaughton, 1983]. While several studies have focused on investigating how anthropogenic actions, most notably logging, affect animal (especially primate) populations [Chapman et al., 2000; Guo et al., 2008; Plumptre and Reynolds, 1994; Rao and van Schaik, 1997], few studies have explicitly tried to link long-term vegetation changes (food availability) to changes in animal population density and vice

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versa [but see Augustine and deCalesta, 2003; Chapman et al., 2010; Gill et al., 1996; Plumptre, 1996].

Historical/longitudinal changes in habitat availability/vegetation cover and suitability of endangered animal species and populations have been assessed in some cases via remotely sensed imagery [Homewood et al., 2001; Pringle et al., 2009]. While such applications can be reliable for detecting changes in distributional properties of land cover types and structure and cover of woody vegetation [Ringrose et al., 2002; Sharp & Bowman, 2004], establishing changes in abundance (density and biomass) of the herbaceous layer necessitates ground surveys on a finer scale. Here we present a detailed analysis of how the resource base of the critically endangered mountain gorilla (*Gorilla beringei beringei*) in Volcanoes National Park (Rwanda) varies spatially and has changed over a 20-year period.

Only about 880 mountain gorillas remain in two small, isolated populations: Bwindi Impenetrable National Park, Uganda (330 km^2) and the Virunga Massif (450 km^2) of Rwanda, Uganda, and the Democratic Republic of Congo. These are island populations that are surrounded by extremely densely populated areas. The Virunga gorilla population has increased from 250 gorillas in the mid-1980s to 480 in 2010, most likely due to intensive conservation activities including daily protection unit, patrolling for illegal activities, tourism, in situ veterinary care, and educational programs [Gray et al., in press; Robbins et al., 2011]. Despite the high growth rate of the population, threats continue to include poaching, political instability, diseases, and habitat disturbance. The positive growth rate and the inability to expand into additional habitat may eventually push the gorillas to their carrying capacity, that is, "the natural limit of a population set by resources in a particular environment" [Caughley, 1976].

Differences in habitat structure and/or in the intensity of anthropogenic disturbance may be responsible for the uneven distribution of gorillas throughout the Virunga landscape [Gray et al., 2010, in press; Harcourt et al., 1981; Robbins et al., 2011; Weber & Vedder, 1983]. Plant species composition and the biomass and density of foods consumed by gorillas are heterogeneous across different vegetation zones [McNeilage, 1995; Plumptre, 1991; Vedder, 1984; Watts, 1984]. The diet of the Virunga gorillas consists primarily of herbaceous leaves and stems that are generally abundant and evenly distributed within the gorillas' preferred habitat types [McNeilage, 2001; Watts, 1984]. Variation in the spatial distribution, abundance, and nutritional quality of food plants has an influence on the frequency and duration of visits to particular locations by gorilla groups [McNeilage, 1995; Vedder, 1984; Watts, 1998a]. The area where habituated gorillas of the Dian Fossey Gorilla Fund's Karisoke Research Center (KRC) have been studied since 1967 (southeastern central region; Fig. 1) has the highest density of gorillas of the Virungas [Gray et al., in press; Harcourt et al., 1981; Robbins et al., 2011; Weber & Vedder, 1983].

The Karisoke study area is characterized by the highest gorilla food biomass in the Virungas [McNeilage, 1995; Robbins et al., 2011]. The diet of the gorillas in this area is composed of 54 plant species [McNeilage 2001; Watts, 1984; Grueter et al., unpubl. data], with six species making up 87% of the diet (*Galium* spp., thistles [*Carduus nyassanus*], wild celery [*Peucedanum linderi*], bamboo [*Yushania alpina*], blackberries [*Rubus* spp.], and nettles [*Laportea alatipes*] [Table I]). Food availability and growth rate of vegetation does not vary seasonally, with the exception of bamboo shoots [Fossey & Harcourt, 1977; Watts, 1984]. Typically, the gorillas ingest only the stems and leaves, so this partial defoliation does not necessarily cause systematic mortality to most food plants. However, biomass is reduced through consumption and the competitiveness of grazed plants may be reduced [Crawley, 1988]. Moreover, trampling of tall herbs by gorillas has been found to result in higher primary productivity and stem density [Watts, 1987], and gorillas appear to time revisits to particular areas so as to allow sufficient time for herbs to grow back [Watts, 1998b]. Nonetheless, a modeling exercise predicted that if the gorilla population increased to around 600 individuals, the single most important food plant in their diet (*Galium* spp.), would become extinct in less than a 1-year period in the Karisoke area, resulting in a decline of the gorilla population to 0.8 times the original density observed in 1989 [Plumptre, 1991, 1996].

Given the high growth rate of gorillas in this area (∼3–4% annual growth rate; [Robbins & Robbins, 2004; Robbins et al., 2011]), the large increase in absolute number of gorillas using the area, and their heavy reliance on only a few plant species, it is important to monitor temporal and spatial dynamics of their food resources. Furthermore, upward shifts in the altitudinal distribution of plants related to global warming have been documented elsewhere [Kelly & Goulden, 2008; Lenoir et al., 2008; Walther et al., 2005] and tropical montane cloud forests are particularly vulnerable to the effects of climatic change [Foster, 2001; Still et al., 1999].

The main goal of this study was to replicate in 2009–2010 a study conducted in 1988–1989 [Plumptre, 1991] that measured the biomass of plant species consumed by the gorillas in 496 plots (5.8 km^2) in the Karisoke study area. We predicted that we would observe a decreased presence of major gorilla food plants as a likely result of density-dependent overharvesting by gorillas. Second, because the area covered in the first part of this study is small, we conducted baseline measures of food availability in a larger area (25.1 km^2) that is

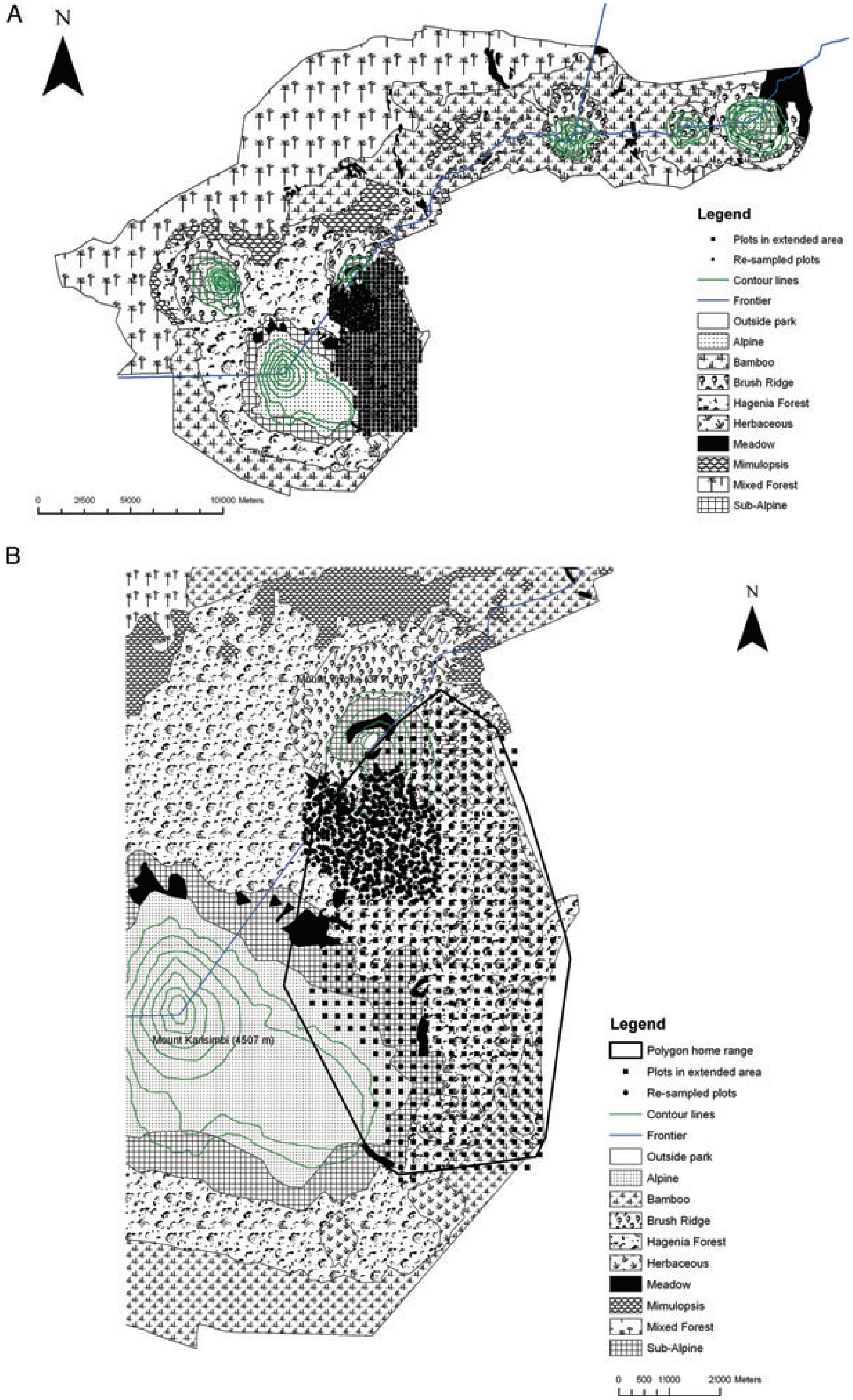

Fig. 1. The locations of the vegetation plots superimposed on a land cover map of the Virunga Volcanoes. The filled circles denote the re-sampled plots and the filled squares the extended area. (A) View of the whole Virunga Conservation Area, (B) Karisoke study area, with the polygon showing the home range of the KRC study groups. Vegetation distribution layer courtesy of Maryke Gray (International Gorilla Conservation Programme).

currently occupied by roughly 25% of the gorilla population (125 gorillas in nine groups). Third, we report changes in altitudinal distribution of food plants.

METHODS

Data Collection

The study was conducted in Volcanoes National Park and adjacent border areas of Virunga National Park in DRC (1°50′S, 29°30′E), a montane cloud forest that ranges in altitude from 2,300 to 4,500 m and supports a patchwork of distinct vegetation communities. The vegetation varies markedly along an ascending altitudinal gradient. Eight habitat types were identified. The classification followed Plumptre [1991] and was modified after Fossey and Harcourt [1977], McNeilage [2001], and Watts [1983]: (1) mixed forest and Mimulopsis: mixed species montane forest with understorey of dense *Mimulopsis* spp. at ca. 2,500–2,700 m; (2) bamboo (*Y. alpina*) forest at 2,500–2,800 m; (3) Hagenia-Hypericum woodland (found in the "saddle" between the volcanoes) at 2,800–3,300 m; (4) meadows at 3,100–3,400 m; (5) Hypericum woodland on volcano slopes (brush ridge) at 3,000–3,300 m; (6) herbaceous vegetation (dense tall herbs with no tree cover) at 2,800–3,300 m; (7) giant lobelia (*Lobelia stuhlmannii*) stands and thickets of *Rubus* spp. at ca. 3,300–3,600 m on the Visoke volcano (subalpine zone); and (8) Alpine community (*Dendrosenecio erici-rosenii* at the summit of Mt. Visoke, interspersed with small glades containing *Alchemilla johnstonii* at 3,600–3,700 m). In the Karisoke research area, the focus of this study, gorilla groups range from the park boundary (ca. 2,500 m) up to 3,700 m. Annual rainfall in the Virungas is ca. 2,000 mm [Plumptre 1991], with a distinct "long" dry season June–August, a less distinct "short" dry season December–February, a "long" heavy rainy season March–May, and a less heavy "short" rainy season September–November.

First, we established a total of 496 sampling plots within the same area (ca. 6 km^2) as the study conducted by Plumptre in 1988–1989 on the slopes of Mt. Visoke and in the saddle area stretching toward Mt Karisimbi (Fig. 1A, B). In the following, we refer to this area as the "re-sampled area." We relocated the sites of the earlier plots based on estimated Universal Transverse Mercator (UTM) coordinates (but not the exact plots themselves, as they were not permanent plots and GPS data did not exist from the late 1980s). The original design for vegetation sampling involved a stratified random sampling technique and the placement of one plot per grid cell of roughly 100 by 100 m [for details see Plumptre, 1991]. To allow for direct comparisons with the earlier study, we chose the same number of plots and the same sampling design (see below). No plots fell into the bamboo zone for this part of the study as all plots were above 3,000 m. Second, 473 additional plots were sampled in an "extended area" (ca. 25 km^2) that encompassed the home range of all gorilla groups monitored by the KRC in 2009–2010 (Fig. 1B). These additional data allowed us to establish whether food availability/abundance differs between the re-sampled and extended area.

Vegetation was sampled in circular plots, in which we counted the number of stems of 17 species most commonly consumed by gorillas (identified from herbarium material at KRC and Troupin [1978]). This species list was generated from previous studies of gorilla diet in the area [McNeilage, 2001; Vedder, 1984; Watts, 1984; KRC long-term records]. Additionally, we sampled two plants that are not consumed by the gorillas but are among the most characteristic and dominant plants in the park (*Hypericum revolutum* and *Lobelia giberroa*), the latter being (Table I) an important plant for nest building by the gorillas [Fossey, 1983]. We also included *Hagenia abyssinica* and *Crassocephalum ducis-aprutii*, which are very rarely consumed by the gorillas (0.1% of diet; KRC, unpubl. data) because *H. abyssinica* is the main canopy tree in Volcanoes National Park and *C. ducis-aprutii* is the most abundant herb. Different plot sizes were used for different plant types: 1 m^2 for herbs and vines, 5 m^2 for shrubs (e.g. *Lobelia* spp., *Rubus* spp.), 10 m^2 for trees (e.g. *H. abyssinica*, *D. erici-rosenii*).

The length of each stem in the plots was measured. For herbs, we measured from ground level, that is, where enters ground or where branches from horizontal stem, to the meristem at the apex/growth tip. For *Rubus* spp. (mostly *Rubus runssorensis*, but also some *R. kirungensis*), we measured also the length of compound leaves, inside the plot up to a height of 2 m. To obtain dry biomass of each herbaceous item in each plot, we used dimension analysis, which is based on the assumption that various plant characteristics are correlated and that one characteristic can be predicted from another that is more easily measured [Higgins et al., 1996; Whittaker, 1965]. For stems and leaves of all tall herbs, stem lengths were transformed to total dry plant biomass and leaf mass by solving phytometric regression equations [see Plumptre, 1991 for details]. For *Peucedanum* spp., *Carduus* spp., and *Echinops hoehnelii* (which grow as rosettes initially with no stem), we also measured length of all leaves and then performed regressions of both leaf length to leaf mass and stem length to stem mass. If a plant branched significantly, length of each branch was measured and regressions were run separately for each stem. For *Rubus* spp., we collected 50 leaves (including petioles) and obtained the average weight, which we subsequently used for biomass estimates. For *Galium* spp. (which grows in tangles on herbaceous stems and on woody plants) and other vine

TABLE I. Plant Density, Frequency, and Biomass for the Re-Sampled Area in 1989 and 2010 as well as for the Extended Area in 2010

Species	Family	Life form	Dietary importance (%)	Frequency (% plots)			Stem density			Biomass		
				1989	2010	Extension	1989	2010	Extension	1989	2010	Extension
Galium spp.	Rubiaceae	Vine	27.0	42.9	30.2	29.2	NA	NA	NA	1.93	0.92	1.14
Carduus nyassanus	Asteraceae	Herb	20.1	34.1	38.3	8.0	1.24	1.50	0.25	18.52	45.33	8.77
Peucedanum linderi	Apiaceae	Herb	18.7	8.5	10.5	9.5	0.24	0.32	0.24	5.80	6.60	4.79
Yushania alpina	Poaceae	Bamboo (shrub)	14.8	0	0	7.0	0	0	0.44	NA	NA	NA
Laportea alatipes	Urticaceae	Herb	2.9	52.4	45.4	30.2	8.27	3.18	1.57	47.39	36.42	20.74
Rubus spp.	Rosaceae	Shrub	3.6	1.2	26.0	35.5	0.01	0.15	0.24	0.07	4.92	7.25
Vernonia adolfi-frederici	Asteraceae	Shrub	2.5	0	1.2	3.1	0	0.01	0.01	NA	NA	NA
Droguetia iners	Urticaceae	Vine	2.0	5.6	11.1	17.1	NA	NA	NA	0.09	0.52	0.99
Dendrosenecio erici-rosenii	Asteraceae	Tree	2.0	3.6	6.0	16.1	0.01	0.02	0.04	NA	NA	NA
Peucedanum kerstenii	Apiaceae	Herb	0.4	1.8	4.2	4.7	0.09	0.14	0.15	0.14	0.28	0.51
Echinops hoehnelii	Asteraceae	Herb	0.3	0	3.6	0.2	0	0.07	0.00	NA	NA	NA
Helichrysum formossissimum	Asteraceae	Herb	0.1	0	1.6	2.3	0	0.03	0.05	NA	NA	NA
Crassocephalum ducis-aprutii	Asteraceae	Herb	0.1	59.5	73.0	42.7	8.36	8.97	4.75	77.67	127.82	68.26
Urtica massaica	Urticaceae	Herb	0.1	4.4	6.5	3.0	0.40	0.35	0.17	NA	NA	NA
Rumex ruwenzoriense	Polygonaceae	Herb	0.1	0.2	5.4	5.0	0.002	0.33	0.21	NA	NA	NA
Hagenia abyssinica[a]	Rosaceae	Tree	0.1	2.0	4.8	3.8	0.004	0.01	0.01	NA	NA	NA
Lobelia stuhlmannii	Campanulaceae	Woody plant (shrub)	0.1	6.5	3.0	7.2	0.08	0.01	0.05	NA	NA	NA
Lobelia giberroa	Campanulaceae	Woody plant (shrub)	0	41.9	37.9	2.6	0.41	0.35	0.20	NA	NA	NA
Hypericum revolutum	Hypericaceae	Shrub/tree	0	15.9	12.1	11.2	NA	NA	NA	NA	NA	NA

Frequency is the percentage of plots containing a plant. Density is the number of stems per m^2. Biomass estimate is given in grams of dry mass per m^2. Dietary importance (in descending order) of plants sampled in this study, as estimated from the KRC records of all monitored gorilla groups ($n = 8$) in 2008/2009. Dietary importance refers to the time spent foraging on particular plants, calculated from instantaneous activity samples taken at 10-min intervals during focal follows.

NA, data not available.

[a] Including seedlings and saplings.

leaves and stems: all the vines (leaves and stems) in the plots were harvested, dried, and weighed. For shrubs and trees, we counted the number of plants and measured the circumference at breast height. Plants were weighed to the nearest 0.1 g at the research station. Samples were sun-dried until there was no further loss in weight.

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The research conducted adhered to the legal requirements of Rwanda and the American Society of Primatologists principles for the ethical treatment of primates.

Data Analysis

To assess changes in plant occurrence over time and space, we fitted a generalized linear mixed model (GLMM) [Baayen, 2008; Zuur et al., 2009] with binomial error structure (yes/no) and logit link function. Fixed effects were year, altitude, squared altitude, and the two-way interactions year-altitude and year-squared altitude. Altitude was squared because we assumed it to have a nonlinear effect in the sense of an optimum altitude for plants. Habitat type was not included as a predictor, since given the altitudinal stratification of vegetation types and the somewhat subjective allocation of a plot to a given vegetation zone, altitude was assumed to be the better predictor. We controlled for repeated measurements by including plot identity as a random factor in the model. The response variable was occurrence (i.e. presence/absence at sampling point). We modeled occurrence instead of density (i.e. the number of stems per m^2) due to the fact that the density and biomass was heavily zero-inflated [cf. Zuur et al., 2009]. We ran the model separately for each species. We included only the following plants: *Galium* spp., *P. linderi*, *C. nyassanus*, *L. alatipes* (important food plants), *C. ducis-aprutii*, *L. giberroa*, and *H. revolutum* (important plants in habitat). The other species could not be modeled since they occurred in only very few plots in either 1989 or 2010 or both (but changes in density and frequency as well as altitudinal distribution over time were examined descriptively).

The occurrence of plant species was likely to show spatial autocorrelation in the sense of plots being close to one another being more likely to show the same value than plots being more distant, even after accounting for the effects of the predictors considered. Such spatially autocorrelated data may lead to nonindependent residuals, violating a crucial assumption of the analysis and leading to erroneous estimates of the effects [Haining, 1990; Legendre, 1993; Valcu & Kempenaers, 2010]. To account for autocorrelation in the model, we first ran the model as described above and deriving the residuals from it. We then, separately for each plot, averaged the residuals of all other data points from the same study period, with the contribution of the residuals being weighted by their distance to the respective plot. The resulting values were then included as an additional "autocorrelation term" into the full model. The weight function had the shape of a Gaussian density function with a mean at distance equal to zero, and its standard deviation was estimated by maximizing the likelihood of the full model with the autocorrelation term included. In case the autocorrelation term appeared insignificant ($P > 0.05$), we removed it from the full model.

Significance testing was done by first comparing the full model with the null model (comprising only the autocorrelation term and the random effect) using a likelihood ratio test [Dobson, 2002], conducted as an overall test of the significance of all fixed effects as a whole. Only once this overall test revealed significance we considered the significance of the individual parameters. If the interaction between year and altitude-squared was significant, we concluded that year and altitude significantly affected the occurrence of the investigated plant species, and did not consider any of the other P-values (because none of them is informative in the context of this interaction). If this interaction was nonsignificant, we removed the interaction from the full model and next inspected the interaction year-altitude. In case of also this being nonsignificant we removed it from the model as well. The autocorrelation term included into all these potential models was generally the one revealed from the full model.

Prior to fitting the model, we subtracted the minimum altitude from all altitude values and then squareroot transformed the resulting variable. We then z-transformed altitude to a mean of zero and a standard deviation of one. The two study periods were coded as 0 (1988/1989) and 1 (2009/2010). All analyses were conducted in R [R Development Core Team, 2010]. GLMMs were conducted using the function "lmer" of the R package lme4 [Bates & Maechler, 2010], and likelihood ratio tests we ran using the R function "anova" with the argument "test" set to "Chisq." The autocorrelation term was calculated using a self-written procedure based on the R function "optimize."

Comparisons of plant frequencies between the re-sampled and extended area were done using a generalized linear model (GLM) with binomial error structure and logit link function. The model contained area (re-sampled vs. extended) as a binary main predictor and altitude as a control predictor. No interactions were included in this model. Models were run in R.

RESULTS

Spatio-Temporal Changes in Gorilla Food Plant Availability

Of the five most frequently consumed foods that make up >70% of the gorillas' diet (excluding bamboo), two (*Galium* spp., *L. alatipes*) showed a decrease and three (*Rubus* spp., *P. linderi*, *C. nyassanus*) showed an increase in frequency (i.e. the percentage of plots in which it occurs) from 1989 to 2010 (Table I). *Galium* spp. showed the largest decrease in frequency (30%) and also biomass (52%). *Laportea alatipes* decreased by 13% in frequency and 23% in biomass. *Carduus nyassanus* experienced a 12% increase in frequency, and its biomass was 2.5 times higher in 2010. *Peucedanum linderi* increased by 24% in frequency and 14% in biomass. *Rubus* spp. increased from being present in only 1% to 26% of the plots. Among the less important food plants and nonfood plants, *H. abyssinica* increased from being in 2% to nearly 5% of the plots. Both species of lobelias decreased in both density and frequency (*L. stuhlmannii*: 53% in frequency, 86% in density; *L. giberroa*: 10% in frequency, 13% in density). *Crassocephalum ducis-aprutii* was already very abundant in the 1980s (found in 59.5% of plots), and was even more abundant in 2010 (73%). Proportional changes in density and biomass of plants were correlated with changes in frequency (density vs. frequency, $r_s = 0.943$, $n = 6$, $P = 0.005$; biomass vs. frequency: $r_s = 0.786$, $n = 8$, $P = 0.021$).

Within a GLMM framework, we first performed an overall test of the significance of all fixed effects combined. These likelihood ratio tests were highly significant (all $\chi^2 > 16.3$, all df = 5, all $P < 0.006$), so we further explored the effects of individual predictors and interactions on the response, that is, the frequency of plant species. A significant interaction between two predictors makes an interpretation of the main effects impossible, and the associated P-values are meaningless. A significant interaction in our case implies that a change in one variable was dependent on the other, that is, year had an effect on plant occurrence, but this differed among altitudes. Significant multiplicative effects between year and altitude were found for the important food plant *C. nyassanus* (0.001), and significant multiplicative effects between year and altitude-squared were found for the important food plant *P. linderi* ($P = 0.032$), and the nonfood plant *L. giberroa* (0.012). Additive effects (both year and altitude significant) were found for the unimportant food plant *C. ducis-aprutii*. For the most important food plant *Galium* spp., only year had an effect on the frequency of the plant (a negative one, $P < 0.001$), and for the nonfood plant *H. revolutum* only altitude had an effect ($P = 0.004$) (Table II).

The five main food plants and four other plants experienced changes in altitudinal distribution (Fig. 2). The two species that experienced the most pronounced changes altitudinal density distribution were *H. abyssinica* and *C. nyassanus*. *Hagenia abyssinica* has become more common at higher altitudes while the opposite was true for *C. nyassanus*. *Lobelia giberroa* was associated mainly with woodlands at moderate elevations (up to 3,400 m), but appears to have expanded into higher altitudes. *Crassocephalum ducis-aprutii* was rare at altitudes above 3,400 m in the 1980s, but seems to be establishing itself in the afroalpine zone.

Comparison Between Re-Sampled and Extended Area

Galium spp., *P. linderi*, and *L. alatipes* did not occur at different frequencies in the re-sampled and extended area, *C. nyassanus* was present in significantly fewer plots in the extended area ($P < 0.001$), and *Rubus* spp. was present in significantly more plots in the extended area ($P < 0.001$) (Table III).

DISCUSSION

Possible Causes of Changes in Plant Availability

Our study found mixed support for the prediction that the increased density of gorillas has led to a decline in their resource base over the past two decades. Among the five most commonly consumed species, two (*Galium* spp., *L. alatipes*) decreased in availability and abundance whereas three (*C. nyassanus*, *Rubus* spp., *P. linderi*) increased. However, we cannot rule out the possibility that the food availability has fluctuated in the interim period. Additionally, factors other than food depletion by the gorillas may be responsible for changes in abundance and distribution of the plant species they consume. First, competition with sympatric herbivores (buffalo, duiker, and bushbuck) that could limit or reduce the availability of food consumed by the gorillas can be excluded a priori because there is little dietary overlap with these species [Plumptre, 1991, 1996]; only elephants could have an impact but they were rare in the study area during both sampling periods. Second, changes in the vegetation could be due to a recovery from the impact of cattle grazing that was common inside the park until the mid-1970s [Curry-Lindahl, 1969; Plumptre, 1993; Spinage, 1972]. Given the relatively fast turnover rate of herbs [Watts, 1987] we believe that any such recovery likely occurred by the time of the first vegetation sampling in the late 1980s.

Galium spp., the most frequently consumed food species, was present in 43% of the plots in the 1989 study, but only in 30% of the plots in the 2010 study, and it declined by more than 50% in biomass. *Galium*

TABLE II. Results of a GLMM with Plant Presence/Absence Being the Response Variable, and Year, Transformed Altitude, Altitude-Squared, and Autocorrelation Being the Predictors and Covariates

Response variable	Predictor variable	Estimate	Standard error	*z*	*P*
Important food plants					
Frequency	Intercept	0.377	0.125		
Laportea alatipes	Year	−0.403	0.156		
	Altitude	−1.090	0.157		
	Altitude (squared)	−0.519	0.102	−5.091	<0.001
	Ac.term	0.800	0.080	9.962	0.001
	Year * altitude	−0.386	0.202	−1.913	0.056
Frequency	Intercept	−0.455	0.107		
Carduus nyassanus	Year	0.174	0.137		
	Altitude	0.274	0.115		
	Altitude (squared)	−0.260	0.057	−4.559	<0.001
	Ac.term	0.307	0.068	4.484	<0.001
	Year * altitude	−0.546	0.163	−3.345	<0.001
Frequency	Intercept	−3.025	0.250		
Peucedanum linderi	Year	1.017	0.306		
	Altitude	−0.885	0.284		
	Altitude (squared)	0.074	0.173	0.426	0.670
	Ac.term	0.581	0.092	6.327	<0.001
	Year * altitude	0.768	0.358	2.145	0.032
	Year * altitude (squared)	−0.464	0.256	−1.817	0.069
Frequency	Intercept	−0.300	0.093	–	
Galium spp.	Year	−0.600	0.136	−4.425	<0.001
	Altitude	0.106	0.069	1.534	0.125
	Ac.term	0.275	0.068	4.044	<0.001
Other plants					
Frequency	Intercept	−0.037	0.121		
Lobelia giberroa	Year	−0.458	0.174		
	Altitude	−0.504	0.138		
	Altitude (squared)	−0.491	0.115		
	Ac.term	0.811	0.077	10.553	<0.001
	Year * altitude	0.005	0.180		
	Year * altitude (squared)	0.355	0.142	2.501	0.012
Frequency	Intercept	0.623	0.120		
Crassocephalum duci-aprutii	Year	0.858	0.161	5.341	<0.001
	Altitude	−0.345	0.084		
	Altitude (squared)	−0.235	0.054	−4.339	<0.001
	Ac.term	1.117	0.085	13.166	<0.001
Frequency	Intercept	−1.736	0.154		
Hypericum revolutum	Year	−0.341	0.202	−1.687	0.092
	Altitude	0.328	0.143		
	Altitude (squared)	−0.264	0.093	−2.852	0.004
	Ac.term	0.506	0.084	6.033	<0.001

Important food plants are the top four herbs in the diet of the gorillas.
Ac.term, autocorrelation term; *, interaction.
z- and *P*-values were not indicated when they have no meaningful interpretation (in case of the intercept and of terms being involved in an interaction or also occurring squared).

may have been even more frequent throughout the Karisoke study area in the late 1970s, as shown by its occurrence in 51% of 900 sampled plots in roughly the same area [Watts, 1984] (but results are not directly comparable since sampling area, effort, and methods were not identical). The reduction in the biomass of the gorillas' main food plant may well be a direct consequence of unsustainable herbivory or local density-dependent depletion by the gorillas.

A negative response of *Galium* spp. to herbivory has also been demonstrated in the Pacific Northwest of the United States [Riggs et al., 2000] and in a British grassland [del-Val & Crawley, 2004], but reactions to herbivory differ among species of *Galium* [e.g. Jutila, 1999], and also probably depend on life form and regenerative strategies. While trampling of herbaceous vegetation can stimulate productivity [Watts, 1987], *Galium* spp.—a vine—may benefit less from posttrampling growth spurts. Our findings provide empirical support for a model [Plumptre, 1991, 1996] that showed that *Galium* spp. would become extinct at some point under a hypothetical (but biologically reasonable) herbivory regime in the Virungas. *Galium* spp. was equally rare in both the

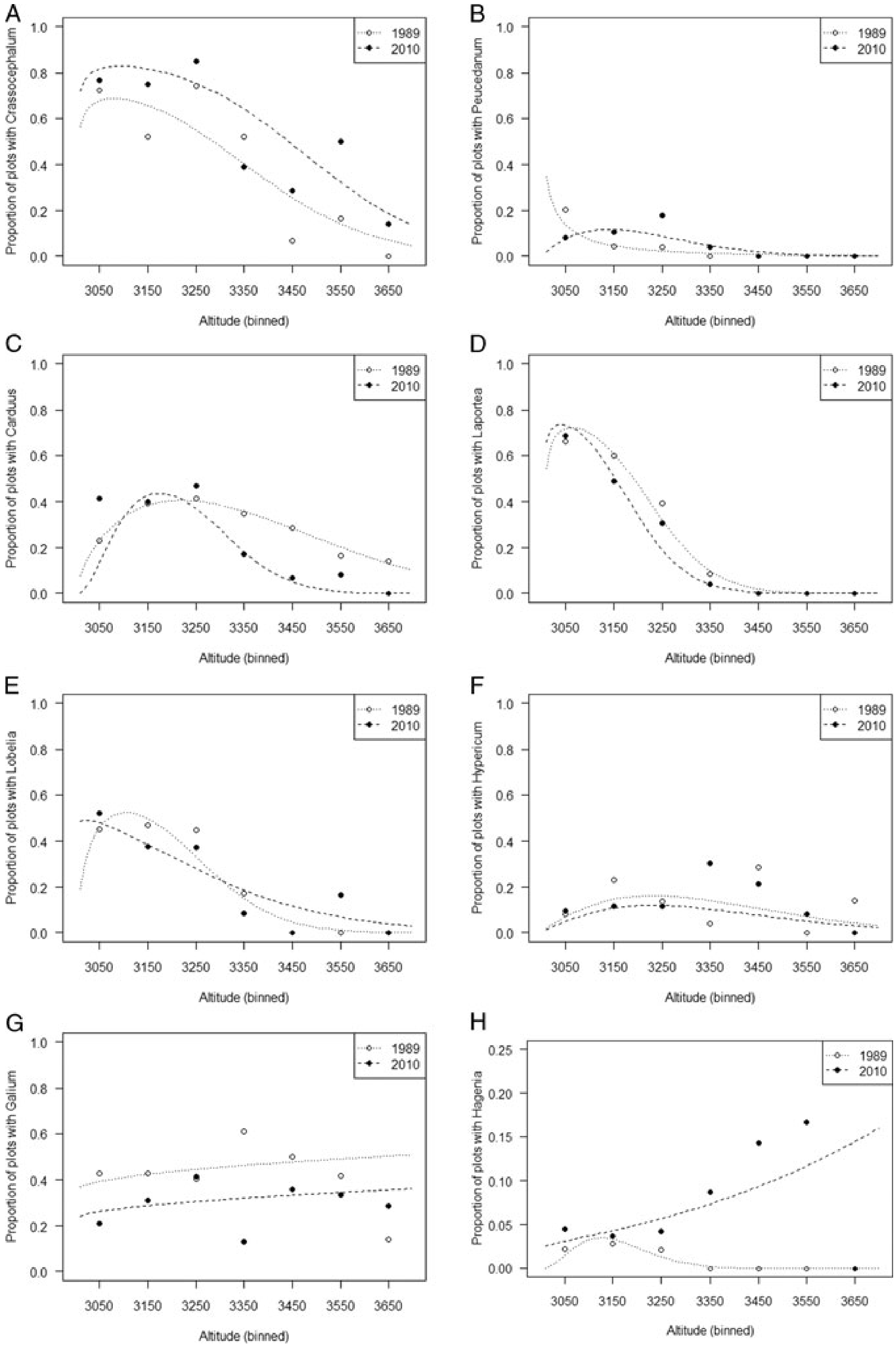

Fig. 2. Proportion of plots with plant species across altitudes in 1989 and 2010 in the Karisoke re-sampled area. Sampling effort deceased with increasing altitude: $n_{\text{plots}}(3{,}000\text{–}3{,}200\ \text{m}) = 347$, $n_{\text{plots}}(3{,}200\text{–}3{,}400\ \text{m}) = 117$, $n_{\text{plots}}(3{,}400\text{–}3{,}700\ \text{m}) = 33$.

TABLE III. Results of a GLM, Comparing the Availability of Food Plants Between the Re-Sampled Area and the Extended Area

Response variable	Predictor variable	Estimate	Standard error	*z*	*P*
Frequency	Intercept	−0.833	0.100		
Galium	Altitude	0.137	0.082	1.680	0.093
	Altitude (squared)	−0.085	0.053	−1.598	0.110
	Area	0.080	0.153	0.525	0.600
Frequency	Intercept	−0.219	0.104	−2.110	0.035
Carduus nyassanus	Altitude	0.103	0.159		
	Altitude (squared)	−0.887	0.179	−4.959	<0.001
	Area	−1.400	0.207	−6.753	<0.001
	Ac.term	−0.198	0.083	−2.383	0.017
Frequency	Intercept	−2.032	0.152		
Peucedanum linderi	Altitude	−0.532	0.202		
	Altitude (squared)	−0.676	0.191	−3.534	<0.001
	Area	0.314	0.238	1.321	0.187
Frequency	Intercept	−0.940	0.109		
Rubus spp.	Altitude	1.084	0.114		
	Altitude (squared)	−0.369	0.066	−5.601	<0.001
	Area	0.656	0.158	4.159	<0.001
	Ac.term	0.339	0.083	4.103	<0.001
Frequency	Intercept	−0.040	0.106		
Laportea alatipes	Altitude	−2.158	0.224		
	Altitude (squared)	−1.560	0.191	−8.190	<0.001
	Area	−0.286	0.180	−1.588	0.112
	Ac.term	0.348	0.078	4.457	<0.001

The frequency of plots with a particular plant species is the response variable, area (re-sampled vs. extended) is the main predictor, and altitude and altitude-squared and the autocorrelation term are control predictors.
Ac.term, autocorrelation term; *, interaction.
z- and *P*-values were not indicated when they have no meaningful interpretation (in case of the intercept and of terms occurring squared).

re-sampled area and the extended area. Unfortunately since we do not have earlier data for this area, it is not possible to determine if this is because similar ecological pressures have acted in the extended area or if it was lower in abundance there previously.

The second-most important food plant of the Virunga gorillas, *C. nyassanus*, was more abundant in the re-sampled area in 2009–2010 (found in 38% of the plots) than in 1989 (24%), but was much less common in the extended area (8% of plots). The lower frequency of *C. nyassanus* in the extended area was not an artifact of different availability of habitat types in the two areas, as the pattern held when we controlled for habitat/altitude. The difference in the availability of *C. nyassanus* might be related to differential intensity of use by the gorillas in the two areas, but this has yet to be demonstrated. *Carduus nyassanus* had a much slower growth rate than *P. linderi* and *L. alatipes* [Watts, 1987], which may explain why the difference in frequency between the two areas is so much more pronounced in *C. nyassanus* than in the other two herbs following harvesting by the gorillas.

Peucedanum linderi has shown a slight increase and *L. alatipes* a decrease over time, but the underlying reasons are not clear. Interestingly, *P. linderi* increased twice as much in density than in total biomass, which means that we see more branching of stems but smaller stems overall. This could be a response of the plant to increased harvesting since the gorillas do not eat the small stems and leaves. *Rubus* spp. showed the largest increase, being nearly 30 times more frequent than in the late 1980s, and the extended area contains an ever higher abundance. Species of the genus *Rubus* spp. have the capacity to spread quickly when introduced to new areas [Stratton, 1996]. As gorillas do not appear to digest the seeds of *Rubus* spp., they may act as important dispersal agents and contribute to the spread of plant.

The decrease in the presence of the nonfood *L. giberroa* may be related to the fact that they are easily damaged and killed, both by the machetes of field workers and by the gorillas when extracting the pith, using them as nesting material, and during social interactions. Afroalpine giant lobelias have slow growth rates [Young, 1994].

Consequences of Changes in Plant Availability

What do the observed changes in food abundance, especially the decline of *Galium* spp., suggest in terms of the gorillas' diet? It is difficult to establish if changes in food abundance have lead to some changes in the diet of the gorillas because of the lack of directly comparable data and lack of control for food availability. A rough comparison of the dietary composition of a mountain gorilla group ranging on the slopes of Visoke between the late 1970s [Vedder, 1984] and several groups using this area in 2008–2009 [KRC, unpubl. data] reveals some variation in diet among extant groups, but no obvious dietary changes consistent with changes in the resource base between the two time periods.

The question arises as to whether gorillas can show enough flexibility in their diet to compensate for changes in food availability [see also Lehmann et al., 2010]. Other studies on primates have shown that dietary plasticity is a crucial adaptation to a dynamic and altered habitat [Olupot, 1998; Riley, 2007; Wieczkowski & Kinnaird, 2008]. Primates are also known to meet their nutritional needs from a range of food species by varying their diets [Conklin-Brittain et al., 1998; Rothman et al., 2007; Ryan et al., in press; Twinomugisha et al., 2006].

Eastern gorillas exhibit a lot of flexibility in their diet because the availability of food varies so much across their habitat [Ganas et al., 2004; McNeilage, 2001; Nkurunungi et al., 2004; Robbins et al., 2006]. Gorillas have some scope for changing to a more fruit-based diet (as shown by several populations of western and eastern gorillas, e.g. Ganas et al., 2004; Head et al., 2011; Remis, 1997; Yamagiwa et al., 2005), and this could provide them with some buffering against the effects of climate change (rising temperatures and changing rainfall patterns). However, such a scenario is not applicable to the Virungas where fruits are notoriously scarce. However, the gorillas at Karisoke have incorporated new species of herbs and vines into their diet since the earlier studies in the 1970s (five species, now accounting for 4% of the diet: McNeilage, 2001; KRC [unpubl. data]), implying that the mountain gorillas living in the KRC area have some capacity for dietary adaptability. Gorillas are selective foragers, and most of their major food items are relatively high in crude protein and energy and low in fiber compared to rarely eaten plants [Plumptre, 1995; Rothman et al., 2007; Watts, 1983; Grueter et al., unpubl. data], so further study would be necessary to understand if other plants of similar nutritional composition are available to compensate for changes in food availability.

Conclusions, Implications for Conservation Management, and Areas for Future Research

Our study provides useful information pertaining to resource availability and thus viability of one of the rarest ape populations in the world. However, establishing a causal relation between gorilla population density and resource abundance is difficult due to other variables that might affect plant availability, especially global and regional warming. Studies on livestock grazing also found a substantial degree of inconsistency in the response of plant species to grazing [Vesk & Westoby, 2001]. Among five primate species at Kibale National Park, Uganda, there were also inconsistent patterns in changes of primate group density and food availability over a three-decade period [Chapman et al., 2010].

To best understand the dynamics among the gorilla population and their food availability, it would be useful to repeatedly measure the availability and abundance of these main food plants, preferably every 5–10 years. While herbaceous vegetation in the Virungas can withstand the damaged caused by trampling herbivore browsers [Plumptre, 1993] and gorillas appear to adjust their revisit intervals to allow food resources to recover from depletion due to feeding and trampling [Watts, 1998b], more research on regeneration time, the effects of trampling, and revisitation rates is needed, especially as the density of gorillas increases. An additional line of inquiry pertains to how chemical composition of food plants changes as a result of frequency of harvest and climate change.

Our study also provides preliminary evidence that some plant species have tended to shift their distribution centers along an altitudinal gradient, with some species having undergone downward movements and others upward movements. Tropical montane cloud forests are particularly vulnerable to the effects of climatic change [Foster, 2001; Still et al., 1999], and it is reasonable to assume that these shifts were caused by changes in climatic patterns. Although climatic parameters have not been consistently recorded in the Virungas, Picton Phillips and Seimon [2010] predicted an increase in temperature (1°C and 3.7°C by the year 2030 and 2090, respectively) within the Albertine Rift region, of which Volcanoes National Park is part. Similar observations have been recorded on other African mountains [e.g. Kilimanjaro: Altmann et al., 2002; Hemp, 2005]. Further climate monitoring is of great importance to understand vegetation dynamics. However, additional factors, such as soil, local topography, and groundwater level, may also influence plant species distributions on a landscape [Iverson & Prasad, 2002].

Previous researchers suggested that the mountain gorilla population had the capacity for expansion in both absolute numbers and distribution [McNeilage, 1995; Plumptre, 1991]. While estimating carrying capacity is beyond the scope of this analysis, it is clear that the productivity of vegetation has been high enough to allow the gorilla population to grow in recent decades [Robbins et al., 2011], but we do not know how much more the population can increase. However, caution should be taken when assuming that if a population is growing there are sufficient resources to sustain it. When a population is in a nonequilibrium state, the relation between food biomass changes and animal population changes may be blurred [Chapman et al., 2010]. Populations may also not exhibit the expected density-dependent response to depletion of food resources (e.g. elephant population in Addo National Park, South Africa [Gough & Kerley, 2006]). Similarly, many ungulates have shown an irruption-like pattern of population fluctuations, whereby the population (particularly after introduction to new range or release from harvesting/predation) increases rapidly in size until resources are depleted, the carrying capacity of the habitat is surpassed, the population plummets to a lower abundance, and then settles at a reduced carrying capacity [Caughley, 1976; McCullough, 1997]. A similar scenario could be envisaged for the Virunga gorillas, but the gorillas' dietary flexibility may buffer them to some degree to such depletion effects. Nevertheless, the reduction of some key food species highlights the importance of continuous monitoring of the vegetation, the gorillas' habitat use and possible changes in diet.

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REFERENCES

Altmann J, Alberts SC, Altmann SA, Roy SB. 2002. Dramatic change in local climate patterns in the Amboseli basin, Kenya. Afr J Ecol 40:248–251.

Altmann J, Hausfater G, Altmann SA. 1985. Demography of Amboseli baboons, 1963–1983. Am J Primatol 8:113–125.

Augustine DJ, deCalesta D. 2003. Defining deer overabundance and threats to forest communities: from individual plants to landscape structure. Ecoscience 10:472–486.

Baayen, RH. 2008. Analyzing linguistic data. Cambridge: Cambridge University Press.

Bates D, Maechler M. 2010. lme4: linear mixed-effects models using S4 classes. R package version 0000375-35. http://cran.rproject.org/web/packages/lme4. Accessed April 20, 2011.

Caughley G. 1976. Wildlife management and the dynamics of ungulate populations. In: Coaker TH, editor. Applied biology, volume 1. New York: Academic Press. p 183–246.

Chapman CA, Balcomb SR, Gillespie TR, Skorupa JP, Struhsaker TT. 2000. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. Cons Biol 14:207–217.

Chapman CA, Struhsaker TT, Skorupa JP, Snaith TV, Rothman JM. 2010. Understanding long-term primate community dynamics: implications for forest change. Ecol Appl 20:179–191.

Conklin-Brittain NL, Wrangham RW, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. Int J Primatol 19:971–998.

Crawley MJ. 1983. Herbivory: the dynamics of animal-plant interactions. Oxford: Blackwell Scientific.

Crawley MJ. 1987. Benevolent herbivores? Trends Ecol Evol 2:167–168.

Crawley MJ. 1988. Herbivores and plant population dynamics. In: Davy AJ, Hutchings MJ, Watkinson AR, editors. Plant population ecology. Oxford: Blackwell Scientific. p 367–392.

Crawley MJ. 1990. The population dynamics of plants. Phil Trans R Soc B 330:125–140.

Curry-Lindahl K. 1969. Disaster for gorilla. Oryx 10:7.

del-Val E, Crawley MJ. 2004. Importance of tolerance to herbivory for plant survival in a British grassland. J Veg Sci 15:357–364.

Dobson AJ. 2002. An introduction to generalized linear models. Boca Raton: Chapman & Hall/CRC.

Fossey D. 1983. Gorillas in the mist. Boston: Houghton Mifflin.

Fossey D, Harcourt AH. 1977. Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*). In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes. New York: Academic Press. p 415–447.

Foster P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. Earth Sci Rev 55:73–106.

Ganas J, Robbins MM, Nkurunungi JB, Kaplin BA, McNeilage A. 2004. Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. Int J Primatol 25:1043–1072.

Gill RMA, Johnson AL, Francis A, Hiscocks K, Peace AJ. 1996. Changes in roe deer (*Capreolus capreolus* L) population density in response to forest habitat succession. Forest Ecol Manag 88:31–41.

Gough KF, Kerley GIH. 2006. Demography and population dynamics in the elephants *Loxodonta africana* of Addo Elephant National Park, South Africa: is there evidence of density dependent regulation? Oryx 40:434–441.

Gray M, Fawcett K, Basabose A, Cranfield M, Vigilant L, Roy J, Uwingeli P, Mburanumwe I, Kagoda E, Robbins MM. in press. Genetic census reveals increased but uneven growth of a critically endangered mountain gorilla population. Biol Cons.

Gray M, McNeilage A, Fawcett K, Robbins MM, Ssebide B, Mbula D, Uwingeli P. 2010. Censusing the mountain gorillas in the Virunga Volcanoes: complete sweep method vs monitoring. Afr J Ecol 48:588–599.

Guo S, Ji W, Li B, Li M. 2008. Response of a group of Sichuan snub-nosed monkeys to commercial logging in the Qinling Mountains, China. Cons Biol 22:1055–1064.

Haining R. 1990. Spatial data analysis in the social and environmental sciences. Cambridge: Cambridge University Press.

Harcourt AH, Fossey D, Sabater-Pi J. 1981. Demography of *Gorilla gorilla*. J Zool 195:215–233.

Head JS, Boesch C, Makaga L, Robbins MM. 2011. Sympatric chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon: dietary composition, seasonality, and intersite comparisons. Int J Primatol 32:755–775.

Hemp A. 2005. Climate change driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. Glob Change Biol 11:1013–1023.

Higgins KF, Oldemeyer JL, Jenkins KJ, Clambey GK, Harlow RF. 1996. Vegetation sampling and measurement. In: Bookhout T, editor. Research and management techniques for wildlife and habitats. Bethesda, MD: The Wildlife Society. p 567–591.

Homewood K, Lambin EF, Coast E, Kariuki A, Kikulai I, Kiveliai J, Said M, Serneels S, Thompson M. 2001. Long-term changes in Serengeti-Mara wildebeest and land cover: pastoralism, population, or policies? Proc Nat Acad Sci 98:12544–12549.

Iverson LR, Prasad AM. 2002. Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. Forest Ecol Manag 155:205–222.

Jutila H. 1999. Effect of grazing on the vegetation of shore meadows along the Bothnian Sea, Finland. Plant Ecol 140:77–88.

Kelly AE, Goulden ML. 2008. Rapid shifts in plant distribution with recent climate change. Proc Nat Acad Sci 105:11823–11826.

Legendre P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673.

Lehmann J, Korstjens AH, Dunbar RIM. 2010. Apes in a changing world—the effects of global warming on the behaviour and distribution of African apes. J Biogeogr 37:2217–2231.

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771.

McCullough DR. 1997. Irruptive behaviour in ungulates. In: McShea WJ, Underwood HB, Rappole JH, editors. The science of overabundance: deer ecology and population management. Washington, DC: Smithsonian Institute Press. p 69–98.

McNaughton SJ. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329–336.

McNeilage AR. 1995. Mountain gorillas in the Virunga Volcanoes: feeding ecology and carrying capacity [Ph.D. thesis]. Bristol: University of Bristol.

McNeilage A. 2001. Diet and habitat use of two mountain gorilla groups in contrasting habitats in the Virungas. In: Robbins MM, Sicotte P, Stewart KJ, editors. Mountain gorillas: three decades of research at Karisoke. Cambridge: Cambridge University Press. p 265–292.

Morrison M, Marcot B, Mannan R. 1998. Wildlife-habitat relationships: concepts and applications. Madison: The University of Wisconsin Press.

Nkurunungi JB, Ganas J, Robbins MM, Stanford CB. 2004. A comparison of two mountain gorilla habitats in Bwindi Impenetrable National Park, Uganda. Afr J Ecol 42:289–297.

Olupot W. 1998. Long-term variation in mangabey (*Cercocebus albigena johnstoni* Lydekker) feeding in Kibale National Park, Uganda. Afr J Ecol 36:96–101.

Picton Phillips G, Seimon A. 2010. Potential climate change impacts in conservation landscapes of the Albertine Rift. WCS Albertine Rift Climate Assessment, whitepaper report no 2.

Plumptre AJ. 1991. Plant-herbivore dynamics in the Birungas [Ph.D. thesis]. Bristol: University of Bristol.

Plumptre AJ. 1993. The effects of trampling damage by herbivores on the vegetation of the Parc National des Volcans, Rwanda. Afr J Ecol 32:115–129.

Plumptre AJ. 1995. The chemical composition of montane plants and its influence on the diet of the large mammalian herbivores in the Parc National des Volcans, Rwanda. J Zool 235:323–337.

Plumptre AJ. 1996. Modelling the impact of large herbivores on the food supply of mountain gorillas and implications for management. Biol Cons 75:147–155.

Plumptre AJ, Reynolds V. 1994. The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. J Appl Ecol 31:631–641.

Pringle RM, Syfert M, Webb JK, Shine R. 2009. Quantifying historical changes in habitat availability for endangered species: use of pixel- and object-based remote sensing. J Appl Ecol 46:544–553.

R Development Core Team. 2010. R: A language and environment for statistical computing R Foundation for Statistical Computing. Vienna, Austria.

Rao M, van Schaik CP. 1997. The behavioral ecology of Sumatran orangutans in logged and unlogged forest. Trop Biodiv 4:173–185.

Remis MJ. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of variable resources. Am J Primatol 43:87–109.

Riggs RA, Tiedemann AR, Cook JG, Ballard TM, Edgerton PJ, Vavra M, Krueger WC, Hall FC, Bryant LD, Irwin LL, Delcurto T. 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains Ecological Province. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Riley EP. 2007. Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. Int J Primatol 28:107–133.

Ringrose S, Chipanshi AC, Matheson W, Chanda R, Motoma L, Magole I, Jellema A. 2002. Climate- and human-induced woody vegetation changes in Botswana and their implications for human adaptation. Env Manag 30:98–109.

Robbins MM, Gray M, Fawcett KA, Nutter F, Uwingeli P, Mburanumwe I, Kagoda E, Basabose A, Stoinski TS, Cranfield MR, Byamukama J, Spelman LH, Robbins AM. 2011. Extreme conservation leads to recovery of the Virunga mountain gorillas. PLoS ONE 6:e19788.

Robbins MM, Nkurunungi JB, McNeilage A. 2006. Variability of the feeding ecology of eastern gorillas. In: Hohmann G, Robbins MM, Boesch C, editors. Feeding ecology in apes and other primates: ecological, physical and behavioral aspects. Cambridge: Cambridge University Press. p 25–47.

Robbins MM, Robbins AM. 2004. Simulation of the population dynamics and social structure of the Virunga mountain gorillas. Am J Primatol 63:201–223.

Rothman JM, Plumptre AJ, Dierenfeld ES, Pell AN. 2007. Nutritional composition of the diet of the gorilla (*Gorilla beringei*): a comparison between two montane habitats. J Trop Ecol 23:673–682.

Ryan AM, Chapman CA, Rothman JM. In press. How do differences in species and part consumption affect diet nutrient concentrations? A test with red colobus monkeys in Kibale National Park, Uganda. Afr J Ecol. Available online ahead of print: DOI: 10.1111/j.1365-2028.2012.01346.x

Sharp BR, Bowman DMJS. 2004. Patterns of long-term woody vegetation change in a sandstone-plateau savanna woodland, Northern Territory, Australia. J Trop Ecol 20:259–270.

Spinage CA. 1972. The ecology and problems of the Volcano National Park, Rwanda. Biol Cons 4:194–204.

Still C, Foster PN, Schneider SH. 1999. Simulating the effects of climate change on tropical montane cloud forests. Nature 398:608–610.

Stratton L. 1996. The impact and spread of *Rubus ellipticus* in ‘Ola’a Forest Tract Hawai’i Volcanoes National Park. Honolulu, Hawai’i: Cooperative National Park Resources Studies Unit, University of Hawai’i at Manoa.

Troupin G. 1978. Flore du Rwanda: spermatophytes. Tervuren, Belgium: Musée Royale de l’Afrique Centrale.

Twinomugisha D, Chapman CA, Lawes MJ, O'Driscoll Worman C, Danish LM. 2006. How does the golden monkey of the Virungas cope in a fruit-scarce environment? In: Newton-Fisher NE, Notmann H, Patterson JD, Reynolds V, editors. Primates of Western Uganda. New York: Springer. p 45–60.

Valcu M, Kempenaers B. 2010. Spatial autocorrelation: an overlooked concept in behavioral ecology. Behav Ecol 21:902–905.

Vedder AL. 1984. Movement patterns of a group of free-ranging mountain gorillas (*Gorilla gorilla beringei*) and their relation to food availability. Am J Primatol 7:73–88.

Vesk PA, Westoby M. 2001. Predicting plant species' responses to grazing. J Appl Ecol 38:897–909.

Walther G-R, Beißner S, Burga CA. 2005. Trends in the upward shift of alpine plants. J Veg Sci 16:541–548.

Watts DP. 1983. Foraging strategy and socioecology of mountain gorillas (*Pan gorilla*) *beringei* [Ph.D. thesis]. Chicago: University of Chicago.

Watts DP. 1984. Composition and variability of mounain gorilla diets in the Central Virungas. Am J Primatol 7:323–356.

Watts DP. 1987. Effects of mountain gorilla foraging activities on the productivity of their food plant species. Afr J Ecol 25:155–163.

Watts DP. 1998a. Long-term habitat use by mountain gorillas (*Gorilla gorilla beringei*). 1. Consistency, variation, and home range size and stability Int J Primatol 19:651–680.

Watts DP. 1998b. Long-term habitat use by mountain gorillas (*Gorilla gorilla beringei*). 2. Reuse of foraging areas in relation to resource abundance, quality, and depletion. Int J Primatol 19:681–702.

Weber AW, Vedder A. 1983. Population dynamics of the Virunga gorillas, 1959–1978. Biol Cons 26:341–366.

Whittaker RH. 1965. Branch dimensions and estimation of branch production. Ecology 46, 365–370.

Wieczkowski J, Kinnaird M. 2008. Shifting forest composition and primate diets: a 13-year comparison of the Tana River mangabey and its habitat. Am J Primatol 70:339–348.

Yamagiwa J, Basabose AK, Kaleme K, Yumoto T. 2005. Diet of Grauer's gorillas in the montane forest of Kahuzi, Democratic Republic of Congo. Int J Primatol 26:1345–1373.

Young TP. 1994. Population biology of Mount Kenya lobelias. In: Rundel PW, Smith AP, Meinzer FC, editors. Tropical alpine environments: plant form and function. Cambridge: Cambridge University Press.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. Berlin: Springer.