Oecologia (Berlin) (1983) 60:244–249

Oecologia

Digestibility, digestion-inhibitors and nutrients of herbaceous foliage and green stems from an African montane flora and comparison with other tropical flora

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Summary. A total of 21 kinds of mature leaves and 12 kinds of green stems from the herbaceous flora of an afro-montane forest have been analysed for moisture content, dry matter digestibility in pepsin and cellulase enzymes, total phenolics, condensed tannins, acid detergent fibre, protein, and the micronutrients phosphorus, potassium, calcium and magnesium. Leaves were found to be significantly more digestible than stems, to contain less fibre but more total phenolics, and to be richer in protein and all micronutrients except potassium. Condensed tannins were found in very few samples, in contrast to their widespread occurrence in foliage from tropical rain forests in Africa and India. An analysis of the correlates of digestibility suggested that in green stems this was largely controlled by fibre content: the overall relationship with all measures being very similar to that recorded previously for rain forest foliage. Rather surprisingly the leaves failed to exhibit a similar relationship and none of the measures taken correlated strongly with digestibility. Compared with foliage from rain forest trees the leaves analysed in this study were found to be more digestible, richer in phosphorus and deficient in both fibre and tannin-based digestion-inhibitors. The two types of foliage are compared as sources of food for herbivores and findings discussed in the light of prevailing hypotheses of plant anti-herbivore chemistry.

Introduction

In a previous paper (Choo et al. 1981) we reported the use of a simple in vitro assay of dry matter digestibility, involving the sequential treatment of an item with pepsin followed by cellulase enzymes of fungal origin (CDIG assay) to estimate the digestibility of a total of 94 different kinds of foliage originating from emergent and canopy trees growing in the rain forests of Cameroon, Uganda and southern India. According to the defense chemistry hypotheses developed by Feeny (1976) and Rhoades and Cates (1976) this is to be regarded as a highly apparent food resource for herbivores and as such would be expected to invest heavily in digestibility-reducing compounds. If these hypotheses are correct then it would be anticipated that CDIG values are likely to differ markedly for foliage from plants growing in different environments. To test this hypothesis we have embarked on a series of studies of CDIG levels, and factors influencing them, in foliage from a number of different tropical ecosystems. In this paper we report the results of a study of a subset of the herbaceous species from the afro-montane vegetation of the Parc National des Volcans in Rwanda and the contiguous Parc des Virungas in Zaire. Analysis of foliage and green stems of herbs and shrubs was undertaken; with species being selected because of their relevance to the diet of the mountain gorilla (*Gorilla gorilla beringei*) found in these areas.

Materials and methods

Study site

Plant specimens were collected from a study site located in the Virunga mountain range of north-western Rwanda and eastern Zaire (1°50′S, 29–30° E). The site, covering approximately 16 km^2 on the south flank of Mt. Visoke, extends from 2,680 up to 3,710 m in elevation. The monthly rainfall during the year of specimen collection (1978–1979) ranged from 2.5 mm to 246.5 mm, with most of the rain falling during the period of mid-February to mid-May and September to December. Mean monthly temperatures recorded during an eight month period (January–August) showed maxima ranging from 12.4 to 16.8° C and minima of 2.3 to 5.4° C.

This area is characterized by relatively distinct vegetation zones which vary with altitude, as described by Schaller (1963) and Fossey (1974). In brief, it is an area of open canopy forest, dominated by *Hypericum revolutum* and *Hagenia abyssinica*, with a dense herbaceous understorey. The forest is interrupted by steep, shrubby ravines and is bordered by thick stands of the bamboo (*Arundinaria alpina*) at lower elevations and subalpine vegetation (*Lobelia launuriensis* and *Senecio johnstonii*) on the upper slopes of the mountain.

Collection of plant material

Selection of plant materials to be collected was based on their having some significance in the diet of mountain gorillas observed in the study area. The foliage and stems discussed in this paper were from herbs or shrubs with plants

Table 1. Moisture content (H_2O), digestion-inhibitor levels (TP, CT, ADF), protein content (PROT), cellulase digestibility (CDIG), and levels of various micronutrients (P, K, Ca, Mg), in leaves (L) and stems (S) of some Virunga species. Values as % dry wt., except for H_2O (% fresh wt)

Family *species*	Plant part	H_2O	CDIG	PROT	TP	CT	ADF	P	K	Ca	Mg
Asteraceae											
Carduus leptacanthus Fres.	L	87	61.3	11.03	3.50	0.00	36.8	0.16	1.40	2.90	0.29
	S	87	30.5	4.03	1.68	0.00	48.5	0.18	5.40	1.20	0.31
Carduus nyassanus R. E. Fries	L	86	69.2	18.55	1.76	0.00	33.8	0.33	5.80	2.80	0.35
	S	87	68.7	4.55	1.89	0.00	38.1	0.18	1.78	0.81	0.25
Gynura ruwenzoriensis S. Moore	L	94	52.2	15.93	2.47	0.00	27.8	0.39	4.40	1.77	0.62
Helichrysum foetidum Cass.	L	86	51.2	18.73	6.73	0.00	38.2	0.40	3.36	1.32	0.41
Helichrysum formosissimum Sch.	L	88	64.0	11.73	5.97	0.00	38.6	0.22	2.52	1.40	0.45
Helichrysum ?newii Oliv. & Hiern	L	90	49.3	11.43	5.27	0.00	41.8	0.18	3.46	1.68	0.09
Latuca attenuata Stebbins	L	90	34.9	15.50	3.07	0.00	29.6	0.38	3.60	1.72	0.45
Micanopsis sp.	L	87	72.2	19.60	2.18	0.00	28.3	0.34	1.00	1.32	0.40
Senecio trichopterygius Muschl.	L	88	46.3	25.38	4.30	0.00	36.0	0.55	1.00	0.78	0.41
Senecio maranguensis O. Hoffm.	L	85	71.1	15.93	3.76	0.00	31.0	0.31	3.48	1.15	0.35
Sonchus exauriculatus O. Hoffm.	L	88	62.6	17.33	6.74	0.00	21.7	0.38	4.60	2.90	0.37
Balsaminaceae											
Impatiens burtonii Hook. *f.*	S	96	87.3	8.93	0.74	0.00	28.6	0.14	2.64	0.47	0.03
Basellaceae											
Basella alba L.	L	93	67.6	18.55	1.65	0.00	49.3	0.49	1.38	1.73	0.41
Boraginaceae											
Cynoglossum amplifolium Hochst.	S	73	37.0	5.25	0.77	0.00	54.8	0.13	3.52	0.44	0.15
Cynoglossum geometricum Baker & Wright	S	71	26.2	3.85	0.78	0.00	58.6	0.67	2.40	0.36	0.15
Cyperaceae											
Carex bequaertii De Wild.	L	74	49.9	8.40	1.38	0.00	42.1	0.13	2.20	0.34	0.19
	L base	92	62.9	10.85	3.50	0.00	62.4	0.19	3.06	0.31	0.13
Loranthaceae											
Englerina woodfordioides Balle	L	79	40.7	13.30	17.08	14.95	30.1	0.37	2.16	1.66	0.27
Poaceae											
Arundinaria alpina K. Schum	L	62	23.4	17.15	1.23	0.00	42.6	0.18	1.00	0.32	0.41
Polygonaceae											
Rumex ruwenzoriensis Chiov.	S	94	49.5	8.93	5.87	0.00	37.8	0.24	0.24	0.25	0.15
Polypodiaceae											
Pleopeltis excavata Hook. *f.*	L	80	61.8	10.33	4.49	0.00	34.8	0.23	2.66	0.52	0.40
Rosaceae											
Rubus kirungensis Engl.	L	60	53.2	14.18	14.84	0.00	29.1	0.13	1.26	0.84	0.36
	S	65	13.3	7.18	5.31	0.00	63.4	0.12	0.84	0.26	0.14
Rubiaceae											
Galium ruwenzoriensis Ehrend.	L	85	78.0	16.63	2.35	0.00	38.6	0.50	3.72	1.92	0.10
Umbelliferae											
Anthriscus sylvestris Auct. *non* L	S	86	37.5	3.50	0.94	0.00	53.4	0.23	0.84	0.80	0.23
Peucedanum kerstenii Engl.	S	91	38.6	5.08	1.80	0.00	46.0	0.20	1.60	2.20	0.62
Peucedanum linderi Norman	S	90	42.5	7.18	0.86	0.00	49.1	0.17	5.00	1.20	0.11
Urticaceae											
Droguetia iners Schweinf.	L	72	47.9	15.58	9.23	6.18	25.0	0.31	1.94	2.55	0.60
Laportea alatipes Hook. *f.*	L	84	65.8	20.00	3.62	1.56	26.9	0.33	2.26	2.95	0.75
	S	83	26.3	5.78	2.52	8.69	59.5	0.13	2.74	0.68	0.40
Urtica massiaca Mildbr.	S	87	35.6	9.98	0.68	0.00	53.6	0.37	3.72	1.30	0.32

that appeared sickly or damaged being avoided. Samples of each item collected during 1978–1979 consisted of material taken from several plants to give at least 200 g wet weight. Stem samples were prepared, as would be done by a gorilla, by removal of the epidermis of the stem.

Specimens were placed in paper bags and dried in a ventilated metal oven over a wood-burning stove until weights stabilized. Dry weights were recorded, and samples were then sealed in plastic bags and stored until transported for laboratory analysis.

Assay procedures

The pepsin/cellulase assay was performed on powdered plant material using the method reported previously (Choo et al. 1981). Assays for total phenols and condensed tannins were performed on extracts prepared with 50% aqueous ethanol and methanol respectively; assays being measured against the same standards as employed by Gartlan et al. (1980). Acid detergent fibre was assayed carrying out the method described by van Soest (1963) except that in some cases shortage of plant material required samples to be scaled down to 300 to 400 mg with comparable scaling down of other reactants. Crude protein content and levels of calcium, magnesium, potassium and phosphorus were analysed using standard methods (Greweling 1976).

Results

Moisture content (H_2O), pepsin/cellulase digestibility (CDIG), and dry wt content of total phenolics (TP), condensed tannins (CT), acid detergent fibre (ADF), protein (PROT), phosphorus (P), calcium (Ca), potassium (K) and magnesium (Mg) were measured for a total of 21 different kinds of mature foliage and 12 kinds of green herbaceous stems. The results of these assays are given in Table 1.

Comparisons between leaf and stem samples

Table 2 presents the basic statistics for each assay performed on leaf and stem samples, together with the results of the Mann-Whitney *U*-test for variance between levels in the two plant parts. These data show that for seven of the 10 measures taken levels in leaf tissues differ significantly from those found in stem tissues. The three where no differences were observed were H_2O, K and CT; in the case of the latter no comparison exists because condensed tannins appear to be generally absent, being found only in *Englerina woodfordioides, Droguetia iners* and *Laportea alatipes* among the 28 species investigated.

For the seven analyses where differences are significant leaf tissue was significantly more digestible than stem tissue and had higher levels of PROT, TP, Ca and Mg. On the other hand levels of ADF are greater in stem tissues. Differences appeared greatest with respect to PROT where there is little overlap between the two data sets; foliage ranged from 8.40% to 25.38% PROT and stems from 3.50% to 9.98%. Differences are almost as clearly marked for TP which averaged about two and a half times greater for leaf samples than for stem samples. However, in the other five measures differences appear less pronounced. This may be somewhat misleading in the case of CDIG, where values for stems are consistently lower than those for leaves with two notable exceptions: the stems of *Impatiens burtonii* (at 87.3% CDIG the most digestible item analysed) and *Carduus nyassanus*. The more direct comparison of four species for which both leaf and stem were available further confirms the greater CDIG of leaf material (mean 62.4%) over stem (mean 34.7%). In three of the four comparisons leaf CDIG is over twice that of the stem.

Table 2. Basic statistics and Mann-Whitney *U*-test for difference for the measures listed in Table 1 – leaf and stem samples

Assay	Leaves ($N=21$)			Stems ($N=12$)			U_s	
	mean	s.d.	c.v.	mean	s.d.	c.v.		
H_2O	83.33	9.29	11%	84.17	9.59	11%	130	NS
CDIG	56.45	13.46	24%	41.08	19.91	49%	194	$P<0.05$
PROT	15.53	4.05	26%	6.19	2.21	36%	249	$P<0.001$
TP	5.01	4.19	84%	1.99	1.79	90%	204	$P<0.01$
CT	1.08	3.46	320%	0.72	2.51	349%	–	
ADF	35.45	9.19	26%	49.28	10.24	21%	209	$P<0.01$
P	0.31	0.12	39%	0.23	0.15	65%	186	$P<0.05$
K	2.68	1.33	50%	2.56	1.63	64%	134	NS
Ca	1.57	0.88	56%	0.83	0.57	69%	192	$P<0.01$
Mg	0.37	0.16	43%	0.24	0.16	67%	189	$P<0.01$

The range of ADF levels found in leaves and stems is similar; 21.7% to 62.4% in the former and 28.6% to 63.4% in the latter. However, the average value for ADF within the 12 stem samples is about 14% greater than the average within the 21 leaf samples, and the two data sets are significantly different using the Mann-Whitney *U*-test. This distinction is again confirmed by turning to the four species for which both leaf and stem are present. In these leaf samples the mean ADF was 31.7% compared with a value of 52.4% for the corresponding stems; there being no overlap between the two sets of measures.

Correlates of CDIG in leaf and stem

Table 3 presents the correlation coefficients for CDIG against the other nine measures, for leaf and stem samples separately. In both kinds of plant part there is a weak but significant positive correlation between H_2O levels and CDIG. In the case of the leaf samples no other correlations that approach significance are found. On the other hand with stem samples there is a very strong negative correlation observed between digestibility and ADF but, other than this, no correlations of significance with CDIG.

Analysis of the complete correlation matrices for the two data sets show few correlations between measures other than those in Table 3. For the stems there is a strong negative relationship between H_2O and ADF ($r=-0.80$, $P<0.01$), which is of particular interest in view of the apparent relationship of both H_2O and ADF to CDIG, and an equally strong positive relationship between Ca and Mg ($r=+0.78$, $P<0.01$). For leaves the only strong correlation observed is between PROT and P ($r=+0.71$, $P<0.001$). Weaker positive correlations ($P<0.05$) are found between PROT and Mg, H_2O and P, and H_2O and K; with similar weak negative correlations between ADF and both Ca and Mg.

Factors influencing CDIG were further analysed by means of a stepwise multiple linear regression, the results of which are presented in Table 4. These analyses confirm

Table 3. Correlation coefficients for all measures against CDIG, for leaves ($N=21$) and stems ($N=12$)

CDIG of	Correlation against								
	H_2O	PROT	TP	CT	ADF	P	K	Ca	Mg
leaves	+0.44*	+0.05	−0.24	−0.29	+0.03	+0.18	+0.26	+0.31	−0.11
stems	+0.69*	+0.28	−0.23	−0.23	−0.93***	−0.22	−0.05	−0.04	−0.30

$^*P<0.05$; $^{***}P<0.001$

Table 4. Stepwise multiple linear regression of all measures against CDIG for leaves and stems

Leaves ($N=21$)		Stems ($N=12$)	
Variable entered	r^2	Variable entered	r^2
H_2O	0.1916	ADF	0.8673
CT	0.2346	TP	0.9069
Ca	0.2935	Ca	0.9440
Mg	0.3286	K	0.9536
TP	0.3342	P	0.9681
P	0.3372	PROT	0.9756
PROT	0.3445	CT	0.9779
K	0.3495	H_2O	0.9840
ADF	did not enter	Mg	0.9880

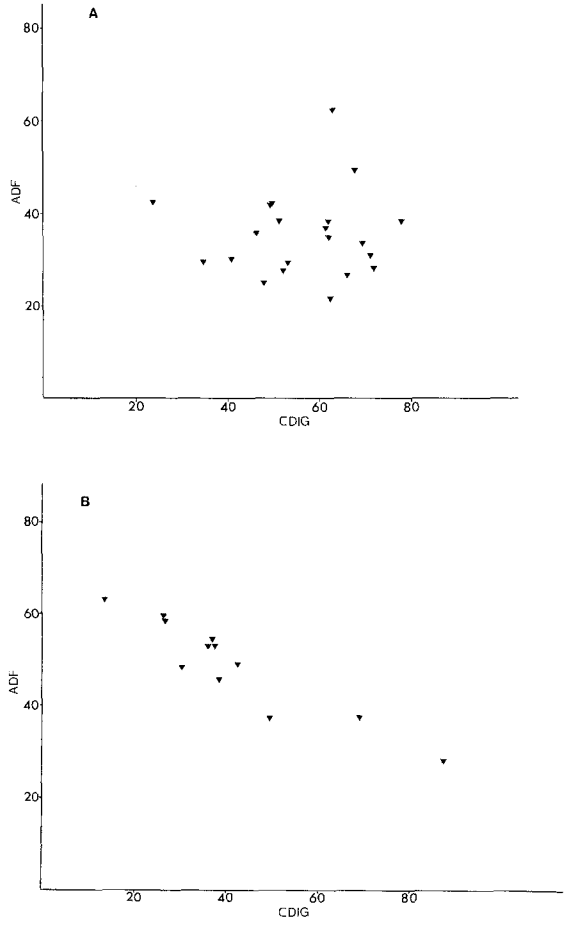

Fig. 1. Relationship of CDIG to ADF: (**A**) for leaves ($N=21$), and (**B**) for green stems ($N=12$)

the apparent differences between factors governing CDIG in the two tissue types. In leaves, the total contribution of eight variables (ADF did not enter the regression) is unable to predict 40% of the observed CDIG and, apart from H_2O, no variable is able to make a significant contribution. By contrast, for stems the total contribution of all nine variables is able to account for over 98% of observed CDIG with ADF alone accounting for over 85% and ADF and TP together (measures that should include all phenolic digestion-inhibitors) for over 90% of the observed variation. The strong relationship between ADF and CDIG in stems and the absence of any similar relationship in leaves is shown graphically in Fig. 1. The absence of a major contribution to the regression from PROT or from any of the measures of micronutrients is not surprising in view of the nature of the CDIG assay, which measures only the activity of the two isolated enzymes and takes no account of any physiological effects of the nutrient content of the plant material on either the animal or its gut microflora.

The regression obtained for the stem samples shows a close relationship to that reported previously (Choo et al. 1981) for a regression on CDIG for mature leaves of rain forest trees. In that study also ADF was the first variable to enter the regression and accounted for over 80% of observed CDIG and TP was again the second variable to enter the equation. By contrast, the regression found here for 21 kinds of mature leaves from herbaceous plants and shrubs showed no similarity to that recorded for mature foliage from other study areas.

Comparison of levels of digestion-inhibitors, digestibility, protein and phosphorus in foliage of afro-montane herbs and shrubs and the foliage of rain forest trees

Table 5 presents a comparison of means and Mann-Whitney *U*-test comparisons for levels of TP, CT, ADF, CDIG, PROT and P in the afro-montane foliage studied here and previously reported data on the mature foliage of rain forest tree species from Cameroon, Uganda and southern India (Oates et al. 1980, Waterman et al. 1980, Choo et al. 1981). For four of the six measures there are significant differences between the two types of leaves; the two exceptions being TP and PROT. The most striking difference is seen in CT levels which average about four times greater in the forest tree foliage. This difference is not the product of generally lower levels of CT in the foliage studied here but is due to their complete absence from 18 of the 21 species. By contrast CT's occur in a high proportion of the leaves examined from rain forest trees. The levels of ADF are also significantly lower in this study in comparison with rain forest examples, although differences are not as extreme as with the tannins. In view of the higher levels of CT

Table 5. Means and Mann-Whitney *U*-test results comparing various measures in foliage from this study and from studies of the foliage of rain forest trees

Assay	Afro-alpine vegetation		Rain forest vegetation		U_s
	mean	*N*	mean	*N*	
TP	5.01	21	5.73	48	589 NS
CT	1.08	21	4.30	48	854 $P<0.001$
ADF	35.45	21	45.83	48	712 $P<0.01$
CDIG	56.45	21	35.58	48	848 $P<0.001$
PROT	15.53	21	13.75	48	648 NS
P	0.31	21	0.13	34	649 $P<0.001$

and ADF it is hardly surprising to find that average CDIG levels are about 20% lower among mature leaves from rain forest trees than are those measured here. Finally, P levels also appear greatest in the afro-alpine foliage.

The data for rain forest foliage used in the above comparison is taken from three areas that differ markedly among themselves (Gartlan et al. 1980, Choo et al. 1981, Waterman and Choo 1981). Where each rain forest site is considered separately the differences outlined are found to be greatest when the Douala-Edea site, in Cameroon, is used for the comparison. In addition for this site PROT levels are significantly lower (mean 12.42%, $U_s = 313_{[21,20]}$, $P<0.05$) than those of the leaves of the Virunga sample. This observation is to be expected in view of the extreme nature of the chemistry of Douala-Edea tree foliage (Gartlan et al. 1980). Foliage from the Indian site at Kakachi shows a pattern of differences from Virunga foliage similar to that for Douala-Edea, except that there is no significant difference in ADF levels. The Kibale site, in Uganda, is recognised as producing the smallest amounts of digestion-inhibitors and most PROT-rich and P-rich foliage of any of the forest sites analysed (Waterman and Choo 1981) and is much more similar in all respects to the Virunga material. However, Kibale foliage remains relatively deficient in P, richer in CT, and marginally poorer in terms of CDIG.

Contrary to the leaves reported upon here the chemistry of the green stems of a number of Virunga plants appears in most ways comparable to the leaves of many rain forest trees. Stems do, however, appear to be generally lower in PROT content and, like the leaves of the Virunga species, contain CT's in only a few cases.

Discussion

The results reported here suggest that the foliage of herbaceous species from an afro-montane forest is poorer in digestibility-inhibitors, and consequently more digestible, and at least marginally richer in nutrients than a set of foliage from trees (most of them evergreen) growing in African and Indian closed-canopy rain forests. The most striking single distinction between the two types of foliage is the near absence of CT's from the herbaceous species. Furthermore, the chemical variation between the two types of foliage may be deeper than a simple change of emphasis on contents because the anticipated correlation between CDIG and ADF, so apparent in the foliage from rain forest sites, is absent for the afro-alpine foliage. To date it has not been possible to discover what chemical factors are delimiting the CDIG of the Virunga foliage. One possibility is that proteinase-inhibitors, which may occur more widely in herbaceous species and could have survived the drying process (Ryan 1979), may be making a far greater contribution than in the foliage of arboreal species.

However, while the CDIG of the herbaceous leaves and factors influencing it are very different in many respects from what has been observed previously, the CDIG of the green stems of Virunga herbs and the inhibitory impact of ADF they contain does appear directly comparable to previous findings for rain forest tree foliage. Thus, as a generalization, it would appear that in consuming the green stems of herbaceous plants from Virunga a herbivore will be faced with similar problems relating to digestibility, and therefore to rate of throughput, as would be faced by an arboreal folivore in an evergreen rain forest such as Douala-Edea or Kakachi. The nutritional gain from such a diet, at least in terms of PROT, would, however, be less than the arboreal folivore would be expected to obtain from leaves. On the other hand a terrestrial folivore consuming the leaves of Virunga herbs would be utilising a nutrient-rich food source that could be processed relatively rapidly and which could be capable of maintaining mammalian herbivores without the major gut adaptations necessary to permit large-scale microbial fermentation (Vedder, Watts and Waterman – in preparation).

According to current theories concerning plant anti-herbivore chemistry the generally short-lived, herbaceous vegetation of the Virunga site examined in this paper would be considered unapparent and suitable for defense by toxins rather than digestion-inhibitors. As yet we have no information regarding the occurrence of toxins in the foliage analysed but it is certainly clear that, as predicted, there is less emphasis on digestion-inhibitors than has been found in the more apparent vegetation of climax rain forest trees. The sharpest division would appear to be in the occurrence of tannins, which are widespread among climax forest species but rare in herbaceous growth forms. However, whilst the relative paucity of tannins does comply with the situation anticipated by anti-herbivore theory it also conforms with the earlier suggestion (Bate-Smith and Metcalfe 1957, Bate-Smith 1962) that tannin production is linked to the woody habit. While these two concepts are not mutually exclusive they can not both be looked upon as the primary factor governing the distribution of tannins. In this context it is important to recognise that some of the most common plant families in the study, notably the Asteraceae and Umbelliferae, are wholly herbaceous in habit and probably completely lacking in tannins. On the other hand the Urticaceae is a family with an arboreal element and the occurrence of condensed tannins in two of the three species from Virunga should perhaps be viewed in that light. Likewise the Rosaceae has a large arboreal element and *Rubus kirungensis* yields considerable quantities of hydrolysable tannins, the only species examined from this site to produce this type of tannin.

Acknowledgements. Laboratory analyses performed at the University of Strathclyde were financed by Grant No. GR 3/3455 from the Natural Environment Research Council (to P.G.W.). Field work was supported by the New York Zoological Society and the Society of the Sigma Xi (to A.L.V.) and by Grant No. 5T32 MH 15181-03 (Dr. S. Altmann, grant supervisor) from

the National Institute of Mental Health (to D.W.). The National Geographic Society is thanked for permission to use their facilities and Dian Fossey for permission to work in her camp. L'Office Rwandaise des Parcs Nationaux et Tourisme is gratefully acknowledged for permission to work in the Parc des Volcans. Additional nutritional analyses were performed at the National Agricultural Laboratories of Kenya, with thanks due, in particular, to Mr. P.G. Otieno and Mr. S. Otiende.

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Received April 27, 1983