FOOD PREFERENCE DATA BY FAECAL ANALYSIS FOR AFRICAN PLAINS UNGULATES

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INTRODUCTION

There is little published information, particularly of a quantitative nature, concerning the preferences shown for different plant species by African ungulates, especially grazers.

The data obtained so far are very largely qualitative. Thus a number of lists have been published of plants recorded as being eaten either by wild animals alone (eg. Anon. 1962; Brynard & Pienaar 1960; Eloff 1959, 1961, 1962; Glover, Stewart and Gwynne 1966; Grzimek and Grzimek 1960; Mitchell 1963; Van der Schijff 1959; Wilson 1965), by both wild and domestic animals (Dougall, Drysdale and Glover 1964), or by domestic animals only (Dougall and Bogdan 1958). A list of plants identified in the faeces of waterbuck *Kobus defassa* by Kiley (1966) provides more detailed information in that it is related to the plants available in the habitat. Various authors, e.g. Bogdan (1958), Edwards and Bogdan (1951), Eggeling (1947), Scott (1955) and Wilson and Bredon (1963), have described the extent to which different plants are of value as fodder to domestic stock.

Preferences for different vegetation types, particularly with reference to grazing succession among different wild animals, have been studied by Orr (1964), Vesey-Fitzgerald (1960, 1965) and Watson and Kerfoot (1964). Leistner (1959) and Roberts (1963) discuss the nutritive value of various vegetation types to wild animals.

Quantitative data on species selection, however, appear to be limited to those published by Lamprey (1963) and Talbot (1962). They compare the proportions of each of a number of plants in the diet of different wild animals, the data being obtained by direct observation and by analysis of stomach contents respectively. Talbot's data are subdivided according to plant parts. Talbot and Talbot (1963) provide quantitative data on the diet of a single wild species, the wildebeest *Gorgon taurinus hecki*. Quantitative work on domestic stock in Africa has been concerned with preferences for different plant parts rather than species (Bredon and Marshall 1962).

There would appear to be no published quantitative data, for either wild or domestic African ungulates, comparing the preferences shown for plant species with the composition of the available pasture. An increasing amount of effort is, however, being directed towards obtaining such data, particularly for wild animals, and in addition to the work described in this paper food preference studies are under way in several parts of Eastern and Southern Africa (Bell, Field, Hirst, McAllister, Norris-Rogers, Nature Conservator-Kruger National Park: personal communications). Several of these studies are making use of the technique, usually known as faecal analysis, involving the identification of plant fragments in faeces by reference to the characteristics of leaf and sheath epidermis. Whilst other techniques, such as the direct observation of wild or tamed animals and the examination of digestive tract contents from dead or fistulated animals, may be preferred, in many circumstances faecal analysis is useful under conditions in which it may be difficult or impossible to apply other metods. In addition it allows the sampling of any number of animals, under entirely natural conditions, and causes little or no disturbance of the animals concerned.

Whilst faecal analysis has been used successfully with large mammals in other parts of the world (Hercus 1960; Martin 1954; Storr 1961), albeit largely to provide qualitative data only, it had not been tried out in the complex situations often found in Africa, involving many plant and animal species, prior to the current studies. Because of its potential usefulness Stewart (1967) carried out an evaluation of the possibilities and limitations of the method under African conditions. By means of feeding experiments with captive wild animals a satisfactory sampling technique was derived. It was also shown that whereas it is not practicable to obtain precise information on the proportions of different grasses eaten, except possibly in intensive studies involving a limited number of plant and animal species, quantitative data on a frequency basis can be obtained. These can be used to illustrate differences in food preferences between animals, as well as to indicate the extent to which each plant is utilised in relation to its abundance in the pasture.

This paper presents results obtained from a series of analyses carried out in Masailand, southern Kenya. The eight animals involved were cattle *Bos indicus*, wildebeest *Connochaetes taurinus*, hartebeest *Alcelaphus buselaphus*, topi *Damaliscus korrigum*, Grant's gazelle *Gazella granti*, Thomson's gazelle *G. thomsonii*, eland *Taurotragus oryx* and zebra *Equus burchelli.*

METHODS

Collection of faeces

Areas were chosen in which animals of several species were feeding on the same pasture. The animals were located daily for six days and identified as far as possible by means of counts and individual characteristics. Early on the seventh day ten fresh piles of droppings from each species were located; c. 70g (fresh weight) of faeces were collected from each pile and stored in formalin acetic alcohol. An attempt was thus made to sample ten different individuals of each species, although it is possible that occasionally more than one pile of droppings had been deposited by the same animal.

Pasture survey

After the collection of faeces a record of the vegetation in the area covered by the animals during the preceding six days was made. Grasses were each given an abundance symbol and notes were made about their degree of maturity, height and condition. Dicotyledons present, and monocotyledons other than grasses, were listed. Stewart (1967) showed that after six days few if any fragments of grasses eaten prior to this period will be found in the faeces. The list thus made should therefore contain all the species which might be found in the faecal samples; in addition to allowing a comparison between food available and food selected such a list of "possibles" greatly reduces the time required to identify epidermal fragments in the faeces.

Treatment of faecal samples

A 1 g. sub-sample from each faecal sample was macerated in 4 ml. concentrated nitric acid over a water-bath for 2-3 minutes and then placed in 200 ml. water which was boiled and stirred to complete the clearing of fragments. The supernatant fluid was then removed by centrifuging; the sub-sample was washed and centrifuged a second time and finally stored in 5 ml. formalin acetic alcohol.

Analysis

Using a shallow scoop of appropriate size sufficient material was removed from the storage tube, after agitation of the latter, to provide a suitable density of fragments under a 3.8 x 1.9 cm. (1½ x ⅞in.) coverslip; if too much material is placed on the slide fragments overlap making identification difficult. The slides were marked with parallel lines whose distance apart was slightly less than the diameter of the microscope field of view at a magnification of x 100. The slide was traversed systematically along alternate pairs of lines; every fragment of grass epidermis which could be identified using a key, reference slides, descriptions and microphotographs of epidermis (Stewart 1965), and which fell wholly or partly between the lines, was recorded. Alternate traverses were omitted to avoid duplicate recordings of fragments overlapping the lines. Fragments which were large enough to bear sufficient characters for identification, but which nevertheless could not be identified, were listed as "unidentified" and included in the total of 100 fragments recorded from each sample.

The relative abundance of material from dicotyledons in each sample was recorded by means of an abundance scale.

RESULTS

The results of analyses in six areas of *Acacia-Themeda* scattered tree grassland (Edwards 1959), involving from three to six animal species feeding together on each area, are presented in Tables 1-6.

Data in the Tables are arranged as follows :—

1. The grasses recorded in the area covered by the animals during the six days preceding the collection of faeces are listed, together with abundance symbols (*a* abundant, *f* frequent, *o* occasional, *r* rare, *la* locally abundant, etc.). (In Table 1 the latter are omitted since the pasture consisted of a new flush of growth after a burn and, although species were identified from unburnt plants, abundance data was not obtained. In Table 3 only the presence or absence of the grasses in the unburnt and burnt parts of the pasture are given.) Nomenclature follows Bogdan (1958).

2. The results of the analysis of ten faecal samples from each animal species are presented in two ways. Columns headed *n* (figures in heavy type) give frequency data, namely the number of samples containing $\geqslant 5$ fragments of the grass concerned. Samples containing < 5 fragments have been omitted in case of occasional misidentifications. Columns headed $\bar{x}$ give the mean number of fragments of each grass recorded per sample.

(In certain cases it was not possible to obtain ten samples from every animal species; the actual number obtained is therefore noted on the Table (*n*/10, *n*/8 etc.). In other cases,

TABLE I

ANALYSIS OF FAECES FROM GRANT'S GAZELLE (G), THOMSON'S GAZELLE (TG), WILDEBEEST (W) AND ZEBRA (Z) (PASTURE SHORT, GREEN AFTER RECENT BURN)[1]

Pasture composition[2]	*Analysis of faeces*								
	G		TG		W		Z		*Total*
	n/10	$\bar{x}$	n/10	$\bar{x}$	n/10	$\bar{x}$	n/10	$\bar{x}$	N/40
Aristida adoensis	6	4·8	9	13·3	9	7·8	9	13·5	33
Bothriochloa insculpta	1	1·4	—	0·3	—	1·0	—	1·6	1
Cynodon dactylon	10	55·5	9	22·1	9	22·4	10	26·5	38
Digitaria milanjiana	—	—	—	—	—	0·4	—	0·6	—
Eragrostis spp.[3]	—	0·9	2	2·4	9	8·0	5	4·9	16
Eustachys paspaloides	—	0·3	—	—	—	—	—	—	—
Panicum massaiense	—	0·2	—	—	—	0·4	—	—	—
Pennisetum mezianum	2	3·3	2	3·0	—	1·0	3	3·2	7
Setaria setulosa	3	3·7	1	3·2	2	2·7	4	6·0	10
Themeda triandra	10	22·3	10	55·5	10	55·4	10	42·2	40
Harpachne schimperi[4]	—	—	—	—	—	0·1	—	—	—
Unidentified grasses[4]	—	0·1	—	0·2	—	0·8	—	0·8	—
Dicotyledons a[5]	9		1						
f	1		1						
o			5		1		2		
r			3		9		8		
nil									

[1]Mara, southwest Kenya 13.8.63. [2]Species identified from unburnt plants; no abundance data obtained.
[3]*E. paniciformis*, *E. tenuifolia* recorded in pasture; species not separated in faecal analysis.
[4]Recorded in faeces only.
n/10=no. of samples scoring>5 fragments, out of a total of 10 samples per animal species.
$\bar{x}$ = mean no. of fragments per sample.
[5]See text for symbols.

where the diet of a particular animal had consisted largely of dicotyledons, it was impracticable to record as many as 100 fragments of grass epidermis since these were so sparse on the slide; in such instances the numbers of fragments of each grass actually recorded were converted to percentages before *n* and $\bar{x}$ were assessed.).

3. Unidentified fragments of grasses, and fragments of grasses which were identified in faecal samples but not listed in the pasture, are also recorded.

4. The relative abundance in the samples of material from dicotyledons is recorded by giving the number of samples in which such material was abundant (*a*), frequent (*f*), occasional (*o*), rare (*r*) or nil.

DISCUSSION

Although no comprehensive picture of the preferences of the animals concerned in different situations and at different seasons has yet been obtained certain preliminary conclusions can be drawn from the six series of analyses which have been carried out.

TABLE II

ANALYSIS OF FAECES FROM CATTLE (C), THOMSON'S GAZELLE (TG) AND WILDEBEEST (W) (PASTURE PARTLY SHORT AND GREEN AFTER BURN; PARTLY MATURE, BROWN)[1]

	Pasture composition[2]		*Analysis of faeces*						
	U	B	C n/10	C $\bar{x}$	TG n/10	TG $\bar{x}$	W n/10	W $\bar{x}$	*Total* N/30
Aristida adoensis	f	f	7	6·3	—	0·5	6	6·2	13
Bothriochloa insculpta	o	—	—	1·2	—	0·6	—	0·3	—
Cynodon dactylon	—	o	10	27·8	10	22·0	10	32·8	30
Eragrostis spp.[3]	..	..	8	5·7	—	1·5	8	13·3	16
Eustachys paspaloides	a	a	—	—	—	0·1	—	—	—
Microchloa kunthii	o	o	—	0·1	—	—	—	0·1	—
Panicum massaiense	la	f	—	0·9	1	1·0	—	0·8	1
P. repens	—	lf	—	0·8	—	0·6	—	—	—
Pennisetum mezianum	f	f	—	0·6	1	2·2	—	2·3	1
Themeda triandra	a	f	10	55·9	10	70·0	10	42·8	30
Harpachne schimperi[4]	..	..	—	0·1	—	—	—	—	—
Digitaria milanjiana[4]	..	..	—	—	1	0·5	—	0·2	1
Unidentified grasses[4]	..	..	—	0·8	—	1·0	1	1·2	1
Dicotyledons a	..	..			3				
f	..	..	1		5				
o	..	..	8		1		2		
r	..	..	1		1		8		
nil	..	..							

[1]Mara, southwest Kenya 12.8.63. [2]Abundance (see text for symbols) of species recorded separately on unburnt (U) and burnt (B) part of pasture.
[3]*E. aulacosperma* (-, f), *E. braunii* (-, o), *E. paniciformis* (la, la), *E. tenuifolia* (a, a) recorded in pasture; species not separated in faecal analysis.
[4]Recorded in faeces only.

1. *Relative importance of different grasses as foodplants*

The frequency data provide the most accurate indication of the extent to which different grasses have been utilised. The mean numbers of fragments recorded must be regarded with caution since different species tend to break into fragments varying significantly in size and different grasses may be digested to varying extents (Stewart 1967). Nevertheless large differences between grasses in this respect are probably meaningful.

Examination of the frequency data (columns headed *n*) shows that with respect to their utilisation the grasses tend to fall into three categories.

(*a*) Species consistently eaten by most of the animals present, irrespective of whether the grasses concerned are abundant in the pasture or not: two grasses, *Themeda triandra* and *Cynodon dactylon* (plus *C. plectostachyus* in Table 5), fall into this category, *Themeda* being the most popular in all six series, closely followed by *Cynodon*. (Note: the epidermis of *Themeda* tends to break into many small fragments which are particularly easy to identify; the mean

TABLE III

ANALYSIS OF FAECES FROM TOPI (T), GRANT'S GAZELLE (G), THOMSON'S GAZELLE (TG) AND ZEBRA (Z) (PASTURE PARTLY SHORT AND GREEN AFTER BURN, PARTLY MATURE AND MOSTLY BROWN)[1]

Pasture composition[2]			*Analysis of faeces*								
	U	B	T n/10	$\bar{x}$	G[5] n/8	$\bar{x}$	TG n/9	$\bar{x}$	Z n/10	$\bar{x}$	*Total* N/37
Aristida adoensis	.. +	+	1	2·2	2	3·5	3	3·4	3	3·4	9
Bothriochloa insculpta	.. —	+	—	0·9	1	2·2	—	0·9	—	1·6	1
Cynodon dactylon	.. +	+	2	3·0	7	34·0	8	11·1	10	24·1	27
Eragrostis spp.[3] ..	..	..	—	1·2	1	1·7	—	0·5	3	3·1	4
Eustachys paspaloides	.. +	+	—	—	—	—	—	0·1	—	—	—
Microchloa kunthii	.. —	+	—	—	—	—	—	—	—	—	—
Panicum massaiense	.. +	+	—	0·5	—	0·5	—	1·0	1	1·7	1
Pennisetum mezianum	.. +	+	—	1·8	2	3·0	1	2·7	3	3·9	6
Themeda triandra	.. +	+	10	89·5	8	53·7	9	79·3	10	59·1	37
Digitaria milanjiana[4]	..	..	—	0·1	—	—	—	—	—	0·1	
Unidentified grasses[4]	..	..	—	0·8	—	1·2	—	0·7	3	3·0	
Dicotyledons a..	..	..			8						
f..	..	..					8				
o	..	..	1				1				
r	..	..	8						9		
nil	..	..	1						1		

[1]Mara, southwest Kenya 12.8.63. [2]Abundance data not obtained; presence in unburnt (U) or burnt (B) part of pasture indicated by +.
[3]*E. paniciformis* (—, +), *E. tenuifolia* (+, +) recorded in pasture; species not separated in faecal analysis.
[4]Recorded in faeces only.
[5]Data corrected for < 100 fragments recorded per sample (see text).

numbers of fragments recorded therefore probably represent a considerable overestimation in relation to the other grasses, but the frequency data are unaffected.) In two of the four series where abundance data were obtained for the grasses in the pasture *Themeda* was recorded as "abundant" and might have been eaten to a large extent for this reason alone; in the other two, however, it was present in small quantities only and the results thus suggest that it was deliberately selected. The same applies to *Cynodon*. The high degree of utilisation of these two species is in accord with previous findings regarding domestic stock; *Themeda* is stated by Bogdan (1958) and Edwards and Bogdan (1951) to be a particularly important food-plant and both *Cynodon dactylon* (at least in some growth forms) and *C. plectostachyus* are also important. With regard to wild animals Bayer (1955) notes that *Themeda* largely supported the vast herds of antelopes which formerly existed over large areas of South Africa. Lamprey (1963) found that in the Tarangire Game Reserve of Tanzania the percentage of *Themeda* in the diet of wildebeest, zebra and buffalo *Syncerus caffer* merely reflected the percentage available in the pasture, but that *Cynodon dactylon* was probably deliberately selected. Talbot

TABLE IV

ANALYSIS OF FAECES FROM CATTLE (C), WILDEBEEST (W) AND ZEBRA (Z) (PASTURE MATURE AND MOSTLY BROWN)[1]

Pasture composition[2]		*Analysis of faeces*						
		C		W		Z		*Total*
		n/10	$\bar{x}$	n/10	$\bar{x}$	n/10	$\bar{x}$	N/30
Aristida spp.[3]	..	**1**	2·1	**2**	1·7	—	0·3	**3**
Bothriochloa insculpta ..	f	**4**	4·6	**6**	6·3	—	0·8	**10**
Brachiaria eruciformis ..	..	**1**	1·8	**2**	2·2	—	0·7	**3**
Chloris pycnothrix	..	—	0·3	—	0·1	—	0·1	—
Cymbopogon pospischilii ..	..	—	1·0	—	1·5	**2**	2·2	**2**
Cynodon dactylon	f	**10**	58·2	**9**	37·2	**10**	61·2	**29**
Dactyloctenium aegyptium	..	—	—	—	—	—	—	—
Enneapogon elegans ..	..	—	0·1	—	—	—	0·4	—
Eragrostis spp.[3]	..	—	2·6	**4**	3·4	**4**	5·5	**8**
Eriochloa nubica	..	—	0·8	**4**	7·4	—	1·2	**4**
Harpachne schimperi ..	..	—	0·4	—	0·1	—	0·1	—
Microchloa kunthii	..	—	—	—	—	—	—	—
Pennisetum mezianum ..	f	**1**	1·3	**3**	5·3	**2**	1·4	**6**
Setaria pallide-fusca ..	..	—	0·1	—	0·5	—	0·1	—
Sporobolus pyramidalis ..	lf	—	0·5	—	0·5	—	0·5	—
Themeda triandra	..	**10**	17·3	**10**	23·0	**10**	13·4	**30**
Tragus berteronianus ..	..	—	—	—	—	—	—	—
Dinebra retroflexa[4] ..	..	**1**	1·2	**4**	3·1	**7**	6·6	**12**
Panicum coloratum[4] ..	..	**1**	2·3	—	—	**1**	0·7	**2**
Unidentified grasses[4] ..	..	**5**	5·2	**5**	7·1	**4**	4·7	**14**
Dicotyledons a	..	2		5		2		
f	..	6		4		3		
o	..	2		1		4		
r	..					1		
nil	..							

[1]Nairobi National Park, southern Kenya 23.2.62. [2]Species without an abundance symbol (see text) were present in small quantities only.
[3]*A. adoensis, A. adscensionis, A. elytrophoroides* and *E. aulacosperma, E. braunii, E. cilianensis, E. exasperata, E. superba, E. tenuifolia* (f) recorded in pasture; species not separated in faecal analysis.
[4]Recorded in faeces only.

(1962) also found that *C. dactylon* was important to the four species he studied (wildebeest, Thomson's and Grant's gazelle, and impala *Aepyceros melampus*) although *Themeda* formed a large part of the diet of wildebeest and impala only. Grzimek and Grzimek (1960), however, who noted the grasses which did or did not show signs of having been grazed at a series of stations in the Serengeti, concluded that *Cynodon dactylon* was a preferred foodplant of the Serengeti plains animals but that *Themeda* was largely refused.

(*b*) Species sometimes eaten by many of the animals present but often largely ignored:

TABLE V

ANALYSIS OF FAECES FROM GRANT'S GAZELLE (G), THOMSON'S GAZELLE (TG), ELAND (E), HARTEBEEST (H), WILDEBEEST (W) AND ZEBRA (Z) (PASTURE MATURE, BROWN)[1]

Pasture composition[2]		*Analysis of faeces* G[5] n/10	$\bar{x}$	TG n/10	$\bar{x}$	E[5] n/10	$\bar{x}$	H n/10	$\bar{x}$	W n/10	$\bar{x}$	Z n/10	$\bar{x}$	*Total* N/60
Aristida spp.[3]	..	—	0·3	—	0·2	—	—	—	0·2	—	0·8	—	0·8	—
Bothriochloa insculpta	o	—	0·4	—	0·2	2	0·2	—	0·1	—	0·4	—	0·8	2
Brachiaria eruciformis	r	—	0·5	—	0·1	1	1·6	—	0·1	—	0·2	—	0·1	1
Chloris pycnothrix	..	—	—	—	—	—	—	—	—	—	—	—	—	—
Cynodon spp.[3]	..	7	30·4	10	14·7	9	12·7	1	1·5	7	10·1	9	7·5	43
Dinebra retroflexa	o	—	0·2	—	—	—	—	—	—	—	0·4	—	—	—
Echinochloa colonum	..	—	—	—	0·1	—	0·2	—	—	—	—	—	—	—
Eragrostis spp.[3]	..	—	1·0	4	5·1	3	4·8	—	—	4	5·3	2	1·7	13
Harpachne schimperi	f	—	0·4	3	4·3	2	3·4	—	—	2	2·9	2	1·5	9
Ischaemum brachyatherum	f	—	0·4	—	0·2	—	—	1	1·6	—	—	3	4·1	4
Lintonia nutans	o	—	—	—	—	—	—	—	—	—	—	—	—	—
Microchloa kunthii	r	—	0·9	—	0·9	—	0·4	—	—	—	0·1	—	0·2	—
Panicum spp.[3]	..	1	1·8	—	0·4	2	3·0	—	0·1	—	0·4	—	0·4	3
Pennisetum mezianum	a	7	13·7	10	18·8	10	13·7	3	3·0	8	10·7	10	16·8	48
Sporobolus discosporus	o	—	—	—	0·1	—	0·2	—	—	—	—	—	—	—
S. pyramidalis	..	—	—	—	0·2	—	—	—	—	—	—	—	—	—
Themeda triandra	a	9	42·9	10	51·0	10	49·8	10	92·1	10	64·1	10	62·9	59
Digitaria milanjiana[4]	..	1	5·3	4	3·1	3	4·2	1	0·8	1	2·0	1	1·8	11
Unidentified grasses[4]	..	1	1·4	—	0·6	3	4·0	—	0·5	1	1·7	1	1·4	6
Dicotyledons a	..	10				10								
f	..			8						2		1		
o	..			2				2		5		3		
r	..							7		3		6		
nil	..							1						

[1]Kajiado, southern Kenya, 15.7.63.

[3]*A. adscensionis* (f), *A. keniensis*; *C. dactylon*, *C. plectostachyus* (la); *E. aulacosperma* (o), *E. ciliatensis* (r) *E. tenuifolia*; *P. atrosanguineum*, *P. coloratum*, *P. repens* recorded in pasture: species not separated in faecal analysis.

[4]Recorded in faeces only.

[5]Data corrected for <100 fragments recorded per sample (see text).

Aristida adoensis (see Tables 1, 2, 3), *Eragrostis* spp. (Tables 1, 2, 4, 5,) and *Harpachne schimperi* (Tables 5, 6) are among the grasses which come into this category. The available data on the abundance of these species in the pasture suggest, however, that when they were eaten to a considerable extent it may simply have been because they were common; the fact that on other occasions they were largely ignored supports this conclusion. In addition when *Aristida adoensis*, which is usually regarded as of low grazing value, was eaten to a considerable extent it was present in the form of new growth after a burn, when it is probably at its most palatable stage.

(*c*) Species consistently eaten to little or no extent whether abundant or not: the remaining grasses in Tables 1-6 include some which were probably largely ignored simply because they were uncommon in the pasture. Others were largely refused despite being common; these include *Eustachys paspaloides*, *Panicum massaiense* and *P. repens* (Table 2). *Panicum poaeoides* and *Sporobolus pellucidus* (Table 6), and especially *Pennisetum mezianum* (Tables 2, 4, 6) with one

TABLE VI

ANALYSIS OF FAECES FROM GRANT'S GAZELLE (G), THOMSON'S GAZELLE (TG), HARTEBEEST (H) AND WILDEBEEST (W) (PASTURE MATURE, BROWN)[1]

Pasture composition[2]		*Analysis of faeces*								
		G[5] n/10	$\bar{x}$	TG n/10	$\bar{x}$	H n/10	$\bar{x}$	W n/10	$\bar{x}$	*Total* N/40
Aristida spp.[3]	..	—	0·2	—	0·2	2	2·3	1	2·0	3
Bothriochloa insculpta ..	lf	—	0·8	—	0·5	1	1·2	4	3·6	5
Chloris pycnothrix ..	..	—	—	—	—	—	0·1	—	—	—
Cynodon dactylon ..	a	10	59·4	10	66·4	1	3·8	10	32·4	31
Digitaria scalarum ..	..	—	—	—	0·2	—	—	—	0·2	—
Echinochloa stagnina ..	..	—	—	—	—	—	—	—	—	—
Enneapogon elegans ..	..	—	—	—	0·1	—	—	—	—	—
Eragrostis spp.[3]	..	1	1·5	2	3·0	—	0·5	5	5·6	8
Harpachne schimperi ..	a	2	3·3	8	16·0	1	1·0	6	6·3	17
Ischaemum brachyatherum	lf	1	4·4	—	0·2	9	30·3	4	7·7	14
Lintonia nutans	lf	—	0·1	—	—	—	—	—	—	—
Microchloa kunthii ..	..	—	—	—	—	—	—	—	—	—
Panicum infestum ..	..	—	0·6	1	0·8	—	—	—	0·4	1
P. poaeoides	lf	—	0·1	—	—	—	0·2	—	0·3	—
Pennisetum mezianum ..	a	—	1·0	—	0·7	—	0·7	1	1·5	1
Rhynchelytrum repens ..	..	—	—	—	0·5	—	0·1	—	0·5	—
Setaria setulosa	lf	—	0·3	—	0·2	—	0·1	1	1·3	1
Sporobolus discosporus ..	..	—	—	—	—	—	—	—	—	—
S. pellucidus	f	—	—	—	0·2	—	—	—	—	—
S. phyllotrichus	..	—	—	—	—	—	—	—	—	—
Themeda triandra ..	..	6	19·0	10	7·0	10	58·4	10	33·1	36
Dinebra retroflexa[4] ..	..	—	0·3	—	0·1	—	0·4	—	—	—
Panicum coloratum[4] ..	..	—	0·7	1	1·0	—	—	—	0·4	1
Unidentified grasses[4] ..	..	6	7·9	4	2·9	—	0·9	4	4·5	14
Dicotyledons a.. ..	..	8								
f.. ..	..									
o ..	..	1		3		4		3		
r ..	..	1		7		6		7		
nil ..	..									

[1]Nairobi National Park, southern Kenya 1.8.63.

[2]*A. adoensis, A. keniensis, E. aulacosperma, E. cilianensis, E. exasperata* (lf), *E. tenuifolia* (a) recorded in pasture; species not separated in faecal analysis.

[4]Recorded in faeces only.

[5]Data corrected for <100 fragments recorded per sample (see text).

notable exception when it occured in 48 out of 60 samples (Table 5). *P. mezianum* is usually regarded as of little value except possibly when young (Bogdan 1958; Edwards and Bogdan 1951) but several of the other species are known to be of value to stock (Bogdan 1958).

The grasses shown as having been recorded in the faeces only, and the unidentified grasses, are likely to have been species which were overlooked during the analyses of the pastures because they were not in flower. In a current study pastures are being analysed in greater detail on a percentage leaf cover basis, both in order to provide a more objective basis for comparison with the faecal analyses and also to make the list of the grasses present more complete. Species which are not in flower are being identified by means of macroscopic or microscopic vegetative characters.

2. *Preference differences between animal species*

The frequency data again provide the most reliable source of information but large differences between animals with respect to the number of fragments of any one grass recorded are probably meaningful, and can be used with caution to qualify the frequency information. Thus in Table 1 nearly all individuals of the four animal species concerned had eaten *Cynodon* and *Themeda*, but the Grant's gazelle show a much higher mean number of *Cynodon* fragments and a much lower number of *Themeda* fragments than the other three animals. Likewise in Table 6 all ten samples from Thomson's gazelle, hartebeest and wildebeest contained *Themeda*, but the mean number of *Themeda* fragments was far lower in the Thomson's gazelle than in the other two species.

Tables 1-6 show that there is a considerable overlap in the preferences of the animal species involved since *Themeda* and *Cynodon* figure very largely in the diet of almost all animals. A notable exception concerns the hartebeest; in each of the two series involving this species (Tables 5 and 6) only one sample out of ten contained *Cynodon*. There are greater differences between animal species in the use made of a number of other grasses, *vide Eragrostis* spp. (Tables 1, 2, 4, 6), *Bothriochloa insculpta* (Tables 4, 6), *Eriochloa nubica* and *Dinebra retroflexa* (Table 4), and *Harpachne schimperi* and *Ischaemum brachyatherum* (Table 6).

Lamprey (1963), Turner and Watson (1965) and Bell (personal communication 1967) have found that there is considerable overlap in the diets of plains animals as far as the plant species taken are concerned, but that separation of diet is achieved by preference for different plant parts, different growth stages, or different feeding levels. Talbot (1962) also found that taking into account not only species, but also plant parts and growth stages, diets were complementary rather than overlapping. The present results, involving leaf and sheath epidermis only, suggest that there is considerable overlap in the use of *Themeda* and *Cynodon*, although it is still possible that in some cases there was differential selection of older or younger leaves and stems by different animals.

3. *Numbers of grasses eaten by different animal species*

Table 7 records the mean number of grasses eaten by each animal species in the different series. A comparison, using the F test, was made of the variance between animal species with the variance between individuals (same species). This showed that significant differences

TABLE VII

MEAN NUMBER OF GRASSES[1] EATEN BY DIFFERENT ANIMAL SPECIES

Table	*Total grasses available*	C	T	G	TG	E	H	W	Z	*Significant differences (see text)*
1	11			5·9	5·7			6·2	7·0	Z-TG
2	12	5·9			4·9			5·9		
3	10		5·4	3·4	5·0				6·2	Z-G, TG-G, T-G
4	19	8·4						9·0	7·5	
5	18			5·1	6·6	5·8	3·8	6·2	6·5	TG-H, Z-H, W-H, E-H
6	23			6·2	6·5		5·2	8·7		W-H, W-G, W-TG

[1]All grasses scoring one or more fragments in a sample have been taken into account.
C=cattle; T=topi; G=Grant's gazelle; TG=Thomson's gazelle; E=eland; H=hartebeest; W=wildebeest; Z=zebra.

between animal species, with respect to the number of grasses eaten, were present in Tables 3, 5 and 6 ($P < 0{\cdot}01$) and Table 1 ($P < 0{\cdot}05$). Use of the sequential Q test (Snedecor 1956) showed that the significant differences in each case were as follows :—

Table 1: the zebra had taken significantly more grasses than the Thomson's gazelle (and nearly significantly more than the Grant's gazelle and wildebeest).

Table 3: the Grant's gazelle had taken significantly less grasses than the zebra, Thomson's gazelle and topi.

Table 5: the hartebeest had taken significantly less than the Thomson's gazelle, zebra, wildebeest and eland.

Table 6: the wildebeest had taken significantly more than the hartebeest, Grant's and Thomson's gazelle.

The differences between animals in these four series are not very great, but there is some evidence that zebra tend to be the most catholic in their choice of grasses whereas Grant's gazelle and hartebeest appear to use fewer grasses than the other species.

4. *Utilisation of dicotyledons*

Although the assessment of material from dicotyledons was made on a subjective basis it clearly reveals the relative extent to which the animals concerned make use of plants other than grasses. The dicotyledons listed in the study areas included *Acacia drepanolobium* and shrubs or herbs such as *Aspilia multiflora*, *Becium* sp., *Cassia hildebrantii*, *Commicarpus pedunculosus*, *Crotalaria spinosa*, *Cucumis* sp., *Gnaphalium declinatum*, *Hibiscus flavifolius*, *Indigofera* spp., *Lysimachia* sp., *Monsonia longipes*, *Rhamphicarpa* spp., *Rhynchosia chrysadenia*, *Sida* spp. and *Solanum incanum*.

Samples from Grant's gazelle (Tables 1, 3, 5, 6) all or nearly all contain a large amount of dicotyledonous material; in a number of samples grass fragments were very sparse. In the one collection of eland samples examined (Table 5) these also all contained large quantities of material from dicotyledons, and in four of the ten samples grass fragments were sparse.

Most Thomson's gazelle samples (Tables 1, 2, 3, 5, 6) contain a considerable amount of dicotyledonous material (Table 6 being an exception), noticeably less than Grant's gazelle or eland samples but usually distinctly more than hartebeest (Tables 5 and 6), wildebeest (Tables 1, 2, 4, 5, 6) or zebra (Tables 1, 3, 4, 5) samples. (Table 4 is exceptional in the case of wildebeest and zebra.)

The two series involving cattle (Tables 2, 4) indicate that they made moderate use of dicotyledons in these instances.

5. *Seasonal changes in preference*

The growth stage and condition of a grass, affecting its palatability and nutritive value, are clearly of great importance in influencing food preferences. The six series of analyses presented here were not intended to provide data on seasonal changes in preferences since they concern six different areas and do not cover the full range of seasonal changes in conditions. Nevertheless Tables 1-3 involve pastures which had been wholly or partly burnt and contained short, green grass whilst Tables 4-6 refer to pastures where the grass was mature and partly or wholly brown. An indication of a seasonal change in preference is afforded by *Aristida*, which was utilised to a considerable extent when available as young growth (Tables 1-3) but to a very small extent when mature (Tables 4-6). The effects of changes in growth stage and condition are being more closely examined in a current study where food preferences are being studied at intervals on a single pasture.

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SUMMARY

Data, particularly of a quantitative nature, on the food preferences of African plains ungulates are scarce.

Because of the difficulty, in certain conditions, of applying other methods of studying preferences an increasing amount of attention is being paid to the use of faecal analysis, whereby plant epidermis is identified in faeces.

The results of applying faecal analysis to six areas of *Acacia-Themeda* grassland in southern Kenya on which 3-6 mammal species were grazing together are described. The species involved were cattle, wildebeest, hartebeest, topi, Grant's and Thomson's gazelles, eland and zebra.

With regard to the relative importance of different grasses as foodplants, two species—*Themeda triandra* and *Cynodon dactylon*—were consistently eaten by most of the animals irrespective of whether these grasses were abundant in the pasture or not. A number of other grasses, such as *Aristida adoensis*, *Eragrostis* spp. and *Harpachne schimperi*, were sometimes

eaten by many of the animals present but were largely ignored on other occasions or by other animals. Even when these species were eaten, however, it may simply have been because they were abundant in the pasture rather than that they were being selected in preference to other species. A third category of grasses contained those which were usually or always ignored even when abundant. *Pennisetum mezianum* was the most prominent example in this category, frequently being very common in the areas concerned but rarely being eaten to any extent.

Because of the popularity of *Themeda* and *Cynodon* amongst almost all the animals (with the exception of hartebeest which largely ignored *Cynodon*), there was considerable overlap in diets.

There were no great differences with regard to the numbers of grasses eaten by different animal species, but there was some evidence that zebra tended to take more grasses than other animals, and that hartebeest and Grant's gazelle tend to take fewer.

Grant's gazelle and eland samples contained large amounts of dicotyledonous materials in relation to the amount of grasses they consumed. Thomson's gazelle made considerable, and cattle moderate, use of dicotyledons whereas the hartebeest, wildebeest and zebra appeared to use considerably less dicotyledonous material than the other animals.

REFERENCES

ANON. 1962. Foods and feeding. *Lammergeyer* 2 (1): 62-71.

BAYER, A. W. 1955. The ecology of grasslands. *In* MEREDITH, D. (ed.) *The grasses and pastures of South Africa*. Cape Town: Central News Agency.

BOGDAN, A. V. 1958. *A revised list of Kenya grasses*. Nairobi: Govt. Printer.

BREDON, R. M. and MARSHALL, B. 1962. Selective consumption by stall-fed cattle and its influence on the results of a digestibility trial. *E. Afr. agric. For. J.* 27 (3): 168-172.

BRYNARD, A. M. and PIENAAR, U. DE V. 1960. Annual report of the Biologist, 1958/1959. *Koedoe* 3:127-167.

DOUGALL, H. W. and BOGDAN, A. V. 1958. Browse plants of Kenya with special reference to those occurring in South Baringo. *E. Afri. agric. J.* 23: 236-245.

DOUGALL, H. W., DRYSDALE, V. M. and GLOVER, P. E. 1964. The chemical composition of Kenya browse and pasture herbage. *E. Afr. Wildl. J.* 2: 86-121.

EDWARDS, D. C. 1959. *In* BUTLER, R. J. (ed.). *Atlas of Kenya*. Nairobi: Survey of Kenya.

EDWARDS, D. C. and BOGDAN, A. V. 1951. *Important grassland plants of Kenya*. Nairobi: Sir Isaac Pitman and Sons.

EGGELING, W. J. 1947. *An annotated list of the grasses of the Uganda Protectorate*. 2nd ed. Entebbe: Govt. Printer.

ELOFF, F. C. 1959, 1961, 1962. Observations on the migration and habits of the antelopes of the Kalahari Gemsbok Park, Part II, III, IV. *Koedoe*, 2: 30-51; 4: 18-30; 5: 128-136.

GLOVER, P. E., STEWART, J. and GWYNNE, M. D. 1966. Masai and Kipsigis notes on East African plants. I-Grazing, browse, animal associated and poisonous plants. *E. Afr. agric. For. J.* 32 (2): 184-191.

GRZIMEK, M. and GRZIMEK, B. 1960. A study of the game of the Serengeti plains. *Z. Säugetierk.* 25: 1-61.

HERCUS, BARBARA H. 1960. Plant cuticle as an aid to determining the diet of grazing animals. *Proc. 8th int. Grassld Congr.*: 443-447.

KILEY, MARTHE 1966. A preliminary investigation into the feeding habits of the waterbuck by faecal analyses. *E. Afr. Wildl. J.* 4: 153-157.

LAMPREY, H. F. 1963. Ecological separation of the large mammal species in the Tarangire Game Reserve. Tanganyika. *E. Afr. Wildl. J.* 1: 63-92.

LEISTNER, O. A. 1959. Notes on the vegetation of the Kalahari Gemsbok National Park with special reference to its influence on the distribution of antelopes. *Koedoe* 2: 128-151.

MARTIN, D. J. 1954. Features of plant cuticle: an aid to the analysis of the natural diet of grazing animals, with especial reference to Scottish hill sheep. *Trans. Proc. bot. Soc. Edinb.* 36: 278-288.

MITCHELL, B. L. 1963. A first list of plants collected in the Kafue National Park. *Puku*, 1: 75-191.

ORR, D. J. C. 1964. *Grazing succession of game animals in Ngorongoro Crater*. Tanganyika Game Department, Dar es Salaam (typescript).

ROBERTS, B. R. 1963. Ondersoek in die plantegroei van die Willem Pretorius Wildtuin. *Koedoe*, 6: 137-164.

SCOTT, J. D. 1955. Pasture plants for special purposes. *In* Meredith, D. (ed.). *The grasses and pastures of South Africa*. Cape Town: Central News Agency.

SNEDECOR, G. W. 1956. *Statistical methods applied to experiments in agriculture and biology*. Fifth edition. Ames, Iowa: Iowa State University Press.

STEWART, D. R. M. 1965. The epidermal characters of grasses, with special reference to East African plains species. *Bot. Jb.* 84: 63-174.

STEWART, D. R. M. 1967. Analysis of plant epidermis in faeces: a technique for studying the food preferences of grazing herbivores. *J. appl. Ecol.* 4 (1): 83-111.

STORR, G. M. 1961. Microscopic analysis of faeces, a technique for ascertaining the diet of herbivorous mammals. *Aust. J. biol. Sci.* 14: 157-164.

TALBOT, L. M. 1962. Food preferences of some East African wild ungulates. *E. Afr. agric. For. J.* 27 (3): 131-138.

TALBOT, L. M. and TALBOT, MARTHA, H. 1963. The wildebeest in Western Masailand, East Africa. *Wildl. Monogr.* no. 12: 1-88.

TURNER, M. I. M. and WATSON, R. M. 1965. An introductory study on the ecology of hyrax (*Dendrohyrax brucei* and *Procavia johnstoni*) in the Serengeti National Park: *E. Afr. Wildl. J.* 3: 49-60.

VAN DER SCHIJFF, H. P. 1959. Weidingsmoontlikhede en weidingsprobleme in die Nasionale Krugerwildtuin. *Koedoe*, 2: 96-127.

VESEY-FITZGERALD, L. D. E. F. 1960. Grazing succession among East African game animals. *J. Mammal.* 41 (2): 161-172.

VESEY-FITZGERALD, D. F. 1965. The utilisation of natural pastures by wild animals in the Rukwa Valley, Tanganyika. *E. Afr. Wildl. J.* 3: 38-48.

WATSON, R. M. and KERFOOT, O. 1964. A short note on the intensity of grazing of the Serengeti plains by plains game. *Z. Säugetierk.* 29 (5): 317-320.

WILSON, V. J. 1965. Observations on the greater kudu *Tragelaphus strepsiceros* Pallas from a tsetse control hunting scheme in Northern Rhodesia. *E. Afr. Wildl. J.* 3: 27-37.

WILSON, J. G. and BREDON, R. M. 1963. Nutritional value of some common cattle browse and fodder plants of Karamoja, Northern Province, Uganda, *E. Afr. agric. For. J.* 28 (4): 204-208.