Feeding behaviour of sable *Hippotragus niger niger* (Harris, 1838) in the Rhodes Matopos National Park, Zimbabwe

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Sable, *Hippotragus niger niger* (Harris, 1838) were studied in the Rhodes Matopos National Park, Zimbabwe. They spent more time feeding during the hot dry months than the hot wet months, cropped grass at 40 to 140 mm above the ground, showed preference for a grass sward of below 160 mm when feeding and were highly species selective. Selection of food components was directed at a high crude protein content and low crude fibre content in plant parts eaten.

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Die swartwitpens, *Hippotragus niger niger* (Harris, 1838) is in die Rhodes Matopos Nasionale Park in Zimbabwe bestudeer. Hulle het meer tyd aan wei spandeer gedurende die warm droë maande as in die warm nat maande; gras teen 40 tot 140 mm bokant die grond gevreet, grasveld van laer as 160 mm verkies en was baie spesies selektief. Seleksie van plantkomponente was gerig op hoë ru-proteïen en 'n lae ruveselgehalte in die plantdele wat gevreet is.

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A multitude of studies have been undertaken to investigate animal populations in relation to their environment, in particular their food source. This aspect was examined for sable *Hippotragus niger niger* (Harris, 1838) in the Rhodes Matopos National Park in Zimbabwe as part of a study in population dynamics (see Grobler 1978).

The main objectives were to determine daylight feeding patterns, the level at which sable fed, area and species selection, the nutrient quality of grass components and the grass swards selected and rejected.

Methods

A breeding herd of sable which numbered up to 31 and was conditioned to human presence formed the study group for detailed observation. The herd occupied an area of diverse vegetation types and all individuals of the group could be identified from photographs. Observations were carried out from a vehicle and on foot at a range of 15 to 100 m using a portable taperecorder and 10 × 50 mm binoculars during the period August 1977 to May 1978, and between 06h30 and 18h00.

Daylight activity

Major activities (feeding, walking, grooming, drinking, etc) were spot recorded at five-minute intervals for up to six adult females at any one time. These females ranged in age from 3 to over 10 years old and the same individuals were used for the full observation period and in successive observations. Results on daylight activity were obtained when nutrient quality of the grass was at its lowest (August, September, October) and at its highest (November, December) for 1977.

For comparative purposes the activities of the adult females were combined into three categories: feeding, lying down and 'other activities'. No successful nocturnal observations were made although sable were seen feeding on moonlight nights, were active before sunrise and sometimes continued feeding after 18h00.

Feeding level and species selection

It was apparent during observation periods that sable were selective of the level at which they fed. To quantify this, five-minute interval spot feeding records were taken over a six-month period (August 1977 to January 1978) while daylight activity was being observed. Feeding levels were divided into: (a) below the knee, (b) between the knee and the sternum, (c) between the sternum and back, and (d) above the level of the back.

As most of the feeding was taking place at level (a), actual bite height above the ground was measured for this level at feeding stations, in a vertical line from the ground to the bite. For comparative purposes, where impala *Aepyceros melampus*, wildebeest *Connochaetes taurinus* and tsessebe *Damaliscus lunatus* were feeding in the same area as sable, bite heights were measured for these.

Feeding stations where high density feeding (over 60 min) took place were examined in detail. Such sites were distinct during the dry months but less so in the wet months when food was superabundant. Ten randomly placed square-metre quadrates were examined at feeding stations and the following recorded in each: grass species present, number of tufts present, number of tufts bitten in each species, bite height, plant components eaten, greenness in the plant (subjective estimate of green to brown ratio), leaf to stem ratio for each species (subjective estimate) and the mean cover height. Mean cover height was measured on a board placed randomly throughout the feeding station (Joubert 1976).

Chemical composition

For the purpose of investigating the chemical composition of accepted and rejected components of the same plant or different species, about 20 g of material were collected from randomly selected plants for analysis. Collecting of rejected components took place within square-metre quadrates where feeding had taken place. Without physically removing food items from the animal after ingestion there was no way the actual parts eaten could be analysed. Food material was then taken from a plant which had been fed on by sable and usually involved collecting components which were not accessible to the sable but were by all indications the same as those that had been eaten. Rejected components were those on plant species not eaten but available for consumption by sable.

To assess mean habitat quality of selected and rejected feeding sites as they affect sable, the grass layer from ten randomly placed square-metre quadrates from each were clipped and chemically analysed. Initially an analysis was carried out for all the grass in each square-metre quadrate, but this was later refined to a separate analysis for the 40 to 160-mm layer and that which occurred above 160 mm.

The chemical analysis was carried out using the proximate analysis as in the Association of Official Agricultural Chemists or 'AOAC handbook', Horwitz (1965). The proximate analysis system of nutrient analysis has many shortcomings but was the only one available for the study. The protein extract appears to be one of the most reliable parts of it and fortunately is the most important aspect of the analysis.

Because of the inherent calcium and phosphorus deficiency in granite soils (D. Richardson *pers comm.*), the presence of these were investigated in selected and rejected foodplants by analysing the material collected for the protein and crude fibre analysis. Faecal nitrogen was also determined from fresh faecal samples of up to six individual adult females while they were feeding on a selected area under observation. Faecal samples were collected on the day after feeding was observed so that they could be compared to food eaten and perhaps give an indication of habitat quality.

Area selection

For comparative purposes, what appeared to be suitable feeding areas, but rejected by sable and adjoining the feeding stations, were analysed for grass composition and chemical composition using the same methods as above.

Results

Daylight activity

A total of 623,5 sable hours representing 87 285 five-minute spot recordings were covered during the exercise. The herd never moved more than 1,75 km (mean 1,22 km, range 0,75 to 1,75 km) during a daylight period and never spent more than a total of 60 min away from feeding stations. Time spent away from feeding areas involved walking from one feeding station to another or walking to a watering point. Sable in the study area were never more than 1 km from water and the study herd were recorded drinking daily, mainly between 12h00 and 13h00. Drinking was a collective function involving the whole herd and intermittent feeding took place en route to watering points, which were small secluded springs or pools in a stream.

Adult male activity was less synchronised than the cycles of other herd members (from casual observations), a feature also noted by Estes (1974). There was also tremendous individual variation in adult male activity and to interpret this meaningfully would require a separate study.

Feeding patterns during August to October were similar (Table 1, Fig. 1) with peak feeding from 06h00 to 09h00 and 16h00 to 17h00 (August, September) and 14h00 to 17h00 (October) with a second peak at midday. The midday peak was often associated with drinking. The ratios of feeding to all other activities during the three-month period were 0,87:1, 1,06:1 and 0,90:1 respectively.

Table 1 Mean time in hours spent on various activities by selected adult female sable during daylight (06h30 to 18h00) in the Matopos, Zimbabwe in 1977

Month	Feeding	Lying	Other	*n*
August	5,35(0,21)	5,69(0,27)	0,44(0,04)	16
September	5,98(0,18)	4,77(0,14)	0,88(0,06)	15
October	5,52(0,16)	5,45(0,15)	0,65(0,07)	10
November	5,10(0,21)	6,00(0,10)	0,48(0,10)	5
December	4,89(0,08)	5,98(0,04)	0,62(0,05)	6
*August	8,09(0,08)	2,28(0,05)	1,14(0,07)	3

Standard Error of the mean in parenthesis
n = number of sable in sample (August, September, October include 3 combined samples)
* = control sable (see text)

During November the herd moved to an area which had been burnt where food of a high nutrient quality was readily available. Only one full daylight period of observation was possible as the herd fed over a large area, but two unsuccessful attempts provided partial confirmation of a pattern involving a series of distinct feeding and resting periods. The sable would feed actively for two to three hours, then rest for two to three hours. The ratio of feeding to all other activities during November was 0,71:1.

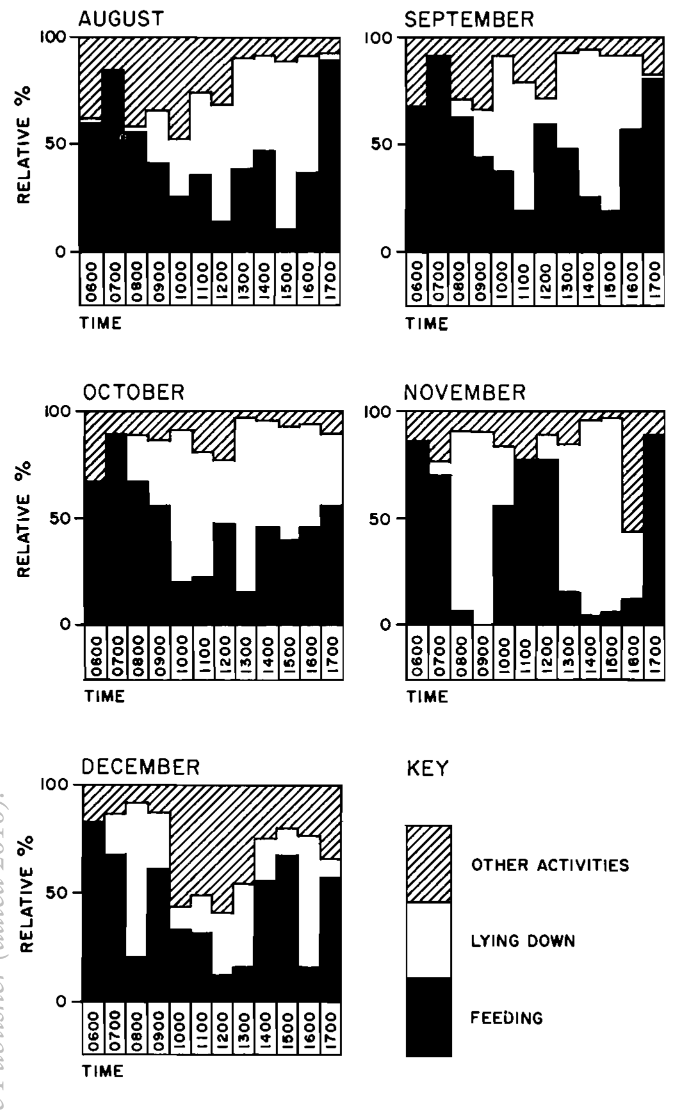

Fig. 1 Daylight activity patterns of selected adult female sable in the Matopos, Zimbabwe.

By December, due to good rainfall, food was readily available, visibility was poor and observations were often hampered by rain. Again only one full daylight observation period was achieved which once more conformed with two halfday observation periods. The pattern for December was intermittent feeding and resting throughout the day at a ratio of 0,74:1.

Group size in the Matopos sable reached a maximum during the hot dry months (Grobler 1974) when they concentrated on selected (limited) food sources available to them. They spent more time feeding during the hot dry months (September, October) than in the hot wet months (November, December), (P<0,0002) using the non-parametric Mann-Whitney U test as in Siegel (1956) and the correction formula:

$$Z = \frac{\dfrac{U - N_1N_2}{Z}}{\sqrt{\left(\dfrac{N_1N_2}{N(N-1)}\right)\left(\dfrac{N_3 - N}{12} - \Sigma T\right)}}$$

The sable were in poor physical condition during the food limiting period and in good condition during the rains when food was abundant.

During October, three partly free-ranging adult sable in a control paddock of about 5 ha were subjected to unfavourable range and lost condition rapidly. A full daylight observation period on the control sable and wild sable on the same day by independent observers showed feeding to other activity ratios of 2,37:1 and 0,87:1 respectively.

Feeding level, species selection and area selection

A total of 3 394 five-minute interval spot feeding records showed 3 373 to be below the knee (level a), 13 between the knee and sternum (level b), four between the sternum and back (level c) and four above the level of the back (level d). Of the sable bites measured, 96,42% were between 40 and 140 mm above the ground (Table 2) despite the fact that suitable food components were readily available below 40 mm and above 140 mm on many occasions.

Table 2 Feeding levels of sable, impala, wildebeest and tsessebe as grazers in Matopos, Zimbabwe, during August 1977 to April 1978

Bite height in mm	Number of bites measured			
	Sable	Impala	Wildebeest	Tsessebe
10–19	0	8	0	0
20–29	0	41	8	8
30–39	7	98	23	32
40–49	57	78	44	28
50–59	58	17	49	27
60–69	79	9	42	18
70–79	78	5	25	16
80–89	78	1	27	17
90–99	71	1	3	3
100–109	79	0	2	3
110–119	17	0	0	0
120–129	12	0	0	0
130–139	11	0	0	1
140–149	3	0	0	0
150–159	2	0	0	1
160–169	3	0	0	0
170–179	1	0	0	0
180–189	2	0	0	0
190–199	1	0	0	0
200–209	0	0	0	0
Totals	560	258	223	154

During late September and most of October 1977 the study herd had access to new growth on a burnt (crude protein 12,1%) area but remained in inferior quality grassland (crude protein 2,8%) adjacent to this. An assessment of the burnt area revealed open (accessible) grass tufts with a high leaf ratio, the leaves themselves containing high crude protein (over 12%) and relatively low crude fibre (less than 40%) and all the grass was 100% green. The mean cover height of the newly flushed grass was however, 42 mm (SE $\bar{X}$ 0,20) above the ground and was kept at this level by grazing impala *Aepyceros* *melampus*, wildebeest *Connochaetes taurinus* and tsessebe *Damaliscus lunatus*. Impala were feeding at 20 to 60 mm above the ground and tsessebe at 30 to 90 mm (Table 2).

Rain in early November increased the vigour of growth on the burn, the mean cover height of the grass increased to 60 mm and 70 mm in two sample areas (SE $\bar{X}$ 2,15 and 3,45) and the sable started feeding on the burn. Towards the end of November grazing pressure from the four species in question reduced the mean cover height to below 50 mm and the sable once more commenced feeding on adjacent, inferior habitat with a crude protein content of 3%. By the first week in December the rains had set in and the mean cover height on the burn increased to 62 mm (SE $\bar{X}$ 2,17) and the sable moved back on to the burn for the remainder of the month.

No sable bites were recorded below 40 mm above the ground while impala were feeding almost to ground level and wildebeest and tsessebe down to 20 and 29 mm. Although sable were shown to graze over a greater range of height above the ground, competition from other species may occur at the lower levels, during the crucial time of the year. The sable were for example the last of the four species under discussion to start utilizing new grass growth (*e.g. Digitaria milanjiana*) which became available immediately after the late dry season when times are critical.

The upper limits may be equally critical to sable. They will for example only feed extensively on the highly nutritious *Panicum maximum* during the hot dry season when it is low enough as it would require feeding above 140 mm above the ground during the wet season.

The partly free-ranging (control) sable were feeding on new growth of *Danthoniopsis pruinosa* during September 1977, at a level between the knee and the sternum. Most of the other grass species normally favoured had been eaten down to the 40 mm level in the control paddock. The crude protein content of the *D. pruinosa* was high (10,5%) and the crude fibre low (37,1%) yet the sable were losing condition rapidly and would have died if left on this pasture. The reason for this was not clear, but may have been due to excess energy expended by being forced to feed at the higher level.

Close scrutiny of grazing sable did not yield any conclusive evidence as to why they should not feed below 40 mm and rarely above the level of the sternum. The presence of tactile hairs on the lips may influence the lower level and the distance that the lip can physically be pulled back might also influence the level of feeding but no evidence could be obtained to substantiate this. It may even be in the physical build of the sable. When drinking, sable will avoid lowering their heads too far either by walking into the water, by kneeling down to drink, by bending one foreleg or by drinking from a sloping bank. One adult female was observed kneeling down to feed on the creeping grass *Digitaria gazensis* during September.

Area selection depended on the composition of the grass layer in terms of structure (of plants available for consumption and of the grass layer), nutrient content and succulence. The highest degree of selection took place during September and October of the study period, when moist areas were sought. The selection for moist areas (which retained greenness longest) could be demonstrated by comparing the density (at feeding stations) of 'indicator species' of grass comprising six species common to moist areas and six common to dry areas (Table 3) as represented in ten square-metre sampling sites on each occasion.

Grass stems often impeded access to the leaf components and the bulk of the material above 160 mm in the Matopos grass layer consisted of stems except in stands of *Panicum maximum*. Area selection was thus directed at grass stands below 160 mm.

Grass species composition of selected areas varied tremendously and no indications were obtained of significant differences between generally accepted and rejected areas. Dense stands of *Pennisetum glaucocladum* were avoided except when cut or burnt after which the nutritious green flush was heavily utilized. Fairly pure stands of *Pogonathria squarrosa* were rejected as were mature stands of *Loudetia simplex*. Areas with a large amount of moribund grass and at the other extreme,

Table 3 Sable selection for moist areas during the dry season in Matopos (Zimbabwe) as demonstrated by the density per square metre of 'indicator' species at feeding stations

Month	Aug		Sept			Oct		Nov (on burn)		Dec		Jan		Feb	Mar	Apr
Day	19	24	9	22	28	5	12			6	21	12	19	16	23	12
Wetland species																
Eragrostis inamoena	–	–	–	1,9	–	0,1	4,1	–	–	–	–	–	–	–	–	–
Fuirena pubescens	–	–	0,2	16,0	9,4	17,4	16,8	–	–	–	0,3	–	–	–	–	–
Digitaria gazensis	–	–	–	6,3	–	2,6	4,4	–	–	–	–	–	–	–	–	–
Eragrostis stapfii	–	0,8	1,5	3,0	3,7	0,5	2,4	–	–	–	–	–	–	–	–	–
Sorghastrum fresii	–	–	–	8,0	–	18,3	3,3	–	–	–	–	–	–	–	–	–
Brachiaria humidicola	–	–	3,8	3,0	12,1	0,1	2,5	–	–	–	–	–	–	–	–	–
Dryland species																
Digitaria pentzii	16,9	22,9	40,8	–	6,0	–	–	–	–	–	10,9	4,7	–	5,6	8,5	18,9
Eragrostis rigidior	4,4	0,8	8,8	–	1,8	–	–	–	–	1,3	1,9	0,8	0,1	0,7	2,0	0,3
Rhynchelytrum repens	5,9	2,7	0,5	–	2,2	–	–	–	–	1,6	1,6	1,4	3,5	0,6	–	2,8
Schizachyrium jeffreysii	3,9	7,0	1,8	–	2,2	1,0	–	–	–	–	1,1	1,2	–	–	–	5,2
Pogonathria squarrosa	7,4	8,0	4,6	–	4,6	–	–	–	–	3,2	2,7	3,0	–	–	–	1,0
Brachiaria nigropedata	0,7	1,5	4,5	–	2,3	–	–	–	–	0,3	3,3	0,6	4,5	6,1	–	1,0

denuded areas were avoided while feeding. Tall dense grassland was also rejected although some areas of *Hyperthelia dissoluta* (a tall grass) were open enough for the sable to feed on other species between the tufts.

With the actual tufts eaten, there was selection for green plants and at no time were sable recorded feeding on any grass that was entirely dry. In the majority of species, the components selected by sable were the leaves, the exceptions being sedges (Cyperaceae) and *Schizachyrium jeffreysii* where both leaves and stems were eaten. Stems were also consumed when eating the fresh shoots of grasses. Selection was further directed at grass species with a high leaf to stem ratio (3:1 or greater) with the exception of *S. jeffreysii* and *Hyperthelia dissoluta*. In the latter the leaves at the base were accessible to sable even though the bulk of the plant consisted of stem components.

There was always a high degree of species selection within a grass sward, except on burnt areas. On burnt areas most species had the right qualities for sable consumption, exceptions were the very small species (cover height less than 40 mm) such as *Microchloa kunthii, Tripogon minimus, Sporobolus festivus*, aromatic species such as *Cymbopogon excavatus* and species with a high stem portion even in early growth stages (e.g. *Aristida junciformis*).

The degree of selection is illustrated in Table 4 which shows the relative abundance in terms of density, the number of plants eaten and number available for each selected species, and the total number of species at a feeding station. The selection index shown is an expression of the percentage of individual plants of a particular species in relation to the number of individuals utilized. Species selection on burns was not included as difficulty was experienced in identifying grass species in the initial growth stages.

Table 4 Species selection by sable in the Matopos (Zimbabwe) in relation to species and plants available

Date	Food Plant	*d*	*E*	*T*	*S*	Spp
19.8.77	*Brachiaria nigropedata*	0,7	7	7	100	15
	Panicum maximum	0,8	8	8	100	
24.8.77	*B. nigropedata*	1,5	14	15	93,3	19
9.9.77	*B. nigropedata*	4,5	35	45	77,8	17
	Hyperthelia dissoluta	0,9	3	8	37,5	
	Heteropogon contortus	1,0	3	8	37,5	
22.9.77	*Loudetia simplex*	6,6	1	66	1,5	14
	Digitaria gazensis	6,3	13	63	20,6	
	H. contortus	1,0	9	10	90,0	
28.9.77	*H. dissoluta*	6,8	4	68	5,9	21
	H. contortus	3,8	4	38	10,5	
	Eragrostis gumiflua	3,6	8	36	22,2	
5.10.77	*Sorghastrum friesii*	18,3	7	183	3,8	16
	Fuirena pubescens	17,4	17	174	9,8	
	Sedge spp	2,9	6	29	20,7	
	Hyparrhenia filipendula	5,7	5	57	8,8	
	L. simplex	0,7	1	7	14,3	
	D. gazensis	2,6	2	26	7,7	
12.10.77	*L. simplex*	2,4	1	24	4,2	13
	F. pubescens	16,8	13	168	7,7	
	H. contortus	0,7	2	7	28,6	
6.12.77	*H. filipendula*	1,5	2	15	13,3	17
	Eragrostis rigidior	1,3	2	13	15,4	
	H. contortus	9,2	9	92	2,2	
	B. nigropedata	0,3	1	3	33,3	
	Digitaria milanjiana	3,2	20	32	62,5	
21.12.77	*Themeda triandra*	3,2	5	32	15,6	20
	B. nigropedata	3,9	11	39	28,2	
	D. pentzii	3,7	1	37	2,7	
	Diheteropogon amplectens	1,3	3	13	23,1	
	Eragrostis superba	0,4	2	14	50,0	
21.12.77	*F. pubescens*	0,3	1	3	33,3	19
	B. nigropedata	3,3	6	33	18,2	
	Schizachyrium jeffreysii	1,1	4	11	36,4	
12.1.78	*H. contortus*	3,9	1	39	2,6	19
	S. jeffreysii	1,2	6	12	50,0	
	Hyparrhenia sp	5,5	8	55	14,5	
	B. nigropedata	0,6	2	6	33,3	
19.1.78	*H. contortus*	3,0	3	30	10,0	22
	T. triandra	3,9	2	39	5,1	
	D. milanjiana	14,2	4	142	2,8	
	E. rigidior	0,1	1	1	100	
16.2.78	*B. nigropedata*	6,1	3	61	4,9	19
	H. contortus	1,9	2	19	10,5	
	D. pentzii	5,6	5	56	8,9	
	T. triandra	1,0	2	10	20,0	
3.3.78	*Sporobolus ioclades*	16,0	3	97	3,1	14
	D. milanjiana	44,0	236	264	89,4	
23.3.78	*Bothriochloa insculpta*	1,1	7	11	63,6	16
	D. milanjiana	44,8	300	448	67,0	
	T. triandra	2,6	22	26	84,6	
	E. superba	0,9	7	9	77,8	
	Urochloa bolbodes	0,5	2	5	40,0	
12.4.78	*B. nigropedata*	1,0	2	10	20,0	15
	D. pentzii	18,9	9	189	4,8	
	S. jeffreysii	5,2	7	52	13,5	
	H. dissoluta	2,0	5	20	25,0	
5.5.78	*H. contortus*	5,2	4	26	15,4	14
	T. triandra	3,0	20	25	80,0	
18.5.78	*B. nigropedata*	2,6	16	17	94,1	16
25.5.78	*P. maximum*	(Clumped distribution)			15,0	
	B. nigropedata	3,0	18	21	85,7	13

Food plants = only those species eaten on that particular day.
d = density/square metre;
E = number of plants with bites;
T = total number of plants available in ten square-metre quadrates on each date/site;
S = selection index $E/T \times 100\%$;
Spp = total number of grass and sedge species recorded in 10 square-metre quadrates placed randomly 10 metres apart at feeding stations.

In the analysis of feeding stations, of 4 637 food plants available only 486 (10%) were utilized. These can be grouped into five categories as follows:

(a) Preferred species which also formed the principle food of sable and were utilized at all seasons. There was only one species in this category, *Brachiaria nigropedata*.

(b) Preferred species, these were generally quite rare at feeding stations: *Diheteropogon amplectens* and *Eragrostis superba*.

(c) Principle food species utilized all year round and contributing significantly to bulk intake: *Heteropogon contortus*.

(d) Seasonally important species. Certain species were important seasonally and formed both preferred food plants and principle food plants on occasions. In the hot dry season *Fuirena pubescens, Digitaria gazensis, Eragrostis gumiflua* and *Panicum maximum* were important and in the mid wet season *Digitaria milanjiana* and *Schizachyruim jeffreysii*. Although not encountered in the intensive study area, *Pennisetum glaucodadum* was heavily utilized after a burn (see Grobler 1974).

(e) Species eaten occasionally. These included *Hyperthelia dissoluta, Loudetia simplex, Sorghastrum friesii, Hyparrhenia filipendula, Eragrostis rigidior, Digitaria pentzii* and *Sporobolus ioclades*.

The only woody species recorded as browsed by sable during the feeding study from 1977 to 1978 were *Tarchonanthus camphoratus* and *Rhus pyroides*. These were browsed during the hot dry season but only accounted for four observations in nearly 4 000. The newly flushed leaves and buds were eaten in both species. On one occasion during this period an adult female was seen to strip the leaves off one *Phragmites mauritianus* plant. Several species of sedges (Cyperaceae) were eaten around drinking sites, including *Scirpus inclinatus, S. muricinux* and *Cyperus esculentus*. They were regarded as incidental and related to drinking even though the leaves and stems were of good nutrient quality (crude protein 9 – 11%).

There were others such as *Panicum maximum* which was utilized in its initial growth phase between 40 and 160 mm above the ground. Once above the 160-mm level the species was, for several months, rarely fed on in spite of having the right structural and chemical qualities. From May onwards *P. maximum* has a tendency to collapse and intermittent feeding on the plant took place. This feeding increased in frequency into the hot dry food limiting period, often at above the 160 mm level, but large dense stands still remained untouched at the end of the season.

The only consistent differences between selected and rejected components were in crude protein contents and crude fibre contents (Fig. 2). Of the two, percentage crude protein showed the least overlap between accepted and rejected material. The main exceptions were aromatic species such as *Cymbopogon excavatus* which were presumably rejected because of taste and *Panicum maximum* which was available at the wrong feeding level. Browse species analysed were *Rhus pyroides* and *Tarchonanthus camphoratus*. Both had high protein contents (13,8 and 11,1%) and low crude fibre (33,0 and 24,7%) when compared to grass.

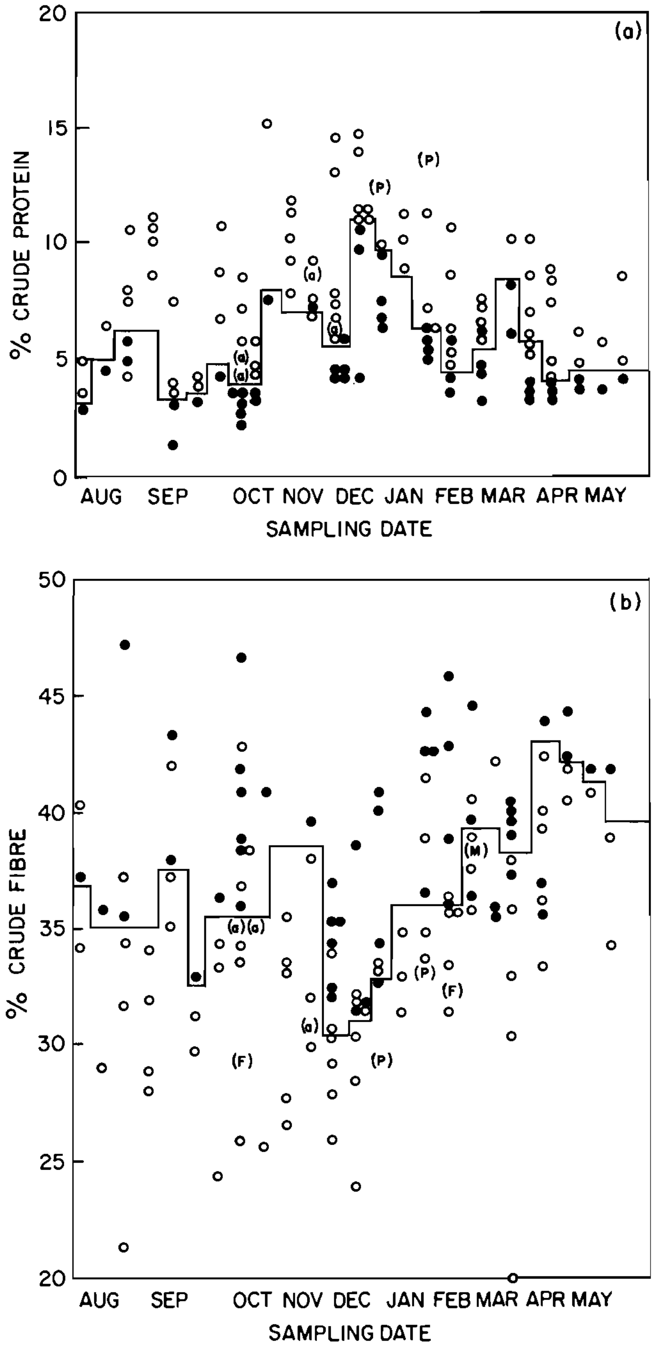

Fig. 2 Sable food selection for (a) crude protein and (b) low crude fibre content as shown from the analysis of accepted (o) and rejected (●) grass species/components at feeding sites.

Chemical composition of plants and grass swards

Protein levels were at their highest during mid November to mid December and at their lowest during August and mid September to early October with a slight peak during September caused by feeding on small moist areas. Differences in protein content were evident between components of the same plant (leaves, stems), on the same species growing in different areas, between different species growing in the same area and the same species growing in the same area (often at a different growth stage), and the same species at different times of the year.

Percentage crude fibre (insoluble carbohydrate) showed more overlap than protein, between accepted and rejected material. Protein in the same plant species decreased with increased fibre content but no correlation existed between percentage protein and percentage fibre for plant components collectively. As with protein, differences in fibre content were found between components on the same plant, between the same species in different areas and at different times and between different species in the same place.

Almost complete separation between accepted and rejected components was obtained when the crude fibre to crude protein ratios were plotted (Fig. 3). A slightly high crude fibre content may for example be offset by an equivalent rise in crude protein content. More than 40 species of plants were sampled in the study area (see Grobler 1978 for results) at feeding sites selected by sable and it was concluded that selection was directed at high crude protein and low crude fibre within the plant components eaten.

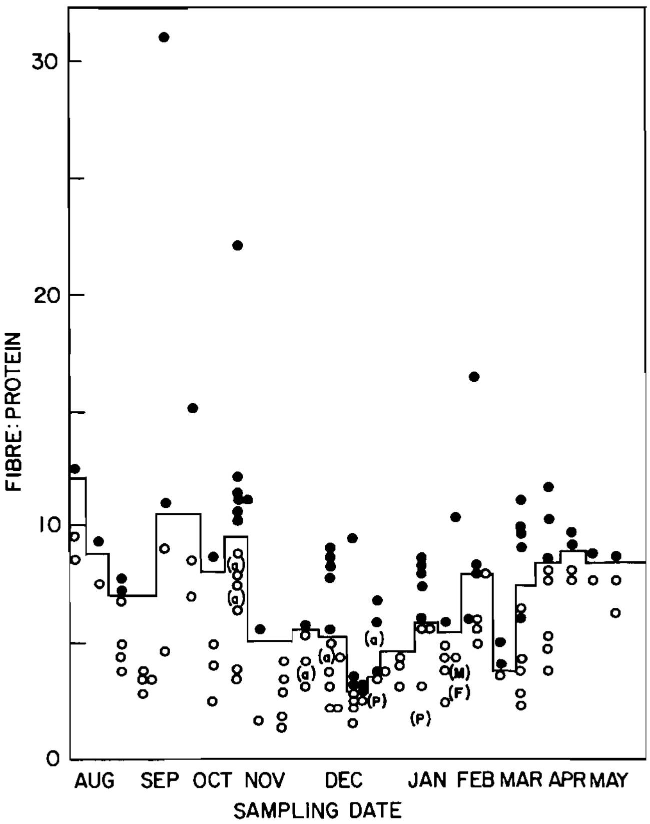

Fig. 3 Sable food selection (o) and rejection (●) based on crude fibre: crude protein ratio in grass plant components.

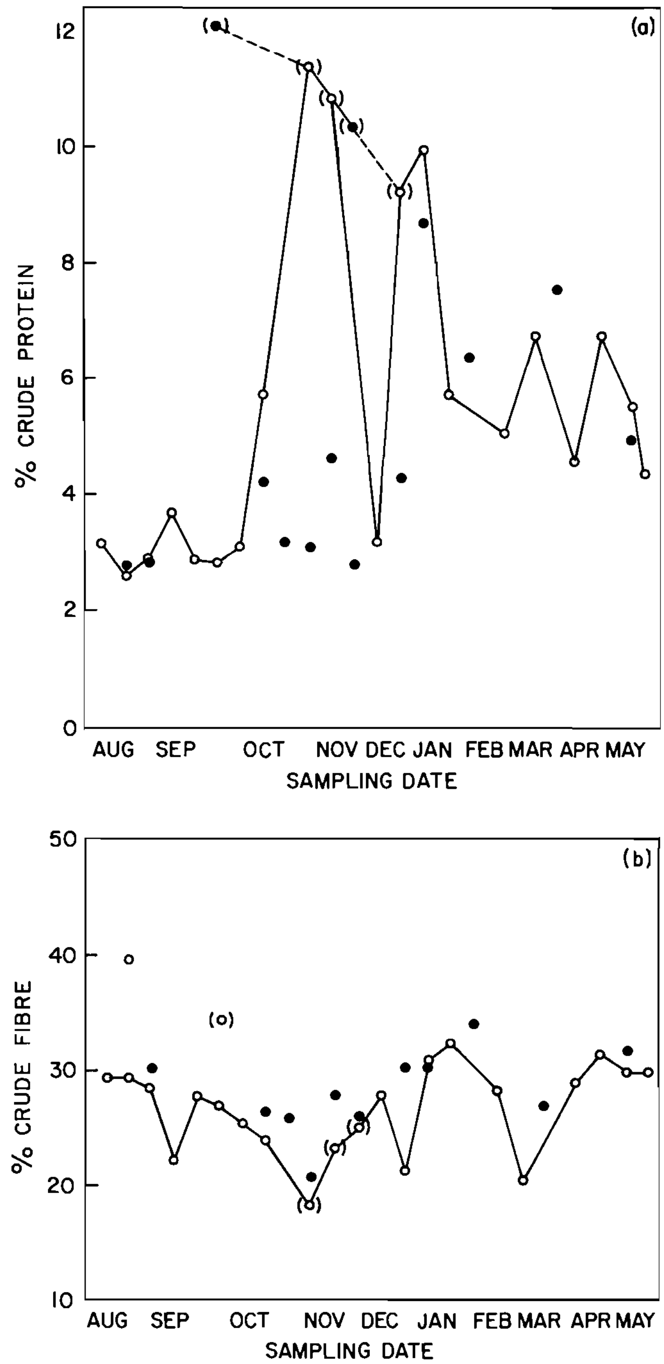

Fig. 4 Sable feeding site selection (o) and rejection (●) on the basis of (a) mean crude protein and (b) mean crude fibre of the grass sward. (Burnt area shown as ()).

A total of 40 feeding stations and rejected sites were analysed between August 1977 and April 1978. The 40 to 160-mm layer of grass invariably had a higher protein content and lower fibre content than the over 160-mm layer when this was present. However, using a mean for the two layers in each transect sampled there was a fairly consistent difference between feeding stations and rejected areas (Fig. 4).

From August to early October there was little difference between the selected and rejected sites indicating poor quality habitat and sparse distribution of suitable food components. With the onset of the rains the sable were in a position to utilize the burnt areas which had a far higher mean habitat quality. This reached a peak in November and slowly declined thereafter as the grass matured, flowered and increased in amount of stalk. A trough in December resulted when the sable were forced to move off the burn by the grazing pressure exerted by wildebeest, impala and tsessebe.

There was no detectable difference between phosphorus and calcium content of accepted and rejected food plants. The phosphorus content of grasses analysed was a mean of 0,34% (SD $\bar{X}$ 0,07, $n = 103$) and the mean calcium content was 0,33% (SD $\bar{X}$ 0,17, $n = 97$).

A correlation with $r = 0,69$ occurred between faecal nitrogen and the mean protein content of the food components in 11 of 13 samples (Fig. 5). The only two exceptions were when the tame sable were living under stress conditions, and when food samples were taken at a drinking site. The latter did not reflect the mean protein intake but rather the highest protein source available at that particular time.

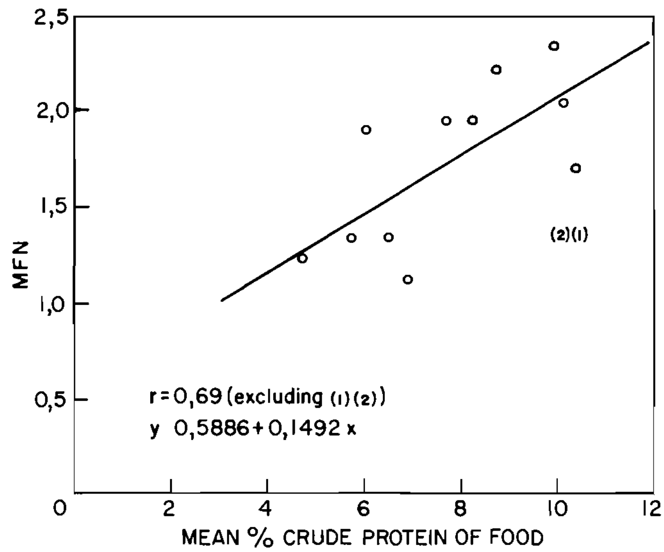

Fig. 5 Mean crude protein of sable food in relation to faecal nitrogen (MFN) in the Matopos, Zimbabwe.

Discussion

Daylight activity

The activity patterns of various species of antelope have been studied and described (see Spinage 1968, Jarman & Jarman 1973, Walther 1973, Duncan 1975). The basic activity pattern of sable is adapted to the mode of feeding (alternation of food gathering and rumination) and to its physiological requirements (thermoregulation, water dependence). The annual pattern of activities would, as Leuthold (1977) states, be governed generally by more or less regular changes in certain environmental factors such as temperature, precipitation, light (photoperiod), through the effects these have on distribution and abundance of resources or on the animal's physiology. From the present study the results indicated that to maintain physical condition, sable in the Matopos need to spend at least the same amount of time feeding as on other activities.

Feeding level, species selection and area selection

The pattern of pasture use by African grazing ungulates has developed in response to the characteristic distribution within the herb layer of physical structure, mechanical properties and chemical composition (Bell 1970). Bell suggests further that for wildebeest and topi *Damaliscus korrigum*, because of differences in their structure particularly in their jaws and teeth, wildebeest are more successful in the herb layer with a low frequency of stem and where leaves incline to the horizontal, while topi utilize a herb layer with a higher frequency of leaves inclined to the vertical. The result is that the two species become alternate members of the grazing succession according to the structure of the herb layer.

Detailed investigation of feeding levels of grazers may illustrate factors separating the different species during times when competition may arise. Joubert (1976) indicates that roan *Hippotragus equinus* customarily feed on the higher parts of the food plants while Field (1976) gives feeding levels for buffalo *Syncerus caffer* indicating them to be high level feeders. For reasons that remain speculative the sable have specialised in feeding over a limited range of heights and this form of specialization may well be one of the critical factors which to some extent separate different herbivore species, affecting them most when competition arises at times when food is limiting.

The physical regulation of voluntary intake of food is directly related to stomach structure and the inherent food preferences and thus diet itself (Hofmann 1973). Recent trends in wildlife research have been to investigate the nutritional qualities of food components, plant structure and food intake of various ruminants (Sinclair & Gwynne 1972, Duncan 1975, Field 1976, Von Richter & Osterborg 1977, Stanley-Price 1977). This has resulted in a great improvement in understanding the feeding behaviour of ruminants.

Physical structure of the vegetation was used to separate habitats used by sable and roan and suggested as a limiting factor in their distribution (Joubert 1976). The nutritional value of food plants as a limiting factor in sable was looked at briefly by Wilson & Hirst (1977) although they indicated disease to be the main cause.

With non-ruminants the apparent digestibility of crude protein is markedly depressed by crude fibre, whereas with ruminants the depression is only slight (Glover & Duthie 1958). The same authors showed the digestibility coefficient (y) is related to the percentage crude protein (x) of the food by the expression $y = a + b \log x$, with the equation $y = 70 \log (x - 15)$ providing a reasonable fit for most data. Using this formula the digestibility coefficient for sable ranged from 25% in the hot dry season to 60% on the burnt area during the hot wet season. This gives some indication of the range sable had to adapt to as a result of variation in quality and quantity of food.

French (1957) demonstrated that the ruminal activity in cattle may be depressed when the diet contains less than 7% crude protein. The sable were recorded feeding on food components with a mean crude protein content as low as 4,05% and during the food limiting period the level rarely rose above 7%. Nutrient values of different grass components have been shown to vary seasonally in the Matopos (Plowes 1957) and over a 12-month period (Sinclair 1974).

Amount of crude fibre may affect palatability (Theron & Booysen 1966) but may not be insoluble to ruminants because of the presence of micro-organisms which can break down cellulose to produce volatile fatty acids that are absorbed from the rumen and supply energy to the host animal (Moen 1973). Seven sable sampled in the study area gave an average of $1{,}79 \pm 0{,}30 \times 10^5$ protozoa per ml of rumen fluid, a relatively low figure typical of grazing ungulates (Van Hoven, Hamilton-Attwell & Grobler 1979).

Calcium and phosphorus content of food components produced nothing conclusive. Osteophagia by sable in the study area was observed but never to the extent described by Sekulic & Estes (1978). South African pastures show a decline of phosphorus from January to July or August followed by a rise of varying intensity to November or December. This was inversely related to the amount of crude fibre present (Du Toit, Louw & Malan 1940).

As a method of evaluating veld quality faecal nitrogen may not be entirely suitable. The chemical composition of faeces may indicate food quality but gives no indication of the quantity available. In a study on springbok *Antidorcas marsupialis* (Erasmus, Penzhorn & Fairall 1978) it was shown, however, that acid detergent lignin, ether extract, neutral detergent fibre and acid detergent fibre in faeces showed seasonal variation which could be related to changes in body mass and fat reserves, as well as rainfall.

Consistent morphological features of the stomach on one hand, and principally similar feeding habits directed towards feeds with a comparable composition of contents as regards nutritional value, digestibility and fermentability on the other, were considered by Hofmann (1973) who grouped East African wild ruminants into three main categories. One of these categories, the bulk roughage or grass eaters was divided further into (a) fresh grass grazers dependent upon water, (b) roughage grazers not dependent upon water and generally ingesting poorer forage and (c) dry region grazers. Although Hofmann did not investigate sable anatomically he wrongly classified them in the second category. It was concluded from the present study that sable, as surmised by Leuthold (1977), are fresh grass grazers dependent on water.

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