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SEASONAL VARIATION OF DIET AND FAECES COMPOSITION OF BLACK RHINOCEROS *DICEROS BICORNIS* IN THE ADDO ELEPHANT NATIONAL PARK

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Abstract — The feeding habits of black rhinoceros were studied in the Addo Elephant National Park, Republic of South Africa, using the "feeding track" method and recording bites taken. A total sample of 59 feeding tracks, 5 540 plants and 17 191 bites were recorded from June 1976 to March 1977. The rhino fed largely on woody shrubs but also took forbs, grass and succulent plants. During dry periods the rhino were selecting succulent plants with a high moisture content rather than woody plants. A total of 111 plant species were utilized. During dry months the feeding rate was greater than wet months. Physical analysis of faeces composition confirmed conclusions drawn from observations. Chemical analyses of faeces indicated that mean crude protein values varied with rainfall and herbage quality, ash values were strongly influenced by the intake of plant roots and dust during dry periods, acid detergent fibre was highest during unfavourable periods and low during favourable periods.

Introduction

Black rhinoceros *Diceros bicornis michaeli* originating from eastern Kenya were

translocated to the Addo Elephant National Park (AENP) in 1961 and 1962 (Hall-Martin & Penzhorn 1977). They were confined to a 210 ha paddock until late 1977. The crude population densities (affected by recruitment, mortality and changes made to the area of paddock available) varied from 1.3 to 5.2 rhinoceros per km^2 and were generally far in excess of maximum densities recorded elsewhere in Africa (Mukinya 1973; Hitchins 1976; Hall-Martin & Penzhorn 1977). These high densities resulted in serious damage to the vegetation as evidenced by degradation of thicket and its replacement in part by open scrub and dwarf shrub communities.

In the present study the seasonal composition of the diet of black rhinoceros was investigated by direct observation and by faecal examination. Furthermore, the chemical composition, hence the quality, of the forage consumed was indirectly examined by analysis of faecal samples. The harvesting of a sample of forage was not contemplated as it has been shown (Engels, Van Schalkwyk, Malan & Baard 1971) that even when working with domestic animals, the harvest of the investigator does not correspond with the harvest of the animal because of the highly selective nature of the animal's feeding. The collection of stomach contents could not be considered because of the rarity of the species involved. Faecal indicator techniques used to estimate feed intake and/or digestion coefficients for specific nutrients as an index of the quality of the forage consumed could also not be considered. The only practical approach was to use the animal as the sampler and to analyse samples collected via the animal (i.e. faeces) as an indicator of forage quality (Erasmus, Penzhorn & Fairall 1978; Zimmerman 1980).

Digestive processes on the food consumed result in changes in the chemical composition of the food material as it passes through the gut. However, certain substances such as lignin, due to its low digestibility by herbivores (Van Soest 1975) occur in the faeces in roughly the same quantities as in the feed. Lignin content of faeces was shown to be correlated with the quality of the food consumed in feeding trials using both domestic and wild animals (Erasmus *et al.* 1978). Faecal nitrogen content usually accurately reflects nitrogen content of the food and its digestibility (Jarrige 1965; Louw 1969; Engels & Hyam 1975; Stanley-Price 1977; Erasmus *et al.* 1978; Zimmerman 1980). Analyses of rhinoceros faeces might therefore be expected to yield useful information on the quality of forage consumed and hence habitat quality. Stressful periods of low nutrition, if these occurred during the study period, might then be identified.

Study Area

The AENP, 7 735 ha in extent, is situated in the south-eastern Cape Province of South Africa at 33° 13'S, 25° 45'E. The rhinoceros enclosure, in the south-western corner of the Park, lies at an altitude of 75-100 m a.s.l. Three easily recognized plant communities constituted the original vegetation of the enclosure. The greater part of the enclosure (44%) was covered by a dense, evergreen, semi-succulent shrub thicket classified by Acocks (1953) as Valley Bushveld. The shrub species are mostly multi-stemmed, growing to a height of about 3 — 4 m and are dominated by *Portulacaria afra, Euclea undulata, Schotia afra, Capparis sepiaria* var. *citrifolia* and *Azima tetracantha*. The understory herbs are dominated by the genera

Sansevieria, *Crassula*, *Euphorbia*, *Asparagus* and *Commelina* and grasses are scarce.

The second vegetation type (39%) is known locally as Karoo-bushveld and is an open community of low drought resistant dwarf shrubs and herbs such as *Justicia orchioides*, *Pteronia paniculata*, *Felicia* spp., *Crassula* spp., *Galenia pubescens*, *Lampranthus productus*, *Ruschia* spp. and *Pentzia globosa* with scattered clumps of tall shrubs and small trees such as *Rhus longispina*, *Maytenus* spp. and *Putterlickia* spp. Grasses such as *Panicum maximum*, *P. deustum*, *Themeda triandra*, *Digitaria eriantha* and *Setaria neglecta* are common in the herb layer over large areas. The third vegetation type distinguished (covering 17% of the area) is best described as Karoo-grassland. This is a herb community dominated by grasses of the above species and succulent herbs chiefly of the family Aizoaceae.

The climate is semi-arid with rain falling during all seasons. The wettest months usually being August (late winter) and March to May (late summer to autumn). Mean annual rainfall for the period 1961-1975 was 377.7 mm. The summer months (November-March) are hot and the winters (June-August) mild; frost is rare. Fires are unknown at Addo.

Besides the black rhinoceros the enclosure supported a few reedbuck *Redunca arundinum* and grey duiker *Sylvicapra grimmia;* one eland *Taurotragus oryx* and one red hartebeest *Alcelaphus buselaphus*.

Methods

Because of other priorities it was not feasible to use time-consuming methods of study such as the "feeding stations" of Goddard (1968) or the "feeding-minutes" technique (Field 1970). The feeding track observation technique, also used successfully by Mukinya (1977), was therefore applied. A feeding rhinoceros was located early in the day and when it had moved off a safe distance its feeding track was followed on foot. All plants on which the animal had fed, the number of bites taken from each plant and the height of each bite were recorded. A bite was scored for any isolated severed shoot or branch and where numbers of contiguous shoots or branches were bitten off at the same level, such as was commonly found in multi-stemmed and freely branching dwarf shrubs, then all severed shoots less than 5 mm thick occurring within a hypothetical circle of 5 cm in diameter were recorded as one bite. Severed branches greater than 5 mm in diameter were recorded as single bites. Field observations were made for four days each month from June 1976 to March 1977 with no observations being made in September 1976.

During the course of the field work, fresh faecal samples were also collected, lightly sprayed with formalin, sun-dried and stored in polythene bags. Samples were later equally divided; half of the material was kept for sorting into easily recognised physical components and half was analysed chemically. The material for physical analysis was spread on a flat surface and randomly divided as described by Hall-Martin (1974) until a sub-sample of approximately 500 g dry weight was extracted. This was then sorted by shaking through a graded series of large wire mesh sieves. From the coarser material the remains of woody plants (twigs, spines, leaves), succulent plants (stems, epidermal material, leaves) and grasses were extracted. The

remaining material was divided into fine material (passing through a grid 1,68 mm) and miscellaneous material. The component categories of each sample were then weighed and the results expressed on a percentage mass basis. The material for chemical analysis was ground and subsamples taken for determination of crude protein (CP) (Kjeldahl: N X 6,25); acid detergent fibre (ADF) and acid detergent lignin (ADL) according to Goering & Van Soest (1970); ash was determined after incineration at 600°C overnight. All the results are expressed as percentage dry matter.

Results

Validity of data

From 59 feeding tracks a total of 5 549 plants belonging to 111 species were found to be utilised and 17 191 bites were recorded (Table 1).

Table 1

Record of feeding tracks, plants used and bites taken by black rhinoceros during the feeding study, Addo Elephant National Park, June 1976 to March 1977

Month	Feeding tracks	Plants	Bites	No. of plant species	Species	Bites/ plant
June 1976	5	353	1 047	51	51	2.97
July 1976	8	657	2 548	54	22	3.88
Aug. 1976	9	718	2 725	55	12	3.80
Oct. 1976	10	838	2 343	52	5	2.80
Nov. 1976	5	345	1 221	36	5	3.54
Dec. 1976	6	494	1 410	45	6	2.85
Jan. 1977	5	707	1 548	45	3	2.19
Feb. 1977	8	1 002	3 347	53	4	3.34
Mar. 1977	3	426	1 002	28	3	2.35
Total	59	5 540	17 191		111	

The number of feeding tracks sampled each month varied (Table 1), as did the length of the individual feeding tracks which represented from 45-195 minutes of feeding per animal. It is difficult therefore to decide whether the data represent valid monthly samples of the diet of the black rhinoceros. The number of species detected by increasing samples of plants utilised were therefore plotted to give species/plant curves (Fig. 1) which are analogous to the species/ area curves used for fixing the minimum sample areas in vegetation studies (Mueller-Dombois & Ellenberg 1974). The minimum number of plant species constituting an adequate sample of those utilised by the rhinoceros would be approximately indicated by the

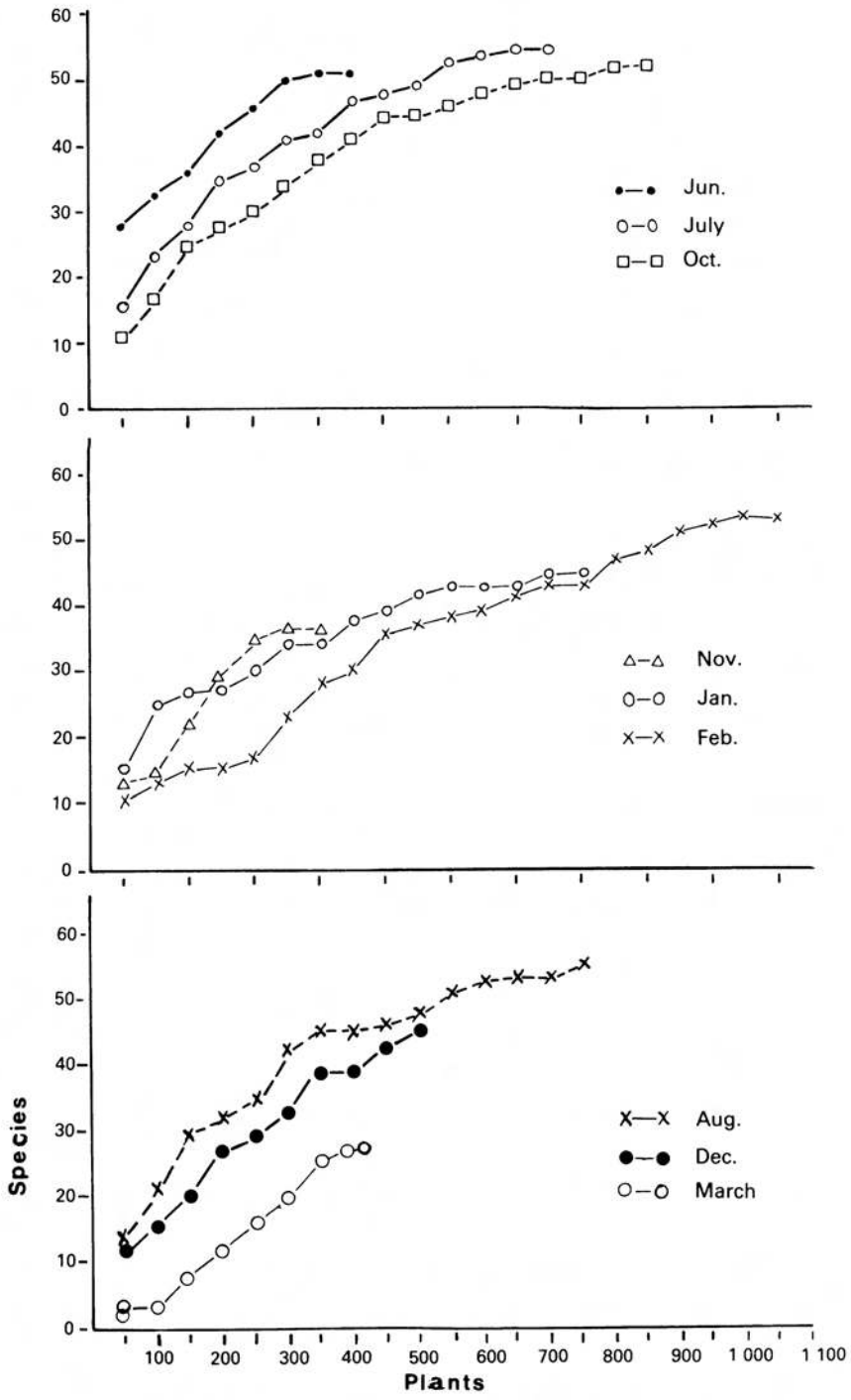

Fig. 1. The relationship between plant species diversity with increasing number of plants fed on by black rhinoceros.

asymptote of the curve. The curves tended to start flattening out at the 400-500 plant level (Fig. 1) for all months except December 1976 and February 1977. These curves were therefore interpreted as indicating that samples were adequate to account for the variation in species eaten by the rhinoceros except for these latter two months.

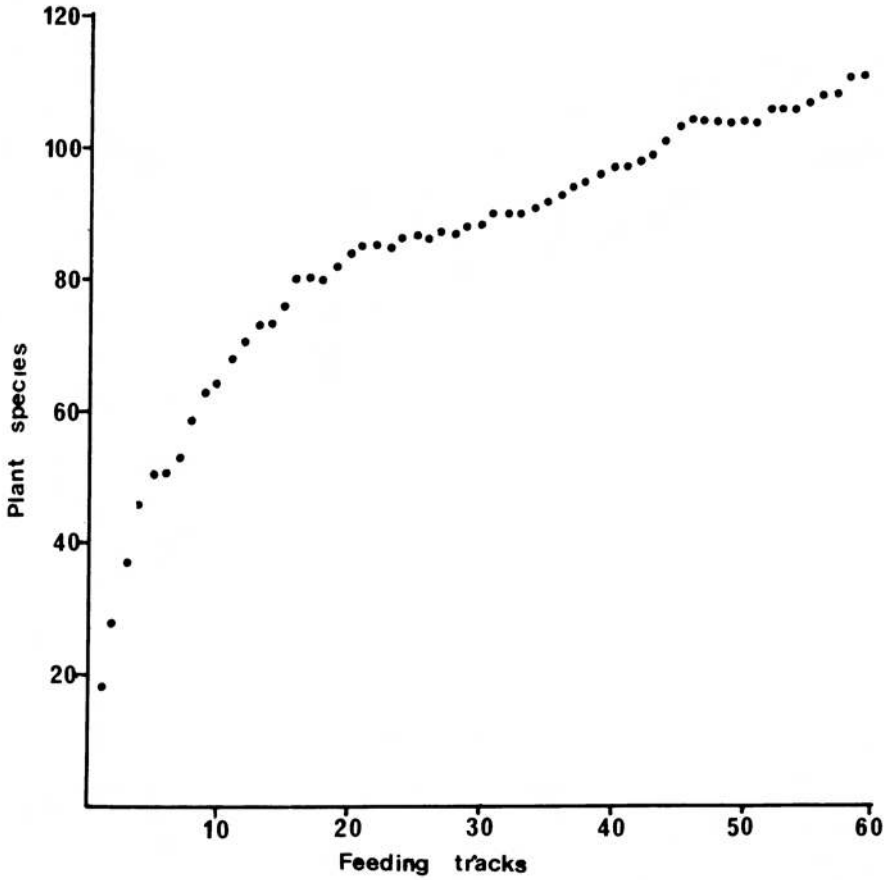

Fig. 2. The relationship between plant species diversity and the increasing sample size as represented by the number of feeding tracks examined.

The number of plant species known to be utilised by rhinoceros throughout the seasons was plotted against the increasing number of feeding tracks (Fig. 2). This resulted in a curve which rose steeply up to about the 20 track level and thereafter the rate of increase declined. This curve shows that though not all the plant species likely to be eaten by rhinoceros were accounted for by the 59 feeding tracks examined; most of them, and certainly all the important species will have been included.

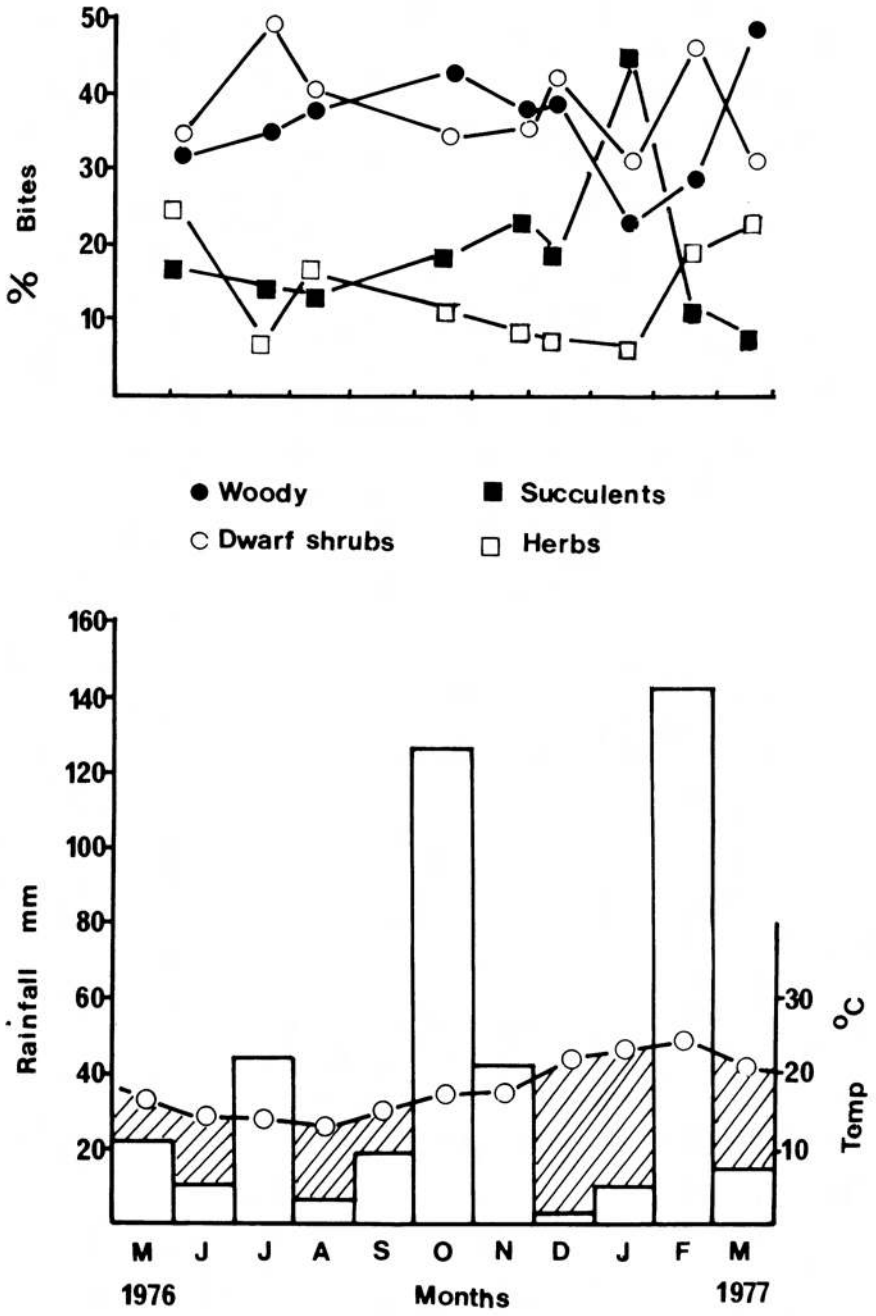

Fig. 3. Utilisation of different categories of plants by black rhinoceros in relation to rainfall and temperature, May 1976 — March 1977.

Table 2

Woody plant composition of the diet of black rhinoceros at the Addo Elephant National Park

Plant family and name	% of all bites				% of woody bites			
	Jun. to Aug.	Oct. to Dec.	Jan.	Feb. and Mar.	June to Aug.	Oct. to Dec.	Jan.	Feb. and March
Capparidaceae								
Capparis sepiaria L. var citrifolia (Lam.) Töelken	5,0	3,6	3,5	0,5	14,7	9,3	16,8	1,7
Cadaba aphylla (Thunb.) Wild	0,5	0,2	0,6	0	1,4	0,4	3,1	0
Maerua caffra (DC.) Pax.	0,1	0,6	0,2	0	0,2	1,6	0,9	0
Boscia oleoides (Burch.ex DC) Töelken	0,1	0	0	0	0,1	0	0	0
Leguminosae								
Acacia karroo Hayne	0,1	0	0	0	0,4	0	0	0
Schotia afra (L.) Thunb.	3,8	4,9	2,4	1,1	11,1	12,7	11,5	3,6
Zygophyllaceae								
Zygophyllum morgsana L.	6,2	3,8	0	1,7	18,0	9,9	0	5,3
Anacardiaceae								
Rhus longispina Eckl. & Zeyh.	3,2	1,6	1,4	0,5	9,2	4,2	6,9	1,8
R. undulata Jacq.	0,1	0,5	0	0	0,1	1,2	0	0
Celastraceae								
Maytenus polyacantha (Sond.) Marais	2,2	1,9	1,0	0,3	6,5	5,0	4,7	1,0
M. heterophylla (Eckl. & Zeyh.) N Robson	0	0,1	0	0	0	0,4	0	0
Putterlickia pyracantha (L.) Szyszyl	0,1	0	0	0	0,2	0	0	0
Vitaceae								
Rhoicissus tridentata (L.f.) Wild & Drummond	0,1	0,2	0	0,1	0,2	0,5	0	0,3
Tiliaceae								
Grewia occidentalis L.	0,1	0	0	0	0,4	0	0	0
G. robusta Burch.	2,2	3,3	3,2	17,8	6,5	8,4	15,6	56,3
Ebenaceae								
Euclea undulata Thunb. var. undulata	0,4	0,5	0,9	0,8	1,2	1,2	4,4	2,7
Salvadoraceae								
Azima tetracantha Lam.	6,3	14,0	4,8	1,8	18,4	36,2	23,4	5,8
Apocynaceae								
Carissa haematocarpa (Eckl.) A. DC.	1,1	2,5	2,4	0,2	3,3	6,5	11,5	0,7
Asclepiadaceae								
Fockea edulis (Thunb.) K. Schum.	0,1	0,1	0,1	0,1	0,1	0,2	0,6	0,2
Solanaceae								
Lycium campanulatum E. Mey.	2,7	0,9	0,1	3,9	8,0	2,3	0,6	12,3
Bignoniaceae								
Rhigozum obovatum Burch.	0	0	0	2,6	0	0	0	8,3
	34,4	38,7	20,6	31,4	100,0	100,0	100,0	100,0

Table 3

Dwarf or karroid shrub composition of the diet of the black rhinoceros of the Addo Elephant National Park

Plant family and name	% of all bites				% dwarf shrub bites			
	Jun. to Aug.	Oct. to Dec.	Jan.	Feb. and Mar.	June to Aug.	Oct. to Dec.	Jan.	Feb. and March
Liliaceae								
Asparagus africanus Lam.	0	0,8	0,1	0,1	0	2,2	0,2	0,3
A. racemosus Willd.	0,7	0,2	0	0,3	1,8	0,6	0	0,8
A. striatus (L.f.) Thunb.	3,3	0,6	7,3	0,7	8,1	1,6	24,3	1,7
A. suaveolens Burch.	0,9	0,6	0	0,5	2,2	1,8	0	1,3
A. subulatus Thunb.	0	0,2	0	0	0	0,5	0	0
Chenopodiaceae								
Chenopodium sp.	0,7	0	0	0	1,8	0	0	0
Aizoaceae								
Mestoklema sp.	3,0	1,4	0,4	0,1	7,3	4,1	1,3	0,1
Crassulaceae								
Crassula tetragona L.	0	0,8	0	0	0	2,3	0	0
Leguminosae								
Indigofera sessilifolia DC.	0,1	0	0	0	0,3	0	0	0
Malvaceae								
Hibiscus pusillus Thunb.	0,1	0	0	0	0,1	0	0	0
Sida ternata L.f.	0,1	0	0	0	0,1	0	0	0
Sterculiaceae								
Hermannia pallens	1,9	11,3	0,3	3,9	4,5	32,0	1,1	9,6
Labiatae								
Lasiocorys capensis Benth.	0,1	0,2	0	0	0,2	0,5	0	0
Solanaceae								
Solanum coccineum Jacq.	0,1	0,1	0,1	0,2	0,2	0,4	0,4	0,6
Scrophulariaceae								
Sutera foliosa (Benth.) Hiern.	0,1	0	0	0	0,2	0	0	0
Selaginaceae								
Walafrida geniculata Rolfe	4,9	9,2	3,5	7,8	11,8	26,1	11,9	19,0
Acanthaceae								
Barleria pungens L.f.	0,6	0,2	0	3,4	1,4	0,6	0	8,4
Blepharis capensis (L.f.) Pers	0	0,2	0	0,1	0	0,6	0	0,1
Hypoestes verticillaris (L.f.) R.Br.	0,3	0,1	0	0,1	0,8	0,3	0	0,1
Justicia orchioides L.f.	7,9	6,8	18,1	6,7	19,1	19,2	60,6	16,3
Compositae								
Pteronia paniculata Thunb.	7,9	0,3	0	0	19,1	0,7	0	0
Felicia fascicularis DC	0,1	0	0	1,0	0,1	0	0	2,4
F. filicifolia Burtt Davy	7,7	0,7	0	0,5	18,6	2,1	0	1,2
F. muricata subsp. muricata	0	0,1	0	13,9	0	0,4	0	33,8
Chrysocoma tenuifolia Berg.	0	0,8	0	0	0	2,2	0	0
Helichrysum pentzioides Less.	0	0	0	0,8	0	0	0	2,0
H. rosum (Berg.) Less.	0,1	0,5	0	0	0,2	1,5	0	0
Pentzia incana (Thunb.) Kuntze	0,1	0	0	0,4	0,2	0	0	0,9
P. globosa Less.	0	0	0	0,3	0	0	0	0,7
Senecio longifolius L.	0,7	0,1	0,1	0,2	1,7	0,3	0,2	0,6
Unidentified RH 117	0,1	0	0	0	0,1	0	0	0
	41,5	35,2	29,9	41,0	99,9	100,0	100,0	99,9

Table 4

Herbaceous plant composition of the diet of the black rhinoceros at the Addo National Park Elephant

Plant family and name	% of all bites				% of herb bites			
	Jun. to Aug.	Oct. to Dec.	Jan.	Feb. and Mar.	June to Aug.	Oct. to Dec.	Jan.	Feb. and March
Gramineae								
Panicum deustum Thunb.	0,2	0	0	0,6	1,7	0	0	3,2
P. maximum Jacq.	0,1	0,2	0	0,6	0,7	3,0	0	3,4
Cynodon incompletus Nees	0	0	0	0,1	0	0	0	0,4
Eragrostis curvula (Schrad.) Nees	0	0	0	tr	0	0	0	0,1
Commelinaceae								
Commelina africana L	0,1	0	0	0	0,7	0	0	0
C. benghalensis L.	0,1	tr	0	0	0,8	0,2	0	0
Liliaceae								
Bulbine frutescens (L.) Willd.	0,3	0,2	0	0,4	2,8	2,0	0	2,0
B. narcissifolia Salm-Dyck	0,2	1,9	0	7,7	2,3	23,3	0	41,3
B. natalensis Bak.	0	0,1	0	0	0	1,7	0	0
Haworthia viscosa Haw.	tr	0,3	0	0	0,1	3,5	0	0
Albuca sp.	0,4	tr	0,5	0,6	3,9	0,2	8,8	3,4
Urginea altissima (L.f.) Bak.	0,7	0	0	0	6,2	0	0	0
Ornithogalum sp	0	tr	0	0	0	0,2	0	0
Sansevieria aethiopica Thunb.	0,5	0,3	0,1	0	4,4	4,2	2,2	0
S. guineensis (L.) Willd.	0,2	0,3	1,6	0	2,3	4,2	27,5	0
Asparagus asparagoides (L.) Wight	0,2	0,1	0	0,1	2,3	1,2	0	0,2
Gasteria sp.	0	0	0,3	0	0	0	4,4	0
Iridaceae								
Tritonia securigera (Ait.) Ker.	0,1	0	0	0	0,4	0	0	0
Loranthaceae								
Viscum obscurum Thunb	tr	0,1	0	0	0,3	1,0	0	0
Polygonaceae								
Polygonum aviculare L.	0	0	0	0,2	0	0	0	1,1
Chenopodiaceae								
Chenopodium album L.	0	tr	0,4	tr	0	0,5	7,7	0,1
Aizoaceae								
Galenia pubescens (Eckl. & Zeyh.) Druce	5,8	4,2	2,9	7,6	51,8	51,6	49,4	40,6
Crassulaceae								
Crassula capitella Thunb. subsp. thyrsiflora (Thumb) Toelken	tr	0	0	0	0,1	0	0	0
C. lycopodioides Lam.	0,1	0,1	0	0	1,3	0,2	0	0
Sterculiaceae								
Hermannia athaeoides Link	0,2	tr.	0	0,5	2,1	0,5	0	2,5
Solanaceae								
Solanum guineense L.	tr	0	0	0	0,3	0	0	0
Acanthaceae								
Barleria obtusa	1,7	0,1	0	0,1	14,8	1,7	0	0,4
Cucurbitaceae								
Kedrostis nana (Lam.) Cogn. var. schlechteri (Cogn.) A. Meeuse	0	tr	0	0,2	0	0,5	0	1,1
Campanulaceae								
Cyphia sylvatica Eckl.	0,1	0	0	tr	0,6	0	0	0,1
	11,0	7,9	5,8	18,7	99,9	99,7	100,0	99,9

Table 5

Succulent plant composition of the diet of black rhinoceros at the Addo Elephant National Park

Plant family and name	% of all bites				% succulent bites			
	Jun. to Aug.	Oct. to Dec.	Jan.	Feb. and Mar.	June to Aug.	Oct. to Dec.	Jan.	Feb. and March
Liliaceae								
Aloe africana Will.	tr	0	0	0	0.1	0	0	0
Santalaceae								
Thesium triflorum Thunb. ex L.f.	tr	tr	0.1	0	0.2	0.1	0.1	0
Aizoaceae								
Carpobrotus sp.	0.1	0	0	0	0.4	0	0	0
Aridaria plenifolia N.E. Br.	4.4	2.0	3.2	0.4	33.7	10.9	7.4	5.0
Delosperma uniflorum L. Bol.	0	3.0	0.1	tr	0	16.6	0.1	0.3
Drosanthemum floribundum (Haw.) Schwant.	0.3	0.3	0	0	2.4	1.8	0	0
Drosanthemum sp.	tr	0	0	0.2	0.1	0	0	1.9
Mesembryanthemum aitonis Jacq.	0.3	0	0.1	0.1	2.5	0	0.1	0.8
Ruschia knysnana (L.Bol.) L. Bol.	0.2	2.4	14.9	3.6	1.6	13.5	34.4	41.1
R. orientalis L. Bol.	0	0.2	0	0	0	1.6	0	0
R. uncinella (Haw.) Schwantes	0.1	0.5	0	0.1	0.7	3.0	0	0.8
Ruschia sp.	0	0.7	0.3	0	0	3.7	0.7	0
Spalmanthus radicans (L. Bol.) L. Bol.	0.3	1.6	1.4	0.1	2.3	8.7	3.1	1.1
Unidentified Aizoaceae RH 210	0	0	0	0.8	0	0	0	9.3
Portulacaceae								
Portulacaria afra Jacq.	2.4	3.3	11.9	2.4	18.6	18.5	27.5	22.8
Crassulaceae								
Cotyledon campanulata Marloth	1.4	0.6	0.6	0	11.1	3.3	1.5	0
C. orbiculata L.	0.2	0.1	0	0	1.8	0.4	0	0
Crassula acutifolia Lam.	0.3	0.2	0.1	0	2.7	1.0	0.3	0
C. expansa Dryand in Ait.	0.1	0	0	0	0.4	0	0	0
C. trachysantha (Eckl. & Zey.) Harv.	0	0.2	0.2	0.2	0	1.2	0.5	2.1
Euphorbiaceae								
Euphorbia caterviflora N.E. Br.	0.9	0.7	0.3	0.1	7.3	3.7	0.6	0.8
E. clava Jacq.	tr	0	0	0	0.2	0	0	0
E. inermis Mill.	tr	0.2	0.8	0.1	0.2	1.3	1.8	0.8
E. mauritanica L.	0	0	0.9	0	0	0	2.1	0
E. rhombifolia N.E. Br.	0.1	0	0.1	0	0.6	0	0.1	0
Apocynaceae								
Pachypodium succulentum (L.f.) A.DC.	0.1	0.4	0.7	0.1	0.4	2.0	1.6	1.6
Asclepiadaceae								
Sarcostemma viminale (L.) R.Br.	0.7	0.7	0.3	0.5	5.6	3.8	0.7	5.8
Compositae								
Senecio radicans (D.C.) Sch. Bip.	0.7	0.8	7.4	0.1	5.2	4.4	17.0	0.8
Othonna carnosa (L.f.) Less.	0.2	0	0.1	0	1.7	0	0.1	0
Unidentified RH 164	0	0.1	0	0	0	0.4	0	0
	12.8	18.0	43.5	8.8	99.8	99.9	99.7	100.0

Plant types eaten

To facilitate the analysis of the data the plant species were classified into four groups (woody, dwarf shrub, succulent and herb). Woody plants include trees and shrubs with woody stems, dwarf shrubs include Karroid shrubs (small much-branched shrublets), succulent plants include all herbaceous plants both dicotyledonous and monocotyledonous.

The number of bites from plants of each life form expressed as a percentage of all bites recorded in each month are shown in Fig. 3, together with rainfall and monthly mean temperatures. These data show that the black rhinoceros at the AENP is predominantly a browser with shrubs and shrublets providing the bulk of the diet. There is an increase in woody plant utilisation from June to October as rainfall increases, and a significant drop to minimum values in January during a hot dry period followed by a recovery to higher levels in February and March with the advent of rains and a new flush of green leaves and flowers in many plants. The data for dwarf shrubs described much the same pattern except that the percentage bites were high in July. As with the woody plants there was a drop to minimum values during the January period. Herbs were high in June, and did not feature prominently again until their rapid rise after the rains in February and March. The percentage utilisation of succulent plants remained relatively constant from June to December and then showed a spectacular rise during the hot dry January period followed by an equally spectacular fall after the rains of early February.

Plant species selection

The species eaten by the rhinoceros, divided into four groups (woody, dwarf shrub, succulent and herb) are shown in Tables 2-5. Because of similarities in climatic conditions and the composition of the diet in some months, the data were combined into four groups representative of a cool, dry winter period (June-August), a warm spring period (October-December), a hot dry summer period (January) and a wet summer period (February-March).

Among the woody plants (Table 2) there are clearly some species which are of great importance throughout the year such as *Schotia afra*, *Grewia robusta*, *Azima tetracantha* and *Capparis sepiaria*. Deciduous species like *Grewia robusta*, *Lycium campanulatum* and *Rhigozum obovatum* were used less during the months when few leaves were available and were particularly heavily used in February and March when the summer rains had brought on a new flush of leaves and flowers.

The most important dwarf shrubs (Table 3) are *Asparagus striatus*, *Hermannia pallens*, *Walafrida geniculata* and *Justicia orchioides*. Few of the herbs (Table 4) are consistently taken except for *Galenia pubescens* which is apparently sought out even in the driest periods. Fairly regularly used succulent plants (Table 5) are *Portulacaria afra* and *Aridaria plenifolia*. However, the most striking aspect of the frequency of bites made on succulent plants is their importance during extreme hot and dry periods such as January 1977 when succulent plants made up 43,5% of all bites taken (Table 5).

When the frequency of bites within each category of plants for the periods in Tables 2-5 were tested by X^2 it was found that significantly more herbs than usual were taken in February and March 1977 ($P<0.025$), more succulent plants were used during January 1977 ($P<0.001$) and significantly less during February and March

(P<0.01). Although woody plants were taken less frequently during the dry period the difference was only just not significant at the 5% level of probability. Taken together, these data and the trends indicated in Fig. 3 are interpreted as showing that rhinoceros can modify their diet to suit environmental conditions. Thus they are opportunist to the extent that (within selected categories) they will use those plants or plant parts most readily available, such as the flush of new leaves and various herbs after the mid-summer rains of February. The data also suggest that during dry periods (though water was always available) the rhinoceros can cut down on the amount of high fibre material consumed (woody plants and dwarf shrubs) and increase their intake of succulent water-containing and possibly more nutritious plants.

Selection for plant types

Although the availability of different categories of plants under different seasonal conditions was not measured during this study, the availability and hence selection for or against, at the species level can be examined. All the 193 species of vascular plants known to occur in the rhinoceros enclosure were classified into the four categories used above. The selection at the species level within the four categories was then tested (Table 6a). It was found that there was significant selection for woody plants and dwarf shrubs, selection against herbs and that succulent species were neither selected for nor against.

Table 6

Black rhinoceros feeding habits — selection for or against certain categories of plants in the Addo Elephant National Park

a.

Category	No. of species		Chi-square	P (d.f.=1)	Selection
	Eaten	Available			
Woody	21	29	5,82	<0,025	For
Dwarf shrubs	30	35	17,86	<0,001	For
Herbs	30	79	4,56	<0,05	Against
Succulents	30	50	2,00	<0,050	None
	111	193			

b.

Category	No. of species		Chi-square	P (d.f.=1)	Selection
	Eaten	Available			
Climbers	9	9	9,00	<0,005	For
Grass/Sedge	4	23	11,56	<0,001	Against
Other herbs	26	56	0,28	>0,50	None
	39	88			

When some of the plant species falling in the above-mentioned four categories were examined on a different basis (Table 6b) it was found that there was strong selection for climbers, strong selection against grasses and sedges (which accounted for the selection against herbs shown in Table 6a) and no selection for other herbs (i.e. other than grass and sedges).

Feeding rate

On 13 occasions throughout the study period the time spent on a feeding track by a rhinoceros was recorded. Though not a good sample, these data may be indicative of the true feeding rate and are interpreted as such. The mean number of bites per minute taken by the black rhinoceros during wet months (July, October) was 1,78 and during dry months (June, August, January) was 2,53. The number of bites per plant (Table 1) during wet months (July, October, November and February) was found to be 3,38 and for the dry months it was 2,83. Though not differing significantly, these data are nevertheless probably indicative of a trend which might be found from better samples.

That many plants, particularly in the herb layer, can respond very rapidly to rainfall was observed during the study period. In the case of woody plants the response of the plant might be expected to take longer. Wilting and drying out of plants during December and January was observed and a spectacular flush of leaves and flowers followed the February rains. The observed changes in feeding rate may well, therefore, be in response to differing quality and quantity of food available to the rhinoceros.

Faecal analysis

Material from 24 defaecations was examined and it was found that only three categories of plant material could consistently be distinguished at the superficial level at which identifications were done. These categories were woody plants, succulents and grass and their percentage composition by mass is shown in Fig. 4a. Though there was considerably more variation than seen in the field observations, the main points to emerge are in accord. Thus woody material was generally more important than succulent plants. However, during the very dry period, as sampled in January 1977, there was a marked increase in succulent material. This was followed by relatively high values for woody material during February and March while percentage of succulent material identified from the faeces declined steeply. In general the values for woody and succulent plants opposed each other, while values for grass were independant but followed the rainfall pattern.

The results for percentage grass as shown in Fig. 4a are apparently much greater than those given in Table 4. A possible indication that the amount of grass recorded in the field was underestimated. The seasonal trends in grass utilisation are, however, very similar to those shown by the field observations (Table 4), with the highest values occurring in the late summer after the rains, and low values during the dry periods (August and December, Fig. 3). The values for fine and miscellaneous material did not follow any easily explained pattern (Fig. 4b) but could nevertheless be related to some extent to the composition of the diet and seasonal effects.

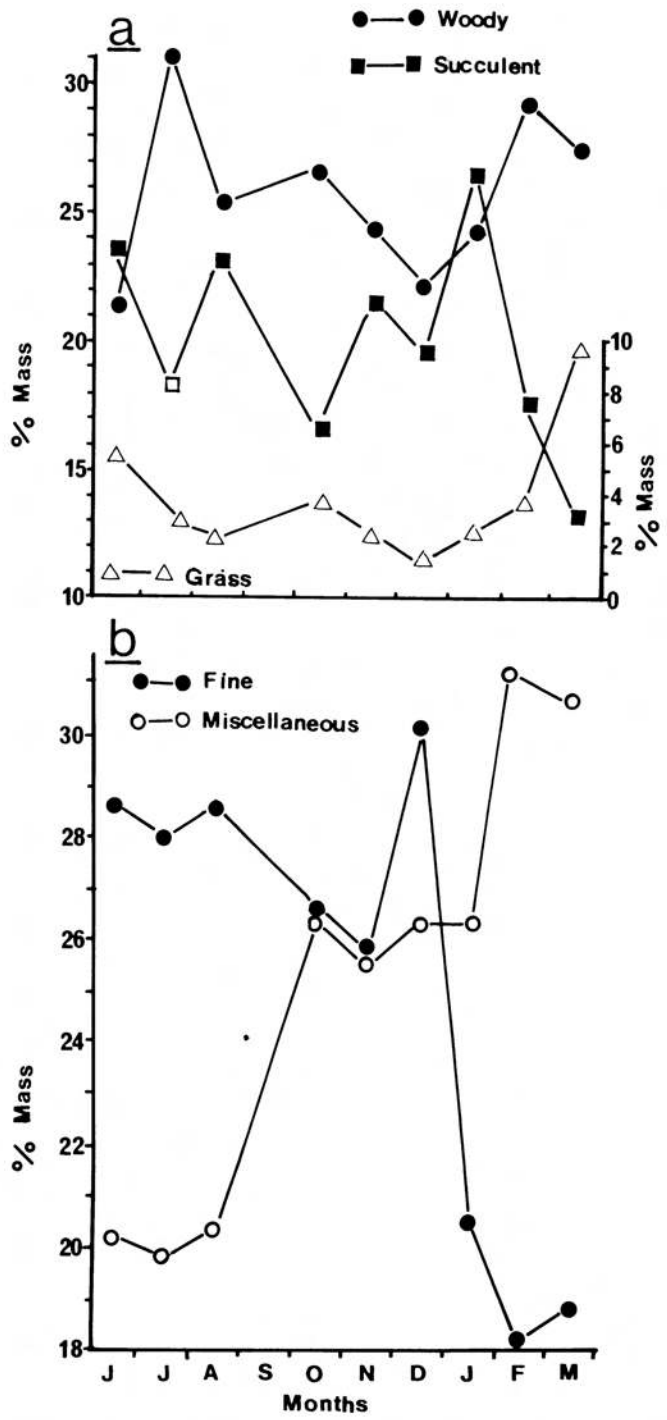

Fig. 4. Analyses of black rhinoceros faeces showing (a) monthly mean percentage woody, succulent and grass material; (b) percentages of fine and miscellaneous material.

Thus the values for miscellaneous material increased steadily as the plant growing season advanced and temperatures rose and reached a maximum in February. Fine material declined, except for December, and reached minimum values in February.

Chemical composition of the herbage

It was beyond the scope of the present study to investigate the quantity or quality of the available herbage. However, some data on chemical composition are available for comparison.

Data on the chemical composition of seven species of shrubs (including five regularly eaten by black rhinoceros at the AENP) taken from Aucamp (1972) are shown in Table 7. The general pattern of these values indicates that protein, crude fibre, and cellulose were high during spring and summer, declining during the autumn and winter. Percentage lignin and fat content (ether extract) were more variable.

Table 7

Composition of pooled samples of seven plant species from Valley Bushveld during four seasons 1970/77. Data from Aucamp (1972)*

Season	Percentages				
	Protein	Crude fibre	Lignin	Cellulose	Ether extract
Spring (October)	11,03	47,65	14,13	33,60	4,56
Summer (December)	9,27	45,90	8,24	36,63	4,72
Autumn (April)	8,77	38,16	9,50	27,36	6,96
Winter (June)	8,91	34,89	11,47	24,36	5,51
Mean	9,49	41,65	10,84	30,49	5,44

* Locality was the farm Greenfields, Uitenhage district, situated 28 km south west of Addo Elephant National Park.

Despite the obvious limitations these data can be taken as indicative of the general trend of change in nutritional quality with season in the Valley Bushveld vegetation type. The feed value of these plant species is influenced by rainfall (Aucamp 1972) and it can be expected that during higher rainfall periods quality will improve and during low rainfall periods it will decline. The selectivity for certain plants or plant parts by the rhinoceros can also be expected to influence the quality of the diet (Goddard 1968, 1970).

Chemical composition of faeces

The mean crude protein values are plotted in Fig. 5a. The winter samples (June — August) are low, then there is a gradual increase in October and November which is probably due to the effect of the spring rains. A dramatic drop coincides with the dry period of December and January and then, presumably as a result of the abun-

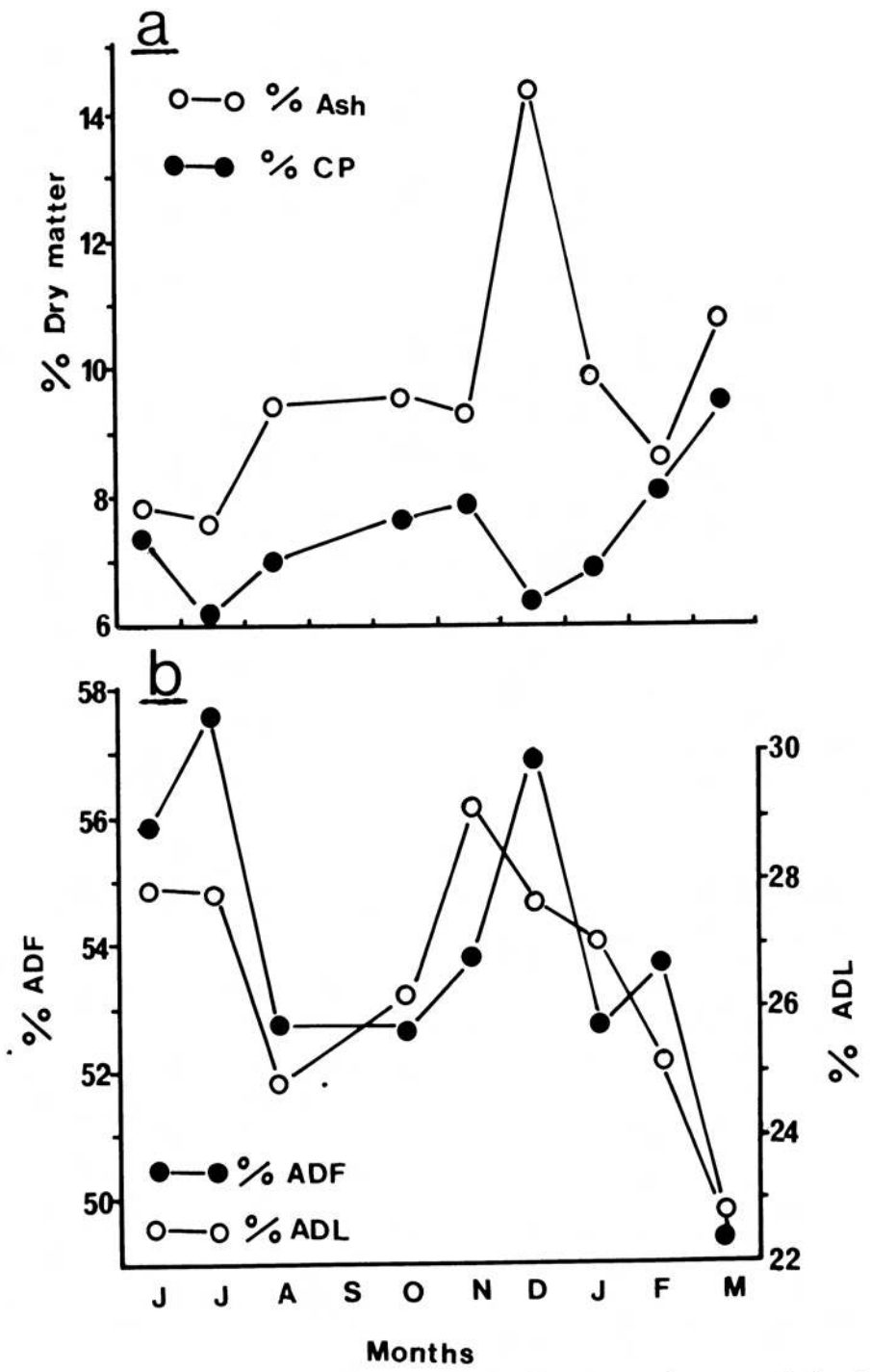

Fig. 5. Analyses of black rhinoceros faeces showing (a) percentage dry matter of ash and crude protein and (b) percentage acid detergent fibre and acid detergent lignin.

dant flush of new plant material with the February rains, there is a dramatic increase in protein. In some respects the percentage ash in the faeces (Fig. 5a) follows a similar course, thus it is low in the winter, higher in the spring but it then rises dramatically during December, before falling to nearly average values in January and February with an increase again in March. The higher percentage ash recorded during December and January may reflect a combination of the effects of eating more creeping succulents (Fig. 3, Fig. 4a) including the roots and an increase in dust on the plants during the summer drought (Fig. 3). The rise in ash in March may also be explained by dust.

The pattern of % ADF (Fig. 5b) seems roughly to be high values during unfavourable periods such as during winter and during the summer drought and lower values during the more favourable spring period and high rainfall late summer period. The pattern followed by % ADL is similar.

Discussion

The vegetation of the AENP, being a largely evergreen, semi-succulent thicket with an admixture of drought resistant Karoo elements and completely lacking fire as an ecological mover, is very different from the habitats in which black rhinoceros feeding has previously been studied (Goddard 1968, 1970; Jarman 1971; Mukinya 1977). Thus there are no rapid and drastic fluctuations in food quantity and quality such as might be expected in habitats subject to fire and deciduousness, but the vegetation nevertheless responds to rainfall (Aucamp 1972). In East Africa the black rhinoceros has been found to be a browser, highly selective for herbs and shrubs and showing a marked preference for legumes (Goddard 1968, 1970; Mukinya 1977). At the AENP the black rhinoceros shows a similar selection for shrubs but herbs are much less important, possibly due to the virtual absence of legumes. Succulents, an important component of the ground layer, were well used, particularly during dry periods.

Though subject to a great deal of variation the information derived from the physical analysis of faeces did agree with the observations derived from the feeding tracks. The chemical analysis of faeces and in particular the protein values, confirmed the subjectively identified stress period i.e. a dry period when preferred foods were not available or as nutritious as usual.

The trend of all the data, taken together, was that periods of generally adverse conditions, especially low rainfall, could be distinguished from optimum conditions by low utilisation of woody plants, higher utilisation of succulent plants, relatively higher feeding rate i.e. more bites per minute, fewer bites per plant indicative that less material was available, high cell wall fibre and lignin content of faeces, and low protein values. Studies on other wild herbivores showed a similar decline in protein (nitrogen) in the faeces during periods of low rainfall (Erasmus *et al.* 1978; Zimmerman 1980).

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