Diet selection and forage quality factors affecting woody plant selection by black rhinoceros in the Great Fish River Reserve, South Africa

Nkqubela M. Ganqa^{1*}, Peter F. Scogings² & Jan G. Raats³

¹Döhne Agricultural Development Institute, Private Bag X15, Stutterheim, 4930 South Africa ²Department of Agriculture, University of Zululand, Private Bag X1001, KwaDlangezwa, 3886 South Africa ³Faculty of Agriculture & Environmental Science, University of Fort Hare, Private Bag X1314, Alice, 5700 South Africa Received 26 October 2004, Accepted 3 March 2005

Diet selection of black rhinoceros and forage quality factors affecting diet selection were investigated in the Great Fish River Reserve. Plant species, number of bite marks, heights and diameters of bites, and diameter of the largest bite were recorded. Five woody species were sampled to quantify forage quality factors that could influence diet selection. Twigs 2, 6, 10 and 14 mm in diameter were collected from each species for determining the dry mass (DM), crude protein (CP) and neutral detergent fibre (NDF) of the leaves and wood of browseable material as well as leaf:stem ratio (LSR). *Azima tetracantha* and *Plumbago auriculata* were the most preferred woody plants in winter and summer. *Euphorbia bothae* was the most preferred succulent species in summer while in winter it was *Jatropha capensis*. Most browsing occurred below 1 m and most browsed twigs were <6 mm in diameter. Twig bites were larger during summer than winter. Forage quality factors varied across the plant species. Plant preference was significantly related to CP and LSR. Relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relationships between plant preference and CP were positive while the relati

Key words: crude protein, *Diceros*, diet, forage, herbivore, leaf:stem ratio, preference, rhinoceros, subtropical, season.

INTRODUCTION

The Great Fish River Reserve is in the Eastern Cape Province of South Africa and divided by the Great Fish (Nxuba) River into Sam Knott Nature Reserve, Andries Vosloo Kudu Reserve and Double Drift Game Reserve. Today the Great Fish River Reserve is home to a population of black rhinoceros (Diceros bicornis L.) (rhino) that consists of close to 70 individuals. In 1986 the first group of black rhinos was introduced in the Andries Vosloo Kudu Reserve. Since then high reproductive rates have been observed (B. Fike, pers. comm., 2000) indicating adequate habitat guality. However, little is known about their feeding ecology in this reserve as few studies have been conducted. Ausland et al. (2001) compared forage guality of preferred plants to that of non-preferred plants in autumn. Preferred plants did not differ from rejected plants in terms of dry mass per twig, leaf dry mass, neutral detergent fibre or

*To whom correspondence should be addressed.

E-mail: nkqubela@dohne.agric.za

crude protein concentrations. As a result black rhinos were suspected to use other nutritional and non-nutritional factors not measured in the study for diet selection in autumn (Ausland *et al.* 2001).

We understand that forage quality is not the only factor determining diet selection in black rhino andthat habitat factors may also be relevant. For example, utilization of woody browse by black rhinos in Western Itala Game Reserve was affected by habitat factors such as slope and abundance of paths, which affected the accessibility of an area. This may have an important influence on the degree to which certain parts of the reserve are utilized (Kotze & Zacharias 1993).

The objective of this study was to investigate forage quality factors that might affect the diet selection of rhinos. The specific aims were (i) to identify plant species preferred by black rhino in this reserve, (ii) compare variation of plant species selection between seasons and (iii) identify forage factors that determine diet selection of black rhino.

METHODS

Study area

Fieldwork was conducted during winter (June/ July 2000) and early summer (November/December 2000) in Andries Vosloo Kudu Reserve in the eastern part of the 45 000 ha Great Fish River Reserve. Andries Vosloo Kudu Reserve is approximately 6500 ha in size and is located between 33°04' and 33°09'S and 26°37' and 26°49'E, 35 km northeast of Grahamstown (Palmer 1981). The altitude varies from 183 to 548 m above sea level (Palmer 1981). The region in which the reserve falls is generally considered to be semiarid, with an average annual rainfall of 435 mm, varying from 500 mm/annum in the high-lying areas to 250 mm/annum in the low-lying parts (Palmer 1981; Hahndiek et al. 1998). Temperature ranges are great, with maxima in summer exceeding 40°C and winter minima as low as 0°C (Palmer 1981). Geologically the area comprises the Middleton formation (Adelaide subgroup of the Beaufort Group, Karoo Super Group) and consists predominantly of grey and 'red' mudstone and sandstone (Johnson & Keyser 1976).

The vegetation in the reserve is classified by Acocks (1975) as Fish River Scrub of the Valley Bushveld. It is known as a vegetation type with a semi-succulent thorny scrub, about 2–3 m high. Overgrazing by cattle has resulted in prickly pear (*Opuntia ficus-indica*) and *Euphorbia bothae* invasion (Acocks 1975). Evans *et al.* (1997) described three principal communities within the reserve: (i) short succulent thicket, (ii) medium succulent thicket and (iii) mesic bush clump savanna.

Together with rhinos the study area supports a wide variety of mammals. The browsing species that represents the highest biomass in the reserve is great kudu (*Tragelaphus strepsiceros*) with an estimated density of 11–16 ha/animal (B. Fike, pers. *comm.*, 2000). Other browsers and mixed feeders are Cape eland (*Taurotragus oryx*), steenbok (*Raphicerus campestris*), springbok (*Antidorcas marsupialis*), grey duiker (*Sylvicapra grimmia*) and bushbuck (*Tragelaphus scriptus*), which are present in relatively small numbers (B. Fike, pers. comm., 2000).

Diet selection

Backtracking was used to study the diet selection of the rhinos (Hall-Martin *et al.* 1982; Oloo *et al.* 1994; Atkinson 1995). Researchers, accompanied by experienced field rangers, used a vehicle to search for foraging rhinos. After a rhino was located and had moved off at a safe distance, its feeding path was followed on foot. Occasionally fresh tracks of rhino were observed and the foot impressions of the rhinos were generally clearly visible on the ground. These together with characteristic bite marks, damage to plants, marking of territory, resting/sleeping sites and scratch marks on trees and termite mounds formed the main criteria for the identification of tracks.

At each plant where fresh bite marks were found along the track, the plant species browsed was identified. Twig diameters and heights of bite marks were categorized into four classes: 0-5 mm, 6-10 mm, 11-15 mm and >15 mm; and 0-0.5 m, 0.51-1.0 m, 1.1-1.5 m and >1.51 m, respectively. In each class the number of twigs browsed was recorded. The diameter of the maximum or thickest bite mark was measured with a vernier calliper.

Forage factors

Five woody species (Acacia karroo, Azima tetracantha, Diospyros lycioides, Maytenus polyacantha and Plumbago auriculata) were selected for quantification of forage quality in summer. These were selected because they are among the most frequently browsed woody species by rhinos, making up 10.5% of all browsed plants (Ausland et al. 2001). More importantly, they represent various canopy retention patterns (deciduous versus evergreen), physical defences (spinescent versus non-spinescent) and shoot growth patterns (short-shoots versus long-shoots). Acacia karroo, D. lycioides and P. auriculata are deciduous. The spinescent species are A. karroo, A. tetracantha and *M. polyacantha*, which all have long, straight spines. Acacia karroo and M. polyacantha produce most of their new leaves in discrete clusters (whorls or tufts) of large primary leaves and small secondary leaves at the nodes of old shoots or branches. Such an arrangement of leaves is known as heterophylly, which may be characterized by the nodes being raised into short-shoots or spurs (Bell 1991). Conversely, the remaining species produce all their new leaves on new long-shoots, which bear one or two leaves per node.

Plant samples were taken in areas where browsing of the species by black rhino occurred. Three composite samples of twigs 2 mm, 6 mm, 10 mm and 14 mm in diameter were cut from each species

Plant species*	Relative abundance	Sun	nmer	Winter		
	(%)	Utilization (%)	Pref. index	Utilization (%)	Pref. index	
Acacia karroo	10.04	1.59	0.16	1.06	0.11	
Azima tetracantha	0.59	2.22	3.77	8.51	14.42	
Brachylaena eliptica	5.56	0.32	0.06	0.00	0.00	
Carissa haematocarpa	0.20	0.00	0.00	1.06	5.32	
Cassine crocea	0.05	0.00	0.00	0.27	5.32	
Coddia rudis	1.03	0.32	0.31	0.00	0.00	
Diospyros lycioides	2.81	0.95	0.34	0.00	0.00	
Ehretia rigida	4.53	0.00	0.00	4.26	0.94	
Euclea undulata	3.30	1.59	0.48	1.06	0.32	
Euphorbia bothae	3.00	68.89	22.96	3.99	1.33	
Grewia occidentalis	0.44	0.00	0.00	1.06	2.42	
Grewia rubusta	6.84	6.67	0.97	16.22	2.37	
Jatropha capensis	0.59	0.95	1.61	5.85	9.92	
Maytenus heterophylla	1.43	0.00	0.00	3.72	2.60	
Maytenus polyacantha	5.91	0.63	0.11	1.60	0.27	
Olea europaea	1.08	0.00	0.00	0.27	0.25	
Opuntia ficus-indica	0.69	1.59	2.30	0.27	0.39	
Ozora mucronata	1.18	0.32	0.27	0.27	0.23	
Pappea capensis	2.61	0.00	0.00	0.27	0.10	
Phyllanthus verrucosus	3.20	0.00	0.00	0.27	0.08	
Plumbago auriculata	2.21	5.08	2.30	25.53	11.55	
Rhus longispina	2.21	0.00	0.00	1.06	0.48	
Rhus refracta	4.23	0.00	0.00	0.27	0.00	
Schotia afra	2.61	0.00	0.00	0.53	0.20	

Table 1. Plant species browsed by black rhino in the Great Fish River Reserve, South Africa, during summer and winter, indicating relative abundance, relative utilization and preference index.

*Plant species not recorded during determination of relative abundance of plants in the reserve but browsed by black rhino during observation of diet selection are not included in this table.

for determining the dry mass and crude protein of the leaves and wood of browseable material. From each plant species sample a known number of twigs of each diameter class were collected and placed into plastic bags, to obtain an average estimate of the amount of dry mass, crude protein and leaf:stem ratio per twig. Samples were ovendried at 60°C for three days, after which the leaves and wood were separated. The dried leaves and wood were weighed separately and analysed for crude protein (CP) (Tecator 2300 Kjeltec Analyser) and neutral detergent fibre (NDF) (ANKOM 200/220 Fibre Analyser) according to standard procedures.

Data analysis

Preference for a plant species was determined as the ratio of relative utilization (number of times a plant species was browsed relative to total number of times of all plant species were browsed) to relative abundance (number of plants of the species relative to total number of plants of all species). The values of relative abundance of plants species in Andries Vosloo Kudu Reserve were provided by W.S.W. Trollope and S. Nibe (unpubl. data). Values of maximum twig diameter cut or thickest bite mark from each plant were pooled together and the *t*-test was used to test differences in log-transformed values between seasons. Variation in forage quality factors among species was modelled with ANOVA. Wood DM and LSR were square-root transformed, but the other factors were not. Simple linear regression analysis was used to model the relationships between forage quality and preference.

RESULTS

During the observation period 377 and 315 feeding stations were recorded in winter and summer, respectively. In summer 15 plant species were observed to be browsed by black rhino while there were 26 species browsed in winter. The two most preferred woody species in winter and summer were *A. tetracantha* and *P. auriculata*

Season

Summer

Winter

0–5

86.3

96.3

 Table 2. Percentage twigs browsed by black rhinos during summer and winter in the Great Fish River Reserve, South Africa, at four height classes.

Season		Height class		
	0–0.5 m	0.6–1.0 m	1.1–1.5 m	>1.5 m
Summer	66.5	23.9	7.7	1.9
Winter	59.8	30.1	10.1	0.0

Percentages in the table are pooled data of different plant species.

Table 3. Percentage twigs browsed by black rhinosduring summer and winter in the Great Fish RiverReserve, South Africa, at four diameter classes.

6-10

12.3

3.4

Diameter class (mm)

11-15

1.4

0.2

>15 mm

0.0

0.1

	Percentages in the table are from a pooled data of different plant
1	species excluding Euphorbia bothae due to difficulties in measuring
1	stem diameter.

(Table 1). Euphorbia bothae was the most preferred succulent species in summer while Jatropha capensis was most preferred succulent in winter. The most utilized woody species were *P. auriculata* and *G. robusta* in winter and summer, respectively. The most abundant species was *A. karroo.* Although *A. tetracantha* was the most preferred woody species in winter, it was less utilized than *P. auriculata.* Some plants were utilized only in one season, *e.g., Schotia afra* was utilized in winter, while others were important food sources in both seasons *e.g., A. tetracantha, E. bothae* and *G. robusta,* though levels of utilization varied between seasons.

The majority of browsed twigs were less than half a metre above the ground in both seasons (Table 2). Most twig browsing occurred at smaller diameter twig sizes in both seasons (Table 3). Percentage twigs browsed below 5 mm diameter in summer and winter were 86.3% and 96.3%, respectively. As the twig diameter increased, fewer twigs were browsed. The maximum browsed point differed between seasons (t = 6.08; d.f. = 451; P < 0.05). In summer the mean maximum browsed point was 6.0 (S.E.M. \pm 0.26) mm while in winter it was 4.4 (S.E.M. \pm 0.13) mm.

Plant species varied in terms of leaf CP (F = 290.391, n = 5, P < 0.001) and wood CP (F =86.879, *n* = 5, *P* < 0.001). *P. auriculata* and *A.* tetracantha had the highest leaf and wood CP, while *M. polyacantha* had the lowest (Table 4). Plant species also varied in leaf NDF (F = 48.555, n = 5, P < 0.001) and wood NDF (F = 30.297, n = 5, *P* < 0.001). Leaf NDF was highest in *D. lycioides* and P. auriculata, but lowest in A. tetracantha (Table 4). Wood NDF was lowest in A. tetracantha and D. lycioides, but highest in M. polyacantha and P. auriculata. Leaf DM did not vary across species, but wood DM did (F = 93.366, n = 5, P < 0.001). Plumbago auriculata had the highest wood DM, while D. lycioides had the lowest (Table 4). Leaf:stem ratio varied among plant species (F =35.509, *n* = 5, *P* < 0.001) (Table 4). *D. lycioides* had the highest LSR and *M. polyacantha* had the lowest.

Table 4. Forage quality (\pm S.E.) of leaves and wood of five woody species browsed by black rhinos during the summer season in the Great Fish River Reserve, South Africa. Superscript letters indicate significant differences among plant species according to the Least Significant Difference (n = 5, P < 0.05).

Plant species	Leaves			Wood			
	CP (%)	NDF (%)	DM (g)	CP (%)	NDF (%)	DM (g)	
A. karroo	13.2°	46.6 ^c	10.8	5.1 ^b	68.2 ^b	39.0 ^b	2.0 [°]
	(0.19)	(1.40)	(3.57)	(0.28)	(1.32)	(4.14)	(0.06)
A. tetracantha	16.0 ^d	31.3ª	11.5	7.7 ^d	63.6 ^ª	52.5 [°]	1.7 ^b
	(0.50)	(2.79)	(4.28)	(0.59)	(2.86)	(9.40)	(0.06)
D. lycioides	12.5 ^b	54.4 ^d	10.2	5.7 ^b	64.2 ^ª	26.3 ^a	2.9 ^e
	(0.29)	(1.15)	(2.33)	(0.47)	(1.71)	(7.67)	(0.07)
M. polyacantha	7.4ª	40.2 ^b	13.6	4.2 ^a	70.4 [°]	51.7°	1.4 ^a
	(0.31)	(0.55)	(3.46)	(0.38)	(2.39)	(16.06)	(0.02)
P. auriculata	16.6 ^d	51.5 ^d	13.3	7.0 ^c	71.6 ^c	78.8 ^d	2.2 ^d
	(0.42)	(1.58)	(3.91)	(0.37)	(1.70)	(25.30)	(0.10)

CP = crude protein, NDF = neutral detergent fibre, DM = dry mass and LSR = leaf: stem ratio.

Plant factor	Plant part	Twig size (mm)	а	b	R^2	Р
Crude protein (%)	Leaf	2	-3.994	0.385	0.508	0.003
		6	-2.822	0.317	0.632	< 0.001
		10	-2.343	0.285	0.564	0.001
		14	-1.783	0.248	0.347	0.021
	Wood	2	-4.770	0.783	0.784	<0.001
		6	-2.932	0.685	0.599	0.001
		10	-3.198	0.908	0.641	<0.001
		14	-2.842	0.894	0.560	0.001
	All	2	-5.168	0.301	0.697	<0.001
		6	-3.115	0.230	0.660	<0.001
		10	-2.719	0.226	0.608	0.001
		14	-2.207	0.205	0.416	0.009
Neutral detergent fibre (%)	Wood	2	9.052	-0.131	0.277	0.044
5	Leaf	6	4.186	-0.065	0.346	0.021
	All	6	7.363	-0.055	0.297	0.036
Drv mass (g)	Leaf	6	3.673	-0.562	0.425	0.008
,	Wood	14	-1 121	0.018	0.379	0.015
	All	14	-1.409	0.017	0.391	0.013
Leaf-stem ratio		6	5 865	-6.901	0 460	0.005
		10	6 174	_0 110	0.386	0.013
		10	0.174	-3.119	0.300	0.013

Table 5. Linear relationships (y = a + bx) between preference index (y) and forage factor (x) in the Great Fish River Reserve, South Africa, during summer (n = 15).

Plant preference among the group of five frequently browsed woody species was significantly related to leaf and wood crude protein at all diameter levels (Table 5). Wood fibre was significantly related to preference only at 2 mm twig diameter while leaf fibre was only significant at 6 mm diameter. The relationship between preference and crude protein was positive and between preference and fibre was negative. No relationship was significant between preference and dry mass at 2 and 10 mm diameter but at 6 mm diameter leaf dry mass was significant and at 14 mm wood dry mass was significant. The relationship between preference and dry mass was negative at 6 mm diameter and positive at 14 mm diameter. The relationship between preference and leaf:stem ratio was significant only at 6 and 10 mm diameter and the relationships were negative related (Table 5). Generally, crude fibre and dry mass were not related to preference but crude protein was consistently related to preference. Leaf:stem ratio related to preference only for the intermediate diameter twigs.

DISCUSSION

Diet selection

Black rhinos are selective feeders (Goddard 1968; Loutit *et al.* 1987; Oloo *et al.* 1994; Muya &

Oguge 2000). A preferred plant species is defined by the extent to which the species is consumed in relation to its availability in the environment (Barnes 1976). A highly preferred plant is one which is consumed in greatest quantities relative to its occurrence. The highly preferred plants in winter were A. tetracantha and P. auriculata and in summer were E. bothae and A. tetracantha. When ranking plant species by utilization index and preference index, it is noticeable that in winter A. tetracantha was the most preferred species although less utilized than P. auriculata which was more available than A. tetracantha. This suggests that preference is dependent on plant availability in the environment. Therefore food preference should be considered in relation to the kinds and amounts of different foods on offer (Barnes 1976).

In East Africa Muya & Oguge (2000) found that when browseable species are widely available to black rhino they tend to be highly utilized. However, in this study this was not apparent. The most abundant plant *A. karroo* was less utilized than available; conversely, the most utilized plants were less available. This indicates that browse is plentiful for black rhino in the reserve. The exceptional high reproductive rate of rhino on the reserve supports the observation of ample quality forage available. Seasonal variation has an important effect on the feeding ecology of black rhinos (Oloo et al. 1994). As shown in the results some plants were important food sources during a particular season. Succulents, including Euphorbia species, are eaten by black rhino elsewhere in Africa during dry periods (Goddard 1968; Joubert & Eloff 1971; Hall-Martin et al. 1982; Loutit et al. 1987). The above studies imply that succulents were used as water sources. This was reinforced in Great Fish River Reserve, where E. bothae was highly preferred during the hottest and driest period. In the present study A. tetracantha was preferred in both seasons. Hall-Martin et al. (1982) found A. tetracantha was of great importance throughout the year in the diet of black rhinos at Addo Elephant National Park.

When comparing black rhino diet selection in previous studies with the present study, there were similarities in the plant species selection. The findings that *E. bothae* and *A. tetracantha* are among the important plants browsed by black rhino in the Great Fish River Reserve are confirmed by previous studies. (Goddard 1968; Owen-Smith 1988; Hall-Martin *et al.* 1982; Corcoran 1994).

Forage factors affecting diet selection

Plant guality has been determined to be one factor determining diet selection of black rhino (Muya & Oguge 2000). However, previous work on black rhino in the Great Fish River Reserve indicated no relationship between quality and preference during autumn (Ausland et al. 2001). Black rhinos were suspected to use other nutritional and non-nutritional factors, not measured in that study, for diet selection. In the current study forage factors affecting diet selection were measured in woody species preferred by rhinos. The study revealed that plant structure is important in diet selection. Black rhinos in the Great Fish River Reserve tended to prefer twigs <6 mm in diameter. This confirms the observations of Ausland et al. (2001). They also bite more large twigs during summer than winter. Even though there were seasonal differences in maximum twig bite, a plant that presents browseable twigs <6 mm diameter could be at greater risk of losing more biomass than a plant that presents twigs with diameters >6 mm. Therefore characterization of plants browsed by rhinos in this reserve would help to develop better understanding and management of their impact on the vegetation they utilize.

The majority of twigs browsed by black rhinos were below 1 m in both seasons. This is consistent

with the findings from other studies as summarized by Owen-Smith (1988). Black rhinos are reported to be highly selective for both plant species and size (Emslie & Adcock 1994). Therefore when assessing habitat suitability for black rhino it is important to consider both plant species and height of available forage. These findings suggest that a key habitat factor important in black rhinoceros conservation includes diverse plant species which are at a height below 2 m (Kotze & Zacharias 1993; Muya & Oguge 2000).

As shown in the results that there are significant relationships between preference and forage quality factors at different twig diameter sizes. Plant preference was positively related to crude protein, therefore woody plants with high protein content were highly preferred by rhinos. As shown in the results the two preferred woody plants in summer were *A. tetracantha* and *P. auriculata* which have high crude protein content compared to other species tested in this study. In the Zambezi Valley the nutrient composition of selected browse consumed by black rhinos also contained high crude protein (Dierenfeld *et al.* 1995).

Elsewhere in Africa, black rhino have been observed to prefer plants with high fibre (Muya & Oguge 2000). In our study this was not apparent. Of the two preferred woody species in summer one had high fibre content and the other had low fibre content in both leaves and wood. Therefore our results do not explain whether black rhino were selecting for or against plants with high fibre content. Though the results indicate significant negative relationships between plant preference and leaf:stem ratio in the five woody species sampled, these were only for certain twig sizes. Generally leaf:stem ratio was variable for the highly preferred plants and the intermediately preferred plant. Therefore dry mass and leaf:stem ratio did not follow the same trend as that of crude protein.

Based on our observations of diet selection and forage quality factors affecting diet selection of woody plants by black rhinos in the GFRR, we found that crude protein was the major factor determining preference. Therefore we postulate that foraging black rhinos optimize nutrient intake rather than energy intake (Owen-Smith & Novellie 1982; Senft *et al.* 1987; Shipley *et al.* 1999). Black rhinos at GFRR preferred to select plants with high crude protein content in twigs less than 6 mm diameter. Nitrogen concentration and digestibility are negatively related to twig diameter, while fibre is positively related to twig diameter (Palo *et al.*, 1992). In larger twigs the ratio of fibre to crude protein is low making them less suitable as forage for black rhino.

ACKNOWLEDGEMENTS

NUFU (Norway), the National Research Foundation (South Africa) and the Royal Society of London (U.K.) funded the research. Brad Fike and staff of the Great Fish River Reserve assisted with data collection.

REFERENCES

- ACOCKS, J.P.H. 1975. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa 28.
- ATKINSON, S.J. 1995. Maintenance of captive black rhinoceros (*Diceros bicornis*) on indigenous browse in Zimbabwe: Energetics, nutrition and implication for conservation. MSc thesis, University of Zimbabwe, Harare.
- AUSLAND, C., SVEIPE, A., GANQA, N.M., RAATS, J.G. & PALMER, T. 2001. Feeding behaviour of black rhino (*Diceros bicornis minor*) in the Great Fish River Reserve, South Africa. Proceedings of the 5th International Wildlife Ranching Symposium, 20–23 March 2001. Pretoria, South Africa.
- BARNES, D.L. 1976. A review of plant-based methods of estimating food consumption, percentage utilisation, species preference and feeding patterns of grazing and browsing animal. *Proc. Grassld. Soc. sth. Afr.* 11: 65–71.
- BELL, A. D. 1991. Plant form. Oxford University Press, Oxford.
- CORCORAN, B. J. 1994. Foraging behaviour of black rhinoceros (*Diceros bicornis*) in the Valley Bushveld. B.Sc. (Hons) thesis, University of Port Elizabeth, South Africa.
- DIERENFELD, E.S., DU TOIT, R. & BRASELTON, W.E. 1995. Nutrient composition of selected browse consumed by black rhinoceros (*Diceros bicornis*) in the Zambezi Valley, Zimbabwe. J. Zoo Wildl. Med. 26(2): 68–74.
- EMSLIE, R.H. & ADCOCK, K. 1994. Feeding ecology of black rhinos. Proceedings of a Symposium on 'Rhinos as Game Ranch Animals', 9–10 September 1994. Onderstepoort, South Africa.
- EVANS, N.V., AVIS, A.M. & PALMER, A.R. 1997. Changes to the mid-Fish River Valley, Eastern Cape, South Africa, in response to land use, as revealed by a direct gradient analysis. *Afr. J. Range. For. Sci.* 14: 68–74.

- GODDARD, J. 1968. Food preferences of two black rhino populations. *East Afr. Wildl. J.* 6: 1–18.
- HAHNDIEK, Q., FIKE, B. & VAN EEDEN, D. 1998. Great Fish River Reserve management plan (Draft). Great Fish River Reserve, Grahamstown, Eastern Cape, South Africa.
- HALL-MARTIN, A.J., ERASMUS, T.& BOTHA, B.P. 1982. Seasonal variation of diet and faeces composition of black rhino (*Diceros bicornis*) in Addo Elephant Park. *Koedoe* 25: 63–82.
- JOHNSON, M.R. & KEYSER, A.W. 1976. Explanatory notes. 1:250000 Geological Series 3226 KWT. Government Printer, Pretoria, South Africa.
- JOUBERT, E. & ELOFF, F. C. 1971. Notes on the ecology and behaviour of back rhinoceros (*Diceros bicornis* L. 1758) in South West Africa. *Madoqua* 1: 5–53.
- KOTZE, D.C. & ZACHARIAS, P.J.K. 1993. Utilization of woody browse and habitat by the Black rhino (*Diceros bicornis*) in Western Itala Game Reserve. Afr. J. Range. For. Sci. 10: 36–40.
- LOUTIT, B.D., LOUW, G.N. & SEELY, M.K. 1987. First approximation of food preferences and chemical composition of the diet of desert dwelling black rhinoceros *Diceros bicornis* L. *Madoqua* 15: 35–54.
- MUYA, S.M. & OGUGE, N.O. 2000. Effects of browse availability and quality on black rhino (*Diceros bicornis michaeli* Groves 1967) diet in Nairobi National Park, Kenya. *Afr. J. Ecol.* 38: 62–71.
- OLOO, T.W., BRETT, R. & YOUNG, T.P. 1994. Seasonal variation in feeding ecology of black rhinoceros (*Diceros bicornis* L.) in Laikipia, Kenya. *Afr. J. Ecol.* 32: 142–157.
- OWEN-SMITH, N. & NOVELLIE, P. 1982. What should a clever ungulate eat? *Amer. Nat.* 119: 151–178.
- OWEN-SMITH, N. 1988. Megaherbivores: the influence of a very large body size on ecology. Cambridge University Press, Cambridge.
- PALMER, A.R. 1981. A study of the vegetation of Andries Vosloo Kudu Reserve, Cape Province. MSc thesis. Rhodes University, Grahamstown, South Africa.
- PALO, R.T., BERGSTRÖM, R. & DANELL, K. 1992. Digestibility, distribution of phenols, and fibre at different twig diameters of birch in winter. Implication for browsers. *Oikos* 65: 450–454.
- SENFT, R.L., COUGHENOR, M.B., BAILEY, D.W., RITTENHOUSE, L.R., SALA, O.E. & SWIFT, D.M. 1987. Large herbivore foraging and ecological hierarchies. Landscape ecology can enhance traditional foraging theory. *BioScience* 37: 789–799.
- SHIPLEY, L.A., ILLIUS, A.W., DANELL, K., HOBBS, N.T., & SPALINGER, D.E. 1999. Predicting bite size of a mammalian herbivores: a test of a general model of diet optimisation. *Oikos*: 84:55–68.