Habitat use and feeding behaviour of the buffalo and the white rhinoceros in the Hluhluwe-Umfolozi Game Reserve

M. R. Perrin* & R. Brereton-Stiles

School of Botany and Zoology, University of Natal, Private Bag X01, Scottsville 3209, Pietermaritzburg, Natal, South Africa

Resource partitioning by buffalo (*Syncerus caffer*) and white rhinoceros (*Ceratotherium simum*) was compared during the dry season in the Hluhluwe section of Hluhluwe-Umfolozi Park, KwaZulu-Natal, South Africa. High buffalo densities had been perceived as a potential competitive threat for grazing with co-existing populations of white rhino which have a high conservation status. Feeding behaviour was compared at different scales to identify exploitative competition or facilitation between the two study species; variables considered were use of grass species, grass height, and habitat preference. No significant differences were observed in the use of the common grasses *Themeda triandra* and *Panicum maximum*. However, resource partitioning occurred through use of grass of different height. Habitat facilitation was inferred from the observed interaction, since buffalo grazed grass to heights optimal for use by white rhino. Partitioning also occurred with reference to topography and gradient; white rhino occurred in valley bottoms, whereas buffalo displayed an even distibution across the catena. Resources were abundant during the study and no competition was evident between buffalo and white rhino. Management of the area optimises resource use.

Keywords: *Ceratotherium simum*, grazing, habitat use, resource partitioning, *Syncerus caffer*.

*   To whom correspondence should be addressed

Introduction

The maintenance of large coexisting, ungulate species populations requires insight into habitat requirements, habitat-use and interspecific competition to prevent undesirable habitat changes (Scogings, Theron & Bothma 1990). Between 1983 and 1994 estimated buffalo numbers increased from 800 to 1800 in the Hluhluwe Game Reserve (HGR) section of the Hluhluwe-Umfolozi Park causing concern for wildlife managers (KwaZulu-Natal Nature Conservation Service records, Balfour pers. comm.). It supports 20% - 30% of Africa's white rhinoceros (*Ceratotherium simum*) population, a species of high conservation value (Emslie pers. comm.; Emslie & Adcock 1995). Competition for grazing between buffalo (*Syncerus caffer*) and white rhino could reduce the viability of the white rhino populations owing to the increasing buffalo populations.

The purpose of this study was to define the trophic niches and spatial requirements of buffalo and white rhino and to identify areas of possible niche overlap which could lead to exploitive competition under conditions of resource limitation. It also examined whether buffalo play a facilitatory role in the maintenance of white rhino populations through pre-emptive grazing behaviour.

The niche concept is associated with resource use for practical reasons (Melton 1987), and resource partitioning reduces interspecific competition between coexisting grazing ungulates (Caughley & Sinclair 1994). White rhino and buffalo may interact with forage differently to optimise energy and nutrient intake (Plumb 1992). Large herbivores confront an apparent food surplus which is not only of low and varied nutritional quality (Senft, Coughenour, Bailey, Rittenhouse, Sala & Swift 1987; Owen-Smith 1992), but is widely dispersed over the landscape (Monro 1980; Buys 1990). Since

large herbivores use forage at various scales of ecological resolution, examining occurrence and use of an ecosystem's spatial heterogeneity is an effective tool in understanding their foraging strategies and resource requirements.

Only when an ungulate's foraging behaviour under optimal resource conditions is known, can it serve as an index of habitat quality (Melton & Heard 1992). Habitat selectivity can be a more sensitive indicator of population status and trend than density estimates (Melton & Heard 1992). Here, the northern HGR, which has a higher grass biomass than the southern region of the park, but which at times can be sub-optimal for grazers because of high cellulose:protein ratios, was selected as an area indicative of optimal resource use by buffalo and white rhino.

Food resources of large generalist herbivores have been studied at several scales: micropatch (feeding stations of plants), community, or the landscape level (Senft *et al.* 1987). Resource partitioning at these scales in large African herbivores has been quantified in terms of habitat choice (Monro 1980; Melton 1987; Scogings *et al.* 1990; Pienaar, Bothma & Theron 1992, 1993); grass species eaten (Field 1976; Hansen, Mugambi & Bauni 1985; Buys 1990; McNaughton & Banyikwa 1995); plant parts eaten (Bell 1970; Field 1976; Sinclair 1977); and preferred leaf table height (Page & Walker 1978; Melton 1987).

Examination of differential use of leaf table height and plant parts is important in understanding the dynamics and facilitation (Vesey-FitzGerald 1960; Caughley & Sinclair 1994) of coexisting ungulates. Studies have not investigated facilitation between buffalo and white rhino, but buffalo are involved in grazing successions where, through trampling and grazing of the taller grasses, they prepare habitats for other ungulates (Okigbo 1985). Hence, buffalo favouring tall

BAARD, E.H.W. 1995b. Growth, age at maturity and sexual dimorphism in the geometric tortoise, *Psammobates geometricus*. *J. Herpetol. Assoc. Afr.* 44:10-15.

BERRY, K.H. (Ed.). 1984. The status of the desert tortoise (*Gopherus agassizii*) in the United States. Report to U.S. Fish and Wildlife Service from the Desert Tortoise Council on Order No. 11310-0083-81.

BRANCH, W.R. (Ed.) 1988. South African Red Data Book - Reptiles and Amphibians. *S. Afr. Nat. Sci. Prog. Rep.* No. 151:1-241.

BRANCH, W.R., BENN, G.A., & LOMBARD, A.T. 1995. The tortoises (Testudinidae) and terrapins (Pelomedusidae) of southern Africa: their diversity, distribution and conservation. *S. Afr. J. Zool.* 30(3):91-102.

BROADLEY, D.G. 1993. A review of the southern African species of *Kinixys* Bell (Reptilia: Tesudinidae). *Ann. Transv. Mus.* 36:41-52.

BURNHAM, K.P., ANDERSON, D.R. & LAAKE, J.L., 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monograph.* 72:1-202.

CAUGHLEY, G. 1977. Analysis of Vertebrate Populations. New York: John Wiley and Sons, 234pp.

FLOYD, D.A. & ANDERSON, J.E. 1987. A comparison of three methods for estimating plant cover. *Journal of Ecology.* 75:221-228.

FREILICH, J.E., & LARUE, E.L. Jr. 1998. Importance of observer experience in finding desert tortoises. *J. Wildlife. Mgt.* 62:590-596.

GROOMBRIDGE, B. (Ed.). 1993. 1994 IUCN Red List of threatened animals. Cambridge, UK: IUCN, 286 pp.

IVERSON, J. 1992. A revised checklist with distribution maps of the turtles of the world. Richmond, Indiana: Privately published, 363 pp.

KEYSTONE VIEW CO., 1961. Manual for the Keystone Visual Survey Tests. Meadville, Pennsylvania.

SEBER, G.A.F. 1982. The estimation of animal abundance and related parameters. London: Charles Griffin and Co., 654pp.

SEN, A.R. 1983. Review of some important techniques in wildlife sampling and sampling errors. *Biometrical Journal.* 25:699-715.

grasses (Sinclair 1977; Page & Walker 1978) may create areas of preferred short grass for white rhino (Owen-Smith 1988). In the Umfolozi Game Reserve, Emslie (pers. comm.) found that buffalo preferred intermediate height tillers (40 - 75 cm), with limited fibre relative to leaf material.

Buffalo and white rhino share the common problem of obtaining maximum quality and adequate quantity in a diet dominated by fibrous, low nutritive tropical C4 grasses (Du Doit & Owen-Smith 1988; Owen-Smith 1992). However, they have different gastrointestinal morphologies and capacities and feed in different ways to maximise nutrient intake. As ruminants, buffalo require a combination of high quality grass and high fibre content (Beekman & Prins 1989). Since grass species and grass parts differ markedly in their nutrient contents (Owen-Smith 1992; McNaughton & Banyikwa 1995), buffalo select for relatively nutritious grass species and parts in order to maximise intake of proteins and carbohydrates (Sinclair 1977). Buffalos select grass species (Field 1976, McNaughton & Banyikwa 1995) which differ from grasses preferred by other ungulates (Sinclair 1977). Furthermore, buffalo eat particular plant parts (Sinclair 1977), prefer relatively tall grass (Beekman & Prins 1989), and avoid grass species high in secondary plant compounds (Owen-Smith 1992). This selectivity may result in reduced niche overlap with white rhino.

White rhino graze unselectively on low quality material to maximise quantity, although quality is also relevant (Monro 1980). They are relatively unselective for grass species (Melton 1987) but graze short grasses (Owen-Smith 1988).

The aim of this study was to compare resource use between coexisting buffalo and white rhino with reference to: grass species, grass leaf table height and habitat.

Within the Hluhluwe-Umfolozi Complex, the Umfolozi Game Reserve (UGR) is prone to periods of resource shortage (Melton 1987; Melton & Heard 1992), and has a relatively larger buffalo than white rhino population. The northern HGR, however, with its unique climate and high annual rainfall, results in the occurrence of a high availability of palatable grasses of different heights. Research in this area was used to show the differential use of habitat types, grass species and grass heights by buffalo and white rhino under optimal conditions where little or no interspecific competition occurred. This enabled comparison of resource partitioning between the two species in the HGR during the dry season, when high buffalo populations and limiting resources may result in asymmetric competition. Patterns of resource use by each species were used as an indication of competition and habitat depletion. With the optimal grazing conditions in the northern HGR during mid-1995, it was possible to investigate facilitation between the species pair.

Study area

The HGR (225km²), the northern section of the larger Hluhluwe-Umfolozi Park, is situated in central Zululand, South Africa (Figure 1). It forms part of the catchment of two large river systems, the Hluhluwe and Nzimane Rivers. The reserve is characterised by hot, wet summers and mild, dry winters, and a mean annual rainfall of 1041 mm (at Hilltop Camp) which peaks between October and March. Rainfall at the study site was probably less than average per annum, how-
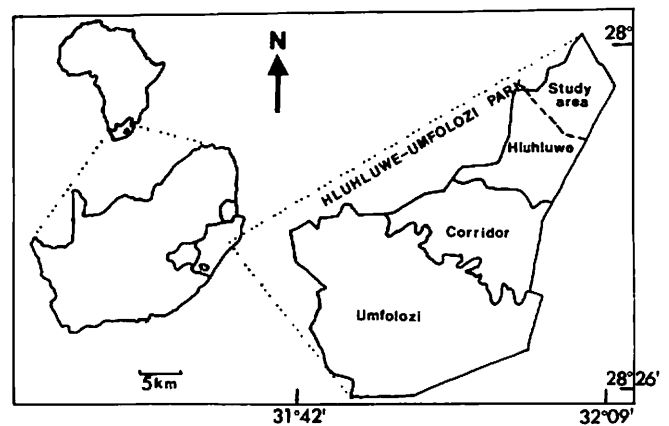

Figure 1   Location of the study area at Hluhluwe-Umfolozi Park, South Africa.

ever, field work was conducted during the dry season (May to July) when average monthly rainfall was higher than the average (100.2mm, 58.5mm and 79.3mm respectively).

The study area was located in the northern half of the HGR (110km²) in the Manzibomvu management section (28°41'1"S; 32°8'1"E). The terrain is broken by numerous hills and valleys with altitudes ranging from 80 m a.s.l. in the river valleys, to 450 m a.s.l. in the highlands. The predominant vegetation type was *Celtis africana-Harpephyllum caffrum* forest in higher lying areas and *Acacia nilotica-Euclea divinorum* woodland which generally occurs between 120m and 400 m above sea level. Fire-induced *Dichrostachys cinerea-Acacia nilotica* thicket, having the appearance of grassland, with an average shrub height of 0.7m, was less common. There are also extensive areas dominated by *A. caffra* and *A. karoo* on hill slopes with high fire frequencies. Towards the river there are areas of *Spirostachys africana* and *Acalypha glastrata*. Along the floodplain of the major water course, *Panicum maximum* grassland was found. The hilltops above 300m a.s.l. supported tall *Themeda triandra-Cymbopogon excavatus* grassland which included areas of *Hyparrhenia hirta*. Along the perennial and semi-perennial streams and rivers, *Acacia robusta-Ficus sycamorus* riverine forest occurred in a belt up to 60m wide. The northern HGR was burned every year between 1990 and 1995 except for 1992, and bush-clearing has occurred since the 1960s, owing to the encroachment of large tracts of forest. The *A. nilotica* areas have changed to lowland forest dominated by *E. racemose-Berchenia ceyheri* but much of the clearing has taken place in *A. karoo and M. senegalensis* woodland areas which can no longer be regarded as terraced forest.

Method

The distribution of the two study species were obtained by driving transect routes along the main roads of the reserve at an average speed of 25km/h between 07:00 and 18:00; fifty-one and fifty-seven samples were obtained for buffalo and white rhino respectively. Habitat data were collected at each sighting of buffalo or white rhino when seen within 500m of the vehicle. Habitat variables recorded in 10x10m animal-centred quadrats were: distance from water (m); aspect (cardinal points); slope (°); catenal position (upland, midland or

lowland); and percentage tree canopy cover (%): and percentage shrub cover (%).

The physiognomic types recorded were closed woodland-forest, bushland, shrubland, thicket, and grassland. When buffalo or white rhino were accessible, their grazing behaviour was recorded; transect data were collected at 19 and 23 sites for buffalo and white rhino respectively. When the animals moved from the 10x10m grid their grazing was recorded. A transect was laid through the centre of the grazed area and a minimum of five patches (0.65 x 0.65m) were sampled. The following variables were recorded within the patches: grass leaf table height (cm) for each grass species; freshly-grazed height (*i.e.* the height to which the study species grazed the grass); and preferred height of previously eaten grass (*i.e.* the height to which the grass was grazed by ungulates on previous occasions). For these parameters, the percentage of each grass grazed by each herbivore species was recorded.

Species codes used in tables and figures were as follows: *Panicum maximum* and *P. deustum* (*Pan*); *Themeda triandra* (*Tt*); *Eragrostis curvula* (*Ec*); *Dactyloctenium australe* (*Da*); *Bothriocloa insculpta* (*Bi*); *Chloris gayana* (*Cg*); *Sporobilis pyramidalis* (*Sp*); *Setaria* spp. (*Set*); *Hyparrhenia hirta* (*Hh*); *Digitaria* spp. (*Dig*); *Cymbopogon excavatas* (*Ce*).

Previously-grazed height (PGH) within the patch indicated the leaf table height available to the subjects on arrival at a site, whereas new freshly-grazed height (FGH) represented the level of herbage made available to other ungulates after the study species had eaten. A comparison between the FGH left by buffalo and the PGH used by white rhino was used to test for facilitation.

Percentage cover was recorded as total grass cover within each patch (%), and the cover of each grass species was given as a % of the total cover of all species. Spearman's rank correlation (Zar 1974) with a Bonferroni-z-statistic ($P < 0.005$; Byers, Steinhorst & Krausman 1984) was used initially to determine the relative availability of each grass species. This was done to decrease the number of G-test (Zar 1974) comparisons; which determined differences between the presence and absence of unassociated grasses in sites where buffalo and white rhino co-occurred.

Availability (Av) was calculated by Av = PA x C, where PA = the proportion of a particular grass species occurrence within the patches along a transect, C = the average percentage area cover of the grass species in the patches where it occurred. Av was then categorised: 1 (Av = 0-12); 2 (Av = 13-30); 3 (Av > 30). PA values were not computed for *Panicum deustem*, which occurred at 16 localities, since it has a similar nutritional value and ecology to *P. maximum*. *Panisum* spp. thus refers to *P. maximum* and *P. deustem* combined.

Tables of graze availability (Av) with amounts eaten (E) indicated preference for a grass species within a patch. E represented percentage area cover of fresh grazing for each grass species per patch. E was assigned four different classes of grazing: low (0-30%); medium (31-70%); high (71-100%); not recently grazed.

PGH and FGH were recorded as the average for the patches along the transect. If no PGHs were present, ungrazed heights were recorded. Only the heights of the dominant grass species *T. triandra, P. maximum* and *P. deustem* were analysed, using

a Mann-Whitney U-test (Zar 1974). Categories assigned to grass heights were as follows: short (0-12cm); medium (13-30cm); tall (>30cm)

A log-linear analysis was used to assess differences in the occurrence of buffalo and white rhino in various habitat types. The method does not require information on habitat availability, since a record of habitat variables at each animal location is sufficient (Scogings *et al.* 1990). Certain habitat variables (vegetation, gradient and aspect) were coded further to increase the resolution of the test; vegetation was coded into four categories: shrubland, grassland, woodland and forest; and grassland into a further two sub-categories: tree cover < 10% (almost unwooded); tree cover 11 - 50% (wooded grassland). Gradient was separated into three classes: gentle slope (0-10°); medium slope (11-25°); steep slope (26-50°) and aspect into four: N (315 - 45°) S (136 - 225°); E (46 - 135°) and W (226 - 314°). The log-linear analysis determined the effect of the habitat variables on the presence of buffalo or white rhino at a site. Forward selection was used to derive the best-fit model (Johnson & Riess 1982) which was tested using maximum likelihood methods to compare observed and expected frequencies.

Results

Spearman's rank correlation showed that of the thirteen grass species examined, none had an availability which correlated significantly with any other species, owing to small sample size, and hence low power of the test. Thus all grass species were used in the G-test.

Resource partitioning of the most extensively consumed grass species (*Panicum* spp. and *T. triandra*) was not evident between buffalo and white rhino which may represent interspecific exploitive competition. There was no significant difference in the occurrence of grass species between the buffalo
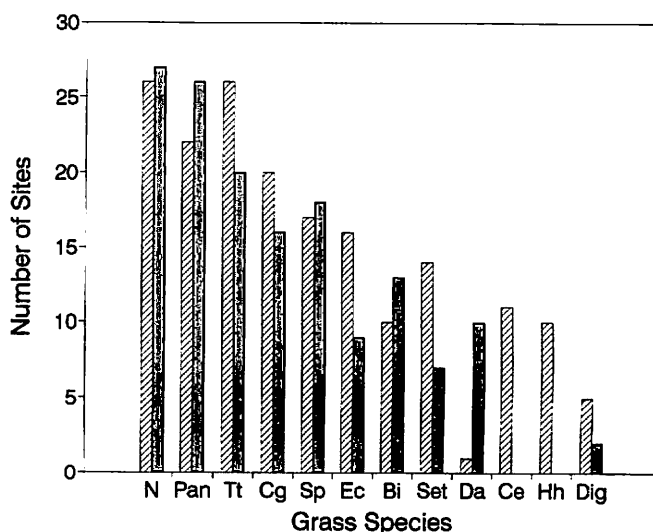

Figure 2 Presence of grass species at transect sites of buffalo and white rhino: (///) = white rhino, (shaded) = buffalo. N = sample sizes.

Pan = *Panicum* spp., Tt = *Themeda triandra*, Cg = *Chloris gayana*, Sp = *Sporobolis pyramidalis*, Ec = *Eragrostis curvula*, Bi = *Bathriochloa insculpta*, Set = *Setaria* spp., Da = *Dactyloctenium australe*, Ce = *Cymbopogon excatavus*, Hh = *Hyparrhenia hirta*, Dig = *Digaria* spp.

Table 1 Results of presence/absence G-test for the grass species

Bonferroni confidence intervals: $P < 0.005$

GRASS SPECIES	CODE	G	P
Panicum spp.	Pan	3.2	$P < 0.072$
Themeda triandra	Tt	5.85	P = N.S.
Eragrostis curvula	Ec	3.69	$P < 0.055$
Dactyloctenium australe	Da	10.44	$P < 0.001$
Bothriocloa insculpta	Bi	0.68	$P < 0.41$
Chloris gayana	Cg	1.34	$P < 0.25$
Sporobolis pyramidalis	Sp	0.08	$P < 0.78$
Setaria spp.	Set	5.0	$P < 0.025$
Hyparrhenia hirta	Hh	16.2	$P < 0.001$
Digitaria spp.	Dig	1.5	$P < 0.2$
Cymbopogon excavatus	Ce	18.1	$P < 0.001$

and white rhino grazing sites (Figure 2; Table 1) which were grazed extensively (Figure 3 to 6).

T. triandra was more common at buffalo (26) than at white rhino (20) grazing sites and *Panicum* spp. were less common at the buffalo (22) than at the white rhino sites (26);($P <$ 0.072; Figure 2). Buffalo frequently occurred at sites dominated by large stands of *T. triandra*, whereas white rhino were more strongly associated with moist bottomlands where *Panicum* spp. were abundant.

Strong trends in species-specific use of the leaf table height were evident (Figure 7). Buffalo predominantly grazed patches of tall grass which differed significantly in height from those used by white rhino (PGH median: 31.5cm vs

10.7cm; Mann-Whitney U-test=4.05; $P < 0.00005$). This indicated that buffalo ate mature, possibly more senescent grass with relatively high fibre to nutrient ratios, while white rhino consumed highly nutritious young grasses low in fibre. Results were counter to those anticipated. Grasses were grazed to significantly different heights by buffalo and rhino (FGH, median: 24.9 vs. 6.1; U = 4.05; $P < 0.00005$).

The FGH's and PGH's of buffalo were considered separately. Buffalo grazed grass to medium height (13-30cm) at 13 grazing sites whereas white rhino occurred in patches with PGH of medium height at ten sites. That is, the buffalo grazed predominantly taller grasses at an optimal height for consumption by white rhino, inferring facilitation.

There was a significant difference in the occurrence of grass species at the buffalo and rhino sites (Table 1); *H. hirta*
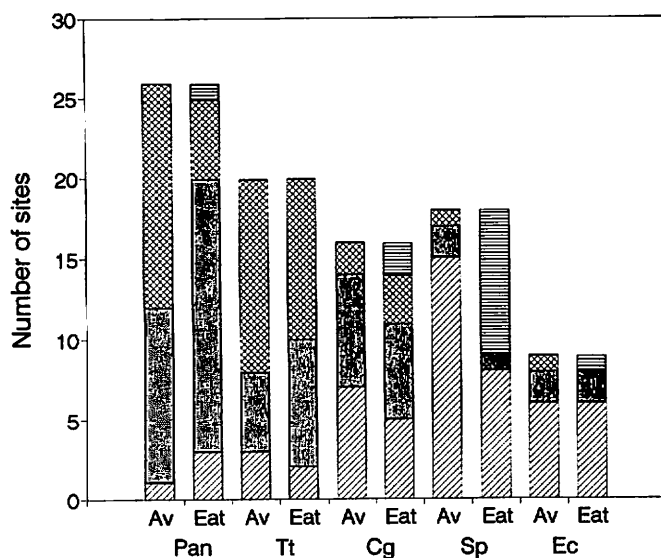

Figure 4 Graze availability and use of the less abundant grass species at the white rhino transect sites. Abbreviations for plant species are as in Figure 2 and for leaf table heights are as in Figure 3.

Figure 3 Graze availability and use of the more abundant grass species at the white rhino transect sites.

Leaf table height; (///) = low, (shaded) = medium, (hatch) = high, (=) = not known. Abbreviation of plant species names are as given in Figure 2.
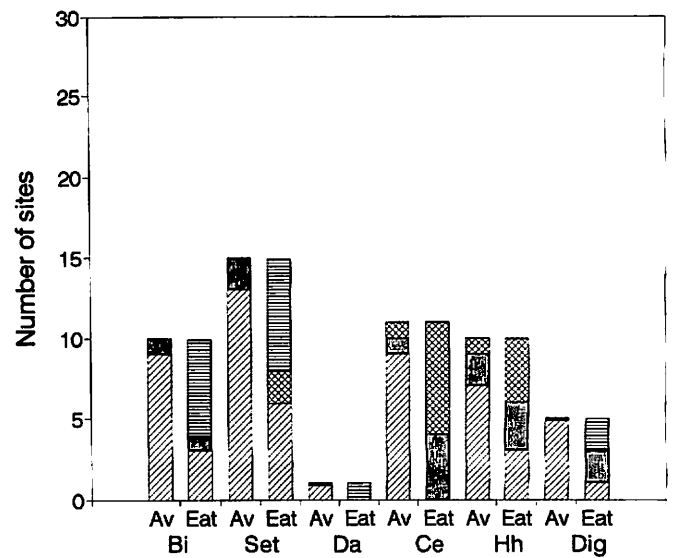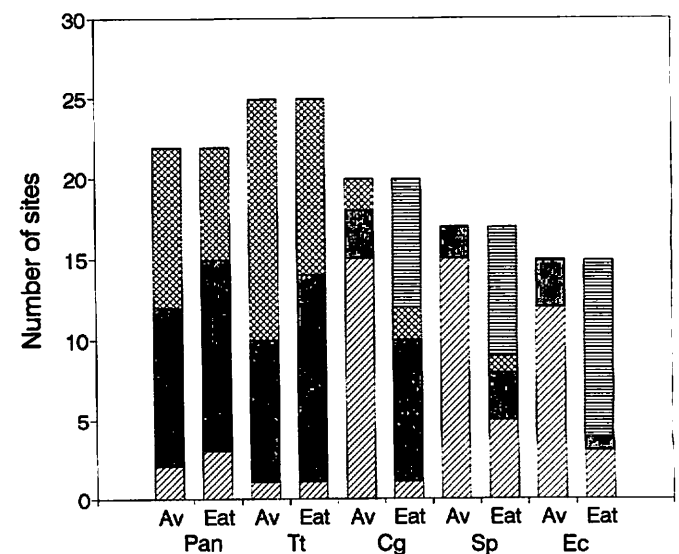

Figure 5 Graze availability and use of the more abundant grass species at the buffalo transect sites. Abbreviations for plant species are as in Figure 2 and for leaf table height are as given in Figure 3.
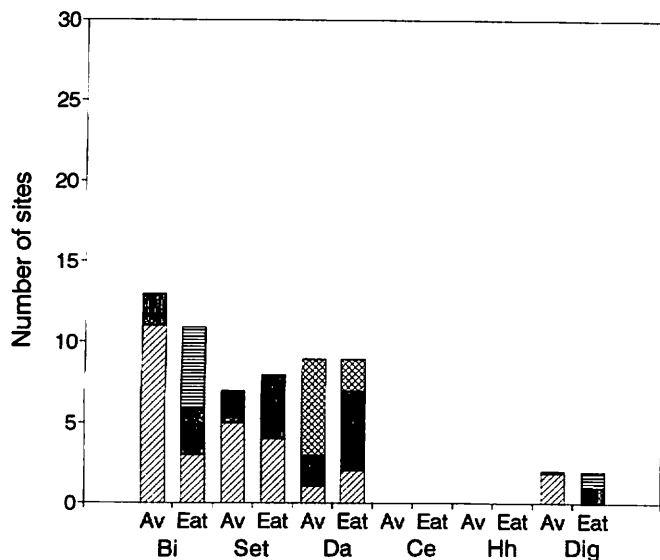
Figure 6 Graze availability and use of the less abundant grass species at the buffalo transect sites. Abbreviations for plant species are as in Figure 2 and for leaf table height are as given in Figure 3.

Table 2 Results of log-linear habitat analysis considering transect and non-transect sites

1.Baseline model A BCDE $L^2 = 51.1$ Df = 107 $P < 1.0$				
Equation	Factor	L^2	Df	P	R^2
AB BCDE	Gradient	8.2	2	$P < 0.02$	16.0
AC BCDE	Vegetation	3.2	3	$P = $ N.S.	6.3
AD BCDE	Topography	17.4	2	$P < 0.001$	34.1
AE BCDE	Freshly-grazed height	30.1	2	$P < 0.001$	58.9

2. Baseline model A BCDE $L^2 = 47.3$ Df = 7 $p < 0.09$				
Equation	Factor	L^2	Df	P	R^2
AB BCDE	Drainage	3.1	1	$P > 0.05$	6.6
AC BCDE	Vegetation	3.2	3	$P = $ N.S.	6.8
AD BCDE	Topography	17.5	1	$P < 0.01$	37.0
AE BCDE	Freshly-grazed height	30.1	2	$P < 0.01$	63.6

and *C. excavatus* were not available at white rhino transect sites (Figure 4) but occurred at buffalo sites 10 and 11 (Figure 6). These grass species are possibly indicative of more sour areas, on the hillslopes which are exposed to higher rainfall and thus more leaching than other sites; they were characteristic of sites grazed by buffalo. Both these grass species had low availability, however, and did not contribute substantially to the total intake of biomass by the buffalo.

Areas grazed by white rhino had a low community diversity with most of the standing crop represented by the dominant species (e.g. *Panicum* spp. or *T. triandra*). *Dactyloctenium australe*, a low-growing species suited to broad muzzled species, was found at ten of the white rhino transect sites with low to medium availability and was eaten on all occasions (Figure 4). It occurred at only one buffalo site with very low availability (Av = 0.5; Figure 6).

The avoidance of certain grass species was displayed by each species (Appendix 2). *Bothriocloa insculpta*, which is chemically defended unless very young, and *Sporobolis pyramidalis*, which occurred at low densities in most patches, were avoided by buffalo and white rhino. Selection was against *B. insculpta* which occurred at few sites at low availability (Figures 2, 4 & 6). *S. pyramidalis*, a ubiquitous species, was not eaten extensively by either grazer (Figures 3 & 5). *Setaria* spp. were largely avoided by buffalo (Figure 6).

C. excavatus was grazed but it occurred in markedly low amounts in the diet (Figure 6). Thus, rejection of the grass was clearly shown. This avoidance behaviour maximised the intake of nutrients by buffalo that spent more time in stands of *T. triandra* and *Panicum* spp. and less in areas of unpalatable species including *H. hirta* and *C. excavatus*.

Buffalo were more selective than white rhino in avoiding less palatable species in a patch (Figures 3 to 6). Although rhino avoided the unpalatable grasses *S. pyramidalis* and *B. insculpta* they showed no preference for other species and consumed grasses according to their availability (Figures 3 & 4). Buffalo, however, avoided *E. curvula* and *C. gayana* more

than did white rhino (Figures 3&4). Avoidance of *C. gayana*, which is palatable, is indicative of extremely high selectivity and is explained by the relatively higher palatability of *T. triandra* and *Panicum* spp.. By avoiding *C. gayana*, buffalo maximised ingestion of more nutritious grasses, including *E. curvula*.

Results of habitat preference highlighted important factors partitioning the two grazers at community and landscape scales (Tables 2 & 3). Differences in leaf table height (*i.e.* previously-grazed heights of *T. triandra* and *Panicum* spp.), displayed the strongest trend for ecological separation of buffalo and white rhino (Table 2) and was highly significant ($P < 0.001$ and $P < 0.01$).

Topography was a significant habitat variable ($P < 0.001$ - $P < 0.02$: Table 2&3). The use by buffalo of the three catenal positions, and the preference of white rhino for generally higher nutrient bottomlands, (Table 4), likely caused differences in use of grass species and grasses of different heights. Buffalo were found significantly more often on the high hillslopes of the midlands and uplands where long stands of *T. triandra* grassland occurred. As uplands are generally drier than lowlands, buffalo were exposed to robust grassland types including *C. excavatus*, *Digitaria* spp., *H. hirta* and *Setaria* spp. White rhino were common in lowlands along drainage lines that were ideal for shade- and moisture-loving grasses including *P. maximum*, *P.deustem* and *D.australe*.

Topography, as a factor partitioning the species, was compounded by gradient (Tables 2 & 3), owing to the correlation between steepness and upper slopes and hilltops, and gentle gradients with valleys.

Some spatial overlap and potential for competition occurred in the lowlands (Table 4). Resource overlap was likely associated with areas of recent burning (October 1994) where *Panicum spp.*, *T. triandra* and *C. gayana* were flushing and leaf table heights were low to medium. Partitioning

Table 3 Results of log-linear habitat analysis considering only non-transect sites

1. Baseline model A BCD
$L^2 = 33.1$ Df = 23 $P < 0.08$

Equation	Factor	L^2	Df	P	R^2
AB BCD	Aspect	4	3	$P = $ N.S.	12.1
AC BCD	Topography	18.9	2	$P < 0.01$	57.1
AD BCD	Drainage	4.2	1	$P < 0.05$	12.7

2. Baseline model A BCDE
$L^2 = 31.1$ Df = 47 $P < 0.96$

Equation	Factor	L^2	Df	P	R^2
AB BCDE	Aspect	2.2	3	$P = $ N.S.	7.1
AC BCDE	Topography	7.8	2	$P < 0.02$	23.6
AD BCDE	Drainage	3.3	1	$P < 0.05$	10.6
AE BCDE	Wooded Grassland	1.1	1	$P = $ N.S.	3.6

3. Baseline model A BCDE
$L^2 = 38.7$ Df = 8 $P = 0$

Equation	Factor	L^2	Df	P	R^2
AB BDE	Topography	28.5	2	$P < 0.001$	47.0
AC BCDE	Vegetation	3.1	3	$P = $ N.S.	5.1
AD BCDE	Gradient	26.7	2	$P < 0.001$	44.2
AE BCDE	Drainage	7.1	1	$P < 0.1$	11.8

4. Baseline model A BC
$L^2 = 38.7$ Df = 8 $P = 0$

Equation	Factor	L^2	Df	P	R^2
AB BC	Previously grazed height	34.1	2	$P < 0.001$	88.1
AC BC	Freshly grazed height	30.1	2	$P < 0.001$	77.8

occurred in relation to grass height and buffalo likely performed a facilitatory role by maintaining grass at medium height.

Drainage was not important in explaining habitat preference differences of white rhino or buffalo (Table 3). Similarly, wooded grassland and aspect were parameters of little importance in determining distribution. White rhino were more frequently associated with water holes than buffalo (67% and 40% of observations respectively). This was partially caused by white rhino's reliance on water not only for daily drinking, but also for mud-wallowing which is an important thermoregulatory process. However, water was readily available during the study following heavy rainfall in the HGR in April, June and July of 1995.

With the exception of the avoidance of forest, vegetation structure was one of the least relevant factors in habitat selection (Table 2 & 3) and the two species were distributed evenly between three of the four parameters *i.e.* grassland, shrubland, and thicket (Table 5). Buffalo and white rhino showed similar preferences for vegetation types.

Buffalo and rhino were rarely recorded grazing in closed woodland or forest despite its high availability, possibly the

Table 4 Log-linear analysis table of species and topography.

	Topography		
	Lowlands	Midlands	Uplands
Buffalo	15	14	22
White rhino	41	12	3

result of reduced grass cover in these areas. Neither buffalo nor white rhino were observed at Isivivaneni Road which is dominated by forest and woodland. White rhino, however, were found in this vegetation type more frequently than buffalo, as grazing lawns of *D. australe* sometimes occurred there in the moist, shady areas provided by the canopy cover. *P. maximum* also occurred under trees.

Discussion

Buffalo and white rhino use *T. triandra*, *P. maximum* and *P. deustem* as their primary sources of graze. As plentiful and highly nutritious species (Tainton, Bransby & Booysen 1979; Clayton & Renoize 1986), *Panicum* spp. and *T. triandra* were
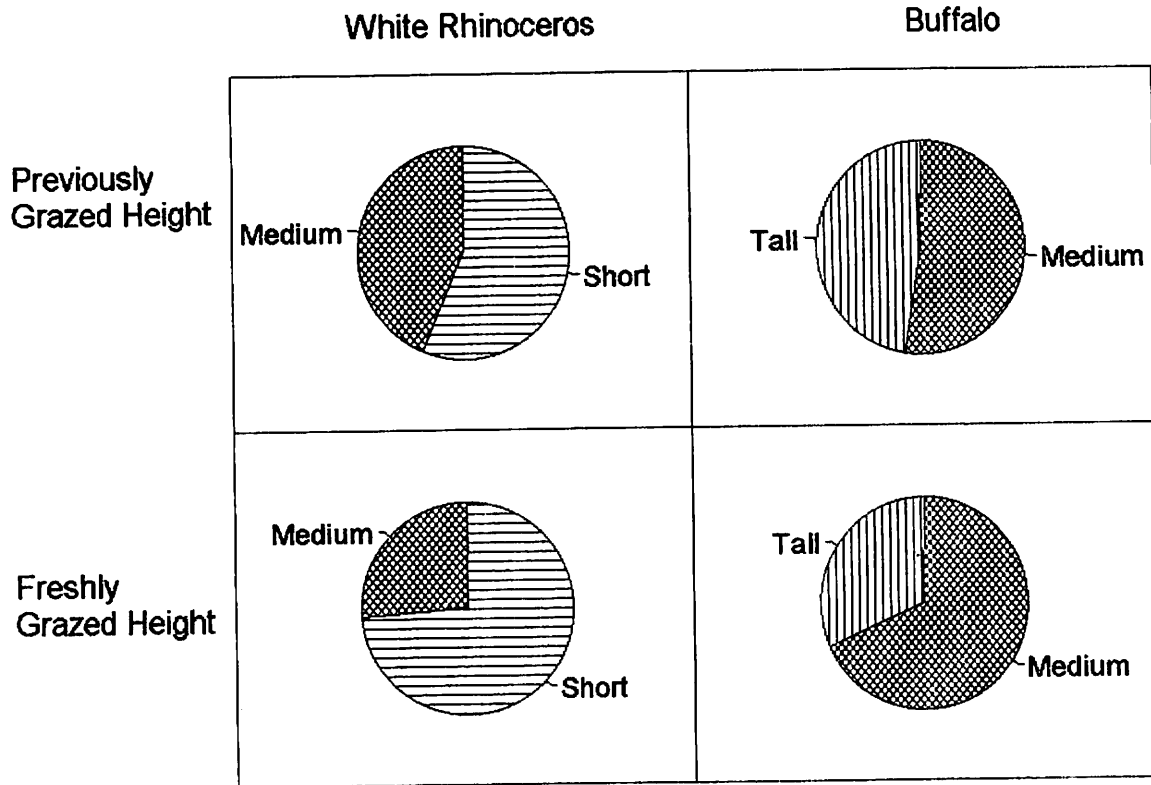
Figure 7 Short (=), medium (hatch) and tall (IIII) previously- and freshly-grazed leaf table heights recorded for buffalo and white rhino.

Table 5 Log-linear analysis table showing the distribution of buffalo and white rhino between vegetation types

	Vegetation			
	Shrubland	Grassland	Thicket	Forest
Buffalo	10	25	14	2
Rhino	16	20	16	5

a significant dietary component of buffalo and white rhino. However, strong ecological separation occurred in terms of the height at which the herbage was grazed and the positioning of the two species in the landscape.

Buffalo occurred more frequently than white rhino on steep upper slopes and hilltops, sites dominated by stands of tall *T. triandra*. They have a high absolute energy requirement (Owen-Smith 1988; Brown 1990) and their digestive system facilitates a slow rate of passage with long retention times, resulting in efficient digestion of a high fibre diet (Demment & Van Soest 1983). Tall swards of possibly less palatable *T. triandra* and *Panicum* spp. provide a large bite mass to maintain foraging efficiency which may account for buffalo using patches with a great herbage mass (Hansen *et al.* 1985; Laca, Distel, Griggs, & Demment 1994). Buffalo use their lower incisors and tongue to twist and cut herbage (Field 1976) and so are precluded from efficient grazing on short grass (Sinclair 1977), hence their preference for *T. triandra* tillers of medium height. However, the narrower muzzle allowed buffalo higher relative selectivity of more nutritious grass species than white rhino, thereby overcoming the problem of low protein content in senescent stands (Page & Walker 1978; Beekman & Prins 1989). At a fine scale, they may be more

selective of plant part (Diamond 1986), hence their preference for taller *T. triandra* tillers, as they are able to select large quantities of leaf and little fibrous culm.

White rhino as large non-ruminants are non-selective bulk grazers able to tolerate a lower minimum dietary quality than buffalo (Owen-Smith 1988). They occurred almost exclusively in more eutrophic lowland areas which had a high occurrence of short, nutritious grasses of high leaf to stem ratio (*P. maximum, P. deustem*, young *T. triandra* and *Dactyloctenium australe*; Buys 1990). As an opportunistic ground cover species, *D.australe* is maintained as extensive 'lawns' by white rhino at heights of <5cm (Owen-Smith 1988). This is interpreted as resource partitioning at the grass species level, since *D.australe* is of high nutritional value (Watson & Dallwitz 1992) and constitutes an important dietary component of white rhino. The broad muzzle enables rapid ingestion of large quantities of undifferentiated plant material, but grass is grazed to heights of 2cm (Owen-Smith 1988). The abundance of high quality grass permitted white rhino to be less selective for plant species than buffalo, although strong avoidance of unpalatable species with high levels of secondary compounds was shown. In areas of low food availability in HGR during the dry season, white rhino were shown to graze tall stands of *T. triandra* demonstrating its ability to process fibrous senescent grasses when necessary. Owen-Smith (1973) recorded that white rhinos move into the hills to utilise *T. triandra* during the crunch period of the dry season. The active maintenance of specific grazing lawns by rhino facilitates rates of resource renewal and encourages the growth of the nutritious ground cover species *D. australe* (Van Oudtshoorn 1992; Dublin 1995).

79

Bothriochloa insculpta which has a low palatability and strong aromatic taste (Clayton & Renoize 1986; Van Oudtshoorn 1992) was often left standing in heavily-grazed patches. Owing to its low palatability and low nutritional value (Tainton *et al.* 1979), *S. pyridimalis* was often left uneaten. *C. excavatus*, a strongly unpalatable and aromatic grass species (Watson & Dallwitz 1992), was only eaten in small amounts.

To evoke interspecific competition, shortage of a common resource is necessary (Caughley & Sinclair 1994); however, the HGR did not have a limiting resource during the dry season. Rainfall was particularly high which resulted in abundant graze of good quality. Under harsh conditions when the abundance of quality grass declines below sub-minimum levels of crude protein, buffalo characteristically switch to browsing owing to the superior nutritive quality of browse (Stark 1986; Buys 1990). Although intake of browse by buffalos often ranges between 5 and 26% (Stark 1986), intake of graze at 50% has been recorded during winter (Sinclair 1977). No browsing was observed by buffalo indicating that graze possessed sufficiently high nutrient levels for maintenance.

Indirect facilitation may occur when buffalo modify the grass sward by trampling and grazing it to levels suitable for consumption by white rhino. However, the two species did not graze in succession and were only found grazing together on three of the 108 observations. Thus, facilitation is indirect and of minor significance and factors including fire, bush-clearing and grazing by other ungulates likely play a role in creating the optimum niche for white rhino. By maintaining grazing lawns, white rhino may facilitate their own optimal grazing conditions. Also buffalo, which revisit the same patches on a rotational basis, especially ridge tops (Emslie, pers. comm.), may facilitate their own optimal grazing conditions by keeping *T. triandra* from senescing.

Acknowledgements

References

BEEKMAN, J. H. & PRINS, H.H.T. 1989. Feeding strategies of sedentary large herbivores in East Africa with emphasis on the African buffalo, *Syncerus caffer*. *Afr. J. Ecol.* 27:129-147.

BELL, R. H. V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. pp 111-124 In A. Watson, (ed). Animal populations and their relation to food sources. Blackwell, Oxford.

BROWN, J. S. 1990. Habitat selection as an evolutionary game. *Evolution* 44:732-746.

BUYS, D. 1990. Food selection by eland in the western Transvaal. *S. Afr. J. Wildl. Res.* 20:16-20.

BYERS, C. R., STEINHORST, R. K. & KRAUSMAN, P. R. 1984.

Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Mgt.* 48:1050-1053.

CAUGHLEY, G. & SINCLAIR, A. R. E. 1994. Wildlife Ecology and Management. Blackwell Science, Massachusetts.

CLAYTON, W. D. & RENOIZE, S. A. 1986. Genera Graminum Grasses of the World. Kew Bulletin Additional Series XIII, London.

DEMMENT, M. W. & VAN SOEST, P. J. 1983. Body size, digestive capacity and feeding strategies of herbivores. Winrock International, Arkansas.

DIAMOND, J.M. 1986. Carnivore dominance and herbivore coexistence in Africa. *Nature*, 320: 112.

DUBLIN, H. T. 1995. Vegetation dynamics of the Serengeti-Mara ecosystem: the role of elephants, fire and other factors. Chapter 4 *in* Sinclair, A. R. E., & Arcese, P. (eds.) Serengeti II. Dynamics, management and conservation of an ecosystem. University of Chicago Press, Chicago and London.

DU DOIT, T. & OWEN-SMITH, N. 1988. Body size, population metabolism, and habitat specialisation among large African herbivores. *Am. Nat.* 133:736-740.

EMSLIE, R. & ADCOCK, A. 1995. White rhino in Hluhluwe-Umfolozi Park, South Africa. Have 800 been "lost"? Unpublished report. I.U.C.N. species survival commission. African rhino specialist group. Key issue report number 1.

FIELD, C. R. 1976. Palatability factors and nutritive values of the food of buffalos (*Syncerus caffer*) in Uganda. *E. Afr. Wildl. J.* 14:181-201.

HANSEN, R. M., MUGAMBI, M. M. & BAUNI, S. M. 1985. Diets and trophic rankings of ungulates of the Northern Serengeti. *J. Wildl. Mgmt.* 49:823-829.

JOHNSON, L.W. & RIESS, R.D. 1982. Numerical Analysis. Addison-Wesley Publishing Company, Reading, Massachusetts.

LACA, E. A., DISTEL, R.A., GRIGGS, T.C. & DEMMENT, M. W. 1994. Effects of canopy structure on patch depression by grazers. *Ecology* 75:706-716.

McNAUGHTON, S. J. & BANYIKWA, F. F. 1995. Plant communities and herbivory. Chapter 3. In Sinclair, A. R. E., & Arcese, P. (eds.) Serengeti II. Dynamics, management and conservation of an ecosystem. University of Chicago Press, Chicago and London.

MELTON, D. A. 1987. Habitat selection and resource scarcity. *S. Afr. J. Sci.* 83:647-651.

MELTON, D. A. & HEARD, D. 1992. Ungulate behaviour and habitat quality: insights from Africa and the Arctic. Pp 185-188 In Spitz, F., Janeau, G., Gonzalez, G. & Aulagnier, S. (eds.) 'Ongules/Ungulates 91'. S.F.E.P.M.-I.R.G.M., Paris & Toulouse.

MONRO, R. H. 1980. Observations on the feeding ecology of impala. *S. Afr. J. Zool.* 15:107-110.

OKIGBO, B. N. 1985. Land use and productive potentials of African savannas. Chapter 9 In Tothill, J. C., & Mott, J. C., (eds.) International Savanna Symposium 1984. Common Agricultural Bureaux, Queensland.

OWEN-SMITH, N. 1973. The behavioural ecology of the white rhinoceros. Unpub. Ph.D. Thesis. University of Wisconsin.

OWEN-SMITH, N. 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge.

OWEN-SMITH, N. 1992. Grazers and browsers: ecological and social constraints among African ruminants. pp 175-181 In Spitz, F., Janeau, G., Gonzalez, G., Aulagnier, S., (eds.) "Ongules/Ungulates 91". S.F.E.P.M.-I.R.G.M., Paris & Toulouse.

PAGE, B. R. & WALKER, B. H. 1978. Feeding niches of four large herbivores in the Hluhluwe Game Reserve, Natal. *Proc. Grassl. Soc. S. Afr.* 13:117-122.

PIENAAR, D. J., BOTHMA, DU P. & THERON, G. K. 1992. Landscape preferences of the white rhinoceros in the southern

Kruger National Park. *Koedoe* 35:1-7.

PIENAAR. D. J., BOTHMA. DU P. & THERON. G. K. 1993. Landscape preferences of the white rhinoceros in the central and northern Kruger National Park. *Koedoe* 36:79-85.

PLUMB. G. E. 1992. Analysis of linear programming models on models of ungulate foraging. Pp. 183-184 In Spitz, F.. Janeau, G., Gonzalez. G.,& Aulagnier, S. (eds.) "Ongules/Ungulates 91". S.F.E.P.M.-I.R.G.M., Paris & Toulouse.

SCOGINGS. P. F., THERON, G. K. & BOTHMA. J. DU P. 1990. Two quantitative methods of analysing ungulate habitat data. *S. Afr. J. Wildl. Res.* 20:9-13.

SENFT. R. L.. COUGHENOUR. M. B.. BAILEY. D. W.. RITTENHOUSE. L. R., SALA, O. A. & SWIFT. D. M. 1987. Large herbivore's foraging and ecological hierarchies. *BioScience*: 37:789-799.

SINCLAIR. A. R. E. 1977. The African buffalo. A study of resource limitations of a population. University of Chicago Press, Chicago & London.

STARK. M. A. 1986. Daily movement, grazing ability and diet of savanna buffalo, *Syncerus caffer brachyceros*, in Benoue National Park, Cameroon. *Afr. J. Ecol.* 24:255-262.

TAINTON, N. M., BRANSBY, D. I. & BOOYSEN, P. DE V. 1979. Common Veld and Pasture Grasses of Natal. Shuter and Shooter, Pietermaritzburg.

VAN OUDSTHOORN, F. (ed.) 1992. Guide to Grasses of South Africa. BRIZA Publikasies, Arcadia.

VESEY-FITZGERALD, D. 1960. Grazing succession among East African game animals. *J. Mammal.* 41:161-172.

WATSON. L.. & DALLWITZ, M. J. (ed.) 1992. Grass Genera of the World. C. A. B. International, United Kingdom.

ZAR. J. H. 1974. Biostatistical analysis. Prentice-Hall inc. London, Sydney. Toronto, New Delhi & Tokyo.