# Forage selection by African buffalo in the late dry season in two landscapes

**Valerio A. Macandza[1], Norman Owen-Smith[1*] & Paul C. Cross[2,3]**

[1]Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, WITS, 2050 South Africa

[2]Department of Environmental Science, Policy and Management, University of California at Berkeley, CA 94720-3112, U.S.A.

[3]Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002 South Africa

Received 27 October 2003. Accepted 10 May 2004

**Forage selection by buffalo and the contribution of grass species to buffalo diet were investigated by comparing two herds occupying granite and basalt landscapes in the Kruger National Park. Observations spanned the late dry season, from July to October 2002. Grass remained greener in bottomlands than in midslopes or uplands within each landscape, but greenness was not significantly different between the basalt and granite landscapes. The favoured grass species remaining highly acceptable to buffalo throughout the late dry season included *Panicum maximum, Panicum coloratum, Cenchrus ciliaris* and *Heteropogon contortus.* However, the dietary contribution by these species declined with the progress of the dry season owing to a reduction in the available forage that they retained. The acceptance frequency as well as the dietary contribution of *Urochloa mosambicensis, Digitaria eriantha* and *Eragrostis superba* increased over time, while *Bothriochloa* spp. became moderately acceptable at the end of the dry season in October. *Themeda triandra,* a species highly rated as forage for cattle, appeared intermediate in its acceptability to buffalo and made a relatively small dietary contribution in both landscapes. In accordance with foraging theory, buffalo expanded the range of grass species accepted, changed the proportions of grass species in their diet and shifted their grazing locations within the landscape.**

**Key words**: African buffalo, diet, grazing behaviour, Kruger National Park, *Syncerus caffer.*

## INTRODUCTION

The availability and quality of forage for large grazing herbivores in savannas varies spatially and seasonally (Bell 1982; Walker 1993). Crude protein concentrations decline and fibre levels increase as grasses become senescent over the course of the dry season (Owen-Smith 1982). Clayey soils are inherently more fertile and grass species growing on them generally offer higher nutrients and less fibre than species prevalent on sandy soils (Bell 1982). However, sandy soils hold subsoil water better than clayey soils (Scholes & Walker 1993), so that grasses may retain green leaves for longer into the dry season. Within landscapes, plants growing towards the bottom of the soil catena have access to soil moisture for longer than plants growing in upland regions (White 1997). Other seasonally variable factors potentially influencing grass species preference by grazing herbivores include grass height and stemminess (Heady 1964).

During the dry season when there is little regrowth, herbivores cause a progressive decline in the standing biomass of favoured forage species. According to foraging theory, this should lead to an expansion of the diet to incorporate less nutritious species and a shift in foraging activity into regions of the landscape where these species occur (Owen-Smith & Novellie 1982). Seasonal changes in selection for particular plant species or types, and consequent changes in diet composition, have been clearly documented for browsing ungulates (Owen-Smith & Cooper 1987, 1989). Variable selection at the plant species level has been recorded for domestic grazers confined within fenced paddocks for periods of a few weeks (O'Reagain & Mentis 1989; O'Reagain & Grau 1995), but little information at this level of detail is available for wild grazers under free-ranging conditions. Understanding the variation in food resources supporting herbivores through the critical dry season period is fundamental for explaining animal movements, the habitat types selected and ultimately population dynamics (Owen-Smith 2002).

As a contribution to a wider study of buffalo herd

*To whom correspondence should be addressed.
E-mail: norman@gecko.biol.wits.ac.za

movements in relation to the spread of bovine tuberculosis within the Kruger National Park, we investigated the food selection and diet composition of two herds occupying different landscape types through the dry season months. We show how the diet of these buffalo widened to incorporate initially less favoured species as the availability of the preferred species declined and report associated changes in use of landscape regions. Relationships between the variable acceptance frequency of grass species and physical characteristics of these species are also considered.

## STUDY AREA

The study was conducted near Satara in the central Kruger National Park, South Africa (24°23′S; 31°47′E). Geologically the area is characterized by predominantly basalt formations in the east and granite formations in the west (Gertenbach 1983). The west also includes a section underlaid by gabbro, which is of volcanic origin like basalt, but coarser in texture. The buffalo herd in the granite region comprised about 350 individuals and moved over a home range of about 29 000 ha. The buffalo herd in the basalt region included about 800 individuals occupying a home range of 15 000 ha.

The mean annual rainfall in Satara is about 550 mm (Gertenbach 1980), with approximately 85–90% falling during the wet season months (October–March). The study period and the preceding wet season were much drier than the long-term mean conditions (Fig. 1).

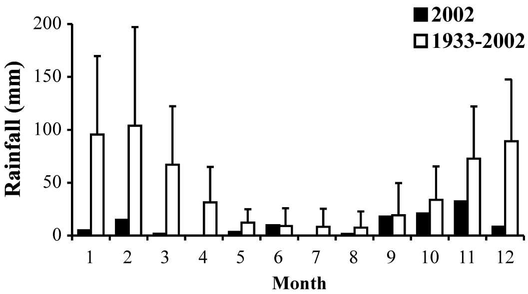


**Fig. 1**. Mean monthly rainfall totals for Satara Camp, Kruger National Park from 1933 to 2002 (open blocks); and monthly rainfall totals for 2002 (solid blocks). Months are labelled from January (1) to December (12). Bars represent standard deviations.

## METHODS

### *Field data collection*

The study extended from July to October 2002. Within this period, observations were made during four sampling periods: 8–24 July, 27 August – 13 September, 17 September – 5 October and 7–25 October. On each day of observation, a pre-selected buffalo herd was located early in the morning using radio telemetry. Information on the grass species available and grazed was collected by backtracking along the foraging path of the herd, identified through the presence of fresh dung, tracks and recent grazing. Four foraging sites (10 × 20 m) were located every 100 m along the direction of foraging movement per sampling day. At each site, five 0.7 × 0.7 m quadrats were placed 5 m apart in two parallel lines along the foraging direction. If the tracks of a particular individual could not be followed, the nearest grazed site along the general direction of movement was sampled. The grass species choices made at feeding stations spaced 5 m apart were assumed to be independent, although the grass species available may have remained similar. In total, 40 quadrats were sampled each day. The landscape position of each foraging site was also recorded.

Within each quadrat, grazed and ungrazed grass tufts were identified from signs of fresh cropping. The total number of tufts and the number of freshly grazed tufts were counted for each grass species within each quadrat. Differences in tuft size were ignored. Grass height was recorded by measuring the height of the tallest basal leaf above ground level for each grass tuft and then grouped into five height classes: 1–10, 11–30, 31–50, 51–70, >70 cm. The proportion of green leaves of each grass species present was estimated subjectively and classified into three greenness classes: 0, 1–10%, 11–25%. The number of emergent culms in each grass tuft was counted and classified into four stem classes: 0, 1–2, 3–4, 5+ stems.

To record grass greenness retention within each landscape type, four randomly located, fixed line transects were placed across the catena. Along each transect, sampling quadrats (0.7 × 0.7 m) were located every 10 m, and each quadrat was scored for the presence or absence of green leaves. These observations were made initially in August and repeated in September before the first rains.

Among the grass species, *Bothriochloa radicans* and *B. insculpta* could not be distinguished reliably in the field, and so were grouped as *Bothriochloa* spp. *Setaria* spp. could also not be identified reliably at species level.

*Faecal analysis*

Ten fresh faecal samples were collected from each foraging pathway and amalgamated to form one composite sample per day for microhistological analysis, following the procedure outlined by Stewart (1967). Composite samples were collected during four days within each previously defined sampling period. Following Hansen *et al.* (1985), the samples were oven-dried at 65°C and milled through a 1 mm screen to avoid the effect of different fragment sizes on identification, then treated with nitric acid to separate epidermal cells. Slides of samples were examined under a light microscope at ×100 and ×400 magnification (Bartolomé *et al.* 1998). The identification of fragments was based on the shape of the silica bodies, shape and size of the silica cells, form of the stomata and presence or absence of hairs, and with the aid of a reference collection previously prepared. About 40–50% of the fragments per slide could be identified. Stewart (1967) suggested that identifying 100 fragments is sufficient to reveal grass species comprising 5% of the diet. In this study, from composite faecal sample of each day, 50 fragments were identified at grass species level as it was considered sufficient to reveal grass species making up 10% of the diet. Only fragments above approximately 2 mm were considered for identification, to avoid bias in favour of grass species that break up into smaller and more numerous fragments during the digestion process. Unidentifiable fragments were classified as monocots or dicots based on the arrangement of the cells of the leaf.

*Data analysis*

Grass greenness was calculated for each landscape type, position and sampling period from the proportion of quadrats retaining green leaves. Quadrats were used as independent units for the calculation of standard errors.

For analysis of dietary changes, the study period was subdivided into four three-week blocks. The availability of each grass species was estimated by its frequency of occurrence, calculated by dividing the number of quadrats where each species was present by the 40 quadrats sampled per day. The frequency of acceptance was calculated by dividing the number of quadrats where the species was eaten by the total number of quadrats in which the species was present. The dietary contribution of each grass species was estimated from plant-based observations by counting the number of tufts of the species that were grazed and dividing this by the total number of grazed tufts of all species for each day. From faecal samples, the proportion contributed by each grass species was estimated by counting the number of identified fragments of that grass species and dividing this by the 50 fragments identified per day for all grass species. Standard errors were calculated assuming independence among the daily samples.

The proportion of quadrats that retained green leaves was compared between two landscapes, two time periods and three landscape positions using a four-way log-linear analysis. This was done using the number of quadrats with and without green leaves for each of the factors included in the analysis (landscapes, time periods and landscape positions). Differences in acceptance frequency among 10 grass species, among four time periods and between two landscapes were assessed by four-way log-linear analysis. Only the 10 grass species that showed a sample size greater than five quadrats for each of the factors were included in the analysis to ensure adequate sample size. Log-linear analysis was performed by backward elimination at 95% significance level ($P < 0.05$) using STATGRAPHICS (Manugistics, Rockville, Maryland, U.S.A.).

The dietary contribution of each grass species in terms of proportion of grazed tufts and proportion of fragments in the dung was compared between landscapes and time periods using a two-way ANOVA. Daily dietary proportions were arcsine transformed prior to statistical analysis. Linear regression was performed to measure the relationship between species acceptance and physical characteristics of the grass species. These physical characteristics of the grass included greenness, height and stemminess. Values for green leaf retention of 0% were changed to 0.1% to enable a log transformation of the green leaf proportions. Two-way ANOVA and regression analysis were done using STATISTICA (Stat Soft Inc., Tulsa, Oklahoma, U.S.A.) at 95% significance level ($P < 0.05$).

The proportions of foraging sites in different landscape positions were derived by dividing the number of foraging sites within each landscape position by the total number of foraging sites sampled for each sampling period.

## RESULTS

### Grass greenness retention

The two landscapes did not differ consistently in

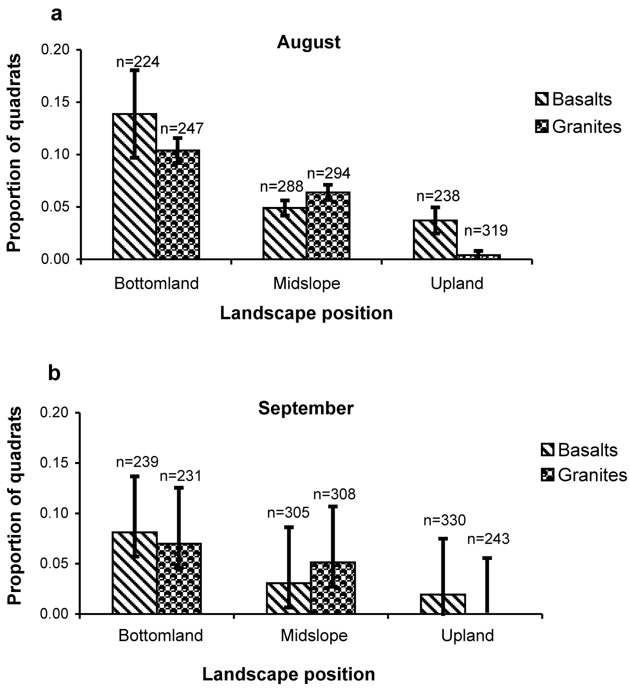


**Fig. 2**. Proportion of quadrats with green leaves within each landscape and landscape position in (**a**) August and (**b**) September. Bars represent standard errors.

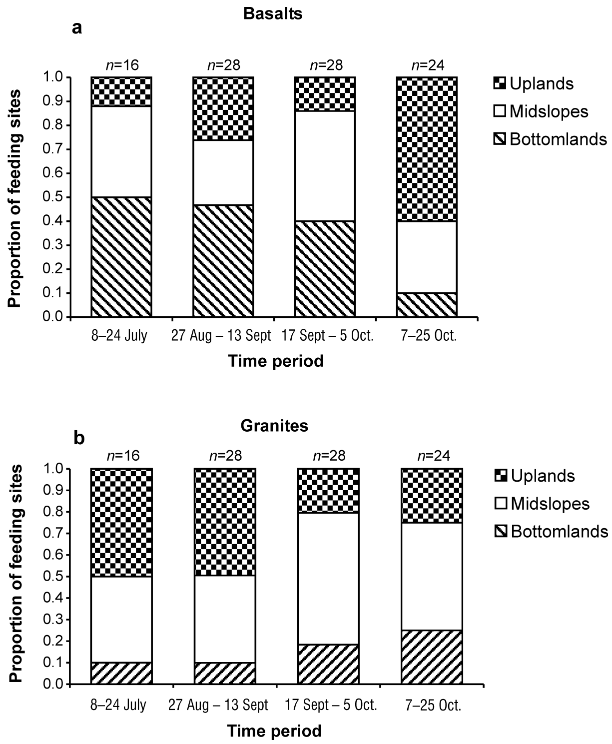


**Fig. 3**. Changes between periods in the proportion of feeding sites located in different landscape positions in the (**a**) basalts and (**b**) granites.

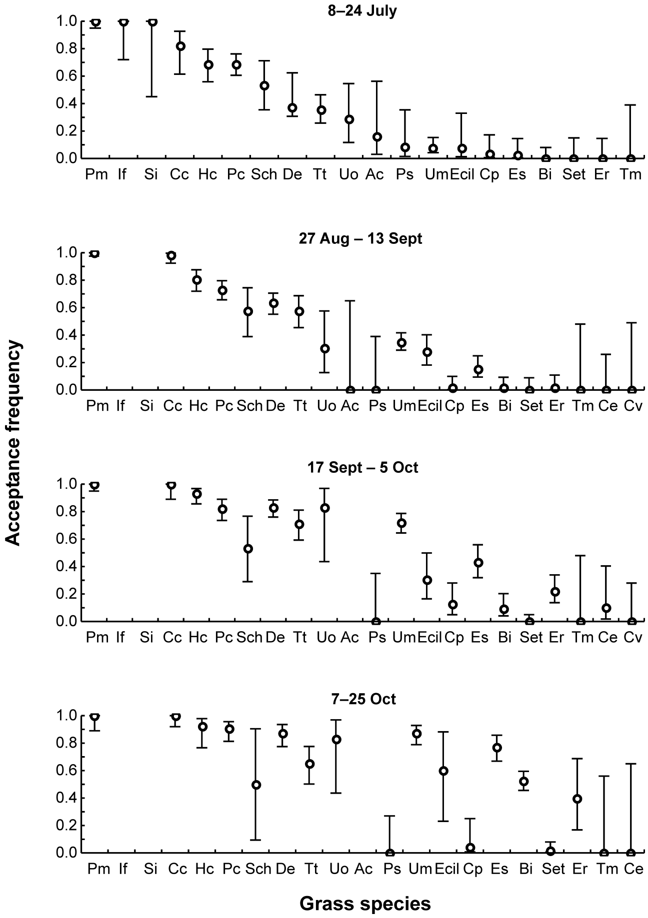


**Fig. 4**. Changes between periods in the acceptance frequency of each grass species. Pm = *Panicum maximum,* If = *Ischaemum fasciculatum,* Si = *Sporobulos ioclados,* Cc = *Cenchrus ciliaris,* Hc = *Heteropogon contortus,* Pc = *Panicum coloratum, Sch = Schmidtia pappophoroides,* De = *Digitaria eriantha,* Tt = *Themeda triandra, Uo = Urochloa oligotricha, A. congesta,* Ps = *Pogonarthria squarrosa,* Um = *Urochloa mosambicensis,* Ecil = *Eragrostis ciliaris,* Cp = *Cymbopogon plurinodis,* Es = *Eragrostis superba,* Bi = *Bothriochloa* spp., Set = Setaria spp., Er = *Eragrostis rigidior,* Tm = *Tricholaena monachne,* Ce = *Cymbopogon excavatus,* Cv = *Chloris virgata.* Vertical lines indicate 95% binomial confidence limits.

their greenness retention, with the basalt apparently greener in the bottomland and upland, and the granite greener only in the midslope region (Fig. 2; $\chi^2 = 3.77$, d.f. = 2, $P = 0.15$). However, grass was consistently greener in bottomlands than elsewhere ($\chi^2 = 14.4$, d.f. = 2, $P = 0.008$). The decline in grass greenness from August to September was small and not statistically significant ($\chi^2 = 2.48$, d.f. = 1, $P = 0.11$).

### Utilization of landscape positions

The herd on basalt used mainly bottomlands and midslopes from July to early October, but concentrated much more on uplands later in October (Fig. 3). The herd on granite occupied mainly uplands prior to mid-September and mainly midslopes thereafter, but made relatively little use of bottomlands. Sample transects indicated that the three regions occupied roughly similar proportions in both landscapes (Fig. 3).

### Grass species selection

Acceptance frequency differed significantly among grass species (Fig. 4; $\chi^2 = 95.9$, d.f. = 9, $P <$ 0.001) and between time periods ($\chi^2 = 126.3$, d.f. = 27, $P<0.001$), but not between buffalo herds in the two landscapes ($\chi^2 = 4.4$, d.f. = 3, $P = 0.221$). Grass species yielding high acceptance values (>0.5) during July remained highly acceptable throughout the dry season. These species included

*P. maximum, P. coloratum, Cenchrus ciliaris* and *Heteropogon contortus.* Grass species that were of low acceptance in July generally showed increasing acceptance with the progress of the dry season. The acceptance of *D. eriantha, U. mosambicensis, U. oligotricha* and *T. triandra* was above 0.5 from late August onwards, whereas the acceptance frequency of *E. superba, E. ciliaris* and *Bothriochloa* spp. increased only in October. Six species remained consistently neglected: *Cymbopogon* spp., *Setaria* spp., *Pogonarthria squarrosa, Tricholaena monachne, Chloris virgata* and *Aristida congesta.* Among the measured features, only grass greenness appeared weakly related to grass species acceptance.

### Grass species availability

The availability of both *Panicum* species at feeding sites tended to decline over the course of the dry season, suggesting depletion of accessible forage on these species and hence a shift towards regions where other species offered more forage (Fig. 5).

*Panicum coloratum, P. maximum, U. mosambicensis, H. contortus* and *C. ciliaris* were the most prevalent species at feeding sites on the basalt. The most commonly available species at granitic feeding sites were *P. maximum, D. eriantha, P. coloratum, H. contortus* and various *Eragrostis* spp. A move to feeding sites where *B. insculpta* was common was evident in October in both granite and basalt landscapes.

### Dietary composition

Estimates of the dietary proportions contributed by different grass species obtained from plant-based observations of grazed tufts, and faecal analysis of epidermal fragments, appeared generally similar (Tables 1 & 2). The two *Panicum* species made the greatest contribution to the diet in both landscapes during July, but declined in importance as the dry season progressed. *Urochloa mosambicensis* became an important food species on the basalt from August to September, and *D. eriantha* on the granite. *Bothriochloa* spp. contributed substantially to the diet in both landscapes in October following the early rains, although hardly eaten earlier in the dry season. *Themeda triandra,* which is regarded as highly important for cattle, contributed less than 10% to the estimated diet of the buffalo in the dry season in both landscapes. Faecal samples confirmed that buffalo consumed little browse during the dry season (Table 2).

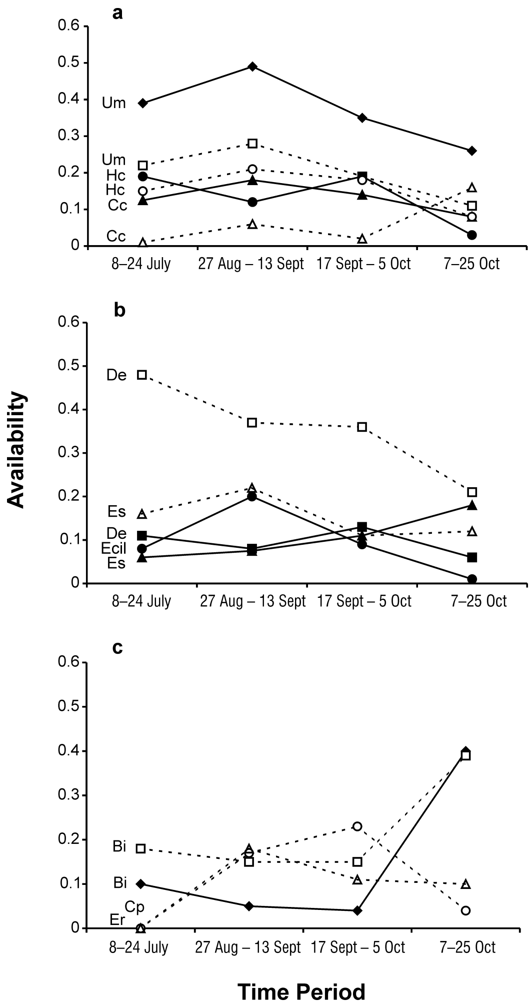


**Fig. 5**. Changes in the availability of grass species in feeding quadrats between the four sampling periods contrasting basaltic (closed lines and closed symbols) and granitic landscapes (dashed lines and open symbols). Sampling was based on 8, 14, 14 and 12 days, respectively, within each period. Acronyms are defined in Fig. 4.

## DISCUSSION

Our findings show how the importance of grass species for buffalo changes during the dry season. The dependence of African buffalo on *Panicum* spp., particularly *P. maximum,* for much of the year has been widely recognized in studies elsewhere (Field 1976; Funston *et al.* 1994; Perrin & Brereton-Stiles 1999). However, both *Panicum* species decreased in dietary contribution as the dry season progressed, presumably because of depletion in the amount of forage that their tufts retained. *Digitaria eriantha* and *U. mosambi-*

**Table 1**. Changes over time in the dietary contribution of different grass species as indicated by plant-based observations on the proportion of grazed tufts, comparing landscapes.

| **Basalts**<br>Grass species | 8–24 July<br>*n* = 4 days<br>Mean ± S.E. | 27 Aug – 13 Sept<br>*n* = 7 days<br>Mean ± S.E. | 17 Sept – 5 Oct<br>*n* = 7 days<br>Mean ± S.E. | 7–25 Oct<br>*n* = 6 days<br>Mean ± S.E. |
|---|---|---|---|---|
| *Panicum maximum* | 0.25 ± 0.08 | 0.16 ± 0.05 | 0.08 ± 0.01 | 0.06 ± 0.02 |
| *Panicum coloratum* | 0.22 ± 0.38 | 0.19 ± 0.06 | 0.14 ± 0.03 | 0.14 ± 0.04 |
| *Urochloa mosambicensis* | 0.02 ± 0.02 | 0.20 ± 0.05 | 0.32 ± 0.08 | 0.21 ± 0.06 |
| *Digitaria eriantha* | 0.06 ± 0.05 | 0.13 ± 0.55 | 0.14 ± 0.08 | 0.09 ± 0.03 |
| *Heteropogon contortus* | 0.14 ± 0.01 | 0.07 ± 0.02 | 0.12 ± 0.10 | 0.03 ± 0.02 |
| *Themeda triandra* | 0.04 ± 0.01 | 0.01 ± 0.01 | 0.04 ± 0.02 | 0.03 ± 0.01 |
| *Cenchrus ciliaris* | 0.06 ± 0.03 | 0.17 ± 0.09 | 0.08 ± 0.09 | 0.06 ± 0.03 |
| *Bothriochloa insculpta* | 0.00 | 0.00 | 0.00 | 0.21 ± 0.07 |
| *Eragrostis superba* | 0.00 | 0.03 ± 0.06 | 0.06 ± 0.05 | 0.15 ± 0.06 |
| *Schmidtia pappophoroides* | 0.06 ± 0.07 | 0.02 ± 0.01 | 0.01 ± 0.01 | 0.01 ± 0.01 |
| *Ischaemum fasciculatum* | 0.09 ± 0.08 | 0.00 | 0.00 | 0.00 |
| Other species[1] | 0.06 | 0.02 | 0.01 | 0.01 |
| **Granites**<br>Grass species | 8–24 July<br>*n* = 4 days<br>Mean ± S.E. | 27 Aug – 13 Sept<br>*n* = 4 days<br>Mean ± S.E. | 17 Sept – 5 Oct<br>*n* = 4 days<br>Mean ± S.E. | 7–25 Oct<br>*n* = 4 days<br>Mean ± S.E. |
| *Panicum maximum* | 0.46 ± .12 | 0.35 ± 0.07 | 0.15 ± 0.02 | 0.06 ± 0.02 |
| *Panicum coloratum* | 0.25 ± 0.08 | 0.11 ± 0.04 | 0.05 ± 0.01 | 0.06 ± 0.02 |
| *Urochloa mosambicensis* | 0.01 ± 0.01 | 0.05 ± 0.02 | 0.13 ± 0.04 | 0.08 ± 0.02 |
| *Digitaria eriantha* | 0.12 ± 0.05 | 0.25 ± 0.22 | 0.38 ± 0.14 | 0.22 ± 0.08 |
| *Heteropogon contortus* | 0.05 ± 0.02 | 0.12 ± 0.14 | 0.12 ± 0.05 | 0.06 ± 0.02 |
| *Themeda triandra* | 0.06 ± 0.03 | 0.09 ± 0.04 | 0.07 ± 0.02 | 0.09 ± 0.04 |
| *Cenchrus ciliaris* | 0.01 ± 0.01 | 0.01 ± 0.04 | 0.01 ± 0.05 | 0.14 ± 0.07 |
| *Bothriochloa insculpta* | 0.00 | 0.00 | 0.01 ± 0.03 | 0.18 ± 0.08 |
| *Eragrostis superba* | 0.00 | 0.00 | 0.01 ± 0.02 | 0.07 ± 0.02 |
| *Schmidtia pappophoroides* | 0.01 ± 0.01 | 0.01 ± 0.01 | 0.00 | 0.00 |
| Other species[2] | 0.03 | 0.01 | 0.07 | 0.04 |

[1]*E. ciliaris, Sporobolos iocladosa.*
[2]*E. rigidior, Cymbopogon* spp., *Urochloa oligotricha.*

*censis,* both regarded as nutritious grasses, but of medium height and thus moderate in the amount of forage they offer, took over as premier food species in the granite and basalt landscapes respectively later during the dry season. *Cenchrus ciliaris* and *Heteropogon contortus* were also highly favoured by the buffalo, but being less common made a smaller dietary contribution.

*Themeda triandra,* a highly rated grass species as important to cattle for its forage value in the dry season (Field *et al.* 1973; O'Reagain & Mentis 1989; Stoltsz & Danckwerts 1990), was only moderately favoured by the buffalo and thus a minor dietary contributor. This could be because in the Kruger Park it grew in a relatively tall and thus quite fibrous form.

Observations in the adjoining Sabi-Sand Game Reserve (Funston *et al.* 1994) as well as in Uganda (Field *et al.* 1973) and Tanzania (McNaughton 1985) likewise indicate that buffalo generally do not favour areas dominated by *Themeda* during the dry season.

*Bothriochloa* spp. are generally regarded as highly unpalatable because of their strong aromatic odour (Field 1976). Nevertheless, these species became important in contributing to the diet of the buffalo in the transition period between the late dry season and the early rains, after available forage presented by the preferred grass species had been depressed. *Bothriochloa* greened up early following the first rains and offered the highest amount of green forage at that time. Both Field (1976) and Perrin & Brereton-Stiles (1999) reported little use of *Bothriochloa* spp. by buffalo. *Eragrostis* spp., especially *E. superba,* which are regarded as of only moderate forage value to

**Table 2**. Changes over time in the dietary contribution of different grass species as indicated by the proportion of epidermal fragments in faecal samples, comparing landscapes.

| **Basalts**<br>Grass species | 27 Aug – 13 Sept<br>*n* = 4 days<br>Mean ± S.E. | 17 Sept – 5 Oct<br>*n* = 4 days<br>Mean ± S.E. | 7–25 Oct<br>*n* = 4 days<br>Mean ± S.E. |
|---|---|---|---|
| *Panicum maximum* | 0.15 ± 0.03 | 0.13 ± 0.02 | 0.09 ± 0.01 |
| *Panicum coloratum* | 0.22 ± 0.06 | 0.28 ± 0.02 | 0.15 ± 0.02 |
| *Urochloa mosambicensis* | 0.24 ± 0.02 | 0.26 ± 0.04 | 0.13 ± 0.02 |
| *Digitaria eriantha* | 0.03 ± 0.02 | 0.10 ± 0.03 | 0.05 ± 0.03 |
| *Heteropogon contortus* | 0.10 ± 0.03 | 0.07 ± 0.02 | 0.04 ± 0.02 |
| *Themeda triandra* | 0.07 ± 0.03 | 0.03 ± 0.02 | 0.04 ± 0.02 |
| *Cenchrus ciliaris* | 0.11 ± 0.02 | 0.08 ± 0.01 | 0.10 ± 0.03 |
| *Bothriochloa insculpta* | 0.01 ± 0.01 | 0.01 ± 0.01 | 0.28 ± 0.02 |
| *Eragrostis superba* | 0.07 ± 0.04 | 0.04 ± 0.04 | 0.12 ± 0.03 |
| Monocots | 0.97 | 0.98 | 0.97 |
| Dicots | 0.03 | 0.02 | 0.03 |
| **Granites**<br>Grass species | 27 Aug – 13 Sept<br>*n* = 4 days<br>Mean ± S.E. | 17 Sept – 5 Oct<br>*n* = 4 days<br>Mean ± S.E. | 7–25 Oct<br>*n* = 4 days<br>Mean ± S.E. |
| *Panicum maximum* | 0.16 ± 0.03 | 0.19 ± 0.04 | 0.11 ± 0.02 |
| *Panicum coloratum* | 0.14 ± 0.02 | 0.13 ± 0.03 | 0.11 ± 0.04 |
| *Urochloa mosambicensis* | 0.18 ± 0.03 | 0.11 ± 0.03 | 0.08 ± 0.02 |
| *Digitaria eriantha* | 0.36 ± 0.08 | 0.33 ± 0.04 | 0.17 ± 0.03 |
| *Heteropogon contortus* | 0.03 ± 0.02 | 0.06 ± 0.03 | 0.10 ± 0.03 |
| *Themeda triandra* | 0.04 ± 0.02 | 0.03 ± 0.01 | 0.06 ± 0.03 |
| *Cenchrus ciliaris* | 0.02 ± 0.01 | 0.04 ± 0.02 | 0.08 ± 0.04 |
| *Bothriochloa insculpta* | 0.01 ± 0.01 | 0.05 ± 0.02 | 0.22 ± 0.06 |
| *Eragrostis superba* | 0.06 ± 0.04 | 0.06 ± 0.04 | 0.07 ± 0.03 |
| Monocots | 0.97 | 0.97 | 0.95 |
| Dicots | 0.03 | 0.03 | 0.05 |

cattle, also made an increased dietary contribution towards the end of the dry season.

In accordance with the predictions of foraging theory, many initially neglected grass species became increasingly accepted as the availability of the more preferred species declined over the dry season. Nevertheless, there were certain grass species that remained consistently rejected, or eaten very little, throughout the dry season. These included *Cymbopogon plurinodis,* which like *Bothriochloa* is an aromatic grass regarded as highly unpalatable to cattle (Field 1976). Other rejected species are mostly fibrous grasses regarded as of low nutritional value, like *Pogonarthria squarrosa and Aristida* spp. However, why the buffalo avoided eating *Setaria* spp., rated as moderate in nutritional value, remains obscure.

Other studies have documented a general shift by buffalo to bottomland regions, which retain soil moisture and hence green grass leaves for longer than upland areas, during the course of the dry season (Sinclair 1977). We did not observe this pattern, and the buffalo herd occupying the granite landscape made relatively little use of the bottomland region (see Fig. 3). This may be because, rather than presenting high grass biomass, much of the bottomland region in the granite landscape consists of sodic soils with grasses consequently heavily grazed. Hence, contrary to expectations, the basalt landscape retained greener grass in the bottomland region than the granitic region (Fig. 2). The study period was very dry, and patterns of grassland use could differ under other conditions.

Overall, results show how African buffalo, despite being regarded as relatively unselective bulk grazers (Sinclair 1977; Prins 1996), adjusted their grass species selection and feeding localities in relation to seasonally changing forage quantity and quality through the critical dry season period. The importance of *Bothriochloa* spp., generally regarded as unpalatable, for bridging the critical transition period between the late dry season and the start of the rains was also previously undocumented.


## ACKNOWLEDGEMENTS

A United States National Science Foundation Ecology of Infectious Disease Grant DEB-0090323 to Wayne M. Getz funded field expenses. We are indebted to South African National Parks for allowing us to conduct this study in the Kruger National Park. David Ward provided helpful comments on earlier drafts of the manuscript. Steve Henley helped guide the microhistological analysis of faecal samples. Justin Bowers, Craig Hay, Fernando Mlhovu, Augusta Mabunda and Kutani Bulunga assisted with fieldwork.


### REFERENCES


BARTOLOMÉ, J., FRANCH, J., PLAIXATS, J. & SELIGMAN, N.G. 1998. Diet selection by sheep and goat on Mediterranean hearth-woodland range. *J. Range Manage.* 51: 383–391.

BELL, R.H.V. 1982. The effect of soil nutrient availability on community structure in African ecosystems. In: B.J. Huntley & B.H. Walker (Eds), Ecology of tropical savannas (pp. 193–213). Springer-Verlag, Berlin.

FIELD, C.R., HARRINGTON, G.N. & PRATCHETT, D. 1973. A comparison of the grazing preferences of buffalo (*Syncerus caffer*) and Ankole cattle (*Bos indicus*) on three different pastures. *E. Afr. Wildl. J.* 11: 19–29.

FIELD, C.R. 1976. Palatability factors and nutritive values of the food of buffaloes in Uganda. *E. Afr. Wildl. J.* 14: 181–201.

FUNSTON, P.J., SKINNER, J.D. & DOTT, H.M. 1994. Seasonal variation in movement patterns, home range and habitat selection of buffaloes in a semi-arid habitat. *Afr. J. Ecol.* 32: 100–114.

GERTENBACH, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe* 23: 35–43.

GERTENBACH, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe* 26: 9–122.

McNAUGHTON, S.J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.* 55: 259–294.

O'REAGAIN, P.J. & MENTIS, M.T. 1989. The effect of plant structure on the acceptability of different grass species to cattle. *J. Grassl. Soc. South. Afr.* 6: 163–169.

O'REAGAIN, P.J. & GRAU, E.R. 1995. Sequence of species selection by cattle and sheep on South African sourveld. *J. Range Manage.* 48: 314–321.

OWEN-SMITH, N. 1982. Factors influencing the transfer of plant products into large herbivore populations In: B.J. Huntley & B.H. Walker (Eds), Ecology of tropical savannas (pp. 359–404). Springer-Verlag, Berlin.

OWEN SMITH, N. 2002. Adaptive herbivore ecology: from resources to populations in variable environments. Cambridge University Press, Cambridge.

OWEN SMITH, N. & NOVELLIE, P. 1982. What should a clever ungulate eat? *Amer. Natur.* 119: 151–178.

OWEN SMITH, N. & COOPER, S.M. 1987. Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology* 68: 319–331.

OWEN-SMITH, N. & COOPER, S. M. 1989. Nutritional ecology of a browsing ruminant, the kudu, through the seasonal cycle. *J. Zool., Lond.* 219: 29–43.

PERRIN, M.R. & BRERETON-STILES, R. 1999. Habitat use and feeding behaviour of the buffalo and the white rhinoceros in the Hluhluwe-Umfolozi Game Reserve. *S. Afr. J. Wildl. Res.* 29: 72–81.

PRINS, H.H.T. 1996. Ecology and behaviour of the African buffalo – Social inequity and decision making. Chapman and Hall, London.

SCHOLES, R.J. & WALKER, B.H. 1993. An African savanna – Synthesis of the Nylsvley study. Cambridge University Press, Cambridge.

SINCLAIR, A.R.E. 1977. The African buffalo–A study of resource limitation of populations. University of Chicago Press, Chicago.

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

STOLTSZ, C.W. & DANCKWERTS, J.E. 1990. Grass species selection patterns on rotationally-grazed Dohne Sourveld during autumn and early winter. *J. Grassl. Soc. South. Afr.* 7: 92–96

TAYLOR, R.D. 1989. Buffalo and their food resources: the exploitation of Kariba lakeshore pastures In: P.A. Jewell & G.M.O. Maloiy (Eds), The biology of large mammals in their environments. *Symp. Zool. Soc. Lond.* 61: 51–70.

WALKER, B.H. 1993. Rangeland ecology: understanding and managing changes. *Ambio* 22: 80–87

WHITE, R.E. 1997. Principles and practice of soil science: the soil as a natural resource (3rd edn). Blackwell Science, Oxford.