Dietary shifts: do grazers become browsers in the Thicket Biome?

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The diet of buffalo (*Syncerus caffer*) and Burchell's zebra (*Equus burchelli*) was investigated in the Addo Elephant National Park to test the hypothesis that the shortage of grass associated with thicket vegetation results in grazers increasing the proportion of dicotyledonous plant species in their diet. Diet composition, estimated from faecal analysis, indicated that 19 and 21 plant species were identified in the faeces of zebra and buffalo, respectively. Buffalo proved to have a higher percentage dicotyledonous (28.1 % *vs.* 8.5 %) and lower percentage monocotyledonous (71.9 % *vs.* 91.5 %) species in their diet than zebra. The grass *Eragrostis curvula* was found to be the dominant food item for both buffalo (18 % of diet) and zebra (39 % of diet) during the period of study. The present study indicated that a great proportion of the buffalo diet does in fact consist of grass, thereby refuting the perception that the Addo buffalo are primarily browsers. Both buffalo and zebra are specialised grazers and unsuited to a diet of browse. The probability of dietary shift by these grazers in the grass limited thicket vegetation is therefore challenged.

Key words: browse, buffalo, diet, graze, thicket, zebra.

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Introduction

Diets reflect the interplay between the availability and quality of food items and the animals' ability to ingest and digest various food items (its dietary adaptations). Dietary shifts occur when a species alters its diet in response to some extrinsic factor, and are perceived as an adaptive response to varying dietary availability (Smith 1990). Cape buffalo (*Syncerus caffer*), which are generally considered to be specialised grazers, persist within the thicket biome of the Eastern Cape, despite the limited availability of grass in this browse-dominated landscape (e.g. Stuart-Hill & Aucamp 1993). De Graaff *et al.* (1973) suggested that this involved a shift in diet, as they recorded a dominance of browse (rumen analysis) in the diet of a sample of buffalo from the Addo Elephant National Park. We investigated this with an analysis of the diets of buffalo and Burchell's zebra in the Addo Elephant National Park.

Study Site

The study was conducted within the elephant enclosure of the Addo Elephant National Park (AENP), which covers an area of more than 11 708 ha (Urquhart *et al.* 1997).

The region in which the AENP falls is generally considered to be semi-arid. Mean daily temperatures range from 32.4 °C in summer to 13.5 °C in winter with temperatures in excess of 40 °C frequently occurring in summer (Stuart-Hill 1992). Rainfall occurs throughout the year with peak rain periods in late summer (February - March) and spring (October - November). The mean annual precipitation, measured at the park headquarters, is 445 mm (Paley & Kerley 1998).

The vegetation of Addo is considered to be Kaffrarian Succulent Thicket, sub order Xeric Succulent Thicket (Lubke 1996), which is characterised by a dense, impenetrable tangle of succulent and spinescent shrubs and lianas 2-4 m high (Penzhorn *et al.* 1974).

The basal covering of grass within thicket is very low (Aucamp 1976), and extremely unreliable between years (Stuart-Hill & Aucamp 1993). Small scattered patches of grassland may however be found in a vegetation community known as Bontveld (Urquhart *et al.* 1997).

Materials and Methods

Microhistological dietary determination

Faecal analysis involved the identification of plant epidermal fragments by reference to a collection of epidermi that was prepared from as many grass species as could be found (n = 16) within the elephant enclosure of the AENP. The slides were prepared following MacLeod *et al.* (1996). A reference collection of dicotyledonous species was available from a previous study (Koekemoer 2001). Note that rumen and faecal dietary estimates have been shown to provide similar results (e.g. Anthony & Smith 1974).

Fourteen fresh faecal samples were collected for each species (buffalo and zebra) from April through July 2000. The samples were oven dried for three days at 60 °C and stored until analysis. Ten and 14 faecal samples were used for plant species identification for buffalo and zebra, respectively, as determined by plotting cumulative frequency curves (Fig. 1) of identified plant species in each sample. Guevara *et al.*'s (1997) recommendation of 15 samples was thus not followed. This is in agreement with Ellis *et al.* (1977) who used only eight samples.

The microscopic technique used to analyse diet samples is based on the procedures of Sparks & Malechek (1968), in which the relative proportions of plant fragments are assessed from their epidermal characteristics. The method indicates the intake of each plant category on a dry matter basis and its characteristics, accuracy and biases have been well documented (Anthony & Smith 1974; Vavra & Holechek 1980). The comparative approach used here makes this technique relatively robust. The procedure used in this study is detailed in MacLeod *et al.* (1996).

Analysis of variance procedures (One-Way ANOVA on Ranks, Tukeys test) (Zar 1999) were used to test for differences in total species richness and monocotyledonous species richness of plant species found in the diet of buffalo and zebra. Analysis of variance procedures (One-Way ANOVA, Tukeys test) of arcsine-transformed data (Zar 1999) tested for differences in the percentage contribution of different plant growth forms to the diet of buffalo and zebra. Differences in dicotyledonous species richness were tested using a One-Way ANOVA (Tukeys test) (Zar 1999). Only the first eight samples for each herbivore were used for statistical analysis, to equalise sample sizes. Degrees of freedom are reported as between groups, within groups. All statistical analyses were done using the statistical package "Sigmastat Version 2.0" (SPSS 1997).

Principal dietary items, defined by Petrides (1975) as those foods eaten in greatest quantities, were identified as the plant species which contributed to more than 3 % of the diet of the animals.

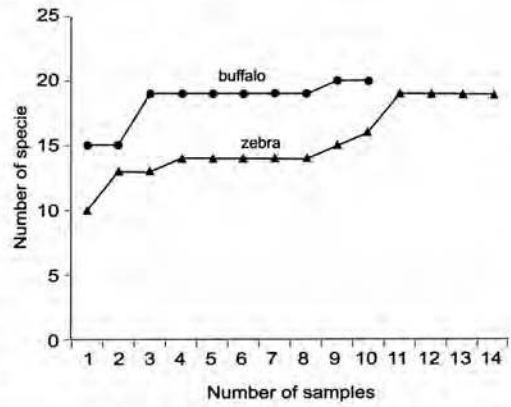

Fig. 1. The cumulative number of dietary plant species recorded per sample for buffalo and zebra.

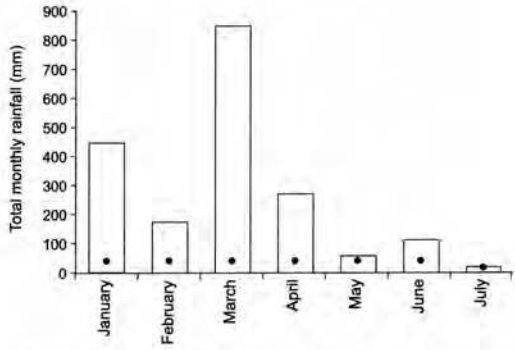

Fig. 2. Total monthly rainfall recorded within the Addo Elephant National Park for the period January 2000 to July 2000 (bars) and the mean monthly rainfall for the park for the period 1989- 1998 (•).

Results

The rainfall immediately preceding and during the early part of this study was high (Fig. 2).

Nineteen (Fig. 3a) and 21 (Fig. 3b) plant species were identified in the faeces of zebra and buffalo, respectively, indicating the significantly greater diversity (species richness) ($H = 12.327$; $df = 1$; $P = < 0.001$) of plant species found in the diet of buffalo. A total of 26 plant species were identified in the diets of buffalo and zebra (App. 1). Fourteen of these plant species were found to be consumed by both buffalo and zebra.

Zebra had a significantly lower diversity (species richness) of dicotyledonous ($F = 60.529$; $df = 1, 14$; $P = < 0.001$) and higher diversity of monocotyledonous ($H = 0.157$; $df = 1$; $P = 0.721$) species in their diet when compared with buffalo. The grass *Eragrostis curvula* was the dominant food item for both zebra (39 %) (Fig. 3a) and buffalo (18 %) (Fig. 3b) during the period of study. *Cynodon dactylon*, which is most commonly found on the open pastures formerly cleared for agriculture (Paley & Kerley 1998), contributed minimally to the diet of the two species.

The dominant dicotyledonous species found in the diet of both buffalo and zebra was the cucurbit *Kedrostis nana* (Fig. 3a & 3b). The principal food items in the diet of zebra were *E. curvula*, *E. obtusa*, *K. nana*, *Pennisetum clandestinum*, *Melinis repens* and *Themeda triandra* and constituted approximately 83.7 % of the total dietary composition (Fig. 3a). Buffalo had a higher species richness (11 spp.) of principal dietary items, contributing to approximately 85.5 % of their total diet, including *E. curvula*, *P. clandestinum*, *K. nana*, *M. repens*, *T. triandra*, *Cynodon dactylon*, *Cenchrus ciliaris*, *Aristida diffusa*, *Grewia robusta*, *Capparis sepiaria* and *Ptaeroxylon obliquum* (Fig. 3b).

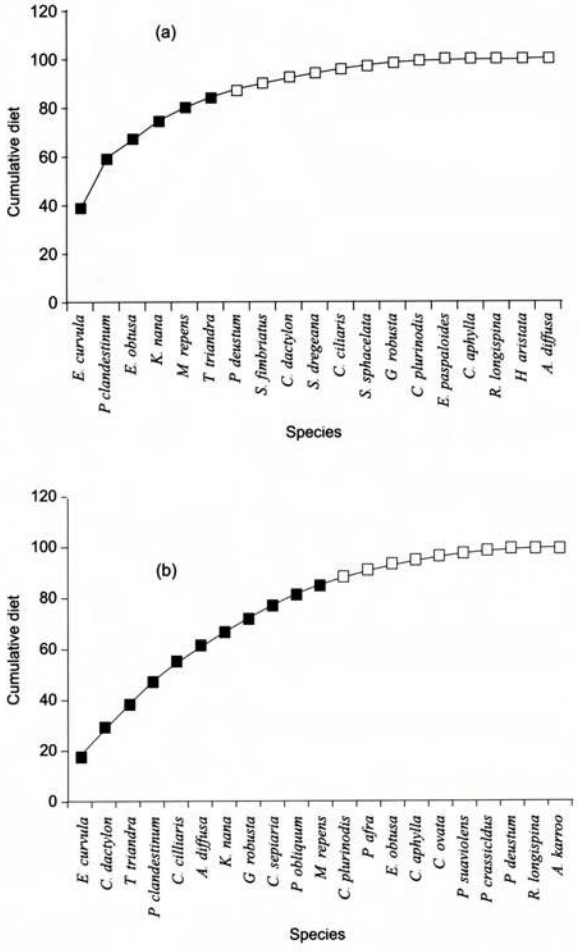

Fig. 3. The cumulative contribution of different plant species to the diet of (a) zebra and (b) buffalo, ranked in order of decreasing importance (principal foods (■), non-principal foods (□)).

Plants identified in the diets of buffalo and zebra were grouped into woody shrubs, succulents, grasses, climbers and herbs. When compared to zebra, buffalo proved to have a significantly higher percentage dicotyledonous (28.1 % *vs.* 8.5 %) (comprising climbers, woody shrubs, herbs and succulents) ($F = 8.895$, $df = 1.14$, $P = 0.010$) and significantly lower percentage monocotyledonous (71.9 % *vs.* 91.5 %)

Table 1
The relative percentage contribution of different plant growth forms to the diet of zebra and buffalo in the Addo Elephant National Park

	Grass %	Herbs %	Woody shrubs %	Climbers %	Succulents %	Total % dicot species
Zebra	91.5	0.1	1.5	6.9	0	8.5
Buffalo	71.9	0	18.4	5.4	4.3	28.1

($F = 17.711$, $df = 1.14$, $P = < 0.001$) species in their diet (Table 1).

Discussion

The present study indicated that the buffalo of Addo are largely grazers, selecting only a relatively small percentage of dicotyledonous plants. The results obtained in this study reflect the diet of buffalo after a period of exceptionally high rainfall. A different set of results may be expected if the relatively low annual rainfall, normally associated with the region, occurred.

Studies done elsewhere in Africa (Stewart & Stewart 1970; Ben-Shahar 1991; Bodenstein *et al.* 2000) on the diet of Burchell's zebra, show similar results to those obtained in the present study. Here it is confirmed that in thicket Burchell's zebra are primarily grazers, selecting an even smaller proportion of dicotyledonous plant species than buffalo.

On numerous occasions in the past, die-offs of the buffalo population in the AENP have occurred during periods of very pronounced and enduring droughts (De Graaff *et al.* 1973). De Graaff *et al.* (1973) found that the rumens of the buffalo that had died during such a drought contained a large proportion of dicotyledonous plant species. Based on these observations, they concluded that the buffalo of Addo show a shift in dietary requirements during periods of drought, and could be considered browsers, rather than grazers. The perception that the Addo buffalo are browsers has been uncritically accepted in the general literature (e.g. Urquhart *et al.* 1997).

Hofmann (1989) showed that the digestive system of buffalos is typical of bulk and roughage grazers, and therefore unsuited to a diet of browse. The animals studied by De Graaff *et al.* (1973) were thus evidently forced by the scarcity of grass at the time to ingest a diet to which they were not adapted (Novellie *et al.* 1991). The present study, having shown that a great proportion of the buffalo diet does in fact consist of grass, has thus disproved the perception that the Addo buffalo are primarily browsers. Zebra, being typical roughage grazers (Van Soest 1982), are even more unsuited to a diet of browse when compared to buffalo. The probability of dietary shift by these specialist grazers, in the grass-limited thicket vegetation, is therefore challenged. If such shifts are observed, it is predicted that the animals will be under severe nutritional stress and that large-scale die-offs (as observed by de Graaff *et al.* 1973) can be expected.

Numerous wildlife-based ventures have introduced large grazing herbivores, e.g., white rhinoceros (*Ceratotherium simum*), into the thicket-dominated areas of the Eastern Cape. Based on the above, we therefore hypothesise that these animals may suffer the same fate as the Addo buffalo during periods of drought, calling into doubt the wisdom of these introductions.

Acknowledgements

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Appendix 1

List of plant species mentioned in this study

Monocotyledonous species	Dicotyledonous species
Aristida diffusa	*Acacia karroo*
Cenchrus ciliaris	*Cadaba aphylla*
Cymbopogon plurinodis	*Crassula ovata*
Cynodon dactylon	*Capparis sepiaria*
Eragrostis curvula	*Grewia robusta*
Eragrostis obtusa	*Hypoestes aristata*
Eustachys paspaloides	*Kedrostis nana*
Melinis repens	*Portulacaria afra*
Panicum deustum	*Ptaeroxylon obliquum*
Pennisetum clandestinum	*Protoasparagus crassicladus*
Setaria sphacelata	*Protoasparagus suaveolens*
Sporobolus fimbriatus	*Rhus longispina*
Stipa dregeana	
Themeda triandra	