Diet composition and habitat selection of eland in semi-arid shrubland

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Abstract

This study investigated the diet composition and habitat selection of eland in semi-arid shrubland, dominated by microphyllous and leptophyllous browse species offering low leaf : stem ratios. Browse (succulent, forb and woody species) contributed 94% to the annual diet of eland. The annual proportion of grass in eland diet was low (6%), even though palatable grass species were abundant in habitats favoured by eland. Most grass was eaten in the early wet season when grasses offered young green foliage. Woody species comprising dwarf shrubs and shrubs made up the bulk of the food eaten by eland. In each season, favoured woody species contributed substantial proportions to the diet of eland. Eland used the plateau habitats in the early wet season, but valleys and slopes in the late wet and dry seasons. Habitats favoured by eland contained high abundances of plants of woody species favoured by eland. Chemical analysis indicated that woody species favoured by eland offered lower total fibre contents than other woody species available to eland. The results of the study indicated that eland are browsers that select browse of low fibre content.

Key words: diet, eland, habitat, karoo, semi-arid, ungulate

Résumé

Cette recherche a étudié la composition du régime alimentaire et le choix de l'habitat des élands dans les zones buissonneuses semiarides dominées par les espèces de microphylles et de leptophylles présentant des feuilles basses à leur consommation : les taux de jeunes tiges. La consommation de feuilles (de plantes succulentes, de buissons et d'espèces ligneuses) représente 94% du régime alimentaire annuel des élands. La proportion des herbacées dans le régime annuel des élands est basse. Les élands mangent de l'herbe surtout au début de la saison des pluies lorsqu'elle présente de jeunes feuilles vertes. Les espèces ligneuses comprenant des buissons, nains ou pas, constituent la part la plus importante de l'alimentation des élands. A chaque saison, les espèces ligneuses favorites contribuent en grande partie au menu des élands. Ceux-ci fréquentent les habitats de plateau au début de la saison des pluies, puis les pentes et les vallées à la fin et en saison sèche. Les habitats préférés des élands contiennent des grandes quantités des espèces ligneuses qu'ils préfèrent. Leur analyse chimique montre que les espèces ligneuses préférées des élands ont un contenu en fibres inférieur à celui des autres espèces ligneuses disponibles. Les résultats de cette étude montrent que les élands sont des consommateurs de feuilles qui sélectionnent celles qui contiennent le moins de fibres.

Introduction

Based on rumen anatomy, eland (*Taurotragus oryx* Pallas) have been classified as intermediate feeders preferring browse (Hofmann & Stewart, 1972; Hofmann, 1973). Most field studies support this classification (e.g. Kerr, Wilson & Roth, 1970; Jankowitz, 1982; Buys, 1990), while in others eland were found to be predominantly grazers (Lamprey, 1963; Underwood, 1975; Nge'the & Box, 1976). In all studies, where the contribution of forbs to the diet was assessed, such herbaceous browse formed an appreciable percentage of the diet (e.g. Kerr *et al.*, 1970; Field, 1975; Jankowitz, 1982).

Eland have been recorded on a wide variety of vegetation types, including montane grassland, savanna and

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semi-arid shrubland, but no studies have examined the diet composition and habitat use of eland in semi-arid shrubland. This represents a gap in the understanding of eland feeding ecology, especially since modelling (Owen-Smith, 1985) has indicated that eland should favour vegetation types offering high abundances of browse species with high leaf : stem ratios (e.g. forb rich grassland/savanna; broad-leafed savanna). Eland have performed well since being introduced into Mountain Zebra National Park (MZNP; P. A. Novellie, unpublished observations). Forb abundance is low in MZNP and vegetation ranges from grass dominated communities to communities dominated by microphyllous dwarf shrubs (van der Walt, 1980; Watson, 1997). The study had the following objectives: (a) to determine the change in the diet composition of eland through the seasonal cycle, at the plant form and plant species level; (b) to determine the habitat preference of eland; (c) to determine if the habitat selection of eland was related to the abundance of favoured woody species.

Materials and methods

Study area

Mountain Zebra National Park (MZNP) is situated 24 km from Cradock, in the Eastern Cape Province of South Africa. The vegetation of MZNP is classified as Eastern Mixed Karoo and is dominated by mesophytic grasses and dwarf shrubs (van der Walt, 1980). The veld types present in MZNP according to Acocks (1988) are: Karroid *Merxmuellera* Mountain Veld, Karroid *Merxmuellera* Mountain Veld replaced by Karoo Veld and False Karroid Broken Veld.

The rainfall in MZNP is unevenly distributed. Highest rainfall occurs in the southern regions, while the western areas receive more rain than the eastern areas (van der Walt, 1980). Rainfall and topography influence the distribution of the vegetation communities in MZNP (van der Walt, 1980), which may represent distinct habitat types for eland. The mean annual rainfall recorded at Babylonstoren in the north of MZNP, over the period 1962–89, was 395 mm. Temperatures in MZNP may exceed 40°C in summer and fall below freezing in winter (P. A. Novellie, unpublished observations).

Eland diet composition was monitored during the period August 1988–July 1989, and eland habitat selection during the period November 1987–May 1989. The mean annual rainfall recorded in MZNP for the 2-year period July 1988–June 1989 was 507 mm (P. A. Novellie, unpublished observations). The year was divided into three seasons with respect to rainfall during the study: (a) the early wet season (November–January), (b) the late wet season (February–May), (c) the dry season (June–October).

Eland were studied only in the northern half of MZNP, because of difficulties of access to other parts. The study area comprised two land forms: (a) the plateau regions of Rooiplaat, Boesmanplaat and Vergesigplaat, (b) the valleys and slopes (Watson, 1997). All sections of the study area were within line of sight from various vantage points.

The 1979 management plan for MZNP set the permissible number of eland at 100 (P. A. Novellie, unpublished observations). The eland population numbered 166 in May 1988 and 219 in May 1989, while 115 eland were removed during the period 1984–88 (P. A. Novellie, unpublished observations).

Feeding observations

A single adult female was fitted with a radio collar. Over the study period, this animal was located six to thirteen times each month ($\bar{x} = 11$). Once located, the female and her companions were observed from a distance of 50–300 m. The first animal seen feeding was chosen as a focal animal (Altmann, 1974) and observed while feeding. To ensure that observations collected in different habitats were comparable, only feeding observations of 3–6 min were chosen for feeding site surveys. Two to four feeding observations were made at each location (13–28 per month). To ensure independence of observations, each feeding observation was made on a different focal animal. Although a single radio collared female was used to locate animals for observation, the size and composition of the herd associated with her varied throughout the year (mode = 6–10; range = 3–170). Feeding observations were therefore considered representative of the eland population in MZNP.

Feeding site surveys

An assistant was directed to plants eaten by the focal animal and marked these plants. Marked plants served as indicators of the feeding path followed by the focal animal. The feeding site was designated as the area 2 m on either side of the feeding path followed by the animal (typically 5–10 m in length). A total of 253 feeding sites was surveyed during the study (Table 1), representing a total feeding time of 1007 min.

All plants within a feeding site were identified at species level and examined for evidence of fresh grazing or browsing. Plant species eaten by eland were divided into five plant forms: grasses (graminoids), succulents (dicotyledons with fleshy leaves), forbs (soft-stemmed dicotyledons), dwarf shrubs (woody-stemmed dicotyledons < 1 m in height when mature), shrubs (woody-stemmed dicotyledons > 1 m in height when mature). No distinction was made between shrubs and trees. Succulents, forbs, dwarf shrubs and shrubs collectively made up the browse component of eland diet.

At each feeding site, the number of bites taken per grass tuft and the number of shoots eaten per browse plant were counted. Three shoots per browse plant were randomly selected from one plant per species per site, and the diameter at the point of browsing was measured with a calliper. Eland bites from grass tufts were taken to be 60 mm in diameter.

Percentage contribution of plant forms to eland diet

The number of grass bites and number of browse shoots recorded as eaten by eland are quantitatively not comparable. Hence grass bites and browse shoots were converted to dry weight in order to estimate dietary proportions. For grasses twenty samples representative of an eland bite were collected from *Cymbopogon plurinodis* ((Stapf) Stapf ex Burtt Davy), the grass most commonly eaten by eland during the study. Samples were dried to constant weight and the mean dry weight per bite calculated ($\bar{x} = 0.85$ g, SE = 0.05). For a representative browse species, the mean shoot diameter at the point of browsing was calculated from records collected during the study. This diameter (x) was converted to shoot dry weight consumed (y) using equations of the type $y = ae^{bx}$. For the forb *Pseudognaphalium undulatum* ((L.) Hilliard & Burtt), the dry weight of 50 shoots was plotted against shoot diameter, using the SAS procedure 'Nlin' to generate the appropriate equation ($y = 0.035e^{1.146x}$, $r^2 = 0.90$). *P. undulatum* was considered representative of most forbs, so this formula was applied to all forbs. *Rhus pallens* was used as the standard for shrubs ($y = 0.019e^{1.849x}$, $r^2 = 0.92$). The equation derived by Hobson (1988) for *Pentzia incana* ($y = 0.016e^{1.5x}$, $r^2 = 0.53$) was used for dwarf shrubs. Due to the low number of succulents recorded as eaten by eland, the equation for dwarf shrubs was also used for succulents.

For each month, the dry weight (pf_i) of plant form i in the eland diet as a percentage was estimated as $pf_i = (dw_i N^{-1}) \times 100$, where dw_i is the dry weight of plant form i in eland diet, and N is the total dry weight of all the plant forms in the sampled diet for that month.

For each plant form, monthly estimates were non-normal (Shapiro-Wilks test; Zar, 1984). To test for difference in the monthly contribution of plant form i to eland diet between season, the Kruskal–Wallis one-way ANOVA by ranks was used (Zar, 1984).

Table 1 The monthly contributions to eland diet of the plant forms estimated by percentage of dry weight consumed. Sites = the number of feeding sites surveyed

	Season												
	Dry			Early wet			Late wet				Dry		
Plant form	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Mean
Grasses	0.0	0.0	1.7	6.3	45.3	10.2	1.2	0.4	1.2	2.4	0.0	0.0	5.7
Succulents	0.0	0.0	0.0	0.0	0.0	5.1	0.2	0.5	0.0	0.0	0.0	0.0	0.5
Forbs	0.0	0.3	0.7	1.0	4.8	1.7	7.9	10.2	1.8	1.1	0.0	0.0	2.5
Dwarf shrubs	46.8	45.2	44.1	40.3	36.1	54.5	30.7	53.5	48.7	45.7	36.0	44.0	43.8
Shrubs	53.2	54.5	53.5	52.4	13.8	28.5	60.0	35.4	48.3	50.8	64.0	56.0	47.5
Sites	26	28	28	26	17	20	25	16	19	20	13	15	21.1

Percentage contribution of browse species to eland diet

For each season, shoot counts of browse species i were used to calculate the percentage of browse species i in the sampled eland diet.

Crude protein and total fibre content of woody species

Fourteen woody species commonly encountered by eland were classified into species favoured and neglected by eland (Watson, 1997). For each of these species, leafy shoots ($\pm$60 mm in length) were collected from five plants per season (early, mid and late wet seasons of 1988/89). Samples were collected in the early morning and placed in separate brown bags for drying at room temperature. Chemical analyses were done at the Forestek Laboratory in George. Nitrogen was determined for all replicate samples per species per season by the Kjeldahl method, and crude protein calculated as $6.25 \times$ the nitrogen concentration. Acid detergent fibre (ADF) was chosen to represent the total fibre content of plant material and was determined using sequential detergent analysis (Goering & van Soest, 1970) without sodium sulphite (Mould & Robbins, 1981). Replicate samples per species per season were amalgamated for analysis.

For woody species i, the mean crude protein and total fibre content of leafy shoots was calculated for the wet season. Because the acceptability of neglected species varied over the wet season (Watson, 1997), for neglected woody species i, the mean for each chemical factor was calculated from records obtained when that species was neglected by eland.

For each chemical factor, Student's t-test tested the two tailed hypothesis of no difference between the content in favoured and neglected woody species.

Habitat use and availability

Eland were located weekly, three to four times per month, and the habitat occupied and the number/composition of the herd recorded. Because individuals within a herd are not statistically independent, each sighting of a herd was considered a single observation (Alldredge & Ratti, 1986). To reduce auto-correlation of data, only records made 24 h apart were used (Swihart, Slade & Bergstrom, 1988). In order to relate habitat use to food resources, observations made near water points were ignored.

Land form use by eland varied seasonally, with the plateau land form favoured during the early wet season and the valley/slope land form favoured during both the late wet and dry seasons (Watson, 1997). Habitat use within land forms was assessed for the periods when each land form was favoured. Observations for all months within seasons were summed for analysis. Observations recorded in the late wet and dry seasons were summed and referred to as the late wet/dry period.

Habitat availability was measured as the proportional area of each habitat within the study area. A planimeter was used to measure habitat area from the vegetation map constructed by van der Walt (1980).

Habitat preference

Chi-squared goodness-of-fit analysis was used to test for significant difference between the expected use and the observed frequency of use of habitats by eland (Byers & Steinhorst, 1984). This test was applied under the condition that the expected use of each habitat was $\geqslant 5$ (Roscoe & Byars, 1971). To meet this requirement some habitats were combined. If the chi-squared test was significant, the Bonferroni method was used to determine which habitats were positively selected or avoided (Byers & Steinhorst, 1984).

Habitat surveys

As an index of habitat quality, an estimate was made of the abundance of plants of favoured woody species per feeding site per habitat. In each habitat $\geqslant 10$ sites (4×10 m) were surveyed and the number of plants recorded for favoured woody species i (Watson, 1997). For favoured woody species i, the mean number of plants per feeding site per habitat was calculated (x_i). The index of habitat quality was calculated as Σx_i for all favoured woody species recorded in that habitat.

ANOVA and the Tukey test compared habitat indices of favoured, neglected and neutrally selected habitats.

Results

Plant form composition

Grasses contributed 5.7% to the estimated annual diet of eland, compared to 94.3% by browse. Grass consumption by eland varied significantly between seasons (one-way Kruskal–Wallis ANOVA by ranks; $\chi^2 = 8.244$, df = 2, $P < 0.05$). The grass proportion was highest in the early wet season, peaking in December (Table 1). Grass consumption fell below 2.0% in the late wet season, while no grasses were eaten in the dry season, except for a small amount in October (Table 1).

The low proportion of succulents consumed annually (0.5%) probably reflected the low abundance of succulents in MZNP.

Forbs formed 2.5% of the annual recorded diet and varied significantly between seasons (one-way Kruskal–Wallis ANOVA by ranks; $\chi^2 = 8.601$, df = 2, $P < 0.05$). Forbs were eaten mostly during the wet season, with peaks in December, February and March (Table 1). Forb consumption appeared to be related to the abundance of forbs in the habitats used by eland.

Dwarf shrubs and shrubs formed the bulk of the diet, contributing similar proportions annually (Table 1). For these woody forms, consumption did not vary significantly between seasons (one-way Kruskal–Wallis ANOVA by ranks; dwarf shrubs $\chi^2 = 0.503$, df = 2, $P > 0.50$; shrubs $\chi^2 = 5.804$, df = 2, $P > 0.05$).

Grass species composition

Although *Cymbopogon plurinodis* is considered unpalatable to cattle and sheep, it formed the bulk of the grass recorded as eaten by eland (55.5%), followed by the more palatable *Digitaria eriantha* (Stend.) (24.4%) and *Themeda triandra* (Forssk.) (13.8%). The remaining grasses eaten by eland were unidentified.

Browse species composition

Seventy browse species were identified as eaten by eland during the study. Of these species, only eighteen contributed > 1.0% to the percentage of browse shoots recorded as eaten annually. All eighteen species were woody species (thirteen dwarf shrubs and five shrubs), making up 84.4% of the browse component annually (Table 2).

The dwarf shrubs *Felicia muricata*, *Helichrysum dregeanum* and *Walafrida geniculata* ranked highest in the proportion of browse shoots consumed (Table 2). These species were classified as favoured by Watson (1997), and together with other favoured browse species (*Grewia occidentalis*, *Pentzia sphaerocephala* and *Rhus erosa*) formed between 42 and 63% of the browse shoots eaten by eland in each season (Table 2).

Crude protein and total fibre content of woody species

The mean crude protein content of favoured ($\bar{x} = 114.7$, SD = 38.7) and neglected woody species ($\bar{x} = 96.1$, SD = 11.5) over the wet season did not differ significantly ($t = 1.295$, df = 12, $P > 0.05$), while the mean total fibre content of favoured species ($\bar{x} = 83.5$, SD = 12.8) was significantly lower than that of neglected species ($\bar{x} = 123.0$, SD = 31.6) ($t = 2.862$, df = 12, $P < 0.05$).

Habitat use and quality

For both the early wet season and the late wet/dry period, observed habitat use differed significantly from that expected from relative habitat area (early wet season $\chi^2 = 10.749$, df = 3, $P < 0.05$; late wet/dry period $\chi^2 = 115.503$, df = 4, $P < 0.001$).

For the plateau land form favoured in the early wet season, the *Setaria sphacelata*/*Acacia karroo* habitat was positively selected, while the *Eragrostis lehmanniana*/*Pentzia incana* and *Becium burchellianum* habitats combined were used less than expected from availability (Table 3).

For the late wet/dry period, when the valley/slope land form was favoured, the *Grewia occidentalis*/*Rhus lucida* habitat, and the *Walafrida saxatilis*/*Felicia filifolia* and *Pentzia sphaerocephala* habitats combined were positively selected by eland (Table 4). The *Diospyros lycioides*/*Acacia karroo*, *Merxmuellera disticha*/*Selago corymbosa*, *Merxmuellera disticha*/*Euryops annuus* and *Heteropogon contortus*/*Rhus erosa* habitats combined were avoided by eland (Table 4).

Indices of habitat quality, measuring the abundance of plants of favoured woody species per feeding site per habitat, varied significantly between favoured, neglected and neutrally selected habitats ($F = 47.81$, df = 10, $P < 0.0001$). Habitats favoured by eland had significantly higher abundances of plants of woody species favoured by eland ($\bar{x} = 35.5$, SD = 3.5), than habitats neglected by eland ($\bar{x} = 9.1$, SD = 5.4) (Tukey test). Favoured habitats and neutrally selected habitats ($\bar{x} = 37.4$, SD = 5.3) had similar abundances of plants of woody species favoured by eland.

Discussion

Grass consumption

Reported grass proportions in eland diet have mostly varied between 20 and 45% (Field, 1975; Buys, 1990).

Table 2 Browse species that contributed > 1.0% to the annual proportion of browse shoots recorded as eaten by eland. Numbers without brackets indicate the percentage of shoots eaten by eland. Numbers in brackets indicate the rank order of each species according to the percentage shoots eaten by eland in each season. Codes: habit and growth form; D = deciduous, E = evergreen, d = dwarf shrub, s = shrub. Classification: F = favoured, N = neglected.

				Season %		
Species	Habit	Classification	Annual %	Early wet	Late wet	Dry
Felicia muricata (Thunb.) Nees	Dd	F	15.8	2.2 (10)	39.6 (1)	5.7 (6)
Walafrida geniculata (L.f.) Rolfe	Dd	F	11.2	30.4 (1)	2.8 (6)	0.4 (15)
Helichrysum dregeanum Sond. & Harv.	Ed	F	9.4	10.4 (2)	2.8 (6)	14.9 (1)
Dodonaea augustifolia L.f.	Es	–	7.1	8.3 (4)	0.0 (17)	13.0 (2)
Rhus erosa Thunb.	Es	F	6.1	1.3 (14)	4.6 (4)	12.4 (3)
Rhus pallens Eckl. & Zeyh.	Es	N	5.2	3.0 (7)	7.4 (3)	5.1 (8)
Grewia occidentalis L.	Ds	F	4.6	2.9 (8)	10.1 (2)	0.7 (13)
Pentzia incana (Thunb.) Kuntze	Dd	N	3.7	6.9 (5)	4.2 (5)	0.1 (17)
Pentzia sphaerocephala DC.	Ed	F	3.6	0.2 (18)	2.7 (8)	7.9 (5)
Felicia filifolia (Vent.) Burtt Davy	Ed	N	3.3	1.5 (12)	0.4 (14)	8.1 (4)
Pentzia globosa Less.	Dd	–	2.9	8.8 (3)	0.0 (17)	0.0 (18)
Walafrida saxatilis (E. Mey.) Rolfe	Ed	–	2.3	2.6 (9)	2.0 (10)	2.2 (10)
Nenax microphylla (Sond.) Salter	Ed	–	2.0	0.8 (15)	0.0 (17)	5.3 (7)
Pelargonium ramosissimum (Cav.) Willd.	Ed	–	1.9	0.6 (16)	1.2 (13)	3.9 (9)
Acacia karroo Hayne	Ds	N	1.8	3.3 (6)	1.7 (11)	0.3 (16)
Chrysocoma ciliata L.	Ed	N	1.4	1.4 (13)	1.7 (11)	1.0 (12)
Pegolettia retrofracta (Thunb.) Kies	Dd	–	1.3	0.5 (17)	2.6 (9)	0.7 (13)
Eriocephalus ericoides (L.f.) Druce	Ed	–	1.0	1.8 (11)	0.1 (15)	1.1 (11)
Total			84.6	86.9	83.9	82.8

Table 3 Eland habitat preference in the plateau land form during the early wet season ($n = 56$). Codes: p_{ei} = expected proportion; p_{oi} = observed proportion; 95% intervals = Bonferroni 95% confidence intervals

Habitat	p_{ei}[1]	p_{oi}[2]	95% intervals	Preference[3]
Themeda triandra/Felicia filifolia	0.219	0.232	0.146–0.318	o
Themeda triandra/Pentzia globosa	0.547	0.482	0.380–0.584	o
Eragrostis lehmanniana/Pentzia incana and *Becium burchellianum*	0.111	0.025	0.000–0.074	–
Setaria neg;ecta/Acacia karoo	0.123	0.250	0.161–0.339	+

[1]Taken as the relative area of the habitat. [2]Calculated for habitat i as $p_{oi} = n_i N^{-1}$ where n_i is the number of times eland were located in that habitat and N is the total number of observations across all habitats. [3]Preference: + = use significantly greater than expected; – = use significantly less than expected; o = use no different to expected.

The studies of Lamprey (1963), Underwood (1975) and Nge'the & Box (1976) indicating much higher proportions (70–77%) are of dubious reliability. The results of Lamprey (1963) were derived from field scout observations, while Underwood (1975) classified all feeding at ground level as grazing. Nge'the & Box (1976) corralled eland at night and only recorded feeding in grassland paddocks.

Grasses formed 6% of the estimated annual diet of eland in MZNP. Among reported studies, only in *Colophospernum mopane* savanna did grass form a similar low proportion of the diet (Kerr *et al.*, 1970). Because

Table 4 Eland habitat preference in the valley/slope land form during the late wet/dry period ($n = 192$). Codes: p_{ei} = expected proportion; p_{oi} = observed proportion; 95% intervals = Bonferroni 95% confidence intervals

Habitat	p_{ei}[1]	p_{oi}[2]	95% intervals	Preference[3]
Diospyros lycioides/Acacia karroo, Merxmuellera disticha/Selago corymbosa, Merxmuellera disticha/Euryops annuus and *Heteropogon contortus/Rhus erosa*	0.310	0.026	0.000–0.056	–
Grewia occidentalis/Rhus lucida	0.490	0.609	0.519–0.700	+
Walafrida saxatilis/Felicia filifolia and *Pentzia sphaerocephala*	0.046	0.156	0.089–0.224	+
Eragrostis lehmanniana/Pentzia incana	0.076	0.135	0.072–0.199	o
Setaria neglecta/Acacia karoo	0.078	0.073	0.025–0.121	o

[1]Taken as the relative area of the habitat. [2]Calculated for habitat i as $p_{oi} = n_i N^{-1}$ where n_i is the number of times eland were located in that habitat and N is the total number of observations across all habitats. [3]Preference: + = use significantly greater than expected; – = use significantly less than expected; o = use no different to expected.

grasses in semi-arid areas are considered to remain acceptable throughout the year (Huntley, 1984; Danckwerts, 1989), the low proportion of grass recorded in eland diet in MZNP is somewhat unexpected.

Grass consumption by eland peaked at the beginning of the wet season when grasses were young with green foliage. The rapid decline in grass consumption in January probably resulted from the maturation of grasses at this time. Because eland stomach structure is similar to that of browsers, eland probably digest mature grass less well than grazers (Hofmann, 1973; Owen-Smith, 1982).

The decline in grass consumption in January may have been influenced by the phenology of dwarf shrubs. For example, the percentage of *W. geniculata* shoots recorded in eland diet increased from the late dry season through to January. Over this period, the proportion of young shoots on plants of *W. geniculata* increased, while the proportion of senescent shoots decreased (Watson, 1997).

Use of the browse component

The large muzzle and high absolute food requirement of eland reduces their ability to select for leaves. In order for eland to reduce their fibre intake, preferred foods should offer high leaf : stem ratios (e.g. leafy forbs or broad-leafed trees; Owen-Smith, 1985). Reported studies indicate that herbaceous forbs formed appreciable proportions of eland diet (10–27%; Kerr *et al.*, 1970; Field, 1975; Jankowitz, 1982). In contrast, forbs only formed 3% of the annual diet of eland in MZNP, while woody plants, which formed 91% of the diet, were microphyllous and leptophyllous species with low leaf : stem ratios. Nevertheless, eland have thrived since being introduced into MZNP (P. A. Novellie, unpublished observations). This was probably because eland were able to select a diet sufficiently low in total fibre content. This was done by eating young leafy shoots of most woody species encountered, and by consuming large proportions of favoured woody species with low fibre contents.

Habitat selection

Eland typically favour habitats with high abundances of grass species during the wet season (Buys, 1990; Fabricius & Mentis, 1990). Similarly, in the early wet season, eland in MZNP favoured the plateau landform with high abundances of palatable grass species. This landform also supported the highest densities of grazing ungulates in MZNP (Novellie & Bezuidenhout, 1994). Although grass formed 45% of eland diet in December, for the other months of the early wet season it formed 6 and 10% of the diet. Habitat selection by eland was therefore unrelated to the availability of palatable grasses in the habitat.

It is suggested that eland habitat selection in MZNP was determined by the quality of the woody browse offered. Habitats favoured by eland had high abundances of plants of woody species favoured by eland and containing low fibre contents. In MZNP, the quality of woody browse within habitats appeared to be influenced by two important factors. First, in contrast to habitats favoured by eland, most neglected habitats occurred on shallow, leached lithosols (van der Walt, 1980). Woody species on nutrient poor soils are generally highly defended against herbivory (Coley, Bryant & Chapin III, 1985). Second, the neglected *Becium burchellianum* and *Eragrostis lehmanniana*/*Pentzia incana* habitats were degraded due to over utilization prior to our study (van der Walt, 1980).

Eland in MZNP were mainly browsers able to thrive on woody species, which although having low leafiness had low fibre contents.

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