

Resource partitioning within a browsing guild in a key habitat, the Chobe Riverfront, Botswana

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Abstract: Resource partitioning between elephant, giraffe, kudu and impala was assessed. This was to address concerns that elephant population increase adversely affects other species through depleting their food in key areas close to permanent water. Resources considered were woody species browsed, height browsed and plant parts browsed. Animals were observed as they browsed and the plant species, browsing heights and plant parts browsed were recorded. Observations were made over 1 y and the data were divided between wet and dry season. Schoener's index of resource use overlap was calculated for plant species, browsing heights and plant parts eaten and differences in overlap between wet and dry season were tested. Levin's measure of niche breadth in plant species utilized by the different browsers was calculated. Woody species identity was the main separator between food resources that elephant used and those giraffe, impala and kudu used. Giraffe, kudu and impala mainly browsed the same species and plant parts but browsed at different heights. There was no difference in resource use overlap between seasons with different resource availability. Since elephant browsed different woody species from those browsed by the others, it is unlikely that the increasing elephant population will deplete food resources for the other browsers.

Key Words: Botswana, browsing, elephant, giraffe, impala, kudu, niche breadth, overlaps

INTRODUCTION

Resource partitioning is the differential use of resources such as food and space by species in the same community (Schoener 1974, Voeten & Prins 1999). Resource partitioning between animal species has been described for many taxa in various ecosystems (Gordon & Illius 1989, Hansen & Reid 1975, Jarman & Sinclair 1979, Leuthold 1978, McDonald 2002, Mysterud 2000, Putman 1996, Voeten & Prins 1999). Species coexist despite overlaps in fundamental niches provided the overlap in potential resource use is incomplete (Putman 1996). Each species can occupy a distinct and non-overlapping 'realized' or 'post-interactive' niche in the presence of the other potentially competing species (Putman 1996).

The Jarman–Bell principle, that relates body size to diet quality, states that larger ungulates can tolerate a wider range of diet quality than smaller ungulates (Bell 1971, Jarman 1974, Stokke & du Toit 2000). This 'body size hypothesis' has been used to explain differences in

resource use depending on different metabolic demands both within and between species (Jarman & Sinclair 1979, Stokke & du Toit 2000). The dilemma faced by animals is that high-quality forage is rare whereas low-quality forage is common (Demment & Van Soest 1985). Partition of resources by animal species could, however, also be explained by the scramble competition hypothesis (Hughes 1980, Illius & Gordon 1987, Stokke & du Toit 2000). The scramble competition involves exploitation and interference components whereby an animal species displaces other species from prime areas or diets forcing them to feed in lower quality areas or to accept poorer diets. Stokke & du Toit (2000) described scramble competition in detail for elephant. When dealing with animal species that differ in body size, it could be predicted that small animal species browse at lower heights of tree canopies displacing animal species of intermediate size which will in turn force large animal species to browse high in the tree canopy. Food availability might also be the reason behind browsing height stratification between animal species of different body sizes. It has been suggested that giraffe browse higher in the tree canopy to gain a bite-size advantage by browsing above the reach of smaller species (Woolnough & du Toit 2001).

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Table 1. Descriptions of the studied animal species. Feeding and digestion types for all species and measurements for giraffe and kudu are according to Skinner & Smithers (1990). Elephant measurements are according to Haltenorth & Diller (1980) while impala measurements are according to Smithers (1992).

Species	Shoulder height (m)		Weight (kg)		Feeding type	Digestion type
	Male	Female	Male	Female		
Elephant	3.5	2.7	4550	2350	mixed feeder	hindgut fermenter
Giraffe	3.0	2.7	1192	828	browser	foregut fermenter
Kudu	1.4	1.3	228	157	browser	foregut fermenter
Impala	0.90	0.85	55	40	mixed feeder	foregut fermenter

Resource use overlap between competing species is expected to be high during the periods of food abundance (wet season) and low during the periods of food scarcity (dry season). This is because during the periods of food abundance both species have enough food even if resource use overlaps (Gordon & Illius 1989, Myrsetrud 2000). However, when food becomes scarce one of the competing species turns to feed on less suitable food and reduce competition (Gordon & Illius 1989, Myrsetrud 2000).

The Chobe Riverfront in Chobe National Park, northern Botswana has high abundance and diversity of wild animals including the elephant population that is increasing at an annual rate of 6% (Gibson *et al.* 1998). The Chobe Riverfront is here referred to as a key habitat in reference to its high importance to the water-dependent animal species compared to other surrounding areas. The Chobe–Zambezi river system is the only dry-season water source in the ecosystem. This forces all water-dependent animals to use the Riverfront during the dry season (Ben-Shahar 1993, Gibson *et al.* 1998, Omphile & Powell 2002, Skarpe *et al.* 2004, Stokke & du Toit 2002, Verlinden & Gavor 1998). In this habitat, herbivores that mainly browse woody species during the dry season include elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), steenbok (*Raphicerus campestris*) and bushbuck (*Tragelaphus scriptus*). However, little is known on resource partitioning between these coexisting species, and there is concern that the increasing elephant population may deplete food resources for other browsers. Information on resource partitioning between these species in this key habitat would therefore be an indicator of how they share resources when they use the same area and whether the elephants are likely to compete with other browsers for food. It should, however, be noted that elephant, giraffe and kudu do not entirely depend on food resources in the study area even during the dry season but also forage in the woodlands further away from the river (Omphile & Powell 2002, Stokke & du Toit 2002). Animal nomenclature accords to Skinner & Smithers (1990).

The study estimates resource partitioning between impala, kudu, giraffe and elephant. Steenbok and bushbuck are rare and they are not considered. Resource

partitioning between the species was expected to be according to difference in body size and digestive system (Table 1). Particularly the study addressed the following questions: (1) Do impala, kudu, giraffe and elephant browse different woody species? (2) Do impala, kudu, giraffe and elephant browse at different heights? (3) When browsing the same species, do impala, kudu, giraffe and elephant browse different plant parts? (4) Is overlap in resource use within the browsing guild larger during the period of food abundance (wet season) than when food is scarce (dry season)?

METHODS

Study site

The research was conducted in the northern part of Chobe National Park (17°49'–17°55'S, 24°50'–24°59'E) in semi-arid northern Botswana. The northern boundary of the study area is the Chobe River. The rainfall is seasonal, with the wet season in summer between November and April. Annual average rainfall is about 640 mm (Botswana Meteorological Service Department, unpubl. data). The period from May to October, is the dry season. Mean maximum and mean minimum monthly temperatures during October (hottest month) are 39 °C and 14 °C, respectively and in July (coldest month) 30 °C and 4 °C, respectively (Botswana Meteorological Service Department, unpubl. data).

The vegetation in the study area tends to form zones from the river changing with soil type and herbivore impact. Along the river on the alluvial soils is a thin strip of riparian forest followed by shrublands dominated by *Capparis tomentosa* and *Combretum mossambicense* (Mosugelo *et al.* 2002, Skarpe *et al.* 2004). Over the past decades woodland has gradually retreated away from the Chobe Riverfront (Mosugelo *et al.* 2002). The area that is now shrubland on the alluvial soils earlier had large *Acacia* and *Combretum* trees, and before that it was open flats (Skarpe *et al.* 2004). Further away from the river, on Kalahari sand, woodlands with *Baikiaea plurijuga* occur (Mosugelo *et al.* 2002, Skarpe *et al.* 2004). Plant nomenclature accords to Coates Palgrave (2002).

Data collection

The study was done for 1 y from July 2002 to June 2003. Impala, kudu, giraffe and elephant were observed while browsing. A vehicle was driven at 20 km h⁻¹ along the road network in the study area. Whenever a group or a single animal of the four species was sighted, the vehicle was stopped and the animal or any animal seen browsing in the group was observed as it browsed. With the aid of a pair of binoculars, woody species and plant parts browsed were identified. The plant parts were categorized as leafless shoots, shoot with leaves, leaves only and bark. After records were made, the plant was visited to measure the browsing height and to verify the plant species and part browsed. The point browsed was in most cases easy to locate because the fresh wet bites could be seen. Browsing height was measured with a measuring rod to the nearest 10 cm. If the animal had browsed several points on an individual tree, each point was recorded and height measured. In such a case the average height browsed was used in the calculations. Browsing heights of elephant were sometimes estimated when animals did not move away from the browsed plant.

A total of 2885 observations were made. They comprised 670 for elephant, 461 giraffe, 971 impala and 783 for kudu. More animals were observed browsing during the dry season than during the wet season because most of the elephants, giraffe and kudu move out of the study area during the wet season. Impala and elephant shift more to grazing than browsing during the wet season whereas they predominantly browse during the dry season. During the dry season the observations were distributed as 517 elephant, 352 giraffe, 595 impala and 669 kudu. The wet season observations were distributed as 153 elephant, 109 giraffe, 376 impala and 114 kudu.

Data analysis

The data were analysed both for the whole year across seasons and separated into wet and dry season. The proportion contributed by each plant species to the total observed browsing by each herbivore species, here referred to as 'diet composition' was calculated from the data of observed browsing. Spearman rank correlation based on these proportions was used to compare diet compositions of each pair of herbivore species. Overlap in resource use in terms of browsed species, browsing height and plant parts browsed were assessed using the Schoener's index (Schoener 1970). This measure has been recommended by Abrams (1980) because it meets all the criteria required in choosing an overlap measure. The Schoener's index used for browsed species overlap

was:

$$O_{jk} = 1 - \frac{1}{2} \sum_{i=1}^n |P_{ij} - P_{ik}|$$

where O_{jk} is the overlap between herbivore species j and k . P_{ij} is the proportion of all browsing events on plant species i by the herbivore species j , while P_{ik} is the same proportion, but for the herbivore species k and n is the number of plant species. In calculating browsing height overlaps, the browsing height section replaced plant species in the above Schoener's index. Heights were categorized into classes of 20-cm intervals and each interval represented browsing height section (i) in the Schoener's index. To calculate browsed parts overlaps, the Schoener's index was:

$$O_{jk} = 1 - \frac{1}{2} \sum_{i=1}^n |P_{hij} - P_{hik}|$$

where O_{jk} is the overlap between herbivore species j and k . P_{hij} is the proportion of all browsing events on plant part i on plant species h by the herbivore species j , P_{hik} is the same proportion, but for the herbivore species k .

The Schoener's index ranges from zero to one. It is zero when species do not share any resources and one when they use identical resources (Wallace 1981). Overlap indices are generally considered significant when the value exceeds or equals 0.60 (Wallace 1981, Zaret & Rand 1971). The Mann-Whitney U-test was applied to test the difference between the wet and dry season overlaps in plant species and parts eaten by comparing the $|P_{ij} - P_{ik}|$ part of the overlap index equation.

The niche breadth of the use of plant species by herbivores was assessed using Levins' measure (Levins 1968),

$$B = 1 / \sum_{i=1}^n P_i^2$$

where B is the niche breadth, P_i is the proportion of all feeding observations on woody species i and n is number of woody species browsed (Menard *et al.* 2002, Mishra *et al.* 2004). It was then standardized to a scale of 0–1 using Hurlbert's (1978) procedure.

$$B_s = (B - 1)/(n - 1),$$

where B_s is the standardized niche breadth. B is the niche breadth and n is the number of species recorded eaten at least once by at least one of the herbivore species during that season. Zero on the standardized niche breadth scale refers to an ultimate specialist herbivore that browses only one species and ignores others, while 1 refers to a perfect generalist herbivore that browses all species without preferences (Hurlbert 1978).

The Welch's robust ANOVA test (Quinn & Keough 2002) that does not assume equal variances was applied to test the differences in browsing heights by different

herbivore species. It was applied after the Levene's test of equality of group variances and the inspection of box plots revealed that variances were not equal. The Welch's robust ANOVA test was followed by multiple comparisons test using the robust Dunnett's T3 test that also does not assume equal variances (Quinn & Keough 2002). In comparing browsing heights it was assumed that browsing heights were independent of plant species. The above was done using data of browsing heights each herbivore species browsed on any woody species. Calculations were also done using only the data when giraffe, impala and kudu browsed *Capparis tomentosa*. All statistical procedures were undertaken in the SPSS for Windows (version 12.0.1) statistical package.

RESULTS

Woody plant species browsed

A total of 35 woody species were observed browsed by at least one of the four herbivore species during either the wet or the dry season. Few woody species, between three and six, contributed more than 5% to the diet composition of each herbivore species during the two seasons (Table 2). The top two or three most-browsed woody species contributed more to the diet composition of giraffe, kudu and impala than to that of the elephant (Table 2). Contribution of *Capparis tomentosa* to the diet compositions of giraffe, kudu and impala increased during the dry season while that of *Combretum mossambicense* decreased (Table 2). Levins' standardized niche breadth for plant species browsed was slightly broader for elephant than for the other herbivore species (Figure 1). The

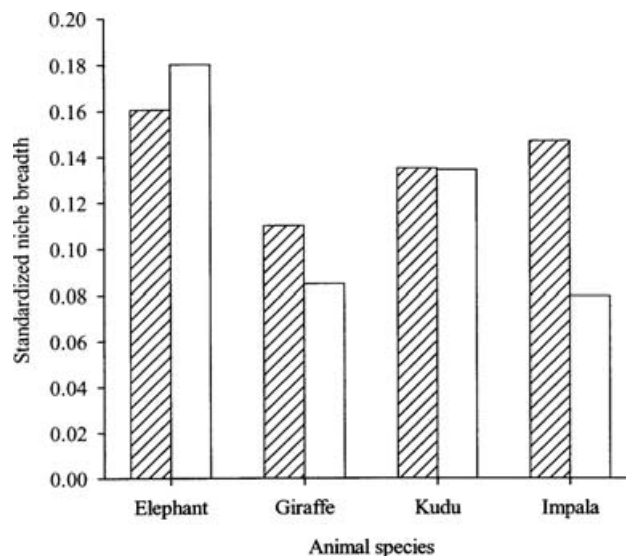


Figure 1. Seasonal standardized niche breadth of woody plant species browsed, represented by Levins' (1968) niche breadth index, standardized to a scale of 0–1 following Hurlbert (1978). Wet (hatched) and dry (open) seasons.

browsed species niche breadth for giraffe and impala were broader during the wet season than during the dry season (Figure 1).

Plant species browsed by elephant did not significantly overlap (Schoener's index < 0.6) with those browsed by the other herbivore species (Table 3). The overlap in woody species browsed by giraffe, kudu and impala was significant between impala and giraffe during the dry season and between impala and kudu during both seasons (Table 3). The overlap between giraffe and kudu during both seasons was not significant but still high (Schoener's

Table 2. Diet composition of each member of the browsing guild studied. The values are percentage contribution by each plant species to the observed browsing by each herbivore species. The table only shows plant species that contributed at least 5% to the observed browsing by at least one of the animal species. Plant species that contributed less than 5% are grouped as others. Plant names are according to Coates Palgrave (2002) while plant type and evergreenness are according to van Wyk & van Wyk (1997). Deciduousness of *Friesodielsia obovata* is from own observation.

Plant species	Leaf fall	Plant type	Elephant		Giraffe		Kudu		Impala	
			Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
<i>Boscia albitrunca</i>	E	ST	0.0	0.2	1.3	5.5	0.0	1.5	0.3	1.0
<i>Canthium glaucum</i>	D	Sh/ST	0.0	1.4	0.0	0.5	1.8	2.4	8.0	0.8
<i>Capparis tomentosa</i>	E	Sh/ST	5.7	0.8	45.6	50.3	20.2	23.9	11.2	50.4
<i>Combretum apiculatum</i>	D	ST/MT	0.0	9.1	0.0	0.5	0.0	0.0	0.0	0.2
<i>Combretum elaeagnoides</i>	D	Sh/ST	39.6	29.8	0.0	0.5	0.0	10.2	0.0	0.7
<i>Combretum mossambicense</i>	D	Sh/ST	1.9	1.4	20.3	15.7	42.1	35.7	42.0	19.2
<i>Croton megalobotrys</i>	D	ST/MT	9.4	22.1	1.3	0.8	1.8	0.7	0.8	0.3
<i>Dichrostachys cinerea</i>	D	Sh/ST	7.5	3.5	10.1	0.5	2.6	1.3	6.4	3.5
<i>Friesodielsia obovata</i>	D	Sh/ST	5.7	2.5	0.0	0.0	0.9	1.3	1.9	1.8
<i>Philenoptera nelsii</i>	D	ST/MT	3.8	7.7	0.0	3.1	5.3	1.8	1.3	1.2
<i>Markhamia zanzibarica</i>	D	ST	0.0	0.6	3.8	6.5	8.8	3.6	6.1	3.7
<i>Flueggea virosa</i>	D	Sh/ST	3.8	6.2	11.4	3.7	5.3	6.3	12.8	8.2
<i>Strychnos potatorum</i>	D	ST/MT	15.1	3.3	0.0	2.1	2.6	2.4	0.5	0.7
Others			7.5	11.6	6.3	10.2	8.8	8.8	8.8	8.2
Number of species that contributed with > 5%			6	5	4	4	5	4	6	3

D, deciduous; E, evergreen; Sh, shrub; ST, small tree; MT, medium tree.

Table 3. Schoener's indices of resource-use overlap during the dry and wet seasons for the studied browsing guild.

Species pair	Plant species overlap (S)		Height overlap (H)		Plant part overlap (P)		Species × height (H × S)		Combined overlap (S × H × P)	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Elephant/impala	0.24	0.22	0.46	0.44	0.12	0.07	0.11	0.10	0.01	0.01
Elephant/giraffe	0.23	0.20	0.35	0.40	0.10	0.10	0.08	0.08	0.01	0.01
Elephant/kudu	0.24	0.32	0.45	0.58	0.15	0.14	0.11	0.18	0.02	0.03
Impala/giraffe	0.58	0.82*	0.10	0.04	0.49	0.70*	0.06	0.03	0.03	0.02
Impala/kudu	0.76*	0.63*	0.35	0.32	0.72*	0.59	0.27	0.20	0.19	0.12
Giraffe/kudu	0.56	0.57	0.33	0.37	0.52	0.55	0.18	0.21	0.10	0.12

* Values above or equal to 0.6 are considered significant for single variables (species, height and plant parts).

Table 4. Spearman rank correlation coefficients between animal species' diet compositions (woody species that at least contributed with 5% and the rest grouped as others) during the wet season (bottom left section of the table) and during the dry season (upper right section of the table). $n = 14$ in all cases and is the number of pairs of woody species in the correlation test.

	Elephant	Giraffe	Kudu	Impala
Elephant	–	–0.382	–0.178	–0.426
Giraffe	–0.043	–	0.657	0.687
Kudu	–0.027	0.714	–	0.663
Impala	–0.148	0.754	0.815	–

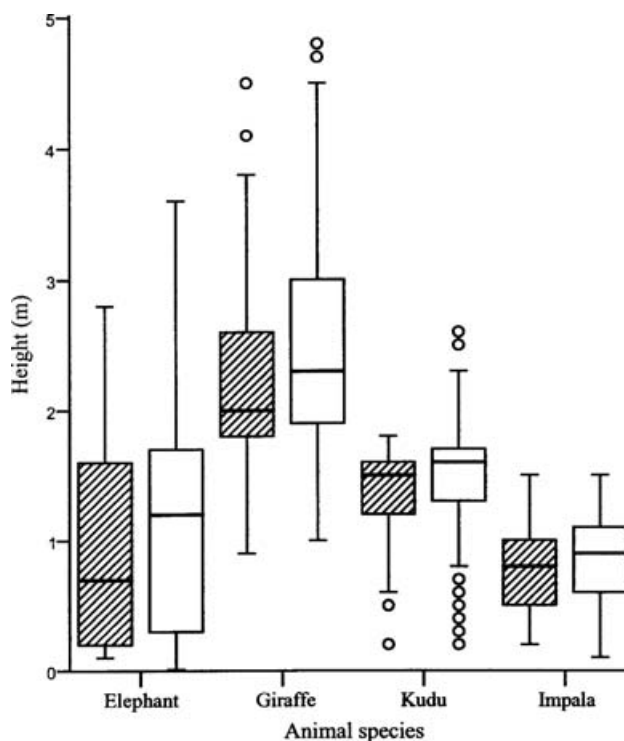
index > 0.5). The Spearman rank correlation between diet compositions for the different browsers (Table 4) supported the diet overlaps shown by the Schoener's index. There was a positive correlation in diet composition between giraffe, kudu and impala but no correlation between the diet composition of elephant and the other species (Table 4). The rank correlation coefficients were slightly weaker in the dry season (Table 4).

There was no difference in overlap of plant species eaten by the herbivores between the wet and the dry season ($P > 0.05$, Mann–Whitney U-test).

Browsing height stratification

The browsing height ranges by elephant and giraffe during both wet and dry seasons were much wider than of impala and kudu (Figure 2). There was no difference in browsing heights between the wet and the dry season for elephant ($F_{1,65} = 2.39$, $P = 0.13$) or kudu ($F_{1,52} = 3.29$, $P = 0.07$). Browsing height was higher in the dry season than in the wet season for both giraffe ($F_{1,126} = 10.9$, $P = 0.001$) and impala ($F_{1,350} = 6.63$, $P = 0.01$). Browsing height differed between the herbivore species during both the wet season ($F_{3,106} = 123$, $P = 0.001$) and the dry season ($F_{3,995} = 602$, $P = 0.001$). Multiple comparisons showed that mean browsing heights by elephant and impala were not different.

The overlaps in browsing heights between all pairs of species were not significant (Schoener's index < 0.6) during any of the seasons (Table 3). Even if not significant, the index was higher when elephant was

**Figure 2.** Box plots showing location and variation in heights browsed by animal species during the wet (hatched) and dry (open) seasons. The lines in the box are sample medians, the lower and upper box ends are 25th and 75th quartiles respectively, and the lines outside the box extend to the minimum and maximum values within the next 25th quartile from the box hinges while the symbols beyond the lines are outlying observations.

included than when the other species were paired between themselves (Table 3). The overlap was lowest when giraffe was paired with impala. Browsing height stratification between giraffe, impala and kudu was even stronger when considering heights they browsed on *Capparis tomentosa*, a species they both heavily browse during the dry season. During the dry season the browsing height overlap between giraffe and impala when browsing on *Capparis tomentosa* was 0.03, while between impala and kudu was 0.23 and between kudu and giraffe was 0.29. The mean browsing heights on *Capparis tomentosa* by giraffe, impala and kudu were different ($F_{2,648} = 547$,

Table 5. Percentages each plant part was observed browsed by each animal species throughout the year.

Plant part	Animal species			
	Elephant	Giraffe	Kudu	Impala
Leafless shoots	34.1	2.2	1.9	0.2
Shoots + leaves	26.1	25.9	22.6	24.3
Leaves only	39.6	65.1	72.2	74.6
Bark	0.2	1.7	0	0.7
Flowers/fruits	0	5.2	3.3	0.2

$P < 0.001$). Multiple comparisons of mean browsing height on *Capparis tomentosa* between each pair of the three species were significantly different ($P < 0.001$).

Browsed plant parts

Elephant browsed fairly equal proportions of leaves, leafless shoots and shoots with leaves whereas giraffe, kudu and impala mostly browsed leaves (Table 5). When *Combretum elaeagnoides* had leaves, the elephant stripped off the leaves and ate the leafless shoots. Contrary to the elephant, the kudu was observed eating the leaves of *Combretum elaeagnoides* but not the shoots. The elephant, however, stripped the leaves of *Croton megalobotrys* to eat, leaving the shoots. Bark eating by giraffe was mainly on *Markhamia zanzibarica*.

There was no overlap in plant parts browsed between elephant and the other species (Table 3). Impala and giraffe overlapped in plant parts browsed during the dry season while impala and kudu overlapped in the wet season (Table 3). Overlap between plant parts browsed by giraffe and impala was lower during the wet season than during the dry season ($P < 0.05$). There was no difference between the dry- and wet-season overlaps in plant parts browsed by other species.

Woody species, browsing height and browsed plant parts combined overlaps

The products of browsed plant species and height overlaps were low for all species pairs, with those for impala and kudu and for giraffe and kudu being higher than for other species pairs (Table 3). The combined overlaps (plant species \times height \times plant parts) were also low, with that for impala and kudu, and giraffe and kudu pairs being higher than for other pairs (Table 3).

DISCUSSION

Woody plant species browsed

The elephant predominantly browses woody plant species different from those mostly browsed by impala, kudu and giraffe (Table 2). The choices of woody plant species

browsed by each of the four herbivores agree with those reported in other studies conducted in the same area (Omphile 1997, Stokke & du Toit 1999). The difference in woody species browsed by elephant and those browsed by the other species could be explained by a combination of differences in body sizes and digestive systems (Table 1). Relative energy requirement decreases with increasing body size, whereas total energy requirements and retention times increase, while the gut capacity remains virtually constant in relation to body mass (Bell 1971, Clauss *et al.* 2003, Demment & Van Soest 1985). This allows the larger animal species to use forage of lower quality, which in most cases is available in large quantities while small animal species meet their high relative energy requirements by browsing rare high-quality foods (Clauss *et al.* 2003, Demment & Van Soest 1985, Jarman 1974). The elephant, a hindgut fermenter, however, has comparatively fast passage rate and achieves only low digestibility coefficients (Clauss *et al.* 2003) which allow it to use forage of even lower quality than other large herbivore species that are foregut fermenters like the giraffe. The body size hypothesis is not supported by the data in this study because the giraffe, a large foregut fermenter, browses largely the same woody species as browsed by the smaller foregut-fermenting kudu and impala.

Browsed plant parts

The difference in digestive system appears also to be the reason for the absence of overlaps between elephant and other species in plant parts browsed. The rate of passage of food in ruminants is low when the diet contains much cell wall material particularly if heavily lignified (Bell 1971). By feeding on plant parts with high lignin content or fibrous tissues, a ruminant fails to assimilate enough protein for its maintenance requirement. This forces a ruminant to select components of vegetation that have thin cell walls and high concentration of protein such as leaves and fruits (Bell 1971, Jarman 1974). The hindgut-fermenting elephant browses shoots more than the other species do (Table 5). This might be explained by the fact that shoots pass through the gut of an elephant relatively faster, even if less digested, than they will pass through the guts of the other ruminant species (Bell 1971, Clauss *et al.* 2003). The bark contribution to diet compositions of animals was low (Table 5). However, shoots were probably ingested more for the bark than for the woody material. Barks of some woody species have low lignin content hence they might improve the digestibility of ingested shoots (Malan & Van Wyk 1993).

The elephant eat shoots of *Combretum elaeagnoides* but not its leaves whereas the kudu eat the leaves but not its shoots, possibly because the two herbivore species have

different tolerance for plant chemical defences. Types and quantity of secondary metabolites can differ between parts of an individual plant (Palo 1984). Hindgut fermenters like the elephant may be more sensitive to rapidly absorbed toxins like alkaloids whereas foregut fermenters like kudu may be more sensitive to digestibility-reducing compounds (Palo 1987).

Food quality changes with season (Senft *et al.* 1987), as does food availability. The increase of *Capparis tomentosa* and a decrease of *Combretum mossambicense* in diet composition of giraffe, kudu and impala during the dry season may be due to these herbivore species mostly browsing leaves (Table 2 and 5). *Capparis tomentosa* is evergreen whereas *Combretum mossambicense* is deciduous (Table 1). This might also explain why the browsed species niche breadth of giraffe and impala shrinks during the dry season whereas that of elephant expands (Figure 1). When deciduous species lose their leaves, animal species that mostly eat leaves have fewer woody species to choose from. The elephant, that mostly eats shoots, can instead distribute its browsing to more species during the dry season when food becomes scarce.

Browsing height stratification

Browsing height stratification reduces overlap in the use of browse resources among browsers (du Toit 1990, Leuthold 1978). Browsing height stratification considerably reduced the overlap in resources used by impala, kudu and giraffe but it more effectively reduced overlap between impala and giraffe (Table 3, Figure 2). This agrees with results found in Kruger National Park, South Africa (du Toit 1990). An elephant often uses its trunk to collect food (Owen-Smith 1988), and thus overlaps with other species in browse height. I suggest that browsing height stratification between impala, kudu and giraffe can, apart from body size differences (Leuthold 1978), be explained by the scramble competition hypothesis that relates to food availability (Hughes 1980, Illius & Gordon 1987, Stokke & du Toit 2000). At lower levels of the tree canopy, the smaller browsers like impala reduce food quality by taking small selective bites and removing individual leaves (Woolnough & du Toit 2001). Giraffe therefore profit from browsing at higher levels in the canopy than impala and kudu as predicted by the scramble competition hypothesis (Hughes 1980, Illius & Gordon 1987, Stokke & du Toit 2000). This might also be the reason why the mean heights browsed by giraffe and impala were higher during the period of food scarcity (dry season) than during the period of food abundance (wet season). When animals deplete the food lower in the canopy they search for food at higher reachable levels. The likely explanation for no difference in mean heights browsed by kudu between the

two seasons might be that they do not profit from browsing higher up in the canopy during the dry season. The mean heights browsed by kudu during both seasons were above the reach of impala that selectively picks leaves.

Resource partitioning at the Chobe riverfront

I did not find support for the hypothesis that overlap in resource use within the browsing guild is higher during the period of food abundance (wet season) than when food is scarce (dry season) which could have indicated interspecific competition between species (Gordon & Illius 1989, Mysterud 2000). Overlap in resources did not increase during food scarcity as predicted for an optimally foraging ungulate (Owen-Smith & Novellie 1982). The species widened their foraging without increasing overlap in resource use between each other. The elephant achieved that by expanding its browsed species niche breadth without a change in browsing height. Giraffe and impala reduced their browsed species niche breadth but they browsed higher in the canopy during food scarcity. The kudu was the only exception because neither its browsed species niche breadth (Figure 1) nor its browsing height differed between the two seasons.

Since the elephant browse different woody species from those browsed by the other browsers the increase in elephant population is unlikely to cause an increase in interspecific competition between it and the other three species. It is likely to cause intraspecific competition within the elephant population, but Stokke & du Toit (1999) found no evidence of this in the same study area. The concerns that elephant population increase could result in them depleting food for impala, kudu and giraffe thus, negatively affecting their population is not supported by this study. It would therefore not be appropriate to manipulate the elephant population on the basis that it competes for food with impala, kudu and giraffe. However, there may be social and economic reasons to limit elephant numbers outside the Park, as suggested by Skarpe *et al.* (2004). It should also be noted that this study did not take into account other factors that elephant population increase can have on other species, such as behavioural intolerance, changing vegetation structure offering shelter and hiding, interference at water sources, disease and parasites shared. It also did not consider the benefits the effect of elephant has on other browsers such as opening dense thickets and keeping trees and shrubs down to a level reachable by smaller browsers.

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LITERATURE CITED

- ABRAMS, P. 1980. Some comments on measuring niche overlap. *Ecology* 61:44–49.
- BELL, R. H. V. 1971. A grazing ecosystem in the Serengeti. *Scientific American* 225:86–93.
- BEN-SHAHAR, R. 1993. Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation* 65:249–256.
- CLAUSS, M., FREY, R., KIEFER, B., LECHNER-DOLL, M., LOEHLEIN, W., POLSTER, C., RÖSSNER, G. E. & STREICH, W. J. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia* 136:14–27.
- COATES PALGRAVE, K. C. 2002. *Trees of southern Africa*. (Third edition). Struik Publishers, Cape Town. 1212 pp.
- DEMMENT, M. W. & VAN SOEST, P. J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* 125:641–672.
- DU TOIT, J. T. 1990. Feeding-height stratification among African browsing ruminants. *African Journal of Ecology* 28:55–61.
- GIBSON, D. C., CRAIG, G. C. & MASOGO, R. M. 1998. Trends of the elephant population in northern Botswana from aerial survey data. *Pachyderm* 25:14–27.
- GORDON, I. J. & ILLIUS, A. W. 1989. Resource partitioning by ungulates on the Isle of Rhum. *Oecologia* 79:383–389.
- HALTENORTH, T. & DILLER, H. 1980. *Mammals of Africa including Madagascar*. Collins field guide. HarperCollins Publishers, London. 400 pp.
- HANSEN, R. M. & REID, L. D. 1975. Diet overlap of deer, elk, and cattle in Southern Colorado. *Journal of Range Management* 28:43–47.
- HURLBERT, S. H. 1978. The measurement of niche overlap and some relatives. *Ecology* 59:67–77.
- HUGHES, G. 1980. Larval competition in serially transferred population of *Drosophila melanogaster*. *Oecologia* 45:396–403.
- ILLIUS, A. W. & GORDON, I. J. 1987. The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* 56:989–999.
- JARMAN, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215–267.
- JARMAN, P. J. & SINCLAIR, A. R. E. 1979. Feeding strategy and the pattern of resource partitioning in ungulates. Pp. 130–163 in Sinclair, A. R. E. & Norton-Griffiths, M. (ed.). *Serengeti – dynamics of an ecosystem*. University of Chicago Press, Chicago.
- LEUTHOLD, W. 1978. Ecological separation among browsing ungulates in Tsavo east National Park, Kenya. *Oecologia* 35:241–252.
- LEVINS, R. 1968. *Evolution in changing environments: Some theoretical explorations*. Princeton University Press, Princeton. 120 pp.
- MALAN, J. W. & VAN WYK, A. E. 1993. Bark structure and preferential bark utilisation by the African elephant. *IAWA Journal* 14:173–185.
- MCDONALD, R. A. 2002. Resource partitioning among British and Irish mustelids. *Journal of Animal Ecology* 71:185–200.
- MENARD, C., DUNCAN, P., FLEURANCE, G., GEORGES, J. Y. & LILA, M. 2002. Comparative foraging and nutrition of horses and cattle in European wetlands. *Journal of Applied Ecology* 39:120–133.
- MISHRA, C., VAN WIEREN, S. E., KETNER, P., HEITKÖNIG, I. M. A. & PRINS, H. H. T. 2004. Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *Journal of Applied Ecology* 41:344–354.
- MOSUGELO, D. K., MOE, S. R., RINGROSE, S. & NELLEMAN, C. 2002. Vegetation changes during a 36-year period in northern Chobe National Park, Botswana. *African Journal of Ecology* 40:232–240.
- MYSTERUD, A. 2000. Diet overlap among ruminants in Fennoscandia. *Oecologia* 124:130–137.
- OMPHILE, U. 1997. *Seasonal diet selection and quality of large savanna ungulates in Chobe National Park, Botswana*. Ph.D. thesis, University of Wyoming, Laramie, Wyoming. 136 pp.
- OMPHILE, U. & POWELL, J. 2002. Large ungulate habitat preference in Chobe National Park, Botswana. *Journal of Range Management* 55:341–349.
- OWEN-SMITH, N. & NOVELLIE, P. 1982. What should a clever ungulate eat? *American Naturalist* 119:151–178.
- OWEN-SMITH, R. N. 1988. *Mega-herbivores: The influence of very large body size on ecology*. Cambridge University Press, Cambridge. 369 pp.
- PALO, R. T. 1984. Distribution of birch (*Betula* spp.), willow (*Salix* spp.), and poplar (*Populus* spp.) secondary metabolites and their potential role as chemical defense against herbivores. *Journal of Chemical Ecology* 10:499–520.
- PALO, R. T. 1987. Chemical defence in a woody plant and the role of digestive system of herbivores. Pp. 103–107 in Provenza, F. D., Flinders, J. F. & McArthur, E. D. (eds.). *Proceedings. Symposium on plant-herbivore interactions*. United States Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report. INT-222.
- PUTMAN, R. J. 1996. *Competition and resource partitioning in temperate ungulate assemblages*. Chapman and Hall, London. 131 pp.
- QUINN, G. P. & KEOUGH, M. J. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge. 537 pp.
- SCHOENER, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- SENFT, R. L., STILLWELL, M. A. & RITTENHOUSE, L. R. 1987. Nitrogen and energy budgets of free-roaming cattle. *Journal of Range Management* 40:421–424.
- SKARPE, C., AARRESTAD, P. A., ANDREASSEN, H. P., DHILLION, S., DIMAKATSO, T., DU TOIT, J. T., HALLEY, D. J., HYTTEBORN, H., MAKHABU, S., MARI, M., MAROKANE, W., MASUNGA, G.,

- MODISE, D., MOE, S. R., MOJAPHOKO, R., MOSUGELO, D., MOTSUMI, S., NEO-MAHUPELENG, G., RAMOTADIMA, M., RUTINA, L., SECHELE, L., SEJOE, T. B., STOKKE, S., SWENSON, J. E., TAOLO, C., VANDEWALLE, M. & WEGGE, P. 2004. The return of the giants; ecological effects of an increasing elephant population. *Ambio* 33:276–282.
- SKINNER, J. D. & SMITHERS, R. H. N. 1990. *The mammals of the southern African subregion*. University of Pretoria, Pretoria. 771 pp.
- SMITHERS, R. H. N. 1992. *Land mammals of southern Africa: A field guide*. (Second edition). Southern Book Publishers, Halfway House. 229 pp.
- STOKKE, S. & DU TOIT, J. T. 1999. Sex differences in feeding-patch choice in a megaherbivore: elephants in Chobe National Park, Botswana. *Canadian Journal of Zoology* 77:1723–1732.
- STOKKE, S. & DU TOIT, J. T. 2000. Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography* 23:70–80.
- STOKKE, S. & DU TOIT, J. T. 2002. Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology* 40:360–371.
- VAN WYK, B. & VAN WYK, P. 1997. *Field guide to trees of southern Africa*. Struik Publishers, Cape Town. 536 pp.
- VERLINDEN, A. & GAVOR, I. K. N. 1998. Satellite tracking of elephants in northern Botswana. *African Journal of Ecology* 36:105–116.
- VOETEN, M. M. & PRINS, H. H. T. 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* 120:287–294.
- WALLACE, R. K. 1981. An assessment of diet-overlap indexes. *Transactions of the American Fisheries Society* 110:72–76.
- WOOLNOUGH, A. P. & DU TOIT, J. T. 2001. Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. *Oecologia* 129:585–590.
- ZARET, T. M. & RAND, A. S. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* 52:336–342.