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Patterns of resource use within the browsing ruminant guild in the Central Kruger

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1984a; this study) because of time spent (a) searching *for cows in oestrus* and (b) repelling other bulls. I suggest that within the time available for feeding, it would be more profitable for bulls to feed on relatively abundant new shoots at full neck stretch than to search for new shoots within the feeding height range of cows and sub-adult males. The predation risk is the trade-off.

4.4.2.4 *Feeding preference and dietary tolerance*

In certain months (dry season), giraffe spent up to a quarter of their feeding time cropping pods of *Dichrostachys cinerea* and *Acacia tortilis*. In other months (late dry season) they fed extensively on *A. nigrescens* flowers, and in the spring flush fed almost entirely off new shoots. *By contrast*, impala and steenbok searched avidly for fallen pods when they were *available but actually spent* less time feeding on them than did giraffe. Flowers of woody plants were usually inaccessible to the smaller browsers.

The above findings are contrary to predictions of the Jarman-Bell principle. Although *A. tortilis* pods might not be exceptionally rich in nutrients (Gwynne, 1969; Altmann *et al.*, 1987), they constitute an easily harvested and obviously very palatable food favoured by a variety of mammals, large and small (Coe and Coe,

1987; personal observations). The nutritional value of *A. nigrescens* flowers has not been analysed, but the alacrity with which they are eaten by giraffe, kudu and baboons (*Papio ursinus*) indicates that they also must be relatively nutritious. New leaves and shoots of *Acacias* are extremely nutritious, containing up to 30% crude protein (Pellew, 1984a). Hence giraffe feed very selectively at certain times of the year, and the same has been reported for black rhinoceros in Tsavo National Park, Kenya (Goddard, 1970). But giraffe cannot always select a high quality diet, as there are periods in the late dry season when flowers, fruits and new shoots are not available. At such times giraffe feed on mature leaf, often from sclerophyllous evergreens (e.g. *Euclea divinorum*), chewing and swallowing woody shoot ends with the leaves (see also Innis, 1958; Hall-Martin, 1974a).

Giraffe feeding preferences and dietary rankings were not related to measures of nutritional quality, and a similar result was found for giraffe in the Serengeti (Pellew, 1984a). My findings could have been influenced by the choice of plants assayed, but the giraffe diet (entirely woody browse) clearly had a much higher condensed tannin content than those of the smaller browsers, which selected strongly against condensed tannin in the woody browse components of their diets. This raises the point that browsers differ from grazers

in that the quality of their diets is not only influenced by fibre, but secondary chemistry too.

Tannins are only some of the secondary defence compounds produced by plants, and Freeland and Janzen (1974) suggest that herbivorous mammals generally spread their diets over numerous plants to prevent a build-up of specific toxins. However, giraffe in the mid- dry season (July, observed for 24 hours, including 18 hours feeding) were recorded to allocate 99% feeding time to just three species of *Acacia* (Appendix B1). It could be that giraffe are specifically adapted for an *Acacia* diet, but in an area adjacent to the KNP it was found that *Colophospermum mopane*, a generally unpalatable and semi-evergreen woody plant, made up almost 70% of the giraffe diet in August (Hall-Martin, 1974b). Giraffe in another area of the Transvaal lowveld were found to consistently ignore *C. mopane* due to the availability of preferred *Acacia* and *Combretum* species (Oates, 1973).

Hence it seems that giraffe have the facultative ability to cope with relatively high doses of plant secondary compounds when they have to. A similar ability has been reported for the desert-dwelling black rhinoceros (*Diceros bicornis*) in Damaraland, South West Africa/Namibia (Loutit *et al.*, 1987). By way of contrast with smaller browsers, there is circumstantial

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evidence that kudu in fenced paddocks (with low browse diversity in the dry season) will limit their intake of foliage from the few woody plant species available, and may even starve despite an apparent adequacy of browse (van Hoven, 1984). A captive steenbok had to be released from an enclosure of natural range after showing distinct signs of starvation after 43 days, although forbs and woody browse were still available (Huntley, 1972). These findings suggest that the larger *the browser the more* tolerant it is of plant secondary compounds. If the secondary compounds are digestion inhibitors (e.g. tannins), then tolerance for these would be expected to increase with increasing body size, just as the Jarman-Bell principle predicts for fibre. If they are toxins then it could be that the larger the browser the larger its store of nutrients used as conjugation materials in microsomal enzyme detoxii ation (Freeland and Janzen, 1974).

Clearly, a principle that can explain the scaling of ungulate diet quality with body size would have to accommodate (a) the ability of certain very large species (e.g. giraffe) to select high quality foods at times, and (b) the influences of both secondary chemistry and fibre on diet quality. Such a principle may be constructed from an important observation made by Bell (1971), but missed by Geist (1974). This was that the optimum diet preferred by *all* ungulates is

highly nutritious and digestible. Ungulate species differ only in their tolerance for foods that depart from the optimum, and this tolerance increases with increasing body size. Hence a principle that applies to browsers and grazers alike may be stated as follows:

> *The body size and population biomass of ungulate species is a function of the range in diet quality they can tolerate.*

A prediction of the above is that larger ungulates, being tolerant of a wider range in diet quality, should be able to occupy a wider range of habitats. Among browsers in the central KNP there is every indication that this prediction holds (*Chapter 3*; du Toit and Owen-Smith, in press). Further, if larger ungulates can tolerate a wider range in diet quality *and occupy a* wider range of habitats, then their share of resources in local ecosystems will be much larger than that available to smaller ungulates. Consequently population metabolism (energy use per species population) should be highest among the largest species in an ungulate community. This does in fact apply for various herbivores, including desert rodents (Brown and Maurer, 1986), and African savanna ungulates (Owen-Smith, 1988; du Toit and Owen-Smith, in press).

4.5 SUMMARY

Giraffe, kudu, impala and steenbok in the central KNP all depend to a large degree on woody browse in the dry season. However, they were found to differ in the *proportions of woody browse, forbs, and grass* in their mean annual diets. Giraffe fed almost exclusively on woody browse throughout the year, including relatively large proportions of pods and flowers when available. Kudu allocated approximately a third of their feeding time to forbs and creepers. Woody browse made up the bulk, especially in the dry season. Impala were mostly grazers in the wet season, but in the mid- dry season about half the diet was composed of forbs and woody browse. Steenbok fed mainly on forbs when they were abundant, but depended heavily on woody browse and *Acacia tortilis* pods in the dry season.

The dry season convergence on woody browse was associated with a tendency for giraffe, kudu and impala to spend proportionally more time feeding in habitats of the lower catena. Mean dietary diversity and diet *overlap increased to a peak in the late dry season.* Although not in the wet season, feeding preferences of (a) giraffe and kudu and (b) impala and steenbok were strongly related in the dry season. Preferences of the larger pair were most similar with respect to certain

tree species, and the smaller pair shared preferences for certain shrub species. Within each pair, giraffe and kudu separated by *feeding height* while impala and steenbok s[illegible]rated by *catenary position* (steenbok remained on the upper catena when impala moved downslope in the mid- dry season).

Wet season feeding preferences of kudu, impala and steenbok were strongly negatively related to leaf condensed tannin levels in their woody food plants. This relationship fell away in the dry season, and did not apply to giraffe during either season.

It was apparent that certain differences in feeding preference between browser species were due to differential accessibility of woody browse, as influenced by the relationships between body size and plant spinescence, canopy density, and canopy height above ground. Separation of browsers by feeding level only applies for the larger browsers. Giraffe cows browsed above the level of kudu, and giraffe bulls browsed above the level of cows.

Contrary to predictions of the Jarman-Bell principle (as stated by Geist, 1974; but see Bell, 1971, 1984), giraffe fed very selectively at times, ingesting larger proportions of certain high quality plant parts than even steenbok. At other times giraffe diet quality was

relatively low, and giraffe were apparently less sensitive than smaller browsers to plant secondary compounds. Hence for ungulates it is clear that dietary tolerance varies more closely with body size than absolute diet quality does.

CHAPTER 5

BROWSER - WOODY PLANT INTERACTIONS

In previous chapters, the focus has been on the ways in which browsing ruminants may be influenced by the distribution, abundance, and chemical composition of their food plants. In this chapter the focus shifts to the ways in which *Acacia savanna* vegetation may be influenced by browsing ruminants. By Crawley's (1983) analysis, this is an investigation into how timing, intensity, selectivity and spatial pattern of animal feeding interact with the establishment, growth, chemical composition and seed set of plants. Here I consider these issues in addressing two questions: Firstly, what are the effects of severe selective browsing around surface water? Secondly, when giraffe feed on *Acacia* flowers, are they predators or pollinators?

5.1 BROWSING, *ACACIA* TREES AND SOIL AT A SAVANNA WATERHOLE

5.1.1 Introduction

5.1.1.1 *Browsing and plant compensation*

McNaughton (1984:881) proposed that "individual grazers obtain a foraging advantage by membership in a herd because of the greater forage yield per bite from grazing lawns compared with lightly grazed vegetation." A *grazing lawn* is a patch of dense, closely grazed grass that is more productive and nutritious than tall, sparser grass growing on the lightly grazed periphery. McNaughton (*op. cit.*) suggests that the *dense, highly branched canopy* surface of heavily browsed woody plants is analogous to a grazing lawn. Indeed, giraffe browsing has been found to stimulate *Acacia* shoot production in the Serengeti (Pellew, 1983*b*) and in Sweden, browsing by moose (*Alces alces*) on birch (*Betula* spp.) can induce compensatory growth which is more palatable than foliage on unbrowsed plants (Danell *et. al.*, 1985; Danell and Huss-Danell, 1985). In this section I consider the applicability of McNaughton's grazing lawn hypothesis to browsing ruminants and *Acacia nigrescens*, one of the principal food plants of browsers in the central KNP.

In the *Solerocarya birrea / Acacia nigrescens* savanna landscape of the central KNP (Gertenbach, 1983), *A. nigrescens* trees predominate on the basalt plains but are relatively less abundant near surface water (Codd, 1951), where their canopies are typically pruned by impala from below and giraffe from above (personal observations). This pruning results in a clear browse-line beneath a dense, highly branched canopy, which may be sculptured into a cone, sphere, or hour-glass shape as is characteristic of severe browsing by giraffe (Sinclair and Norton-Griffiths, 1979; Pellew, 1984b; *Coe and Coe*, 1987). The browse-line is caused by impala which are mixed feeders with a high rate of water turnover (*Fairall and Klein, 1984*), and in the KNP are seldom found more than a few kilometres from surface water (Young, 1972; this study). The *browse-line* is maintained by many impala each taking a little browse from woody plants in a localised area. The reason for giraffe exerting such a high browsing pressure at waterholes is rather less apparent however.

Unlike grass, woody foliage retains a high preformed water content through the dry season, which enables savanna browsers to be largely independent of surface water (Taylor, 1969; Western, 1975; Louw, 1984). Giraffe, kudu, and steenbok do drink when water is available, but not by necessity (except obviously during droughts). This is evident from the fact that

during the two dry seasons of this study, at least two out of the four kudu cow groups monitored by radio telemetry (Chapter 3) did not visit surface water once. Neither did the two radio-collared steenbok. Although giraffe were often observed drinking, they were also often observed feeding around waterholes and then moving off without drinking. During a dry season in the East African Amboseli ecosystem, the highest density of giraffe was found 30-35 km from water, while zebra and wildebeest were concentrated 5-10 km from water (Western, 1975).

Since browsers are largely water-independent it is to be expected that they should actively avoid waterholes. The central KNP supports one of the highest densities of lions in Africa (± 13 adults per 100 km^2), and the distribution of pride core areas is closely related to the distribution of waterholes (Smuts, 1982). Lions are attracted to waterholes by a high biomass of prey, mainly wildebeest and zebra, which are often ambushed by lions as they come to drink (Schaller, 1972). From my observations it is clear that kudu in the central KNP are sensitive to the predation risk associated with waterholes, which they do actively avoid. This does not apply for giraffe however. To the contrary, dense sculptured *A. nigrescens* canopies are evidence of the fact that giraffe are actually attracted to waterholes.

Because giraffe risk a high predation threat in order to visit waterholes that they do not need to drink from, especially in the wet season, the most likely explanation is that they are attracted there by food. Since the browse (*A. nigrescens* foliage) that giraffe spend most time feeding on at waterholes is equally (or more) abundant elsewhere, this suggests that browse at waterholes might be more palatable than elsewhere. Hence this investigation was designed to test the hypothesis that severe browsing by giraffe and impala results in compensatory growth of enhanced palatability in *A. nigrescens* patches that are frequented by both species.

5.1.1.2 *Browsing and Acacia savanna dynamics*

In African semi-arid savanna ecosystems, selective feeding by concentrations of indigenous large herbivores can profoundly influence vegetation dynamics (Walker, 1986). In areas of subsistence pastoralism, overstocking causes encroachment of less preferred woody plants, soil erosion, and desertification (Walker *et al.*, 1981; du Toit, 1985; Sweet and Mphinyane, 1986). The influence of browsing on semi-arid savanna dynamics is inextricably linked with the influences of soil moisture, grazing and fire (Walker and Noy-Meir, 1982; Pellew, 1983a), and in conservation areas the impact of elephants (*Loxodonta africana*) is a major

factor on its own (Laws, 1970; Norton-Griffiths, 1979). Hence it is difficult to identify the effects of browsing ruminants in isolation. It is nevertheless worth considering their influences on savanna vegetation dynamics, and that is the concern of this section.

In savanna vegetation of the central KNP there is a strong relationship between herbivore impact and a shift in plant species composition. This shift is from lightly grazed *Sclerocarya birrea / Acacia nigrescens* savanna (Gertenbach, 1983) to a heavily grazed and trampled *Acacia tortilis / Dichrostachys cinerea association* in the vicinity of riverlines waterholes, where herbivore concentrations occur (Coetzee, 1983). One factor responsible for this shift is undoubtedly the influx of *A. tortilis* and *D. cinerea* seeds deposited in the dung of large herbivores (Wolhuter, 1940; Lamprey, 1967; Gwynne, 1969; Lamprey et al., 1971; Coughenour and Detling, 1986; Coe and Coe, 1987). This does not, however, account for the thinning of *A. nigrescens* trees and the stunted, severely pruned canopies of those that persist near surface water.

Large browsing ruminants feed on *A. nigrescens* in preference to *A. tortilis* and *D. cinerea* (Chapter 4). This raises the question of whether several selective

herbivory could lead to replacement of preferred woody food plants by better defended species at herbivore concentration points, such as waterholes. In boreal forests it has been found that herbivore-driven changes in woody plant community structure may be associated with reduced rates of nutrient cycling (Bryant and Chapin, 1986). In this section I consider the possibility of a similar effect occurring in a savanna ecosystem, where herbivores concentrate around surface water.

5.1.2 Methods

i. Experimental design

Three sites were chosen on the upper catena on basaltic clay soil in the *Sclerocarya birrea / Acacia nigrescens* savanna landscape of the central KNP (described by Gertenbach, 1983).

One site was at a seasonal waterhole that had formed in a shallow depression enlarged by wallowing elephant and buffalo. The heavily grazed and trampled area immediately about this waterhole was vegetated with *Acacia tortilis* and severely pruned *A. nigrescens* trees. Five mature trees were chosen at random from both species at this site, and each tree was individually labelled. On each tree ten growing shoots

were marked with individually numbered plastic tags, which were tied with string approximately 50 cm in from the canopy surface. The tags were distributed all round the canopy from the lower browse-line to the upper surface. The length of shoot (including all side-branches) distal to each tag was precisely measured using a length of string which was then compared against a ruler. Tagging was done in mid- September, just before the spring flush.

A second site, the *A. nigrescens* control site, was in a monospecific stand of mature, lightly browsed *A. nigrescens* trees 7 km from the waterhole and more than 3 km from alternative water. The herb layer at this site, which supported a relatively low density of large herbivores, consisted mainly of tall, lightly grazed *Themeda triandra grass*. Here, five trees were chosen at random, and individually marked and tagged in the same way (and during the same week) as at the waterhole site.

A third site, the *A. tortilis* control site, was in a monospecific stand of *A. tortilis* at the Tshokwane ranger station, 4 km from the waterhole. Large herbivores visited this site relatively infrequently due to the disturbance of human activity. It was nevertheless representative of the surrounding *A. tortilis* savanna vegetation, which is heavily grazed

and trampled by large herbivores drawn to permanent water in pools of the Nwaswitsontso River (less than 1 km from the *A. tortilis* control site). Five mature trees were chosen at random and individually marked, and ten shoots on each were tagged in the same way (and during the same week) as previously described.

All three sites were revisited during the same week at 3-monthly intervals, in late December (after the early growing season), early April (after the late growing season), early July (after the early dry season), and early October (after the late dry season period of dormancy). On each visit all tagged shoots were inspected for signs of recent browsing (recorded on a *presence/absence* basis) and the length of shoot distal to each tag was carefully measured (including all side-branches).

ii. Estimation of browsing pressure and net shoot extension

The proportion of tagged shoots showing signs of recent browsing was calculated for each marked tree of each species at each site, during each quarter of the seasonal cycle. The four proportions were then averaged to give an index of mean browsing pressure per marked tree per species per site for the complete seasonal cycle. The five mean proportions of browsed shoots per

species per site were arcsine-transformed and browsing pressure was compared across species and sites using the SAS ANOVA procedure with the *a posteriori* Student-Newman-Keuls test option (SAS Institute Inc., 1985*b*).

Net annual shoot extension (total growth minus browsed growth) was calculated for each tagged shoot as the difference between the length of shoot measured after one year, and the length of shoot measured at the time of tagging. Net annual shoot extension was compared across *Acacia* species and sites using the same statistical procedure (ANOVA and SNK) as described for browsing pressure comparisons.

iii. Chemical analyses

In December (mid- wet season), leaf and soil samples were collected on the same day at each marked tree at each site. Leaf samples were collected by plucking leaves at random all round the canopy over the same height range as the tagged shoots. For each marked tree, the plucked leaves were well mixed and a handful was placed in a labelled paper packet, giving five replicate samples (one from each tree) per species per site. These packets were hung in the shade to dry, and then milled and stored at low temperature until analysed in the USA. Leaf samples were analysed for condensed tannin, total nitrogen, and total phosphorus.

Methods of analysis were those described by Bryant *et al* (1985) and outlined in this thesis in Chapter 4.

Soil samples were collected beneath each marked tree at each site by scraping away surface litter and removing a spade-full of soil to a depth of ± 10 cm at four places (at each point of the compass) beneath the canopy, 1 m out from the stem. These four samples were well mixed and one sub-sample was placed in a labelled paper packet. This resulted in five replicate samples of soil collected from beneath each tree species at each site. These were air-dried and stored at low temperature in the USA until analysed. Soil samples were analysed for total nitrogen, nitrate nitrogen, ammonium nitrogen, total phosphorus, and water soluble phosphorus. Total nitrogen and phosphorus were analysed by the methods described by Bryant *et al* (1985) and outlined in this thesis in Chapter 4. Soil nitrate (NO_3), ammonium (NH_4), and water soluble phosphorus (P) were assayed by standard agronomic methods (Black, 1982): NO_3 and NH_4 were extracted for 1 hr from 15 g soil with 75 ml of 2-normal KCl; water soluble P was extracted overnight from 2-3 g soil with double-distilled deionized water (7 ml H_2O/g soil). These extracts were analysed colorimetrically on a Technicon autoanalyser.

iv. Assumptions

This experiment was designed to compare browsing pressure, net shoot extension, leaf chemistry, and local soil nutrients available to specific trees of two *Acacia* species across a gradient of herbivore density. It is not assumed that measurements from each site are representative of the regions in which they occur, as the experimental design would then be flawed by pseudoreplication (Hurlbert, 1984). Intrinsic site differences (i.e. excluding herbivory-induced differences) were minimized by choosing sites in the same landscape and soil type, and in the same position at the top of the catenary drainage sequence. The furthest distance between sites was 10 km (the two control sites) and so rainfall differences are assumed to be negligible.

6.1.3 Results (Table 5.1)

i. Browsing pressure

The overall conclusion of the Student-Newman-Keuls (SNK) multiple range test ($\alpha \approx 0.05$) was as follows:

$$BP_{WAN} \neq BP_{WAS} \neq BP_{CAN} = BP_{CAS},$$

where *BP* is browsing pressure on tree samples denoted

Table 5.1. Plant and soil data from waterhole and control sites.

Variable	Mean value (± S.E.) per variable per site							
	A. tortilis				A.nigrescens			
	Control	Diff*	Waterhole	Diff	Waterhole	Diff	Control	
Browsed shoots[1] (mean %)	0.50 (0.56)	<	12.08 (4.73)	<	30.75 (6.90)	>	3.41 (1.[illegible])	
Mat shoot extension (cm yr⁻¹)	31.20 (5.58)	ns	35.81 (9.19)	>	10.47 (3.26)	ns	15.28 (3.10)	
Leaf tannin[2] (Abse)	0.26 (0.02)	ns	0.32 (0.02)	>	0.21 (0.02)	<	0.42 (0.01)	
Leaf total N (% dry mass)	3.06 (0.05)	ns	2.97 (0.11)	<	3.67 (0.20)	>	3.01 (0.05)	
Leaf total P (% dry mass)	0.14 (0.001)	ns	0.14 (0.006)	<	0.16 (0.007)	>	0.15 (0.005)	
Soil total N (mg kg⁻¹)	1174 (123)	<	1949 (303)	ns	1934 (247)	<	2784 (156)	
Soil nitrate N (mg kg⁻¹)	0.81 (0.13)	<	3.97 (0.89)	ns	5.74 (1.17)	>	2.00 (0.25)	
Soil ammonium N (mg kg⁻¹)	4.67 (0.19)	<	13.61 (1.68)	ns	14.16 (1.85)	>	8.52 (0.48)	
Soil total P (mg kg⁻¹)	355 (16)	<	1303 (51)	ns	1163 (62)	ns	1109 (43)	
Soil soluble P (mg kg⁻¹)	Trace	<	10.29 (2.63)	ns	16.32 (2.35)	>	3.62 (0.61)	

*Comparisons indicate differences determined by the Student-Newman-Keuls multiple range test ($\alpha = 0.05$).
[1]Percentage of marked shoots within each sample of trees that showed signs of recent browsing, averaged over 4 quarterly inspections.
[2]Absorbance value obtained in the proanthocyanidin assay.

by the subscripts (*wan*, waterhole *A. nigrescens*; *wat*, *waterhole A. tortilis*; *can*, control *A. nigrescens*; *cat*, control *A. tortilis*), ranked from highest (BP_{wan}) to lowest (BP_{cat}). This result shows that *A. nigrescens* at the waterhole site was browsed significantly more heavily than at the *A. nigrescens* control site. Furthermore, *A. nigrescens* was browsed more heavily than *A. tortilis* at the waterhole site, where browsing pressure on *A. tortilis* was also higher than that at the *A. tortilis* control site. Browsing pressure did not differ significantly between *A. nigrescens* and *A. tortilis* at the two control sites.

ii. Shoot extension

The overall conclusion of the SNK test was as follows:

$$NSE_{wat} = NSE_{cat} + NSE_{can} = NSE_{wan},$$

where *NSE* is net shoot extension over one seasonal cycle, in the tree samples denoted by the subscripts (as previously described), ranked from highest on the left to lowest on the right. Sample sizes (n_i) were as follows: *wat*, 41; *cat*, 49; *can*, 46; *wan*, 46. Although 50 shoots were tagged in each case, some shoots died during the year and only shoots still alive after one year were included in this analysis.

The comparison shows that net annual shoot extension was greater in *A. tortilis* than *A. nigrescens* at both waterhole and control sites. Within each species, net annual shoot extension did not differ significantly between waterhole and control sites. This finding is important, as it shows that despite being browsed almost 10 times more severely, *A. nigrescens* at the waterhole site achieved a net annual growth increment per shoot equivalent to that at the control site. In order to achieve this, compensatory growth in heavily browsed *A. nigrescens* trees must have been exceptionally high to compensate for continual removal *and* to achieve a net annual growth increment per shoot equivalent to that of lightly browsed trees.

iii. Leaf chemistry (Table 5.2)

Leaves on heavily browsed *A. nigrescens* trees at the waterhole were significantly lower in condensed tannin, and higher in total nitrogen and total phosphorus, than leaves on any of the other tree samples.

iv. Soil chemistry (Table 5.3)

a). Soil total nitrogen was highest at the *A. nigrescens* control site and lowest at the *A. tortilis* control site. The waterhole site was intermediate.

Table 5.2. Leaf chemistry comparisons across *Acacia* species and sampling sites.

Leaf chemistry *variable*	SNK grouping[1]	Sample[2]
Condensed tannin	a	*A. nigrescens* control
	b	*A. tortilis* control
	b	*A. tortilis* waterhole
	c	*A. nigrescens* waterhole
Total nitrogen	a	*A. nigrescens* waterhole
	b	*A. nigrescens* control
	b	*A. tortilis* waterhole
	b	*A. tortilis* control
Total *phosphorus*	a	*A. nigrescens* waterhole
	b	*A. nigrescens* control
	b	*A. tortilis* waterhole
	b	*A. tortilis* control

[1]Samples with the same letter are not significantly different ($\alpha = 0.05$).
[2]*Ranked by mean value of each chemical variable*, with the sample with the highest mean value at the top in each case.

Table 5.3. Soil chemistry comparisons across *Acacia* species and sampling sites.

Soil chemistry variable	SNK grouping[1]	Sample[2]
Total nitrogen	a	*A. nigrescens* control
	b a	*A. tortilis* waterhole
	b a	*A. nigrescens* waterhole
	b	*A. tortilis* control
Total phosphorus	a	*A. tortilis* waterhole
	b a	*A. nigrescens* waterhole
	b	*A. nigrescens* control
	c	*A. tortilis* control
Nitrate nitrogen	a	*A. nigrescens* waterhole
	b a	*A. tortilis* waterhole
	b c	*A. nigrescens* control
	c	*A. tortilis* control
Ammonium nitrogen	a	*A. nigrescens* waterhole
	b a	*A. tortilis* waterhole
	b c	*A. nigrescens* control
	c	*A. tortilis* control
Water soluble phosphorus	a	*A. nigrescens* waterhole
	a	*A. tortilis* waterhole
	b	*A. nigrescens* control
	b	*A. tortilis* control

[1]Samples with the same letter are not significantly different ($\alpha = 0.05$).
[2]Ranked by mean value of each chemical variable, with the sample with the highest mean value at the top in each case.

b). Soil total phosphorus was highest at the waterhole and lowest at the *A. tortilis* control site. The *A. nigrescens* control site was intermediate. This was the same conclusion for nitrate nitrogen and ammonium nitrogen.

c). Water soluble phosphorus was higher in soil at the waterhole than at the two control sites.

d). In all comparisons, the *A. tortilis* control site had the lowest levels of soil nutrients assayed.

e). At the waterhole site, soil nutrient levels beneath *A. nigrescens* canopies were not significantly different to those beneath *A. tortilis* canopies in all comparisons.

v. Variation *in leaf nutrients with respect* to variations in soil nutrients and browsing pressure

a). In both *Acacia* species leaf N and P levels were not significantly correlated with soil N and P levels ($P > 0.05$ in all cases).

b). Browsing pressure on *A. nigrescens* was strongly positively correlated with leaf total nitrogen

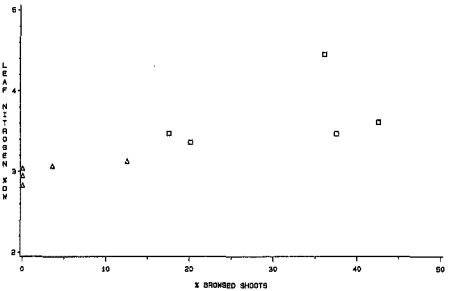


Figure 5.1. *Acacia nigrescens* leaf nitrogen content (percent dry weight) plotted against the average percentage of marked shoots that were browsed (see section 5.1.2), for trees at control (triangles) and waterhole (squares) sites.

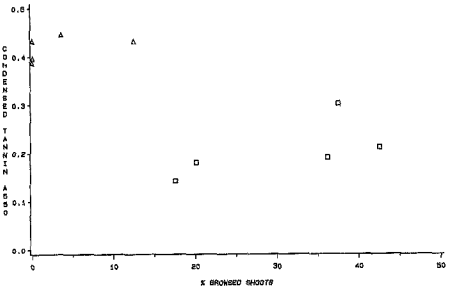


Figure 5.2. *Acacia nigrescens* leaf condensed tannin content (A_{550})* plotted against the average percentage of marked shoots that were browsed (see section 5.1.2), for trees at control (triangles) and waterhole (squares) sites.
*The absorbance value (at 550 nm) in the proanthocyanidin assay (see section 4.3.6).

content (Fig. 5.1; $r = 0.80$, $P < 0.01$, $n = 10$), and negatively correlated with leaf condensed tannin content (Fig. 5.2; $r = -0.70$, $P < 0.05$, $n = 10$).

c). Browsing pressure on *A. tortilis* was not correlated with any of the leaf chemistry variables assayed ($P > 0.05$ in all cases).

5.1.4 Discussion

5.1.4.1 *Browsing and plant compensation*

In a mixed stand of *Acacia tortilis* and *A. nigrescens* at a seasonal waterhole, browsing pressure was significantly higher on *A. nigrescens* than on *A. tortilis*. Browsing pressure on *A. nigrescens* was also very much higher at the waterhole than at a control site. To replace tissue lost to browsers, compensatory shoot growth occurred in *A. nigrescens* at the waterhole, so that net annual shoot extension was not significantly less than that among lightly browsed control trees. Furthermore, the nutritional quality of foliage on severely browsed *A. nigrescens* trees was significantly higher (higher in nutrients and lower in condensed tannin) than that of foliage on lightly browsed trees.

The difference between *A. tortilis* and *A. nigrescens* in

terms of browsing pressure at the waterhole arises from differences in feeding preference. Large browsers feed on *A. nigrescens* in preference to *A. tortilis* (Chapter 4), probably because of the greater spinescence and smaller leaf size of the latter (Cooper and Owen-Smith, 1986). The higher browsing pressure on *A. nigrescens* at the waterhole, relative to the control site, is to be expected from the higher quality of forage at the former. Foliage that is high in nutrients and low in *condensed tannin* is preferred by most browsing mammals (Bryant *et al.*, 1983; Danell and Huss-Danell, 1985; Cooper and Owen-Smith, 1985; Cooper *et al.*, 1988; Bryant *et al.*, *in press*; *this study*, Chapter 4). The crux of this investigation is to present an hypothesis that can account for *why* foliage on severely browsed *A. nigrescens* trees should be more palatable than that *on* lightly browsed trees. This requires consideration of two possibilities.

Firstly, it could be argued that severe browsing at the waterhole resulted from the high leaf nutrient levels expected among trees growing in soils enriched with dung. However in both *Acacia* species, *leaf total* nitrogen and phosphorus levels were not related to total levels of these nutrients in the soil. "Available" soil nutrients in the form of ammonium, *nitrate, and water* soluble phosphorus were all highest at the waterhole site, and so both *A. tortilis* and

A. nigrescens leaf nutrients should also have been higher at the waterhole than at the control sites. This was not the case, however. In fact, *A. tortilis* leaf nitrogen at the waterhole site did not differ significantly from that at the *A. tortilis* control site, which had the lowest soil nutrient levels out of all three sites. Finally, soil nutrient differences cannot account for the significant difference between waterhole and control sites with respect to *A. nigrescens* leaf condensed tannin levels, as no such difference was detected for *A. tortilis*.

An alternative hypothesis is that severe browsing induces a physiological response in some woody plants that increases palatability, leading to a feedback loop of further browsing. The mechanics of this feedback loop (refer to Fig. 5.3) are outlined as follows:

Browsing ruminants such as giraffe, kudu, impala and even steenbok often bite off or damage shoot ends during feeding (Dunham, 1980; Pellew, 1984a; Cooper, 1985; personal observations). This is equivalent to *pruning* (step 1) which induces a plant physiological response quite different to that induced by severe *defoliation* such as by insects (Danell and Huss-Danell, 1985; Bryant *et al.*, in press). Pruning the shoot system of mature woody plants reverses ageing (step 2), reducing between-shoot competition for nutrients

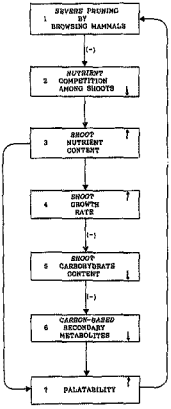


Figure 5.3. Cause-and-effect model of woody plant chemistry changes induced by severe browsing, showing positive effects on palatability that induce further browsing. Arrows between boxes indicate positive effects unless marked (-). Small arrows within boxes indicate directions of change.

(Moorby and Wareing, 1963). The result is increased concentrations of nutrients in remaining shoots (step 3), stimulating growth (step 4). From this study it appears that the pruning effect, widely employed in orchard management, also works to the advantage of browsing ruminants. Evidence is compensatory growth of shoots and significantly higher levels of leaf nitrogen and phosphorus in severely pruned *A. nigrescens* relative to less pruned *A. nigrescens* and *A. tortilis* (Table 5.1). Furthermore, carbohydrate demands incurred by compensatory growth (step 5) cause substrate limitation (step 6) of carbon-based secondary metabolite synthesis (Bryant *et al.*, 1983; Danell and Huss-Danell, 1985; Bryant *et al.*, 1987; Bryant *et al.*, in press). Hence leaf condensed tannin levels in heavily browsed *A. nigrescens* at the waterhole were significantly reduced (halved) relative to lightly browsed plants at the control site (Table 1). Reduced chemical defence and increased shoot nutrients (steps 6 and 3) increase the palatability (step 7) of most woody plants (Bryant *et al.*, 1983; Danell and Huss-Danell, 1985; Cooper and Owen-Smith, 1985; Cooper *et al.*, 1988; Bryant *et al.*, in press; this study, Chapter 4), thereby attracting increased browsing pressure (feedback loop to step 1).

For the above cause-and-effect system to be initiated and maintained, it requires browsing pressure to become

focused on a localised patch of *A. nigrescens*. I suggest that this focus is provided by waterholes, to which impala are attracted for their water requirements, and where they severely browse *A. nigrescens* to the upper limit of their feeding height range. Even moderate browsing by giraffe would then raise the browsing pressure on these patches above the "background" level. If this was sufficient to produce the pruning effect leading to increased palatability, then more giraffe would be attracted to these patches and the browsing feedback loop would come into effect.

Stimulation of *Acacia* shoot production by browsing has been demonstrated in controlled experiments with giraffe (Pellew, 1983b) and domestic goats (Teague, 1987). Pellew (*op. cit.*) suggests that this could be induced by salivary plant-growth-promoting agents (Reardon *et al.*, 1972; Dyer, 1980; McNaughton, 1985). Evidence from this study indicates that browsing not only stimulates *Acacia* shoot production, but also promotes browse quality. Hence the effects of concentrated feeding by browsing ruminants could be considered analagous to the effects of gregariousness in grazers, which modify the sward to the benefit of individual grazers in a herd (McNaughton, 1984; see also Chapter 6, section 6.9). The next important step is to consider the degree to which *A. nigrescens* can

continue to compensate for tissue loss, and by so doing maintain the browsing system.

5.1.4.2 *Browsing and* Acacia *savanna dynamics*

At the waterhole site, where *A. tortilis* was more abundant than in the surrounding *Sclerocarya birrea / A. nigrescens* savanna, pruning by browsers on *A. nigrescens* was significantly more severe than on *A. tortilis*. In the previous section it was suggested that compensatory growth enhances the palatability of severely browsed *A. nigrescens*, leading to a feedback loop of further browsing. Here I propose that this cycle of severe browsing eventually results in *A. nigrescens* being replaced by less preferred competitors, such as *A. tortilis*, where large herbivores concentrate around surface water.

Whether herbivory may actually benefit plants, and if so at what level, are issues of hot debate (Owen and Wiegert, 1976; McNaughton, 1983; Belsky, 1986; McNaughton, 1986; Belsky, 1987). McNaughton (1979) found that even under very intense grazing in the Serengeti ecosystem, productivity was maintained by grazer-adapted grasses to which conventional definitions of overgrazing *may* be inapplicable. Pellew (1984b) suggests that *Acacia* species are able to withstand severe browsing as the result of evolutionary

selection for tolerant genotypes. However, Crawley (1983) analysed the potential for compensation in plant-herbivore interactions and concluded that plants would not be expected to compensate for continuous attack by food-limited herbivores.

Continually severe herbivory depresses plant fecundity (Crawley, 1983), and in *Acacias* flowering and fruiting is suppressed by severe browsing (Coe and Coe, 1987). Hence in areas of high browser density, a strong selective advantage will be derived by plants well defended against browsing (structurally or chemically), with herbivore-adapted means of propagation. *A. tortilis* and *Dichrostachys cinerea* are examples of such plants. These species are very thorny, have fine leaves (particularly *A. tortilis*), and produce palatable indehiscent pods. By contrast *A. nigrescens* bears small hooked thorns, the largest leaflets of all African acacias (Coates Palgrave, 1981), and dehiscent pods. Spinescence and small leaf size reduce the bite size obtained by browsing ruminants (Dunham, 1980; Cooper and Owen-Smith, 1986; Pellew, 1984*b*), while consumption of pods facilitates seed dispersal and reduces the risk of infestation by seed-boring bruchid beetles (reviewed by Coe and Coe, 1987). It is not surprising then that *A. tortilis* and *D. cinerea* tend to encroach in areas of high herbivore density where the grass layer has been weakened (Codd, 1951; Coetzee, 1983; Sweet and

Mphinyane, 1986). Indeed, one of the first rangers in the KNP (Wolhuter, 1948) ascribes the spread of *D. cinerea* in the southern KNP to population increases among ruminants (particularly impala, but also kudu and giraffe) after the rinderpest epizootic and subsequent protection from hunting.

An alternative to the herbivory hypothesis could be that *A. tortilis* and *D. cinerea* are adapted for nutrient-rich soils, and replace *A. nigrescens* near surface water because of local enrichment of soils by dung. This is not supported by the present investigation however, which found that soils at the *A. tortilis* control site had the lowest nutrient levels of all three sites sampled. Furthermore, total soil nitrogen was in fact higher at the *A. nigrescens* control site than at the waterhole. A second alternative could be that *A. tortilis* out-competes *A. nigrescens* where the water-table is near the surface, such as near riverlines. *A. tortilis* at the waterhole and control sites were at the top of the catena though, and the small seasonal waterhole would have had an insignificant influence on soil moisture in the surrounding area. Thirdly, it could be argued that elephants are the prime agents of vegetation change near surface water. This may be so, but then one would expect *A. tortilis* to be affected as much as *A. nigrescens*, because for example in Lake Manyara

National Park, Tanzania, it is elephant damage to *A. tortilis* that is causing most concern (Laws, 1970; Mwalyosi, 1987). Finally it must be recognised that heavy grazing and trampling remove the fuel load near surface water. Consequently reduced burning could cause species changes in woody vegetation as a distal effect of herbivory, but the effects of reduced burning and herbivory are difficult to separate.

Considering possible alternatives, severe selective herbivory remains the most likely factor promoting the establishment of *A. tortilis* / *D. cinerea* thorn-scrub near surface water in the central KNP. Associated with this thorn-scrub are various sclerophyllous evergreens such as *Maytenus senegalensis* and *Euclea divinorum* (Codd, 1951; van Wyk, 1984; personal observations). These species are generally low-preference food plants to browsing ruminants (Chapter 4). I suggest that this woody plant association could develop where severe selective browsing *reduces* the fitness of preferred species such as *A. nigrescens*. Similar vegetation changes occur in the boreal forests of North America, where selective herbivory favours encroachment of inherently slow-growing chemically defended sclerophyllous evergreens (Bryant and Chapin, 1986). The relatively small amount of fibrous, tanniniferous litter produced by these plants decomposes and mineralises slowly (Lewis and Starkey, 1968; Swift *et*

al., 1979), thus impeding nutrient cycling (Bryant and Chapin, 1986).

A potentially important finding of the present investigation is that total soil nitrogen was highest at the lightly browsed and grazed *A. nigrescens* control site, intermediate at the waterhole site, and lowest at the *A. tortilis* control site. Being near the *Nwaswitsontso* River, the latter site had a history of severe herbivory and trampling. Sampling would have to be replicated using more sites to determine if total soil nutrient levels are always higher in *A. nigrescens* savanna than around waterholes or in *A. tortilis* savanna. Nevertheless the pattern I describe is the exact reverse of that described by Hatten and Smart (1984) for the effects of long-term exclusion of large herbivores on soil nutrient status in Murchison Falls National Park, Uganda. Weir (1971) found extensive destruction of trees of certain species around artificial pans in Wankie National Park, Rhodesia (now Zimbabwe). Dung accumulated at these pans, where soil phosphorus levels were high, but the phosphorus levels declined steadily outwards for approximately 4 km to the woodland fringes, and then increased again. Apart from Weir's study, the influence of African large herbivores on nutrient distribution, redistribution and cycling has received little attention (Cumming, 1982). On purely theoretical grounds, Botkin *et al.* (1981)

suggested that large herbivores may be important in the maintenance of a nutrient pool near the soil surface, but this is mainly in high rainfall areas where soils are susceptible to leaching. These authors also acknowledge that cycling of nitrogen through herbivores could in fact increase nutrient losses via volatilization of ammonia from urine and faeces.

I suggest that severe selective herbivory in arid and semi-arid ecosystems could retard nutrient cycling near surface water, resulting in a local decline in soil fertility. The process by which this could occur (refer to Fig. 5.4) is as follows:

Where browsing ruminants concentrate they impact most heavily on *A. nigrescens*, which produces compensatory growth of enhanced palatability, attracting further browsing (this study). Severe browsing reduces litter fall from *A. nigrescens*. Litter production is further reduced by removal of the herb layer through severe grazing and trampling, which also causes soil compaction. This decline in litter production is important as the organic matter content of soil represents a mineralizable resource of organic nitrogen, which through ammonification and nitrification replenishes the plant-available pool of ammonia-nitrogen and nitrate-nitrogen respectively (Hatten and Smart, 1984). *A. nigrescens* is replaced by

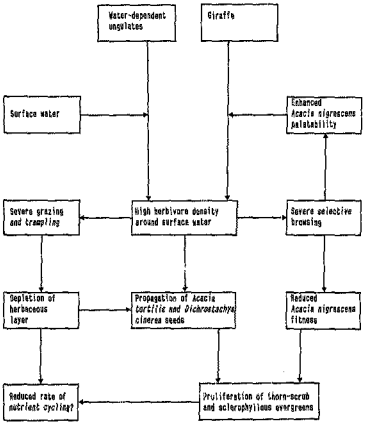


Figure 5.4. Cause-and-effect model of vegetation changes that could occur in the vicinity of surface water in the *Sclerocarya birrea / Acacia nigrescens* landscape of the central KNP.

finer-leafed and thornier species such as *A. tortilis* and *D. cineres*, which typically encroach in areas of high herbivore density (Wolhuter, 1948; Codd, 1951, Coetzee, 1983; Sweet and Mphinyane, 1986), and tend to be associated with sclerophyllous evergreens such as *Euclea divinorum* (Codd, 1951; personal observations). The return flux of nutrients through litter decomposition in this heavily grazed and trampled thorn-scrub association is likely to be significantly lower than in lightly utilized *A. nigrescens* savanna. The end result could be local depletion of soil nutrients, as is indicated by results of this study and the general occurrence of *D. cineres* on impoverished soils (*Costes* Palgrave, 1981).

Notwithstanding the limited scope of the investigation reported here, the results indicate that severe selective herbivory could have a significant influence on nutrient cycling in the vicinity of surface water. I suggest that this be investigated further, with particular attention to monitoring for changes in soil nutrient levels around artificially introduced waterpoints throughout the KNP.

5.2 GIRAFFE FEEDING ON *ACACIA* FLOWERS: PREDATORS OR POLLINATORS?

5.2.1 Introduction

Pollination by nonflying mammals has been reported for primitive primates (Coe and Isaac, 1965; Sussman and Raven, 1978), rodents (Carpenter, 1978; Wiens and Rourke, 1978) and marsupials (Turner, 1982). Many other nonflying mammals feed on blossoms, which although destructive could also result in pollination in some cases (Faegri and van der Pijl, 1979). The largest mammals to be implicated in pollen dispersal are genets (*Genetta tigrina*) in West Africa (Lack, 1976) and lemurs (*Lemur mongoz*) in Madagascar (Sussman and Raven, 1978). Mammals are able to transport large quantities of pollen for a long time in their fur, but the effectiveness of nonflying mammals as cross-pollinators is generally limited by their inability to fly from one plant to another (Faegri and van der Pijl, 1979). Here I consider the potential for pollen dispersal by a very large and highly mobile nonflying mammal, the giraffe.

The diet of giraffe in the eastern Transvaal includes a relatively large proportion of flowers at certain times of the year (Hall-Martin, 1974a; this study, Chapt. 4). These are mainly from *Acacias*, some of which bloom in profusion in the late dry season when the abundance of

deciduous browse is most limited. For the two *Acacias* most common in savanna vegetation of the central KNP, I investigated timing of flowering, flower characteristics, and patterns of flower exploitation by browsing ungulates to assess the potential of giraffe as a pollen vector.

5.2.2 Methods

Phenology of flowering was monitored in the two most common *Acacia* species in the Tshokwane area of the central KNP: *A. nigrescens* and *A. tortilis*. From July 1984 to January 1987, mature stands of each were inspected on a regular basis (usually once a week) at various locations in the study area. When flowering was in evidence, a qualitative assessment of the "degree" of flowering was made as follows:

From high ground overlooking stands of mature trees, the rating system of Anderson and Walker (1974) was used to score the percentage of trees in flower. By this system a percentage class was selected by eye, namely 0, 1-10, 10-25, 25-50, 50-75, 75-90, 90-99, or 100. Depending on the class selected, a score (1 for 1-10% and 7 for 100%) was assigned to each weekly inspection. These were averaged to give a general index of flowering for each month. The index was then scaled for each *Acacia* species so that the month (or months)

out of the whole study period during which flowering was most profuse scored 7, and scores for other months were scaled relative to this. This method provided a convenient "relative flowering index".

Time allocated to feeding on flowers was recorded during feeding observations on giraffe, kudu, impala, and steenbok as described in Chapter 4. For this analysis feeding data from January 1985 to December 1986 were used.

5.2.3 Results

i. Phenology of flowering in *A. nigrescens* and *A. tortilis*

Flowering in *A. nigrescens* occurred regularly, over a short period in the late dry season each year; from July to September 1984, August to September 1985, and August to September 1986. Flowering in *A. tortilis* was less regular, peaking in January (mid- wet season) and lasting for varying periods depending on rainfall; from December 1984 to January 1985, December 1985 to May 1986, and resuming in December 1986.

Flowering in both species during 1985 was weaker than 1986 (Fig. 5.8), probably because of lower rainfall

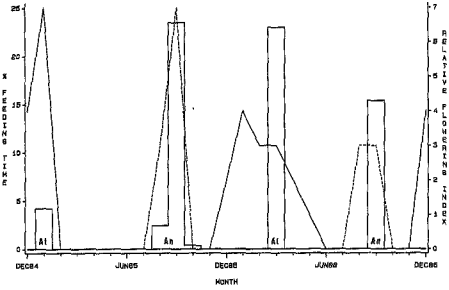


Figure 6.5. Giraffe percentage feeding time allocated to flowers of *Acacia tortilis* (bar, At) and *A. nigrescens* (bar, An) during each month between December 1984 and December 1986, plotted with the relative flowering index of *A. tortilis* (solid line) and *A. nigrescens* (dashed line) over the same period.

during the wet season of 1985/86 relative to 1984/85 (439 mm c.f. 809 mm).

ii. Flower consumption by browsers

Giraffe were the only browsers for which flowers of woody plants constituted an important food resource. During September in both years over which feeding data were collected (1985 and 1986), giraffe consumed *A. nigrescens* flowers in large quantities while they were available (Fig. 5.5). This accounted for 23.5% of feeding time recorded during September 1985 (out of 11.5 hours of observation time spread over 5 days), and 15.3% in September 1986 (out of 16.5 hours spread over 5 days). The lower value for 1986 corresponds with the weaker flowering of *A. nigrescens* that year. *A. tortilis* flower consumption did not always occur when flowers were available (Fig. 5.5). It accounted for 4.2% of giraffe feeding time recorded in January 1985 (17.5 hours spread over 6 days), and 29.5% in March 1986 (out of 5.3 hours spread over 2 days). Other flowers making a significant contribution to the giraffe diet were *Acacia gerrardii* in the wet season and *Combretum hereroense* in the dry season (Fig. 5.5). Flowers making a minor contribution to the diet were *Maytenus senegalensis*, *M. heterophylla*, *Combretum paniculatum*, *Rhotia brachypetalia*, *Diospyros mespiliformis*, and *Kigelia africana* (Appendix B1).

These plants are all associated with riverlines and bloom in the dry season.

Kudu were unable to reach the flowers on most *Acacia* trees, but did feed on the few *A. nigrescens* flowers that were encountered on low-hanging branches. This was during September and accounted for 3.4% of feeding time for that month, averaged over the two years. Other flowers eaten by kudu included *Grewia flavescens*, *Kigelia africana*, *Euclea divinorum*, *Maytenus senegalensis*, *M. heterophylla*, *Dichrostachys cinerea*, and *Combretum mossambicense* (Appendix B2).

Impala and steenbok were not observed feeding on the flowers of any woody plants, these being mainly above their reach.

5.2.4 Discussion

Acacia flowers are an attractive food resource to giraffe, particularly in the dry season when many savanna trees are bare. If giraffe feeding was detrimental to the reproductive success of flowering trees, strong selection for defence against flower predation would be expected. Indeed, long straight thorns are a formidable defence for the capitate ("pom-pom") inflorescences of *A. tortilis*, which have short peduncles and cluster close to the stem. Consequently,

although a giraffe might stand nibbling at *A. tortilis* flowers it is unlikely that much damage is done to the flower mass as a whole. By contrast the spicate ("bottle-brush") inflorescences of *A. nigrescens* stand well proud of small recurved prickles, and are borne in clusters on terminal shoots where they are easily cropped in large quantities by giraffe. In some areas a giraffe browse-line may even form in the flower mass (Hall-Martin, 1974a), although this is unusual in the KNP (personal observations).

The relationship between inflorescence structure and spinescence separates the African *Acacia* species into two distinct groups (Ross, 1979). Firstly, almost all the species with spicate inflorescences have non-spinescent stipules and are armed with recurved prickles, while nearly all the species with capitate inflorescences are well armed with spinescent stipules. Secondly, all the species with spicate inflorescences have pale creamy-white flowers while a large proportion of species with capitate inflorescences have bright golden or orange-yellow flowers. Furthermore out of 26 southern African *Acacia* species, Coetzee (1956) found significant morphological differences between the pollen grains of species with capitate and spicate inflorescences. Pollen grains from species with capitate inflorescences had furrowed surfaces, as did those from 31 Australian species examined. These

furrows were not found on any pollen grains from African species with spicate inflorescences.

Acacia pollination is attributed mainly to insects, although the breeding systems and pollinating agents of many African species remain unexplained (Ross, 1979; Coe and Coe, 1987). The pollen grains are too large to be dispersed by wind (Coetzee, 1955), and despite conspicuous aggregations of insects on the flowers of some species, most African *Acacias* have a remarkably low pod:flower ratio (Ross, 1979). Many (and possibly all) African *Acacia* inflorescences consist of bisexual and male flowers in varying proportions, and Ross (*op. cit.*) suggests that sterile or male flowers are possibly the functional equivalents of petals, with the production of vast quantities of blossom creating a visual attractant to pollinating agents.

In light of the above, feeding by giraffe on *A. nigrescens* flowers is much less destructive than it may seem. The removal of flowers that are unlikely to be fertilized anyway will have little effect on the reproductive success of the plant. By feeding in the flower mass though, giraffe are certain to collect large quantities of pollen in the hair of their heads and necks. Giraffe are highly mobile, and using radio telemetry on adult females I have recorded daily movements of up to 20 km, while one radio-collared bull

was found to move a straight-line distance of 60 km in two weeks (this study, Chapter 3). By feeding in the canopy and moving over such distances I suggest that giraffe are potentially as efficient pollen vectors as bats, which have been shown to carry pollen over distances of up to 30 km (Faegri and van der Pijl, 1979).

A basic principle of biotic pollination is that a "relationship" of *some form* must exist between vector and plant, *so* that regular visits to the plant are part of the *vector's* normal activity pattern (Faegri and van der Pijl, 1979). Such a relationship exists between giraffe and *A. nigrescens*. The foliage of this species is a "staple" food of giraffe in the central KNP (this study, Chapter 4), where the KNP giraffe population has always been concentrated (Pienaar, 1963) and where *A. nigrescens* is most common (Gertenbach, 1983). The very regular phenology ensures flowering when alternative giraffe food types are least abundant in the late dry season, shortly before deciduous trees come out in palatable new leaf. The only browsing ungulates really capable of reaching the *flowers of* mature *A. nigrescens* trees are giraffe, *to* which distally-borne clusters of spicate *inf* rescences with non-spinescent stipules *constitute* an easily harvestable, high quality food resource. Hence it is not surprising that giraffe almost always feed on

flowering *A. nigrescens* trees when they are encountered (personal observations).

The pale flowers of *A. nigrescens* conform with the general tendency for dull flower coloration in pollination systems involving mammals (Sussman and [illegible]n, 1978), though other vectors such as insects and birds are possibly important too. By contrast it would seem that the *Acacia* group bearing thorn-protected capitate inflorescences, many of which are a bright yellow colour, are adapted for pollination by insects only.

Co-evolution with ungulates is clearly evident among the African *Acacias* that produce aromatic, highly palatable indehiscent pods. These are specifically adapted for consumption by ungulates, preventing bruchid beetle infestion and resulting in the dispersal of scarified seeds in dung (reviewed by Coe and Coe, 1987). That one group of African *Acacias* produces masses of palatable, undefended, pale, spicate inflorescences with heavy pollen suggests that co-evolution with ungulates has not only resulted in ungulate-adapted systems of seed dispersal, but perhaps pollen dispersal too.

5.3 SUMMARY

5.3.1 Browsing and waterholes

At a seasonal waterhole, *A. nigrescens* trees were more heavily browsed than thornier and finer-leafed *A. tortilis* trees. Foliage of heavily browsed *A. nigrescens* had higher levels of nutrients and lower levels of condensed tannin than foliage of lightly browsed *A. nigrescens* at a control site. It is suggested that severe pruning by browsers reduces intershoot competition for nutrients, promoting compensatory growth. Carbohydrate demands of compensatory growth reduce carbon-based secondary metabolite synthesis. The result is a patch of highly palatable browse that attracts further browsing, generating a browsing - compensatory growth feedback loop. I suggest that this is analogous to the grazing lawn phenomenon.

In the *Sclerocarya birrea / Acacia nigrescens* savanna landscape of the central ENP, there is a tendency for *A. tortilis* and *Dichrostachys cinerea* to dominate in heavily grazed and trampled patches around surface water. These species are physically well defended against herbivory, have herbivore-adapted means of propagation, and hence are successful where severe selective browsing reduces the fitness of competitors

such as *A. nigrescens*. Associated with *A. tortilis / D. cinerea* thornscrub are various sclerophyllous evergreens. I suggest that the lower quality and quantity of litter produced by this association could impede nutrient cycling, and ultimately lead to relatively lower soil fertility in the vicinity of water points. The management implications of this need consideration in the planning of artificial waterpoints.

5.3.2 Giraffe and *Acacia nigrescens* flowers

Flowers of *A. nigrescens* are an important food resource to giraffe in the late dry season. This is not necessarily deleterious to the plant, however. Most or all African *Acacias* have very low pod:flower ratios, as many flowers are sterile. Such factors as inflorescence colour and structure, pollen characteristics, and thorn structure indicate that one group of *African Acacias* could be pollinated by ungulates. The phenology of flowering in *A. nigrescens*, and the close association between *A. nigrescens* and giraffe in the central KNP, suggest that giraffe could be a pollen vector for this species.

CHAPTER 6

FINAL DISCUSSION

6.1 Overview

The questions posed at the beginning of this thesis address the issues of how syntopic browsing ruminants use shared food resources, how preferences for habitats and food plants differ, and some of the implications of resource use on resource abundance and quality. The conceptual framework within which these issues were addressed was that of resource partitioning within a guild. In this chapter I synthesise my findings on the use by browsers of habitats and food plants, and discuss these with respect to the resource partitioning hypotheses presented in the introduction. I present my conclusions on resource partitioning within the browsing ruminant guild, consider the importance of interspecific competition to the guild's structure, and compare the browsing and grazing guilds. Finally, I assess the value of the guild approach and suggest how future research could build on the results of this study.

6.2 The use of habitats

My findings confirm that giraffe, kudu, impala and steenbok use different habitats (vegetation communities) with different intensities over the seasonal cycle as a whole (section 3.3.3), as proposed for ungulates by Lamprey (1963) and McNaughton and

Georgiadis (1988). In the dry season however, giraffe, kudu and impala converge on habitats of the lower catena (riverine and watercourse vegetation). Movement down the catena in the dry season has also been described in the Serengeti for grazers (Bell, 1970), and the Zambezi valley for both browsers and grazers (Jarman, 1972). Such widespread overlap in habitat use during the lean season challenges the assertion (Lamprey, 1963; McNaughton and Georgiadis, 1986) that an important factor contributing to resource partitioning among African savanna ungulates is the occupation of different habitats in the same season. It is actually only the smaller species, such as steenbok, that remain on the upper catena and so are ecologically separated from the larger species by virtue of a difference in habitat use during the dry season.

More important than separation by habitat, syntopic browser species feed along qualitatively distinct foraging paths, as measured in terms of the woody plant species encountered by each browser species when foraging (section 3.3.4). A multivariate statistical technique would have to be employed to prove that this separation of species at the scale of the foraging path is more distinct than at the scale of the habitat. Such an analysis was not performed, however, in view of the conclusions of two previous studies. Firstly, Ferrar and Walker (1974) found that by results of discriminant

function analysis, plant associations at feeding sites were more important than physical habitat structure in the ecological separation of savanna ungulates. Secondly, in a pilot study in the KNP, Beardall *et al.* (1984) tested the usefulness of correspondence analysis as a technique to analyse herbivore/habitat associations. They concluded that while this technique is more suitable than alternative multivariate techniques, a fundamental problem is identifying the particular habitat features that are most important to each species in question. For herbivores I suggest the best way to avoid this problem is to work at the scale of the foraging path, recording by direct observation the plant associations selected by individuals of each species when feeding (see also Wiens, 1976; Senft *et al.*, 1987).

6.3 The use of food plants

6.3.1 *Grass, forbs and woody browse*

The four species studied were found to differ not only with respect to the proportions of grass and browse in their diets (see McNaughton and Georgiadis, 1986), but the proportions of forbs too (section 4.3.1). Hence species clumped at the browser end of the grazer-to-browser continuum may be separated according to the mix of forbs and woody forage types that they consume.

Hofmann and Stewart (1972) separated African browsing ruminants ("selectors of juicy, concentrated herbage") into (a) "tree and shrub foliage eaters" and (b) "fruit and dicot (tree, shrub or forb) foliage selectors". The former group included giraffe and kudu and the latter group included duiker and klipspringer, but not steenbok, which was classified with impala as an intermediate feeder. This classification was made on the basis of stomach structure and field observations published [illegible]. My findings on diet composition (section 4.[illegible]al inconsistencies with Hofmann and Stewart's classification. Of the four species studied, giraffe allocated the highest proportion of feeding time to fruits and flowers, which would warrant its inclusion in group (b) above. Steenbok hardly grazed at all (see also Cohen, 1976), feeding on forbs, woody foliage and *Acacia tortilis* pods, which would also warrant its inclusion (with giraffe) in group (b) of Hofmann and Stewart's classification.

The above examples illustrate the difficulties of separating ungulate species into *categories* on the basis of diet. If browser species are to be classified by diet, I suggest that they be *graded* on the basis of the relative proportions of herbaceous and woody browse that they consume. For example, gerenuk (*Litocranius walleri*) feed almost exclusively on woody browse

(Leuthold, 1970), and so are trophically more similar to giraffe than are kudu, which feed on forbs as well as woody browse. Black rhinoceros also feed on both forbs and woody browse (Goddard, 1970), and so in terms of their food requirements they are more similar to kudu than to giraffe and gerenuk. Such similarities and distinctions were not considered by Hofmann and Stewart, who placed giraffe, kudu and gerenuk in the same category ("tree and shrub foliage eaters"), and did not consider black rhinoceros as this species is not a ruminant.

6.3.2 *Seasonality*

Among kudu, impala and steenbok, the proportion of woody browse in the diet rose sharply in the dry season to compensate for a reduced abundance of green herbaceous forage types (section 4.3.2). The proportion of forbs in the impala diet also rose in the dry season, but this was contributed mainly by desiccated tissue of dead or dormant forbs that kudu and steenbok ignored. The ability of impala to use this forage type is probably related to the dependence of impala on surface water, while steenbok and kudu depend on preformed water in their diets.

Dietary diversity and overlap among species increased from the late wet season to a peak in the late dry

season (the lean season), and declined after the spring flush (sections 4.3.3 and 4.3.4). According to the hypothesis adhered to by Smith *et al.* (1978) and Schoener (1982, 1986a), this finding indicates a low probability that interspecific competition prevails over intraspecific competition for food. This is because if interspecific competition was prevalent it would be most intense in the lean season, and then each species would be expected to retreat to the food resource set to which its phenotype was selected. By this hypothesis niche overlap should be greatest in the fat season, when species converge on abundant high quality food types, even those that some species are not specifically adapted to feed on. For example, it was found that Darwin's ground finches (*Geospiza* spp.) converge on abundant and easily handled seeds and fruits in the wet season, but each species resorts to separate food types in the dry season (Smith *et al.*, 1978; but see Wiens, 1984). A similar wet season convergence occurs in the KNP, when various mammals such as elephant, kudu, impala, warthog and baboon converge on marula (*Sclerocarya birrea*) fruits (personal observations). However, among the browsing ruminants studied, the proportional contribution of marula fruits to the wet season diet (Appendix B) was not sufficient for this convergence to result in increased dietary overlap.

The possibility that seasonal variation in competition results in seasonal variation in niche overlap is in fact untestable, as variation in niche overlap cannot be measured in the absence of potential competitors. In the absence of potential competitors there is no niche overlap to measure. Furthermore, niche overlap is only related to competition when the ratio of resource density to consumer density is so low that resources are limiting (Schoener, 1974*b*; Abrams, 1980; Lawlor, 1980; Wiens, 1984; Moermond, 1986). Hence dietary similarities among species are best investigated by comparing resource-use patterns after resource abundances have been taken into account, i.e. by comparing electivities (Ivlev, 1961; Schoener, 1974*b*, 1986*a*; Lawlor, 1980).

6.3.3 *Electivities*

Dietary similarities among the four species studied, as measured using electivities for woody plants (section 4.3.5.1), were high in the dry season between giraffe and kudu (G/K), and impala and steenbok (I/S). Similarities between the two pairs, G/K and I/S, were very low, confirming the low probability of competition between them (discussed further in section 6.7). Separation was by virtue of G/K having relatively higher preferences for certain tree species, and I/S

having relatively higher preferences for certain shrub species.

Wet season feeding preferences of kudu, impala and steenbok were strongly negatively related to leaf condonsed tannin levels in their food plants (section 4.3.6.1). This relationship fell away in the dry season when the choice of woody forage types was reduced. A negative relationship between condensed tannin level and feeding preference conforms with previous observations on savanna ruminants (van Hoven, 1984; Cooper and Owen-Smith, 1985). However, I found no such relationship to apply during either season in the case of giraffe. A relationship could have been masked by accessibility-related factors influencing giraffe feeding preferences for some of the woody plants assayed (section 4.4.2.3). Nevertheless giraffe clearly tolerated relatively high levels of dietary tannins during certain periods of the dry season, when they fed entirely on tanniniferous foliage, almost all from *Acacia* trees (Appendix B1). Deactivation of tannins with proline-rich salivary proteins (Mehansho *et al.*, 1987) has been suggested as a means by which deer avoid the digestion-inhibiting effects of tannins in their food plants (Robbins *et al.*, 1987*b*). It could well be that the same applies for savanna browsers, and giraffe in particular, as proline-rich proteins are reported (*op. cit.*) to impart viscosity to saliva, and giraffe

saliva is particularly viscous (section 4.4.2.2).

6.4 The influence of body size on resource use

A dominant theme running through the results of this investigation is that resource-use differences are related to body size differences among species. This is not a new finding. Huxley (1942) and Lack (1947) asserted that coexisting species using the same food resources usually differ in body size. Hutchinson (1959) concluded that for two such species the ratio of linear dimensions of the larger to the smaller should be approximately 1.3. This empirical ratio, Hutchinson suggested, indicates the kind of difference necessary to permit two species to coexist at the same level of the food web.

Scores of examples of conformity with "Hutchinson's Rule" have now been published (see Greene, 1987). Indeed, Owen-Smith (1985) showed that African browsing ungulates are discretely graded in size, with the cube root of the average body size ratio between successive species being very near 1.3. Owen-Smith suggested that this grading reflects the distribution of leaf sizes and leaf:stem ratios prevailing among woody plants and forbs. However, there is now evidence that Hutchinson's rule is based on a statistical artefact. A ratio near 1.3 will result from comparing the linear dimensions of

many objects (even some inanimate ones) in nature that are log-normally distributed, and occur in assemblages with standard deviations less than one (Eadie *et al.*, 1987). Why this size distribution should prevail among sympatric species is unclear, as competition alone cannot be the cause in many cases (reviewed by Pagel and Greenough, 1987). Irrespective of the way in which species are graded in size, the fact that size differences exist was found to have the following important consequences for resource use among the browser species studied:

6.4.1 *Body size and dietary tolerance*

My results show that giraffe select new shoots, pods and flowers (mainly from *Acacia* species) when these are available (section 4.3.1). In fact giraffe allocated a higher proportion of feeding time (on average over the seasonal cycle) to fruits and flowers of woody plants than did steenbok. This finding conforms with that of Pellew (1984a) that giraffe are highly selective feeders. Such findings contradict the general understanding that because a herbivore as large as giraffe has low mass-specific metabolic costs but a high food intake rate, it should feed relatively unselectively on high-fibre foods (Geist, 1974; Jarman, 1974; Demment and van Soest, 1985; McNaughton and Georgiadis, 1986). However, Bell (1971) noted that the

optimal diet for all herbivores is that which is highly nutritious and digestible. It is *tolerance* for departures from this optimum that increases with increasing body size. Indeed, when high quality plant parts are not available the giraffe diet is relatively low in quality, both in terms of fibre and plant secondary compounds (section 4.4.2.4; see also Hall-Martin, 1974*a*,*b*).

The influences that differences in body size and digestive system (i.e. ruminant/non-ruminant) have on the feeding ecology of large herbivores have been interpreted largely in terms of differences in the fibre contents of selected diets (e.g. Janis, 1976; Demment and van Soest, 1985). While this may be a suitable interpretation for grazers, it is becoming increasingly apparent that plant secondary chemistry is an additional factor to be considered, particularly for browsers (Cooper and Owen-Smith, 1985; Robbins *et al.*, 1987*a*; Cooper *et al.*, 1988; this study, section 4.4.2.2). Whether or not body size influences the abilities of browsers to withstand plant secondary compounds is unknown, but circumstantial evidence indicates that it might do (section 4.4.2.4) and this requires investigation. Either way, the influence of body size on the feeding ecology of herbivores is more accurately interpreted in terms of the range in diet

quality tolerated, than dietary fibre content *per se* (see also Bell, 1984).

6.4.2 *Body size and habitat specialisation*

My findings indicate that increased dietary tolerance with increased body size enables the larger herbivore species to feed in a more diverse range of habitats than the smaller species (section 3.3.1). The generality of this habitat-use / body size trend requires further investigation, although among African ungulates it appears to be well supported. Among five general styles of feeding behaviour among African antelope, Jarman (1974) recognised a tendency for small species to remain in one vegetation type throughout the year, and progressively larger species to feed in a progressively wider range. If the trend is generally applicable to African ungulate species, then it will provide an explanation (du Toit and Owen-Smith, in press) for why population metabolism (energy use per species population) tends to increase with increasing average body size among these species (Owen-Smith, 1988). Simply stated, larger species are able to spread more evenly through ecosystems by feeding in a wider range of habitats, and so metabolise a larger fraction of available plant biomass than smaller species can (section 3.4.1).

The above hypothesis has important implications for resource partitioning. If small-bodied ungulate species specialise on using different habitats to each other then niche overlap among these species will be negligible. Evidence for this in the KNP is the complete ecological separation of the following small browsers: steenbok, which occur in open patches of savanna; klipspringer, which occur only on rocky outcrops; and bushbuck, which occur in riverine thickets (Pienaar, 1963; Smithers, 1983). Larger species may encroach on these habitats but the impact of their feeding is distributed by their use of other habitats too.

6.4.3 *Body size and home range area*

For the four species studied I found a close relationship between body mass and home range area (section 3.3.2). The body mass exponent (1.38) in this relationship is significantly higher than 0.75, the exponent expected if home range area is assumed to scale with body mass in proportion to metabolic requirements (McNab, 1963). Other studies on home range scaling among herbivorous mammals (Harestad and Bunnell, 1979; Swihart *et al.*, 1988) have also found body mass exponents significantly greater than 0.75, and not significantly different to that reported here.

My data set is not extensive enough to resolve the current debate on why animals feed over a disproportionately larger area than they are expected to require for their metabolic needs (reviewed in section 3.1.2). Current theories, based on published estimates of home range from a variety of studies conducted in different regions, are concerned with modifying McNab's (1963) original hypothesis. That is, home range area must vary as a function of the minimum area an individual *has* to cover in order to feed itself (Schoener, 1968; Harestad and Bunnell, 1979; Damuth, 1981b; Lindstadt *et al.*, 1986). I propose that this assumption is not supported by adequate evidence from field studies. I found no evidence that my study animals were forced (by resource limitation) to cover the distances that they did in order to survive. Giraffe, for example, would walk steadily through *Acacia* savanna in which trees were in full leaf, to feed in patches of *Dichrostachys cinerea* that were in pod (section 3.4.3). Hence I consider a more realistic approach is to assume an animal will cover as much ground as it profitably *can*. This area will vary as a function of benefits and costs. Benefits would be determined by the productivity and heterogeneity of the environment, and costs by various size-dependent variables, including metabolic rate, speed and energetics of locomotion, dietary tolerance, etc. (section 3.4.2).

6.5 Feeding height separation

Almost all giraffe feeding was at a higher level in the vegetation than that used by kudu, but for species smaller than kudu the overlap in feeding levels was considerable (section 4.3.7). This finding questions the generality of Lamprey's (1963) hypothesis that differently-sized browsing ungulates tend to partition their resources vertically by feeding at different levels in the vegetation (see also McNaughton and Georgiadis, 1986). For savanna browsers I suggest that feeding height separates only giraffe from other species. Giraffe are quite capable of feeding at low levels though, so even this separation might not always be complete. For example in Tsavo East National Park, Kenya, giraffe have been found to allocate about 50% feeding time to browsing below a height of 2 m (Leuthold and Leuthold, 1972). This gave rise to the suggestion (see also Leuthold, 1978) that reduction of the woody layer by elephants and fire could bring giraffe into competition with smaller browsers.

Although giraffe have exclusive access to the upper canopy of mature trees, these trees grow from saplings and seedlings, which are food to other browsers. If herbivory on saplings and seedlings was excessive then replacement of the mature canopy, where damaged by

elephants for example, would be retarded. Hence the possibly of long-term exploitative competition (*sensu* Schoener, 1983) between the smaller browsers and giraffe must be considered. This type of competition is evident in the boreal forests of North America. There snowshoe hares (*Lepus americanus*) can impact so heavily on preferred woody food plants, such as *Salix alaxensis*, that the abundance of browse used by moose (*Alces alces*) is severely reduced during peak hare densities (Wolff, 1980; Belovsky, 1984). I consider it unlikely that such an interaction is of much importance among browsers in African savannas though (but see French, 1985, for grazers), where the smaller browsers do not reach the high densities that snowshoe hares do in North America.

6.6 Browser - woody plant interactions

Results of this aspect of the study (section 5.1.3) indicate that severe browsing on *Acacia nigrescens* induces compensatory growth of shoots, which bear foliage that is more nutritious and palatable than that on lightly browsed trees. This result conforms with previous findings on the nutritional quality and growth of woody plant shoots following pruning by large browsing mammals (Danell *et al.*, 1985, Danell and Huss-Danell, 1985; Pellew, 1983b; Teague, 1987; Bryant *et al.*, in press).

The above results are in contrast to the much publicized assertion by van Hoven (1984) that foliage on savanna trees *decreases* in palatability as a result of chemical defences induced by browsing. However, the time-scale to which van Hoven refers is very short. He proposes that palatability returns to normal within a period of between 50 and 100 hours following damage to foliage. Furthermore, the effects of herbivory on plant chemistry vary greatly depending on timing (i.e phase of the seasonal cycle), duration, and intensity (reviewed by Bryant *et al.*, in press). Finally, the method van Hoven used to simulate browsing was to thrash trees with belts and whips, which I suggest is more a simulation of defoliation (such as by insect attack) than of pruning (such as by large mammals). The physiological responses of deciduous woody plants to (a) defoliation and (b) pruning are quite distinct (discussed by Bryant *et al.*, in press).

If severe pruning can have a positive influence on woody browse quality then this introduces a new slant to interspecific relations among browsers. For example, where giraffe and impala exert a combined "attack" on *Acacia nigrescens* trees, they are feeding at different heights and so competition is not involved. Rather, compensatory growth, raised leaf nutrients, and reduced leaf condensed tannin suggest facilitation. In fact

Rhoades (1985) proposed exactly this on theoretical grounds, postulating that herbivores should be either stealthy or opportunistic in countering plant defences. Stealthy herbivores should minimise damage to plants so that defence responses are not invoked (but see Schultz, 1988), while opportunists should employ mass-attack behaviour and thereby take advantage of stressed plants. As with many other plant-herbivore relations, the validity of the above hypothesis awaits further investigation.

The induction of compensatory growth of *Acacia nigrescens* shoots by severe browsing would result in a feedback loop of further browsing (section 5.1.4.1). The scope of the study was too limited to reach a conclusion, but I suggest that a feedback loop of this kind could result in the eradication of preferred woody browse plants where herbivores concentrate, such as near surface water. Herbivory by large mammals is not always deleterious to savanna woody plants though. Some plants, particularly the *Acacias*, have evolved seed dispersal mechanisms that depend upon the consumption of pods by ungulates (reviewed by Coe and Coe, 1987). In addition I suggest that *A. nigrescens*, and perhaps other species too, might benefit from the consumption of their flowers by giraffe, which have the potential to be very effective pollen vectors (section 5.2).

6.7 How does resource partitioning occur?

From the results of this study I conclude that resource partitioning is clearly evident among browsing ruminants in the central KNP. This is by virtue of the following:

a). Habitat specialisation among the smaller species (steenbok, klipspringer, bushbuck, etc.) results in separation between some or most of these species. The tendency for larger species to use a more diverse range of habitats (i.e vegetation communities) lessens their impact on browse resources in habitats ch smaller species are specifically adapte on 6.4.2).

b). Syntopic species feed along distinctly different foraging paths, as defined by the woody plants associated with feeding sites (section 6.2), and giraffe feed at higher levels in the vegetation than other species do (section 6.5).

c). Syntopic species differ in the proportions of grass, forbs, and woody browse in their diets (section 5.3.1). Such dietary differences do not separate species completely, but reduce dietary overlap among them.

d). Because of morphological variations among browsers and plants, foliage on certain plants is more accessible to some browsers than it is to others. For example, giraffe (being taller) can feed in the upper canopy where kudu cannot reach, and impala (having a narrower muzzle) can pluck leaves from between the thorns of *Acacia tortilis*, which are an effective deterrent against kudu (Cooper and Owen-Smith, 1986; see also section 4.4.2.3)

e). Dietary tolerance increases with body size (Bell, 1971; see also section 6.4.1), so the larger browser species may consume forage types of lower nutritional quality than can be tolerated by smaller species.

f). Because of factors d) and e), electivities for woody plants tend to differ, particularly between large and small species (section 6.3.3).

The dry season is the lean season in the KNP, so the factors that result in resource partitioning during this period are those most deserving of attention. For the four species studied, niche separation in the dry season occurs by spacing along three axes (Fig 6.1). Giraffe and kudu are separated by feeding height. Impala and steenbok are separated by the tendency for steenbok to remain on the upper catena when impala are

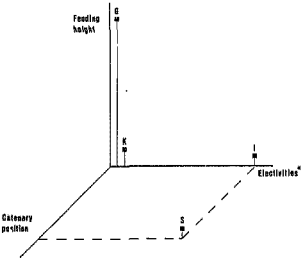


Figure 6.1. Niche separation (in the dry season) between giraffe (G), kudu (K), impala (I), and steenbok (S). Positions of each species along the three axes are relative to other species, and the distance between positions indicates the degree of separation.
*Electivities for woody food plants.

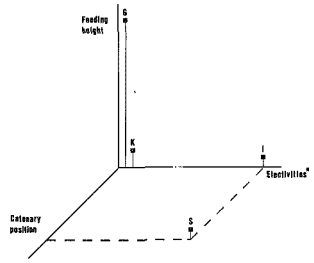


Figure 6.1. Niche separation (in the dry season) between giraffe (G), kudu (K), impala (I), and steenbok (S). Positions of each species along the three axes are relative to other species, and the distance between positions indicates the degree of separation.
*Electivities for woody food plants.

feeding mainly along the riverlines. The larger pair (giraffe and kudu) are separated from the smaller pair (impala and steenbok) by differences in their electivities for woody plants. The larger pair share preferences for certain tree species while the smaller pair share preferences for certain shrub species.

6.8 Why does resource partitioning occur?

Considering the degree to which the browse resource is partitioned among browsing ruminants, it is apparent that interspecific competition is largely or entirely avoided. This raises the following questions: (1) is resource partitioning maintained by present-day competition? (2) is resource partitioning the product of competition through evolutionary time? (3) is resource partitioning the product of competition at all, or would it also occur in a randomly assembled group of ungulate species?

Firstly, if niche separation is maintained by present-day competition, then niche expansion is to be expected in the absence of potential competitors. However, among the species studied, the potential for niche expansion is limited by morphology and physiology. For example, kudu cannot feed any higher than they do, and impala cannot disperse away from riverlines in the dry season

because they cannot go without water (Fairall and Klein, 1384).

Secondly, competition through evolutionary time could have caused the smaller browsers, which share a requirement for relatively rare high quality foods, to specialise on separate habitats. However, it could also be that selection for predator avoidance is the reason that klipspringer are adapted for running on rocks, steenbok for fast zig-zag escape in short grass savanna, and bushbuck for crypsis in riverine thickets.

Thirdly, if ungulate species were picked at random and introduced to a different (and predator-free) environment to that in which they originated, it is indeed possible that differences among these species, and between introduced and indigenous species, would be sufficient for such species to coexist. Evidence is provided by the variety of ungulate species introduced to Australia, which are now feral and coexist in the Northern Territory (Hume, 1987). Such species include water buffalo (*Bubalus bubalis*), cattle, horses, donkeys, goats and pigs. Instead of competing with indigenous large herbivores, the introduced species have actually improved range conditions for the large grazing kangaroos (*Macropus* spp.) by transforming tall grass tussocks to short grassland (Hume, 1987).

Hence the role of competition in shaping large herbivore guilds is unclear. Sinclair (1985) proposes that among African ungulates, predation is as important as competition in this regard. Demment and van Soest (1985) propose that if competition is important in structuring herbivore guilds, then body size differences are the most likely result. This is because body size differences promote partitioning of shared food resources on the basis of nutritional quality. Bell (1971, 1984) asserts that the key factor in the feeding ecology of herbivores is the range in diet quality that is tolerated, and this range increases with body size. Jarman (1974) argued that body size differences are related to differences in both feeding style and social organisation among antelope. Considering the graded body size of African savanna browsers (Owen-Smith, 1985), and the influence that body size has on resource-use patterns within the guild (this study), I concur with Demment and van Soest (1985) that competition through evolutionary time is a feasible explanation for this graded size distribution. Differences among adaptations to predation and the physical environment (e.g. water dependence, heat tolerance, etc.) are undoubtedly important contributing factors promoting coexistence, particularly among similar-sized species.

6.9 Browsers and grazers compared

The feeding ecology of African savanna ungulates is currently understood mainly in terms of grazer-oriented research findings (for reasons outlined in the introduction). My study is the first to include a range of browsers that were studied together and by the same methods. Hence this provides an opportunity to consider the applicability to the browsing guild of principles established for the grazing guild. These include the following:

1). Diet quality varies as a function of fibre content, and dietary fibre content increases with body size (Geist, 1974). This, the Jarman-Bell principle, applies to browsers if it is adjusted to allow for (a) the fact that forage quality varies as a function of both secondary chemistry and fibre content (section 4.4.2.2), and (b) that dietary tolerance varies more closely with body size than does average diet quality *per se* (Bell, 1971, 1984; section 4.4.2.4).

2). Species move down the catenary sequence in the dry season (Bell, 1970; Jarman, 1972; Jarman and Sinclair, 1979). Although this does apply to browsers, particularly giraffe (Hall-Martin, 1974b; Pellew, 1984a; section 4.3.2.2), the very small

browsers such as steenbok and klipspringer do not exhibit this pattern. These species remain in their specific habitats on the upper catena throughout the seasonal cycle.

3). Smaller species depend on larger species to trample and remove coarse plant matter, so as to facilitate access to high quality plant parts (Vesey-Fitzgerald, 1960; Gwynne and Bell, 1968; Bell, 1970, 1971; McNaughton, 1976; Maddock, 1979). This principle, termed "grazing succession" does not apply to browsers, as the feeding actions of large species (elephant excluded) do not physically modify woody vegetation to the benefit of smaller species. Note that there is debate as to whether smaller grazing species follow larger grazing species because: (a) this improves their feeding efficiency (as is generally assumed); (b) they benefit by predator protection (Sinclair and Norton-Griffiths, 1982; Sinclair, 1985); or (c) they actually displace the larger species as the outcome of scramble competition that favours the smaller, narrower-muzzled species (Illius nd Gordon, 1987).

4). Gregariousness may increase foraging efficiency (McNaughton, 1984). This is by the modification of vegetation structure to increase food yield per

bite to the individual in a herd (*op. cit.*). This "grazing lawn" principle does indeed seem applicable to browsers, although not directly. Where browsing preasure is concentrated, food yield per bite (with the yield being digestible nutrients) is indeed improved, but not for reasons of altered plant structure. Rather, severe pruning results in altered leaf chemistry, with nutrient levels enhanced and condensed tannin levels depressed (section 5.1.4.1).

From the above comparisons I conclude that currently accepted principles in African ungulate feeding ecology are loosely applicable to browsers. The major exception is that of grazing succession, and others (specifically the Jarman-Bell principle and the grazing lawn hypothesis) would be more applicable to browsers if it was accepted that diet quality varies not only as a function of fibre, but of secondary chemistry as well.

6.10 The value of the guild approach, and the next step

Section 6.9 (above) demonstrates an advantage of adopting a guild approach to investigating consumer/resource relations. That is, if principles of feeding ecology are established for representatives of a particular taxonomic group (e.g. ungulates) within a particular guild, these principles may be tested on

representatives of the same group in another ("control") guild. The comparison might then show where modifications are required to increase the predictive value of such principles to the taxonomic group as a whole.

Another advantage of the guild approach is that because it is resource-defined, it is flexible in the taxonomic range over which consumer-resource and consumer-consumer relations may be studied. This flexibility is demonstrated by a long-term study on the desert granivore guild (Brown *et al.*, 1979; Brown *et al.*, 1986). The study was initially established to test for competition between rodents and ants, and was later expanded when results indicated that rodents compete not only with ants, but with birds as well.

I suggest that the above example is illuminating, in that the work embodied in this thesis could be developed upon by expanding the guild to include other groups of animals that depend upon dicotyledonous foliage for food. Insects are a priority in this regard, particularly in view of the fact that insect herbivory does not only remove part of the browse resource, but may alter the nutritional quality of that which remains (reviewed by Schultz, 1988).

A more immediate step by which the results of this

study may be built upon is to employ ecological modelling (see Starfield and Bleloch, 1986). A number of relationships have been identified among the feeding patterns of browsers, and these lend themselves to incorporation into predictive models. Some examples include: the relationships between rainfall and diet composition, with the identification of thresholds below which such relationships come into effect; the influence of phenology (flowering, fruiting, leaf flush etc.) among certain plant species on diet composition; the relationship between rainfall and movement across the catenary sequence; the relationship between feeding preference and leaf condensed tannin content; the relationship between browsing pressure and shoot production and nutritional quality; the relationships between body size and dietary tolerance, as well as diversity of habitat use; the relationship between body size and home range area; etc.

I suggest that a particularly useful management application of the results of my study would be the inclusion of the above relationships in an expert system for the Transvaal lowveld, for assessing the suitability of private holdings for stocking with indigenous browsing ruminants.

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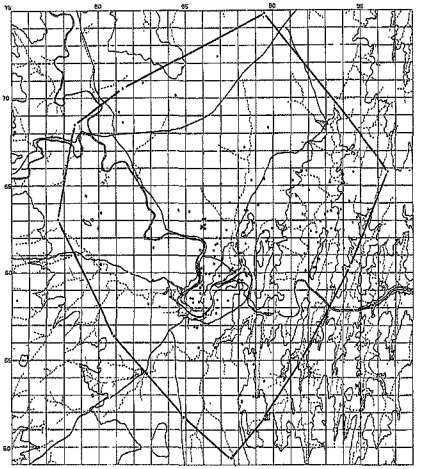
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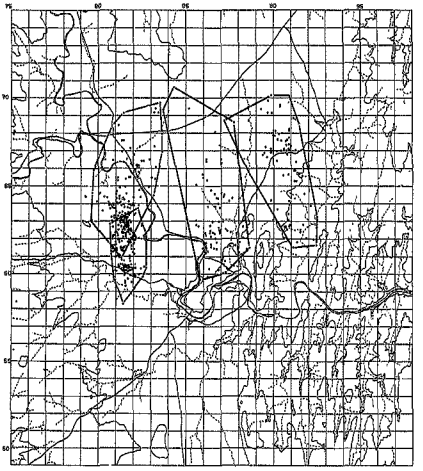
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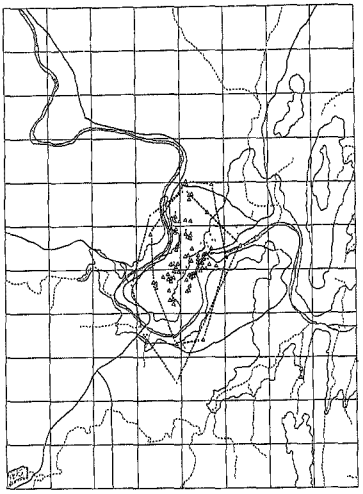
APPENDICES



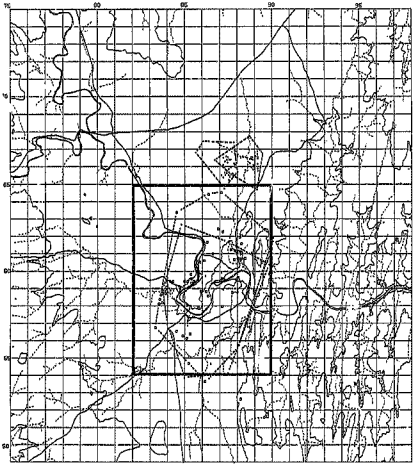
Appendix A1. Giraffe (G920) home range and location points. Scale: 1 grid square = 1 km².



Appendix A2. Kudu home ranges and location points. Top overlay: K905 (west), K925 (east); bottom overlay: K910 (north), K900 (south). Scale: 1 grid square ≙ 1 km².



Appendix A3. Steenbok and impala home ranges and location points.
Top overlay: steenbok; S902 (west), S907 (east).
Middle overlay: impala; I912 (squares), I91 (circles).
Bottom overlay: impala; I913 (circles), *I909 (triangles)*.
Scale: 1 grid square = 1 km^2.



Portion of study area enlarged in map that follows.

Plant species	Plant part[1]	Monthly percentage feeding time allocation												Year average	Sample size[2]
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Acacia nigrescens	Fol	51.44	46.15	31.10	5.10	10.30	15.90	20.60	11.30	35.82	25.57	54.53	45.67	31.14	302542
Acacia tortilis	Fol	14.22	16.85	43.35	55.84	7.13	11.40	19.50	11.20	9.31	4.71	2.72	1.56	16.14	81711
Dichrostachys cinerea	Fol	8.66	5.45	3.20	12.55	0.31	6.30	0	0.36	0.09	0.12	0.34	12.22	4.05	24870
Acacia xanthophloea	Fol	2.25	6.15	7.19	0	0	15.00	0	14.61	1.01	0.62	0.15	1.70	3.88	20630
Leucheosperma capasse	Fol	2.67	3.22	0.10	0	0	0.94	0	0	0.66	0.22	14.10	1.25	1.91	15006
Combretum hereroense	Fol	3.25	0.23	4.35	1.00	4.87	0.95	6.15	0.44	2.53	5.18	2.12	1.18	2.69	19479
Dichrostachys cinerea	Frt	0	0	0	23.37	0	5.45	8.37	0	1.01	0	0	0	2.88	10880
Acacia gerrardii	Fol	0.28	0.52	0	0.20	5.40	0.98	10.17	1.96	9.02	0.10	1.04	0	2.56	17294
Ziziphus mucronata	Fol	9.79	0	0	0.54	4.79	1.84	0	0.31	0.62	0.62	6.41	14.43	3.44	14012
Maytenus senegalensis	Fol	0.43	0	0	0	0	1.26	0.04	0.48	0.90	1.38	1.33	3.40	1.16	14524
Euclea divinorum	Fol	0	0	0	1.27	0.67	1.32	0	10.91	2.28	0.62	0.21	4.43	1.81	11852
Acacia nigrescens	Flr	0	0	0	0	0	0	0	0.96	16.53	0.25	0	0	1.55	15175
Acacia robusta	Fol	0.21	0	0	0.82	0.24	0.13	0	10.72	0.51	0	0	0	1.56	10966
Acacia tortilis	Frt	0	0	0	2.98	0	15.54	0	0	0	0	0	0	1.54	9295
Acacia gerrardii	Flr	0	0	0.02	0	0.24	0.48	0	0	0	0	0	0	1.33	5262
Sesamothamnus lugardii	Fol	0.39	0.35	0.98	1.00	0	0.84	0.91	0	0.20	0	0.86	5.91	1.22	8941
Combretum imberbe	Fol	2.43	4.67	0.38	0.14	1.97	0.68	0	2.24	0.30	0.72	0.12	0.35	1.18	6686
Spirostachys africana	Fol	0	0	1.62	0	0	0	0	0.76	0.66	0	0	4.11	0.87	5495
Grewioxa	-	0	1.42	0.26	1.93	0	0.23	0	1.73	1.06	0	0.15	0.21	0.80	3987
Capparis tomentosa	Fol	0	0	0	0	0	0.20	0	3.64	1.03	0.08	0	0.94	0.71	4969
Acacia tortilis	Flr	2.90	0	0.35	0	0	0	0	0	0	0	0	0	0.59	3674
Combretum hereroense	Flr	0	0	0	0	0	0	0	0.54	3.52	0	0	0	0.51	3662
Rhus gueinzii	Fol	0.65	0	0.09	0	0.53	2.17	0	0.96	1.61	0.82	0	0	0.51	2890
Pelthophorum africanum	Fol	0.83	0	0	0.34	0	0	0	0	2.43	0.12	1.18	0.63	0.48	4748
Acacia welwitschii	Fol	0	0	0	3.86	0	0.59	0	0	0	0	0	0	0.37	1284
Acacia exuvialis	Fol	0.45	0	0.11	1.96	0.36	0.10	0	0	0	0	0.21	0.15	0.21	1286
Combretum zeyheri	Fol	0	0	0	3.43	0	0	0	0	0	0	0	0	0.29	997
Acacia gerrardii	Flr	0.35	0	0	0	0	0	0	0	0	0	0	0	0.28	1005
Lannea stuhlmannii	Fol	1.54	1.54	0.24	0	0	0	0	0	0	0	0	0	0.25	1164
Combretum apiculatum	Fol	0	0	0	0.24	1.65	0	0	0	0.64	0.42	0.24	0.16	0.24	1422
Ochthocrys schinzyllon	Fol	0.56	0	0	0	0	0	0	0	0.93	0	1.66	0.49	0.23	1607
Acacia grandicornuta	Fol	0	0	1.10	0.66	0	0	0	1.56	0	0	0	0	0.23	1393
Acacia nilotica	Fol	0	0	0	0.35	0.15	0.26	0	0	0	0	0.15	0.15	0.22	1270
Ochthocrys schinzyllon	Frt	2.17	0	0	0	0	0	0	0	0	0	0	0	0.18	867
Maytenus heterophylla	Fol	0	0	0	0	0.61	0	0	0	0.26	0	1.26	0	0.17	1002
Combretum mossambicense	Fol	0	0	0.16	0	1.19	0	0	0	0	0	0	0.12	0.13	665
Euclea divinorum	Frt	0	0	0.16	0	0	1.65	0	0	0	0	0	0	0.16	537
Garcinia volkensii	Fol	0.66	0	0.22	0	0	0	0	0	0	0	0.66	0	0.15	974
Tephrosia serices	Fol	0.72	0	0	0.79	0	0	0	0	0	0	0	0.13	0.14	981
Galiniches saxatilis	Fol	0	0	0.03	0.52	0	0	0	0	0.49	0	0	0	0.12	833
Diospyros amplifolia	Fol	0	0	0	0	0	0	0	0	0.49	0.92	0	0	0.09	1157
Strychnos spinosa	Fol	0	0	0	0	0	0	0	0.22	0.73	0	0	0	0.08	598
Maytenus senegalensis	Flr	0	0	0	0	0	0	0	0.65	0	0	0	0	0.07	465
Albizia petersiana	Fol	0	0	0	0.88	0	0	0	0	0	0	0	0.06	0.07	248
Unidentified	Fol	0	0.17	0	0.19	0	0	0.06	0.21	0	0	0	0.09	0.07	335
Cassine transvaalensis	Fol	0	0	0.52	0	0	0	0	0.22	0	0	0	0	0.06	365
Combretum paniculatum	Fol	0	0	0	0	0	0	0	0.20	0.38	0	0	0	0.06	496
Combretum paniculatum	Flr	0	0	0	0	0	0	0	0.61	0.05	0	0	0	0.06	325

Continued overleaf

Appendix B1 Continued.

Plant species	Plant part[1]	Monthly percentage feeding time allocations												Year average	Sample size[2]
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Phyllanthus reticulatus	Fol	0	0	0	0	0	0	0	0.31	0.55	0	0	0	0.05	491
Sclerocarya birrea	Fol	0	0.14	0	0	0.31	0	0	0	0	0	0	0	0.04	138
Acacia nigrescens	Fol	0	0	0	0	0	0	0.19	0.29	0	0	0	0	0.03	227
Peltophorum africanum	Fol	0.22	0	0	0	0	0	0	0	0	0	0	0	0.03	151
Securinega virosa	Fol	0	0	0	0	0	0	0	0	0	0	0	0.24	0.02	177
Albizia harveyi	Fol	0	0	0	0.55	0.55	0	0	0	0	0.01	0.15	0	0.02	198
Manilkara mochisia	Fol	0	0	0	0	0.24	0	0	0	0	0	0	0	0.02	74
Grewia flavescens	Fol	0	0	0	0.08	0	0	0	0	0	0.01	0	0	0.01	42
Schotia brachypetala	Flr	0	0	0	0	0	0	0	0	0	0.08	0	0	0.01	26
Ehretia amoena	Fol	0	0	0	0	0	0	0	0	0	0	0.08	0	0.01	64
Maytenus heterophylla	Flr	0	0	0	0	0	0.11	0	0	0	0	0	0	0.01	35
Ximenia caffra	Fol	0	0.04	0	0	0	0	0	0	0.04	0	0	0	0.01	38
Dalbergia transvaalica	Fol	0	0	0	0	0	0	0	0	0	0.08	0	0	0.01	101
Grewia bicolor	Fol	0	0.08	0	0	0.06	0	0	0	0	0	0	0	0.01	42
Grewia monticola	Fol	0	0	0.13	0	0	0	0	0.03	0	0	0	0	0.01	74
Grewia microthyrsa	Fol	0	0	0	0	0.06	0	0	0	0	0	0	0	0.01	19
Kigelia africana	Fol	0	0	0	0	0	0	0	0.13	0	0	0	0	0.01	74
Diospyros mespiliformis	Flr	0	0	0	0	0	0	0	0	0	0.05	0	0	0	11
Schotia brachypetala	Fol	0	0	0	0	0	0	0	0	0	0.03	0	0	0	38
Maytenus senegalensis	Frt	0	0	0	0	0	0	0	0	0	0.02	0	0	0	21
Ximenia caffra	Frt	0	0	0	0	0	0	0	0	0	0	0.05	0	0	55
Unidentified	Frt	0	0	0	0	0	0	0	0	0.02	0	0	0	0	11
Kigelia africana	Flr	0	0	0	0	0	0	0	0	0.02	0	0	0	0	11
Croton megalobotrys	Fol	0	0	0	0	0	0	0	0.03	0	0	0	0	0	38
Maerua parvifolia	Fol	0	0	0	0	0	0	0.06	0	0	0	0	0	0	34
Acacia burkea	Fol	0	0	0	0	0	0	0	0.04	0	0	0	0	0	24
Herbs	-	0	0	0	0	0	0	0	0	0.01	0	0	0	0	9
Sample size[2]		41571	26513	46535	31998	31565	35155	63715	35813	28019	133468	65225	46865	53468	640182

[1] Fol, foliage; Frt, fruit; Flr, flower.
[2] Sample size in seconds, indicating total feeding time recorded in each case.

Plant species	Plant part[1]	Monthly percentage dietary time allocation												Year average	Sample size[2]
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Forbs	-	37.72	22.13	37.36	45.82	48.15	29.19	16.49	23.32	10.44	29.53	18.34	45.51	29.80	119154
Acacia digressens	Fol	6.95	10.20	10.12	15.21	8.78	15.71	24.84	15.11	37.88	33.15	13.65	3.43	19.23	76957
Securinega virosa	Fol	18.16	26.19	6.28	5.52	7.62	3.24	0.92	3.54	0.21	5.89	6.47	16.51	8.57	33349
Dichrostachys cinerea	Fol	6.30	4.41	2.55	2.37	6.88	8.45	8.36	6.29	3.40	2.15	6.98	4.14	5.24	23155
Grewgark	-	5.96	4.35	20.14	4.92	3.44	0.36	0.81	2.61	0.61	0.25	3.20	7.48	4.63	18574
Lonchocarpus capassa	Fol	2.25	0.81	4.62	0	0.02	0.95	0	0.22	0.68	15.64	12.60	4.74	3.39	21481
Combretum hereroense	Fol	0.54	0.22	0.26	2.61	1.93	0	1.33	1.33	5.59	4.93	1.20	0.79	2.14	18922
Acacia gerrardii	Fol	3.63	0.52	0	1.04	0.23	2.96	8.49	5.16	0.86	0.03	0.65	0	2.62	12617
Combretum imberbe	Fol	1.28	2.39	0.84	1.74	2.14	1.06	2.97	0.21	5.01	0.53	0.15	0.67	1.42	11817
Grewia scpurpus trichocarpus	Fol	0.53	2.73	0.93	0	0.47	13.36	3.20	0.20	1.01	0.17	0.55	0.09	2.08	6499
Grass	-	0.27	0.03	0	2.29	0.22	0	0	0	0	0.45	5.51	1.14	1.26	6409
Grewia flavescens	Fol	0.72	0.04	0	1.24	1.44	16.46	1.06	0.01	1.83	0.20	0.20	0.74	1.68	6282
Ehretia amoena	Fol	0.74	1.19	1.15	2.56	1.51	1.61	0.79	1.90	0.66	0.58	0.54	0.31	1.15	6077
Sclerocarya birrea	Frt	1.49	7.83	3.56	0	0	0	0	0	0	0	0	0	1.55	3336
Dalbergia melanoxylon	Fol	1.37	3.19	0.72	0	0.19	0	0.14	0.35	0	0.61	0.49	2.31	0.77	6256
Acacia tortilis	Fol	0.24	0	1.52	4.36	0.73	2.25	0.45	1.15	4.79	1.33	0	0.51	1.11	6756
Dichrostachys cinerea	Fol	0	0	0	0	0.49	10.56	0.27	0	0	0	0	0	1.10	3637
Albizia harveyi	Fol	0.30	1.10	2.10	0	0	0	0.21	0.15	0.14	3.46	1.39	0.98	0.81	4761
Gardenia volkensii	Fol	0.51	2.96	1.17	0	0	0.87	0.83	0.68	0.36	0	0	0.56	0.72	2292
Euclea divinorum	Fol	0	0	0	0	0	0.14	0.13	2.84	2.88	0.29	0.31	0.07	0.61	2975
Capparis tomentosa	Fol	0	0	0	0.39	0	0	3.67	2.25	0	0.08	0	0	0.61	3264
Lannea stuhlmannii	Fol	1.15	0.15	0.39	0.28	2.26	0.67	0.51	0.57	0	0.16	0.12	0.63	0.56	2215
Ziziphus mucronata	Fol	0.27	0.22	0.26	0	0.06	0	0	0.92	1.46	2.18	0	0.51	0.53	3469
Maytenus heterophylla	Fol	0	0.18	0	1.68	0.48	1.15	1.96	0.11	0.22	0.03	0.22	0.18	0.39	1679
Cassia abbreviata	Fol	0	0.64	0.68	0.72	2.18	1.15	0	0.04	0.17	0.11	0.17	0	0.43	1918
Solanum pseudoquinum	Fol	0	0	0	0	0.44	0	0	0.04	0.88	0.01	0.61	0.05	0.42	2571
Diospyros mespiliformis	Fol	0	0	0	0	0	0.19	0	0.71	0.23	1.18	0	0.92	0.36	2956
Acacia xanthophloea	Fol	0	0	0	3.86	0	0	0	0	0	0.12	0	0	0.33	732
Ximenia caffra	Fol	0.14	0	0	0	0	1.11	0.13	1.44	0.41	0.49	0	0.06	0.32	1733
Acacia nigrescens	Flr	0	0	0	0	0	0	0	0.23	3.44	0.04	0	0	0.31	1972
Securinega virosa	Frt	0	0	0	0	0	0	0	0	0	0	0	5.53	0.26	1372
Combretum apiculatum	Fol	0.20	0.80	0.05	0	0.72	0	0	0.24	0	0.44	0	1.02	0.29	1332
Combretum mossambicense	Fol	0	0	0	0	0.12	0.17	0.01	0.05	0	0	0	0.19	0.27	1924
Sclerocarya birrea	Fol	0.24	0.92	5.18	0	0.20	0.18	0.19	1.09	0.44	0.38	0.08	0.27	0.97	1481
Ximenia caffra	Frt	0	0	0	0	0	0	0	0	0	0	2.84	0.20	0.26	1442
Rhus gueinzii	Fol	0	0	0	0.23	0	0	0.15	1.95	0.32	0.49	0	0.35	0.25	1728
Albizia petersiana	Fol	0	1.68	0	0	0	0	0	0	0	1.81	0	0.11	0.24	1215
Peltophorum africanum	Fol	0	0	0	0	0.06	0.11	0	0.04	0.71	1.52	0.81	0	0.21	1586
Maytenus senegalensis	Fol	0	0	0	0	0	0	0	0.18	0.61	1.13	0	0	0.21	1781
Grewia flavescens	Flr	0	0	0	0	0	0	0	0	0	2.17	0	0	0.20	1276
Acacia albidus	Fol	0	0	0	0	0	0	0	0.22	0.38	1.38	0	0	0.17	1366
Acacia permixta	Fol	0	0	0	0	0	0	0	0	1.88	0	0	0	0.16	953
Acacia nilotica	Fol	0	0.15	0.08	0	0	0	0.09	0.02	0.24	0.08	0	0	0.15	954
Strychnos spinosa	Fol	0	0	0	0	0	0	0.43	1.18	0	0	0	0	0.13	837
Unidentified	Fol	0	0	0.36	0.39	0.65	0.88	0.09	0.53	0.02	0	0	0.04	0.13	559
Ziziphus africana	Flr	0	0	0	0	0	0	0	1.26	0	0	0	0	0.12	665
Cassia petersiana	Fol	0	0	0	0	0	1.31	0	0	0	0	0	0	0.11	591
Euclea divinorum	Flr	0	0	0	0	0	0	0	0	0.16	0	0	0.55	0.09	537

Continued overleaf

Appendix B2 continued.

Plant species	Plant part[1]	Monthly percentage feeding time allocation												Year average	Sample size[2]
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Hyptenes senegalensis	Flr	0	0	0	0	0	0	0	1.06	0	0	0	0	0.09	527
Pterocarpus rotundifolius	Sol	0.66	9.34	0.23	0	0	0	0	0	0.28	0	0.01	0.09	0.89	471
Acacia sieberiana	Fol	0	0	0	0	0	0	0	0	0	0	0	1.12	0.09	563
Almeida americana	Frt	0	0	0	0	0	0	0	0	0	0	1.01	0	0.09	473
Acacia robusta	Fol	0	0	0	0	0.13	0	0	5.65	0	0	0.76	0	0.96	535
Spirostachys africana	Fol	0	0.41	0	0	0	0	0	0.56	0	0	0	0	0.08	413
Grewia monticola	Fol	0	0	0	0	0	0.18	0	0.41	0.14	0	0.28	0	0.08	483
Ficus cordifolia	Frt	0	0	0	0.76	0.04	0	0	0	0	0.01	0.18	0	0.08	885
Schotia brachypetalla	Fol	0	0	0	0	0	0	0	0.36	0	0.48	0	0	0.07	567
Acacia grandicornuta	Fol	0	0	0	0	0	0.37	0	0.57	0	0	0	0.06	0.06	394
Acacia gerrardii	Frt	0	0	0	0	0.02	0	0	0	0	0	0	0	0.05	153
Acacia tortilis	Frt	0	0	0	0	0	0	0.46	0	0	0	0	0	0.04	164
Dombeya rotundifolia	Fol	0	0.15	0	0	0	0	0	0	0.01	0.34	0	0	0.04	287
Solanum quadrangulare	Frt	0	0.11	0.07	0	0	0	0	0	0	0	0	0.29	0.04	183
Acacia burkeae	Fol	0	0	0	0	0	0	0	0	0.43	0	0	0	0.04	515
Hyptenes heterophylla	Flr	0	0	0	0	0	0.01	0	0	0	0	0	0	0.03	69
Phyllanthus reticulatus	Fol	0	0	0	0	0	0	0	0.26	0	0	0.09	0	0.03	193
Hyptenes senegalensis	Frt	0	0	0	0	0	0	0	0	0	0.22	0	0	0.02	167
Balsanthes speciosus	Fol	0	0	0	0	0.15	0	0	0	0	0.11	0	0	0.02	119
Cinnafzegeria fiddebrauttii	Fol	0	0	0	0	0	0	0	0.16	0	0.08	0	0	0.02	152
Solanum panduraeforme	Flr	0	0	0.25	0	0	0	0	0	0	0	0	0	0.02	67
Grewia microthyrsa	Fol	0	0	0	0	0	0	0	0.13	0.18	0.04	0	0	0.03	155
Boscniakzeneia ambensis	Fol	0	0	0	0	0	0	0.25	0	0	0	0	0	0.02	60
Vigelia africana	Fol	0	0	0	0	0	0	0	0.24	0	0	0	0	0.02	139
Grewia bicolor	Frt	0	0	0	0	0	0	0	0.04	0.10	0	0	0	0.02	122
Terminalia sericea	Frt	0	0	0	0	0	0	0	0	0	0	0	0.10	0.02	60
Dichrostachys cinerea	Flr	0	0	0	0	0	0	0	0	0	0	0.12	0	0.01	55
Calpicila transvaalica	Fol	0	0	0	0	0	0	0	0	0	0.07	0	0	0.01	55
Combretum mossambicense	Flr	0	0	0	0	0	0	0	0	0.06	0	0	0	0.01	29
Grewia bensella	Fol	0	0	0	0	0	0	0	0.08	0	0	0	0	0.01	32
Berelebus mannopeloides	Flr	0	0	0	0	0.	0	0	0	0	0	0	0.12	0.01	57
Cordia sinensis	Fol	0	0	0	0	0	0	0	0.11	0	0	0	0	0.01	16
Combretum paniculatum	Fol	0	0	0	0	0	0	0	0.08	0	0	0	0	0.01	49
Unidentified	Frt	0	0	0	0	0	0	0	0	0.06	0	0	0	0.01	43
Croton megalobotrys	Fol	0	0	0	0	0	0	0.08	0	0	0	0	0	0.01	26
Protasparagus myastriatulus	Fol	0	0	0	0	0	0	0	0	0.12	0	0	0	0.01	60
Xeromphis obovata	Fol	0	0	0	0	0	0	0	0	0	0	0	0.06	0.01	29
Grewiacarpon trichocarpon	Flr	0	0.03	0	0	0	0	-	0	0	0	0	0	0	6
Acacia welwitschii	Fol	0	0	0	0	0.03	0	0	0	0	0	0	0	0	1
Oxosyphon herbaceus	Sol	0	0	0	0	0	0	0	0.02	0	0	0	0	0	10
Vigelia africana	Frt	0	0	0	0	0	0	0	0	0	0.01	0	0	0	16
Sample size[2]		36623	21337	22691	16310	24693	23241	35627	58157	49658	24616	43721	49419	37252	447904

[1] Fol, foliage; Frt, fruit; Flr, flower.
[2] Sample size in seconds, indicating total feeding time recorded in each case.

Plant species	Plant part[1]	Monthly percentage feeding time allocation												Year average	Sample size[2]
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Grass	-	90.28	79.67	87.56	87.31	86.53	93.86	48.67	38.26	41.58	63.00	82.41	88.72	69.22	232100
Forbs	-	8.39	5.84	5.96	6.53	1.37	41.06	19.42	32.12	21.39	9.97	2.82	3.42	12.96	42917
Acacia tortilis	Fol	4.43	4.71	2.21	4.19	7.34	3.29	17.53	16.66	4.06	16.75	2.33	4.56	7.76	25315
Acacia nilotica	Fol	2.91	3.12	0	0.30	0.81	2.06	5.65	6.05	2.58	5.47	9.53	6.12	3.42	11784
Dichrostachys cinerea	Fol	0.45	2.06	0	1.14	1.11	0.59	3.99	1.59	0.22	0.19	1.26	1.06	1.02	6315
Securinega virosa	Fol	0.51	0.14	0	0.49	0	1.75	1.29	0	2.99	1.39	0.19	0.25	0.73	2282
Ziziphus mucronata	Fol	0.84	0.39	1.61	0	0.25	0.46	0.35	0.86	1.11	0.31	1.39	0.25	0.58	1864
Maytenus senegalensis	Fol	0.19	0	1.07	0	0	0	0.90	1.06	0.29	1.97	0.86	0.19	0.53	1466
Acacia senegal	Fol	0	0	0.19	0	0	1.35	1.55	0	0	0	0.06	1.16	0.31	1005
Grewia monticola	Fol	0	0	0	0	0	0.18	1.02	0.64	0	0	0.11	0	0.19	1559
Grewia flavescens	Fol	0	0	0	0	0.11	0	0.09	0	0.12	0	0.39	0.31	0.10	1368
Acacia hertzii	Frt	0	0	0	0	0	0.54	0.55	0.35	0	0	0	0	0.21	146
Boscia senrifolia	Fol	0.11	0.10	0	0	0	0	0.26	0.30	0.24	0.26	0	0	0.13	961
Lonchocarpus capassa	Fol	0	0	1.29	0	0	0	0	0	0	1.17	0.33	0	0.33	424
Capparis tomentosa	Fol	0	0	0	0	0	0.41	1.52	0	0	0	0	0	0.16	545
Combretum zeberba	Fol	0	0	0	0	0.64	0	0	0	0.12	0	0	0.45	0.10	244
Combretum hereroense	Fol	0	0	0	0	0	0	0.28	0	0.20	0.48	0.06	0	0.09	249
Commiphora schimperi	Fol	0.27	0	0	0	0	0	0	0	0	0	0.11	0.51	0.06	396
Acacia robusta	Fol	0	0	0	0	0	0	0	0	0.05	0	0	0	0.01	267
Rhus quartzeri	Fol	0	0	0	0	0	0	0.17	0	0.61	0	0	0	0.07	237
Dichrostachys cinerea	Frt	0	0	0	0	0	0.57	0	0	0	0	0	0	0.06	153
Ehretia amoena	Fol	0	0	0	0	0	0	0.24	0	0.12	0	0.14	0.34	0.05	215
Pretoriagrewia magnistipulata	Fol	0	0	0	0	0	0	0	0	0.05	0	0	0	0.01	176
Gardenia volkensii	B	0	0	0	0	0	0	0.23	0.03	0	0	0	0.26	0.04	165
Dalbergia melanoxylon	[illegible]	0.06	0	0	0	0	0	0.01	0	0	0	0	0	0.01	161
Solanum panderanifolium		.	0	0	0	0	0	0	0.10	0.05	0	0	0	0.03	105
Acacia nilotica		0	0	0	0	0	0	0	0.01	0	0	0	0	0.00	93
Unidentified		.	.	0	0	0	0.00	0.03	0.11	0	0	0.01	0	0.01	87
Creepers			0	0.13	0.11	0	0.09	0	0	0	0	0	0	0.03	63
Ximenia caffra			0	0	0	0	0	0	0	0	0.19	0	0	0.02	36
Solanecio angulatus	Fol	0	0	0	0	0	0	0.23	0	0	0	0	0	0.02	46
Grewia bicolor	Fol	0	0	0	0	0	0	0.24	0	0	0	0	0	0.02	59
Dracocryne triebocarpus	Fol	0	0	0	0	0	0.22	0	0	0	0	0	0	0.02	59
Acacia greadfocarpa	Fol	0	0	0	0	0	0	0	0.15	0	0	0	0	0.02	75
Boscia dirinoria	Fol	0	0	0	0	0	0	0	0	0.06	0	0	0	0.01	20
Maytenus heterophylla	Fol	0	0	0	0	0	0	0	0	0.09	0	0	0.04	0.01	41
Combretum nossambicense	Fol	0	0	0	0	0	0	0.16	0	0.05	0	0	0	0.01	44
Spirostachys africana	Fol	0	0	0	0	0	0	0.06	0	0	0	0	0	0.01	16
Acacia nilotica	Fol	0	0	0	0.12	0	0	0	0	0	0	0	0	0.01	33
Grewia microthyrsa	Fol	0	0.17	0	0	0	0	0	0	0	0	0	0	0.01	56
Acacia xanthophloea	Fol	0	0	0	0	0	0	0	0	0.06	0	0	0	0	16
Solanum panderanifolium	Frt	0	0	0	0	0	0.04	0	0	0	0	0	0	0	12
Cissus corniflora	Fol	0	0	0	0	0	0	0	0	0	0	0.05	0	0	39
Sample size[2]		25919	20956	8849	27934	8459	26782	28581	29467	30928	19803	37589	33617	29569	300034

[1] Fol, foliage; Frt, fruit; Flr, flower.
[2] Sample size in seconds, indicating total feeding time recorded in each case.

Plant species	Plant part[1]	Monthly percentage feeding time allocation												Year average	Sample size[2]
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Forbs	-	65.35	68.24	64.64	78.91	72.06	48.79	28.16	10.95	10.59	19.68	55.66	62.49	57.36	97143
Securinega virosa	Fol	4.82	11.98	12.43	15.62	13.93	48.61	32.15	3.22	0.29	0	3.76	4.75	12.48	24423
Acacia tortilis	Fol	4.59	5.41	0	2.24	1.65	2.43	0.89	10.61	28.83	44.13	4.03	0.12	9.37	23560
Acacia nigrescens	Fol	0.85	1.30	0	1.21	5.29	6.17	5.87	14.98	19.13	30.25	24.62	1.15	8.19	18605
Acacia tortilis	Fru	0	0	0	0	0	0	1.16	18.21	6.12	0	0	0	2.17	4194
Ziziphus mucronata	Fol	0.65	1.16	0	1.39	5.91	1.23	0	0.79	0.63	0.66	0.32	0	1.04	3214
Acacia permadii	Fol	0	0	0	0	0	0	0	11.72	0	0	0	0	0.98	1330
Creepers	-	1.46	1.48	0	0	0	1.76	0	4.84	1.31	0.64	0.28	0.41	0.96	1850
Maerua parvifolia	Fol	0.65	0	0	0	0	0.35	1.73	5.76	1.73	2.31	0.66	0	0.91	1965
Grewia pyrifolia	Fol	0	0.33	0	0.66	0.52	2.78	6.26	0.19	0.45	0	0	0	0.87	1873
Dichrostachys cinerea	Fol	0.46	1.13	0	1.19	0.26	0.52	0.71	0	0.17	0	0.69	0.46	0.77	1599
Pentarrhaphia senegalensis	Fol	0	0	0	0	0	0	0	0	0	0	5.58	0.03	0.71	582
Dic[illegible]ra angolitoris	Fol	0	0	0	0	0	0	0	2.44	0	1.06	0	0	0.25	571
C[illegible]a senegalensis	Fol	0	0	0	0	0	0	1.07	0	0	1.99	0	0	0.26	732
Commiphora africana	Fol	0	0	2.93	0	0	0	0	0	0	0.64	0	0	0.25	76
Grewia atroviryea	Fol	0	0	0	0	0	0	0	0	0	2.43	0	0.23	0	0.22	351
Peltophorum africanum	Fol	0	0	0	0	0	0	0	1.64	0	0.65	0.29	0	0	0.21	444
Commiphora schimperi	Fol	0	0.51	0	0	0	0	0	0	0	0	0	0.04	0	0.15	444
Ximenia americana	Fol	0	0	0	0	0	0	0.61	0.83	0	0	0	0.01	0	0.20	359
Grass	-	1.13	0.91	0	0.48	0	0	0	0	0	0	0.04	0.56	0.12	0.20	401
Cecina divitorum	Fol	0	0	0	0	0	0	1.83	0.44	0	0	0	0	0	0.14	598
Boscia albitrunca	Fol	0	0	0	0	0	0	1.14	0	0	0	0.08	0	0	0.10	210
Acacia gravellarensis	Fol	0	0.19	0	0	0	0	0.81	0	0	0	0	0	0	0.08	192
Solanum pseudoreforme	Fol	0.24	0.57	0	0	0	0	0	0.06	0	0	0	0	0	0.08	515
Unidentified	Fol	0	0	0	0	0	0	0.40	0.45	0	0.08	0	0	0	0.08	172
Acacia senegal	Fol	0	0	0	0	0	0	0	0.14	0	0	0	0.06	0.38	0.06	75
Securinega virosa	Fru	0	0	0	0	0	0.48	0	0	0	0	0	0	0	0.04	15
Gethyllis melanosyphon	Fol	0.09	0	0	0	0	0	0.08	0	0	0	0	0.04	0	0.04	89
Grewia flavescens	Fol	0	0	0	0	0	0	0.07	0	0	0	0	0	0	0.03	83
Solanum pseudoreforme	Fol	0	0	0	0	0	0.24	0	0.10	0	0	0	0	0	0.03	92
Cleofungosia hildebrandtii	Fol	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0.03	66
Combretum imberbe	Fol	0	0.16	0	0	0	0	0	0	0	0	0	0	0	0.01	24
Rhus pentzii	Fol	0	0	0	0	0	0	0.07	0	0	0	0	0	0	0.01	15
Lannea stuhlmannii	Fol	0	0	0	0	0	0	0	0	0	0	0.04	0	0	0	12
Sample size[2]		19050	25211	2012	14532	3193	21125	17766	11347	13395	21616	15474	12778	15377	184630

[1] Fol, foliage; Fru, fruit; Flr, flower.
[2] Sample size in seconds, indicating total feeding time recorded in each case.

Appendix C. Mean duration of feeding events (in seconds).

Plant*	Giraffe			Kudu			Impala			Steenbok		
	Mean	S.E.	n	Mean	S.E.	n	Mean	S.E.	n	Mean	S.E.	n
Acacia borlase	24	-	1	71.7	51.8	3	-	-	-	-	-	-
Acacia ecuvialis	68	16.4	30	111	15.5	5	34.7	6.67	52	12.7	2.52	6
Acacia gerrardii	514.1	5.3	2554	59.7	4.4	233				148	53.3	9
Acacia grandicornuta	126	26.5	11	64	31.3	6	37.5	15.65	2	95	48	2
Acacia nigrescens	114	2.79	2768	64.6	2.07	1413	42.1	2.63	280	66.7	3.31	317
Acacia nilotica	96.1	54.5	13	66	15.5	25	33	-	1	-	-	-
Acacia robusta	51.4	7.02	126	54.7	6.84	15	63.4	22.47	5	-	-	-
Acacia tortilis	121	6.99	766	92.4	6.55	113	39.8	1.58	910	71.1	4.17	376
Acacia welwitschii	91.7	22.6	14	?	-	1	95	-	1	-	-	-
Acacia xanthophloea	112	9.9	183	95.9	11.3	11	18	-	1	-	-	-
Albizia harveyi	27.6	3.9	9	46.5	4.66	101	-	-	-	-	-	-
Albizia petersiana	61.2	13	4	71.5	14.6	17	-	-	-	-	-	-
Balanites aaupmmii	87.2	48.8	6	-	-	-	-	-	-	-	-	-
Boliasanthus speciosus	-	-	-	29.7	10.1	4	32	9.0	2	-	-	-
Capparis tomentosa	142	22.6	35	78.9	12	43	60.6	9.91	9	-	-	-
Cassia abbreviata	-	-	-	48.8	8.67	27	-	-	-	-	-	-
Cassia petersiana	-	-	-	36.4	7.47	6	-	-	-	-	-	-
Cassiea transvalensis	61	25.7	6	-	-	-	-	-	-	-	-	-
Chanfuepsis hildebrandtii	-	-	-	26.3	4.15	6	-	-	-	-	-	-
Cissus cornifolia	-	-	-	37.8	18.2	5	20.0	-	1	-	-	-
Combretum apiculatum	49	8.29	29	36.6	4.64	38	-	-	-	-	-	-
Combretum hereroense	92.8	7.78	252	67.7	4.47	241	35.8	6.25	7	-	-	-
Combretum imberbe	75.1	6.14	81	66.8	9.54	177	34.9	9.43	7	24.0	-	1
Combretum mossambicense	83.1	30.6	8	64.1	8.35	25	22	6	2	-	-	-
Combretum sesicalatum	58.1	17.3	15	24.3	4.5	3	-	-	-	-	-	-
Combretum zeyheri	79.2	31.3	12	-	-	-	-	-	-	-	-	-
Commiphora africana	-	-	-	-	-	-	-	-	-	35	24	2
Commiphora schlegerii	-	-	-	-	-	-	70	25.7	4	63.4	24	7
Cordia sinensis	-	-	-	76	-	1	-	-	-	-	-	-
Croton megalobotrys	26	-	1	30	-	1	-	-	-	-	-	-
Dalbergia melanoxylon	177	62.3	14	76.6	13.6	55	50.5	31.5	2	20	6.99	4
Dichrostachys cinerea	64.1	4.92	35	67.2	2.69	439	36	3.15	154	30	4.44	40
Diospyros mespiliformis	75.5	19.7	16	68.8	10.6	43	-	-	-	63.4	11.9	9
Dombeya rotundifolia	-	-	-	65.8	4.95	15	-	-	-	-	-	-
Ehretia amoena	27	5	2	43.1	3.54	141	26.9	5.71	8	25.2	5.78	12
Euclea divinorum	117	12.8	107	64.7	10.8	70	20		1	67	16.1	4
Galpinia transvaalica	101	-	1	55	-	1	-	-	-	-	-	-
Gardenia volkensii	139	25.4	7	107	29	21	32	9.61	5	-	-	-
Gossypium herbaceum	-	-	-	10	-	1	-	-	-	-	-	-
Grewia bicolor	-	-	-	40.7	17.7	3	-	-	-	-	-	-
Grewia flavescens	21	1	2	65.7	10	94	45.6	7.23	30	53	-	1
Grewia hexamita	21	1	2	22	-	1	69	-	1	-	-	-
Grewia microthyrsa	19	-	1	-	-	-	-	-	-	-	-	-
Grewia monticola	37	24	2	32.1	3.96	15	52.4	7.44	31	-	-	-
Hexalobus monopetalus	-	-	-	57	-	1	-	-	-	-	-	-

Continued overleaf

Appendix 6 Continued.

Plant*	Giraffe			Kudu			Impala			Steenbok		
	Mean	S.E.	n	Mean	S.E.	n	Mean	S.E.	n	Mean	S.E.	n
Kigelia africana	43.5	30.5	2	159	65.1	9	-	-	-	-	-	-
Lannea stuhlmannii	192	70.5	6	45.4	7.66	51	-	-	-	72	-	1
Lonchocarpus capassa	78.7	5.77	329	57.1	2.98	419	25.5	5.83	10	-	-	-
Maerua parvifolia	34	-	1	233	14.2	4	60.6	40.6	12	48.8	6.79	39
Manilkara mochisia	74	-	1	-	-	-	-	-	-	-	-	-
Maytenus heterophylla	56.1	40.5	12	46	6.18	38	20.6	8.5	2	70	42.1	3
Maytenus senegalensis	65.3	6.35	198	109	54.9	22	29.4	3.26	54	91.8	59.9	9
Neorautanenia amboensis	-	-	-	44	33	2	-	-	-	-	-	-
Oroaxylum trichocaryum	-	-	-	59.2	5.17	170	80	-	1	44.8	6.74	42
Ozoroa engleri	-	-	-	65.4	16.8	11	-	-	-	-	-	-
Peltophorum africanum	82.3	7.44	68	66.7	10.7	56	-	-	-	45.3	8.76	9
Phyllanthus reticulatus	66.8	12.6	9	36.8	11.6	5	-	-	-	-	-	-
Pterocarpus angolensis	-	-	-	60	-	1	175	-	1	41.6	5.72	14
Pterocarpus rotundifolius	-	-	-	65.3	12.6	9	-	-	-	-	-	-
Rhus guineizii	61.8	17.5	33	55.6	8.81	54	69.2	16.6	4	15	-	1
Schotia brachypetala	66	26	2	94.5	37	5	-	-	-	-	-	-
Sclerocarya birrea	33.7	6.15	4	97.6	15.3	55	-	-	-	-	-	-
Securinega virosa	103	21	69	67.5	3.77	320	60.4	12.2	36	69.8	3.61	353
Solanum panduriforme	-	-	-	38.7	3.92	93	16.7	1.66	7	16.3	1.21	17
Spirostachys africana	125	16.2	44	138	55.5	3	18	-	1	-	-	-
Strychnos spinosa	89.4	25.7	7	52.3	7.49	16	-	-	-	-	-	-
Tephrosia caerica	49	26	2	-	-	-	-	-	-	-	-	-
Terminalia sericea	72.7	18.1	8	-	-	-	-	-	-	-	-	-
Xeroderris stuhlmannii	-	-	-	28	-	1	-	-	-	-	-	-
Ximenia caffra	16.7	5.2	9	97.2	11.3	48	36	-	1	-	-	-
Ximenia americana	-	-	-	79.9	47.4	8	60	-	1	40.5	19.2	5
Ziziphus mucronata	103	11.5	135	59.6	9.9	57	65.5	11.4	30	66.6	7.61	56
All woody plants	76.2	0.6	4164	60.6	0.43	5042	45.7	0.76	1381	57.6	0.62	1334
Grass	-	-	-	37.6	3.1	169	53.8	1.16	5820	24.1	12.8	14
Forbs	9	-	1	49.6	1.61	2369	38.4	1.33	1935	29.6	0.86	2478
Creepers	90.9	12.5	43	72.6	5.41	220	15.7	6.84	4	66.1	8.54	32

*Plants listed by species are all woody plants.
†n is the number of feeding events recorded in each case.

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