SEX AND AGE RELATED DISTINCTIONS IN THE FEEDING ECOLOGY OF THE AFRICAN ELEPHANT, *Loxodonta africana*

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DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

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ABSTRACT

Sexual dimorphism in size in the African savanna elephant, *Loxodonta africana*, is pronounced. Allometric differences between the sexes lead to dissimilar nutritional demands, which result in sex related distinctions in feeding ecology. This extension of the Jarman-Bell Principle to an intra-specific level has been referred to as the Body Size Hypothesis (BSH). This study established whether different nutritional requirements of elephant size/sex classes resulted in functional distinctions in feeding ecology between elephant bull groups and family units. Plant based surveys on woody species were conducted at the feeding sites of both bull groups and family units of elephants during the dry season period of resource limitation within the Associated Private Nature Reserves of South Africa. Although similar in terms of plant species composition, the diets of bull groups and family units differed in the plant parts ingested. Family units frequently debarked and defoliated woody plants while bulls tree-felled and engaged in rhizophagy more frequently than cows. Adult bulls had greater bite and break diameters and also fed at significantly higher heights than family units. The management implications of the feeding habits of bull groups as opposed to family units are considered. Furthermore, plant and faecal samples were collected at the feeding sites of both social groups to determine whether diet quality measures differed between them. Near infrared reflectance spectroscopy (NIRS) proved to be a time and cost effective analysis technique when applied to ecological research. NIRS also accurately determined gender in free ranging elephants from faecal samples. Diet quality measures did not differ significantly between elephant groups although family units utilised plant species high in sugar and low in fibre content. Bulls accepted plant species with a high calcium content. In dry months large-adult bulls had significantly lower faecal phosphorus levels together with higher fibre levels than adult females, thereby providing some support for the BSH. Although various factors confounded the interpretation of faecal nitrogen and calcium levels, the results nevertheless suggested that large-adult males ingested diets of poorer quality than adult females when resources were limited. A dry season dietary shift to browse was confirmed by carbon isotope analysis of faecal samples. Finally, the results of this study were compared with those of a similar study conducted within the Kalahari woodlands and a conceptual model was developed to draw comparisons between the sex and age-related feeding behaviour in elephants among diverse savanna ecosystems.

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CHAPTER 1

Introduction

1.1 Inter-specific scaling of metabolic rate with body size

Basal metabolic rate can be approximated over a wide range of taxa according to Kleiber's equation (Kleiber 1961): Metabolic rate=70 kcal per kg$^{0.75}$ Therefore, metabolic rate has a 0.75- power relationship with body mass. As metabolism is the summed energetic cost of an organism's biological processes, the principle of similitude (Thompson 1961) suggests that very different processes should show parallel responses to variations in body size. In general mass exponents of 0.75, 0.25 and -0.25 have been so effective in describing biological phenomena (Peters 1983), that quarter-power allometric scaling has been described as the single most pervasive theme underlying all biological diversity (West *et al.* 1997).

The 0.75 - power relationship that metabolic rate has with body mass would mean that mass specific metabolic rate decreases with an increase in body size (Schmidt-Nielsen 1984). Despite smaller bodied species having higher maintenance costs per unit body weight when compared to large-bodied species, smaller animals are constrained by the fact that gut capacity remains a constant fraction of body mass (Paraa 1978). Small-bodied animals must therefore achieve their required nutritional status either by faster digestion and rate of passage of digesta, or by ingesting a more concentrated diet (Van Soest 1994). This forms the basis of the Jarman-Bell Principle according to which an increase in ungulate body size at inter-specific level is associated with an increased tolerance of low quality (high fibre) diets (Bell 1971, Geist 1974, Jarman 1974, Demment & Van Soest 1985). This tolerance of low quality diets by larger animals may become more pronounced under dry season conditions when resources are limited (Owen-Smith 1988).

1.2 Intra-specific scaling of metabolic rate

To achieve generality across taxa, body size relationships to the 0.75 power have sacrificed precision (Peters 1983). Hence relationships between body weight and energy expenditure for maintenance should only be used as generalisations for interspecific comparisons as approximations would ignore energy expenditure differences between individuals or sexes within species (Robbins 1983, Van Soest 1994). At intra-specific level the exponent of Kleiber's equation ranges quite widely (Hudson & Christopherson 1985). In domestic ruminants (cattle) exponents ranged from 0.46 for steers to 0.60 for dairy cows (Thonney *et al.* 1976). Feldman & McMahon (1983) suggested that the exponent 0.67 best represents intra-specific variation while 0.75 best described the mass exponent for inter-specific variation. In general however, the differences in weight and sex categories within species exhibit power relations substantially less than the 0.75 power. Any mass exponent less than 1.0, implies that smaller animals need more nutrients per unit body weight for maintenance than larger ones (Van Soest 1994).

1.3 Scaling of requirements for nutrients with body size

The scaling of requirements for nutrients like protein and minerals may be dissimilar to that for energy, whether at inter- or intra-specific levels. A few basic concepts are first distinguished before consulting the literature on the scaling requirements for nutrients with body size. A nutrient is defined as any food constituent, or group of food constituents of the same chemical composition, that aids in the support of animal life (Crampton & Harris 1969). The equation that describes the relationship between an animal's body mass (W) and another of its characteristics (Y) take the form of power formula ($Y=aW^b$). The change of Y with W is called the scaling of that characteristic to body size (Peters 1983). Basal metabolic rate (BMR) refers to the minimal energy expenditure of an animal at rest in a thermoneutral environment and in a post-absorptive state (Blaxter 1982). Average daily metabolic rate (ADMR) represents the composites of energy expended for basal metabolism, activity, thermoregulation and the inefficiency of feed utilisation (Robbins 1983) and is usually represented as a multiple of BMR.

Numerous researchers have assumed that other response variables have the same relationship to body mass as does heat production (Thonney *et al.* 1976). According to Crampton & Harris (1969) both basal-energy metabolism and endogenous protein metabolism have mass exponents near 0.7. The general allometric relationship for daily energy requirements have been given as 2x ($293.W^{0.75}$)KJ/day by Belovsky (1978), Peters (1983) and Robbins (1983). The scaling of potential energy intake with body weight was found to average $W^{0.85}$ (Illius & Gordon 1991, 1992). Peters (1983) estimated protein requirements of mammals according to the equation 1.56 $W^{0.75}$g/day. Mineral utilisation rate has been less extensively analysed than energy budgets (Crampton & Harris 1969, Peters 1983) and data on allometric relationships for mineral requirements are lacking.

1.4 Differences in nutrient requirements between the sexes

The main factors that would influence nutrient requirements between the sexes would include body size and reproduction. Barboza & Bowyer (2000) suggested that in large species, within-sex dietary distinctions would be driven by gestational and reproductive costs. Lactation is considered to place greater nutritional demands on females than pregnancy (Crampton & Lloyd 1959, Peters 1983, Oftedal 1985) Expressed as a multiple of BMR, Belovsky (1978) estimated the metabolic energy requirements of a lactating female to be 2.7 times the basal metabolism requirement. Moen (1973) found that the protein demands of lactating white-tailed deer (*Odocoileus virginianus*) could be 60% greater and the energy demands 40% greater than those of non-lactating females. Although Lindsay (1994) was unable to distinguish non-breeding elephant females from lactating and/or gravid females, females in general had the strongest positive correlation between diet choice and protein intake in the wet season and energy intake in the dry season. Elephant bulls had a strong positive correlation between diet choice and energy intake, irrespective of the season in Amboseli National Park, Kenya. Estimates of the nutrient requirements of elephants were calculated according to the methods used by Lindsay 1994) (Appendix A).

Sex differences in reproductive cost would therefore tend to reinforce the effect of size differences between the sexes. Adult males within a species could meet their greater absolute energy demands by digesting fibre more efficiently because of their larger body size compared to smaller bodied females. On the contrary, smaller bodied females would require diets high in protein and possibly minerals to meet their higher mass specific metabolic needs coupled with the added protein and mineral demands of pregnancy and lactation.

1.5 Elephants and sexual dimorphism in body size

Sexual dimorphism in body size is common amongst polygamous herbivores (Skinner & Smithers 1990). Divergent morphological appearances are often favoured under selection because of the different reproductive roles of males and females (Badyaev 2002). Such dimorphism in size leads to differences in energy requirements and food selection between the sexes (Pérez-Barbería & Gordon 1998) and has also been associated with sexual segregation where single-sexed groups segregate in time and/or space (Main *et al.* 1996). Numerous studies have documented sexual segregation in various ungulate species (see Main *et al.* 1996, Mysterud 2000, Ruckstuhl & Neuhaus 2000 for reviews), but the mechanisms that underlie such segregation are still unresolved. Sex related dietary differences could be the cause of, or a consequence of, sexual segregation.

Sexual dimorphism in size in the African savanna elephant, *Loxodonta africana africana* (Blumenbach, 1797) (see Roca *et al.* 2001) is pronounced, as adult bulls can be more than twice the mass of adult females (Laws 1966, Meissner 1982, Owen-Smith 1988). Although Conradt (1999) found that intra-specific body-size differences between red deer (*Cervus elaphus*) hinds and stags were not large enough for the Jarman-Bell Principle to apply, elephants, as the largest land mammal represent the upper end of the body-size continuum and research on sex related feeding distinctions should be directed at such species (Woolnough & du Toit 2001).

Amongst elephant, the sexes are furthermore segregated in different social groups (Laws *et al.*1975, Spinage 1994). Habitat segregation between family units and bull groups has been documented in the African elephant (Laws *et al.* 1970, Croze 1974, Barnes 1982, Moss & Poole 1983, Western & Lindsay 1984, Kabigumila 1993, Frost 2001, Stokke & du Toit 2002). Adult bulls associate in bachelor herds, on their own or occasionally with breeding groups (Moss & Poole 1983, Poole 1982, Poole 1987). Typically males leave their natal family unit by the age of 14 years to form temporary associations in bachelor herds that range in size from 2 to 25 animals (Moss & Poole 1983). As individual adult males do not associate with females for long periods, breeding groups with accompanying adult bulls represent temporary situations (Lindsay 1994), which often coincide with musth in bulls or oestrous in females (Poole 1982). Adult males are known not to compete for oestrus females until 25-30 years of age, and only begin to experience prolonged periods of musth at approximately 30 years of age in areas where older bulls are present (Slotow *et al.* 2000). These older, mature bulls are of social importance to the breeding herds as females preferentially mate with them (Poole & Moss 1981, Poole 1982, Poole 1987).

Females and their offspring form cohesive family units (Spinage 1994). Family units are led by old, experienced matriarchs that strongly influence the social knowledge of the group as a whole (McComb *et al.* 2001). Family units may aggregate into clans, which are possibly structured hierarchically according to kinship bonds (Douglas-Hamilton 1972, Moss & Poole 1983).

Ruckstuhl & Neuhaus (2000) observed that the hypotheses proposed to explain sexual segregation relate either to predation risk, social preferences, forage selection, scramble competition or activity budgets. Sexual segregation due to predation risk may be excluded as predation on elephants within my study area can be regarded as negligible. Hypotheses relating to social affinities (Bon & Campan 1996, Conradt 1999) and activity budgets (Conradt 1998, Ruckstuhl 1998) were beyond the scope of this study. Therefore, this study will focus on the extension of the Jarman-Bell Principle to an intra-specific level, as referred to as the Body Size Hypothesis (BSH) by Stokke & du Toit (2000). Comparisons were made between the feeding strategies of bull groups and family units to determine whether sex-related allometric differences could be one of the underlying factors leading to dissimilar nutritional demands between the sexes. All male groups and lone bulls were considered as bull groups while females and their offspring, with or without accompanying adult males, were regarded as family units.

1.6 Elephants and dietary differentiation between the sexes

Dietary differences between the sexes have been recorded in studies on African (Ruggiero 1992, Lindsay 1994, Stokke 1999, Stokke & du Toit 2000, Frost 2001) and Asian elephants (McKay 1973, Sukamar & Gadgil 1988). Daily food composition and feeding times of elephants were calculated by Guy (1975, 1976) by means of continuous diurnal monitoring. Guy (1975) found that the number of trunksful per minute taken by each sex was different. Bulls tend to have higher plucking rates than cows and these differences become more pronounced in the dry season (Guy 1975 & 1976, Lindsay 1994, Stokke & du Toit 2000). Bulls also spend longer at each browsing site than cows (Barnes 1979, Stokke & du Toit 2000). Lindsay (1994) found that males had higher feeding rates in most food types when compared to females. To ensure high intake rates, male herbivores should select habitats with high forage biomass, select forage species that enable high intake rates and increase their bite size and rate (Miquelle *et al.*1992). By implication, bulls individually may be expected to have a greater impact on the vegetation than cows because of the larger proportion of vegetation biomass that males will remove during feeding bouts. This required further investigation. In support thereof, bulls engage more frequently in tree felling behaviour than cows (Guy 1976, Barnes 1979, Stokke & du Toit 2000) and remove greater amounts of biomass from woody species, due to larger break and bite diameters than cows (Stokke & du Toit 2000).

When reproductive state is considered, lactating elephant cows not only had larger stomach fills when compared to males (Laws *et al.* 1970, Malpas 1977) but the mean daily food intake of lactating cows represented 1.2-1.5% of the body mass. This contrasted with the mean daily food intake of 1.0-1.2 % of the body mass for males and non-lactating elephant cows as estimated from stomach fills (Laws *et al.* 1975). These results suggest that breeding females could compensate for the added nutritional demands of pregnancy and lactation by increasing their gut fill.

Stokke (1999) and Stokke & du Toit (2000) studied the size and sex related differences in the feeding patterns of elephants during the dry season in the dystrophic, savanna system of Chobe National Park, Botswana. Sex related distinctions in habitat use, plant species and plant part use were identified, but questions relating to diet quality differences between the sexes were left unanswered. Hoppe (1977) found that the proportion of stem material in the digesta of various large herbivores increased with increasing body mass. A decline in nutritive value of plants is generally associated with increased lignification and a decreasing ratio of leaves to stems (Van Soest 1994). Smaller bodied female elephants should thus include a smaller proportion of fibrous material in their diet when compared to larger bodied males. In agreement with these predictions Stokke & du Toit (2000) found that females leaf-stripped woody plant more frequently than bulls.

My study was conducted within the semi-arid, eutrophic savanna of the South African lowveld and coupled vegetation surveys with chemical analyses of plant and faecal samples. The underlying rainfall and edaphic factors that characterise my study area combined with a comparatively low density of elephants relative to that of the Chobe National Park, also enabled the predictions of the BSH to be compared over disparate landscape types. My study was primarily aimed at establishing whether different nutritional requirements of elephant age/sex classes, combined with social segregation; result in functional distinctions in feeding ecology between elephant bull groups and family units.

1.7 Objectives

The objective of this study was to achieve an understanding of sex and age related differences in elephant diets in terms of:

1.7.1 forage class selection (graminoids or woody species)
1.7.2 woody plant species and plant height acceptance
1.7.3 use of woody plant parts (foliage, bark, twigs, root or heartwood)
1.7.4 nutritional variables within the selected diets
1.7.5 vegetation impact

Forage class selection (Objective 1.7.1) was determined by faecal analysis of material collected in wet and dry seasons. Objectives 1.7.2-1.7.5 were met by conducting plant-based surveys during the dry season period when sex related differences in feeding ecology would be most pronounced (i.e. high quality food resources would most likely be limited). Plant-based surveys were restricted to woody plant species and did not include surveys of grass and herbs. Elephants primarily consume browse during the dry season (Owen-Smith 1988) so that woody species utilisation by the sexes would not only be of more relevance but also proved to be more practically measurable. According to Van Wyk & Malan (1998), woody plants are perennial plants with stems that do not die back at the end of the growing season. Nutritional variables were investigated by the chemical analyses of both plant and faecal samples.

1.8 Hypothesis and predictions

Constraints associated with body size and reproduction will lead to dietary distinctions between the sexes The following predictions, based on this broadly defined BSH, were evaluated during this study and the specific objectives to which they are related are indicated in parenthesis:

1.8.1 Smaller bodied females and their offspring within family units, having higher relative energy requirements, feed more selectively on particular forage classes, plant species and plant parts when compared to males within bull groups (Objective 1.7.1 - 1.7.3).

1.8.2 Smaller bodied females and their offspring ingest food of higher nutritional quality when compared to larger bodied males found within bull groups (Objective 1.7.4).

1.8.3 Larger bodied bulls have a greater impact on the vegetation than family units because they are capable of larger bite and break diameters than smaller bodied females (Objective 1.7.5).

1.9 Thesis structure

The following chapter (Chapter 2) gives a general description of the history, climate, geology, vegetation and elephant population of the study area. The study methods described in this chapter focuses on the use of near infrared reflectance spectroscopy (NIRS). The applications of the NIRS's results are discussed elsewhere (Chapters 4 & 5).

The plant species and plant height acceptances of bull groups as opposed to family units are described within each social category of elephant. Comparisons in plant part use, i.e. foliage, bark, twigs, roots or heartwood, between bull groups and family units of elephant are made and differences in vegetation impact between bull groups and family units of elephant with regard to woody species bite and break diameters and the proportionate use of various plant parts are also described (Chapter 3). This is followed by an analysis of the differences in forage nutrient content of woody species that were utilised by bull groups and/or family units of elephant (Chapter 4). Sex- and age-related differences in forage class selection (graminoid/dicotyledon) are discussed and faecal indices of diet quality i.e. nitrogen, phosphorus, calcium and fibre content of faecal samples collected from adult female, adult male and small, adult male elephants are compared (Chapter 5). Finally, a conceptual model is developed to compare the findings of this study with a similar study conducted within Chobe National Park. A concluding discussion reviewing the relationship amongst the relevant findings, the limitations and management implications of this study are also discussed (Chapter 6).

Chapters 3-5 follow the format of manuscripts, which has led to some duplication in aspects of the introduction, and method section of each of these chapters.

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CHAPTER 2

Study area and methods

2.1 Study area

2.1.1 Brief history

In 1956 a permanent game protection association, consisting of 45 landowners was formed on the western border of the Kruger National Park (KNP) adjacent to the central district. The Klaserie and Timbavati Private Nature Reserves were officially formed and wardens appointed in 1972 (De Villiers 1994). Over time bordering farms were incorporated to increase the land surface area. The Association of Private Nature Reserves (APNR), which presently consist of the Klaserie, Timbavati and Umbabat Private Nature Reserves (24º 03'- 24º 33' S; 31º 02' – 31º 29'E), comprises approximately 180 000ha (Figure 2.1). The varied land-use history of the farms within the APNR has meant that certain areas of the APNR have been subjected to cattle ranching, heavy and selective hunting of wildlife, intensive creation of artificial water points, control of veld fires and animal populations that were either over protected or possibly over-hunted (Witkowski 1983, Pretorius 1993, Joubert 1996). All three reserves have recently adopted the management principles and policies of the KNP and now form part of the greater Kruger National Park biosphere (Joubert 1996).

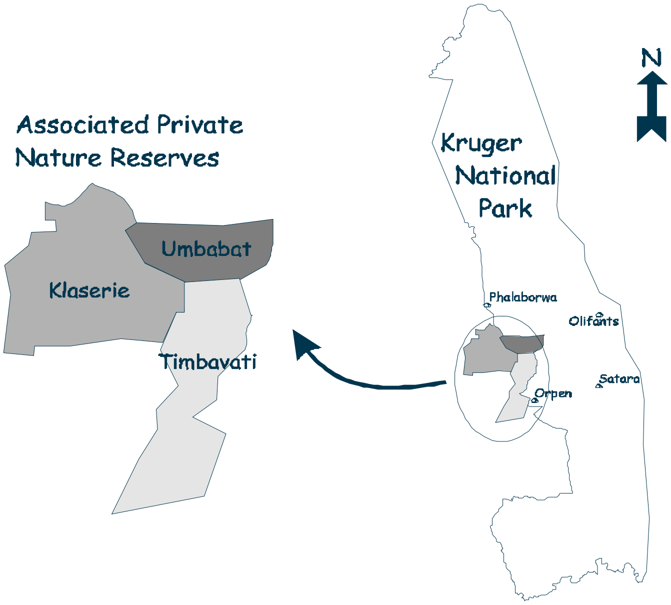

Figure 2.1 Location of the Association of Private Nature reserves relative to the Kruger National Park.

2.1.2 Climate

The climate is semi-arid with a mean annual rainfall of less than 600mm. The annual average temperature is 22°C and frost rarely occurs. Rainfall is known to increase from east to west and from north to south (Gertenbach 1980, Venter & Gertenbach 1986). Total monthly rainfall data were measured within the Umbabat Private Nature Reserve throughout the study period. A climate diagram (Figure 2.2) of the area was constructed from 14 years of data (1977-1990) obtained from the Hoedspruit weather station (Station number: 0638052; Latitude 24º 22'S; Longitude 31º 02' E; Altitude: 513m above sea level), approximately 40 km northwest of the APNR (Anon. 1992), depicting the temperature and rainfall throughout the year (Walter 1985). The rainfall figures of 1999-2001 that were measured within the Umbabat Private Nature Reserve were superimposed on the climate diagram and the seasons were defined accordingly. The climate diagram illustrates that the wet season usually starts in October (where the plot of mean monthly temperature and precipitation intersect). During the study period, however, the start of the wet season was delayed until November. Therefore October of 1999 and 2000 were classified as dry months. The exceptionally high rainfall figures of January-March 2000, with the rainfall of February 2000 being six times as high as the mean monthly level of the past 14 years, are depicted in Figure 2.3.

2.1.3 Topography and geomorphology

The terrain is undulating and is drained by the perennial Klaserie and Olifants Rivers and the seasonal Timbavati River (Gertenbach 1983). Numerous artificial water points with a mean spacing of 2 km, provide a perennial water supply to animals within the APNR (Stalmans *et al.* 2003). Geologically the study site is dominated by granite and gneiss intersected by dolerite intrusions. Gabbro occurs in the central and southern regions. Upland soils weathered from granitic rock are light-coloured, coarse, sandy and gravely with a high infiltration rate and permeability. These soils are leached and of low fertility. The bottomlands of the undulating granites as well as soils originating from gabbro are rich in clay minerals. Clayey and sometimes sodic duplex soils form towards the granite bottomlands. The heavy textured clay derived from Timbavati Gabbro is dark-coloured and rich in iron- and magnesium containing minerals. These soils have a low infiltration rate, are non-leached and contain a dominance of calcium and magnesium in solution (Gertenbach 1983, Brady 1984, Bristow & Venter 1986, Venter 1986, Walraven 1986, Venter 1990).

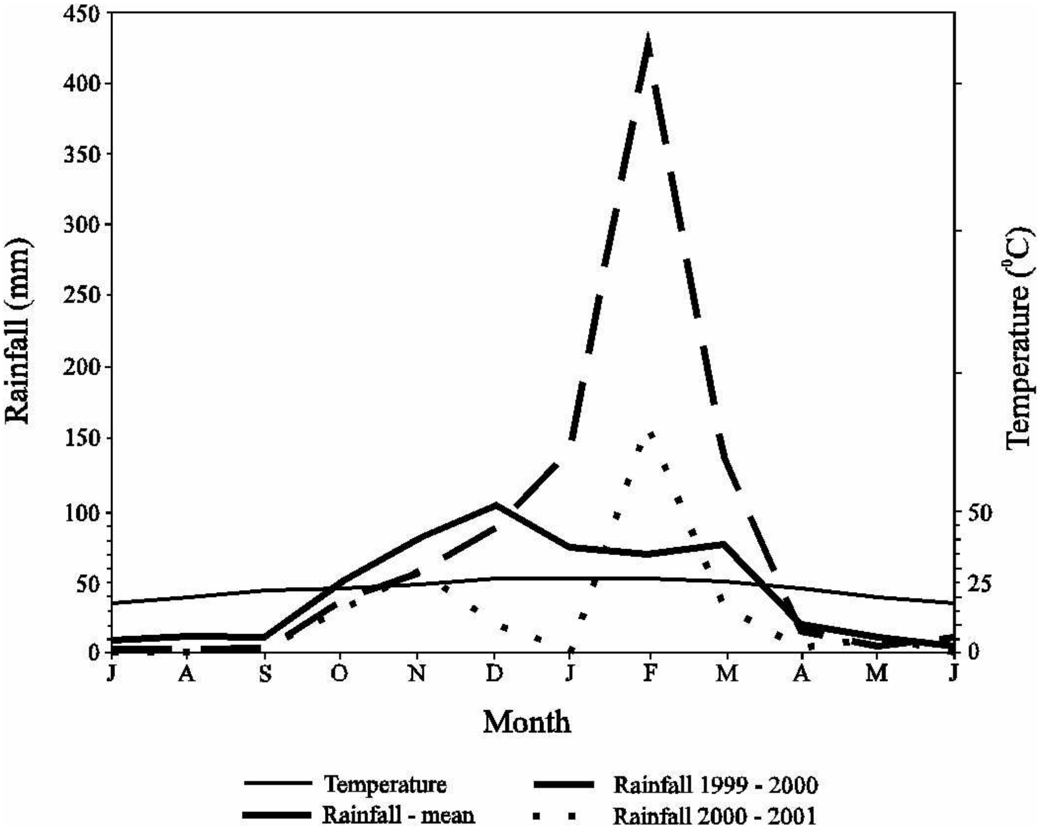

Figure 2.2 Climate diagram of Hoedspruit weather station constructed from 14 years of monthly rainfall and mean monthly temperature data.

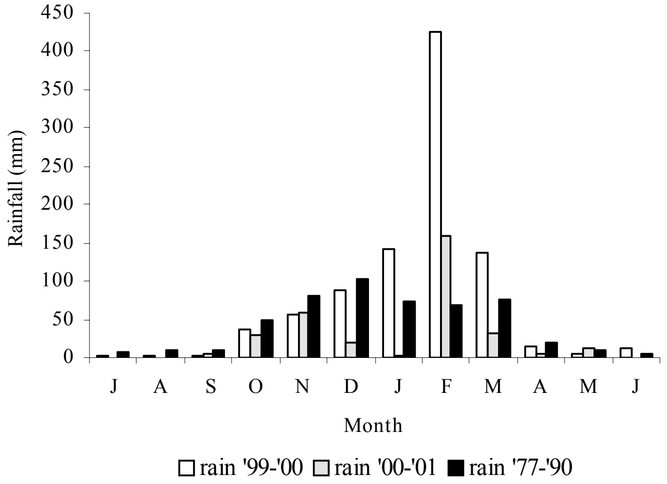

Figure 2.3 The monthly rainfall figures for 1999 and 2000 gathered within the Umbabat Private Nature Reserve and plotted with the mean monthly rainfall collected for 14 years at the Hoedspruit weather station. Note the exceptionally high rainfall of February 2000 and the bimodal distribution of rainfall recorded from July 2000 until June 2001.

2.1.4 Vegetation

Acocks (1975) broadly described the vegetation type as *Acacia nigrescens-Sclerocarya birrea* savanna. *Combretum apiculatum, Colophospermum mopane* and *Grewia* species represent other dominant plant species (De Villiers 1994). Vegetation surveys within the APNR were conducted by Witkowski (1983) and Zambatis (1983) and the vegetation was further more divided into the following landscape types based on Gertenbach's (1983) survey within the KNP and described by De Villiers (1994): (1) *Acacia nigrescens*/*Combretum apiculatum* woodland; (2) *Colophospermum mopane* veld; (3) *Combretum apiculatum* open woodland; (4) *Combretum* spp./*Colophospermum mopane* woodland; (5) *Combretum* spp./*Terminalia sericea* woodland; (6) Mixed *Combretum* spp./*Terminalia sericea* woodland; (7) Mixed veld on Gabbro; (8) Olifants River Rugged veld; (9) Shrub *Colophospermum mopane* veld.

2.1.5 Elephants within the APNR

The indiscriminate hunting of elephants over two centuries ago had largely removed elephants from most of South Africa (Hall-Martin 1992). In 1898 when the Sabi Sand Game Reserve was proclaimed, prior to the creation of the KNP, elephants were believed to have been extirpated in the area (Garaï 1998). At the turn of the nineteenth century, only a few dozen elephants were to be found between the Letaba and Olifants rivers within the present day KNP (Hanks 1979, Ebedes *et al.* 1991, Hall-Matin 1992, Whyte 2001). The KNP was recolonised by elephant immigrants from Mozambique, which also moved westwards into privately owned land (Hall-Martin 1980). In 1960 the KNP started fencing their western boundary to arrest the spread of foot-and-mouth disease (Joubert 1996). The fence disrupted the east-west migration of wildebeest and zebra and led to a substantial decrease in both populations (Whyte 1985, Whyte & Joubert 1988). According to Kettlitz (1962), no elephants were resident outside the borders of the KNP prior to 1962. A decade later Lambrechts (1974) estimated that *ca* 220 resident elephants occurred within the private nature reserves in the lowveld.

Annual aerial censuses indicate that elephant numbers have increased within the APNR in recent years. Elephant numbers increased from 189 in 1983 to over 500 in 1992 (De Villiers 1994), appeared to stabilise at just over 500 from 1992 until 1996 and then steadily increased to over 800 in 2001 (I. Whyte pers.comm.). These increases are thought to represent an influx of elephants from the KNP following the removal of fences between the private reserves and the western boundary fence in 1993/1994. The APNR is furthermore adjacent to a so-called high elephant density zone within the KNP where the Park have allowed elephant numbers to increase following the termination of culling operations in 1995 and the implementation of a new elephant management policy (Whyte *et al.* 1999). The elephants within the APNR presently represent the largest elephant population on privately owned land (Hall-Martin 1992).

As in the rest of Africa, elephants within the APNR occur either as socially distinct bachelor herds, lone bulls or cohesive family units, which consists of females and their offspring and are led by a matriarch (Owen-Smith 1988). De Villiers & Kok (1997) found that male herd size within the APNR seldom exceeded five animals. The minimum and maximum range areas required by males in the APNR varied between 157 and 342 km^2. Female home ranges within the APNR were estimated at 115 and 465 km^2, with core areas comprising on average 10.1 % of their home range. Family units of elephants thus required core areas of a minimum and maximum of 11.5 and 46.5 km^2 respectively, in which they spent 80% of their time. Significant differences in range size were found between females in the Klaserie and Timbavati Private Nature Reserves (De Villiers & Kok 1997).

Since 1985, elephant bulls have been hunted within the APNR. The revenue thus generated being used to fund various conservation initiatives within the reserves. Hunted animals have been aged at 26 years and older, and only two individuals carried ivory less than 18kg, which were not considered as acceptable trophies (De Villiers 1994). Since 1998, elephant bulls within the Timbavati Private Nature Reserve have formed part of a ‘green’ hunt initiative where trophy bulls are darted and fitted with satellite collars for research purposes (I. Douglas-Hamilton pers. comm.). An environmental impact assessment is currently being carried out to identify the potential environmental, socio-economic and cultural heritage impacts of hunting within the APNR (Stalmans *et al.* 2003).

2.2 Study methods

The methods pertaining to plant sample and elephant faecal collection and classification are described in chapter 4 and chapter 5 respectively. Chapters 3 describe the methods that were used to conduct plant-based surveys.

This section focuses on the use of near infrared reflectance spectroscopy (NIRS) to predict the nutrient concentrations of plant and faecal samples and to determine the sex of collected faecal samples.

2.2.1 Introduction

Near infrared reflectance spectroscopy was developed by Norris *et al.* (1976) and has been used extensively in the agricultural and manufacturing industries (Foley *et al.* 1998). The use of NIRS in ecological research has been a recent development and the technique has proved to be a useful tool in the measurement of forage quality attributes, which determine plant-herbivore interactions (Woolnough & Foley 2002).

Within an African context, elephant feeding preferences have been explored by NIRS, albeit only qualitatively (Lister *et al.* 1997). Near infrared reflectance spectroscopy has furthermore been used to predict the nutritional status of the diet of roan antelope (*Hippotragus equines*) following faecal analysis (Dörgeloh *et al.* 1998) and the technique has been applied to determine browse quality of tree canopies exposed to African browsing ungulates (Woolnough & du Toit 2001). Determination of sex in livestock (Godfrey *et al.* 2001) as well as in four wildlife species (Tolleson *et al.*2001), including the African savanna elephant (*Loxodonta africana africana*), has been accomplished via faecal NIRS.

In this study we used NIRS to compare the browse quality of bull groups and family units of elephants after collecting the spectra from a wide range of dicotyledonous plant species and plant parts. We also used the technique to establish whether the sex of adult elephants could be determined from faecal samples. Faecal samples from each of the abovementioned social groups of elephant were analysed to determine the ratio of graminoid:dicotyledon material, based on $\delta^{13}C$ values, and the levels of nitrogen (N), phosphorus (P), calcium (Ca) and fibre indices such as neutral-detergent fibre (NDF) and acid-detergent fibre (ADF). The interpretation of these results within the framework of the Body Size Hypothesis (Stokke & du Toit 1996) will be discussed elsewhere and do not form the focus of this section.

As the sampling intensity exceeded the practical capacity to apply conventional analysis techniques, a cost- and time-effective technique such as NIRS became essential to this study. However, for NIRS to be applicable to ecological research, broad based calibrations should be robust enough to predict diet quality attributes from a diverse array of plant species collected at different times and from various locations (Foley *et al.* 1998, Woolnough & Foley 2002). We therefore evaluate whether NIRS could be used to (1) discriminate between male and female faecal samples (2) predict the $\delta^{13}C$ values of faecal samples (3) predict the levels of N, P, Ca, NDF and ADF of faecal samples and (4) predict the levels of N, P, Ca, NDF and total soluble sugar content of the collected plant samples with sufficient accuracy and precision.

2.2.2 Methods

Spectra collection

All faecal and plant samples (excluding leaf samples) were first hammer milled (Retsch SM1, Haan, Germany) through a 1-mm sieve. To ensure that variability in particle size would not influence the NIRS results (Shenk & Westerhaus 1991), samples were passed through a 1-mm screen of a cyclone mill (Udy Corporation, Fort Collins, Colorado). Near infrared spectra (1100 to 2500 nm) were collected at 2 nm intervals with a NIRSystems model 4500 monochromator equipped with a spinning sample module (NIRSystems Inc. Model 4500, Silver Spring, MD, USA). The instrument was housed at the Range and Forage Institute of the Agricultural Research Council at Roodeplaat and was operated under constant temperature (22°C) and relative humidity (55%). Repeatability of the near infrared spectra was measured by deviations in optical data (log 1/R) at each wavelength using an internal ceramic reference tile with duplicate spectra not exceeding a root mean square of 45 (Shenk & Westerhaus 1992). Each dried, ground sample was scanned in duplicate according to the standard procedures developed by the American Society for Testing & Material (ASTM 1995). After centering the collected spectra, the ISI software (ISI version 3.10, Infrasoft, Port Matilda, Pennsylvania, USA) selected a representative or calibration set of samples to include the spectral variability of the remaining spectra. The calibration set of samples were analysed by conventional laboratory procedures (refer to the section below).

Initially a total of 245 faecal samples were collected from September 1999 until January 2000. The CENTER and SELECT algorithms of the ISI software selected 95 samples to represent the calibration set. After the spectra from an additional 137 faecal samples, which were collected from July until November 2000 were added to the existing spectra file, the calibration set was extended with a further 47 samples.

Plant samples were collected from July until November 2000. The spectra of 479 plant samples and an additional 62 composite samples were stored once the samples were ground and scanned. After centering the spectra a calibration set of 138 samples was selected using the ISI software.

Laboratory analyses of the calibration set

Three separate calibration sets were analysed during this study. The faecal calibration set of 95 was analysed for the percentage carbon (%C) and the percentage nitrogen (%N) via combustion in a Carlo Erba CHN analyser prior to carbon isotope determination. Carbon isotope ($\delta^{13}C$) determination took place in a Finigan Matt 252 mass spectrometer operating in the continuous flow mode. The $\delta^{13}C$ values are expressed as parts per million (‰) relative to Pee Dee Belemnite (PDB) standard as follows (Graig 1957):

$\delta^{13}C$ ‰$=\{[(^{13}C/^{12}C)$ sample$/(^{13}C/^{12}C)$standard$]-1\}$ x 1000

The faecal calibration set of 142 samples was analysed by conventional laboratory procedures for total N, P, Ca, NDF and ADF. The automated, simultaneous determination of N, Ca and P was conducted in a continuous-flow analysis system as described by the Agri Laboratory Association of S.A. (ALASA 1998). Neutral-detergent fibre was determined according to the methods of Robertson & Van Soest (1981) and ADF according to the methods described by Goering & Van Soest (1970).

The calibration set of 138 samples was analysed as mentioned above, by conventional laboratory analyses for N, P, Ca and NDF. Total soluble sugar according to Jachmann (1989), was determined by Luff-Schoorl titration after extraction with ethanol and reaction with Carrez I and II (ICUMSA 1994). Samples were analysed in duplicate where sufficient sample material was available and the averaged laboratory values were used in the infrared evaluation. All values are expressed as percentage dry matter.

Predictive equation development and calibration procedures

Predictive equations were derived from the laboratory results of the calibration set similarly to the protocol described by Foley *et al.* (1998) and Woolnough & Foley (2002). To ensure that the best predictive equation was developed and used in subsequent analyses, a variety of mathematical transformations and smoothing functions were applied. The first number in the formula is the order of the derivative, the second number is the segment gap (number of data points over which the derivative is calculated) and the third and fourth numbers are the number of data points used during smoothing (number of data points in the moving average). The following 10 mathematical transformations and smoothing functions were applied to a model using a default regression technique of modified partial least-squares (MPLS): 0,4,4,1; 1,4,4,1; 2,4,4,1; 0,5,5,1; 1,5,5,1; 2,5,5,1; 0,8,8,1; 1,8,8,1; 2,8,8,1 and 1,10,10,1. MPLS regression is reported to be a more stable and accurate algorithm than partial least squares (PLS) and principle components regression (PCR) (Shenk & Westerhaus 1994). Initially, scatter corrections were set to include both standard normal variate and detrend methods of scatter corrections, which are also recommended to improve the accuracy of the prediction (Barnes *et al.* 1989, Shenk & Westerhaus 1991, Baker *et al.*1994). Models with mathematical transformations that produced the lowest standard error of the cross-validation (SECV) and standard error of the calibration (SEC) statistics concurrently with the highest coefficient of determination (r^2) and one minus the variance ratio (1-VR) were then re-run using a combination of either PLS or PCR regression techniques combined with standard normal variate or no scatter correction techniques. All equations were subsequently ranked with the preferred equation having the lowest SECV, SEC and the highest coefficient of determination and 1-VR of all the equations that were developed. The variance ratio is the explained variance divided by the total variance and refers to the percentage of the variation in the reference method that is explained by NIRS (Shenk & Westerhaus 1992). Several calibration runs were carried out with spectral outliers eliminated after each run. Although Smith *et al.* (1998) found that this procedure did not lead to more accurate predictions; elimination of spectral outliers is common practice during the development of NIRS calibration equations according to the protocols developed by Shenk & Westerhaus (1991). Predicted values with *H*-values three times the average distance from the centre of the population were replaced with the actual laboratory reference values, and if necessary the sample was eliminated from the calibrations (Shenk & Westerhaus 1995). The *H* statistic is the distance of the sample from the population centroid and is standardised to have unit variance (Walker *et al.* 2002).

Validation procedures

An internal validation set of samples was used and the following statistics were determined to evaluate the success of the NIRS predictions: coefficient of determination (r^2), slope, bias and the standard error of prediction (SEP). The SEP was estimated by cross-validation, which is preferable to limiting the number of samples in the calibration set (Meuret *et al.* 1993, Shenk *et al.* 1993, Foley *et al.* 1998). Cross-validation prevents over-fitting by optimising the number of factors (Shenk & Westerhaus 1994). As described by Walker *et al.* (2002), the coefficient of determination describes the amount of variation in the dependent variable that is explained by NIRS predictions and is an indicator of the precision of the calibration equation. Increases in unexplained error are associated with a decrease in r^2. The slope and bias are estimates of the accuracy of the calibration. Decreases in accuracy occur as deviations from a slope of 1 and an intercept of 0 respectively for the regression between NIRS and reference values. The SEP includes error due to poor precision (i.e. lack of fit) and systematic error as a result of slope and bias deviations from 1 and 0 respectively. Foley *et al.* (1998) cautioned that the quality of NIRS-based predictions was entirely dependent on the quality of the reference method used to generate the model. Therefore the standard error of the laboratory (SEL) was determined according to the methods of Smith & Flinn (1991) as SEL = $[\sum(y_1-y_2)^2/n]^{0.5}$, where y_1 and y_2 are duplicates of the laboratory analyses and *n* represents the number of samples in the calibration set.

Discrimination between male and female faecal samples

The spectra obtained from the faecal samples of 126 adult male and 137 adult female, free-ranging elephants were used as calibration files. A validation set of 77 samples consisted of 51 samples from independent family units of elephant within which all the adult female's faecal samples were pooled prior to near infrared scanning. The adult bulls within 26 different bull groups were also pooled and used as part of this validation set. Discriminant equations were developed using ISI software (ISI version 1.04a, Infrasoft, Port Matilda, Pennsylvania, USA) to predict the sex of the pooled samples of the validation set. The procedure utilised two-block partial least squares (Martens & Martens 2001) to predict a set of indicator variables identified with the calibration spectra. Indicator variables in the calibration set were assigned as follows: a sample belonging to males would be represented as {2,1} in the algebraic matrix; a sample belonging to females would be {1,2}. An unknown sample would be predicted with estimates for both indicator variables. The closer the value to 2.0, the greater the certainty with which the sex of the sample can be determined. A predictor indicator value greater than 1.5 was required for a 'correct' determination of sex. For example, if the predictor values for sample X are {1.9, 1.1}, membership would be assigned to males. The standard error for the discriminant equation represented the precision associated with the prediction of the indicator variables.

2.2.3 Results

The models that produced the best predictive equations (evaluated by means of the lowest SECV, SEC and the highest r^2 and 1-VR) for each nutritive attribute of both faecal and plant samples are given in Table 2.1. The accuracy of the calibrations are depicted in Figure 2.4 & 2.5 where the relationship between the predicted NIRS values and the laboratory references values was highly significant while the slopes of each model were not significantly different from 1 ($P<0.001$). The control limits for bias (equation standard error of the calibration x 0.6) and the standard error of performance corrected for bias (equation standard error of the

Table 2.1 The NIRS model's performance for carbon and nitrogen as determined through combustion (%C and %N respectively), carbon isotope (δ^{13}C), nitrogen (N), phosphorus (P), calcium (Ca), neutral-detergent fibre (NDF) and acid-detergent fibre (ADF) measured within elephant faecal samples. The NIRS model's performance for N, P, Ca, NDF and the total soluble sugar content of plant samples are also given. Results were obtained after evaluation of the best predictive model, which was determined for each of the three calibration sets.

Chemical variable	Equation type	Mean (%DM[a])	Maths treatment	SECV[b]	SEC[c]	SEL[d]	SEP[e]	1-VR[f]	r^2 [g]
Calibration set of 95 faecal samples									
%C	MPLS[h]	44.4	1551	0.83	0.48	-	0.44	0.49	0.85
%N	MPLS	1.13	1881	0.07	0.06	-	0.06	0.95	0.96
δ^{13}C	MPLS	-22.6	2881	0.68	0.51	0.55	0.48	0.92	0.96
Calibration set of 142 faecal samples									
N	MPLS	1.09	2551	0.05	0.04	0.01	0.04	0.97	0.98
P	PLS[i]	0.11	1881	0.02	0.02	0.01	0.02	0.82	0.85
Ca	MPLS	1.31	2441	0.08	0.06	0.05	0.05	0.95	0.97
NDF	MPLS	73.2	2551	1.31	1.02	1.09	0.98	0.90	0.94
ADF	MPLS	60.6	2551	2.66	2.20	1.31	2.13	0.75	0.84
Calibration set of 138 plant samples									
N	MPLS	1.37	1441	0.13	0.11	0.08	0.11	0.97	0.98
P	MPLS	0.09	1441	0.03	0.02	0.02	0.02	0.80	0.88
Ca	MPLS	1.48	1441	0.21	0.15	0.12	0.13	0.93	0.97
NDF	MPLS	49.6	1881	2.01	1.63	2.10	1.54	0.98	0.99
Sugar	MPLS	3.58	2441	0.73	0.64	0.06	0.61	0.78	0.84

[a]Percentage Dry Matter, [b]Standard Error of Cross Validation, [c]Standard Error of Calibration, [d]Standard Error of the Laboratory, [e]Standard Error of Performance, [f]One minus the Variance Ratio, [g] Coefficient of determination, [h]Modified Partial Least Squares, [i]Partial Least Squares.

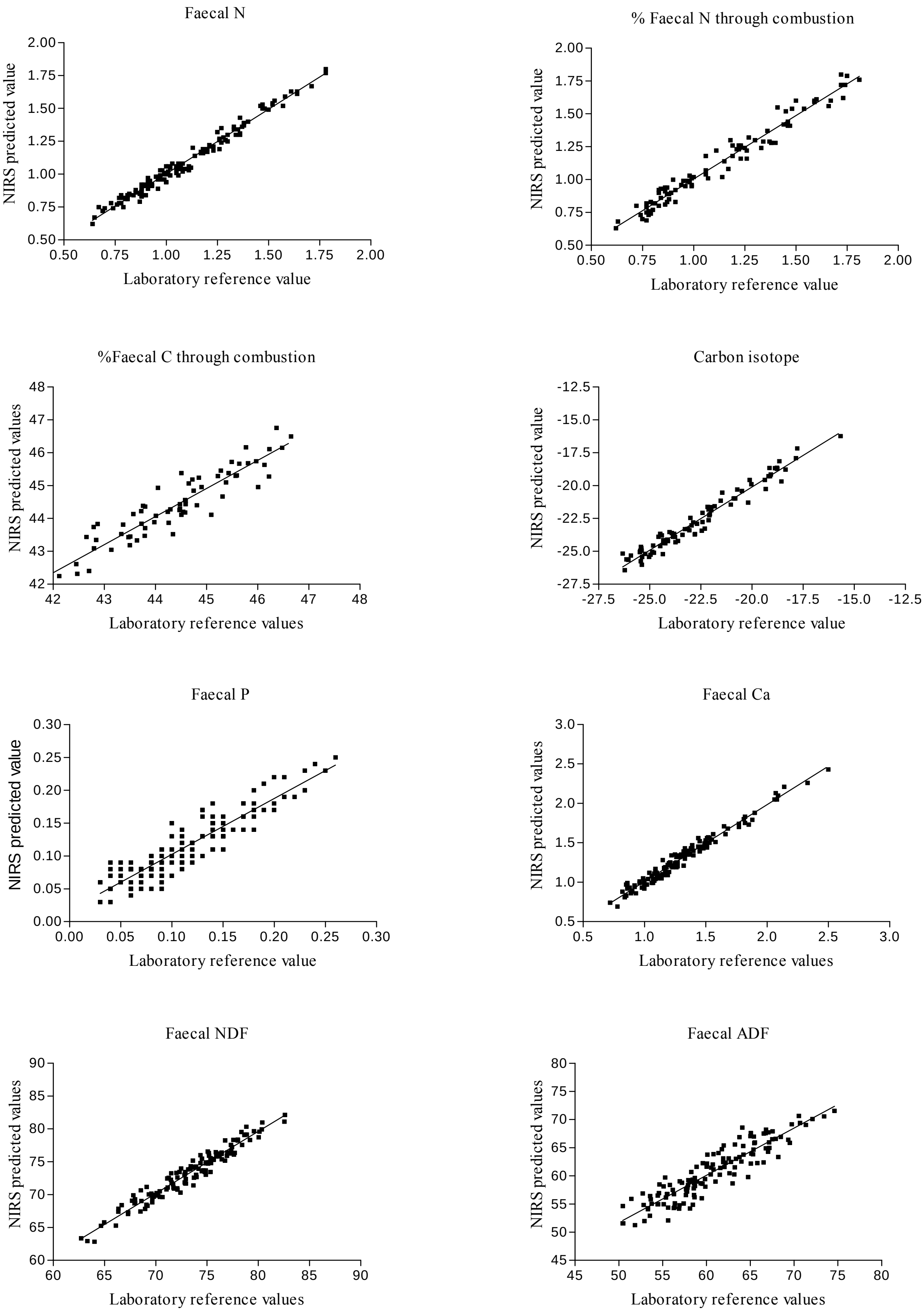

Figure 2.4 Relationship between the laboratory and NIRS predicted values for the calibration sets of the faecal samples.

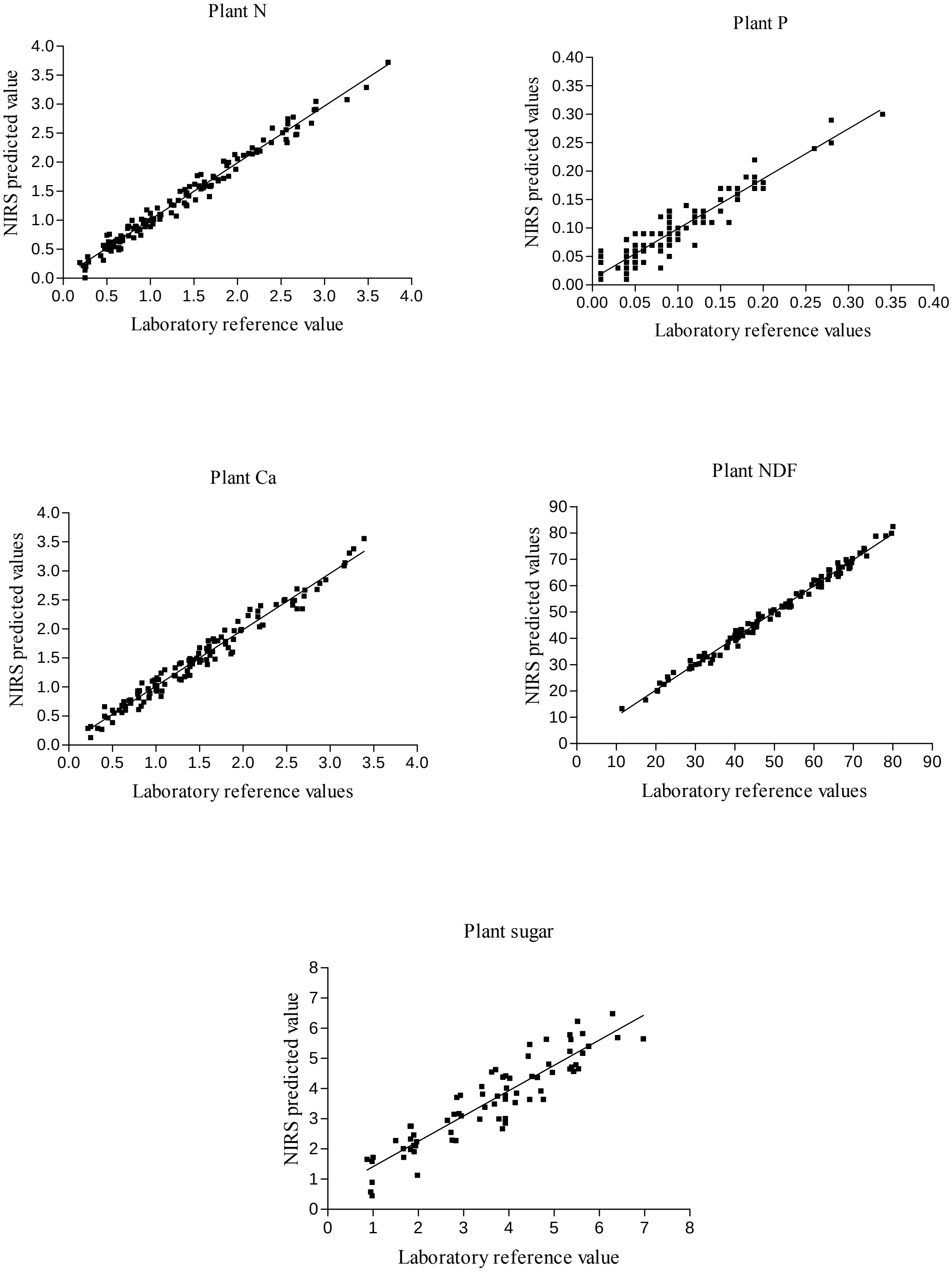

Figure 2.5 Relationship between the laboratory and NIRS predicted values for the calibration sets of the plant samples.

calibration x 1.3) were not exceeded (Shenk *et al.* 1989). The low SECV and SEC for each of the abovementioned quality attribute in both faecal and plant samples reflect the accuracy of the NIRS models that were developed. The predictive model for faecal N, Ca and $\delta^{13}C$ as well as %N, measured by means of combustion, had the highest levels of precision followed by the predictive models generated for Ca, NDF, P, % C and lastly ADF. For plant samples NDF, N and Ca were predicted with high levels of precision, while the models developed for P and sugar could explain more than 80% of the variability of the samples.

Estimates of SECV, SEC and r^2 compared favourably with other studies, which used NIRS to determine faecal nitrogen (Leite & Stuth 1990, Lyons & Stuth 1992, Coates 2000) and faecal $\delta^{13}C$ content. Coates (1999a, 1999b) provided the only published data with which to compare statistics for faecal $\delta^{13}C$ where a good relationship between laboratory reference values and NIRS predicted values was obtained (r^2 of 0.96 and SECV of 0.82). Although the indices of fibre had the highest SECV and SEC, these results were better than those reported elsewhere (SECV of 2.06-2.11) which used NIRS to determined fibre levels within diverse woody foliage (Meuret *et al.* 1993). Potential errors increased when comparing faecal ADF to NDF values because of sequential laboratory analysis. Phosphorus levels in plant samples were predicted with greater precision and accuracy than reported by Clarke *et al.* (1987). De Boever *et al.* (1994) predicted P levels with greater precision but similar accuracy to this study. The P and Ca content of plant samples was also predicted with greater precision and accuracy than those evaluated by Shenk *et al.* (1979) and Stoltz (1990) for agricultural forages and grains. Shenk *et al.* (1979) previously obtained SEP and r^2 for Ca similarly to those of ADF while the r^2 for P appeared to only explain 60-70% of the variation in the forage samples. The total soluble sugar content of the plant samples was predicted with less precision but similar accuracy to other studies that analysed the water-soluble carbohydrate (WSC) content (Smith *et al.* 1998, Woolnough & Foley 2002). Such comparisons may however be misleading as WSC includes both sugar and starch (Van Soest 1994). The absence of similar studies prevented direct comparisons of the models developed for faecal NDF, minerals and percentage C and N obtained through combustion.

The discriminant equation (r^2 = 0.512, SEC =0.274) correctly identified 78% of the female faecal samples and 88% of the male, faecal samples in the validation set.

2.2.4 Discussion

Near infrared reflectance spectroscopy produced robust equations for a variety of diet quality attributes and chemical variables within a diverse range of plant and elephant faecal samples. The high degree of accuracy with which the model can predict nitrogen levels can be ascribed to the numerous C-N and N-H bonds contained in the samples. An increase in near-infrared radiation that a sample absorbs will therefore result in a more detailed spectrum of reflected light that relates to the chemical composition of the sample (Foley *et al.*1998).

The mineral content of plant and faecal samples was predicted with sufficient accuracy and precision. Clarke *et al.* (1987) found that accurate use of NIRS to determine mineral cation composition of forages appeared to be limited to Ca, P, K and Mg. Minerals do not have reflectance spectra as NIRS theoretically responds to vibrating bonding energies of hydrogen. NIRS can therefore only determine some cation concentrations because of their association with organic or hydrated inorganic molecules (Shenk *et al.*1979, Clark *et al.* 1987). Calcium peaks have been found to be similar to those of calcium pectate, a possible component of cell walls (Clarke *et al.* 1987). Phytate, phospholipids, phosphoproteins, mineral phytates and nucleic acids contain P. Although the proportion of total P can vary (0.22-1.25%) between seasons as well as between closely related plant species, De Boever *et al.* (1994) also found that NIRS could be used to predict total P in plant samples.

In this study faecal fibre levels were predicted with less precision and accuracy when compared to the other chemical variables analysed. Cell wall content consists of a large proportion of cellulose, hemicellulose and other less defined polyproponal units called lignin. Although Goering & Van Soest (1970) describe a analytical method for measuring ‘cell wall’, actual cell walls in plant tissue as measured by infrared, are not completely represented (Shenk *et al.* 1979). Dietary fibre exists in several different compounds that confound the assignment of wavelengths to particular chemical entities, resulting in a reduction in precision of the predictive model (Shenk & Westerhaus 1995).

Other types of analyses where NIRS was successfully applied during this study included the determination of faecal $\delta^{13}C$ values as well as sex discrimination of faecal samples obtained from adult elephants. The sex of both cattle and sheep has been determined via faecal NIRS (Tolleson *et al.* 2000, Godfrey *et al.* 2001). Tolleson *et al.* (2001) also found that NIRS could be used as a practical, non-invasive method of determining sex in wildlife and found that large sample sets of species that utilize diverse forages are necessary for faecal NIRS to determine sex in wildlife management situations. Coates (1999a, 1999b) concluded that NIRS provided a cheap, simple and practical means of monitoring dietary non-grass proportions in free ranging cattle through faecal $\delta^{13}C$ determination. Okano *et al.* (1983) found that NIRS could distinguish differences in $\delta^{13}C$ abundance between C_3 and C_4 plants. Clarke *et al*. (1995) suggested that NIRS be used as a suitable alternative to determining carbon isotope discrimination in plants, thereby enabling plants with high water use-efficiencies to be accurately identified. The ability of NIRS to predict carbon isotope discrimination of plant samples is thought to be related to the ash concentrations of the samples (Windham *et al.*1991, Clarke *et al.*1995).

The plant samples that were collected during this study were particularly diverse in that leaf, twig, bark, heartwood and root samples were collected from 42 different woody species that were utilized by free ranging elephants. These samples were not only collected at different locations throughout the study area but were also collected over a five month period in the dry season, the period of resource limitation. Although each species-specific plant part was scanned by NIRS, a single calibration encompassing all plant parts and species was developed. Shenk *et.al.* (1993) found that more than 150 samples were needed to develop custom calibrations while smaller sample sizes were best utilized by extending calibrations of similar samples. Less than 150 heartwood, bark and root samples were collected during this study and separate calibrations could thus not be developed for each of these plant parts. The broad based equations that were developed with NIRS nevertheless proved to be effective in predicting the diet quality attributes of all the samples. Our findings are in agreement with the suggestion of Barton *et al.* (1990) to use broad based calibrations while Smith *et al.* (1998) also found no major advantages in developing plant-part specific NIRS calibrations.

As sample sizes increase, the proportional benefits of savings increase with the use of NIRS. This meant that the isotope analysis costs were cut by 61% (95 samples were analysed out of 245 samples). As 142 out of 382 faecal samples were analysed for protein, mineral and fibre content, the expenditure of traditional analyses were cut by 63%. The analysis of the calibration set developed for plant samples represented a saving of 74% (138 samples were analysed out of 541 samples). Instead of having to analyse over a 1000 samples by conventional laboratory techniques, the use of NIRS meant that just over a third of the samples required wet chemistry analysis. The broad based calibrations that were developed during this study thus lead to a considerable reduction in analytical costs as well as a reduction in time and the use of hazardous chemicals. Moreover, with the spectral information stored, predictions can be modified and new calibration equations expanded to enable NIRS predictions of diet quality at even larger geographic scales. New equations for different constituents can also be developed in the future.

We conclude that NIRS was of considerable value during this study. Near infrared reflectance spectroscopy provided estimates of diet quality attributes of free ranging elephants that previously would have been too time-consuming and too expensive to obtain. The variety of chemical variables that were predicted within both plant and faecal samples were accomplished with adequate predictive accuracy. Near infrared reflectance spectroscopy could furthermore be used as an accurate, non-invasive technique for determining sex in free ranging wildlife species from faecal samples. The diverse range of samples that were predicted from each of the calibration sets demonstrates the scale at which NIRS can be applied to ecological research. The application of these results to broad based ecological comparisons between the feeding ecology of bull groups and family units of elephants will be discussed in the following chapters. We agree with the predictions of Foley *et al.* (1998) and Woolnough & Foley (2002) that the use of NIRS as an invaluable tool in ecology, has merely begun.

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CHAPTER 3

Differential selection for plant species, plant parts and height classes between bull groups and family units of African elephants

3.1 Abstract

The African savanna elephant is sexually dimorphic in size. According to the Body Size Hypothesis these size differences should cause differences in diet selection between the sexes when resources become limited. To test this, plant based vegetation surveys were conducted at the feeding sites of both bull groups and family units of elephants during the dry season period of resource limitation within the Associated Private Nature Reserves of South Africa. Although similar in terms of plant species composition, the diets of bulls and cows differed in terms of plant parts ingested. Elephants of both sexes were mainly stem browsers. Family units frequently debarked woody plants, while bulls engaged in tree felling and rhizophagy more frequently than cows. Cows and immature animals leaf-stripped woody plants more frequently than did bulls. Adult males had greater bite and break diameters than cows, subadults of both sexes and juveniles within family units. Bull groups were thus comparatively more destructive feeders than family units of elephants. Although bull groups fed at significantly higher heights than family units these differences were consistent with the height differences between the sexes among adults. Furthermore, sex related distinctions in feeding height were only significant where the feeding mode involved the breakage of branches to access smaller plant parts such as twigs, bark or heartwood and could be ascribed to males utilising taller trees more commonly than family units.

3.2 Introduction

Various studies have described plant species, plant part and plant height selection in African savanna (*Loxodonta africana*) and forest elephants (*Loxodonta cyclotis*) respectively (Barnes 1982, Jachmann *et al.* 1989, Buss 1990, Tchamba & Mahamat 1992, Hiscocks 1999). With the exception of a study of the elephants within Botswana's Chobe National Park (Stokke 1999, Stokke & du Toit 2000), most studies have ignored the dietary distinctions arising from body size differences between age and sex categories within populations.

Inter-specific variation in body size has been viewed as a possible mechanism for differences in diet selection by ungulates (Demment & Van Soest 1985). According to the Jarman-Bell principle, smaller animals have higher metabolic demands in relation to processing capacity so that an increase in body size can accommodate an expansion in dietary tolerance (Bell 1971, Geist 1974, Jarman 1974). This means that during the dry season, larger bodied herbivores can expand their diet to include lower quality food sources when high quality food becomes scarce. Herbivores are sensitive to differences between functional categories of plant material (Demment & Van Soest 1985) and preferentially feed on nutrient rich plants and plant parts when making foraging decisions (Bergström 1992). Body size is therefore an important determinant of how resources are perceived by herbivores (Ritchie & Olff 1999).

The mean body mass of a female African elephant (2800kg) represents only 56% of the mean body mass of a 5000kg adult bull (Owen-Smith 1988). According to the Body Size Hypothesis (BSH) as stated to by Stokke & du Toit (2000), different energy requirements based on sex related differences in body size could lead to distinctions in nutrient acquisition, plant selection and habitat use between the sexes. This application of the Jarman-Bell Principle to inta-specific level seems appropriate because of the universal quarter-power scaling of circulatory systems underlying allometric scaling (West *et al.* 1997). Furthermore, Feldman & McMahon (1983) described the 0.75 mass exponent of energy metabolism as a reasonable approximation for inter-specific variation while a mass exponent of 0.67 provides a better description of intra-specific variation. Any mass exponent less than 1.0 implies that smaller animals need more nutrients per unit body weight than larger ones (Van Soest 1994). Adult males are also taller and stronger than smaller bodied females and thus have greater power to fell trees or break large branches, and are able to access plant parts out of reach of smaller bodied females. It is likely that differences in reproductive status between the sexes could have a significant influence on dietary distinctions between the sexes. Moen (1973) found that the protein demands of lactating white-tailed deer (*Odocoileus virginianus*) could be 60% greater and the energy demands 40% greater than those of non-lactating females. Hence, differences in body size together with differences in reproductive status between the sexes should be associated with some degree of sexual segregation along dietary axes within populations of large, sexually dimorphic herbivores such as elephants.

Stokke (1999) and Stokke & du Toit (2000) found sex related differences in selectivity at the plant species level within Chobe National Park with its high density of 7.6-25 elephants/km^2 (Gibson *et al.* 1998). Bulls were found to uproot woody species, break larger branches and fell trees more frequently than females within family units. Family units were found to access plant parts from higher heights than bull groups (Stokke & du Toit 2000).

According to the BSH, adult elephant bulls would need to meet their high absolute energy requirements either by selecting habitats with high forage biomass, selecting forage species that enable high intake rates, or by increasing their bite size and rate (Miquelle *et al.*1992). I expect bulls not only to pluck a greater number of parts, irrespective of the type, but also to remove a broader range of plant parts from a browsing site than females. Adult males, with their greater tolerance of low quality diets could stay for longer periods at a browsing site eating more plant parts, albeit of lower quality, than females. Females would have to move to additional feeding patches once only highly fibrous plant parts of low nutritional value (low protein and mineral content) remain at the browsing sites. Furthermore, adult males could broaden the range of plant part types that they use at browsing sites as the intake rate of specific plant part types decrease over time. Adult males' increased strength and ability to procure plant parts out of the reach of smaller-bodied females would give them easier access to such plant parts (roots and large branches at greater heights), whilst females would need to search for more accessible plant parts at other browsing sites. In agreement with these postulates, Stokke & du Toit (2000) found that males spent longer times at each browsing site than females. Consequently, I expect bull groups to be more destructive feeders than family units not only because of the larger proportion of vegetation biomass that males need to remove during feeding bouts (Stokke & du Toit 2000), but also because their increased strength which enables them to remove larger plant parts than females. Smaller bodied females and their offspring should include a lesser proportion of the digestible stem material in their diet than larger bodied males.

Feeding height distinctions between the sexes was considered on the basis of the Scramble Competition Hypothesis (Clutton-Brock *et al.* 1987). According to the SCH, smaller bodied animals can tolerate a lower plant biomass because of lower absolute metabolic requirements and will indirectly exclude larger bodied feeders from preferred feeding sites when resources are limited (Ruckstuhl & Neuhaus 2000). When applied to browsing ungulates during periods of resource shortage, this hypothesis predicts feeding height stratification (du Toit 1990) between the sexes as a result of taller males concentrating their feeding at a higher level than females (Stokke & du Toit 2000, Woolnough & du Toit 2001).

This chapter is concerned with feeding height and foraging distinctions between the sexes at the level of plant species and plant part selection. Dietary distinctions between the sexes at the level of foraging paths are discussed elsewhere (Appendix D). Sex related differences in forage type selection as well as the nutrient composition of utilised plant parts and how these relate to nutrient requirements are reported in Chapter 4. I regard bulls within bull groups and females and their smaller bodied offspring within family units as sexually segregated categories of elephant (Chapter 1). The following predictions were made after considering only the woody plant component of the diet of elephants:

(1) Adult male elephants in bull groups will feed more destructively by breaking main stems, snapping branches, uprooting and debarking woody species more often than females within family units.

(2) Adult males in bull groups will pluck a greater number of plant parts, irrespective of the plant part type, at both the individual plant and food plot level, than females within family units.

(3) Adult males in bull groups will remove a wider range of plant parts at a food plot than females within family units.

(4) Adult males will remove a larger proportion of vegetation biomass by having greater bite and break diameters than females within family units.

(5) Adult males within bull groups will feed at higher browsing heights than females within family units.

3.3 Methods

3.3.1 Study area and study period

Refer to Chapter 2 for a detailed description of the study area.

Plant-based surveys of elephant feeding habits were conducted from July until mid-November 2000 to encompass most of the dry season and the transitional period into the start of the rainy season.

3.3.2 Plant-based surveys

Roads within the Association of Private Nature Reserves (APNR) were traversed daily from 06h00 until 18h00 in search of elephants or fresh tracks (no older than 12 hours). Information on the previous day's elephant sightings were gathered from field rangers within the Timbavati- and Klaserie Private Nature Reserves. A route was taken in the direction of the previous day's reported sightings until the animals were either found or fresh tracks could be followed. Within the Umbabat Private Nature Reserve, a set route was followed unless specific information on elephant sightings was available. To prevent possible duplicate sampling of herds within a week's collection time, care was taken to ensure that each day's starting point was at least 50 km from the previous day's search area. Information recorded during surveys included the date, time, location (GPS co-ordinates), and sex and/or group composition of all elephants encountered. Elephants within family units were assigned to age classes by comparison with adults within the herd, according to the methods of Stokke & du Toit (2000).

Plant-based surveys were conducted once the animals had moved off. If fresh tracks crossed the road, plant-based surveys were also conducted on condition that the group type (bull groups, a single male or family unit) could be discerned from the available tracks. Footprint dimensions (Western *et al.* 1983) as well as bolus dimensions (Jachmann & Bell 1984) of faeces along the foraging path were also used to distinguish elephant group types.

Plant-based surveys were adapted from the methods used by Stokke (1999). The first impacted woody species encountered along a foraging path was used as the centre of a food plot with a 5m radius. The feeding path was followed forward until 2-6 consecutive food plots were surveyed. Each food plot thus had a freshly impacted woody plant at its centre. Impact was considered fresh if the sap of exposed stems had not yet dried or discarded plant parts had not dried out, changed colour or withered. The distance between food plots were measured by pacing (a pace averaged 1.1m). None of the food plots was less than 20m from a neighbouring plot. The possibility of interdependence of plant species utilisation or availability at consecutive food plots was furthermore tested and found to be independent (Appendix A). If the elephant group consisted of many individuals that fed parallel to each other, thus creating a broad feeding path, two to six plots were surveyed in a straight line in the direction of the foraging path. The combined feeding plots surveyed along a foraging path constituted a feeding site. A control plot for every second food plot was surveyed 50m perpendicular to the direction of the feeding path, and thus one to three control plots constituted the control site for a particular feeding site.

Within each feeding plot and control plot all woody plants (utilised as well as unutilised) were recorded by species and height. The following eight height classes of woody species were distinguished: 0 to <0.5m, 0.5 to <1m, 1 to <1.5m, 1.5 to <2m, 2 to <2.5m, 2.5 to <3m, 3 to <5m and >5m. To be included in the survey, a woody species on the periphery of the demarcated area had to have at least half of its stem base inside the feeding patch. This applied to single-stemmed as well as multi-stemmed woody species. Breakage heights of utilised woody plants within feeding plots were recorded to the nearest cm. Remaining or discarded food items were carefully examined at each food plot or within the vicinity thereof to establish whether only the bark/leaves were utilised, the whole branch, the whole root or only the heartwood of branches or roots. Bi-directional measurements of all break and bite diameters were measured with a vernier calliper to the nearest millimetre and the average calculated. All breakage diameters and heights were categorised according to the feeding modes in which they occurred (Appendix C).

Basal circumference measurements were made of all newly impacted woody species whether multi- or single stemmed. A combined circumference measurement was taken for all the stems of multi-stemmed species that were closer than 5 cm apart. Where the stems of multi-stemmed species were further than 5cm apart they were measured individually. A single circumference measurement for a multi- stemmed species was then calculated as the mean of the stem measurements.

Estimates of damage, which refers to the percentage of stems that were removed, were made in the field according to Anderson & Walker's (1974) categories: 0%, 1-10%, 11-25%, 26-50%, 51-75%, 76-90%, 91-99% and 100%. When different types of feeding events occurred on an individual plant, an overall estimate of the damage was given. Feeding modes in which the main stem was pushed over or broken were considered to represent 100% damage. Uprooting events in which all the stems were first removed or flattened were also classified as 100% damage. If the plant was left intact and only a proportion of the roots were utilised at a distance away from the main stem, these were measured and the damage estimated as with the bite and break diameters of branches. For all leaf-stripping feeding modes the damage was estimated as being no more than 10%. A distinction was made between new and old damage (*i.e.* damage incurred prior to the most recent feeding bout along the particular feeding path). Damage that was classified as 'old' was not analysed as no distinction could be made between damage caused by bull groups or family units of elephant.

Uncertainties in species identification meant that *Grewia bicolor, G. flava* and *G. monticola* were grouped as "*Grewia* spp.". Likewise, *Commiphora africana, C. glandulosa, C. neglecta* and *C. pyracanthoides* were grouped as "*Commiphora* spp.".

All breakage diameters were categorised according to the feeding modes in which they occurred (Appendix C).

3.3.3 Data analysis

Plant species acceptance

To assess whether family units and bull groups fed on similar woody plant species I calculated acceptance and availability as well as the relative dietary contributions for all woody plants used at food plots and present at food- and control plots. Availability and acceptance indices were calculated for each woody species on a site-specific basis to represent independent sampling sites (Owen-Smith & Cooper 1987a). Availability indices were calculated by dividing the number of food plots in which the species was present by the total number of food plots that were surveyed at a feeding site. The availability index for control plots was calculated by dividing the number of control plots in which a species was present by the total number of control plots that were surveyed at a control site. Acceptance indices were calculated by dividing the number of food plots where a woody species was utilised by the number of food plots in which it was present at a feeding site. A mean acceptance index as well as a mean availability index was calculated for each woody species across all the sites in which this species was present or had been utilised. Woody species that were available at 10 or more food plots of either family units or bull groups were ranked according to their acceptance frequencies.

Principal foods refer to those that are eaten in the greatest quantities although they may not necessarily be the preferred species (Petrides 1975). Principal foods were thus determined for both bull groups and family units by dividing the number of individual plants that were utilised within a species by the total number of utilised woody plants to obtain species-specific, relative dietary contributions.

Plant part acceptance

To establish whether bull groups selected plant parts in different proportions to family units, I counted the number of plant parts types (stem bark, twigs, heartwood or roots) that were removed per individual plant. Hence each individual breakage point indicated the number of plant parts that were removed within a particular categorised feeding mode (Appendix C). When bark was removed from the main stem it was counted as a single bark-stripping event. Likewise, the number of leaf-stripping events per individual plant was underestimated as separate leaf-stripping events could not be distinguished from each other. Thereafter I summed the number of different plant parts removed across all individuals from all species and calculated the relative dietary contribution of each plant part type by dividing the number of a particular plant part type by the total number of plant parts that were removed by either bull groups or family units.

To test whether bull groups removed more plant parts per individual plant than family units, I counted the number of plant parts removed per individual plant, irrespective of the plant species and then averaged across all individual plants utilised within a particular feeding mode by either bull groups or family units. To determine whether bull groups removed more plant parts per food plot, the number of plant parts within the same feeding mode were summed within each food plot and then averaged across all food plots. The Shannon-Wiener diversity function (*H'*) (Krebs 1985) was used to determine the diversity of plant parts that were utilised at food plots and thereby establish whether bull groups utilised a wider range of plant parts per food plot than family units.

As both bull groups and family units of elephant fed on only one individual plant at the majority of the food plots (69% for bull groups and 74% for family units) and as the acceptance and availability of woody species at consecutive food plots was not autocorrelated (Appendix B), breakage diameters per individual plant were considered independent samples. Breakage diameters categorised according to the abovementioned feeding modes were thus first averaged within individual plants to represent independent samples and thereafter averaged across all species within either bull groups or family units of elephant to test whether bull groups removed a larger proportion of the vegetation than family units.

The number of individual plants within each impact class was counted for both bull groups and family units of elephant to determine whether bull groups damaged more woody plants in the higher impact classes than family units. To determine whether bull groups felled trees more often than family units, the number of trees felled by either of the social units was counted. Trees were defined as perennial woody plants with a single main stem and a distinct upper crown (Van Wyk & Van Wyk 1997). Single stemmed plants with basal measures > 6 cm were used to distinguish trees from shrubs according to the guidelines given by Walker (1976). As the upper crown of smaller trees were on occasion utilised to such an extent that the height of the tree could no longer be accurately measured, heights in excess of 2m were also considered to distinguish trees from shrubs. Trees were felled by either bull groups or family units to access smaller plant parts such as twigs, bark and heartwood or to remove the roots. As all uprooting events by family units included only shrubs (*Grewia* spp.), these were excluded from the analysis.

Plant part consumption and level of impact was calculated at the species level for those species that were available in ten or more feeding plots and utilised in at least five plots by either bull or family units. Six species fell within this category (*Albizia harveyi*, *Colophospermum mopane*, *Dichrostachys cinerea*, *Dalbergia melanoxylon*, *Grewia* spp., and *Lannea schweinfurthii*). Impact levels were obtained by firstly converting stem circumference to stem area for each individual woody plant within a species. The impact class middle frequencies were then weighted by the log transformed stem areas and the average determined within a species for each of the six species as described in Anderson & Walker (1974).

Height class acceptance and browsing heights

To determine whether family units and bull groups browsed at food plots with the same vegetation structure in terms of woody plant height, I calculated height class acceptance values for all woody plants that were used at food plots while height class availability values for woody plants present at both food and control plots were also calculated. The frequency of occurrence of all individual woody plants, irrespective of the species in each of the eight height class intervals, was determined at the food plots and control plots of both family units and bull groups of elephant. Height class acceptance values were obtained by dividing the number of woody plants utilised within a particular height class by the total number of woody species accepted by either bull groups or family units. Height class availability indices were determined by dividing the total number of woody plants present within a height class by the total number of woody plants found at either bull groups or family unit's food plots.

To test whether bull groups browsed at higher heights than family units, breakage heights were firstly categorised according to feeding modes as main stem breakage to access smaller parts, branch breakage to access smaller parts, branch breakage to consume the pith or bark on the proximal end of the branch and twig breakage to bite twigs or leaf strip branchlets. Breakage heights were thereafter averaged within each of these feeding modes per individual plant and then averaged across plants utilised in the same manner. As both bull groups and family units of elephant fed on only one individual plant at the majority of the food plots (69% for bull groups and 74% for family units) and as the acceptance/availability of woody species at consecutive food plots was not autocorrelated, breakage heights per individual plant were considered independent samples. I also compared the mean browsing height between family units and bull groups over all species, irrespective of the feeding mode to compare my results with those of Stokke & du Toit (2000). Thereafter I compared the browsing heights of bull groups and family units in greater detail within each of the various feeding modes described earlier. To test whether the prediction of the Scramble Competition Hypothesis would be more apparent within woody species that were in high demand by both social units of elephant, I pooled browsing height data across woody species that were commonly utilised by both bull groups and family units prior to determining browsing height distinctions between each of social units of elephant.

Statistical analysis

Plant species acceptance and availability indices were grouped into three periods which differed in rainfall conditions. These periods were based on the total monthly rainfall recorded. The three rainfall periods included the early dry- (July-August 2000), dry- (September 2000) and transitional (October-November 2000) months. Three-way ANOVA with period, plant species and elephant group type as factors was used to test whether rainfall influenced plant species acceptance and availability indices at the food plots of bull groups and family units. To avoid reporting rare plants that were utilised as being highly acceptable, all woody species included in the analysis were available at 10 or more food plots and accepted at five or more food plots of both bull groups and family units of elephant (Owen-Smith & Cooper 1987a, 1987b). Proportional data was arcsine transformed prior to ANOVA analyses (Fry 1993). The interaction between period, plant species acceptance or availability and group type (bull groups and family units) did not prove significant (Appendix E). Thereafter, plant species acceptance and availability frequencies were pooled across all months.

I constructed contingency tables and used Pearson's χ^2 test to evaluate whether the expected cell frequencies under the respective model were significantly different from the observed frequencies, thereby indicating an interaction between sex and plant part utilisation and impact levels. Prior to this, I determined whether the abovementioned rainfall periods had a significant effect on the frequency of particular categories of plant parts utilised by either bull groups or family units. The following feeding modes were combined to increase the frequencies of occurrence within each feeding mode: the frequency of branch breaking events to consume either the heartwood or bark, leaf-stripping and twig breakage events and finally main stem breakage and uprooting events were pooled as an 'other' category. As the interaction between period, plant part and group type (bull groups and family units) did not prove significant, the frequency of plant part use was thereafter pooled across all months to increase the sample sizes for further analyses (Appendix E). Pearson's χ^2 test was also used to determine which height classes bull groups and family units utilised more than expected. The same analysis method was used to determine which height classes were more frequently available at the food plots than at the control plots of both bull groups and family units. Individual cell χ^2 values were used to evaluated the degree of deviation between the observed and expected frequencies. Log-linear estimates measured how the proportional mean frequency of all cells within the category deviated from the proportional mean frequency of all the cells in the contingency table. Hence *P*-values for individual cells were approximate and indicated how each cell contributed to the overall significance of the model (Christensen 1990). The details of the log-linear analyses are given in Appendix F. All log-linear analyses were done using SAS (Anon. 1989).

Spearman's rank correlation test (r_s) was used to determine the relationship between the acceptance indices for woody species within bull groups and family units. Fisher exact test (one-sided) was used to test whether bull groups accepted *Colophospermum mopane* and *Lannea schwienfurthii* more frequently than family units. This same method was used to determine whether bull groups felled trees more often than family units (Zar 1996). The relationship between the height class acceptance and availability indices within bull groups and family units was determined with Spearman's rank correlation test.

Browsing height, break diameters, species-specific impact and the number and diversity of plant parts utilised were compared between bull groups and family units of elephant. Data were tested for normality (Kolmogorov-Smirnov test) and homoscedasticity (Barlett's test), and log transformed according to Fry's (1993) ladder of powers to enable parametric, one-tailed, unpaired *t*-tests between bull groups and family units. Proportional data were arcsine transformed prior to comparisons between group types. Residual plots were used to determine whether data transformations were appropriate. Where variances remained unequal after transformation, a *t*-test with Welsch's correction was used. Where samples were too small to test for normality, nonparametric Mann-Whitney *U* tests were used to compare the abovementioned data between bull groups and family units (Zar 1996). All tabulated values represent the sample mean followed by the standard error of the mean**.**

Two-way ANOVA was used to determine what effect sex and height class categories had on browsing heights. The transformed data (log x+1) on the height at which large branches were broken to access smaller plant parts were used as response variable with sex and height class categories as categorical predictor variables. Hence interaction effects were evaluated to determine whether bull groups fed at higher heights in relation to the taller trees that they used when compared to family units. Distinctions were made between small- (0 to <2m), medium- (2 to < 3m) and tall woody plants (>3m) to increase the samples within each category, thereby ensuring balanced designs (Zar 1996).

3.4 Results

3.4.1 Diet selection at the plant species level

Fifty of the 92 woody species recorded in the 250 food- and 90 control plots were not utilised by elephants. All species present at five or more food plots but avoided by either social unit of elephant are listed in Appendix G (Table G1). The relationship between the acceptance index and availability index as well as the categorisation of all woody plants according to their acceptance frequencies by either bull groups or family units are also given in Appendix F. A narrow range of 6-8 plant species made up 70-80% of the diet of elephants. *Grewia* species were the principal food to both family units and bull groups as this set of species made up 41% of the diet utilised by family units and 38% of the diet utilised by bull groups (Figure 3.1). In comparison with other species, *Grewia* species were also more frequently available than other woody species for both group types of elephants (Figure 3.2). Bull groups and family units fed from similar plant species as indicated by the significant positive relationship between the acceptance frequencies for plant species by each of these social units (Figure G1: n=17, r_s=0.747, *P*=0.0006). However, bulls accepted *Lannea schweinfurthii* more frequently than family units (Figure 3.2: 0.46 vs 0.27, *P*=0.0178). Bulls did not accept C*olophospermum mopane* more frequently than family units (Figure 3.2: 0.47 vs 0.29, *P*=0.0676).

3.4.2 Plant part usage

Bull groups and family units differed in their proportional use of plant parts (χ^2=107, *df*=4, *P*<0.0001). Although both social groups consumed large proportions of stems in comparison to other plant parts, family units used bark and leaf-stripped woody plants without stem browsing approximately twice as many times as bull groups. Contrary to family units, bull groups removed almost twice as many roots and snapped twigs more than 1.5 times as frequently as family units (Figure 3.3). Bull groups also removed significantly more (*t*=2.23, *df*= 243,

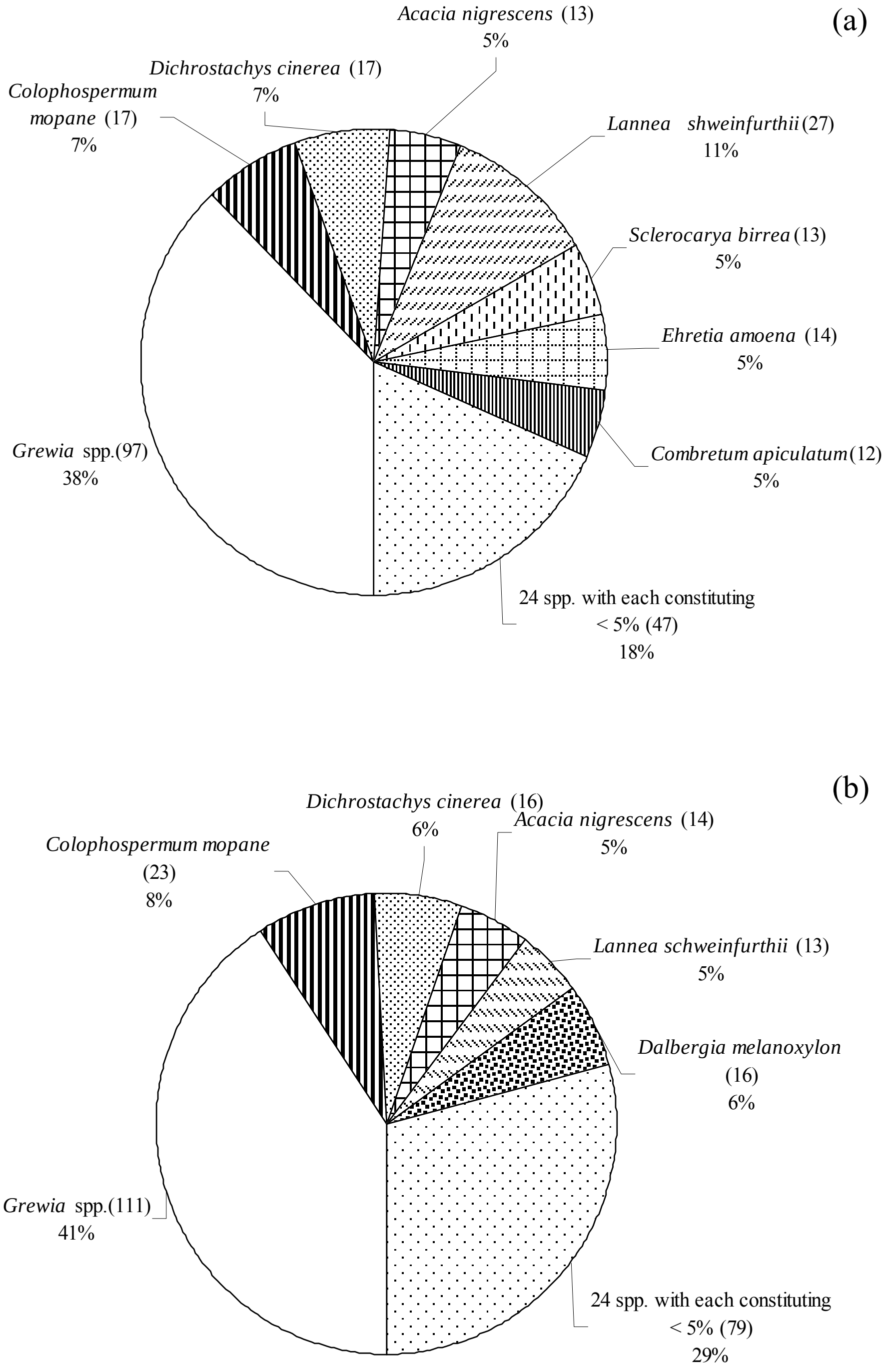
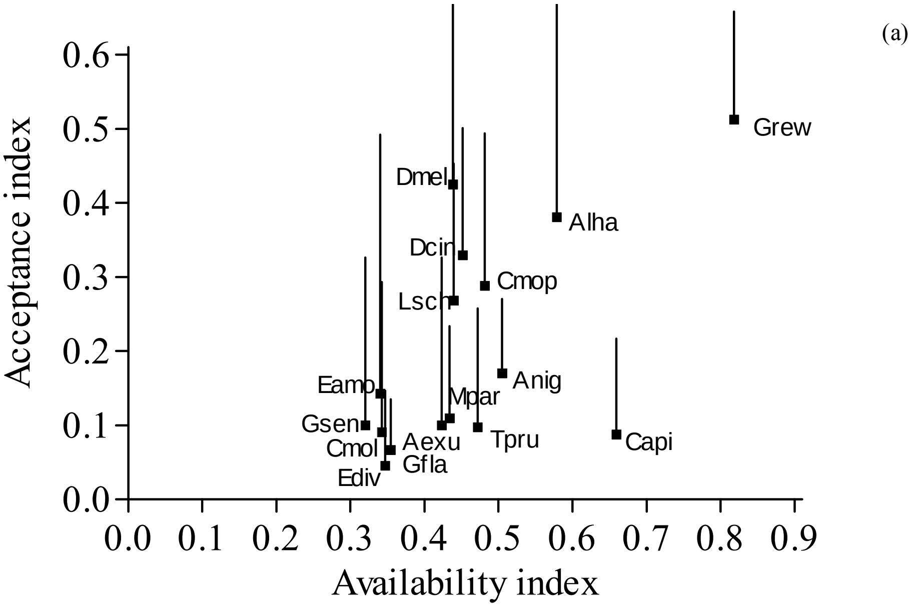


Figure 3.1 Relative dietary contributions of woody plant species that were utilised by (a) bull groups and (b) family units of elephants during the dry season. The number of individual plants of each species is given in brackets.



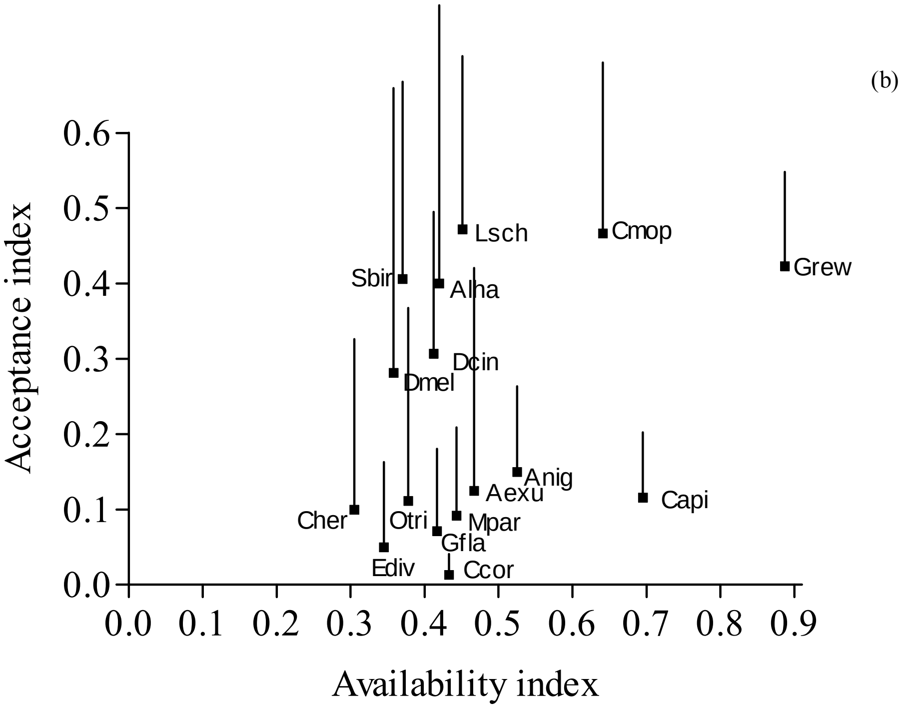


Figure 3.2 Acceptance and availability indices for woody species that were available at 10 or more food plots of either (a) family units or (b) bull groups of elephant. Lines indicate the upper 95% confidence interval for the acceptance indices.

Aexu=*Acacia exuvialis*, Alha=*Albizia harveyi*, Anig=*Acacia nigrescens*, Capi=*Combretum apiculatum*, Ccor=*Cissus cornifolia*, Cher=*Combretum hereroense*, Cmol=*Commiphora mollis*, Cmop=*Colophospermum mopane*, Dcin=*Dichrostachys cinerea*, Dmel=*Dalbergia melanoxylon*, Eamo=*Ehretia amoena*, Ediv=*Euclea divinorum*, Gfla=*Grewia flavescens*, Grew=*Grewia* spp, Gsen=*Gymnosporia senegalensis*, Lsch=*Lannea schweinfurthii*, Mpar=*Maerua parvifolia*, Otri=*Ormocarpum trichocarpum*, Sbir= *Sclerocarya birrea*, Tpru=*Terminalia prunoides*.

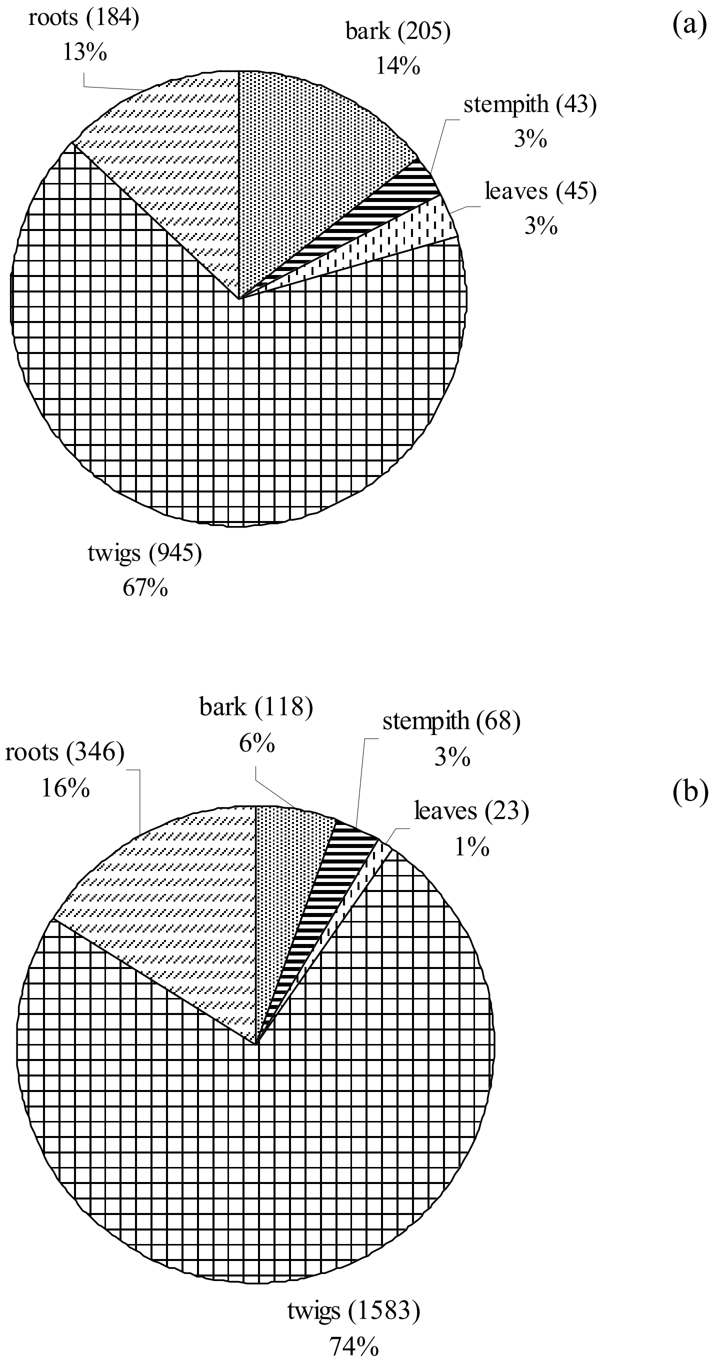


Figure 3.3 Relative dietary contributions of woody plant parts that were utilised by (a) family units and (b) bull groups of elephants during the dry season. The number of individual plants of each species is given in brackets.

P=0.0267) and larger twigs (*t*=2.06, *df*=243, *P*=0.0400) per individual plant than family units (Table 3.1 & 3.2).

Irrespective of the woody species, bull groups removed more plant parts per food plot (19.4 ± 2.58, *n*=124) than family units (12.1 ± 1.36, *n*=126; *t*=1.93, *df*=248, *P*=0.054). These differences could be ascribed to bull groups being less likely to only use one individual plant per food plot when compared to family units and also because they often removed more plant parts, irrespective of the type, per individual plant than family units. The range of different plant parts that were used by either of the elephant group types did not however, differ significantly (*U*=7615, *P*=0.723) as family units had similar Shannon Wiener diversity indices for the types of plant parts that were removed per food plot (0.530 ± 0.0513, *n*=126) when compared to those of bull groups (0.534 ± 0.0476, *n*=124). On a species-specific basis, bull groups removed more plant parts from *Grewia* species (6 vs 4, *t*=2.80, *df*=216, *P*=0.006), *Colophospermum mopane* (6 vs 2, Mann-Whitney *U*=97.5, *P*=0.004) and *Acacia nigrescens* (35 vs 9, Mann-Whitney *U*=46.5, *P*=0.010) than family units (Appendix H, Figure H1). These three species constituted 54% of the total number of plants that were utilised by family units and 50% of the plants that were used by bull groups.

3.4.2 Break diameters

Irrespective of the feeding mode, bull groups had larger break and bite diameters than family units (Table 3.2). However, this difference was not significant for the break diameter of branches broken to consume the heartwood or bark off the proximal end of the broken branch. Bulls had significantly larger break/bite diameters than family units when they snapped off main stems (16 vs 5.7cm, Mann Whitney U=59.0, P=0.026), large branches (3.6 vs 2.7cm, t_{130}=2.24, df=130, *P*=0.026), twigs (0.85 vs 0.73cm, t_{243}=2.06, *P*=0.040) and roots (2.0 vs 1.6cm, t_{65}=2.82, *P*=0.006).

3.4.3 Intersexual differences in vegetation impact

The basal circumference of impacted plants was similar whether used by bull groups (28.2±1.51cm) or family units of elephant (23.0±1.06cm). However, the level of impact differed significantly between the bull groups and family units (χ^2=17.0, *df*=7, *P*=0.0179). Bull groups more frequently uprooted and broke the main stem or large branches of woody plants

Table 3.1 The number of plant parts (mean ± SEM) removed per individual plant subjected to a specific type of feeding mode for family units or bull groups of elephant. The number of individual plants utilised within each category is given in brackets. Significant differences ($P<0.05$) between the social units of elephants are given in bold.

Plant part type[a]	Family units	Bull groups	P-levels
Branch breakage to access smaller parts	1.9 ± 0.25 (52)	3.2 ± 0.52 (80)	U=1749, P=0.0568 [b]
Branch breakage to consume bark on the proximal end of the branch	2.3 ± 0.19 (91)	2.1 ± 0.20 (65)	U=2598, P=0.206
Branch breakage to consume the pith on the proximal end of the branch	3.1 ± 1.5 (7)	7.7 ± 3.2 (6)	U=18, P=0.191
Uprooting to consume the roots	8.0 ± 2.0 (23)	7.9 ± 1.1 (44)	U=504, P=0.490
Twig bite or breakage to consume the whole twig	7.8 ± 1.7 (122)	13 ± 2.0 (123)	**t=2.2, df=197, P=0.0267**[c]

[a] As main stem breakage and leaf-stripping were each counted as single plant-part removing events, these feeding modes were not included in the analysis.

[b] Mann-Whitney U tests (one-tailed).

[c] Unpaired t-test using Welsch's correction for unequal variance (one-tailed).

Table 3.2 The mean diameter ± standard errors of breakage points for all woody species that were utilised by family units and bull groups of elephants. The number of individual plants from which the break diameters were determined is given in parentheses. All values were recorded to the nearest cm. Significant differences ($P<0.05$) between the social units of elephants are given in bold.

Feeding mode	Family units	Bull groups	P-value
Main stem breakage to access smaller canopy parts	5.7 ± 2.0 (11)	16 ± 3.6 (19)	**U=59, P=0.026**
Branch breakage to access smaller parts	2.7 ± 0.26 (52)	3.6 ± 0.31 (80)	**t_{130}=2.2, P=0.026**
Branch breakage to consume bark or heartwood on the proximal end of the branch	2.1 ± 0.14 (98)	2.2 ± 0.19 (71)	t_{167}=0.74, P=0.464
Twig bite or breakage to consume the whole twig	0.73 ± 0.040 (122)	0.85 ± 0.040 (123)	**t_{243}=2.1, P=0.040**
Root breakage to consume the roots	1.6 ± 0.13 (23)	2.0 ± 0.11 (44)	**t_{65}=2.8,P=0.006**

and hence impacted heavily on the vegetation when compared to family units. Family units were found to bark strip small branches and defoliate woody species by means of leaf-stripping and twig biting. The abovementioned greater tendency of family units to leaf strip woody plants was substantiated by the higher occurrence of woody species that were utilised and placed into the low impact category (1-10%), which primarily represented leaf-stripping or light twig browsing, when compared to bull groups. Bull groups, when compared to family units, utilised nearly twice as many woody plants in the highest impact category (100%) where main stems were broken, pushed over, uprooted or ring-barked (Table 3.3). Furthermore, bull groups felled significantly more trees than family units (22 vs 2, Fisher exact test, *P*=0.0002). Appendix I lists the woody species that qualified as 'trees' where either bull groups or family units had broken their main stem to access smaller plant parts or uprooted them to feed on their roots.

Small sample sizes and large variations in the level of impact between individuals of the same species, generally masked significant species-specific differences in the level of impact between bull groups and family units. Although bull groups removed significantly more plant parts from *Acacia nigrescens* than family units (35 vs 2, Mann-Whitney *U*=46.5, *P*=0.010), family units impacted more heavily on *Acacia nigrescens* (Mean percentage impact: 35 vs 29, Mann-Whitney *U*=54.0, *P*=0.038) than bull groups (Appendix G, Figure G2). As family units were found to bark-strip the main stem of this species, the level of impact largely depended on the type of plant part that was removed.

Table 3.3 The frequency distribution of various impact categories of all woody species that were present in the feeding plots of either bull groups or family units of elephant.

Level of impact (%)	Family units	Bull groups
0	2721	2512
1-10	144	108
11-25	51	44
26-50	27	17
51-75	10	16
76-90	12	9
91-99	15	20
100	25	49
Total number utilised	284	263

3.4.4 Browsing height

The proportion of woody plants utilised within particular height classes was dependent upon whether bull groups or family units fed upon them (χ^2=22.0, *df*=7, *P*=0.0025). When comparing the heights of woody plants that were utilised by bull groups with those of family units, each social unit of elephant utilised woody plants at heights of 2-2.5m (*P*=0.0004, Appendix F) and > 5m (*P*=0.0033, Appendix F) differently. Family units utilised more than double the proportion of woody plants with a height of 2-2.5m, when compared to bull groups. Family units utilised only 41% of the proportion of tall woody species (>5m) that bulls utilised

(Table 3.4). Bulls selected feeding sites with taller woody species (>5m) than the surrounding area as the food plots of bull groups had more trees >5m available to them when compared to those of family units (χ^2=20.4, *df*=7, *P*=0.0047), while the opposite was true for the control plots of both social units (χ^2=15.4, *df*=7, *P*=0.0314). The acceptance indices of woody plants abruptly increased above a height of 2m for family units and 2.5m for bull groups while the availability indices for these height classes correspondingly decreased (Figure 3.4). The utilisation of woody species height classes was therefore inversely related to the height class availability for both family units (n=8, r_s=-0.738; $P<0.05$) and bull groups (n=8, r_s=-0.881; $P<0.01$).

Table 3.4 Frequency distribution of all woody plants that were accepted in the food plots and available in both the food plots and control plots of family units and bull groups of elephant.

Numerical value and height interval (m) for height class categories 1-8		Number of woody plants accepted at food plots		Number of woody plants available at food plots		Number of woody plants available at control plots	
		Family unit	Bull groups	Family unit	Bull groups	Family unit	Bull groups
1	0 to < 0.5	14	21	322	295	86	73
2	0.5 to < 1	20	13	638	516	218	135
3	1 to < 1.5	35	32	563	551	190	169
4	1.5 to < 2	45	46	513	479	191	147
5	2 to < 2.5	72	35	397	371	102	98
6	2.5 to < 3	35	37	226	219	80	60
7	3 to < 5	47	43	269	224	78	69
8	> 5	16	36	77	120	41	15
Total		284	263	3005	2775	986	766
Chi square test		χ^2=22, *df*=7, *P*=0.0025		χ^2=20, *df*=7, *P*=0.0047		χ^2=15, *df*=7, *P*=0.0314	

Bull groups had significantly higher browsing heights than family units when tested across all woody species and irrespective of the feeding mode (bull groups: 1.30 ± 0.08m; family units: 1.02 ± 0.04m; t=2.42, *df*=415, *P*=0.008). Contrary to predictions that competition and therefore browsing height distinctions would be more pronounced in plant species that both social units required in large dietary proportions, the differences in browsing height between bull groups and family units were within the same range when compared within common food plants (*Albizia harveyi*, *Colophospermum mopane*, *Dichrostachys cinerea*, *Dalbergia melanoxylon*, *Grewia* species, and *Lannea schweinfurthii*). The difference in browsing height between bull groups and family units for the abovementioned species were

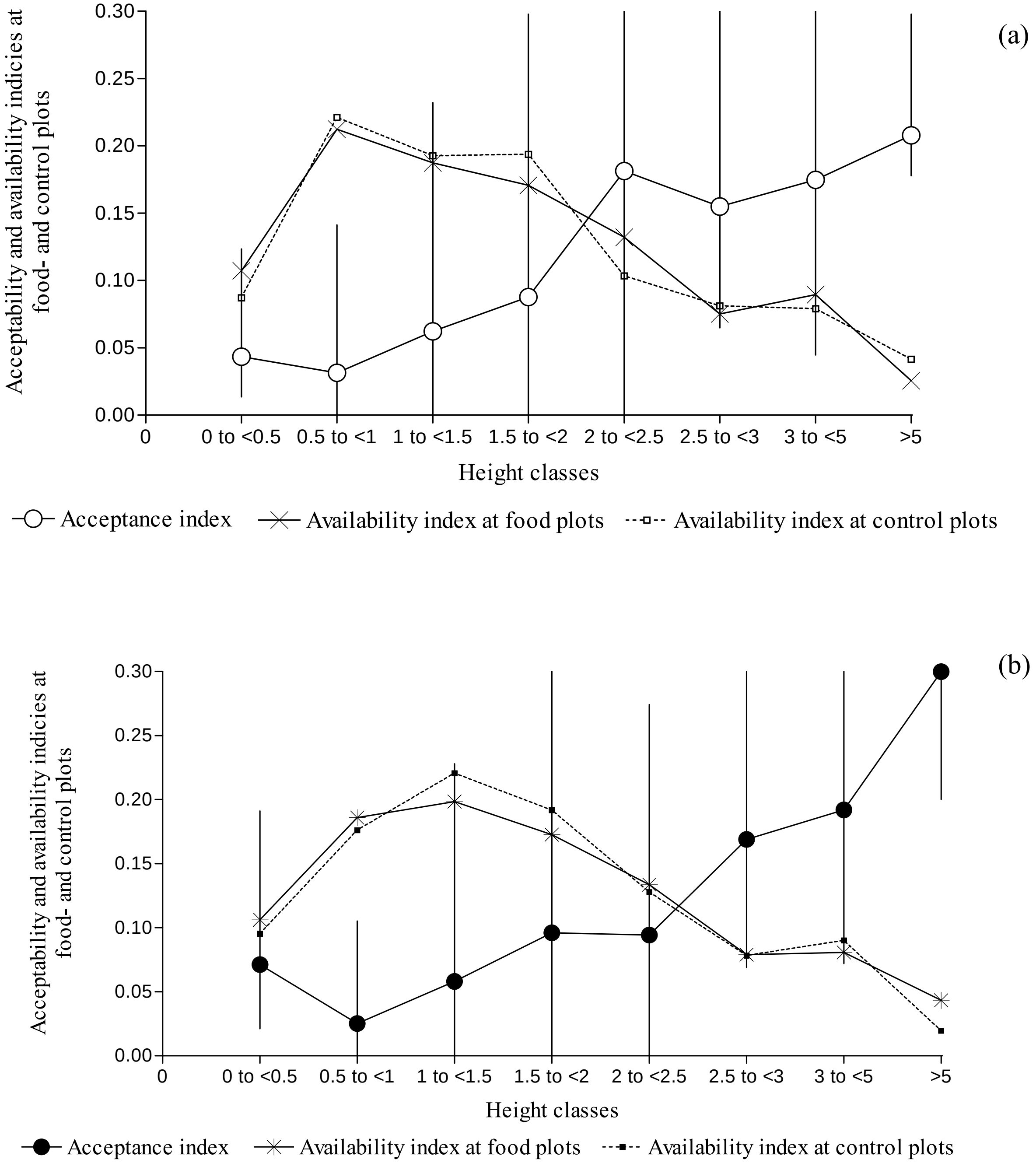


Figure 3.4 The height class acceptability and availability at food plots as well as control plots against height classes for family units (a) and bull groups (b) of elephants. Vertical lines indicate the 95% confidence intervals for the height class acceptance indicies at food plots. All heights were measured in metres.

still within a narrow margin of approximately 30 cm (bull groups: 1.16 ± 0.04m; family units: 0.899 ± 0.09m; *t*=-2.13, *df*=256, *P*=0.0170).

When comparing breakage heights between elephant groups within various feeding modes (Table 3.5), bull groups not only broke large branches more frequently than family units (80 vs 52 woody plants, one sided χ^2=14.9, *df*=1, *P*=0.0001) but also did so at significantly higher heights than family units (2.0 vs 1.4m, *t*=2.74, *df*=93, *P*=0.007). Both the elephant group type and the height class of the browsed plant accounted for 50% of the variance in the height at which large branches were broken (R^2=0.496, $F_{2,107}$=21.0, *P*<0.0001). Hence bull groups increased the breakage height of large branches in relation to the height class of the woody plant that they utilised (Appendix J).

Table 3.5 The mean height ± standard errors of breakage points for all woody species that were utilised by family units and bull groups of elephants. The number of individual plants from which the breakage heights were determined is given in parentheses. Significant differences (P<0.05) between the social units of elephants are given in bold.

Feeding mode	Family units	Bull groups	*P*-value
Main stem breakage to bark strip or to access smaller canopy parts	0.34 ± 0.13 (11)	0.30 ± 0.10 (19)	*U*=86, *P*=0.210
Large branch breakage to access smaller parts	1.4 ± 0.11 (50)	2.0 ± 0.20 (62)	**t_{93}=2.7 *P*=0.007**
Branch breakage to consume bark or heartwood on the proximal end of the branch	0.87 ± 0.060 (91)	1.1 ± 0.15 (54)	t_{68}=1.2, *P*=0.231
Twig bite or breakage to consume the whole twig	1.0 ± 0.071 (104)	1.2 ± 0.082 (93)	t_{195}=1.1, *P*=0.288

3.5 Discussion

Diet selection differences at the plant species level were not apparent when comparing bull groups with family units within the APNR. Contrary to these findings, Stokke (1999) and Stokke & du Toit (2000) found that family units within the Chobe system fed from significantly more woody species than bull groups while their food plots contained the highest density of palatable woody species when compared to the surrounding area. The density of elephants within my study area (0.41 elephants/km^2) was only approximately 5% of density of the Chobe National Park's elephant population (7.6 elephants/km^2) (Hall-Martin 1992, Gibson *et al.* 1998). The higher density of elephants within Chobe National Park would place the vegetation under comparatively more pressure during periods of resource limitation than within the APNR. Hence, social units within Chobe may need broaden their dietary breath at plant species level to obtain sufficient high quality plant parts to meet their nutritional needs.

According to Owen-Smith & Danckwerts's (1997) categorisation of plant part use, elephants within the APNR could primarily be described as stem browsers rather than folivores. Stem browsing represents a critical dry season reserve to both bull groups and family units of elephant when deciduous woody species loose their leaves (Bell 1985). Other 'nutritional stepping stones' (Owen-Smith & Cooper 1989) such as bark and roots also formed important dietary components to elephants. Prior to leaf abscission, protein and minerals are retranslocated from senescing leaves (Bloom *et al.* 1985), making roots and bark a potentially valuable food resource to both bull groups and family units of elephants when deciduous species start losing their leaves.

In support of the prediction that bull groups remove a larger proportion of phytomass per feeding bout, bull groups were involved in tree felling and large branch breaking more frequently than family units and also had greater bite or break diameters within each of these feeding modes when compared to family units. Since bulls spend longer times at food plots than cows (Barnes 1982, Stokke & du Toit 2000), bull groups also removed more plant parts per food plot than family units. Hiscocks (1999) found that elephant bulls were responsible for 94% of uprooted trees while Guy (1976) and Barnes (1979) found that males engaged in tree felling more frequently than females. Social reasons such as dominance displays by bulls have been proposed as a possible causal factor for tree felling (Napier Bax & Sheldrick 1963, Guy 1976, Hiscocks 1999). De Villiers (1996) did however find that bulls utilised the roots and bark of all trees that were felled. In agreement with these findings, I found that all woody plants that were felled by bulls were eaten.

In spite of the overlap in plant part use between bull groups and family units, the results of this study were in agreement with the findings of Stokke & du Toit (2000). Bulls consumed roots, broke branches and felled trees more frequently while cows preferentially leaf-stripped woody plants. Intersexual distinctions in plant part use may depend not only on the nutritional needs of bull groups and family units (Chapter 4). As each plant also differs structurally it presents an animal with diverse harvesting and processing challenges (Shipley & Spalinger 1992). Adult males can ingest large dietary volumes while their larger body size provides them with a greater ability to obtain food items that may require either taller or stronger animals than those found within family units. Both procurement abilities and the amount of food required therefore increase with increasing body size (Janis 1976, Demment & van Soest 1985, Duncan *et al.* 1990, Illius & Gordon 1992). The results suggest that bulls are able to increase their intake rates firstly by procuring more plant parts per utilised plant, thereby decreasing their search effort, and then by having larger bite and break diameters than family units. Bulls could therefore simply remove larger plant parts because they are stronger.

My results as well as those of Guy (1976), Jachmann & Bell (1985) and Stokke & du Toit (2000), show that elephants mainly feed below 2m above the ground. Although bull groups showed significantly higher mean feeding heights than family units, there was still considerable overlap across the range of browsing heights of both bull groups and family units. Laws (1966) measured asymptotic shoulder height differences of 26cm between adult male and female elephants from Queen Elizabeth National Park in Uganda. These differences in feeding height between the social units were therefore consistent with the height differences between the sexes. Nevertheless, the results suggest that at tall trees (>3m) bulls selectively broke larger branches more frequently and from higher heights than family units. Hence, bulls could have exclusive access to high quality resources because larger elephants can reach higher whilst browsing. Contrary to my results, Stokke & du Toit (2000) found that family units fed at higher heights than bulls.

Another factor, which could influence plant part selection between bull groups and family units, could be the different social environments in which group members find themselves. Lindsay (1994) suggested that females might need to move constantly to ensure group cohesion. Furthermore, Lindsay (1982) and Western & Lindsay (1984) found that large elephant aggregations could be maintained if habitat types, such as open grasslands were selected where plants were easily harvested. Likewise, Jarman & Jarman (1979) found that during the dry season, impala (*Aepyceros melampus*) were unable to maintain the same group cohesion whilst browsing when compared to grazing. Barnes (1982) found that elephant bulls in small groups had longer feeding bouts than females in family units while Stokke & du Toit (2000) found that males spent longer at each browsing site than females. The results indicate that plant parts such as roots, may also be nutritionally important to family units when deciduous plant species have lost their leaves, but herd members may be restricted to plant parts that are comparatively easier to harvest to ensure that no group member falls behind whilst feeding. All members of a family unit were frequently observed breaking stems of *Grewia* species and debarking them while moving forward towards the next plant.

In conclusion, these results show that selection at the plant species level may be too broad to look for dietary distinctions between bull groups and family units. Dietary distinctions between the sexes may only be shown by comparing how each social unit feeds on plant parts of the same plant species. Differences in nutritional needs, abilities to procure plant parts and the social environment of bull groups as opposed to family units provided possible explanations for observed sex-related differences in the proportional use of plant parts. In support of the BSH, the results suggest that bulls are ingesting plant parts of higher fibre content than females within family units. However, the nutritional content of the different plant parts and how this relates to feeding distinctions in plant part use between the social units of elephant, requires further investigation. The more destructive feeding habits of bull groups as apposed to family units could be parsimoniously explained by bulls being both stronger and taller than smaller-bodied females. Hence bulls were found to have a higher impact on the vegetation than family units.

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CHAPTER 4

Sex differences in elephant diet selection at the nutrient scale

4.1 Abstract

According to the predictions of the Body Size Hypothesis, family units of elephant should ingest plant tissue of higher quality than bull groups given the reproductive demands of pregnancy and lactation coupled with the higher mass specific metabolic demands of smaller bodied animals within family units. Plant samples were collected at the food plots of bull groups and family units within the lowveld savanna system of southern Africa. Diet quality measures (nitrogen, phosphorus, calcium, fibre and total soluble sugar content) were compared between these two social groups at the feeding site, food plot, plant species and plant part level. Diet quality measures did not differ between elephant groups at either of the spatial scales that were tested. However, the proportional use of plant parts by each of the social units of elephants was in accordance with their nutritional value.

4.2 Introduction

During dry season periods herbivores are frequently protein (Bell 1971, White 1978) or energy limited (Owen-Smith & Novellie 1982, Owen-Smith & Cooper 1989). Numerous studies have also indicated the importance of mineral nutrition to free-ranging ungulates (Weir 1972, Belovsky 1978, McNaughton 1990). Most herbivores select diets which contain high quality green, leafy material when available (Bell 1986). However, as the season progresses and deciduous species loose their leaves; high quality leaf tissue becomes scarce. During such times large herbivores can increase their dietary breath to incorporate other abundant plant tissues albeit of lower quality (Demment & Van Soest 1985). A decline in the nutritive value of plant parts is generally associated with increased lignification and a decreased proportion of leaves to stems. Large herbivore species are, however, more tolerant of low quality forage than smaller bodied species as the increased gut capacity of large herbivores ensures that retention times are sufficient for adequate extraction of slowly digestible nutrients. Furthermore, the large gastrointestinal volume of large bodied animals is best suited for bulky fibrous forage (Van Soest 1994). This forms the basis of the Jarman-Bell principle (Bell 1971, Jarman 1974) according to which larger animals with their lower mass specific metabolic needs and increased gut capacity are more tolerant of low quality diets (higher in fibre and lower in protein content). In agreement with the Jarman-Bell principle, Hoppe (1977) found that the proportion of non-stem material in the digesta of various large herbivores declined with increasing body mass.

Stokke & du Toit (2000) extended the Jarman-Bell principle to intra-specific level and proposed the so-called Body Size Hypothesis (BSH) according to which different metabolic rates based on sex related differences in body size within a species could lead to differential nutritional requirements. This extension of the Jarman-Bell principle to intra-specific level seems justified by the basic structural mechanisms underlying allometric scaling identified by West *et al.* (1997). Furthermore, a mass exponent of 0.67 was found to best represent intra-specific scaling of metabolic rate by Feldman & McMahon (1982). Any mass exponent less than 1.0 implies that smaller animals need more nutrients per unit body weight than larger ones (Van Soest 1994).

According to the BSH, smaller bodied female elephants should be more selective for nutritious plant parts such as leaves or soft shoots when compared to adult males, even though such items may be rare during the dry season. These plant part preferences ensure the ingestion of rapidly digestible plant items high in nutrients and minerals which smaller bodied females require to meet their higher mass specific metabolic demands coupled with the added demands of pregnancy or lactation. The nutritional quality of stems furthermore depends on their diameter and whether they contain heartwood. Stems with larger diameters are generally more fibrous because of increased lignification (Van Soest 1994). A decrease in digestibility with increased twig diameter is also partly caused by a decrease in the bark/heartwood ratio (Hjeljord *et al.* 1982). Previous results confirmed that males had consistently larger stem break and bite diameters and were therefore probably ingesting higher fibre diets when compared to females within family units (Stokke & du Toit 2000). Furthermore, adult male elephants were found to consume roots more frequently, while adult females preferentially leaf-stripped or debarked small branches (Chapter 3). Although numerous studies have documented the comparatively high nutritional value of leaves within the diets of elephants (Napier Bax & Sheldrick 1963, Field & Ross 1976, Jachmann 1989, Holdo 2003), only Barnes (1982) and Stokke & du Toit (2000) found that females and smaller bodied offspring within family units used leaves more frequently than adult bulls. Hence the nutritive value of plant parts chosen by either bull groups or family members requires further investigation.

In sexually dimorphic species such as elephants, females not only have to contend with the metabolic constraints of a smaller body size but also the added nutritional demands of pregnancy and lactation compared with males. Reliable estimates of nutrient requirements for maintenance and reproduction in elephants are not available. Estimates based on the mean values for several allometric equations extracted from the literature and calculated according to the methods of Lindsay (1994) (Appendix A), indicate that adult females at peak lactation, with a mean body mass of 2800kg (Owen-Smith 1988), would require 1.3kg protein per day when compared to the 1.0kg protein that a adult male with a mean body mass of 5000kg (Owen-smith 1988) would require on a daily basis. The energy requirements of an adult female at peak lactation were furthermore estimated to be 259 MJ/day in comparison with the 348 MJ/day of an adult male. The daily calcium requirements of a lactating female were estimated to be lower than those of an adult male (187g as opposed to 214g) while the opposite was true for daily estimates of phosphorus requirements (174g for lactating females as opposed to 139g for males). In comparison with other minerals, phosphorus levels in elephant milk increase steadily as lactation progresses (McCullagh & Widdowson 1970). In accordance with the reproductive demands and the predictions of the BSH, I therefore expect family units to select diets of higher protein and phosphorus content than bull groups.

Haschick & Kerley (1997) found that one of the over-riding factors determining diet selection by goats was the plant's soluble carbohydrate content. Likewise, Tixier *et al.* (1997) concluded that diet preference and/or avoidance by roe deer (*Capreolus capreolus*) was related to concentrations of soluble sugars and not crude protein content. Jachmann & Bell (1985) found that the leaf-stripping of plant species by elephants was related to sodium and protein content of leaves but was not correlated with crude fibre content. Jachmann (1989) furthermore found that elephants utilised plant species with high mineral and total soluble sugar content within the *Brachystegia* woodlands of Kasungu National Park, Malawi.

Although aspects of the protein, fibre and mineral content of woody species selected by African savanna elephants, *Loxodonta africana* have been investigated (Dougall & Sheldrick 1964, Field 1971, Koen *et al.* 1988, Hiscocks 1999), none of the above mentioned studies have distinguished between the diet quality of family units and bull groups. Although sex related feeding differences in elephants have been described by Barnes (1982), Lindsay (1994), Stokke (1999), Stokke & du Toit (2000) and Frost (2001), woody plant tissues selected by either family units or bull groups of elephant have yet to be compared on the basis of their chemical contents. Most studies have furthermore only considered the nutrient content of leaf samples and have not analysed other plant parts utilised by elephants (Jachmann & Bell 1985, Jachmann 1989, Holdo 2003). I therefore compared the nutrient content of plant parts selected by either family units or bull groups of elephant to determine whether:

(1) The high protein and phosphorus requirements of females within family units caused the composite samples of plant parts collected at the feeding sites, food plots and plant species level to have higher overall protein and phosphorus levels than those used by males within bull groups.

(2) The same species-specific plant parts collected at the food plots of females had higher protein and phosphorus levels when compared to those collected at the food plots of bull groups.

(3) Adult males within bull groups ingested diets of higher fibre content at the feeding site, food plot, plant species and plant part levels than females within family units.

4.3 Methods

4.3.1 Sample collection

The methods according to which plant-based surveys were conducted are described in detail in Chapter 3.

Depending on the type of feeding mode that had occurred, leaves, twigs, stem-bark, roots or heartwood was collected at each food plot or in the immediate vicinity thereof to represent the utilised plant part. Samples were collected at similar heights to the woody parts accessed by elephants. This meant that roots were dug up or stem-bark was removed with a pocket knife after breaking or sawing stems of similar diameter to those used by elephants. Where elephants had leaf-stripped flexible branch tips, leaf-stripping feeding modes were imitated by sliding both hands towards the distal end of a group of twigs to severe the leaf petioles. Feeding which involved both twig and leaf consumption was imitated by clipping terminal twig tips with garden shears and placing both leaves and twigs in the same sample bag after immediately plucking all the leaves from the twigs. Composite samples were made from various plants of the same species to represent species-specific feeding at a food plot i.e. if three individual *Acacia nigrescens* were leaf-stripped at a food plot; leaves were collected from each plant and pooled to represent the defoliation event of *Acacia nigrescens* at that food plot. All food plots were grouped according to their use by either family units or bull groups of elephant.

4.3.2 Measuring diet quality

Samples were stored in brown paper bags until they were oven dried over night at 60°C. Individual plant part types were processed and analysed separately. Samples were hammer-milled (Retsch SM1, Haan, Germany) through a 1 mm sieve. Milled samples were ground further for near infrared spectroscopy (NIRS) purposes (refer to Chapter 2), through a 1 mm screen in a cyclone mill (Udy Corporation, Fort Collins, Colorado). In addition to each species-specific sample of a particular plant part type, composite samples were also made to represent the independent feeding sites of either family units or bull groups. A feeding site consisted of 2-6 consecutive food-plots with a browsed woody plant at its centre and spaced no less than 20m apart (refer to chapter 3). Composite samples were made by combining equal proportions by mass of each species-specific plant part utilised at a feeding site. Leaf and twig samples were combined in proportion to their gravimetrical measurements prior to grinding to represent a particular defoliation event at a food plot before being added to other plant part types. According to NIRS procedures, these composite samples thus included the variability of numerous individual samples and would decrease the number of samples chosen as part of the calibration set. Although the details of the NIRS analyses are described in detail in Chapter 2, a brief outline is given here. All 469 plant samples that were ground and the additional 62 composite samples were scanned with a NIRS spectrophotometer (5000: Infrasoft, USA). The spectra of the scanned samples were centred and a calibration set of 138 samples was selected using ISI software (ISI version 3.01; Infrasoft). The calibration set was analysed by conventional laboratory analyses for total nitrogen (N), phosphorus (P), calcium (Ca), neutral detergent fibre (NDF) and total soluble sugar content. Nitrogen, P and Ca were analysed simultaneously in an automated continuous-flow analysis system (ALASA 1998). Fibre content was determined according to the methods of Robertson & Van Soest (1981) while total soluble sugar was determined by Luff-Schoorl titration after extraction with ethanol and reaction with Carrez I and II (ICUMSA 1994). Although soluble sugars are often labile and metabolise if not frozen after collection (Van Soest 1994), our sample collection and processing procedures for the determination of the carbohydrate content of the collected plant samples, followed the protocol of Jachmann (1989) and Woolnough & Foley (2002). Predictive equations, based on the results of the calibration set, were generated with the ISI software and used to predict the values of the remaining samples. The NIRS analyses followed the methods described by Woolnough & Foley (2002). All chemical values are expressed on a percentage of dry matter basis (%DM).

4.3.3 Statistical analysis

All variables measured as proportions were arcsine transformed prior to conducting parametric tests (Fry 1993). Discriminant function analysis (DFA) was used to determine the ability of diet quality indices to distinguish between firstly elephant social groups, secondly plant species and lastly plant parts across all samples. This preliminary analysis provided insight into the structure of the data (Tabachnick & Fidell 1983).

Seasonal effects on the diet quality indices of plant species were tested with MANOVA by testing the effect of rainfall period, plant species (*Albizia harveyi, Colophospermum mopane, Grewia* species) and group (bull groups and family units of elephant) and their interaction on diet quality indices (N, P, Ca, NDF and sugar content). All other plant species had to be grouped as 'other' to ensure balanced designs. Three rainfall periods were distinguished based on total monthly rainfall and included the early dry- (July-August 2000), dry- (September 2000) and transitional (October-November 2000) months. Likewise, MANOVA was used to test the effect of rainfall period, plant parts (leaves, twigs, bark and roots) and group (bull groups and family units) and their interaction on diet quality indices (N, P, Ca, NDF and sugar content). As the interaction between rainfall period and elephant group did not significantly influence the diet quality indices, indices were compared between these elephant social units over the entire dry season period (Appendix E). STATISTICA version 6.0 (Statsoft Inc. 2001) was used to perform all statistical analyses.

Comparisons of diet quality measures at feeding site, food plot and plant species level

To assess whether the feeding sites of family units had a higher nutritional status than the feeding sites of bull groups, diet quality measures (N, P, Ca, NDF and total sugar content separately) were first averaged over all plant species and plant parts that were utilised along a feeding site. The combined value was thus a composite of the different species and various plant parts used along a foraging path. The chemical content of the feeding sites of bull groups were compared with those of family units by averaging the composite values of all feeding sites used by each of these social units and testing for differences in each of the diet quality measures by means of one-tailed unpaired *t*-tests. Where variances remained unequal after arcsine transformations, a one-tailed unpaired *t*-test with Welsch's correction was used (Sokal & Rohlf 1981). Feeding sites were considered independent samples as surveys were done on different days in areas that were further than 50 km from the previous day's elephant sighting (Chapter 3).

At the finer scale, the nutritional value of the plant samples within food plots used by bull groups or family units was compared by averaging the diet quality measures within each plot, irrespective of the plant species type or plant part utilised. All food plots were considered independent as the species present and accepted at consecutive food plots were not autocorrelated (Appendix B). The mean N, P, Ca, NDF and total sugar measure for all bull group food plots was then compared with that of family units by means of one-tailed unpaired *t*-tests within each of the diet quality measures (Sokal & Rohlf 1981).

To test whether family units fed from plant species of higher nutritional quality than bull groups, the mean chemical value for each plant species was derived from the mean value for each of its component plant part types, thereby ensuring equal representation of plant parts in the overall species value. I used a one-tailed paired *t*-test to compare the diet quality indices of the 21 plant species that were utilised by both bull groups and family units of elephants (Sokal & Rohlf 1981).

Comparisons of diet quality measures at the plant part level

To assess the prediction that family units used plant parts of higher quality than bull groups, I used one-tailed Wilcoxon matched paired (*Z*) test to compare the diet quality values (N, P, Ca, NDF and soluble sugar) between each of these social units within species-specific leaf, twig and stem bark samples. The chemical values of plant parts were determined by first averaging values within a specific plant part type for each species that was used by both social units of elephant and thereafter averaging across woody species. Small samples sizes prevented similar analyses of uprooting and heartwood utilisation events. Instead the diet quality attributes of *Grewia* roots and *Lannea schweinfurthii* heartwood utilisation events were directly compared between family units and bull groups by means of Mann-Whitney *U* tests as these plant species constituted the majority of specimens that were uprooted or from which the heartwood was removed.

As the differences in diet quality measures did not differ between social units of elephants at the plant part level, plant parts were thereafter grouped according to type irrespective of whether they were used by bull groups or family units. I used a Kruskal Wallis (*H*) test to compare plant parts (leaf, twig, stem bark, heartwood and roots) within plant species followed by Dunn's Multiple Comparison test to determine which plant part differed significantly from each other in terms of diet quality measures (Sokal & Rohlf 1981). The same procedures were followed when comparing the diet quality indices of plant parts across the range of woody species that were used by both bull groups and family units. The heartwood category was however, omitted from the analyses due to a small number of samples collected over different species within this feeding mode.

4.4 Results

Plant parts separated strongly (low λ value) according to their nutritional value (Table 4.1). The first and second functions of the discriminant function analysis (Figure 4.1) accounted for 97% of the explained variance. The first function weighted most heavily on nitrogen and fibre (standard coefficients of –0.545 and 0.836 respectively) which separated leaves as having the least fibre and the highest nitrogen content while twigs and heartwood were separated from roots and stem bark as being the most fibrous with a low nitrogen content. On a percentage of dry matter basis: nitrogen=2.2, neutral detergent fibre=35 (leaves); nitrogen=0.89, neutral detergent fibre=64 (twigs); nitrogen=0.32, neutral detergent fibre=71 (heartwood); nitrogen=1.4, neutral detergent fibre=49 (stem bark) and nitrogen=0.79, neutral detergent fibre =55 (roots). The second function weighted most heavily on Ca and sugar (standardised coefficients of 0.846 and 0.394 respectively) which separated stem bark and roots with a high and heartwood with a low Ca and sugar contents from leaves and twigs. On a percentage of dry matter basis: calcium=1.3, soluble sugar=4.7 (leaves); calcium=1.3, soluble sugar=2.9 (twigs); calcium=0.34, soluble sugar=3.3 (heartwood); calcium=2.4, soluble sugar=5.2 (stem bark) and calcium=1.9, soluble sugar=4.7 (roots).

Table 4.1 Results of Discriminant Function Analyses to determine whether elephant group type, plant species or plant part were distinct from each other, based on the diet quality indices (N, P, Ca, NDF and total soluble sugar) that were measured. Significant differences (P<0.05) between the categories within the grouping variables are given in bold.

Grouping variable	Description	λ	*F*	*P*
Elephant group type	Family unit or bull group	**0.97**	**2.6**	**<0.0269**
Plant species	32 plant species that were utilised for which more than one plant sample was collected	**0.11**	**7.4**	**<0.0001**
Plant part	Leaves, twigs, roots, stem bark and heartwood.	**0.077**	**85**	**<0.0001**

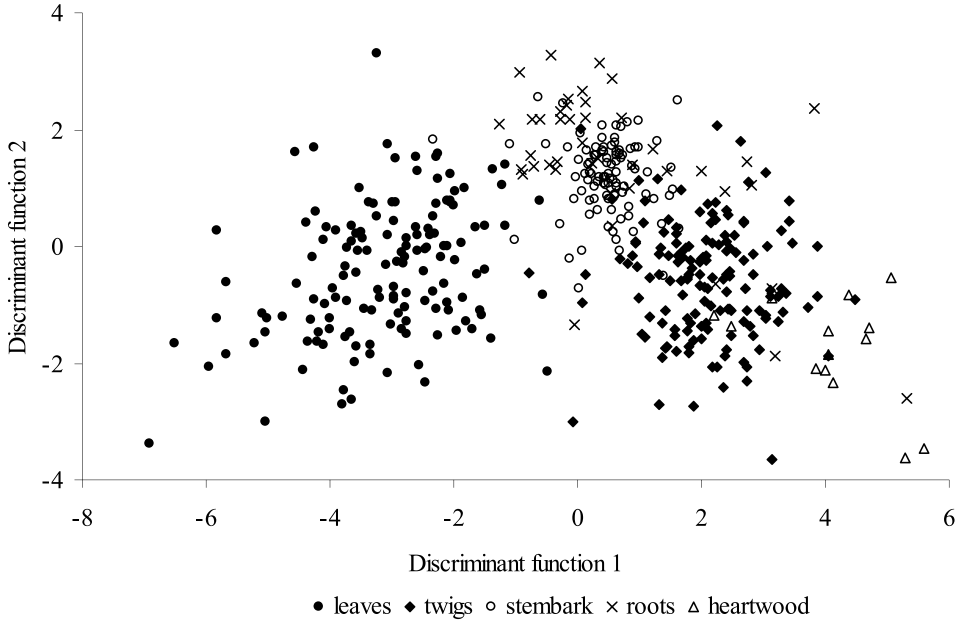

Figure 4.1 Discriminant analysis of leaves, twigs, stem bark, roots and heartwood utilised by both bull groups and family units of elephant.

In spite of differences between bull groups and family units in the proportional use of plant parts (Chapter 3), diet quality measures did not differ significantly between these social units of elephant at either the feeding site or food plot level. The nutritive value of plant species that were used by both bull groups and family units was also similar (Table 4.2).

The same plant part within species that were used by bull groups and family units had similar nutritional values (Table 4.3). Bull groups utilised *Grewia* roots with significantly higher levels of calcium and sugar than those utilised by family units.

The results indicate that leaves were the most nutritious plant parts consumed (high nitrogen and low fibre when compared to the other plant parts (Table 4.3). Leaves obtained from *Lonchocarpus capassa* had the highest nitrogen content followed by those of *Ehretia amoena*, *Dalbergia melanoxylon* and *Acacia nigrescens*. Roots and stem bark had sugar levels equivalent to those of leaves (ca 5%DM). Stem bark had high calcium levels equivalent to those of roots. Heartwood was the least nutritious plant part (low nitrogen and high fibre) content) and consequently both social units of elephant obtained heartwood from only *Lannea schweinfurthii* (Table 4.4 - 4.8). When tested across all species that were utilised for the same plant parts by family units and bull groups, leaves had significantly higher levels of N, P and soluble sugar together with lower levels of fibre when compared to twigs (Dunn's Multiple

Table 4.2 Nitrogen (N), phosphorus (P), calcium (Ca), fibre (NDF) and carbohydrate (total soluble sugar) levels (mean ± standard errors) of plants parts collected at the feeding site, food plot or plant species level of bull groups and family units of elephant. Sample sizes are given in brackets. All values are expressed on a percentage of dry matter basis.

Scale	Diet quality index	Family units	Bull groups	*t*-test
Feeding site	N	1.3 ± 0.055 (29)	1.2 ± 0.045 (31)	*t*=1.6, *P*=0.1089
	P	0.084 ± 0.0040 (29)	0.093 ± 0.076 (31)	*t*=0.93, *P*=0.3577
	Ca	1.7 ± 0.086 (29)	1.6 ±0.080 (31)	*t*=0.030, *P*=0.9760
	NDF	52 ± 1.2 (29)	50 ± 1.1 (31)	*t*=1.3, *P*=0.1891
	Sugar	3.9 ± 0.17 (29)	4.0 ± 0.12 (31)	*t*=0.46, *P*=0.6475
Food plot	N	1.3 ± 0.044 (121)	1.2 ± 0.042 (123)	*t*=1.1, *P*=0.2688
	P	0.081 ± 0.0033 (121)	0.089 ± 0.0050 (123)	*t*=1.2, *P*=0.2496
	Ca	1.7 ± 0.068 (121)	1.6 ± 0.065 (123)	*t*=0.61, *P*=0.5413
	NDF	53 ± 1.2 (121)	51 ± 1.0 (123)	*t*=1.4, *P*=0.1531
	Sugar	4.0 ± 0.18 (121)	4.0 ± 0.13 (123)	*t*=0.040, *P*=0.9682
Plant species	N	1.7 ± 0.19 (21)	1.5 ± 0.14 (21)	*t*=1.1, *P*=0.2872
	P	0.10 ± 0.013 (21)	0.097 ± 0.012 (21)	*t*=0.52, *P*=0.6082
	Ca	1.3 ± 0.12 (21)	1.4 ± 0.10 (21)	*t*=1.6, *P*=0.2606
	NDF	49 ± 2.6 (21)	48 ± 1.4 (21)	*t*=0.13, *P*=0.8989
	Sugar	3.7 ± 0.21 (21)	4.1 ± 0.18 (21)	*t*=1.7, *P*=0.1091

Comparison test, *P* <0.001). Leaves also had significantly higher levels of phosphorus than stem bark and roots (*P*<0.05 and *P*<0.001 respectively). Stem bark had higher levels of Ca than leaves (P<0.05) and a higher soluble sugar content than twigs (*P*<0.001). The chemical content of roots and stem bark proved to be similar according to the diet quality indices that were measured in this study. Although small sample sizes confounded some of the comparisons between plant parts within a species (large variance), leaves again proved to be the most nutritious plant part of all the plant species that were tested, followed by stem bark, roots and lastly twigs (Table 4.4 - 4.8).

4.5 Discussion

The results indicate that there was no difference between nutrient concentrations in plant species or plant parts selected by females and their smaller bodied offspring within family units compared with males within bull groups. However, the analyses showed distinctions in nutrient levels in different plant part categories. The differing dietary contributions by these plant parts to family units and bull groups are described elsewhere (Chapter 3).

Stokke & du Toit (2000) found likewise, that females ingested larger dietary proportions of leafy material than males within bull groups. According to the predictions of the

Table 4.3 Nitrogen (N), phosphorus (P), calcium (Ca), fibre (NDF) and carbohydrate (total soluble sugar) levels for plant parts collected at the food plots of bull groups and family units of elephant (mean levels ± standard errors). Sample sizes are given in brackets followed by the woody species that were compared within each plant part category. All values are expressed on a percentage dry matter basis with tests that proved to be significant ($P<0.05$) given in bold.

Plant part	Family units	Differences between social units	Bull groups
N			
Leaves	2.3 ± 0.17 (18[a])	$Z=35$, $P=0.2263$	2.2 ± 0.13 (18)
Twigs	0.96 ± 0.095 (15[b])	$Z=42$, $P=0.1262$	0.87 ± 0.075 (15)
Stem bark	1.6 ± 0.47 (4[c])	$Z=0.0$, $P=0.5625$	1.3 ± 0.27 (4)
Roots	1.2 ± 0.056 (11[d])	$U=94$, $P=0.3257$	1.2 ± 0.062(19)
Heartwood	0.27 ± 0.097 (5[e])	$U=11$, $P=0.1338$	0.35 ± 0.090 (7)
P			
Leaves	0.14 ± 0.013 (18)	$Z=-8.0$, $P=0.4351$	0.15 ± 0.015 (18)
Twigs	0.060 ± 0.0055(15)	$Z=24$, $P=0.2622$	0.057 ± 0.0055 (15)
Stem bark	0.062 ± 0.0066 (4)	$Z=0.0$, $P=0.5625$	0.051 ± 0.014 (4)
Roots	0.0043 ± 0.0003 (11)	$U=74$, $P=0.0939$	0.047 ± 0.0038 (19)
Heartwood	0.044 ± 0.0025 (5)	$U=14$, $P=0.265$	0.049 ± 0.0044 (7)
Ca			
Leaves	1.4 ± 0.14 (18)	$Z=37$, $P=0.2135$	1.3 ± 0.11 (18)
Twigs	1.3 ± 0.15 (15)	$Z=-6.0$, $P=0.4452$	1.2 ± 0.11 (15)
Stem bark	2.5 ± 0.32 (4)	$Z=-4.0$, $P=0.5780$[f]	2.5 ± 0.25 (4)
Roots	2.5 ± 0.015 (11)	**$U=61$, $P=0.0321$**	2.9 ± 0.14 (19)
Heartwood	0.28 ± 0.11 (5)	$U=13$, $P=0.2650$	0.37 ± 0.072 (7)
NDF			
Leaves	35 ± 2.0 (18)	$Z=23$, $P=0.3121$	34 ± 1.7 (18)
Twigs	63 ± 1.8 (15)	$Z=10$, $P=0.4020$	64 ± 1.7 (15)
Stem bark	49 ± 2.2 (4)	$Z=-6.0$, $P=0.1875$	50 ± 2.3 (4)
Roots	48 ± 1.0(11)	$U=68$, $P=0.0607$	46 ± 1.2 (19)
Heartwood	71 ± 2.7 (5)	$U=17$, $P=0.5000$	71 ± 2.5 (7)
Sugar			
Leaves	4.7 ± 0.26 (18)	$Z=11$, $P=0.4096$	4.7 ± 0.21 (18)
Twigs	2.8 ± 0.24 (15)	$Z=-4.0$, $P=0.4670$	2.9 ± 0.21 (15)
Stem bark	5.0 ± 0.26 (4)	$Z=-2.0$, $P=0.438$	5.0 ± 0.53 (4)
Roots	5.1 ± 0.13 (11)	**$U=65$, $P=0.0467$**	5.8 ± 0.34 (19)
Heartwood	2.8 ± 0.44 (5)	$U=17$, $P=0.4381$	3.6 ± 0.98 (7)

[a] *Acacia exuvialis*, *Acacia gerrardi*, *Albizia harveyi*, *Acacia nigrescens*, *Combretum apiculatum*, *Colophospermum mopane*, *Dichrostachys cinerea*, *Dalbergia melanoxylon*, *Diospyros mespiliformis*, *Ehretia amoena*, *Euclea divinorum*, *Grewia* spp., *Grewia hexamita*, *Lonochocarpus capassa*, *Lannea schweinfurthii*, *Maerua parvifolia*, *Sclerocarya birrea*, *Schotia brachypetala.*

[b] *Acacia exuvialis*, *Acacia gerrardi*, *Albizia harveyi*, *Acacia nigrescens*, *Colophospermum mopane*, *Combretum imberbe*, *Dichrostachys cinerea*, *Dalbergia melanoxylon*, *Ehretia amoena*, *Euclea divinorum*, *Grewia* spp., *Grewia flavescens*, *Grewia hexamita*; *Lannea schweinfurthii*, *Maerua parvifolia..*

[c] *Acacia nigrescens*, *Colophospermum mopane*, *Dalbergia melanoxylon*, *Grewia* spp.

[d] *Grewia* spp.

[e] *Lannea schweinfurthii*

Table 4.4 Nitrogen levels for plant parts that were used within particular plant species by both bull groups and family units of elephants (mean levels ± standard errors). Sample sizes of the number of species involved within each plant part category are given in brackets (last row) while the number of plant parts that were averaged within a species are also provided. All values are expressed on a percentage dry matter basis. The Mann-Whitney statistic (*U*), the Kruskal Wallis statistic (*H*) and the level of significance is given for plant part differences within species (Diff. within spp.) as well as across all the species (Diff. across spp.) that were used by both social units of elephant. Plant parts with superscripts with the same alphabetical letter (a-d) where not significantly different while all significant results (*P*<0.05) are given in bold.

Species*	Leaves	Twigs	Stem bark	Roots	Heartwood	Diff. within spp.
Aexu	2.5 ± 0.23 (2)	0.76 ± 0.045 (3)				*U*=0.0, *P*=0.2000
Ager	2.1 ± 0.080 (2)	0.90 ± 0.12 (6)				*U*=0.0, *P*=0.0714
Alha	2.3 ± 0.13 (2)	0.87 ± 0.038 (11)				**_U_=0.0, _P_=0.0383**
Anig	2.6 ± 0.12 (17)^{a}	0.93 ± 0.041 (18)^{b}	2.2 ± 0.63 (2)^{ab}			**_H_=27, _P_<0.0001**
Capi	2.1 ± 0.14 (8)					na[1]
Cimb		0.47 ± 0.015 (2)				na
Cmop	1.5 ± 0.076 (21)^{a}	0.68 ± 0.036 (7)^{bc}	0.70 ± 0.035 (12)^{c}			**_H_=29, _P_<0.0001**
Dcin	2.4 ± 0.29 (2)	1.2 ± 0.044 (21)				**_U_=0.0, _P_=0.0253**
Dmel	2.7 ± 0.21 (4)^{a}	1.2 ± 0.10 (5)^{b}	1.7 ± 0.10 (6)^{ab}			**_H_=11. _P_<0.0001**
Dmes	2.0 ± 0.16 (5)					na
Eamo	2.8 ± 0.010 (2)	1.6 ± 0.18 (2)				**_U_=0.0, _P_<0.0001**
Ediv	1.6 ± 0.013 (2)	0.96 ± 0.44 (2)				**_U_=0.0, _P_<0.0001**
Gfla		0.58 ± 0.031 (5)				na
Ghex	2.3 ± 0.22 (6)	0.57 ± 0.29 (4)				**_U_=0.0, _P_=0.0095**
Gre	2.2 ± 0.063 (32)^{a}	0.72 ± 0.032 (22)^{b}	1.0 ± 0.013 (73)^{c}	1.2 ± 0.045 (31)^{d}		**_H_=109, _P_<0.0001**
Lcap	4.1 ± 0.45 (2)					na
Lsch	1.4 ± 0.054 (13)^{a}	0.59 ± 0.025 (4)^{abc}		0.40 ± 0.065 (7)^{b}	0.32 ± 0.064 (12)^{c}	**_H_=27, _P_<0.0001**
Mpar	2.2 ± 0.080 (2)	1.3 ± 0.085 (6)				*U*=0.0, *P*=0.0714
Sbir	1.6 ± 0.081 (11)					na
Sbra	1.7 ± 0.14 (4)					na
Diff. across spp.	2.2 ± 0.15 (18)^{a}	0.89 ± 0.082 (15)^{b}	1.4± 0.34 (4)^{ab}	0.79± 0.39 (2)^{ab}	0.32 ± 0.064 (1)	**_H_=25, _P_<0.0001**

*Aexu=*Acacia exuvialis*, Ager= *Acacia gerrardi*, Alha=*Albizia harveyi*, Anig=*Acacia nigrescens*, Capi=*Combretum apiculatum*, Cimb= *Combretum imberbe*, Cmop=*Colophospermum mopane*, Dcin=*Dichrostachys cinerea*, Dmel=*Dalbergia melanoxylon*, Dmes=*Diospyros mespiliformis*, Eamo=*Ehretia amoena*, Ediv=*Euclea divinorum*, Gfla=*Grewia flavescens*, Ghex= *Grewia hexamita*, Grew=*Grewia* spp, Lcap=*Lonochocarpus capassa*, Lsch=*Lannea schweinfurthii*, Mpar=*Maerua parvifolia*, Sbir=*Sclerocarya birrea*, Sbra=*Schotia brachypetala.*

[1] not applicable

Table 4.5 Phosphorus levels for plant parts that were used within particular plant species by both bull groups and family units of elephants (mean levels ± standard errors). Sample sizes of the number of species involved within each plant part category are given in brackets (last row) while the number of plant parts that were averaged within a species are also provided. All values are expressed on a percentage dry matter basis. The Mann-Whitney statistic (*U*), the Kruskal Wallis statistic (*H*) and the level of significance is given for plant part differences within species (Diff. within spp.) as well as across all the species (Diff. across spp.) that were used by both social units of elephant. Plant parts with superscripts with the same alphabetical letter (a-d) where not significantly different while all significant results ($P<0.05$) are given in bold.

Species*	Leaves	Twigs	Stem bark	Roots	Heartwood	Diff. within spp.
Aexu	0.12 ± 0.0050 (2)	0.045 ± 0.0029 (3)				*U*=0.0, *P*=0.2000
Ager	0.083 ± 0.0075 (2)	0.058 ± 0.067 (6)				*U*=1.0, *P*=0.1429
Alha	0.15 ± 0.060 (2)	0.061 ± 0.0042 (11)				***U*=0.0, *P*=0.0383**
Anig	0.14 ± 0.013 (17)^{a}	0.058 ± 0.0045 (18)^{b}	0.043 ± 0.028 (2)^{c}			***H*=26, *P*<0.0001**
Capi	0.17 ± 0.022 (8)					na
Cimb		0.033 ± 0.0075 (2)				na
Cmop	0.090 ± 0.0063 (21)^{a}	0.052 ± 0.0038 (7)^{bc}	0.046 ± 0.0055 (12)^{c}			***H*=20, *P*<0.0001**
Dcin	0.16 ± 0.025 (2)	0.064 ± 0.0035 (21)				***U*=0.0, *P*=0.0253**
Dmel	0.10 ± 0.011 (4)^{a}	0.054 ± 0.012 (5)^{ab}	0.052 ± 0.046 (6)^{b}			***H*=8.3. *P*=0.0066**
Dmes	0.21 ± 0.024 (5)					na
Eamo	0.11 ± 0.020 (2)	0.12 ± 0.0025 (2)				***U*=2.0, *P*<0.0001**
Ediv	0.12 ± 0.010 (2)	0.058 ± 0.023 (2)				***U*=0.0, *P*<0.0001**
Gfla		0.056 ± 0.012 (5)				na
Ghex	0.19 ± 0.022 (6)	0.059 ± 0.0059 (4)				***U*=0.0, *P*=0.0095**
Gre	0.14 ± 0.089 (32)^{a}	0.067 ± 0.0051 (22)^{bc}	0.078 ± 0.0018 (73)^{c}	0.0431 ± 0.0025 (31)^{d}		***H*=98, *P*<0.0001**
Lcap	0.29 ± 0.010 (2)					na
Lsch	0.18 ± 0.069 (13)^{a}	0.058 ± 0.0026 (4)^{a}		0.039 ± 0.0058 (7)^{a}	0.047 ± 0.0028 (12)^{b}	***H*=18, *P*=0.0001**
Mpar	0.080 ± 0.010 (2)	0.022 ± 0.0060 (6)				*U*=0.0, *P*=0.0714
Sbir	0.19 ± 0.016 (11)					na
Sbra	0.11 ± 0.027(4)					na
Diff. across spp.	0.15 ± 0.013 (18)^{a}	0.057 ± 0.0053 (15)^{bcd}	0.055± 0.0081 (4)^{bcd}	0.041± 0.0017 (2)^{bcd}	0.047 ± 0.0028 (1)	***H*=28, *P*<0.0001**

*Aexu=*Acacia exuvialis*, Ager= *Acacia gerrardi*, Alha=*Albizia harveyi*, Anig=*Acacia nigrescens*, Capi=*Combretum apiculatum*, Cimb= *Combretum imberbe*, Cmop=*Colophospermum mopane*, Dcin=*Dichrostachys cinerea*, Dmel=*Dalbergia melanoxylon*, Dmes=*Diospyros mespiliformis*, Eamo=*Ehretia amoena*, Ediv=*Euclea divinorum*, Gfla=*Grewia flavescens*, Ghex= *Grewia hexamita*, Grew=*Grewia* spp, Lcap=*Lonochocarpus capassa*, Lsch=*Lannea schweinfurthii*, Mpar=*Maerua parvifolia*, Sbir=*Sclerocarya birrea*, Sbra=*Schotia brachypetala.*

[1] not applicable

Table 4.6 Calcium levels for plant parts that were used within particular plant species by both bull groups and family units of elephants (mean levels ± standard errors). Sample sizes of the number of species involved within each plant part category are given in brackets (last row) while the number of plant parts that were averaged within a species are also provided. All values are expressed on a percentage dry matter basis. The Mann-Whitney statistic (U), the Kruskal Wallis statistic (H) and the level of significance is given for plant part differences within species (Diff. within spp.) as well as across all the species (Diff. across spp.) that were used by both social units of elephant. Plant parts with superscripts with the same alphabetical letter (a-d) where not significantly different while all significant results ($P<0.05$) are given in bold.

Species*	Leaves	Twigs	Stem bark	Roots	Heartwood	Diff. within spp.
Aexu	1.3 ± 0.28 (2)	1.4 ± 0.24 (3)				U=3.0, P=1.0000
Ager	1.4 ± 0.22 (2)	1.0 ± 0.24 (6)				U=5.0, P=0.8571
Alha	0.69 ± 0.28 (2)	0.74 ± 0.078 (11)				U=8.0, P=0.6217
Anig	1.2 ± 0.16 (17)^{a}	1.4 ± 0.099 (18)^{ab}	3.1 ± 0.099 (2)^{b}			**H=8.5, P=0.0014**
Capi	2.1 ± 0.14 (8)					na
Cimb		2.4 ± 0.24 (2)				na
Cmop	1.4 ± 0.056 (21)^{a}	1.2 ± 0.076 (7)^{ab}	1.7 ± 0.15 (12)^{ac}			**H=10, P=0.0059**
Dcin	1.4 ± 0.035 (2)	1.0 ± 0.079 (21)				U=13, P=0.4132
Dmel	1.4 ± 0.35 (4)^{a}	1.2 ± 0.24 (5)^{ab}	2.7 ± 0.16 (6) ^{ac}			**H=9.7. P=0.0015**
Dmes	1.1 ± 0.11 (5)					na
Eamo	1.9 ± 0.095 (2)	1.3 ± 0.11 (2)				**U=0.0, P<0.0001**
Ediv	1.0 ± 0.24 (2)	1.2 ± 0.080 (2)				**U=1.0, P<0.0001**
Gfla		1.2 ± 0.12 (5)				na
Ghex	2.5 ± 0.34 (6)	2.5 ± 0.34 (4)				U=16, P=0.7619
Gre	2.0 ± 0.11 (32)^{a}	1.4 ± 0.095 (22)^{b}	2.32 ± 0.046 (73)^{c}	2.7 ± 0.11 (31)^{cd}		**H=59, P<0.0001**
Lcap	0.92 ± 0.055 (2)					na
Lsch	1.8 ± 0.093 (13)^{a}	1.4 ± 0.34 (4)^{a}		1.2 ± 0.34 (7)^{a}	0.34 ± 0.061 (12)^{b}	**H=19, P=0.0002**
Mpar	0.78 ± 0.15 (2)	0.49 ± 0.045 (6)				U=0.0, P=0.0714
Sbir	0.83 ± 0.061 (4))					na
Sbra	1.4 ± 0.21 (11)					na
Diff. across spp.	1.3 ± 0.11 (18)^{a}	1.3 ± 0.13 (15)^{a}	2.4± 0.29 (4)^{b}	1.9± 0.79 (2)^{ab}	0.34 ± 0.061 (1)	**H=8.3, P=0.0399**

*Aexu=*Acacia exuvialis*, Ager= *Acacia gerrardi*, Alha=*Albizia harveyi*, Anig=*Acacia nigrescens*, Capi=*Combretum apiculatum*, Cimb= *Combretum imberbe*, Cmop=*Colophospermum mopane*, Dcin=*Dichrostachys cinerea*, Dmel=*Dalbergia melanoxylon*, Dmes=*Diospyros mespiliformis*, Eamo=*Ehretia amoena*, Ediv=*Euclea divinorum*, Gfla=*Grewia flavescens*, Ghex= *Grewia hexamita*, Grew=*Grewia* spp, Lcap=*Lonochocarpus capassa*, Lsch=*Lannea schweinfurthii*, Mpar=*Maerua parvifolia*, Sbir=*Sclerocarya birrea*, Sbra=*Schotia brachypetala.*

[1] not applicable

Table 4.7 Neutral detergent fibre levels for plant parts that were used within particular plant species by both bull groups and family units of elephants (mean levels ± standard errors). Sample sizes of the number of species involved within each plant part category are given in brackets (last row) while the number of plant parts that were averaged within a species are also provided. All values are expressed on a percentage dry matter basis. The Mann-Whitney statistic (*U*), the Kruskal Wallis statistic (*H*) and the level of significance is given for plant part differences within species (Diff. within spp.) as well as across all the species (Diff. across spp.) that were used by both social units of elephant. Plant parts with superscripts with the same alphabetical letter (a-d) where not significantly different while all significant results (*P*<0.05) are given in bold.

Species	Leaves	Twigs	Stem bark	Roots	Heartwood	Diff. within spp.
Aexu	48 ± 4.9 (2)	68 ± 0.66 (3)				*U*=0.0, *P*=0.2000
Ager	31 ± 3.4 (2)	63 ± 1.3 (6)				*U*=0.0, *P*=0.0714
Alha	44 ± 0.96 (2)	65 ± 0.91 (11)				**_U_=0.0, _P_=0.0383**
Anig	32 ± 0.79 (17)^{a}	64 ± 1.1 (18)^{b}	45 ± 1.6 (2)^{ab}			**_H_=28, _P_<0.0001**
Capi	22 ± 1.4 (8)					na
Cimb		61 ± 1.1 (2)				na
Cmop	31 ± 0.38 (21)^{a}	54 ± 1.4 (7)^{bc}	47 ± 1.1 (12)^{c}			**_H_=31, _P_<0.0001**
Dcin	31 ± 1.3 (2)	69 ± 0.79 (21)				**_U_=0.0, _P_=0.0253**
Dmel	2.7 ± 0.21 (4)^{a}	1.2 ± 0.10 (5)^{b}	1.7 ± 0.10 (6)^{ab}			**_H_=11. _P_<0.0001**
Dmes	38 ± 1.1 (5)					na
Eamo	29 ± 0.54 (2)	58 ± 1.6 (2)				**_U_=0.0, _P_<0.0001**
Ediv	37 ± 6.0 (2)	53 ± 7.7 (2)				**_U_=0.0, _P_<0.0001**
Gfla		75 ± 1.6 (5)				na
Ghex	41 ± 0.84 (6)	63 ± 1.7 (4)				**_U_=0.0, _P_=0.0095**
Gre	43 ± 0.63 (32)^{a}	67 ± 0.62 (22)^{a}	53 ± 0.39 (73)^{b}	47 ± 0.89 (31)^{c}		**_H_=112, _P_<0.0001**
Lcap	32 ± 0.59 (2)					na
Lsch	22 ± 0.51 (13)^{a}	57 ± 3.0 (4)^{a}		63 ± 3.1 (7)^{a}	71 ± 1.8 (12)^{b}	**_H_=29, _P_<0.0001**
Mpar	25 ± 0.61 (2)	70 ± 0.85 (6)				*U*=0.0, *P*=0.0714
Sbir	34 ± 2.2 (4)					na
Sbra	42 ± 4.3 (11)					na
Diff. across spp.	35 ± 1.8 (18)^{a}	64 ± 1.6 (15)^{b}	49 ± 2.0 (4)^{ab}	55± 8.0 (2)^{ab}	71 ± 1.8 (1)	**_H_=25, _P_<0.0001**

*Aexu=*Acacia exuvialis*, Ager= *Acacia gerrardi*, Alha=*Albizia harveyi*, Anig=*Acacia nigrescens*, Capi=*Combretum apiculatum*, Cimb= *Combretum imberbe*, Cmop=*Colophospermum mopane*, Dcin=*Dichrostachys cinerea*, Dmel=*Dalbergia melanoxylon*, Dmes=*Diospyros mespiliformis*, Eamo=*Ehretia amoena*, Ediv=*Euclea divinorum*, Gfla=*Grewia flavescens*, Ghex= *Grewia hexamita*, Grew=*Grewia* spp, Lcap=*Lonochocarpus capassa*, Lsch=*Lannea schweinfurthii*, Mpar=*Maerua parvifolia*, Sbir=*Sclerocarya birrea*, Sbra=*Schotia brachypetala.*

[1] not applicable

Table 4.8 Soluble carbohydrate (sugar) levels for plant parts that were used within particular plant species by both bull groups and family units of elephants (mean levels ± standard errors). Sample sizes of the number of species involved within each plant part category are given in brackets (last row) while the number of plant parts that were averaged within a species are also provided. All values are expressed on a percentage dry matter basis. The Mann-Whitney statistic (U), the Kruskal Wallis statistic (H) and the level of significance is given for plant part differences within species (Diff. within spp.) as well as across all the species (Diff. across spp.) that were used by both social units of elephant. Plant parts with superscripts with the same alphabetical letter (a-d) where not significantly different while all significant results ($P<0.05$) are given in bold.

Species	Leaves	Twigs	Stem bark	Roots	Heartwood	Diff. within spp.
Aexu	3.7 ± 0.97 (2)	2.1 ± 0.13 (3)				U=0.0, P=0.2000
Ager	6.0 ± 1.0 (2)	3.5 ± 0.31 (6)				U=0.0, P=0.0714
Alha	4.2 ± 0.46 (2)	2.5 ± 0.11 (11)				**U=0.0, P=0.0383**
Anig	4.5 ± 0.47 (17)^{a}	2.5 ± 0.16 (18)^{b}	6.0 ± 0.59 (2)^{ac}			**H=15, P=0.0005**
Capi	5.0 ± 0.12 (8)					na
Cimb		3.5 ± 0.30 (2)				na
Cmop	5.8 ± 0.25 (21)^{a}	4.7 ± 0.87 (7)^{b}	5.1 ± 0.55 (12)^{ab}			**H=11, P=0.0036**
Dcin	4.7 ± 0.10 (2)	2.5 ± 0.12 (21)				**U=0.0, P=0.0253**
Dmel	4.1 ± 0.37 (4)^{ab}	2.9 ± 0.51 (5)^{a}	5.4 ± 0.85 (6)^{b}			**H=8.1 P=0.0084**
Dmes	3.8 ± 0.22 (5)					na
Eamo	5.5 ± 0.070 (2)	2.8 ± 0.49 (2)				**U=0.0, P<0.0001**
Ediv	4.9 ± 0.45 (2)	4.1 ± 0.21 (2)				**U=0.0, P<0.0001**
Gfla		1.7 ± 0.21 (5)				na
Ghex	3.1 ± 0.41 (6)	3.0 ± 0.44 (4)				U=8.0, P=0.4762
Gre	3.6 ± 0.23 (32)^{a}	2.5 ± 0.094 (22)^{b}	4.4 ± 0.078 (73)^{ad}	5.4 ± 0.23 (31)^{c}		**H=86, P<0.0001**
Lcap	4.7 ± 0.23 (2)					na
Lsch	6.2 ± 0.99 (13)^{a}	3.3 ± 0.29 (4)		3.9 ± 0.79 (7)^{b}	3.3 ± 0.59 (12)^{c}	**H=15, P=0.0017**
Mpar	4.6 ± 0.12 (2)	1.6 ± 0.72 (6)				U=2.0, P=0.2857
Sbir	4.3 ± 0.61 (11)					na
Sbra	4.9 ± 1.5 (4)					na
Diff. across spp.	4.7 ± 0.20 (18)^{a}	2.9 ± 0.22 (15)^{b}	5.2± 0.32 (4)^{ac}	4.7± 0.75 (2)^{abc}	3.3 ± 0.59 (1)	**H=22, P<0.0001**

*Aexu=*Acacia exuvialis*, Ager= *Acacia gerrardi*, Alha=*Albizia harveyi*, Anig=*Acacia nigrescens*, Capi=*Combretum apiculatum*, Cimb= *Combretum imberbe*, Cmop=*Colophospermum mopane*, Dcin=*Dichrostachys cinerea*, Dmel=*Dalbergia melanoxylon*, Dmes=*Diospyros mespiliformis*, Eamo=*Ehretia amoena*, Ediv=*Euclea divinorum*, Gfla=*Grewia flavescens*, Ghex= *Grewia hexamita*, Grew=*Grewia* spp, Lcap=*Lonochocarpus capassa*, Lsch=*Lannea schweinfurthii*, Mpar=*Maerua parvifolia*, Sbir=*Sclerocarya birrea*, Sbra=*Schotia brachypetala.*

[1] not applicable

BSH, nutritious leaves would be sought after by smaller-bodied females with their higher mass specific metabolic demands when compared to larger bodied males. As discussed in the introductory section, lactating females within family units would furthermore have high demands for protein and phosphorus with the costs of lactation being higher than those of pregnancy (Moen 1973, Robbins 1983, Oftedal 1985). I found that leaves had higher nitrogen and phosphorus contents together with comparatively lower fibre contents when compared to twigs, stem bark, roots and heartwood samples. Hence, the increased dietary proportion of leaves that family units ingested when compared to bull groups, was in keeping with their nutritional requirements. Furthermore, faecal indices of diet quality substantiated the finding that females were ingesting diets of higher quality as the faecal samples of adult females contained significantly higher levels of nitrogen and phosphorus together with lower levels of fibre than those of adult males (Chapter 5).

During the dry season the quality of senescing leaves declines as up to 90% of N and P are retranslocated to other plant parts (Chapin 1980). Elephants of both sexes were found to broaden their dietary breath in terms of plant parts, thereby incorporating other more abundant plant tissues (twigs, stem bark, roots and heartwood) of lower quality (high fibre content) in comparison to the leafy material ingested by elephants (Chapter 3).

Roots and stem bark are known to become valuable food sources to elephants when deciduous species start losing their leaves (Williamson 1975a). Although Hiscocks (1999) did not differentiate between debarking incidents caused by bull groups and family units, she also found that elephants frequently bark stripped woody species in the dry season, especially prior to leaf production by deciduous woody species. As developing leaves facilitate their growth in part by the importation of carbohydrates from the phloem, while mature leaves do not normally acquire carbohydrates from other plant parts (Moorby 1977), bark obtained prior to leaf production could be rich in carbohydrates. Williamson (1975b) recorded a high incidence of debarking between September and October and proposed that debarking coincided with the rising of sap from the roots to other plant parts. In accordance with these predictions, I found the soluble sugar content of roots and stem bark to be high. Chemical analyses revealed that the nutritive value of stem bark and roots were also similar in terms of other diet quality indices (nitrogen, phosphorus, calcium and fibre content) However, family units were found to preferentially debark small branches while bulls uprooted plants more frequently than family units (Chapter 3). These results are in agreement with those of Stokke & du Toit (2000). Barnes (1982) also found that bulls utilised roots more frequently than family units. The chemical similarity between stem bark and roots suggests that distinctions in their use by family units or bull groups can be parsimoniously explained by bulls being stronger because of their larger body size (Chapter 3). This would enable bulls to uproot shrubs and trees with greater ease than smaller bodied individuals within family units. Acquiring a similar proportion of roots by family unit members would therefore entail a handling cost of both energy and time which would make it more beneficial for family units to debark small stems of similar nutritional value to roots, when leaves are unavailable.

The proportion of plant parts used by males indicates that males ingested overall diets of higher fibre content than those of females, and were consistent with the predictions of the BSH. Not only did males ingest leaves (low in fibre) less frequently than females but males broke and bit more stems and roots with larger diameters than those of females (Chapter 3), thereby increasing their fibre intake. Furthermore, dietary differences in fibre intake between the sexes were substantiated by males having higher overall faecal fibre levels than smaller-bodied females (Chapter 5). Cell wall content consists of a large proportion of cellulose, hemicellulose and other less defined polyproponol units called lignin (Goering & Van Soest 1970). The caloric value of fibre depends on its fermentability with the products of fermentable fibre including volatile fatty acids (VFA). Estimates of the energy contribution of VFA in non-ruminant species, indicate that VFA form a significant part of digestible energy (Udén 1978). The extent of digestion of cellulose, the most slowly digested carbohydrate is however highly related to retention time. However, retention times increase with an increase in body size while digestibility is in turn a function of retention time (Van Soest 1994). As the fermentation rate required for maintenance is low in large animals, by implication larger bodied males will extract fermentable energy more efficiently than smaller bodied females. Estimates of the absolute energy requirements of adult male elephants indicated that they would require 26% more energy per day than adult females at peak lactation (348MJ/day in comparison with 259MJ/day, Appendix A). The findings of this study therefore indicate that larger males derive an important amount of energy from increased fibre intake in comparison with females.

Estimates of daily calcium requirements indicated that adult males require more calcium than adult female elephants at peak lactation (214g/day as opposed to 187g/day, Appendix A). However, faecal analysis failed to find higher calcium levels in the faeces of males when compared to females (Chapter 5). Napier Bax & Sheldrick (1963) and Williamson (1975a) suggested that calcium deficiencies within the diets of elephants could be filled by selecting bark. The calcium content of stem bark was found to be higher than those of other plant parts but similar to that of roots. Family units did however, bark-strip branches more frequently than bull groups while males ate roots more often than family units (Chapter 3). Hence, adult males could meet their daily calcium requirements by selecting roots. Alternatively, males need not specifically require plant parts high in calcium to meet their nutritional requirements because of their higher fibre intake and as calcium essentially exists as calcium pectate in cell walls (Van Soest 1994).

In conclusion, both bull groups and family units accepted varying proportions of plant part categories in relation to their nutritional requirements. The chemical analysis of plant samples collected at the feeding sites of both social units of elephant complemented the information obtained from faecal analyses as well as the data collected during plant-based surveys. According to Guy (1976) and Hoppe (1984), the total feeding time of elephants varies between 12 and 18h. Chemical analyses of faecal samples, are therefore more representative of the diet quality of longer feeding times. Faecal analysis, coupled with the overall averages of the frequency at which plant parts were removed and the chemical analyses of these plant parts, did provide empirical evidence that bulls were more tolerant of high fibre diets and were possibly ingesting diets with a lower protein and phosphorus content than females. The results of this study suggest that smaller bodied animals within family units adopt feeding strategies which would enable them to feed selectively on more nutritious plant parts. Contrary to this, bulls appeared to eat plant parts of low digestibility for bulk and volume.

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CHAPTER 5

Size- and sex related feeding distinctions amongst African elephants as reflected by faecal indices of diet quality and carbon isotope discrimination

5.1 Abstract

Dimorphism in body size at intra-specific level is expected to lead to differences in the energy requirements and food selection between the sexes according to the predictions of the Body Size Hypothesis. Adult female elephants should have higher relative energy demands than large-adult males not only because of their smaller body size but also because of the demands of pregnancy and lactation. It is therefore predicted that adult females would be selecting a higher quality diet than larger bodied adult males. These feeding distinctions should be reflected in the faecal fibre, protein and mineral content. To determine whether these expectations held, faecal samples were collected from elephants within the private nature reserves bordering the Kruger National Park in South Africa over a two-year period and were chemically analysed for nitrogen, phosphorus, calcium and measures of fibre. We compared these chemical measures where they were most likely to be pronounced. Hence comparisons were made between adult females and large-adult males during the dry season period of resource limitation. To separate the possible effects of reproductive status (pregnancy and lactation in females) from body size differences between the sexes, faecal indices of diet quality were furthermore compared between (1) adult females and large-adult males differing in both size and sex (2) adult females and small-adult males similar in size but differing in sex, and (3) large-adult males and small-adult males differing in size but not sex. As elephants are known to shift from dicotyledon to graminoid dominated diets as conditions progress from dry to wet season, we also examined whether differences in faecal carbon isotope values exist, potentially indicating differences in forage class selection between elephant size/sex categories. Seasonal differences in the relative proportions of browse:grass within size/sex categories of elephants were more pronounced than differences between size/sex categories. Large-adult males showed significantly lower levels of faecal minerals, with the exception of faecal calcium levels, together with higher levels of fibre than adult females during the dry season. These sex related differences in faecal measures could be ascribed to differences in the

reproductive status as well as body size differences between the sexes. When weaned juveniles and subadults were included in the analysis to incorporate a wider range of size categories, irrespective of sex effects, faecal indices of protein and phosphorus were negatively related to body size while the inverse was true for fibre levels during the dry season months. Faecal levels of neutral detergent fibre were also positively related to body size during the transitional and wet season months while faecal phosphorus levels decreased with increasing body size during the transitional period.

5.2 Introduction

Faecal indices of diet quality provide non-evasive, economical alternatives to determine the nutritional contents of diets of free-ranging wildlife species (Erasmus *et al.* 1978, Hobbs *et al.*1981, Leslie *et al.*1989, Dörgeloh *et al.* 1998, Grant *et al* 2001). Furthermore, faecal indices of diet quality in combination with near infrared reflectance spectroscopy (NIRS) have become an important cost effective tool for nutritional profiling in agricultural studies (Lyons & Stuth 1992, Coates 1999, Coates 2000). Hence I used faecal concentrations of protein, minerals and fibre together with NIRS techniques to reflect the dietary intakes of these chemical entities by elephants (Meissner *et al.* 1990, Seydack *et al.* 2000). I assumed that high faecal measures of nitrogen (N), phosphorus (P) and calcium (Ca) together with low levels of neutral detergent and acid detergent fibre (NDF and ADF respectively) are indicative of a high quality diet.

Faecal indices of diet quality are however confounded by various factors, which are specific to the type of nutrient that is being measured within the faeces. Briefly, measures of N have been described as poor predictors of dietary protein for several reasons (Hobbs 1987, Wehausen 1995, Coates 2001). Firstly, faecal N levels are elevated by the protein-complexing properties of plant secondary compounds (Robbins *et al.* 1987). Faecal N levels would thus be high especially if dicotyledons formed a large proportion of the diet (Arman *et al.* 1975, Eramus *et al.* 1978, Holechek *et al.* 1982). Tannins are largely restricted to dicotyledons (White 1957, Swain 1979). Secondly, only a small fraction of faecal N in herbivores can be associated with dietary nitrogen as microbial cells and endogenous N form a large proportion of faecal N (Orskov 1982, Robbins 1983, Van Soest 1994). Lastly, seasonal changes in digestibility of forages also confound the use of faecal N as an index of dietary N (Holloway *et al.*1981), especially when diets of low digestibility are ingested (Wrench *et al.*1997) as during periods of limited resource availability. Contrary to faecal N, accurate estimates of dietary P in livestock can be made from faecal P (Holechek *et al.*1985, Vitti *et al.* 2000, Wu *et al.* 2000).

Faecal P levels have also been seen as a more reliable index to diet quality than faecal N, as faecal P levels are not influenced by tannins (Mubanga *et al.*1985, Grant *et al.* 1995, Wrench *et al.* 1997, Osborn & Jenks 1998, Grant *et al.* 2001). Although dietary Ca levels accurately reflects faecal Ca levels in domestic goats (Diersen-Schade *et al.* 1984), Ca levels will depend on whether monocotyledons or dicotyledons are ingested. Dicotyledons, especially bark (Napier Bax & Sheldrick 1963, Williamson 1975, Hiscocks 1999), have higher Ca levels than grass (McCullagh 1969, Van Soest 1994). Faecal NDF measures the actual undigested forage fraction (cellulose, hemicellulose, lignocellulose, silica, pectins, insoluble starch and bound cell wall protein) in livestock (Manson & Frederiksen 1979) as well as in elephants (Meissner *et al.* 1990). Plant quality as defined by total digestibility can also be indexed by ADF, which is a measure of the total lignocellulose and silica in plant matter (Shenk *et al.*1992).

Macroscopic and microscopic analysis of elephant dung can be used to estimate the ratio of browse to grass in addition to providing information on the seasonal variation of diets (Williamson 1975, Buss 1990). I used stable carbon isotope analyses of faecal samples to establish the seasonal variation in the relative proportions of browse to grass consumed by elephants (DeNiro & Epstein 1978). Different photosynthetic pathways of carbon fixation characterises C_3 (most dicotyledonous forbs, shrubs and trees) and C_4 (primarily grass) plants. Hence it is possible to estimate the dietary contribution of each of these types of plants by determining the $^{13}C/^{12}C$ ratio of plant material found within the faeces of elephants (Tieszen & Imbamba 1980). The $\delta^{13}C$ value is a measure of the amount of heavy (^{13}C) and light (^{12}C) isotopes in a sample relative to a standard and are expressed as parts per thousand (‰) (Peterson & Fry 1987, Kelly 2000). In most areas throughout southern Africa C_4 plants have $\delta^{13}C$ values of approximately –12.5 ‰ while C_3 foliages average values between –26.5 and –28.0 ‰ (Smith & Brown 1973). The isotopic differences between consumed C_3 and C_4 plants are reflected in the body tissue of the animal (Vogel 1978) so that animals dependent on dicotyledonous browse would have $\delta^{13}C$ values close to –28.0 ‰ and grazers would have $\delta^{13}C$ values of approximately –12.5 ‰. A straight line between –12.5 ‰ at a C_3/C_4 or a browse/graze ratio of 0:100 and –28.0 ‰ at a ratio of 100:0 provides a means of estimating the diets of mixed feeders (Van der Merwe *et al.*1988). The $\delta^{13}C$ values of faecal or rumen samples are advantageous in that they represent the immediate dietary proportion of C_3 and C_4 plants actually eaten by the animal and do not estimate the isotope fractionation between the plant and the animal (Tieszen *et al.* 1979, Tieszen *et al.*1983). Coates (1991) found that the

$\delta^{13}C$ of a single cattle faecal sample could reliably reflect the integrated diet over the previous three to four days. Furthermore the inefficient digestive abilities of elephants (Foose 1982, Meissner *et al.* 1990) would ensure that the $\delta^{13}C$ faecal values would not differ much from the actual foliage eaten (Vogel *et al.* 1990).

According to the Jarman-Bell Principle, small ungulates should be more selective for a high quality diet, while large ungulates should be more tolerant of a low quality, high fibre diet (Bell 1971, Geist 1974, Jarman 1974). Hence diet quality is expected to decline with increased body mass, with the tolerance for low quality diets of larger animals becoming more pronounced under dry season conditions (Owen-Smith 1988). As a consequence, larger herbivores should tend to utilise lower quality resources, have a greater dietary breadth, be more resistant to starvation and incorporate more habitat types within their feeding range than smaller species (Owen-Smith 1985, du Toit & Owen-Smith 1989).

Stokke & du Toit (2000) extended the Jarman-Bell Principle to intra-specific level by generalising this Body Size Hypothesis (BSH). The widespread quarter-power scaling of numerous biological processes in nearly all organisms (West *et al.* 1997), indicates that the Jarman-Bell Principle could be applied at intra-specific level where body size differences exist. Furthermore, a mass exponent of 0.67 has been described to best represent intra-specific scaling of metabolic rate (Feldman & McMahon 1982). Any mass exponent less than 1.0 implies that smaller animals need more nutrients per unit body weight than larger ones (Van Soest 1994). Hence, allometric differences between the sexes at intra-specific level should lead to divergence in nutritional demands, which result in sex related distinctions in feeding ecology in response to different metabolic needs. Besides higher mass-specific metabolic rates when compared to their larger bodied male counterparts, females are subject to the added nutritional demands that pregnancy or lactation impose (Crampton & Lloyd 1959, Moen 1973). Consequently, adult females may require high protein diets (Robbins 1983), while males should be more energy limited as Lindsay (1994) found strong positive correlations between diet choice and energy intake in male elephants. Although I was unable to differentiate faecal samples obtained from breeding females from those of non-reproductive females, sex differences in reproductive costs should tend to reinforce the effect of size differences between the sexes.

In African elephants, *Loxodonta africana,* size dimorphism is pronounced, with adult males (maximum body mass of 8000kg) reaching twice the body mass of adult females (maximum body mass of 4000kg) (Laws 1966, Owen-Smith 1988). I here focus on the dietary comparison at the nutritional level, using faecal analyses to investigate whether the predictions of BSH apply to African elephants within the lowveld region of South Africa. I determined faecal nitrogen (N), phosphorus (P), calcium (Ca), neutral detergent fibre (NDF) and acid detergent fibre (ADF) levels for male and female elephants of different size categories in an attempt to quantify size- and sex related dietary differences in these measures. The predictions of the BSH, namely that when resources are limited larger bodied animals will utilise poorer quality diets than their smaller bodied counterparts, were also tested between categories where (1) both size- and sex related differences were linked (large-adult males and adult females), (2) where sex differences occurred independently of size differences (adult females and small-adult males) and (3) where size differences occurred independently of sex differences (small-adult males and large-adult males). The small-adult male category was incorporated into the analysis to distinguish the possible influence of reproductive status apart from body size differences on faecal diet quality measures. Possible differences in diet quality as revealed by faecal indices could furthermore merely reflect differences in forage class selection without indicating feeding distinctions between size/sex categories of elephant among woody plant components. I therefore also considered the size- and sex related distinctions in the relative proportions of browse:grass by stable carbon isotope analyses of faecal samples. Finally, the influence of body size on faecal indices of diet quality was determined across a wider range of body sizes by incorporating findings from the faeces of weaned juveniles and subadult animals.

5.3 Methods

5.3.1 Study area and study period

Refer to Chapter 2 for a detailed description of the study area.

Elephant faecal samples were collected over two years, 1999 and 2000. During 1999, samples were collected during the dry season month of September and for three consecutive months after the onset of the summer rains (November 1999 until January 2000). In 2000, sample collection extended from July until middle November. Based on monthly rainfall measured within the Umbabat Private Nature Reserve the following rainfall months were distinguished: early-dry months (July-August 2000), dry months (September 1999 and September 2000), transitional months (November 1999 and October-November 2000) as well as wet months (December 1999-January 2000). Monthly rainfall was measured within the Umbabat Private

Nature Reserve. Some of the highest rainfall recorded in the recent history of the area, was measured during the summer of 2000 (Chapter 2).

5.3.2 Sample collection and preparation for chemical analyses

During this study, 245 fresh faecal samples were collected from September 1999 to January 2000 and 137 samples from July to November 2000, so that 382 samples were collected in total. Most samples were collected within three hours of defecation (with a range of 25 min to 17 h), which were well within the time frame of seven days suggested by Leite & Stuth (1994) as the maximum amount of field exposure permitted before influencing the spectral integrity of faecal samples. The circumference of faecal samples were measured (to the nearest 0.5 cm) to allocate all boli from a particular individual to a specific size class based on Jachmann & Bell's (1984) circumference measurements of Kasungu elephant droppings in Malawi (Table 5.1). Reilly (2002) had also estimated age in free-ranging Sumatran elephants (*Elephas maximus sumatranus*) based on their dung measurements but these results were not used due to the obvious size differences between African and Indian elephants (Owen-Smith 1988). Most samples were gathered after animals had moved from the area. Faecal samples were also collected in the absence of positive sightings of animals as long as a clear distinction could be made on whether the faeces were from a bull group or family unit, using group size, number of tracks, bolus circumferences and information of sightings provided by landowners. Bolus circumference was thus used to distinguish between sexes within the adult age classes, primarily through the spatial separation of large- and small-adult males within bull groups, from family units. Faecal samples that were collected from small-adult males within family units were classified as obtained from adult females unless the animal was sighted, as considerable overlap in bolus circumference measurements made distinctions between these two size- and sex categories impractical within family units (Figure 5.1).

Samples were collected from family units, which included adult females and subadults as well as juveniles of both sexes. I excluded most unweaned animals from the analyses as pre-weaned diet is not restricted to the vegetation and could bias the results (Cook *et al.* 1994, Wrench *et al.* 1996, Judson & McFarlane 1998). According to the literature, most elephant's weaning commences by the age of three (Bengis *et al.* 1995, Whyte 1996) but usually suckling continues until the birth of the next calf. The average inter-calving period for elephants within

Table 5.1 The classification of elephant faecal samples into size and sex categories based on the bolus circumference measurements. Square brackets are inclusive of the measurement while parentheses indicate exclusivity.

Size category	Abbreviation	Bolus circumference (cm)	Age class (years)
Neonates	N	<20	<1
Juveniles	J	[20-35)	[1-8)
Subadults	SA	[35-40)	[8-12)
Adult females	AF	[40-50)	>12
Large, adult males in family units	AM-f	>50	>25
Small, adult males in bull groups	SM-b	[40-50)	[13-25)
Large, adult males in bull groups	AM-b	>50	>25
Lone males	LM	>40	>13

the Kruger National Park was between 4 and 4.5 years (Whyte 1996, Whyte 2001). Juveniles under the age of five were not included in the analysis by excluding samples with bolus circumference measurements less than 31cm (Jachmann & Bell 1984). This procedure would eliminate most un-weaned animals, although some juveniles that may suckle for extended periods could still have confounded the results of the analyses. Samples collected from adult males included the following categories: large-adult males found in bull groups, small-adult males found in association with these bulls, large-adult males associated with family units and lone males (Figure 5.1).

Entire faecal samples were collected with the exception of that portion in contact with the ground, leaving approximately 1 cm of soiled faecal material behind. During the wet season all insects were manually removed from the samples. Care was taken to prevent the samples from being contaminated by dust during transportation by keeping them in boxes lined with chicken mesh to prevent sweating and covering them with brown paper sheets. Samples were air-dried in a ventilated room while suspended on shade cloth covered with brown paper. Breaking the samples up and spreading them to an even thickness of about 1 cm prevented fungal growth (Wrench *et al.* 1996). After air-drying, the samples were shredded by an electric garden shredder and mixed thoroughly. A 200g sub-sample of each shredded sample was taken to ensure equal representation of all faecal components within the faeces. The samples were stored in paper bags until they could be oven dried overnight. Samples were then hammer milled, cyclone milled and near infrared spectra collected. The application of NIRS enabled the accurate prediction of the protein, mineral, fibre and carbon isotope levels of all the faecal

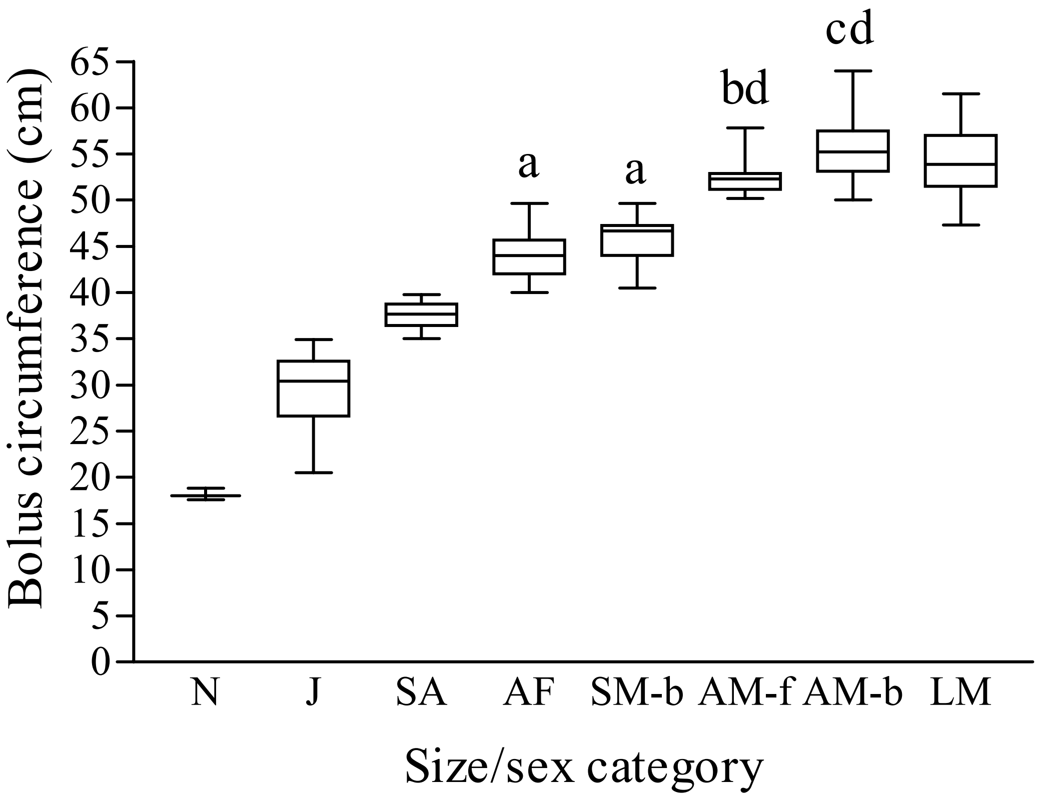

Figure 5.1 Box-whisker plots to show the range of bolus circumference measurements for neonates (N), juveniles (J), subadults (SA), adult females (AF), small-adult males in bull groups (SM-b), large-adult males in family units (Am-f), large-adult males in bull groups (AM-b) and lone males (LM). The box extends from the 25th to the 75th percentile with the horizontal line at the median while the whiskers extend from the smallest to the largest values. Unmarked classes were significantly different from each other (*P* <0.001), while classes that are marked with a 'd' were only significantly different at the 5% level. The other categories with the same letter of the alphabet (a-c) were not significantly different from each other at the 5% level (one-way ANOVA plus Bonferroni multiple comparison correction).

samples (refer to Chapter 2 for details concerning NIRS). Briefly, NIRS procedures involve the collection of near infrared spectral data for all samples. The computer software linked to the spectrophotometer selects a representative set of samples that includes the spectral variability of all the remaining samples. The selected samples were analysed by conventional laboratory procedures for chosen diet quality indices. This calibration set is then used to develop a predictive model calculating the chemical composition of the unknown samples, for which only the infrared spectra has been provided.

5.3.3 Chemical analysis

The ^{13}C to ^{12}C ratio was determined on two replicates of each of the 95 dried and ground faecal samples, which represented the calibration set. The calibration set was selected from 245 samples that were collected from September 1999 until January 2000 (Appendix M). Carbon isotope ($\delta^{13}C$) determination took place in a Finigan Matt 252 mass spectrometer operating in the continuous flow mode. The $\delta^{13}C$ values are expressed as parts per million (‰) relative to Pee Dee Belemnite (PDB) standard as follows (Graig 1957):

$$\delta^{13}C\ ‰=\{[(^{13}C/^{12}C)\ \text{sample}/(^{13}C/^{12}C)\text{standard}]-1\}\ x\ 1000$$

All the $\delta^{13}C$ values were converted to % C_3. We assume that faecal C_3 represents the dietary proportions of dicotyledons that were utilised by elephants. Dicotyledonous forage would thus include mainly the leaves, twigs, roots and bark of trees and shrubs as well as forbs (non-graminaceous herbs) and ingestion of these plant parts will henceforth be referred to as browsing.

A calibration set of a 142 samples which represented the spectra variability of all 382 faecal samples that were collected throughout the study period were analysed by conventional laboratory procedures for nitrogen, mineral and fibre content. The automated, simultaneous determination of N, Ca and P was conducted in a continuous-flow analysis system as described by the Agri Laboratory Association of S.A. (ALASA 1998). NDF was determined according to the methods of Robertson & Van Soest (1981) and ADF according to the methods described by Goering & Van Soest (1970).

5.3.4 Statistical analysis

The results from large-adult males in bull groups, on their own or in association with family units were grouped to represent the large male size category (Figure 6.1). The results from small-adult males found in bull groups or on their own and adult females within family units were analysed separately. Prior to this, the data from individual animals of the same size category and within the same family unit or male group, were pooled and the mean used to ensure independent samples within a particular size/sex category (Fry 1993).

A full factorial design (ANOVA) with period (early-dry, dry and transitional months) and sex (adult females and large-adult males) as factors was used to test for differences between the sexes for each chemical measure across the dry season. As the interaction of sex and period proved to be insignificant (Table 5.2), the interaction effect was left out of the

Table 5.2 Factorial ANOVA results of the higher order interactive effects of sex (large-adult males and adult females) and period (early dry-, dry- and transitional rainfall period) on faecal measures (N, P, Ca, NDF and ADF). Significant *P* values (<0.05) are given in bold.

		N		P		Ca		NDF		ADF	
Effect	Df	*F*	*P*-level	*F*	*P*-level	*F*	*P*-level	*F*	*P*-level	*F*	*P*-level
Sex	1	**8.30**	**0.0050**	**12.6**	**0.0006**	2.57	0.1122	**22.1**	**<0.0001**	**4.10**	**0.0459**
Period	2	**15.9**	**<0.0001**	**19.1**	**<0.0001**	0.41	0.6679	**38.4**	**<0.0001**	**43.4**	**<0.0001**
Sex*period	2	0.42	0.6570	1.19	0.3090	0.34	0.7129	0.50	0.6184	0.53	0.5900

model. The overall effect of sex proved to be significant while controlling for the effect of sampling period and faecal measures between the sexes were therefore compared for each of the categorised dry season periods. Thereafter one-tailed Mann Whitney (*U*) tests were used to test whether the faecal indices of large-adult males were indicative of poorer diets (higher in fibre content and lower in N and mineral content) when compared to adult females within each of the dry season categories (Zar 1996).

To determine the effects of size apart from sex differences on faecal measures, the small-adult male category was included in the dataset. Seasonal effects were tested over a wider range of months/periods by including the wet months in the dataset. Statistical testing was limited by insufficient samples especially for small-adult males, which prevented a multi-factor ANOVA design with sex, size and month/period as factors (Fry 1993). Data on faecal nutrients were assigned to four periods which were based on the total monthly rainfall received during the study period and included early-dry months (July-August 2000), dry months (September 1999 and September 2000), transitional months (November 1999 and October-November 2000) as well as wet months (December 1999-January 2000). The Kruskal Wallis (*H*) test was used to test for differences in faecal indices of diet quality between the four groupings of months for the same size/sex category of elephant and between each of these elephant categories within a block of months. Dunn's Multiple Comparison test was used to determine which size/sex groups within particular blocks of months differed from each other in their protein, mineral or fibre content (Sokal & Rohlf 1981).

Carbon isotope data were assigned to three periods, which did not include the early-dry months. Carbon isotope analysis was conducted on the samples that were collected from September 1999 until January 2000 and consequently data were grouped to represent a dry- (September 1999), a transitional- (November 1999) and a wet month period (December 1999 and January 2000). A straight line between –12.5 ‰ at a C_3/C_4 or a browse/graze ratio of 0:100

and –28.0 ‰ at a ratio of 100:0 provides a means of estimating the diets of mixed feeders (Van der Merwe *et al.*1988). The Kruskal Wallis (*H*) test was used to test for differences in the % C_3 (representing browse) within the same size/sex categories of elephant and between each of these categories within a month/period. Dunn's Multiple Comparison test was used to determine which periods or size/sex groups differed significantly from others in their proportion of faecal browse. To determine whether either faecal N or faecal P levels (dependent variables) were influenced by the proportion of browse in the faeces, General Linear Models of STATISTICA version 6.0 (Statsoft Inc. 2001) were used with month/period as a categorical predictor and the faecal browse component as continuous predictor. Faecal N, P and % C_3 were arcsine transformed prior to the analyses and residual plots were examined to ensure that data transformations were appropriate (Miles & Shevlin 2001).

The relationship between faecal N and P, Ca and fibre indices as well as between N and NDF, irrespective of rainfall period, was determined using Pearson's correlation coefficient after arcsine transformation of faecal measures (Fry 1993). Faecal measures were compared between all size/sex categories of elephant.

Faecal diet quality indices from weaned juveniles and subadult animals were incorporated into the data of adult size categories of elephant to determine the influence of body size on chemical measures over a wider range of size categories. Bolus circumference measurements represented body size, irrespective of the effects of sex. General Linear Models of STATISTICA version 6.0 (Statsoft Inc. 2001) were again used to determine the effect of period (categorical predictor variable) and log of the bolus circumference measurements (continuous predictor variable) on each of the arcsine transformed chemical measures (Zar 1996, Miles & Shevlin 2001). Least squares linear regression was thereafter used within each of the four collection periods to determine whether body size influenced faecal measures while controlling for the effect of sampling period.

5.4 Results

5.4.1 Diet quality as revealed through faecal levels of nitrogen, minerals and fibre

Adult females had significantly higher faecal measures of nitrogen and lower faecal measures of NDF and ADF when compared to large-adult males during the early-dry and dry month periods. The measurement of faecal nitrogen and fibre levels were more variable for adult females than for large adult males during the transitional months and hence the sex differences did not prove to be significant, although they followed the same direction. Phosphorus levels in the faeces of adult females were higher than those of large-adult males for the dry and transitional months. No difference could be found between the faecal calcium levels of adult females and large-adult males for either of the dry season periods that were tested (Table 5.3).

Table 5.3 Mean (±SEM) levels of nitrogen (N), phosphorus (P), calcium (Ca), neutral-detergent fibre (NDF) and acid-detergent fibre (ADF) within the faeces of adult female and large-adult male elephants. Sample sizes are given in parentheses. All values are expressed on a percentage dry matter basis. Significant *P*-values (<0.05) are given in bold.

Chemical measure	Rainfall month	Large adult males	Sex differences (Mann Whitney *U*)	Adult females
N	Early-dry	0.97±0.031 (11)	**_U_=28, _P_=0.0164**	1.1±0.024 (11)
	Dry	0.82±0.020 (27)	**_U_=170, _P_=0.0248**	0.87±0.019 (19)
	Transitional	0.94±0.044 (14)	*U*=63, *P*=0.1459	1.1±0.078 (12)
P	Early-dry	0.11±0.0073 (11)	*U*=39, *P*=0.0836	0.12±0.0068 (11)
	Dry	0.065±0.0043 (27)	**_U_=160, _P_=0.0125**	0.079±0.0048 (19)
	Transitional	0.069±0.0067 (14)	**_U_=41, _P_=0.0143**	0.11±0.016 (12)
Ca	Early-dry	1.2±0.068 (11)	*U*=39, *P*=0.0790	1.4±0.081 (11)
	Dry	1.3±0.047 (27)	*U*=249, *P*=0.4379	1.4±0.080 (19)
	Transitional	1.3±0.051 (14)	*U*=67, *P*=0.1980	1.4±0.085 (12)
NDF	Early-dry	73±0.86 (11)	**_U_=14, _P_=0.0013**	69±0.49 (11)
	Dry	78±0.49 (27)	**_U_=120, _P_=0.0012**	76±0.53 (19)
	Transitional	76±0.47 (14)	*U*=54, *P*=0.0614	73±1.2 (12)
ADF	Early-dry	57±0.47 (11)	**_U_=34, _P_=0.0409**	55±0.54 (11)
	Dry	66±0.86 (27)	**_U_=161, _P_=0.0171**	63±0.83 (19)
	Transitional	61±0.75 (14)	*U*=83, *P*=0.4897	61±1.2 (12)

Comparing small-adult and large-adult males, significant differences were restricted to the early dry months when small-adult males had significantly higher Ca levels than large-adult males (1.6 as opposed to 1.2 %DM, Kruskal Wallis *H*=6.3, *P*=0.0418). Where the influence of only a sex effect on faecal measures was tested by comparing adult females with small-adult males of similar size, a significant difference was found in the early-dry months. Adult females contained lower ADF levels in their faeces than small-adult males (55 as opposed to 58 %DM, Kruskal Wallis *H*=8.0, *P*=0.0191). Large-adult males were found to have higher faecal levels of NDF than adult females in both the early dry (73 as opposed to 69 %DM, Kruskal Wallis *H*=11, *P*=0.0045) and the dry rainfall months (78 as opposed to 76 %DM, Kruskal Wallis *H*=10, *P*=0.0062). Furthermore, adult females had higher faecal levels of phosphorus than large-adult males in the dry rainfall period (0.079 as opposed to 0.065 %DM Kruskal Wallis *H*=6.0, *P*=0.0495, Table 5.4).

Table 5.4 Mean (±SEM) levels of nitrogen (N), phosphorus (P), calcium (Ca), neutral-detergent fibre (NDF) and acid-detergent fibre (ADF) within the faeces of large-adult male (AM), adult female (AF) and small-adult male (SM) elephants. Sample sizes are given in parentheses. All values are expressed on a percentage dry matter basis. The Kruskal Wallis statistic (KW) and level of significance is given. Significant *P*-values (<0.05) are given in bold. Periods with superscripts with the same alphabetical letter (a-d) where not significantly different from each other.

Chemical Measure	Rainfall months	Size/sex diff.	Large, adult males (AM)	Period diff. in AM	Adult females (AF)	Period diff. in AF	Small, adult males (SM)	Period diff. in SM
N	Early-dry	*P*=0.0622	0.97±0.031 (11)^{a}	***P*<0.0001** KW=40	1.1±0.024 (11)^{ac}	***P*<0.0001** KW=29	1.1±0.083 (5)	*P*=0.0763 KW=6.9
	Dry	*P*=0.0604	0.82±0.020 (27)^{a}		0.87±0.019 (19)^{b}		0.91±0.040 (4)	
	Transitional	*P*=0.4858	0.94±0.044 (14)^{a}		1.1±0.078 (12)^{ab}		1.1±0.088 (9)	
	Wet	*P*=0.5130	1.4±0.045 (14)^{b}		1.4±0.053 (10)^{c}		1.5±0.27 (2)	
P	Early-dry	*P*=0.3406	0.11±0.0073 (11)^{ad}	***P*<0.0001** KW=38	0.12±0.0068 (11)^{ad}	***P*<0.0001** KW=27	0.11±0.019 (5)	*P*=0.1034 KW=6.2
	Dry	***P*=0.0495**	0.065±0.0043 (27)^{b}		0.079±0.0048 (19)^{b}		0.079±0.0072 (4)	
	Transitional	*P*=0.0868	0.069±0.0067 (14)^{bc}		0.11±0.016 (12)^{abc}		0.087±0.012 (9)	
	Wet	*P*=0.8850	0.15±0.010 (14)^{d}		0.15±0.011 (10)^{d}		0.17±0.05 (2)	
Ca	Early-dry	***P*=0.0418**	1.2±0.068 (11)^{ab}	***P*=0.0308** KW=8.9	1.4±0.081 (11)^{ab}	***P*=0.0194** KW=9.9	1.6±0.085 (5)	*P*=0.0640 KW=7.3
	Dry	*P*=0.9239	1.3±0.047 (27)^{a}		1.4±0.080 (19)^{ab}		1.3±0.11 (4)	
	Transitional	*P*=0.5667	1.3±0.051 (14)^{ab}		1.4±0.085 (12)^{a}		1.3±0.063 (9)	
	Wet	*P*=0.8881	1.1±0.083 (14)^{b}		1.1±0.070 (10)^{b}		1.1±0.11 (2)	
NDF	Early-dry	***P*=0.0045**	73±0.86 (11)^{ac}	***P*<0.0001** KW=40	69±0.49 (11)^{ad}	***P*<0.0001** KW=28.8	72±0.61 (5)^{ac}	***P*=0.0026** KW=14
	Dry	***P*=0.0062**	78±0.49 (27)^{b}		76±0.53 (19)^{b}		77±0.51 (4)^{b}	
	Transitional	*P*=0.1945	76±0.47 (14)^{ab}		73±1.2 (12)^{bc}		74±0.52 (9)^{abc}	
	Wet	*P*=0.5570	71±0.66 (14)^{c}		71±0.46 (10)^{acd}		71±1.2 (2)^{c}	
ADF	Early-dry	***P*=0.0191**	57±0.47 (11)^{ac}	***P*<0.0001** KW=33	55±0.54 (11)^{a}	***P*<0.0001** KW=25	58±0.54 (5)^{a}	***P*<0.0096** KW=11
	Dry	*P*=0.0091	66±0.86 (27)^{b}		63±0.83 (19)^{b}		66±0.84 (4)^{b}	
	Transitional	*P*=0.9933	61±0.75 (14)^{abc}		61±1.2 (12)^{cb}		62±1.1 (9)^{ab}	
	Wet	*P*=0.7890	59±0.84 (14)^{c}		59±0.69 (10)^{abc}		59±1.5 (2)^{ab}	

Faecal concentrations of N and P for both adult females and large-adult males were found to be substantially higher in the wet months than in the dry or transitional months. Irrespective of the size/sex of the elephant, faecal Ca levels were higher during periods of limited rainfall (early-dry, dry and transitional months) than during wet months. Both nutrient and fibre levels for all size/sex categories of elephant were intermediate between dry and wet months in the transitional period (Table 5.4).

5.4.2 Carbon isotope analyses

Both male and female elephants consistently had higher levels of C_3 plants (browse) in their faeces in the dry season months than in the wet months. No significant forage class distinctions could be discerned among different size/sex related categories of elephant (Table 5.5). Both faecal N and P levels were significantly influenced by month/period of collection ($F_{2,185}$=86.2, P<0.0001 and $F_{2,185}$=57.7, P<0.0001 respectively) with levels of both chemical measures being higher in the transitional and wet months than in the dry rainfall period. After controlling for the effect of period, faecal N levels were found to significantly increase with an increase in the browse component of the diet during September (r=0.30, $F_{1,100}$=9.61, P=0.0025). Faecal P levels were unaffected by faecal browse components, irrespective of the month/period of collection (dry period: r=0.01, $F_{1,100}$=0.02, P=0.8876; transitional period: r=0.23, $F_{1,26}$=1.52, P=0.2291 and wet period: r=0.08, $F_{1,51}$=9.61, P=0.5878).

5.4.3 Relationships between faecal measures

Faecal N levels were positively related to faecal P levels thereby indicating that faecal N and P levels covaried (n=159, Pearson r = 0.817, P<0.0001). High levels of faecal N were associated with low total cell wall content or total fibre (NDF) (n=159, Pearson r = -0.645, P<0.0001). Faecal Ca levels were significantly positively related to ADF levels (n=159, Pearson r = 0.234, P=0.0030) but not to NDF levels.

5.4.5 The influence of body size on faecal indices of diet quality

All faecal measures, with the exception of faecal Ca, were significantly influenced by bolus circumference (Figure 5.2). Faecal N levels decreased with increasing bolus circumference

Table 5.5 Mean (±SEM) monthly estimates of the percentage C_3 (browse) plants within the faeces of large-adult male (AM), adult female (AF) and small-adult male (SM) elephants. Sample sizes are given in parentheses. The Kruskal Wallis (KW) statistic and significance level are given. Significant tests results (*P*<0.05) are given in bold. Months that did not differ significantly from each other are indicated by the same letters of the alphabet (a-b).

Months	Size/sex differences	Large-adult males (AM)	Monthly differences (AM)	Adult females (AF)	Monthly differences (AM)	Small-adult males (SM)	Monthly differences (SM)
Dry	*P*=0.4462	79 ± 1.8 (22)^{a}	***P*<0.0001** KW=29	82 ± 1.9 (12)^{a}	***P*<0.0001** KW=20	83 ± 2.9 (4) ^{a}	*P*=0.0390 KW=5.7
Transitional	*P*=0.4008	66 ± 3.6 (5)^{ab}		68 ± 1.3 (4)^{ab}		71 ± 3.5 (4) ^{ab}	
Wet	*P*=0.5416	52 ± 3.1 (14)^{b}		49 ± 2.9 (10)^{b}		54 ± 9.5 (2) ^{b}	

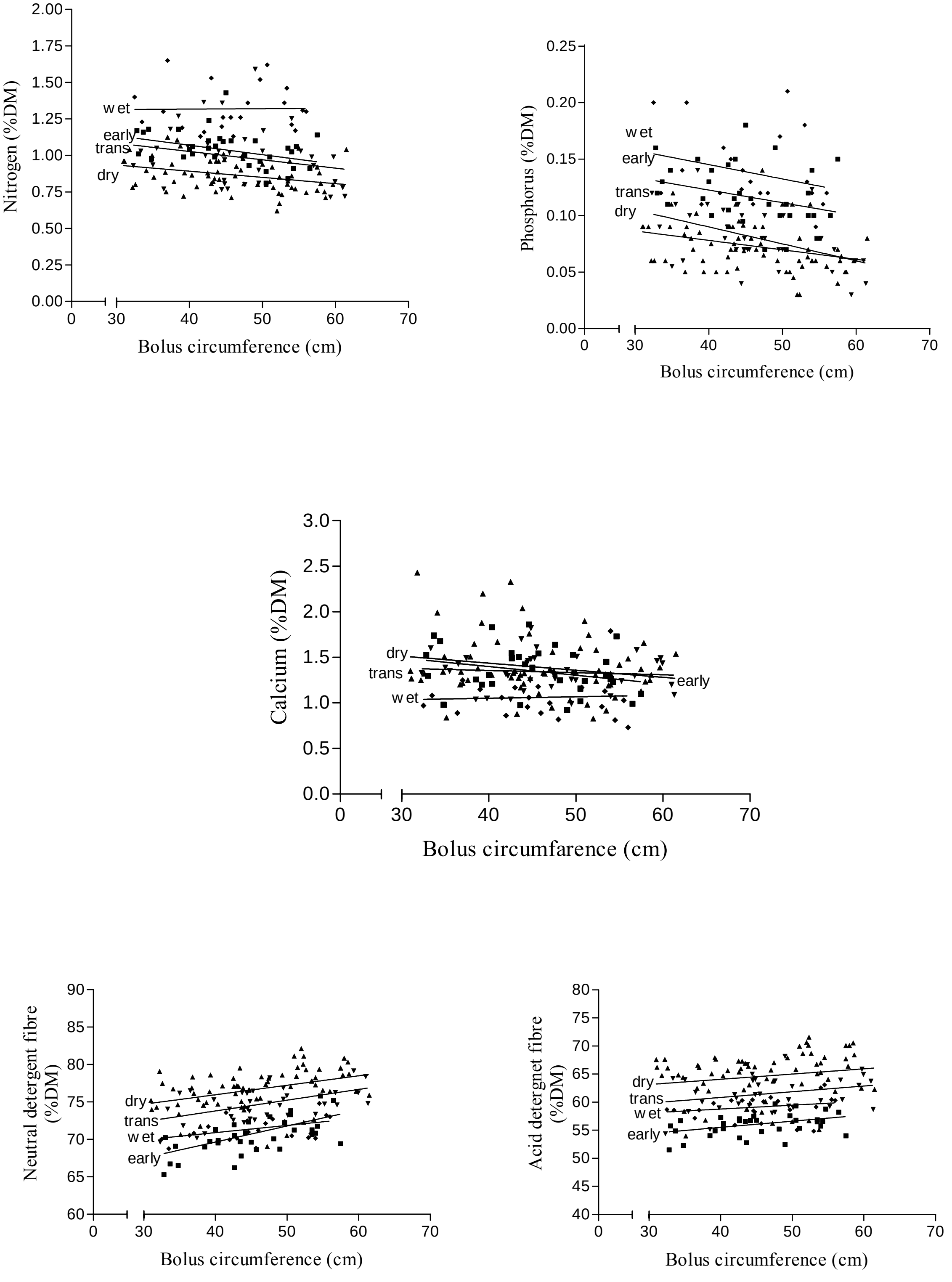

Figure 5.2 The relationship between faecal nitrogen (N), phosphorus (P), calcium (Ca), neutral-detergent fibre (NDF), acid-detergent fibre (ADF) and bolus circumferences for the early dry, dry, transitional and wet month periods.

during the early-dry and dry months (r=-0.39, P=0.0267 and r=-0.33, P=0.0073 respectively). Faecal P levels showed similar trends but only during the dry and transitional rainfall months (r=-0.32, P=0.0088 and r=-0.44, P=0.0071 respectively). Contrary to faecal protein and mineral levels, NDF levels were not only positively related to body size during the early-dry or dry months (r=0.64, P<0.0001 and r=0.39, P=0.0010 respectively) but also during the transition and wet rainfall months (r=0.53, P=0.0008 and r=0.45, P=0.0380). Faecal ADF levels were positively related to bolus circumference only during the early-dry rainfall period (r=0.41, P=0.0173). The interaction between body size and period of collection was not significant as the slopes did not differ between rainfall periods (Table 5.6).

Table 5.6 Regression of faecal nitrogen (N), phosphorus (P), calcium (Ca), neutral-detergent fibre (NDF) and acid-detergent fibre (ADF) against bolus circumferences from a wide range of elephant size categories which included weaned juveniles, subadults, adult females, small-adult males and large-adult males. Significant P-values (<0.05) are given in bold.

Dependent variable	Rainfall period				Comparison of regression lines	
	Early-dry	Dry	Transitional	Wet	Slope	Elevation
N	r=-0.39	r=-0.33	r=-0.24	r=-0.010	$F_{3.151}$=0.57	**$F_{1,154}$=59**
	$F_{1,31}$=5.4	$F_{1,65}$=7.7	$F_{1,35}$=1.8	$F_{1,20}$=0.002	P=0.6362	**P<0.0001**
	P=0.0267	**P=0.0073**	P=0.1836	P=0.9643		
P	r=-0.32	r=-0.32	r=-0.44	r=-0.29	$F_{3.151}$=0.47	**$F_{1,154}$=52**
	$F_{1,31}$=3.6	$F_{1,65}$=7.3	$F_{1,35}$=8.2	$F_{1,20}$=1.8	P=0.706	**P<0.0001**
	P=0.0689	**P=0.0088**	**P=0.0071**	P=0.1969		
Ca	r=-0.26	r=-0.19	r=-0.10	r=-0.02	$F_{3.151}$=0.45	**$F_{1,154}$=10**
	$F_{1,31}$=2.2	$F_{1,65}$=2.4	$F_{1,35}$=0.35	$F_{1,20}$=0.011	P=0.716	**P<0.0001**
	P=0.1512	P=0.1229	P=0.5557	P=0.9186		
NDF	r=0.64	r=0.39	r=0.53	r=0.45	$F_{3.151}$=0.73	**$F_{1,154}$=80**
	$F_{1,31}$=21	$F_{1,65}$=12	$F_{1,35}$=14	$F_{1,20}$=4.9	P=0.5363	**P<0.0001**
	P<0.0001	**P=0.0010**	**P=0.0008**	**P=0.0380**		
ADF	r=0.41	r=0.17	r=0.27	r=0.22	$F_{3.151}$=0.060	**$F_{1,154}$=57**
	$F_{1,31}$=6.3	$F_{1,65}$=2.0	$F_{1,35}$=2.8	$F_{1.20}$=1.0	P=0.9805	**P<0.0001**
	P=0.0173	P=0.1616	P=0.1046	P=0.3289		

5.5 Discussion

During the dry season, when resources were most likely to be limited, I found that faecal differences in nutritional measures (N, P, NDF and ADF) between large-adult male and adult female elephants were evident. Large-adult males had significantly higher levels of fibre but lower levels of N and P in their faeces than adult females, thereby indicating that large males could be ingesting diets of lower quality than adult females. Nutritional requirements, as measured by faecal indices, were most pronounced between large-adult males and adult females as they represented the combined effect of both reproductive costs and allometric differences between the sexes.

In general, the faecal dietary indicators of small-adult males did not differ from those of large-adult males and adult females. The small samples sizes in the small-male category could however have increased my chances of making Type II Errors (failure to detect size or sex differences in diet quality that really exist) and thereby underestimate the biological significance of these results because of insufficient sampling effort within this category (Anderson *et al.* 2001). Larger sample sizes would be necessary to detect the smaller differences where either only a sex effect (adult females and small-adult males) or size effect (large- and small-adult males) was operational (Cohen 1977). Nevertheless, the expected trend with body size was confirmed when an analysis across a wider range of size classes, irrespective of sex, was performed and faecal P and N were found to decrease while fibre levels increased with increasing bolus circumference.

From measuring faecal $\delta^{13}C$ values and the subsequent conversion of these values to percentage C_3, I assumed that faecal C_3 represented the dietary proportions of woody plants i.e. browse that was utilised by elephants. Under this assumption, my results corroborate the findings of other studies, namely that elephants decrease the proportion of grass in their diet and increase the proportion of browse during the dry season (Field 1971, Guy 1976, Kabigumila 1993). The increase in faecal N levels with an increase in faecal C_3 (browse) during the dry season month of September, when the browse component of the diet would be at its highest level, suggests that the influence of plant secondary compounds could have elevated the faecal N component (Bryant *et al.* 1992). Contrary to faecal N, faecal P levels were not significantly affected by the proportion of browse, thereby excluding the possible confounding influences of tannins and enabling significant size/sex related distinctions in faecal P levels to be detected. My results are therefore in agreement with the suggestion of Osborn & Jenks (1998) and Mubanga *et al.* (1985) that faecal P levels probably provided more accurate indices of diet quality than faecal N in the presence of tannins.

Fluctuations in Ca levels were not consistent for elephants of different size or sex, which confounded comparisons between large- and small-male elephants as well as adult females within a rainfall period. The well established increase in the dietary proportion of grass together with a decrease in the use of dicotyledonous plant material by elephants as the season progressed from dry to wet (Guy 1976, Barnes 1982, Riggiero 1992) could cause fluctuations in Ca levels which would not only depend on the rainfall period, but also on the individual variability within elephant size or sex classes in the proportion of browse that was consumed. Weckerly & Nelson (1990) also found no sex and age group contrasts in dietary Ca levels within white-tailed deer, *Odocoileus virginianus*. Elephants of all classes appeared to have the lowest faecal Ca levels during the wet period. During the wet months, faecal fibre levels were also at their lowest. Pectin in plant cell walls consists of galacturonic acid where acid groups are combined with Ca ions. Calcium thus essentially exists as calcium pectate in cell walls. Calcium cross-chain bonding is easily broken during ADF analyses (Van Soest 1994), which explained the positive relationship that we found between faecal Ca and ADF levels. Therefore, the elevated faecal Ca levels during periods of limited rainfall could have been a consequence of ingesting fibrous plant parts (twigs, bark and roots), high in Ca content (Chapter 4). Furthermore, unlike other minerals in plants, Ca is not translocated out of leaves before abscission (Williams 1955).

I found the lowest levels of faecal N and P together with the highest levels of fibre, during periods of limited rainfall. Grant *et al.* (1995, 2001) found similar results for the faecal N and P levels of ruminants within the Kruger National Park. Although the increased tannin content of browse could have elevated faecal N levels, the results indicate that the high fibre diets ingested during periods of limited rainfall were low in soluble cell contents. Bell (1982) suggested that the ratio of metabolic content (protein and soluble carbohydrate cell content) to structural carbohydrate constituents (cellulose, hemicellulose and lignin content of cell walls) were the main determinants of plant quality. Faecal measures therefore suggested that during the dry months diets of lower quality were ingested by elephants, irrespective of size or sex group of elephant. Although leafy browse would offer a higher and seasonally more constant level of protein when compared to grass (Field 1971, Owen-Smith 1982), leafy browse becomes scarce as deciduous woody species loose their leaves which in turn necessitates the use of other plant parts (twigs, bark and roots) by elephants. Previous results have indicated that elephants are essentially stem browsers rather than folivores during the dry season (Chapter 3). Chemical analyses of woody plant parts have also indicated that plant stems were of lower nutritional value than dicotyledonous leafy browse (Chapter 4).

To conclude, the diet quality of different size or sexes of elephant appeared to be most dissimilar when resources were limited. Higher levels of N and P, together with lower levels of fibre found in the faeces of adult females, indicates that large-adult males may be ingesting diets of lower quality when compared to adult females. The influence of seasonal progression was reflected by all faecal indices. Although the statistical power of the differences that were tested between sex/size groups were influenced by small sample sizes, the results suggest that the effects of body size differences (comparisons between large-adult males and small-adult males) or sex differences alone (comparisons between adult females and small adult males of similar size) may not be large enough to lead to significant distinctions in diet quality at intra-specific levels. To detect such differences the combined effect of both body size and sex differences, as between large-adult males and adult females, may be necessary to influence metabolic needs to such a degree that it will lead to diet quality distinctions between the sexes.

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CHAPTER 6

Concluding overview

6.1 Introduction

Here I discuss the overall significance of the preceding chapters. I consider the management implications of my study, evaluate the complementarity of the various methods used to determine the sex- and age related feeding distinctions in the African elephant, *Loxodonta africana*, and discuss the study's limitations. Then I compare the findings of this study with similar work by Stokke (1999) and Stokke & du Toit (2000), following which I develop a conceptual model for comparison of inter-sexual differences in elephants' feeding behaviour between the Kalahari woodlands of Stokke's study area and the lowveld system of my study site. Finally I discuss recommendations for future research beyond the limits of this study

6.2 Synthesis

The Body Size Hypothesis (BSH), as defined by Stokke & du Toit (2000), predicts that sexual dimorphism in size will lead to diverse nutritional demands, which in turn will result in sexual differences in feeding ecology (Ruckstuhl & Neuhaus 2000). Diet quality is expected to decline with increased body mass, with the tolerance for low quality diets of larger animals becoming more pronounced under dry season conditions (Owen-Smith 1988). Mysterud (2000) found that the frequency of sexual distinctions in diet or habitat use (i.e. ecological segregation) increased amongst more dimorphic species. On the continuum of size dimorphism between sexes of different animal species, African elephants approach the upper end of the scale (Loison *et al.* 1999, Woolnough & du Toit 2001), considering that mature bulls within bull groups can be more than twice the size of females and their offspring within family units (Laws 1966, Owen-Smith 1988). This species is therefore eminently suited for testing the predictions of the BSH. Hence I aimed to determine whether nutritional needs of elephant age/sex classes, combined with social segregation, resulted in functional distinctions in feeding ecology between bull groups and family units.

Although numerous studies have looked at the feeding ecology of elephants in general (Barnes 1982, Jachmann *et al.* 1989, Buss 1990, Tchamba & Mahamat 1992), only a few have considered sex related differences in feeding ecology (Barnes 1982, Lindsay 1994, Stokke

1999, Stokke & du Toit 2000, Frost 2001). A seminal work in this regard has been the study by Stokke & du Toit (2000) on which were based the vegetation survey methods used in this study. Feeding distinctions at plant species and plant part level (Stokke 1999, Stokke & du Toit 2000), and habitat segregation between the sexes (Stokke & du Toit 2002), upheld the predictions of the BSH at the levels of plant species and food plots. My results indicate that within the lowveld savanna ecosystem, feeding distinctions between bull groups and family units were most pronounced at a finer scale, namely the relative quantities and types of plant parts used by the social units of elephant. The development of a conceptual model to compare sex differences in elephant feeding ecology between mesic dystrophic and semi-arid eutrophic savanna systems is therefore discussed in greater detail under a separate heading (section 6.5).

Differences in diet quality between the sexes due to distinct nutritional needs have been assumed to cause the observed intersexual distinctions in feeding behaviour within the Kalahari woodlands (Stokke 1999, Stokke & du Toit 2000). However, these diet quality differences were not established through chemical analyses. My study integrated vegetation surveys with chemical analyses of both plant and faecal samples, in an attempt to directly determine diet quality distinctions between bull groups and family units. I found near infrared reflectance spectroscopy (NIRS) to be a useful tool in this regard. Although the technique is subject to the problems inherent in predictive regression techniques (Van Soest 1994, Foley *et al.* 1998), I found that the chemical composition of both plant and faecal samples were predicted with adequate precision. NIRS enabled rapid automated non-destructive analyses of more than a 1000 samples, while only a third of these samples required conventional wet chemical analyses. The application of NIRS therefore proved to be extremely time- and cost effective. The potential utility of NIRS for ecological research was highlighted in that a single calibration set was able to predict the chemical content of 42 different plant species, made up of leaf, root, twig, bark and heartwood specimens, from various localities within the study area, over a six month period (Chapter 2).

During the dry season, vegetation surveys revealed that bull groups and family units frequently subsisted on a very narrow range of six woody species. These six species were not only favoured by both social units, but were utilised in approximately 70% of all plant species feeding events recorded. Hence there was considerable overlap in plant species consumption by both herd structures. Individuals of bull groups brought larger branches within foraging reach more frequently and from greater heights than did family units. Both bull groups and family units were predominantly stem browsers during the dry season. Bull groups, however, were found to engage in tree felling, large branch breaking and rhizophagy (root eating) more frequently than family units, which frequently debarked and defoliated woody species. Previous workers, having observed the tree felling behaviour of bulls, speculated that bull groups are more destructive feeders than family units (Guy 1976, Barnes 1982, Stokke & du Toit 2000). This study quantified the damage inflicted by bull groups compared to family units, for each of the utilised plant species, following the methods of Anderson & Walker (1974). Therefore, this study has contributed empirical evidence towards the question of whether bull groups have a greater impact on the vegetation than family units. The larger body size of mature bulls within bull groups provided underlying theoretical evidence for the observed differential impacts on woody plants, as bulls would not only need to maintain higher intake rates than family units, but their larger gut size would also enable them to be more tolerant of the low quality (high fibre) diets (Bell 1971, Geist 1974, Jarman 1974, Demment & Van Soest 1985). In support of these predictions, bulls were found to have larger bite and break diameters than family units when feeding. Bull groups, furthermore, not only removed more plant parts per food plot, but also broke more branches and twigs per individual plant than did family units (Chapter 3). These findings have management implications, which are discussed in section 6.3.

No difference in diet quality could be found when directly comparing the chemical contents of plant species and plant parts used by bull groups and family units. The large differences in diet quality measures between leaves, stem bark, roots, heartwood and twigs, furthermore clarified why bull groups and family units of elephants used the various plant parts in different proportions. Leaves had the lowest fibre content and together with stem bark had a comparatively high sugar content. Roots and stem bark had high mineral contents and together with twigs and heartwood were found to contain comparatively high fibre levels. Heartwood was the least nutritious of the plant parts and unsurprisingly was rarely ingested by elephants of either sex. By ingesting larger quantities of leaves and stem bark than bulls, family units could insure that they obtained diets of comparatively low fibre content but high carbohydrate levels. Bulls, by frequently ingesting roots and taking bites with large break and bite diameters, were probably ingesting plant tissues high in minerals and fibre. While family units found rare species that were high in sugar and low in fibre highly acceptable, for bulls acceptability appeared to be related to variation in the calcium content of the plant tissues between species. From these results, the conclusion could be drawn that in accordance with the BSH, plant species and plant part use by family units was associated with energy and digestibility requirements, while bull groups utilised plant species in relation to their mineral content irrespective of the fibre content of the plant tissue (Chapter 4).

Carbon isotope analyses of faecal samples confirmed a dietary shift by elephants with the onset of the wet season, from a dicotyledon- to a graminoid-dominated diet (Guy 1976, Barnes 1982, Ruggiero 1992, Kabigumila 1993). It could also be established from the carbon-isotope analyses that this shift in diet was not restricted to any age/sex class. During dry periods, adult females showed marginally higher levels of faecal protein and mineral content, and lower fibre levels, than large, adult males. During transitional and wet periods, faecal measures were similar among age/sex classes. Despite various confounding factors discussed elsewhere (section 6.4), faecal indices of diet quality proved to be of practical use when comparing diet quality measures across a range of age/size classes, including weaned juvenile, subadult, adult female, small-adult male and large-adult male elephants (Chapter 5).

6.3 Management implications

Managers of both small and large reserves with megaherbivores such as elephant, face the following concerns (Owen-Smith 1988):

- changes to specific habitat types within the reserve and possible loss of species that depend on these habitat types;
- local extinction of certain sensitive plant species within the reserve;
- reduced vegetation cover and increased erosion potential, and an overall decline in the productivity of the system;
- depletion of the resource base for the elephants themselves;
- loss of aesthetic landscape features such as mature trees.

While the first four points will apply to elephant populations in general, my results have indicated that the last point is of particular relevance for bull groups. Managers can thus expect changes in the vegetation composition after use by either type of social unit, but the changes will be most apparent following feeding by bull groups. Since these findings have different management implications for small reserves, compared to larger reserves where dispersal of bulls can take place, I firstly highlight some recommendations concerning the reintroduction of elephants to small private nature reserves. Secondly, I will discuss the overall management implications of my study with specific reference to the Association of Private Nature Reserves (APNR).

6.3.1 Re-introductions of elephants into small private nature reserves

Briefly, the biggest problem facing small landowners is a lack of space, considering that more than 50% of small reserves are no bigger than 50 km^2 (Knight *et al.* 1996) while the approximate extent of clans' home ranges varies between 250-500 km^2 (Owen-Smith 1988). Prior to 1994, juvenile elephants from the Kruger National Park (KNP) were introduced into small reserves following the recommendation of 650 ha /elephant for the Eastern lowveld (Garaï 1996, Garaï 1998). The practise of translocating juveniles without their family units was reviewed and terminated in 1995. Subsequent records indicate that until 1999, 72 bulls and 458 animals from family units have been translocated out of the KNP (Whyte 2001). The recommended sex ratio for reintroductions to private reserves has been one large male for each family unit consisting of 1-10 animals (du Toit 1995).

I found that bull groups not only selected feeding sites with trees that were taller (> 5m) than those in surrounding areas, but utilised tall trees more frequently than did family units. These results indicate that small reserve managers may well wish to protect large trees if mature bulls are kept within the reserve. Considering the impact that large bulls have on vegetation, a short term solution would be for, managers to introduce only family units into their reserves, but bearing in mind possible long term social (Slotow *et al.* 2000, Slotow *et al.* 2001, Slotow & van Dyk 2001) and genetic problems (Knight *et al.* 1996). Alternatively, managers could create artificial dispersal networks between small reserves, through the removal and reintroduction of large bulls, should information from monitoring programmes indicate that the composition or structure of the vegetation has been transformed beyond acceptable limits. Scattered, disjunct elephant populations can be viewed as parts of a large, single, meta-population (Knight *et al.* 1996). While bulls may be transferred between reserves for 'green hunting' enterprises (Douglas-Hamilton 1998), this should be subject to strict codes of conduct. Trophy hunting of large bulls provides a profitable alternative to non-consumptive use, but may impact negatively upon tourism because of public disapproval (Dublin 1996). Also, the affects of trophy hunting upon non-target animals have not been established and may prove traumatic (Garaï 1996, Garaï 1998). Where trophy hunting therefore seems unavoidable because of saturated markets for live sale (Benjis 1996), this should be made to replicate the process of dispersal as far as possible (Owen-Smith 1983).

Managers concerned with aesthetic landscapes should also bear in mind that mitigation of the impacts on vegetation by bull groups may not be practical within acceptable time frames, considering how long it takes for mature trees to establish in semi-arid environments. It follows that there are no easy solutions for small landowners owning elephants, or contemplating a reintroduction. I tend to agree with De Villiers (1996) that it is inadvisable to introduce elephants onto game farms smaller than 14 000 ha. It is furthermore imperative for elephant landowners to clearly define their short and long-term objectives and to ensure they will have the corresponding financial means, considering the costs that may be involved. The importance of well-planned, long-term vegetation monitoring programs, preferably commencing *a priori* to elephant introductions, is obvious.

6.3.2 Elephant impact within the APNR

Annual aerial censuses have indicated that elephant numbers within the APNR have increased in recent years to a density of approximately 0.4 elephant/ km^2 (I.J. Whyte pers comm.). The increase is thought to represent an influx of elephants from the KNP following the removal of the western boundary fence in 1993 (Joubert 1996). Further increases in elephant numbers are expected because the APNR population adjoins a so-called high elephant density zone within the KNP, where elephant numbers are allowed to increase following the termination of culling operations in 1994 and the implementation of a new elephant management policy (Whyte *et al.* 1999). Irrespective of which factors are responsible for the increase in elephant numbers, landowners have expressed concern about the effects on woodlands.

Results show that both bull groups and family units utilised only 9% of the 5 780 individual woody plants that were available to them in the study plots. Six woody plant species i.e. *Albizia harveyi*, *Colophospermun mopane*, *Dalbergia melanoxylon*, *Dichrostachys cinerea*, *Grewia* species and *Lannea schweinfurthii* were identified as plants favoured by both types of social unit. In addition, bull groups favoured *Sclerocarya birrea*. These seven woody species were utilised during 72% and 70% of all feeding events by bull groups and family units respectively. *Grewia* species, aesthetically an unimportant species but with high availability, proved to be the staple food plant for both bull groups and family units. Damage by bull groups and family units to 36% and 22% of the woody species utilised by them, respectively, exceeded 50% in each case. Bull groups were the more destructive feeders as they removed larger proportions of phytomass per plant and engaged in destructive activities such as uprooting, felling and branch breaking, more frequently than family units. Bull groups also selected for taller trees compared to family units. All the above indicate that bulls groups have a greater potential for alteration of vegetation structure within the APNR. Of further interest to managers is that De Villiers (1994) found elephants within the APNR to show preference for

Acacia nigrescens, Colophospermun mopane and *Sclerocarya birrea* trees, taller than 7 m. Additionally, my results suggest that the frequent use of *Albizia harveyi, Lannea schweinfurthii* and *Sclerocarya birrea* to bull groups may be of concern to landowners, not only because of the aesthetic appeal but also because of their comparatively high acceptance frequencies coupled with their intermediate availability indices.

Although elephant hunting is forbidden in National Parks such as the KNP, controlled hunting has been permitted in the APNR, based on the premise that the population is large enough not to be negatively affected (age and/or sex ratios, or social structures) by the removal of a few animals. The proportion of the elephant population within the APNR annually removed through trophy hunting is currently 0.1%. The income from hunting in 2002 amounted to R1.3 million and R 2.2 million for the Klaserie and Timbavati Private Nature Reserves respectively, covering 60 to 70 % of their budgets (Stalmans *et al.* 2003). Unlike many reserves in Africa, the KNP has not been subjected to heavy poaching. As elephant tusks grow lifelong (Pilgram & Western 1986), and as hunters (legal and illegal) generally target large-tusked individuals, old individuals are scarce in most populations. Several large-tusked bulls are nevertheless still to be found within the well-protected borders of the KNP. A number of individuals with the potential to grow large tusks have been sighted within the APNR, presumably after immigrating from the KNP. These bulls are of economic and social importance to the area. It has been shown that adult males do not compete for oestrus females until 25-35 of age, only experience prolonged periods of musth from about 30 years of age when there are older bulls present. The older, mature bulls are of social importance to the breeding herds as females prefer to mate with them (Poole & Moss 1981, Poole 1982, Poole 1987).

While selective hunting of trophy bulls within the area may appear to be a logical way to prevent vegetation degradation, the potential impact by bulls on an area cannot really be assessed without knowing how they distribute themselves in time and space. Specific studies aimed at determining recruitment rates and resilience to elephant impact, for each of the favoured woody species, should be conducted before measures are taken. Trophy hunting is highly selective with respect to sex, age and particular physical features, and cannot be regarded as an effective means of controlling the population, or be motivated by such claims (Joubert 1996, Stalmans *et al.* 2003). De Villiers (1994) advised a cautionary approach after constructing population models that predicted a disruption in the adult sex ratio should trophy hunting continue at the then present rate (an average of six bulls were hunted annually from

1985 to 1992). His findings also show that the past hunting rates could not have been sustained without immigration from the KNP population. Without recruitment from the KNP population, trophy bulls within the APNR would be shot out within five to six years. Recently, concern has also been raised that private landowners are benefiting economically from national assets, i.e. immigrations of animals from the KNP since the removal of boundary fences (Stalmans *et al.* 2003).

Although concepts such as 'carrying capacity' have been used to manage wild herbivores since the early twentieth century (Leopold 1933), the term remains a mathematical abstraction rather than a measurement of sustainable population size (Macnab 1985). This is especially true when measured within variable environments, where carrying capacity cannot be viewed as a measurement of long-term equilibrium density, but at most reflects short-term potential density as a function of resource availability (McLeod 1997). If management decisions are to be based on the concept of carrying capacity, ongoing monitoring and continual reassessment are required prior to implementation in environments such as the APNR. Defining carrying capacity levels for elephants, which are capable of migrations the scale of which has yet to be ascertained within the APNR, appears superfluous. A decrease in elephant densities would also not necessarily lead to the substantial elimination of woodland damage, as the loss of certain tree species will inevitably occur even at low elephant densities (e.g., less than 0.2 elephant/ km^2) because of their selective feeding habits (Cumming *et al.* 1997).

I suggest that under natural circumstances, any localised over exploitation of woody vegetation within the APNR would be prevented by dispersal. Contrary to the problems facing elephant populations within small private nature reserves, the APNR represents a reserve of approximately 1800 km^2 and furthermore borders on the KNP with a size of 18 992 km^2 (Whyte 2001), which itself has recently become part of an even larger Transfrontier Conservation Area (Braack 2000). Since the removal of the western boundary fence between the APNR and the KNP, the APNR is likely functioning as a dispersal sink (Owen-Smith 1983). Although not yet documented, I expect bulls to emigrate from the KNP more frequently than family units, as bulls are known to cover larger areas than family units and are generally the first to colonise new areas (Hall-Martin 1992). The vegetation structure and composition can thus be expected to alter as more and more elephants utilise the APNR. While elephants should disperse once their resource base becomes over utilised, the extensive network of artificial water points within the APNR may interfere with this process. The KNP is currently decreasing the number of artificial water points there (Whyte 2001) while waterholes in the APNR are spaced no further than 2 km apart (Stalmans *et al.* 2003). Consequently, elephants may remain in the proximity of the APNR's many water sources during the dry season period instead of seeking out areas offering them more suitable food resources. I suggest that in the long run, landowner's concern for woodlands would best be resolved by the systematic removal of waterholes.

It is apparent that insights into patterns of movement and population growth rates within the APNR are of significance to all the above, including the concerns of landowners and managers. Incorporating green hunting (Douglas-Hamilton 1998) into research methods would permit such information to be obtained, will allow the targeting of large tuskers without depleting the gene pool, and at financial benefit, rather than cost, to the APNR.

6.4 Complementarity of the methods and limitations of the study

This study focussed on the dietary distinctions in the feeding ecology of bull groups and family units of elephants. Plant based surveys, of central importance to the study, were based on the methods of Stokke (1999) and Stokke & du Toit (2000). The elephant population within my study area was less habituated and also of considerable lower densities than the Chobe National Park's population where Stokke conducted his study. As a consequence age/size specific observations could not be made prior to vegetation surveys, which meant that feeding sites were limited to distinguishing between the food plots of bull groups and family units. It was therefore not possible to determine whether more than one animal had fed at a food plot or whether the same animal fed at consecutive food plots. The data recorded at the food plots of family units could have included the feeding behaviour of large, mature bulls. As the association of mature bulls with family units represent a temporary state (see to Chapter 1&2), I considered this possibility of negligible importance. Within bull groups no distinctions were made between the feeding sites of large adult bulls as opposed to small adult bulls. Determining differences in the feeding behaviour of females of varying reproductive status i.e. pregnant or lactating cows (Dublin 1983) also proved impractical even though reproductive status could have had an overriding influence on dietary distinctions between the social units of elephants. The low density of elephants within my study area meant that a driving protocol could not be followed to equalise the distribution of data collection across habitat types (Stokke & du Toit 2000). The influence of habitat type on plant species and plant part selection by bull groups and family units were therefore beyond the scope of this study.

Due to sample size constraints, the effect of seasonal progression on diet choice of bull groups and family units of elephant could not be established. Data were pooled across the entire dry season period. The focus of this study was however to distinguish dietary distinctions between social units of elephant during times of resource limitation, gradual decreases in plant quality and quantity with progression of the dry season were therefore assumed to occur at the same rate for both herd structures. The exceptionally high rainfall that fell during the wet season before vegetation surveys were conducted could have caused a less severe and restricted dry season in comparison with other years. This could have masked sex related distinctions in feeding behaviour as resources may not have been limited enough to observe differences in feeding behaviour between bull groups and family units of elephant.

I acknowledge that numerous other factors such as the environment for plant growth, the age and maturity of the forage and previous impact levels (Van Soest 1994, Owen-Smith & Danckwerts 1997) could affect plant species and plant part acceptance by elephants, but were considered beyond the scope of this study. Despite the abovementioned limitations, vegetation surveys successfully provided insight into the proportions according to which family units and bull groups eat plant parts and their consequential impact on the vegetation. The vegetation structure and composition of the foraging paths of each of these social units of elephant could be compared to the surrounding area by coupling vegetation surveys at food plots with those of control plots. Vegetation surveys furthermore included both diurnal and nocturnal feeding behaviour as some vegetation surveys were conducted without actually sighting the herd structure but on condition that a clear distinction could be made between the feeding sites of bull groups as opposed to family units. This meant that if fresh tracks were found in the early morning, nocturnal feeding sites were often considered fresh enough to warrant plant-based surveys as discarded plant items had not withered and the sap of utilised plants had not dried out.

Plant samples collected at the feeding sites of bull groups and family units complemented the information gathered during plant-based surveys as samples were collected similarly to their utilisation by elephants. During plant-based surveys intersexual feeding distinctions were greatest when considering the type and proportions of plant parts that were used by either bull groups or family units of elephant. Chemical analysis of plant samples lent support to these findings as the largest distinction in the quality of plant tissue was between plant parts and not plant species. Plant samples were analysed for nitrogen (N), phosphorus (P), calcium (Ca), fibre (NDF: neutral detergent fibre) and total soluble sugar content. The importance of plant secondary metabolites and other minerals such as sodium were not analysed due to financial constraints but may have played an important role in the acceptance of particular plant species or plant parts (Jachmann & Bell 1985, Jachmann 1989, Lister *et al.* 1997, Holdo *et al.* 2002). I acknowledge that total soluble sugars could have been metabolised as soluble sugars are often labile if not frozen after collection (Van Soest 1994). As my sample collection and processing procedures for the determination of carbohydrate content followed the protocol of Jachmann (1989) and Woolnough & Foley (2002), the possible metabolisation of carbohydrates were deemed to be within acceptable limits. Plant samples collected at food plots would only represent a small fraction of the total feeding time of elephants, which can be as long as 12-18 h (Guy 1976, Hoppe 1984). Overall averages and repeated plant sample collection at food plots were still considered to provide a reliable estimate of the diet quality of bull groups and family units.

Faecal analyses were important in that age/size distinctions could be made within bull groups or family units. Faecal indices of diet quality were representative of longer feeding times than the plant samples collected at food plots as the mean retention time of digesta in elephants is 33h but may be as long as 50 and 60h (Warner 1981, Foose 1982). Interpretation of faecal indices of diet quality was confounded by various factors, which reduced the complemetarity between diet quality indices of plant and faecal samples. For example faecal indices of N are artificially elevated by the protein-complexing properties of plant secondary compounds (Robbins *et al.* 1987). Only a small fraction of faecal N is furthermore associated with dietary nitrogen as microbial cells and endogenous N form a large proportion of faecal N (Orskov 1982, Robbins 1983, Van Soest 1994). High faecal Ca levels may not necessarily reflect diets rich in Ca, but may instead indicate high fibre intake as most Ca essentially exists as calcium pectate in cell walls (Van Soest 1994). As insoluble starch is the only non-structural carbohydrate likely to appear in faeces and only at very high intake rates (Van Soest 1994), faecal samples could not be analysed for non-structural carbohydrates during this study. Without digestibility trails, which were considered beyond the scope of this study, it was not possible to say whether significantly higher faecal fibre levels in large bulls when compared to females were due to ingestion of high fibre diets or as a consequence of inefficient digestion. During plant-based surveys bulls were found to ingest plant parts high in fibre content whilst also increasing fibre intake by having larger break and bite-diameters than family units. Plant-based surveys coupled with faecal analyses of fibre did therefore provide empirical evidence that bulls were ingesting diets of lower quality (high fibre content) than family units, thereby upholding the predictions of the BSH.

6.5 A conceptual model

Most studies have either described community assemblage differences between landscape types, or compared feeding patterns across different landscapes at similar species densities. I present a conceptual model to compare differences in the feeding ecology of bull groups and family units of elephants, at similar spatial and temporal (dry season period) scales, within and between the Chobe and APNR elephant populations. The model incorporates differences in elephant densities, climatic and edaphic factors, and floristic components, characterising the semi-arid eutrophic and mesic dystrophic savanna systems respectively (Appendix N). After providing some background information, I will firstly describe intra-specific differences in feeding patterns within the two different landscapes and then develop a conceptual model to explain patterns of sex related feeding differences among elephants between the two landscape types. I propose that the elephant density within a particular area will largely determine the degree of feeding variation between family units and bull groups. The underlying geomorphology and climatic characteristics of a landscape will, however, determine the type (quality or quantity driven) of sex related feeding differences between elephant social units.

6.5.1 Distinguishing savanna types

Huntley (1982) referred to savannas as C_4 grasslands, where woody species are either scattered or form dense woodlands. Rainfall occurs during warm, summer months, while fire typically impacts on the system at intervals varying from one to fifty years. Moist savannas are distinguished from arid savannas in that the former generally receive more than 800mm rain per year. Savannas that receive more than 650mm rainfall can best be described as mesic. Floristically, a mesic to moist, dystrophic savanna is characterised by woody species such as *Brachystegia, Jubernardia, Burkea* and *Ochna* that grow on dystrophic acidic sands. Semi-arid or arid savannas predominantly include *Acacia, Commiphora, Colophospermum* and *Rhigozum* species, occupying eutrophic soils. Soils are classified as dystrophic/infertile when they are highly leached and low in soil nutrients (Ca, Mg and K) while eutrophic/fertile soils are generally non-leached and high in soil nutrients (MacVicar 1977). Floristic delineation between semi-arid/arid and mesic/moist savannas may be indistinct as edaphic factors largely determine vegetation structure. For example, arid savanna plant species interject moist savannas on base-rich substrates such as termitaria. Conversely moist savanna plant species can extend into arid savannas where dystrophic acidic sands overlie granites (Appendix N).

6.5.2 Determinants of plant quantity and quality

Bell (1986) found that the interplay of physical inputs and biological influences determined the quantity and quality of vegetation. The main physical factors affecting plant production include water and soil nutrient availability, while biological influences include the presence of other plants and offtake by herbivores. Bell (1982) suggested that the ratio of metabolic content (protein and soluble carbohydrate plant cell content) to structural carbohydrate constituents (cellulose, hemicellulose and lignin content of cell walls) were the main determinants of plant quality. Both the protein production (Grimsdell & Bell 1974) and soluble carbohydrate production (Brendon & Horrell 1963) of plants were, however, found to be functions of soil nutrient availability. Bell (1982) concluded that the total volume and quality of plant production are thus dependent on the availability of water and soil nutrients. These findings led Bell (1982) to describe moist dystrophic savannas as characterised by abundant, low quality vegetation while arid eutrophic savannas generally consist of high quality vegetation low in biomass.

6.5.3 Determinants of herbivore biomass

Coe *et al.* (1976) found a positive relationship between herbivore biomass and rainfall in arid eutrophic savannas. East (1984) not only determined the relationship between community wide herbivore biomass and rainfall but also within individual species such as elephant. Communities where elephants make up more than 75% of the total herbivore biomass are typically woodland areas of low nutrient availability and high rainfall, that is to say moist dystrophic savannas. Bell (1982) concluded that herbivore biomass is not only a function of the total production of vegetation (quantity) but also the availability of vegetation within the usable range of metabolic to structural carbohydrate ratios (quality). An animal's nutrient requirements are controlled by basal metabolic rate, which varies with body mass (Owen-Smith 1982). Bell (1969, 1971) found that most herbivores would select diets of similar quality but their tolerance levels for low quality diets differs as a consequence of size differences. Vegetation use is thus described as a function of quality in relation to biomass and the tolerance range of the herbivore (Bell 1986). The large body size of elephants, coupled with their non-ruminant digestive systems (Meissner *et al.* 1990), would provide them with a high tolerance of low quality forage in comparison with other species. This, in turn, would explain high elephant densities in both arid eutrophic and especially within moist, dystrophic savanna systems.

6.5.4 Predictions on sex related differences in the feeding ecology of elephants within different landscape types

Chobe National Park can be classified as a mesic dystrophic savanna, and will henceforth be referred to as the Kalahari woodlands. In contrast the APNR, where this study was conducted, broadly represents a semi-arid eutrophic savanna and will be referred to as the lowveld ecosystem. As mentioned earlier, edaphic factors can override distinctions between savanna types that were previously defined according to climatic variables (rainfall) (Huntley 1982). Hence, it is possible to find moist savanna plant species at low rainfall on infertile soils. Likewise, arid savanna plant species can occur under high rainfall conditions, as in the Serengeti. The undulating low-rainfall landscape of the APNR is therefore intermediate with dystrophic vegetation on uplands and eutrophic plants in bottomlands. *Colophospermum mopane* woodlands which also characterises some areas within my study, fits neither classification system. Nevertheless, for the purpose of this model, the APNR will generally be classified as a semi-arid, eutrophic savanna.

Chobe National Park is characterised by high elephant densities, which have been subject to minimal human intervention, while elephant densities are comparatively low within the APNR. Although elephant numbers within the APNR have been artificially manipulated through fencing, trophy hunting and the annual culling of elephants within the adjacent Kruger National Park until 1994 (Joubert 1996, Whyte 2001), historical evidence suggests that elephant densities could have been low within the lowveld ecosystem of South Africa (Whyte 2001). According to Bell (1982), herbivore biomass in moist-dystrophic savannas will be dominated by large species, such as elephant, as they have a wide dietary tolerance for the abundant low quality vegetation that characterises this savanna type. Elephants can furthermore obtain population densities that are substantially higher than predicted by the body size/population density relationship because of their combined tolerance of low quality food and wider range of habitats (Owen-Smith 1988, du Toit & Owen-Smith 1989, du Toit 1995).

Within the Kalahari woodlands, Stokke (1999) and Stokke & du Toit (2000) found that family units not only utilised a wider range of woody species but also used different plant parts more and ingested plant parts with smaller break and bite diameters than larger bodied males.

These findings upheld the predictions of the BSH within the Kalahari woodlands by suggesting that family units seek out diets of high quality while bull groups are more tolerant of abundant, low quality food. Woody species that grow on nutrient poor soils also contain high levels of secondary compounds (Bryant *et al*. 1989). Contrary to this, high quality forage that grows on nutrient rich soils are usually characterised by structural repellents such as thorns or spikes (Owen-Smith 1982). While Jachmann (1989) concluded that trees high in total phenols and steroidal saponins are avoided by elephants, elephants are generally not deterred by structural defences (Buss 1990). This would imply that forage quality will be reduced by the prevalence of secondary compounds (Bell 1986). East (1984) found that moist savanna herbivore species are more selective feeders than arid savanna species on a weight for weight basis and proposed that such selective feeding habits were an adaptation to the availability of a large bulk of low quality herbage. On an intra-specific level, Stokke's findings (2000) provide theoretical and empirical evidence that smaller bodied cows or subadult males within family units compensate for variations in vegetation quality by selecting for high quality forage at both plant species and plant part levels within the Kalahari woodlands. I propose that while large elephant numbers within Chobe determined the high degree of sex related differences across more spatial scales, namely at habitat, food plot, plant species and plant part levels, than within the APNR, the soil nutrient and water availability characteristics of the Kalahari woodlands determined the type of sex related distinctions that were observed between elephant group types.

In the lowveld savanna of my study area, family units and bull groups differed primarily in the quantity of forage that each consumed, as forage quality did not appear to be the limiting factor. Within the lowveld ecosystem the only apparent sex related distinction in feeding behaviour occurred at the plant part level. The semi-arid eutrophic nature of this system would mean that less abundant, relatively high quality forage would be available to both social units of elephant during the dry season. As abundance would be the most limiting factor, and not forage quality, results indicate that bull groups are accepting a greater proportion of the available plant biomass albeit of similar quality as that selected by family units.

Assuming that sex related differences in elephant feeding ecology are driven by sex differences in nutritional requirements (Figure 6.1), the inter-sexual differences in feeding patterns to the left of the solid vertical line, that represents more than 685 mm rainfall per annum, will largely be driven by forage quality while distinctions in forage quantity will predominate in areas to the right of the abovementioned line. The density of elephants will

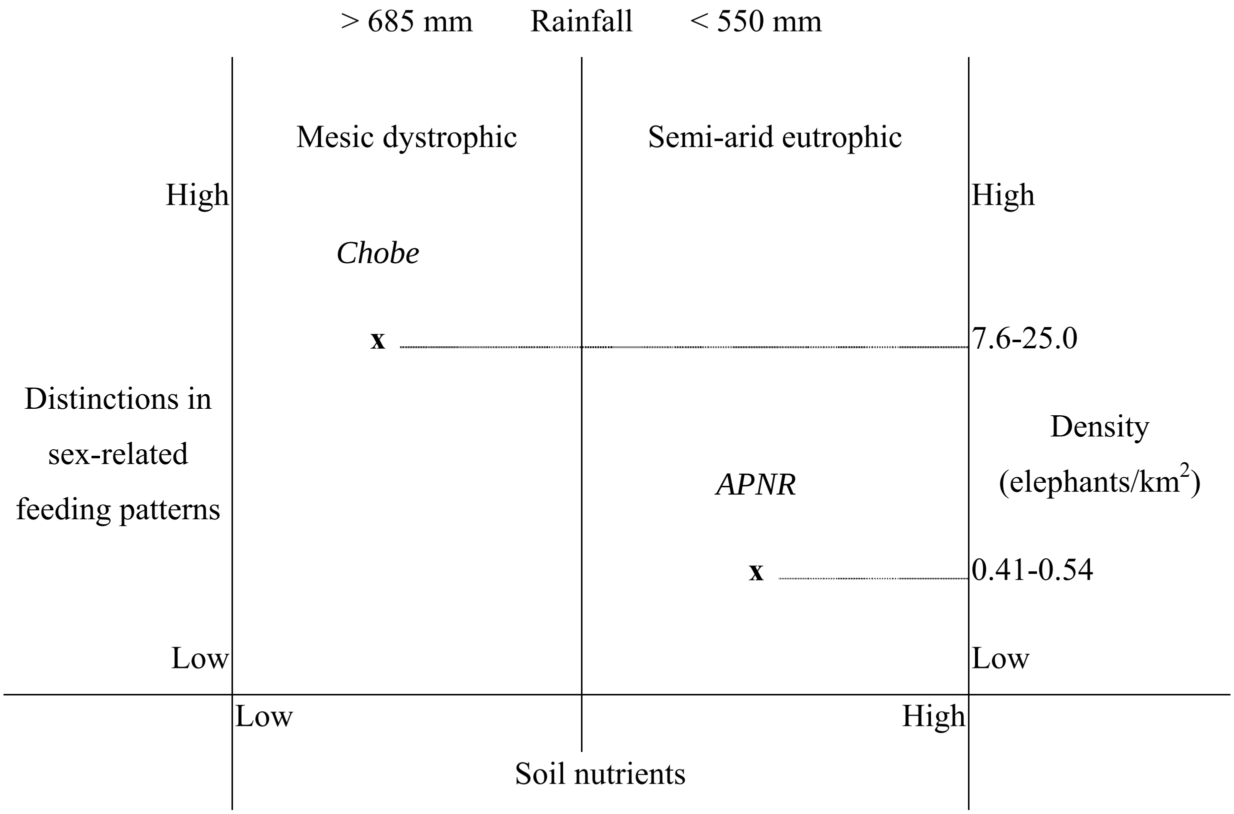

Figure 6.1 Conceptual model depicting the degree of intersexual differences in feeding ecology of elephants at different densities and from regions of differing soil nutrient status and water availability. Chobe National Park (Chobe) represents a mesic dystrophic savanna while the Association of Private Nature Reserves (APNR) represents a semi-arid eutrophic savanna system.

determine the vertical movement (i.e. the level or degree) of the point depicting inter-sexual feeding distinctions within each savanna type. Both rainfall and soil nutrients will determine the horizontal location of the point depicting inter-sexual feeding distinctions in that the differences will either depend on quality or quantity differences in the vegetation.

Fritz *et al.* (2002) not only found support for Bell's hypothesis but also suggested that the competitive interaction between megaherbivores and other mixed feeders and even browsers would be stronger in ecosystems with poor nutrient status. Inter-specific competition is thought to play an important role in structuring African ungulate communities, especially in areas where megaherbivores dominate (Fritz 1997). The apparent decline in bushbuck (*Tragelaphus scriptus ornatus*) with the concomitant increase in elephant numbers in Chobe National Park (Simpson 1975, Addy 1993), highlights the implications of feeding ecology within size structured large herbivore assemblages. My results indicate that abiotic factors, such as soil nutrient status and water availability, also effect sex related feeding patterns on intra-specific level and not only influence herbivore assemblages on an inter-specific level. It would therefore be of relevance to consider sex ratios and sex related size differences of elephants within an ecosystem when evaluating the forage quantity and quality thereof.

6.6 Future research

The preceding sections highlighted some unanswered questions, which require additional research. While this study revealed which plant species were frequently used by both bull groups and family units during the dry season, it would be relevant to future studies to determine the recruitment of seedlings of aesthetically important trees such as *Acacia nigrescens*, *Albizia harveyi*, *Lannea schweinfurthii* and *Sclerocarya birrea* into the category of mature trees. Long-term monitoring programs aimed at determining the resilience of these species to accumulated elephant damage would also be of importance.

An understanding of the temporal (across seasons) and spatial components of habitat selection by social units of elephant will further refine and extend the applicability of the present study. Determining the movements of herd structures within the APNR and adjacent areas will contribute greatly towards establishing how dispersal alleviates the effects of localised utilisation of forage resources. It would be of interest to establish whether food resources, water availability and/or social and safety benefits motivate elephant movements. As certain areas have been identified as potential 'bull areas' (I.J.Whyte pers. comm.) within the APNR, changes to the vegetation structure within these areas favoured by bulls could be monitored to establish whether stem densities increase due to elephant feeding strategies which keep selected species in the coppice phase of regrowth. Alternatively feeding strategies within bull areas could lead to vegetation thinning.

Additional chemical analyses of sodium and plant secondary metabolites of plant tissues may prove to be important determinants of plant species and plant part acceptance indices of bull groups and family units. Within the mesic, dystrophic savanna of Chobe National Park it was assumed that differences in plant quality led to intersexual distinctions in plant species and plant parts use. Chemical analyses of plant tissues collected within the Kalahari woodlands would therefore verify the concepts developed in the model outline in my study.

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APPENDIX A

Estimating nutrient requirements of elephants

Similar methods as those used by Lindsay (1994) were applied to approximate the daily maintenance and reproductive requirements of adult elephants. Existing allometric equations obtained from the literature were used to estimate energy (Kleiber 1961, Peters 1983, Robbins 1983) and protein (McCullagh 1969 Peters 1983, Robbins 1983) requirements. As mineral utilisation has been less extensively analysed in both domestic and wild animals (Peters 1983), estimation of daily calcium and phosphorus requirements were extracted from the literature (McCullagh 1969, Holdo 2002. Lagendijk 2003) or extrapolated from the daily minimum requirements of another cecalid, the horse. Daily maintenance requirements for energy, protein, calcium and phosphorus were compared between adult bulls and cows at peak lactation. Lactation is considered to place greater nutritional demands on females than pregnancy (Crampton & Lloyd 1959, Peters 1983) and lactation was therefore taken as the highest reproductive cost that a female could incur. I did not estimate the influence of gestation on nutrient requirements as the calculation of average daily nutrient requirements of gestation would not address the requirements of a pregnant female at different stages of gestation (Oftedal 1985). The mean body mass of an adult female was taken as 2800kg while an adult elephant bull has a mean mass of 5000kg (Owen-Smith 1988). Although I acknowledge that the results obtained from extrapolating nutrient requirements across taxa can at best provide coarse estimates of energy, protein and mineral requirements for elephants, the paucity of bioenergetic information on elephants necessitated this approach. I here discuss the implications of the estimates that were made. The details of all calculations are presented in Table A1.

When considering the effect of size differences between the sexes, an adult, non-breeding elephant cow will require approximately 225MJ energy, 0.639kg protein, 67.9g calcium and 77.8g phosphorus per day. An adult elephant bull, almost twice as large as an adult female, will require 348MJ energy, 0.987kg protein, 214g calcium and 139g phosphorus per day. The daily requirements of a female elephant at peak lactation were estimated at 259MJ energy, 1.30kg protein, 187g calcium and 174g phosphorus. These results indicate that during peak lactation female elephants will have higher protein and phosphorus requirements than larger-bodied males. Furthermore, the effects of body size alone (non-breeding females versus bulls) were not large enough to indicate that females would be in greater need of any of the reported nutrients than bulls. Bulls appeared to have greater energy demands when compared to reproductive or non-breeding females.

I was unable to measure the influence of reproductive status on dietary distinctions between social units of free-ranging elephants. As Whyte (2001) found that at 14 years 93% of all cows within family units in the Kruger National Park were either pregnant or lactating, I considered females within family units to largely represent breeding females. Based on the calculations above, protein and mineral requirements of family units would thus be greater than those of bulls within bull groups. Theoretically, bull's absolute requirements for energy would be greater than those of females. Bulls in musth should be even more energy limited in the dry season than non-musth bulls as musth bulls are known to spend less time foraging, and more time searching and interacting with family units (Poole 1982). In spite of being unable to determine the possible effects of reproductive status (musth in bulls and pregnancy and/or lactation in females) on nutritional requirements in elephants, differences in body size together with the costs of reproduction are expected to lead to dietary distinctions between bull groups and family units of elephants.

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Table A1. Estimates of daily requirements of metabolisable energy, protein, calcium and phosphorus for adult cows (non-breeding), adult cows at peak lactation and elephant bulls.

Nutritional requirement	Sex	Reproductive status	Equation	Daily requirement	Literature source
Metabolisable energy	Female[1]	Non-breeding	BMR[2]=0.293 x $W^{0.75}$	112.7 MJ	Peters (1983)
			ADMR[3]=2 x BMR	225.4 MJ	Peters (1983), Robbins (1983)
		Peak lactation	ADMR + 0.669 x $W^{0.70}$	225.4 + 173.2 = 398.6 MJ	Oftedal (1985)
			ADMR + 1.519 x $W^{0.52}$	225.4 + 94.2 = 319.6 MJ	Robbins (1983)
				Mean = 259.1 MJ	
	Male[4]	Non-musth	BMR=0.293 x $W^{0.75}$	174.2 MJ	Peters (1983)
			ADMR=2 x BMR	348.4 MJ	Peters (1983), Robbins (1983)
Protein	Female	Non-breeding	ADMR=0.00176 x $W^{0.75}$	0.677 kg	McCullagh (1969)
			ADMR=0.00156 x $W^{0.75}$	0.600 kg	Peters (1983)
				Mean = 0.639 kg	
		Peak lactation	Mean ADMR + 0.001072 x $W^{0.52}$	0.639 + 0.665 = 1.304 kg	Robbins (1983)
	Male	Non-musth	ADMR=0.00176 x $W^{0.75}$	1.047 kg	McCullagh (1969)
			ADMR=0.00156 x $W^{0.75}$	0.928 kg	Peters (1983)
				Mean = 0.987 kg	
Calcium	Female	Non-breeding	2.8 x 8.5 g	23.8 g	McCullagh (1969)
			3.1 x 36 g	112 g	NRC[5] (1989)
				Mean = 67.9 g	
		Peak lactation	-	60 g	Lagendijk (2003)
			3.1 x 101 g	314.2 g	NRC (1989)
				Mean: 187.1 g	
	Male	Non-musth	-	400 g	Holdo *et al.*(2002)
			5 x 8.5 g	42.5 g	McCullagh (1969)
			5.6 x 36 g	200 g	NRC (1989)
				Mean: 214.2 g	

Table A1. (continued) Estimates of daily requirements of metabolisable energy, protein, calcium and phosphorus for adult cows (non-breeding), adult cows at peak lactation and elephant bulls.

Nutritional requirement	Sex	Reproductive status	Equation	Daily requirement	Literature source
Phosphorus	Female	Non-breeding	3.1 x 25 g	77.8 g	NRC (1989)
		Peak lactation	3.1 x 56 g	174.2 g	NRC (1989)
	Male	Non-musth	5.6 x 25 g	138.9 g	NRC (1989)

[1] Mean mass of female = 2800 kg (Owen-Smith 1988)

[2] Basal metabolic rate (BMR) refers to the minimal energy expenditure of an animal at rest in a thermo neutral environment and in a post-absorptive state (Blaxter 1962)

[3] Average daily metabolic rates (ADMR) represent the composites of energy expended for basal metabolism, activity, thermoregulation and the inefficiency of feed utilisation (Robbins 1983) and are usually represented as a multiple of BMR.

[4] Mean mass of male = 5000 kg (Owen-Smith 1988)

[5] Values extrapolated from a 900 kg horse

References

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APPENDIX B

Autocorrelation

Although the distance between consecutive food plots of family units (mean ± SEM: 62.7 ± 3.67 m, range 22-232 m, *n*=94) and bull groups (68.4 ± 4.04 m, range 22-169 m, *n*=92) were large enough to be considered as independent sampling sites (minimum of 15 m, see Gadd 1997), the interdependence in plant species utilization and availability was tested. *Grewia* species were used to test the possibility of autocorrelation in plant species utilisation/availability between consecutive food plots as these woody species were frequently encountered and utilised in food plots of both elephant group types. Availability indices were calculated by dividing the number of individual *Grewia* plants present at a food plot by the number of individuals of all species present at that food plot. Acceptability indices were obtained by dividing the number of individual *Grewia* plants utilised at a food plot by the number of individual *Grewia* plants present at that food plot. Each food plot's availability and acceptability index for *Grewia* plants was paired with the distance from the previous food plot where that species was accepted/available. Where the same distance corresponded to more than one acceptability or availability indices, the average was taken as representative of that particular distance. Least square linear regression analysis of the logit of plant availability or acceptability of *Grewia* plants (the response variables) against the log of the successive distance between food plots (the predictor variable), was used to determine if sampled food plots were independent of each other. If independent, then the acceptability and availability of *Grewia* plants would not be significantly related to the distance between food plots. The Durbin-Watson statistic (*DW*) of successive residuals was used to test the null hypothesis of first order independence between plant species utilisation/availability and distance between food plots and thus no autocorrelation in successive residuals (Fry 1993).

Results

The plant based acceptability and availability of *Grewia* species in food plots of bull groups was not significantly related to the distance between food plots (r^2=0.120, $F_{1,26}$=3.45, *P*=0.07 and r^2=0.0006, $F_{1,53}$=0.0343, *P*=0.854, respectively). The same trend was found within the food plots of family units (r^2=0.0184, $F_{1,29}$=0.544, *P*=0.467 and r^2=0.0150, $F_{1,51}$=0.779, *P*=0.382, respectively).

The *DW* statistic furthermore confirmed that the null hypothesis of first order independence of the residuals could not be rejected for both elephant group types that were tested as $DW > d_u$ and $DW < 4 - d_u$. Within bull groups $DW = 1.78$ and $d_u = 1.48$ for the residuals of acceptability against distance while $DW = 1.90$ and $d_u = 1.60$ for the residuals of availability against distance. Within family units $DW = 2.08$ and $d_u = 1.50$ for the residuals of acceptability against distance while $DW = 2.01$ and $d_u = 1.59$ for the residuals of availability against distance.

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APPENDIX C

Table C1 Categorisation and description of the different feeding modes of elephants.

Feeding mode	Plant part consumed	Description	Data collected
Uprooting	The whole root, the pith of a root or the bark of a root	Roots were utilised after either uprooting the whole plant or pushing the main stem over. It was only possible to determine which part of the root was utilised for larger roots as smaller roots were often completely consumed together with the larger roots.	- Breakage diameter - Number of roots removed per plant
Main stem breakage	These events refer to breakage without consumption	Main stem snapped off or pushed over at the base.	- Breakage height - Breakage diameter - One main stem breakage event was recorded per plant
Large branch breakage	These events refer to breakage without consumption as only smaller branches, which were then broken off these larger branches, were utilised in some way	Large branch breaking was distinguished from main stem breaking when the stem forked into two or more branches below the breaking point (Gadd 1997).	- Breakage height. The height of fracture of all broken branches lying on the ground was not always visible and was consequently not measurable especially in very tall trees with dense canopies - Breakage diameter - Number of large branches broken per plant
Branch breakage	Heartwood or bark	Heartwood/bark was removed on the proximal end of the broken branch. These branch breakage events involved smaller branches than those mentioned previously.	Breakage height Breakage or bite diameter was measured at the break point of the fully consumed twig (Stokke & du Toit 2000) Number of branches broken per plant
Branch biting	Twigs with or without leaves	Utilised twigs were consumed after direct bites to the larger broken branches or by twigs that were severed with the trunk and then consumed. All whole bites were thus recorded as twig usage.	- Breakage height - Breakage diameter - Number of branches bit or broken per plant
Leaf-stripping	Leaves	Leaf-stripping usually occurred when branchlets were very flexible and often included new growth.	- Breakage height - One leaf-stripping event was recorded per plant, as the possible number of leaf-stripping events that may have occurred per individual plant could not be distinguished

References

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APPENDIX D

Dietary distinctions between the sexes at foraging paths

I here focus on sex related foraging distinctions at the level of location selection as defined by Senft *et al.* (1987), where location selection refers to the foraging path when comparing the woody species composition at feeding sites with control sites

Prediction based on the Body Size Hypothesis

Feeding sites of both family units and bull groups will be of similar species diversity but bull groups will select feeding sites with a higher density of woody species than family units, which would potentially provide them with a larger quantity of forage resources than the surrounding area.

Methods

To test whether family units utilised a higher diversity of woody species at both the food plot and feeding site level when compared to bull groups, I determined the diversity of woody species that were utilised at food plots and present at food- and control plots of both bull groups and breeding units of elephants. Woody species richness was calculated as the number of different species present at each plot. Species density was calculated as the number of individual plants, irrespective of the species, at a food plot or control plot divided by the area of the plot. The Shannon Wiener diversity function (H') was used to determine the diversity of available species at each of the food plots and control plots (Krebs 1985). This same function was used to determine the diversity of utilised woody species at food plots. As diversity is both a function of the species richness at a plot as well as the relative abundance of each species, the equitability (E) or evenness of distributions amongst the species present was also calculated according to the following formula (Krebs 1985):

$E=H'/H_{max}$

where H' is the observed species diversity, and H_{max} is the maximum species diversity calculated as $\log_e$ (number of different species in the plot). Equitability values close to one indicate an equal distribution of individual plants across species. Each of these variables was averaged across all food plots and control plots to draw comparisons between bull groups and family units of elephants. To directly compare species richness, density, diversity and equitability between food plots and control plots within either bull groups or family units, the average was taken over all food- and control plot pairs.

Nonparametric Mann-Whitney *U* tests were used to test for differences in species richness, density, diversity and equitability between bull groups and family units of elephants. The nonparametric Wilcoxon signed rank test was used to enable pair-wise food to control plot comparisons within an elephant group type.

Results and discussion

Both social units of elephant exploited food plots with a similar diversity of woody species at which they also utilised a similar diversity of woody species. The control plots of family units had significantly higher species richness than those of bull groups (Table D1).

When comparing the difference between food and control plots within social units, bull groups selected food plots with a higher density of woody plants than their adjacent control plots (Table D2). Hence bulls also selected food plots with a higher species richness than the surrounding area as there was a positive association between species richness and plant density for both bull groups (n=168, r=0.621, P<0.0001) and family units (n=172, r=0.525, P<0.0001). Both social units of elephants nevertheless selected food plots with a similar diversity of available woody species when compared to their surrounding area (control plots). The equitability of woody species was similar at the food and control plots of both elephant group types. These results suggest that elephants, irrespective of herd structure, are not selecting foraging paths at the plant species level. Bull groups do however select foraging paths with denser vegetation than the surrounding area. Presumably, this would enable them to feed at sites which potentially offer them a larger quantity of forage resources in terms of the absolute abundance of available woody species. Although selecting such feeding sites also meant that these foraging paths had a higher species richness when compared to the surrounding area, bull groups commonly fed on the same range of species as family units.

In conclusion, both family units and bull groups selected food plots with identical woody plant densities so that the prediction of the BSH was not upheld at the level of foraging paths. The control plots for bulls were however less dense than those for females, thus making the contrast with the control significant.

References

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Table D1 Plant species richness, woody plant density, equitability and the Shannon-Wiener diversity index for available and utilised woody species at the food plots and control plots of bull groups and family units of elephants. Mean ± standard errors are shown for each variable. The sample size of each plot type is given in parentheses. Significant P values (<0.05) are given in bold.

	Food plot		Mann-Whitney test	Control		Mann-Whitney test
	Bull groups (124)	Family unit (126)		All-male groups (44)	Breeding group (46)	
Woody spp.[1] richness	6.52 ± 0.25	6.56 ± 0.27	ns[2]	5.11 ± 0.33	6.43 ± 0.40	**$U=731$, $P<0.05$**
Woody plant density	0.29 ± 0.01	0.31 ± 0.02	ns	0.22 ± 0.02	0.27 ± 0.02	ns
Diversity of available woody spp.	2.02 ± 0.06	2.03 ± 0.07	ns	1.76 ± 0.10	2.02 ± 0.02	ns
Equitability of woody spp.	0.78 ± 0.01	0.79 ± 0.01	ns	0.78 ± 0.02	0.79 ± 0.03	ns
Diversity of utilised woody spp.	0.35 ± 0.05	0.29 ± 0.05	ns	na[3]	na	ns

1=species
2=not significant
3=not applicable

Table D2 Pair-wise comparison between the control plots and food plots of bull groups and family units of elephants for plant species richness, woody plant density, equitability and the Shannon-Wiener diversity index for available woody species. Mean ± standard errors are shown for each variable. The sample size of each plot type is given in parentheses.

	Bull group		Wilcoxon signed rank test	Family unit		Wilcoxon signed rank test
	Food plot (44)	Control (44)		Food plot (46)	Control (46)	
Woody spp.[1] richness	6.66 ± 0.46	5.11 ± 0.33	**$W=434$, $P<0.01$**	6.43 ± 0.48	6.43 ± 0.40	ns[2]
Woody plant density	0.32 ± 0.03	0.22 ± 0.02	**$W=560$, $P<0.001$**	0.32 ± 0.04	0.27 ± 0.02	ns
Diversity of woody available spp.	2.00 ± 0.11	1.76 ± 0.10	ns	1.95 ± 0.13	2.02 ± 0.10	ns
Equitability of woody spp.	0.76 ± 0.02	0.78 ± 0.02	ns	0.79 ± 0.02	0.79 ± 0.03	ns

1=species
2=not significant

Seasonal effects on plant species use

Factorial ANOVA with period, plant species and elephant group as factors and acceptance indices as response variable. Small acceptance frequencies within certain categories prevented the use of log-linear analysis (Plackett 1964).

Table E1.1 Factorial ANOVA results of the higher order interactive effects of period (early dry-, dry- and transitional rainfall period), plant species which were available at more than ten food plots and accepted at more than five food plots (A*lbizia harveyi, Acacia nigrescens, Colophospermum mopane, Dichrostachys cinerea, Grewia* species and *Lannea schweinfurthii*) and group (bull groups and family units of elephants) on species-specific acceptance indices. Significant *P* values (<0.05) are given in bold.

Effect	Df	*F*	*P*-level
Period	**2**	**3.66**	**0.0273**
Plant species	**5**	**6.38**	**<0.0001**
Group	1	1.71	0.1925
Period*plant species	**10**	**3.94**	**0.0001**
Period*group	2	0.26	0.7681
Plant species*group	5	1.07	0.3781
Period*plant species*group	10	0.425	0.9335

Factorial ANOVA with period, plant species and elephant group as factors and availability indices as response variable

Table E1.2 Factorial ANOVA results of the higher order interactive effects of period (early dry-, dry- and transitional rainfall period), plant species which were available at more than ten food plots and accepted at more than five food plots (A*lbizia harveyi, Acacia nigrescens, Colophospermum mopane, Dichrostachys cinerea, Grewia* species and *Lannea schweinfurthii*) and group (bull groups and family units of elephants) on species-specific availability indices. Significant *P* values (<0.05) are given in bold.

Effect	Df	*F*	*P*-level
Period	**2**	**3.54**	**0.0307**
Plant species	**5**	**25.0**	**<0.0001**
Group	1	0.29	0.5882
Period*plant species	**10**	**2.66**	**0.0046**
Period*group	2	0.75	0.4731
Plant species*group	5	0.63	0.6784
Period*plant species*group	10	0.78	0.6466

References

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Seasonal effects on plant part use

Log linear analysis of the seasonal effects, plant part selection and elephant group

Table E2.1 Frequency distribution of the number of individual woody plants utilised by bull groups or family units of elephant for specific plant parts within the early dry-, dry- and transitional periods.

Period	BBA		BBB and BBP		TW and LS		Other (UR and MS)	
	Bull groups	Family units	Bull groups	Family units	Bull groups	Family units	Bull groups	Family units
Early dry	21	14	20	36	70	69	16	10
Dry	22	14	27	44	19	53	10	15
Transitional	37	24	24	18	57	45	38	12

BBA = Large branch breakage to access smaller parts
BBB = Branch breakage to consume bark on the proximal end of the branch
BBP = Branch breakage to consume the pith on the proximal end of the branch
TW = Twig bite or breakage to consume the whole twig
LS = Leaf-stripping to consume leaves and leaf petiole
UR = Uprooting to consume the roots
MS = Main stem breakage to bark strip or to access smaller canopy parts

Table E2.2 Analysis of maximum likelihood estimates where the interaction of 'period','plant part' and 'group' effects did not prove significant at the 95% level. Significant *P* values (<0.05) are given in bold.

Source	Df	χ^2	*P*-level
Period	**2**	**6.58**	**0.0372**
Plant part	**3**	**72.0**	**<0.0001**
Group	1	0.45	0.5019
Period*plant part	**6**	**50.8**	**<0.0001**
Period*group	**2**	**13.7**	**0.0011**
Plant part*group	**3**	**17.2**	**0.0006**
Period*plant part*group	5	7.28	0.2005

Seasonal effects on plant species and plant part use according to diet quality indices

Factorial MANOVA with period, plant species and elephant group as factors diet quality indices as response variables

Table E3.1 Factorial MANOVA results of the higher order interactive effects of period (early dry-, dry- and transitional rainfall period), plant species (A*lbizia harveyi, Colophospermum mopane, Grewia* species with the rest of all the species pooled as 'other'[1]) and group (bull groups and family units of elephants) on diet quality indices (N, P, Ca, NDF and sugar content). Significant *P* values (<0.05) are given in bold.

Effect	Df	*F*	*P*-level
Period	10	0.769	0.6593
Plant species	**15**	**13.3**	**<0.0001**
Group	5	0.747	0.5886
Period*plant species	30	1.24	0.1743
Period*group	10	0.242	0.9919
Plant species*group	**15**	**1.66**	**0.0534**
Period*plant species*group	30	0.866	0.6442

Factorial MANOVA with period, plant part and elephant group as factors and diet quality indices as response variables

Table E3.2 Factorial MANOVA results of the higher order interactive effects of period (early dry-, dry- and transitional rainfall period), plant parts (leaves, twigs, berk and roots[2]) and group (bull groups and family units of elephants) on diet quality indices (N, P, Ca, NDF and sugar content). Significant *P* values (<0.05) are given in bold.

Effect	Df	*F*	*P*-level
Period	10	1.39	0.1799
Plant part	**15**	**70.8**	**<0.0001**
Group	5	1.54	0.1761
Period*plant part	**30**	**3.69**	**<0.0001**
Period*group	10	1.01	0.4344
Plant part*group	15	1.02	0.4301
Period*plant part*group	30	1.29	0.1333

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[1] Incomplete designs necessitated the pooling of all other plant species into an 'other' category as insufficient samples were collected over all three periods for both bull groups and family units of elephants within these species.

[2] Insufficient samples were collected within the heartwood category over all three periods for both bull groups and family units and thus necessitated the omission of this plant part category.

Log linear analysis of the different height classes that were utilised by bull groups and family units of elephant

Table F1.1 The frequency distribution of plant heights that were accepted in the food plots of family units and bull groups of elephant. Significant *P* values (<0.05) are given in bold.

Height interval (m)	Family units	Bull groups
0 to <0.5	14	21
0.5 to <1	20	13
1 to <1.5	35	32
1.5 to <2	45	46
2 to <2.5	72	35
2.5 to <3	35	37
3 to <5	47	43
>5	16	36
Total number utilised	284	263
Chi square test	**χ^2=22.0, *df*=7, *P*=0.0025**	

Table F1.2 Analysis of maximum likelihood estimates. Significant *P* values (<0.05) are given in bold.

Source	Df	χ^2	*P*-level
Height interval	**7**	**66.29**	**<0.0001**
Group	1	0.00	0.9616
Height interval*group	**7**	**22.00**	**0.0025**

Table F1.3 Parameter estimates for the saturated model. Significant *P* values (<0.05) are given in bold.

Level of interaction	Parameter	Estimate	*P*-level
0 to <0.5, family unit	λ_{11}	-0.2050	0.1911
0 to <0.5, bull groups	λ_{12}	0.2050	
0.5 to <1, family unit	λ_{21}	0.2131	0.1869
0.5 to <1, bull groups	λ_{22}	-0.2131	
1 to <1.5, family unit	λ_{31}	0.0425	0.7144
1 to <1.5, bull groups	λ_{32}	-0.0425	
1.5 to <2, family unit	λ_{41}	-0.0133	0.8969
1.5 to <2, bull groups	λ_{42}	0.0133	
2 to <2.5, family unit	λ_{51}	**0.3584**	**0.0004**
2 to <2.5, bull groups	λ_{52}	**-0.3584**	
2.5 to <3, family unit	λ_{61}	-0.0301	0.7895
2.5 to <3, bull groups	λ_{62}	0.0301	
3 to <5, family unit	λ_{71}	0.0422	0.6824
3 to <5, bull groups	λ_{72}	-0.0422	
>5, family unit	λ_{81}	**-0.4078**	**0.0033**
>5, bull groups	λ_{82}	**0.4078**	

Log linear analysis of the different height classes that were available at the food plots of bull groups and family units of elephant

Table F2.1 The frequency distribution of plant heights that were available in the food plots of family units and bull groups of elephant. Significant *P* values (<0.05) are given in bold.

Height interval (m)	Family units	Bull groups
0 to <0.5	322	295
0.5 to <1	638	516
1 to <1.5	563	551
1.5 to <2	513	479
2 to <2.5	397	371
2.5 to <3	226	219
3 to <5	269	224
>5	77	120
Total number available	3005	2775
Chi square test	**χ^2=20.4 *df*=7, *P*=0.0047**	

Table F2.2 Analysis of maximum likelihood estimates. Significant *P* values (<0.05) are given in bold.

Source	Df	χ^2	*P*-level
Height interval	**7**	**1010.26**	**<0.0001**
Group	1	0.85	0.3562
Height interval*group	**7**	**20.42**	**0.0047**

Table F2.3 Parameter estimates for the saturated model. Significant *P* values (<0.05) are given in bold.

Level of interaction	Parameter	Estimate	*P*-level
0 to <0.5, family unit	λ_{11}	0.0295	0.4396
0 to <0.5, bull groups	λ_{12}	-0.0295	
0.5 to <1, family unit	$\boldsymbol{\lambda_{21}}$	**0.0918**	**0.0022**
0.5 to <1, bull groups	$\boldsymbol{\lambda_{22}}$	**-0.0918**	
1 to <1.5, family unit	λ_{31}	-0.00351	0.9075
1 to <1.5, bull groups	λ_{32}	0.00351	
1.5 to <2, family unit	λ_{41}	-0.0200	0.5262
1.5 to <2, bull groups	λ_{42}	0.0200	
2 to <2.5, family unit	λ_{51}	-0.0196	0.5746
2 to <2.5, bull groups	λ_{52}	0.0196	
2.5 to <3, family unit	λ_{61}	-0.00145	0.9736
2.5 to <3, bull groups	λ_{62}	0.00145	
3 to <5, family unit	λ_{71}	-0.0773	0.0666
3 to <5, bull groups	λ_{72}	0.0773	
>5, family unit	$\boldsymbol{\lambda_{81}}$	**-0.2361**	**0.0003**
>5, bull groups	$\boldsymbol{\lambda_{82}}$	**0.2361**	

Log linear analysis of the different height classes that were available at the control plots of bull groups and family units of elephant

Table F3.1 The frequency distribution of plant heights that was available at the control plots of family units and bull groups of elephant. Significant *P* values (<0.05) are given in bold.

Height interval (m)	Family units	Bull groups
0 to <0.5	86	73
0.5 to <1	218	135
1 to <1.5	190	169
1.5 to <2	191	147
2 to <2.5	102	98
2.5 to <3	80	60
3 to <5	78	69
>5	41	15
Total number available	986	766
Chi square test	**χ^2=15.4, *df*=7, *P*=0.031**	

Table F3.2 Analysis of maximum likelihood estimates. Significant *P* values (<0.05) are given in bold.

Source	Df	χ^2	*P*-level
Height interval	**7**	**355.42**	**0.0000**
Group	**1**	**26.93**	**0.0000**
Height interval*group	**7**	**15.38**	**0.0314**

Table F3.3 Parameter estimates for the saturated model. Significant *P* values (<0.05) are given in bold.

Level of interaction	Parameter	Estimate	*P*-level
0 to <0.5, family unit	λ_{11}	-0.0729	0.3315
0 to <0.5, bull groups	λ_{12}	0.0729	
0.5 to <1, family unit	λ_{21}	0.0847	0.1304
0.5 to <1, bull groups	λ_{22}	-0.0847	
1 to <1.5, family unit	λ_{31}	-0.0963	0.0780
1 to <1.5, bull groups	λ_{32}	0.0963	
1.5 to <2, family unit	λ_{41}	-0.0239	0.6685
1.5 to <2, bull groups	λ_{42}	0.0239	
2 to <2.5, family unit	λ_{51}	**-0.1349**	**0.0478**
2 to <2.5, bull groups	λ_{52}	**0.1349**	
2.5 to <3, family unit	λ_{61}	-0.0110	0.8900
2.5 to <3, bull groups	λ_{62}	0.0110	
3 to <5, family unit	λ_{71}	-0.0936	0.2275
3 to <5, bull groups	λ_{72}	0.0936	
>5, family unit	λ_{81}	**0.3479**	**0.0094**
>5, bull groups	λ_{82}	**-0.3479**	

Log linear analysis of the level of impact and elephant group type

Table F4.1 The frequency distribution of various impact categories of all woody species that were present or utilised at the food plots of either bull groups or family units of elephant. Significant *P* values (<0.05) are given in bold.

Level of impact (%)	Family units	Bull Groups
0	2721	2512
1-10	144	108
11-25	51	44
26-50	27	17
51-75	10	16
76-90	12	9
91-99	15	20
100	25	49
Total number utilised	284	263
Chi square test	**χ^2=17.0, *df*=7, *P*=0.0179**	

Table F4.2 Analysis of maximum likelihood estimates. Significant *P* values (<0.05) are given in bold.

Source	Df	χ^2	*P*-level
Impact level	**7**	**7573.14**	**<0.0001**
Group type	1	0.04	0.8424
Impact level*group type	**7**	**16.92**	**0.0179**

Table F4.3 Parameter estimates for the saturated model. Significant *P* values (<0.05) are given in bold.

Level of interaction	Parameter	Estimate	*P*-level
0%, family units	λ_{11}	0.0503	0.3451
0%, bull groups	λ_{12}	-0.0503	
1-10%, family units	λ_{21}	**0.1542**	**0.0417**
1-10%, bull groups	λ_{22}	**-0.1542**	
11-25%, family units	λ_{31}	0.0841	0.4145
11-25%, bull groups	λ_{32}	-0.0841	
26-50%, family units	λ_{41}	0.2416	0.0928
26-50%, bull groups	λ_{42}	-0.2416	
51-75%, family units	λ_{51}	-0.2247	0.2172
51-75%, bull groups	λ_{52}	0.2247	
76-90%, family units	λ_{61}	0.1542	0.4359
76-90%, bull groups	λ_{62}	-0.1542	
90-99%, family units	λ_{71}	-0.1335	0.3942
90-99%, bull groups	λ_{72}	0.1335	
100%, family units	λ_{81}	**-0.3262**	**0.0059**
100%, bull groups	λ_{82}	**0.3262**	

APPENDIX G

Plant species categories according to acceptance frequencies

Table G1 Categorisation of woody species that were used* by family units and bull groups of elephant. Species were classified according to whether their acceptance frequencies fell below the 25 percentile (low acceptance) or above the 75th percentile (high acceptance) of the median. Woody species that fell within the same categories for both family units and bull groups of elephant are given in bold.

Family units			Bull Groups		
Low [0.01 - 0.15)	Medium [0.15 - 0.5)	High [0.5 - 1.0]	Low [0.01 - 0.15)	Medium [0.15 - 0.5)	High [0.5 - 1.0]
Acacia exuvialis	*Acacia nigrescens*	***Diospyros mespiliformis***	***Acacia exuvialis***	***Acacia nigrescens***	***Diospyros mespiliformi***
Combretum apiculatum	***Albizia harveyi***	***Pterocarpus rotundifolius***	***Combretum apiculatun***	***Albizia harveyi***	***Pterocarpus rotundifolius***
Euclea divinorum	***Colophospermum mopane***	*Acacia erubescens*	***Euclea divinorum***	***Colophospermum mopane***	*Acacia tortillis*
Grewia flavescens	***Dalbergia melanoxylon***	*Acacia gerrardi*	***Grewia flavescens***	***Dalbergia melanoxylor***	*Cissus rotundifolia*
Maerua parvifolia	***Dichrostachys cinerea***	*Acacia robusta*	***Maerua parvifolia***	***Dichrostachys cinerea***	*Combretum imberbe*
Commiphora mollis	***Lannea shweinfurthii***	*Acacia senegal*	*Cissus cornifolia*	***Lannea shweinfurthii***	*Combretum zeyheri*
Ehretia amoena	***Sclerocarya birrea***	*Berchemia discolor*	*Combretum hereroense*	***Sclerocarya birrea***	*Ehretia amoena*
Gymnosporia senegalensis	*Lonchocarpus capassa*	*Cassine transvaalensi*	*Lonchocarpus capassa*	*Acacia gerrardi*	*Grewia hexamita*
Terminalia prunoides	*Combretum imberbe*	*Grewia* species.	*Ormocarpum trichocarpum*	*Grewia* species	*Spirostachys africana*
	Grewia hexamita	*Ozoroa spp.*		*Pappea capensis*	*Unknown mistletoe*
		Schotia brachypetala		*Schotia brachypetala*	Unknown vine
		Unknown vine		*Ziziphus mucronata*	

Both family units and bull groups avoided the following species that were available at their food plots (*n* >5): *Combretum mossambicense*, *Commiphora africana*, *Commiphora glandulosa*, *Commiphora neglecta*, *Commiphora pyracanthoides*, *Euclea natalensis*, *Euclea undulata*, *Flueggea virosa*, *Gardenia volkensii*, *Grewia villosa*, *Gymnosporia buxifolia*, *Peltophorum africanum*, *Terminalia sericea*, *Ximenia americana and Ximenia caffra*

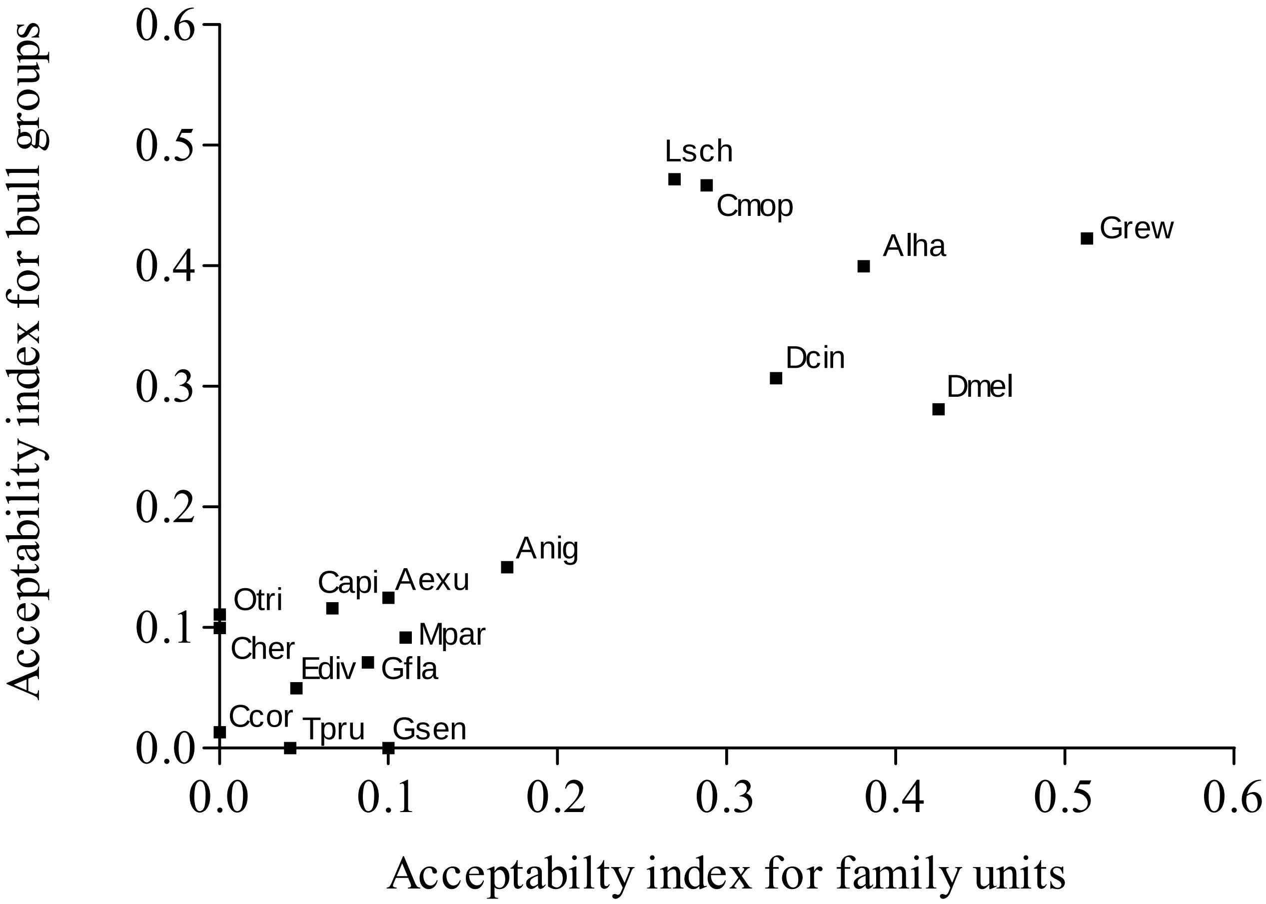

Figure G1 The positive relationship between the acceptability indices of woody species that were available at 10 or more food plots to both bull groups and family units of elephants (n= 17, r_s=0.747, P=0.0006).

Aexu=*Acacia exuvialis*, Alha=*Albizia harveyi*, Anig=*Acacia nigrescens*, Capi=*Combretum apiculatum*, Ccor=*Cissus cornifolia*, Cher=*Combretum hereroense*, Cmop=*Colophospermum mopane*, Dcin=*Dichrostachys cinerea*, Dmel=*Dalbergia melanoxylon*, Ediv=*Euclea divinorum*, Gfla=*Grewia flavescens*, Grew=*Grewia* spp, Gsen=*Gymnosporia senegalensis*, Lsch=*Lannea schweinfurthii*, Mpar=*Maerua parvifolia*, Otri=*Ormocarpum trichocarpum*, Tpru=*Terminalia prunoides.*

APPENDIX H

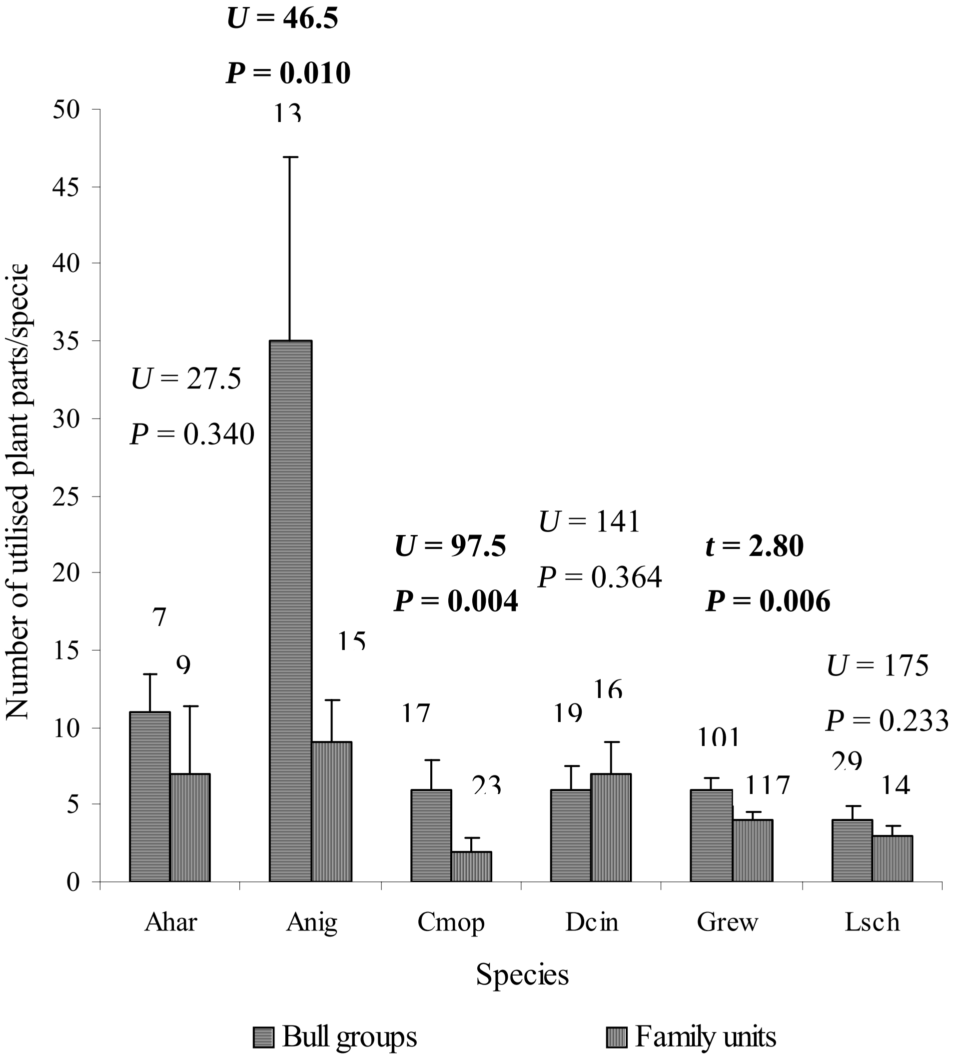

Figure H1 The mean number of plant parts utilised ± standard errors for six plant species that were available at ten or more food plots and utilised at five or more food plots by both bull groups and family units of elephant. The sample sizes are given above the standard error bars while the results of statistical tests to determine whether bull groups utilised more plant parts per species than breeding groups are also included (one-tailed tests). Significant *P* values (<0.05) are given in bold.

Ahar = *Albizia harveyi*, Anig = *Acacia nigrescens*, Cmop = *Colophospermum mopane*, Dcin = *Dichrostachys cinerea*, Grew = *Grewia* spp., Lsch = *Lannea schweinfurthii*.

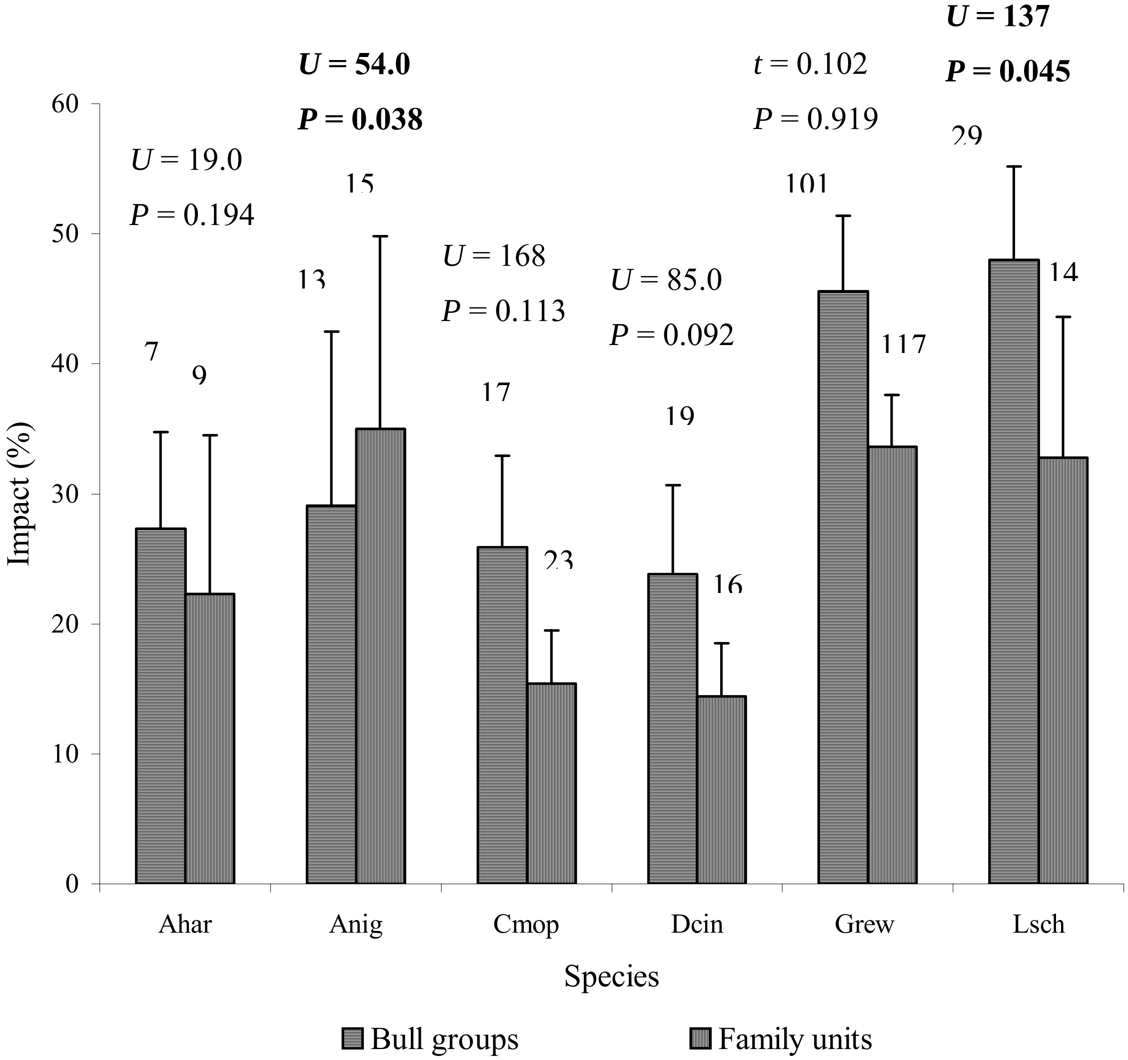

Figure H2 The mean percentage impact ± standard errors for six plant species that were available at ten or more food plots and utilised at five or more food plots by both bull groups and family units of elephant. The sample sizes are given above the standard error bars while the results of statistical tests to determine whether bull groups had a greater impact than breeding groups are also included (one-tailed tests). Significant *P* values (<0.05) are given in bold.

Ahar = *Albizia harveyi*, Anig = *Acacia nigrescens*, Cmop = *Colophospermum mopane*, Dcin = *Dichrostachys cinerea*, Grew = *Grewia* spp., Lsch = *Lannea schweinfurthii*.

APPENDIX I

Tree felling by family units and bull groups

TableI1 The number of individual trees felled or uprooted by family units or bull groups of elephant.

Family units			Bull groups		
Tree species	Feeding mode	Number felled	Tree species	Feeding mode	Number felled
Albizia harveyi	MBA[1]	1	***Acacia exuvialis***	MBA	1
Acacia robusta	MBA	1	***Acacia nigrescens***	MBA	3
			Colophospermum mopane	MBA	1
			***Combretum apiculatum*,**	UR[2]	2
			Lannea schweinfurthii	MBA	6
			Lannea schweinfurthii	UR[2]	4
			Pappea capensis	MBA	1
			Sclerocarya birrea	MBA	3
			Ziziphus mucronata	UR	1
Total number of trees felled		2	Total number of trees felled		22
Total number of trees utilised		80	Total number of trees utilised		93

[1] MBA = Main stem breakage to access smaller canopy parts

[2] UR = Uprooting to consume the roots

APPENDIX J

Browsing height differences between social grouping of elephants in relation to woody plant height categories

Factorial ANOVA with browsing height at which large branches were broken to access smaller plant parts as response variable, and social group and woody plant height class as categorical predictor.

Table J1 Factorial ANOVA results of the higher order interactive effects of height class (small, medium and tall) and group (bull groups and family units of elephants) on the height at which large branches were broken to access smaller plant parts. Significant *P* values (<0.05) are given in bold.

Effect	Df	*F*	*P*-level
Height class		**13.3**	**< 0.0001**
Group		**19.3**	**< 0.0001**
Height class*group		**8.99**	**0.0002**

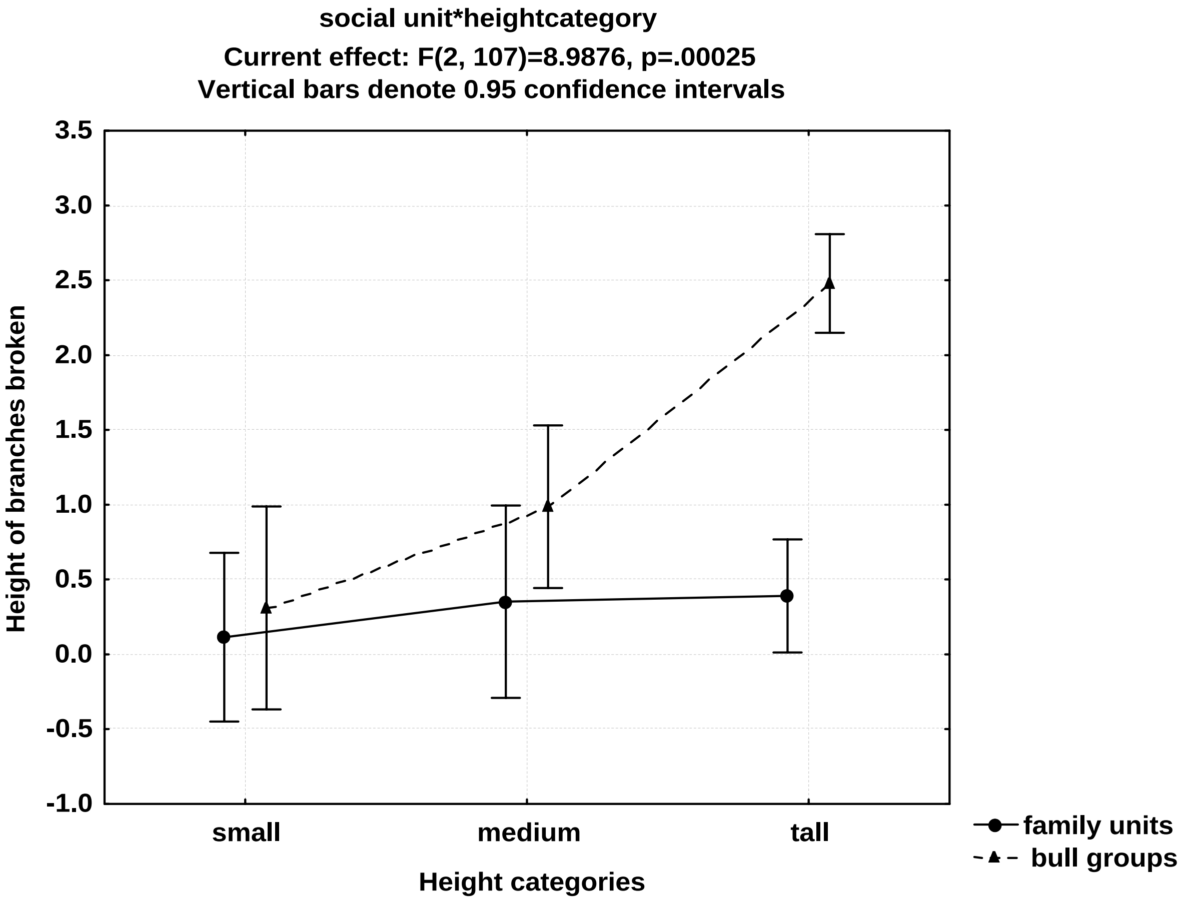

Figure J1 The relationship between the height at which large branches were broken to access smaller plant parts and the height categories of woody plants for family units as well as bull groups. Bull groups broke large branches at significantly higher heights than family units in relation to feeding at taller trees (Tukey test, *P*=0.0001)

APPENDIX K

Chemical variables responsible for plant species acceptance

This section looks at which diet quality indices (N, P, Ca, NDF, and soluble sugar) best distinguish the plant species accepted by elephant family units and bull groups.

Methods

To test whether family units fed from plant species of higher nutritional quality than bull groups, all plant species used by either group were first assigned to one of three categories based on the acceptance indices calculated for each of the species (refer to Chapter 3 for the calculation of acceptance values). Appendix G gives the result of this classification process as well as the numerical intervals of the high-, medium- and low acceptance categories. The mean chemical value for each plant species was derived from the mean value for each of its component plant part types, thereby ensuring equal representation of plant parts in the overall species value. Thereafter diet quality measures were averaged across species within a particular acceptance category for each elephant group type. To assess the prediction that family units utilised woody species of higher nutritional quality than bull groups when compared over the entire range of woody species that were accepted by either bull groups or family units, I used one-tailed Mann Whitney (*U*) tests to test for differences in diet quality measures between herd structures within the abovementioned acceptance categories. To establish whether plant species classified as either high-, medium- or low acceptance differed in their nutritional quality, I used a Kruskal Wallis (*H*) test to compare acceptance categories within a particular elephant social unit. Dunn's Multiple Comparison test was used to determine which categories differed significantly from each other (Sokal & Rohlf 1981).

To test the prediction that family units and bull groups have different acceptance criteria when it comes to the nutritive value of food plants, plant species acceptance indices were regressed against the species-specific diet quality parameters. The calculation of plant species acceptance values for bull groups and family units are reported elsewhere (refer to Chapter 3). As mentioned above, the nutritive value of plant species that were utilised by both bull groups and family units of elephant were determined by first averaging species-specific diet quality measures within the same plant parts and then averaging across plant parts within the same species in an attempt to equally weight the various plant parts utilised within a woody species. This was done for the 21 plant species that both social units fed on as well as for an additional two categories. These two additional categories included species that were in the high acceptance category for bull groups but which weren't utilised by family units and *vice versa* while that same was done for species that weren't shared by both social groups but which fell into the low acceptance category. Plant species acceptance values were calculated for both bull groups and family units by averaging the acceptance values of woody species that fell within either the 'high acceptance' or 'low acceptance' categories. Principle Component Analysis (PCA) was used to extract axes that represented the variation amongst the chemical variables. Three axes were extracted to include all five chemical variables after examination of eigenvalues. Axes were varimax rotated to eliminate the constraint of orthogonality (Fry 1993). Instead of determining the relationship between the species-specific acceptance value and each of the five chemical variables separately, the number of variables used in the least square linear regression was reduced by regressing acceptance values against factor scores obtained from PCA (Tabachnick & Fidell 1983). These procedures were followed for both bull groups and family units to determine which chemical variables affected the acceptance of plant species utilised by either of these social units.

Results

For family units, plant species with high or moderate acceptance indices could be distinguished from species with low acceptance frequencies on the basis of their sugar content as more acceptable species had a comparatively high sugar contents. For bull groups this contrast was associated with differences in the calcium content of the plant samples (Table K1).

The woody species that had high acceptance frequencies for family units as well as high sugar levels included most of the *Acacia* species (*Acacia erubescens, A. gerrardi, A. robusta* and *A. senegal*). Other woody species such as *Berchemia discolor, Cassine transvaalensis, Ozoroa* species, *Pterocarpus rotundifolius* and an unidentified vine were also included into the high acceptance category. Although these species were classified as highly acceptable to family units they were also infrequently available (Appendix G). Family unit's acceptance indices of plant species were thus positively correlated to the factor loadings of axis 1 of the PCA (Table K2). Axis 1 of the PCA represented woody species which offered plant parts with high sugar and low fibre (NDF) contents. In general the positive relationship between the acceptance indices of woody species by family units and their sugar and fibre content was largely determined by the abovementioned few plant species (Figure K1). For bull groups the acceptance indices of plant species were positively correlated to axis 2 of the PCA according to which calcium had a strong positive loading (Table K2). Woody plant species such as *Acacia tortillis, Cissus rotundifolia, Combretum imberbe, Combretum zeyheri, Ehretia amoena, Grewia hexamita, Spirostachys africana,* mistletoe and an unidentified vine had plant parts with high calcium contents but these species were also infrequently available to bull groups. Although the relationship between plant calcium levels and their acceptance by bull groups was also largely determine by a few species with extreme nutritive levels (Figure K1), the results suggests that bulls accept woody species on diet quality attributes other than sugar and fibre content.

Table K1 Nitrogen (N), phosphorus (P), calcium (Ca), fibre (NDF) and carbohydrate (total soluble sugar) levels (mean levels ± standard errors) for plant species that were collected at the food plots of bull groups and family units of elephant. Plant species were assigned to high, medium and low acceptance categories. Plant species categories that were similar are indicated by the same letters of the alphabet (a-b). Sample sizes are given in brackets. All values are expressed on a percentage dry matter basis. Significant *P* values (<0.05) are given in bold.

Acceptability index	Kruskal-Wallis (*H*)	Family units	One-tailed Mann Whitney (*U*)	Bull groups	Kruskal-Wallis (*H*)
N					
High	*H*=1.42,	1.64 ± 0.15 (12)	*U*=61, *P*=0.3909	1.58 ± 0.17 (11)	*H*=2.37,
Medium	*P*=0.4924	1.56 ± 0.35 (10)	*U*=47, *P*=0.2049	1.23 ± 0.01 (12)	*P*=0.3055
Low		1.42 ± 0.17 (8)	*U*=29, *P*=0.2707	1.48 ± 0.29 (9)	
P					
High	*H*=1.06,	0.11 ± 0.01 (12)	*U*=65, *P*=0.4877	0.11 ± 0.02 (11)	*H*=1.11,
Medium	*P*=0.5885	0.10 ± 0.02 (10)	*U*=58, *P*=0.4606	0.08 ± 0.01 (12)	*P*=0.5739
Low		0.09 ± 0.01 (8)	*U*=28, *P*=0.2117	0.10 ± 0.03 (9)	
Ca					**_H_=7.64, _P_=0.0219**
High	*H*=1.06,	1.45 ± 0.16 (12)	*U*=42, *P*=0.0741	1.91 ± 0.24 (11)	**a**
Medium	*P*=0.5873	1.52 ± 0.23 (10)	*U*=59, *P*=0.4870	1.31 ± 0.12 (12)	**a**
Low		1.23 ± 0.18 (8)	*U*=34, *P*=0.4420	1.20 ± 0.09 (9)	**b**
NDF					
High	*H*=0.666,	47.6 ± 3.19 (12)	*U*=55, *P*=0.2591	43.0 ± 4.67 (11)	*H*=1.77,
Medium	*P*=0.7168	49.8 ± 3.56 (10)	*U*=55, *P*=0.3883	52.0 ± 2.60 (12)	*P*=0.4134
Low		52.8 ± 4.31 (8)	*U*=34, *P*=0.4442	51.04 ± 3.83 (9)	
Sugar	**_H_=6.21, _P_=0.044**				
High	**a**	4.80 ± 0.66 (12)	*U*=50, *P*=0.1701	3.83 ± 0.32 (11)	*H*=0.674,
Medium	**a**	4.18 ± 0.31 (10)	*U*=55, *P*=0.3833	4.35 ± 0.45 (12)	*P*=0.7138
Low	**b**	2.92 ± 0.39 (8)	*U*=20, *P*=0.0694	4.02 ± 0.62 (9)	

Table K2 Factor loadings of five diet quality indices on the first three axes extracted by Principle Component Analysis (PCA) for plant species that were used by family units and bull groups of elephant followed by the correlations between acceptance values and these axes. The percentage of the total variance explained by a specific factor is given in brackets. Chemical variables with substantial loadings on each of the three axes are indicated in bold.

Family units				Bull groups			
Correlation coefficients for each chemical variable				Correlation coefficients for each chemical variable			
Diet quality index	Factor 1 (54.0%)	Factor 2 (22.2%)	Factor 3 (14.9%)	Diet quality index	Factor 1 (54.4%)	Factor 2 (19.8%)	Factor 3 (16.6%)
N	0.236	-0.062	**0.864**	N	**-0.884**	-0.092	-0.166
P	0.165	-0.122	**0.909**	P	**-0.910**	-0.078	-0.194
Ca	0.006	**0.992**	-0.117	Ca	0.103	**0.994**	0.039
NDF	**-0.797**	0.119	-0.517	NDF	0.586	0.046	**0.745**
Sugar	**0.971**	0.069	0.114	Sugar	-0.113	-0.034	**-0.970**
Correlation with acceptability values							
r	0.413	0.111	0.009	*r*	0.069	0.458	0.027
$F_{1,21}$	4.345	0.263	0.002	$F_{1,21}$	0.100	5.567	0.004
P	0.049	0.614	0.968	*P*	0.755	0.028	0.952

Discussion

Family units found certain plant species with high sugar and low fibre contents, highly acceptable. Bull groups readily accepted particular woody species that had a high calcium content. As plant parts were initially pooled within species, the positive correlation between calcium content and the acceptance frequency of a species for bull groups could merely reflect the frequent use of particular plant parts such as roots and stem bark, which were rich in calcium. Likewise, family unit's high acceptance frequencies of certain species could be indicative of their tendency to debark and leaf-strip woody plants, thereby selecting plant parts with high sugar and a low fibre contents respectively. Calcium levels in dicotyledonous leaves would also remain high as calcium is not translocated out of senescing leaves before abscission (Williams 1955). The relationship between plant species acceptance indices and nutrient content is furthermore confounded by the finding that 36% of the plant species which family units found highly acceptable because of their high sugar and low fibre content, were not available at the food plots of bull groups. For bull groups only 9% of the highly acceptable woody species with their comparatively high calcium content, were not available at the food plots of family units. Bull groups could thus potentially accept the same woody species that

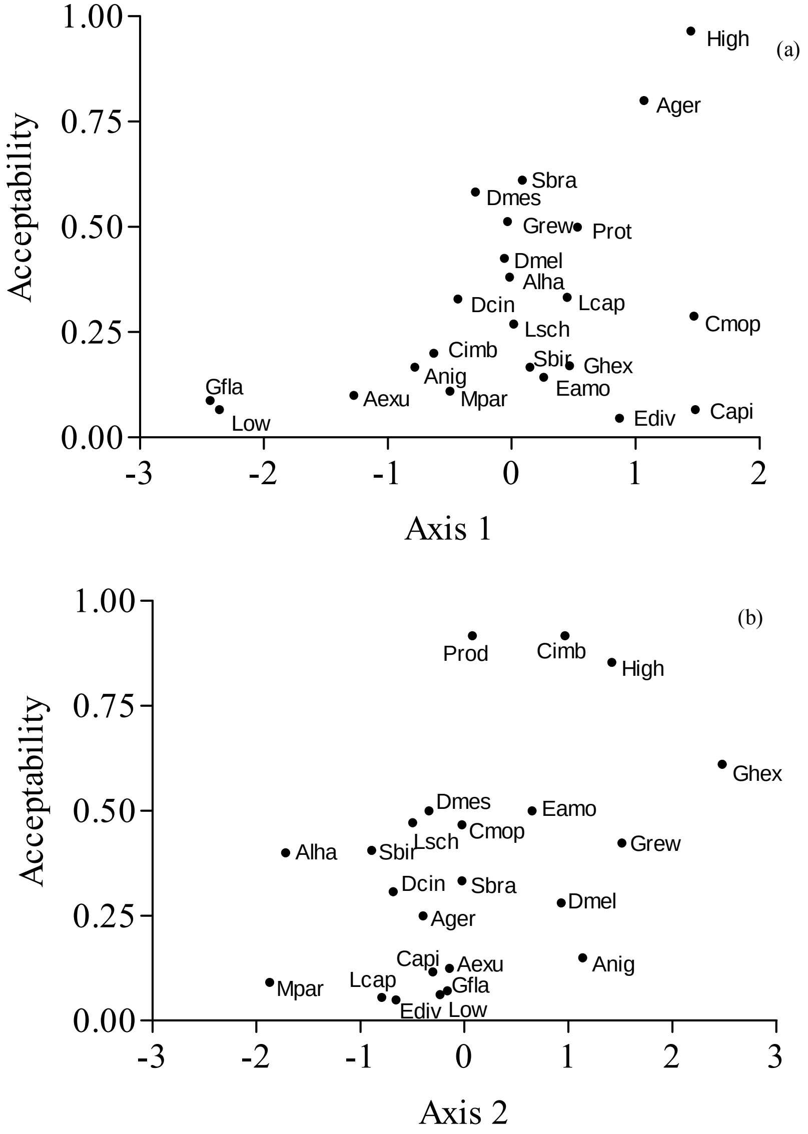

Figure K1 The relationship between the acceptability values of woody species used by family units (a) and axis 1 based on the total soluble sugar and fibre content of the samples as well as the acceptability values of woody species to bull groups (b) in relationship to axis 2, which represents the calcium content of these species.

Aexu=*Acacia exuvialis*, Ager = *Acacia gerrardi*, Alha=*Albizia harveyi*, Anig=*Acacia nigrescens*, Capi=*Combretum apiculatum*, Cimb= *Combretum imberbe*, Cmop=*Colophospermum mopane*, Dcin=*Dichrostachys cinerea*, Dmel=*Dalbergia melanoxylon*, Dmes=*Diospuros mespiliformis*, Eamo= *Ehretia amoena*, Ediv=*Euclea divinorum*, Gfla=*Grewia flavescens*, Ghex= *Grewia hexamita*, Grew=*Grewia* spp, Lcap=Lonchocarpus capassa, Lsch=*Lannea schweinfurthii*, Mpar=*Maerua parvifolia*, Prot=*Pterocarpus rotundifolius*, Sbir=*Sclerocarya birrea*, Sbra=*Schotia brachypetala*.

'High' (family units)=*Acacia erubescens, Acacia robusta, Acacia senegal, Berchemia discolor, Cassine transvaalensis, Ozoroa* spp., vine. 'Low' (family units)=*Commiphora mollis, Terminalia Prunoides.* 'High' (bull groups)=*Acacia tortillas, Cissus rotundifolia, Combretum zeyheri, Spirostachys africana,* mistletoe, vine. 'Low' (bull groups)=*Cissus cornifolia, Combretum hereroense, Ormocarpum tricocarpum.*

family units found highly acceptable and possibly for the same nutritional reasons, if these species were also available to bull groups.

Acceptance of plant species and plant parts by bull groups appears to be associated with the calcium content of woody species. Although studies investigating the dietary importance of calcium to elephants failed to distinguish between the feeding behaviour of bull groups and family units, Napier Bax & Sheldrick (1963) nevertheless found that the utilised bark of trees in Kenya as well as two herbaceous species that were highly sought after by elephants, had high levels of calcium. Williamson (1975) suggested that calcium deficiencies within the diet of elephants could be filled by specific plant species and plant part selection (bark). Although it was proposed that bark stripping by elephants could be a mechanism for acquiring needed calcium, Hiscocks (1999) could not find a difference in calcium levels in the cambium of preferred, less preferred and rarely stripped tree species. After chemically analysing stomach samples of elephants culled in Murchison Falls National Park in Uganda, McCullagh (1969a) concluded that calcium deficiencies were unlikely to affect the feeding behaviour of elephants. According to the literature and in comparison with sodium, calcium is less likely to be limited for elephants (Holdo *et al.* 2002). Nevertheless, I propose a possible explanation for the dietary importance of calcium to bull groups before considering factors, which may have confounded these results. As calcium is an osteotrophic element, calcium could be of particular importance to bulls because of their large skeletons and longer growth curves when compared to females within family units (Georgievskii *et al.* 1981). Although McCullagh (1969b) found no significant differences in the growth rate of male and female elephants during the dry season, males grew considerably faster than females during the wet season. Calcium reserves can thus be deposited in the soft bones and in the trabeculae of the long bones (Lloyd *et al.* 1978, Judson & McFarlane 1998) during the dry season to meet the daily calcium requirements for growth during the wet periods when calcium intake by elephants are significantly lower (McCullagh 1969a). Furthermore calcium is important to tusk formation and although tusk growth is continuous for both males and females, the mean tusk weight of females over 50 is 7.7 kg while males of a similar age have a mean tusk weight which is six times greater (109 kg). The weight of male tusks therefore increases exponentially with age while for females increases in tusk weight are linear (Laws 1966). The abovementioned provides some explanation for the importance of calcium to males but does not clarify why calcium would also not be sought after by pregnant or lactating females within family units as bone calcium is largely metabolised during the formation of milk or of foetal bones (Lloyd *et al.* 1978).

A direct relationship between the concentration of a chemical factor and dietary acceptance is however, rarely found as dietary choice depends on interrelationships amongst chemical factors which either function as attractants or repellents with availability as an overriding factor (Field 1971, Haschick & Kerley 1997). A study conducted on the effects of plant chemicals on foliage selection by elephants in the *Brachystegia* woodlands of Kasungu National park, Malawi, exemplifies the complexity of attributing acceptance of plant species to a single chemical factor (Jachmann & Bell 1985, Jachmann 1989). Jachmann (1989) concluded that sugars and calcium had a positive effect on food selection by elephants whilst also finding that sodium was one of the factors determining browse quality for elephants. The sodium concentration in browse was however related to the concentration of magnesium, which in turn was related to the concentration of calcium (Jachmann & Bell 1985). From the above I cannot conclude that only calcium levels are affecting the ingestion of particular plant species and plant parts by bull groups. Instead I suggest that bull groups may be ingesting large amounts of calcium when uprooting or debarking plants to acquire other minerals. Although sodium concentrations weren't determined in this study the importance of sodium deposits to elephants has already been documented (Weir 1969, Weir 1972, Weir 1973). I suggest that elephant bulls could possibly be procuring plant parts high in calcium as a mere consequence of sodium levels covarying with calcium levels within these tissues.

These results should be interpreted with caution as elevated Ca contents could be an artefact of fibre bound Ca in the form of calcium pectate so that the apparent ingestion of plant parts high in calcium content would not necessarily imply that the calcium is digestible and of physiological use. Furthermore, the measuring of physiological levels of sugar in plants requires careful sampling and handling (Van Soest 1994). As mentioned previously, these findings could also merely reflect each social unit's acceptance of particular plant parts high in Ca or sugar within a species. Hence, I agree with Owen-Smith & Novellie (1982) that categorisation of food plants in terms of individual species is misleading and should preferentially be defined in terms of plant parts of similar nutritive value. Diet quality would primarily depend on parts selected within a species and nutritional analyses should focus on this fine scale (Field 1976, Demment & Van Soest 1985). Differences in plant species used by social units would thus be a secondary consequence of plant part selection.

In conclusion, the mineral content of plant species was associated with the acceptance values of bull groups while high sugar and low fibre content influenced the plant species acceptance frequencies of family units. However, these results were influenced by the inclusion of species with a low availability in the analyses and were largely dependent on which plant parts were selected within a species by either bull groups or family units.

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APPENDIX L

Table L1 The number of plant parts removed per species and the related chemical content from the feeding sites of both bull groups and family units of elephant.

Plant species[1]	Family units									Bull groups								
	SBAv (n)[2]	No. of plants	Plant parts[3]	No. of parts	N	P	Ca	NDF	Sugar	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
Aeru	0.8 (1)	4	MS[4]	-	-	-	-	-	-	na	na	MSA	-	-	-	-	-	-
			BBA[5]	2	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW[6]	40	1.28	0.082	1.77	68.32	2.47			TW	-	-	-	-	-	-
				-	3.305	0.17	0.92	36.05	3.75				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS[7]	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	42	-	-	-	-	-			total	-	-	-	-	-	-
Aexu	0.423 (10)	9	MS	-	-	-	-	-	-	0.467 (8)	2	MSA	2	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	30	0.718	0.043	1.615	67.41	1.945			TW	1	0.83	0.05	0.91	67.7	2.32
				-	2.68	0.125	1.035	52.78	2.89				-	2.225	0.115	1.59	42.9	4.83
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	30	-	-	-	-	-			total	3	-	-	-	-	-
Ager	0.287 (5)	6	MS	-	-	-	-	-	-	0.233 (4)	1	MSA	-	-	-	-	-	-
			BBA	2	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	4	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	11	0.858	0.057	0.958	63.53	3.456			TW	6	1.13	0.06	1.21	57.7	3.63
				-	1.97	0.09	1.59	33.9	4.94				-	2.13	0.075	1.15	27.1	6.97
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	17	-	-	-	-	-			total	6	-	-	-	-	-
Anig	0.505 (25)	15	MS	2	-	-	-	-	-	0.525 (25)	13	MSA	3	-	-	-	-	-
			BBA	5	-	-	-	-	-			BBA	51	-	-	-	-	-
			BBB	1	2.845	0.07	3.165	43.71	5.37			BBB	2	1.58	0.015	2.97	46.9	6.54

Plant species	Family units									Bull groups								
	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	121	0.964	0.05	1.228	63.88	2.801			TW	399	0.909	0.053	1.522	63.6	2.288
				-	-	-	-	-	-				-	2.5	0.133	1.096	32.1	4.407
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	2	2.699	0.145	1.25	31.51	4.634			LS	-	-	-	-	-	-
			total	131	-	-	-	-	-			total	455	-	-	-	-	-
Arob	0.25 (1)	1	MS	1	-	-	-	-	-	0.2 (1)	-	MSA	-	-	-	-	-	-
			BBA	13	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	0.25	0.035	1.1	78.21	1.91			BBP	-	-	-	-	-	-
			TW	15	0.76	0.03	1.5	63.91	3.1			TW	-	-	-	-	-	-
				-	2.81	0.14	1.26	27.67	5				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	29	-	-	-	-	-			total	0	-	-	-	-	-
Asen	0.333 (1)	4	MS	4	-	-	-	-	-	na	na	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	3	1.603	0.053	2.943	57.16	3.21			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	7	0.7	0.05	1.33	62.95	3.62			TW	-	-	-	-	-	-
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	14	-	-	-	-	-			total	0	-	-	-	-	-
Ator	0.225 (2)	0	MS	-	-	-	-	-	-	0.267 (2)	1	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	4	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	-	1.1	0.06	1.52	63.9	2.73
				-	-	-	-	-	-				-	-	-	-	-	-

Plant species	Family units									Bull groups								
	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	0	-	-	-	-	-			total	4	-	-	-	-	-
Alha	0.579 (7)	9	MS	1	-	-	-	-	-	0.42 (10)	7	MSA	1	-	-	-	-	-
			BBA	3	-	-	-	-	-			BBA	18	-	-	-	-	-
			BBB	11	-	-	-	-	-			BBB	11	1.06	0.06	0.708	46.0	7.795
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	45	0.926	0.061	0.857	65.89	2.372			TW	45	0.812	0.06	0.594	64.2	2.634
				-	2.2	0.085	0.975	43.19	3.71				-	2.455	0.205	0.41	45.1	4.63
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	60	-	-	-	-	-			total	75	-	-	-	-	-
Bdis	0.2 (1)	1	MS	-	-	-	-	-	-	na	na	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	-	-	-	-	-	-
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	1	2.17	0.15	2.195	22.08	10.47			LS	-	-	-	-	-	-
			total	1	-	-	-	-	-			total	0	-	-	-	-	-
Ccor	0.313 (19)	0	MS	-	-	-	-	-	-	0.433 (25)	1	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	-	-	-	-	-	-
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	5	0.925	0.095	1.1	49.9	7.94
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	0	-	-	-	-	-			total	5	-	-	-	-	-

Plant species	Family units									Bull groups								
	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
Crot	na	na	MS	-	-	-	-	-	-	0.2 (1)	1	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	1	0.91	0.07	3.46	47.0	3.03
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	0	-	-	-	-	-			total	1	-	-	-	-	-
Cmop	0.481 (17)	23	MS	-	-	-	-	-	-	0.641 (15)	17	MSA	1	-	-	-	-	-
			BBA	2	-	-	-	-	-			BBA	19	-	-	-	-	-
			BBB	7	0.732	0.052	1.632	47.04	4.55			BBB	17	0.744	0.049	1.959	45.8	4.34
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	23	0.68	0.05	0.97	54.12	3.83			TW	69	0.681	0.053	1.220	54.2	4.795
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	15	1.721	0.098	1.261	30.34	6.516			LS	1	1.386	0.075	1.433	31.2	5.494
			total	47	-	-	-	-	-			total	107	-	-	-	-	-
Capi	0.659 (23)	4	MS	-	-	-	-	-	-	0.695 (25)	11	MSA	-	-	-	-	-	-
			BBA	3	-	-	-	-	-			BBA	15	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	39	-	-	-	-	-			TW	339	0.795	0.057	1.735	60.9	2.454
				-	2.446	0.213	0.863	19.95	4.717				-	1.932	0.141	0.917	22.9	5.118
			UR	-	-	-	-	-	-			UR	18	0.455	0.01	2.075	65.7	8.64
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	42	-	-	-	-	-			total	372	-	-	-	-	-
Cher	0.325 (12)	0	MS	-	-	-	-	-	-	0.305 (10)	1	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-

Plant species	Family units									Bull groups								
	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	1	0.59	0.05	1.28	65.5	2.75
				-	-	-	-	-	-				-	1.47	0.08	1.82	23.3	5.8
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	0	-	-	-	-	-			total	1	-	-	-	-	-
Cimb	0.213 (5)	1	MS	1	-	-	-	-	-	0.333 (1)	1	MSA	-	-	-	-	-	-
			BBA	1	-	-	-	-	-			BBA	2	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	2	0.71	0.045	1.47	65.68	2.118			TW	32	0.45	0.04	2.15	62.3	3.19
				-	-	-	-	-	-				-	1.77	0.12	2.25	26.2	5.51
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	4	-	-	-	-	-			total	34	-	-	-	-	-
Czey	0.2 (1)	0	MS	-	-	-	-	-	-	0.433 (2)	1	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	-	-	-	-	-	-
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	1	2.73	0.22	0.7	19.4	3.7
			total	0	-	-	-	-	-			total	1	-	-	-	-	-
Cmol	0.342 (11)	1	MS	-	-	-	-	-	-	0.289 (6)	0	MSA	-	-	-	-	-	-
			BBA	1	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	72	0.48	0.075	0.795	61.47	3.84			TW	-	-	-	-	-	-
				-	2.255	0.165	0.735	34.33	0.96				-	-	-	-	-	-

Plant species	Family units									Bull groups								
	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	73	-	-	-	-	-			total	0	-	-	-	-	-
Ctra	0.225 (2)	1	MS	-	-	-	-	-	-	na	na	MSA	-	-	-	-	-	-
			BBA	5	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	8	0.64	0.01	1.06	66.19	7.8			TW	-	-	-	-	-	-
				-	1.96	0.08	1.4	25.71	5.79				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	13	-	-	-	-	-			total	0	-	-	-	-	-
Dcin	0.452 (20)	16	MS	-	-	-	-	-	-	0.412 (22)	19	MSA	-	-	-	-	-	-
			BBA	2	-	-	-	-	-			BBA	2	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	107	1.294	0.066	1.029	67.90	2.639			TW	115	1.146	0.061	0.972	70.3	2.441
				-	2.65	0.18	1.17	30.14	4.59				-	2.08	0.13	1.1	32.8	4.79
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	109	-	-	-	-	-			total	117	-	-	-	-	-
Dmel	0.438 (10)	16	MS	3	-	-	-	-	-	0.358 (8)	4	MSA	-	-	-	-	-	-
			BBA	3	-	-	-	-	-			BBA	5	-	-	-	-	-
			BBB	17	1.708	0.05	2.626	52.78	5.492			BBB	6	1.92	0.06	2.84	54.9	5.02
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	12	1.36	0.065	1.05	63.06	3.355			TW	12	1.128	0.047	1.315	70.2	2.515
				-	2.568	0.095	1.308	38.45	4.345				-	2.745	0.11	1.51	41.7	3.76
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	35	-	-	-	-	-			total	23	-	-	-	-	-

Plant species	Family units									Bull groups								
	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
Dmes	0.413 (4)	6	MS	-	-	-	-	-	-	0.267 (2)	2	MSA	-	-	-	-	-	-
			BBA	18	-	-	-	-	-			BBA	1	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	38	0.76	0.048	1.307	65.78	2.463			TW	-	-	-	-	-	-
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	2	2.016	0.21	1.066	38.52	3.65			LS	3	2	0.19	1.17	36.2	4.25
			total	58	-	-	-	-	-			total	4	-	-	-	-	-
Eamo	0.34 (7)	3	MS	-	-	-	-	-	-	0.3 (2)	13	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	14	1.76	0.12	1.43	59.85	3.32			TW	50	1.41	0.115	1.22	56.7	2.35
				-	2.79	0.13	1.98	28.11	5.38				-	2.77	0.09	1.79	29.2	5.52
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	14	-	-	-	-	-			total	50	-	-	-	-	-
Ediv	0.347 (11)	2	MS	-	-	-	-	-	-	0.345 (10)	1	MSA	-	-	-	-	-	-
			BBA	5	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	39	1.4	0.08	1.13	45.71	4.34			TW	4	0.525	0.035	1.29	61.1	3.92
				-	1.575	0.13	0.8	42.58	4.46				-	1.6	0.11	1.27	30.6	5.36
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	44	-	-	-	-	-			total	4	-	-	-	-	-
Gfla	0.354 (19)	3	MS	-	-	-	-	-	-	0.417 (21)	2	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-

Plant species	Family units									Bull groups								
	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	8	0.602	0.042	1.273	75.40	1.73			TW	22	0.54	0.078	1.008	73.8	1.685
				-	-	-	-	-	-				-	1.993	0.1	1.67	40.8	3.36
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	8	-	-	-	-	-			total	22	-	-	-	-	-
Ghex	0.356 (3)	5	MS	-	-	-	-	-	-	0.333 (6)	6	MSA	-	-	-	-	-	-
			BBA	7	-	-	-	-	-			BBA	3	-	-	-	-	-
			BBB	15	1.095	0.075	2.585	55.45	4.215			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	5	0.55	0.06	3.18	60.15	3.42			TW	44	0.575	0.058	1.948	63.5	2.843
				-	2	0.13	3.22	40.22	4.03				-	-	-	-	-	-
			UR	1	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	1	2.401	0.2	2.304	41.4	2.89
			total	28	-	-	-	-	-			total	48	-	-	-	-	-
Grew	0.818 (30)	115	MS	1	-	-	-	-	-	0.887 (32)	96	MSA	2	-	-	-	-	-
			BBA	20	-	-	-	-	-			BBA	32	-	-	-	-	-
			BBB	166	0.994	0.076	2.432	52.09	4.553			BBB	85	0.994	0.08	2.197	53.2	4.239
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	102	0.773	0.070	1.335	65.88	2.575			TW	121	0.668	0.065	1.370	67.0	2.457
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	171	1.175	0.047	2.517	48.20	5.109			UR	298	1.199	0.040	2.926	45.5	5.752
			LS	12	2.209	0.141	1.997	41.50	3.516			LS	7	2.235	0.147	1.88	44.6	3.667
			total	472	-	-	-	-	-			total	545	-	-	-	-	-
Gsen	0.32 (10)	1	MS	-	-	-	-	-	-	0.371 (7)	0	MSA	-	-	-	-	-	-
			BBA	2	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	-	-	-	-	-	-
				-	-	-	-	-	-				-	-	-	-	-	-

Plant species	Family units									Bull groups								
	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	2	-	-	-	-	-			total	0	-	-	-	-	-
Lsch	0.44 (18)	14	MS	1	-	-	-	-	-	0.451 (20)	26	MSA	-	-	-	-	-	-
			BBA	18	-	-	-	-	-			BBA	21	-	-	-	-	-
			BBB	2	-	-	-	-	-			BBB	42	0.5	0.078	2.79	43.5	3.135
			BBP	5	0.272	0.044	0.284	71.23	2.814			BBP	6	0.345	0.049	0.372	70.5	3.622
			TW	12	0.565	0.06	0.945	61.72	2.76			TW	11	0.61	0.055	1.905	51.9	3.76
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	1	0.26	0.015	0.255	80.55	0.98			UR	22	0.422	0.043	1.303	59.6	4.43
			LS	3	1.34	0.103	1.86	22.34	7.724			LS	3	1.473	0.244	1.594	22.3	5.364
			total	42	-	-	-	-	-			total	105	-	-	-	-	-
Lcap	0.319 (6)	2	MS	-	-	-	-	-	-	0.311 (6)	3	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	57	-	-	-	-	-			TW	102	-	-	-	-	-
				-	-	-	-	-	-				-	3.6	0.3	0.97	31.8	4.5
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	1	4.495	0.28	0.86	32.99	4.96			LS	-	-	-	-	-	-
			total	58	-	-	-	-	-			total	102	-	-	-	-	-
Mpar	0.434 (19)	11	MS	-	-	-	-	-	-	0.443 (20)	8	MSA	-	-	-	-	-	-
			BBA	3	-	-	-	-	-			BBA	4	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	27	1.28	0.025	0.512	70.78	0.75			TW	4	1.32	0.015	0.45	69.8	3.14
				-	2.13	0.07	0.93	25.59	4.76				-	2.29	0.09	0.62	24.4	4.52
			UR	-	-	-	-	-	-			UR	2	2.645	0.09	0.93	65.5	3.36
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	30	-	-	-	-	-			total	10	-	-	-	-	-

Plant species	Family units									Bull groups								
	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv (n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
Mist	na	na	MS	-	-	-	-	-	-	0.2 (1)	1	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	-	0.46	0.04	1.56	69.9	2.11
				-	-	-	-	-	-				-	1.33	0.1	1.91	42.6	3.57
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	0	-	-	-	-	-			total	0	1.742	0.103	1.318	43.6	4.987
Otri	0.379 (7)	0	MS	-	-	-	-	-	-	0.378 (9)	2	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	4	0.735	0.015	1.325	72.7	0.98
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	0	-	-	-	-	-			total	4	-	-	-	-	-
Oso	0.2 (2)	2	MS	-	-	-	-	-	-	0.2 (1)	0	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	1	0.285	0.065	0.605	31.6	7.77			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	1	0.74	0.065	0.65	61.91	1.96			TW	-	-	-	-	-	-
				-	3.73	0.34	1.215	35.19	4.02				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	2	-	-	-	-	-			total	0	-	-	-	-	-
Pcap	0.2 (1)	0	MS	-	-	-	-	-	-	0.333 (7)	5	MSA	1	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	6	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-

Plant species	Family units									Bull groups								
	SBAv(n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv(n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	35	0.583	0.043	1.238	66.9	1.755
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	1	1.657	0.13	1.363	46.3	4.227
			total	0	-	-	-	-	-			total	43	-	-	-	-	-
Prod	0.328 (3)	2	MS	-	-	-	-	-	-	0.2 (1)	1	MSA	-	-	-	-	-	-
			BBA	2	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	4	1.445	0.035	1.965	50.9	4.88
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	-	-	-	-	-	-
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	1	2.67	0.17	0.78	38.42	3.96			LS	-	-	-	-	-	-
			total	3	-	-	-	-	-			total	4	-	-	-	-	-
Sbra	0.394 (3)	3	MS	-	-	-	-	-	-	0.244 (3)	1	MSA	-	-	-	-	-	-
			BBA	1	-	-	-	-	-			BBA	5	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	1	0.57	0.04	1.38	51.4	4.43
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	3	0.58	0.055	1.395	53.01	0.83			TW	-	-	-	-	-	-
				-	1.742	0.103	1.318	43.61	4.987				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	1.52	0.11	1.52	35.9	4.46
			total	4	-	-	-	-	-			total	6	-	-	-	-	-
Sbir	0.267 (6)	1	MS	-	-	-	-	-	-	0.37 (16)	13	MSA	3	-	-	-	-	-
			BBA	1	-	-	-	-	-			BBA	73	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	22	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	0.255	0.035	0.795	71.7	0.98
			TW	3	-	-	-	-	-			TW	151	0.623	0.1	0.778	56.2	2.152
				-	1.235	0.14	1.25	34.75	5.11				-	-	-	-	-	-

Plant species	Family units									Bull groups								
	SBAv(n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv(n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	5	1.577	0.194	0.784	33.7	4.2
			total	-	-	-	-	-	-			total	254	-	-	-	-	-
Safr	0.417 (4)	0	MS	-	-	-	-	-	-	0.333 (2)	1	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	-	-	-	-	-	-
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	1	1.905	0.13	1.605	11.4	6.18
			total	0	-	-	-	-	-			total	1	-	-	-	-	-
Tpru	0.425 (14)	2	MS	-	-	-	-	-	-	0.361 (14)	0	MSA	-	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	4	0.53	0.06	1.375	67.24	1.68			TW	-	-	-	-	-	-
				-	1.78	0.13	2.9	18.76	5.37				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	-	-	-	-	-
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	4	-	-	-	-	-			total	-	-	-	-	-	-
Vine	0.2 (1)	1	MS	-	-	-	-	-	-	0.2 (1)	1	MSA		-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	4	1.4	0.09	1.29	54.5	9.6			TW	-	-	-	-	-	-
				-	3.48	0.2	1.42	24.45	5.22				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	2	1.52	0.09	2.95	50.7	3.39
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	4	-	-	-	-	-			total	2	-	-	-	-	-

Plant species	Family units									Bull groups								
	SBAv(n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar	SBAv(n)	No. of plants	Plant parts	No. of parts	N	P	Ca	NDF	Sugar
Zmuc	0.375	0	MS	-	-	-	-	-	-	0.233(4)	1	MSA	1	-	-	-	-	-
			BBA	-	-	-	-	-	-			BBA	-	-	-	-	-	-
			BBB	-	-	-	-	-	-			BBB	-	-	-	-	-	-
			BBP	-	-	-	-	-	-			BBP	-	-	-	-	-	-
			TW	-	-	-	-	-	-			TW	-	-	-	-	-	-
				-	-	-	-	-	-				-	-	-	-	-	-
			UR	-	-	-	-	-	-			UR	-	0.875	0.055	1.36	66.8	8.61
			LS	-	-	-	-	-	-			LS	-	-	-	-	-	-
			total	0	-	-	-	-	-			total	0	-	-	-	-	-

[1] Plant species Aeru=*Acacia erubescens*, Aexu=*Acacia exuvialis*, Ager=*Acacia gerrardi*, Anig=*Acacia nigrescens*, Arob=*Acacia robusta*, Asen=*Acacia senegalensis*, Ator=*Acacia tortillas*, Alha=*Albizia harveyi*, Bdis=*Berchemia discolor*, Ccor=*Cissus cornifolia*, Crot=*Cissus rotundifolia*, Cmop=*Colophospermum mopane*, Capi=*Combretum apiculatum*, Cher=*Combretum hereroense*, Cimb=*Combretum imberbe*, Czey=*Combretum zeyheri*, Cmol=*Commiphora mollis*, Ctra=*Cassine transvaalensis*, Dcin=*Dichrostachys cinerea*, Dmel=*Dalbergia melanoxylon*, Dmes=*Diospyros mespiliformis*, Eamo=*Ehretia amoena*, Ediv=*Euclea divinorum*, Gfla=*Grewia flavescens*, Ghex=*Grewia hexamita*, Grew=*Grewia spp*, Gsen=*Gymnosporia Senegal*, Lsch=*Lannea schweinfurthii*, Lcap=*Lonchocarpus capassa*, Mpar=*Maerua parvifolia*, Mist=Mistletoe, Otri=*Ormocarpum trichocarpum*, Oso=*Ozoroa*, Pcap=*Pappea capensis*, Prod=*Pterocarpus rotundifolia*, Sbra=*Schotia brachypetala*, Sbir=*Sclerocarya birrea*, Safr=*Spirostachys africana*, Tpru=*Terminalia prunoides*, Vine=Vine, Zmuc=*Ziziphus mucronata*

[2] SBAv (*n*)=Site-based Availability (*n* = number of independent feeding sites at which the species was present)

[3] Plant parts MSA=Main stem breakage to access smaller plant parts, BBA=Branch breakage to access smaller plant parts, BBB=Branch breakage consume bark on the proximal end, BBP=Branch breakage to consume the pith/heartwood, TW=Twigs, UR=Uprooting to access roots, LS=Leaf stripping for leaves.

[4] No plant parts were chemically analysed as these feeding modes only refer to breakages without consumption.

[5] No plant parts were chemically analysed as these feeding modes only refer to breakages without consumption.

[6] Where twigs were utilised they either had leaves or were without leaves. Leaves and twigs were analysed separately.

[7] During leaf-stripping events, only leaves were removed which were chemically analysed and no twigs.

Table M1 The mean $\delta^{13}C$ (‰) values with the standard deviation (s.d) for elephant faecal samples collected throughout South Africa.

Locality	n	$\delta^{13}C$ (s.d.)	Potential sources of variation for $\delta^{13}C$ estimates	Source
APNR[a]	245	-22.8 (2.2)	Seasonal variation in forage class selection	Present study
KNP[b] (south)	4	-26.3 (0.8)		Vogel *et al.* 1990
	18	-25.5 (0.8)[c]		Van der Merwe *et al.* 1988
KNP (north)	6	-23.4 (2.7)		Vogel *et al.* 1990
	13	-26.0 (1.0)[c]		Van der Merwe *et al.* 1988
Addo Elephant Park	1	-23.1	Influence of ingested CAM plants[d]	Vogel *et al.* 1990
	5	-22.0 (0.4)[c]	Influence of ingested CAM plants[d]	Van der Merwe *et al.* 1988
Knysna	4	-29.1 (0.5)[c]	Recycled CO_2 because of forest canopy[e]	Vogel *et al.* 1990
	1	-28.2[c]	Recycled CO_2 because of forest canopy[e]	Van der Merwe *et al.* 1988
	12	-28.7 (0.7)	Recycled CO_2 because of forest canopy[e]	Seydack *et al.* 2000

[a] Association of Private Nature Reserves

[b] Kruger National Park

[c] Values obtained from bone collagen samples that were converted to faecal $\delta^{13}C$ values by the addition of -5‰ as bone collagen values are enriched by approximately 5‰ relative to the plant food average (Van der Merwe *et al.* 1988; Vogel *et al.* 1990; Seydack *et al.* 2000).

[d] Succulents and euphorbias fix atmospheric CO_2 by crassulacean acid metabolism (CAM) or C_3 photosynthesis or a mix of both (Mooney *et al.* 1977; Van der Merwe *et al.*1988).

[e] In forest environments grasses can be either of the C_3 or C_4 type (Vogel 1978) while recycling of biogenic CO_2 would depend on the position within the forest canopy and the under storey canopy development which would cause unusually low $\delta^{13}C$ values in these environments (Ehleringer *et al.* 1986; Vogel 1990). The C_3 grass type normally dominates in forests.

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APPENDIX N

Table N1 Summary of the climatic, edaphic, vegatational and elephant density components of a mesic dystrophic and a semi-arid eutrophic savanna system.

Savanna type	Semi-arid eutrophic savanna Associated Private Nature Reserves	Mesic, dystrophic savanna Chobe National Park
Location	Western border of Kruger National Park, South Africa 31°02’- 31°29’E and 24°03’- 24°33’	North-eastern Botswana 24°43’- 25°15’E and 17°46’- 18°15’S
Rainfall	450-550mm[2,8,10,19]	685mm[3]
Temperature	Annual average = 22°C[8,10,19]	Annual average = 21.2°C[3]
Frost	Rare occurance[8,10,19]	Rare occurance[3,5]
Wet season	Between October – May[8,9,10,19]	Between October – May[5]
Topography	Undulating terrain on granites Average altitude = 150 – 600m[8,10,19]	Flat to gently undulating Average altitude = 1000m[3,4]
Bedrock	Dominated by granite and gneiss, crisscrossed with many drainage lines, intersected by dolerite. Gabbro in central and southern parts[6,8,10,14,19]	Consists mainly of Karoo sediments, Ghanzi, Kwede and Damara formations. Gneiss of old basement complex[13]
Soil	Upland soils weathered from granite rock: Coarse, sandy and gravely, high infiltration rate and high permeability, low clay forming potential, leached soils of low fertility. Bottomlands of undulating terrain as well as gabbro: Fine-grained clay soils, non-leached soil with low infiltration rate, rich in nutrients, sometimes formation of sodic duplex soils[6,8,10,14,19]	Extensive deposits of aeolian and alluvial sands of the Kalahari beds, high infiltration rate and high permeability. Soils neutral to slightly acidic, poor in nutrients, more fertile soils found on flood plains and in some depressions. The Alkaline Flats that represent a narrow strip on the border of the riverfront supports sodic soils[35]
Vegetation	Broadly classified as *Acacia nigrescens, Sclerocarya birrea* savanna of arid lowveld[1]but *Combretum* dominated on granites	Broadly categorised into the riparian fringe, the alluvial terrace and extensive sandveld woodlands[18]
Characteristic plant species	The *Acacia nigrescens/Combretum apiculatum* woodlands of fertile, lowland soils are considered the most widespread landscape type. Other arid savanna species i.e. *Acacia*, *Commiphora* and *Colophospermum* are present at different densities throughout the reserve[1,6,8,14,19]	Moist savanna species i.e. *Burkea, Brachystegia, Ochna* and *Julbernardia* as well as *Baikiaea plurijuga* are found in sandveld woodlands. Although dominated by *Colophospermum*, depressions and floodplain fringes often have similar species composition to arid savannas[7,15,16,17]
Elephant density	0.41-0.54 elephants/km^2 [12,20]	7.6-25.0 elephants/km^2 [11]

[1]Acocks (1975), [2]Anon (1996), [3]Bekker & de Wit (1991), [4]Ben-Shahar (1996), [5]Bhalotra (1987), [6]Bonsma (1976), [7]Child (1968), [8]De Villiers (1994), [9]Gertenbach (1980), [10]Gertenbach (1983), [11]Gibson *et al.*(1998), [12]Hall-Martin (1992), [13]Hutchins *et al.* (1976), [14]Low & Rebelo (1996), [15]Moroka (1984), [16]Simpson (1975), [17]Sommerlatte (1976), [18]Stokke & du Toit (2000), [19]Witkowski (1983), [20]S.C.J Joubert (*pers. comm.*)

Table N2 Dry season comparisons of intersexual differences in feeding patterns between family units (♀) and bull groups (♂) of elephant at various spatial scales.

Increasing scale of measurement	Semi-arid eutrophic savanna Associated Private Nature Reserves[1]	Mesic dystrophic savanna Chobe National Park[2]
Habitat types	not measured	♂ used a greater diversity of habitat types than ♀
Foraging paths[3]	foraging paths of ♂ higher density of plants than the surrounding area.	foraging paths of both ♂and ♀ had a similar density of species to surrounding area.
	foraging paths of ♂higher species richness than the surrounding area.	foraging paths of both ♂and ♀ had a similar species richness to surrounding area.
	foraging paths of both ♂and ♀ had a similar diversity of species to surrounding area.	foraging paths of both ♂and ♀ had a similar diversity of species to surrounding area.
Food plots	food plots of both ♂and ♀ had a similar density of species.	food plots of ♀ had a higher density of species than food plots of ♂.
	food plots of both ♂and ♀ had a similar species richness.	food plots of ♀ had a higher species richness than food plots of ♂.
	food plots of both ♂and ♀ had a similar diversity of species.	food plots of both ♂and ♀ had a similar diversity of species.
Plant species	21 woody species used by both ♂and ♀	19 woody species used by both ♂and ♀
	31 woody species used by ♀	41 woody species used by ♀
	32 woody species used by ♂	28 woody species used by ♂
	♂and ♀ utilised a similar diversity of woody species.	♀ utilised a higher diversity of woody species than ♂.
Plant parts	♂and ♀ utilised a similar diversity of plant parts.	♂ utilised a higher diversity of plant parts than ♀.
	♂ uprooted, broke branches and tree felled woody species more frequently than ♀.	♂ uprooted, broke branches and tree felled woody species more frequently than ♀.
	♀ debarked and defoliated woody species more frequently than ♂.	♀ debarked and defoliated woody species more frequently than ♂.
	♂ removed more plant parts per *Grewia* species[4] than ♀.	♂ removed more plant parts per *Baphia mossaiensis*[4] species than ♀.
	♂ broke and bit branches of larger diameter than ♀.	♂ broke and bit branches of larger diameter than ♀.
	♂ accessed plant parts from higher heights than ♀.	♀ accessed plant parts from higher heights than ♂.
Chemical analysis	♂and ♀ used plant species and parts of similar quality	not measured

[1] Refer to chapters 4, 5 & 6.

[2] Stokke (1999), Stokke & du Toit (2000).

[3] Food plots compared to their respective control plots were taken to represent chosen foraging paths as opposed to the surrounding area.

[4] Woody species that were the most frequently browsed by both bull and breeding groups of elephant within the APNR and Chobe National Park respectively.

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