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FOOD-RELATED DETERMINANTS OF KUDU CARRYING CAPACITY IN A SEMI-ARID SAVANNA

by

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CHAPTER 1

INTRODUCTION

The recent past has seen a shift away from commercial livestock production, mostly cattle, towards game ranching in South Africa (Behr & Groenewald 1990; Eloff 1996; Robinson & Lademann 1998; Van der Waal & Dekker 2000) and specifically in the savanna areas. Savanna describes vegetation constituting a herbaceous layer, usually graminoids, with an upper layer of woody plants (Edwards 1983; Rutherford & Westfall 1994). These layers are differentially utilised by African ungulate species (Hofmann & Stewart 1972; Giesecke & Van Gylswyk 1975; Hofmann 1989; Du Toit 1995; Owen-Smith 1997), a perceived benefit of multi-species production systems (Tainton, Booysen & Nash 1977; Dekker 1998; Smit 2000). Three distinctive large herbivore feeding groups are evident; grazers which consume mainly graminoids, browsers which feed mainly on forbs and woody plants, and mixed feeders which alternate between forage components (Owen-Smith 1997).

Game ranching in the South African context usually involves relatively small (< 5 000 ha) fenced-in areas (Behr & Groenewald 1990) where natural limitations of water availability, disease and large predators are often controlled (Du Toit 1995). Under these conditions large herbivore populations often overshoot natural densities (Du Toit 1995), which necessitates increased managerial input (Trollope 1990; Bothma 1995).

A fundamental question relating to wildlife management concerns the carrying capacity of an area; how many animals of which species can a given area support (Du Toit 1995; Grossman, Holden & Collinson 1999)? Norms to set initial grazer stocking rates in multi-species systems have been relatively well studied, e.g. Snyman (1989), Peel, Grossman & Van Rooyen (1991a) and Schmidt, Theron & Van Hoven (1995). This is, however, not the case for browsers. A need has consequently been expressed by rangeland scientists to assess the ability of an area of land to sustain browsing ungulate species in order to reach set objectives (Tainton *et al.* 1977; Peel 1990; Melville, Cauldwell & Bothma 1999; Schmidt & Jordaan 1999).

The greater kudu, *Tragelaphus strepciseros* (Pallas), was chosen as the focal species of this study because:

(i) Kudu are widely distributed in the savanna areas of southern Africa (Skinner & Smithers 1990).

(ii) The kudu is a prominent game ranch species in the sub-region (Van Hoven 1991; Van der Waal & Dekker 2000).

(iii) Kudu are predominantly browsers (Wilson 1965; Jarman 1971; Owen-Smith 1997).

(iv) Kudu undergo population crashes (Simpson 1972; Owen-Smith 1990, 1993a), which are apparently amplified by confinement (Wilson 1970; Owen-Smith 1982; Van Hoven 1991; Du Toit 1995). Large-scale mortalities equate to financial losses that raise questions about current management practises.

(v) The habitat use (Simpson 1972; Wentzel 1990; Fabricius 1994; Dekker 1996), feeding ecology (e.g. Novellie 1983; Owen-Smith, Novellie & Cooper 1983; Owen-Smith 1979, 1997; Owen-Smith & Cooper 1987, 1989), reproduction system (Skinner & Huntley 1971; Owen-Smith 1984, 1993b), demography (Owen-Smith 1990) and social organisation (Simpson 1968; Owen-Smith 1993a) of kudu has been well documented. These studies provide a firm background for future ecological investigation.

Most large ungulate species, which also include kudu, are thought to be food limited (Owen-Smith & Cooper 1985; Novellie 1992; Grossman 1994; Wolff 1997). The objective of this study was to quantify food-related factors that limit kudu production in a semi-arid savanna. A comparative study was set up with a view to quantify food resources across a range of availability levels and to relate these to kudu population parameters thought to have a bearing on kudu carrying capacity.

CHAPTER 2

STUDY AREA

2.1 LOCATION

The study involved eight study units located in the north-western part of the Northern Province of South Africa (Figure 2.1). Seven study units were located between the towns of Vivo, Alldays, Tolwe and Maasstroom (Figure 2.1). An eighth study unit was situated approximately 25 km south-west of Louis Trichardt.

2.2 SELECTION OF STUDY UNITS

Study units were chosen along a reported kudu mortality gradient experienced during the dry season of 1998 in the study area. Study units 6 and 8 reported high mortalities (>25 kudu). Study units 1, 2 and 3 reported moderate mortalities (3-8 kudu). The remaining study units, study units 4, 5 and 7 reported few kudu deaths (<3 kudu).

The kudu mortality gradient formed the basis on which the selection of study units was made. Other factors were, however, also considered. Selected study units had the following characteristics in common:

(i) Study units were located in the Arid Sweet Bushveld (Acocks 1988).
(ii) Larger game species' movements in and out of study units were restricted by game fences (>2.3 m high) and excluded at study unit 4 by a concrete wall (>2.5 m) encircling the study unit. Only study unit 7 was subdivided by inner cattle fences (4-5 wire strands). The movements of browsing ungulate species such as impala, eland and kudu are apparently minimally impeded by these obstructions, with the possible exception of very young animals (personal observation).
(iii) Both kudu and impala occurred on properties for at least three years prior to the study period (January 1997 to December 1999).
(iv) Owners of the private game ranches were co-operative regarding the study. They also financed the helicopter game censuses undertaken during 1999 (Chapter 6).

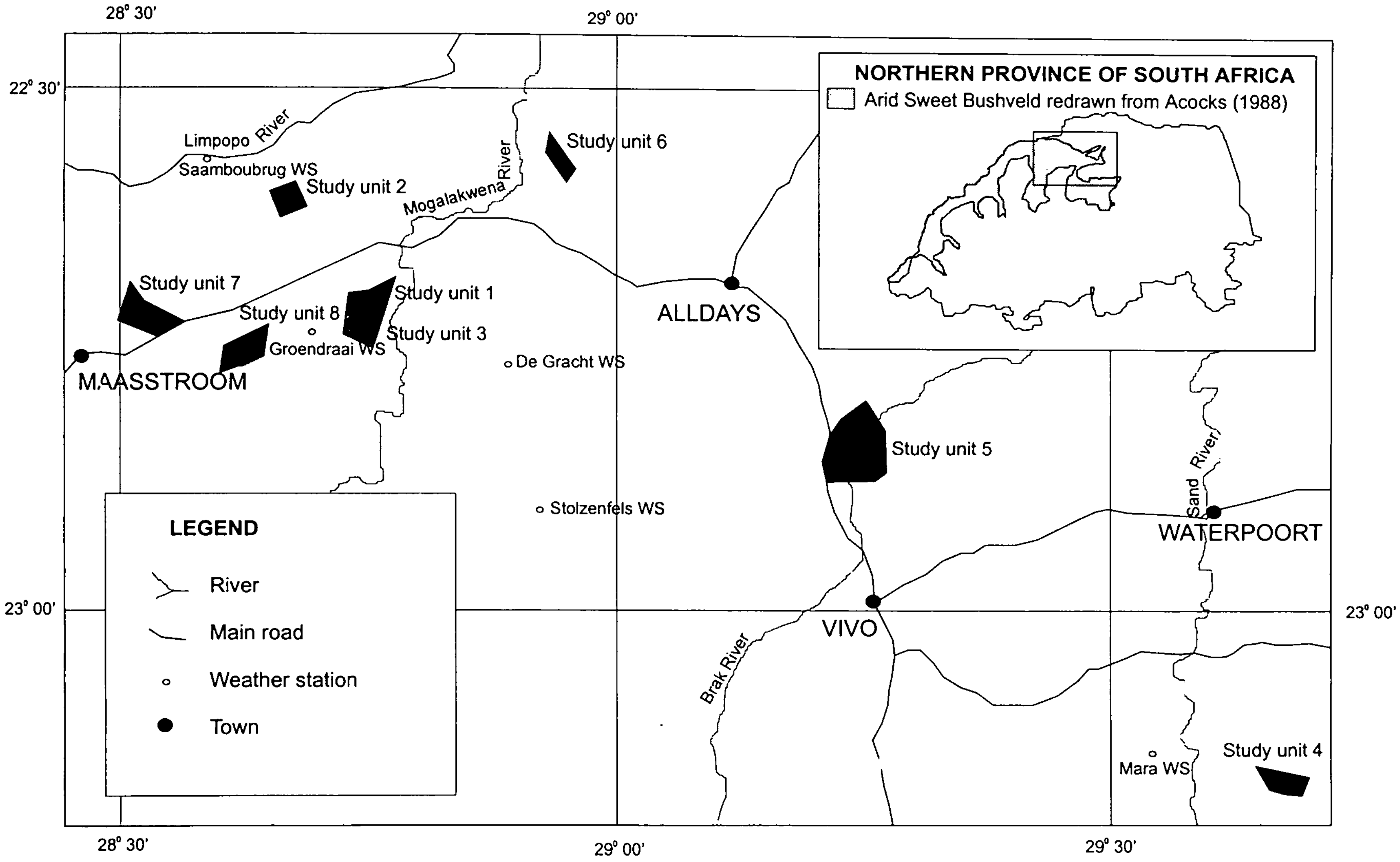

Figure 2.1 A map of the study area illustrating the location of the study units in relation to geographical features. The insert shows the location of the study area in relation to the limits of the Arid Sweet Bushveld (Acocks 1988).

2.3 STUDY UNIT SIZE

The surface area of each of the study units was obtained from the registered title deeds of the properties involved (Table 2.1). In cases where game fences did not follow the boundaries of the registered title deeds, surface areas were calculated with the aid of a planimeter and 1:50 000 topo-cadastral maps (Table 2.1).

The game fenced areas of study units ranged from 750.0 ha to 4 587.5 ha with a mean of 1 549.3 ha (Table 2.1). This mean is close to the mean size of 1 717 ha calculated for 1 701 game ranches in the Northern Province by Van der Waal & Dekker (2000).

2.4 PHYSIOGRAPHY

2.4.1 Topography

The study units are located at altitudes ranging from 680 metres to 980 metres above sea level (Table 2.2). The topography of study units 2, 4, 5 and 8 was flat to gently undulating with a relatively small variation in altitude (Table 2.2). Study units 1 and 7, and to a lesser extent study unit 3, have localised areas raised above the landscape with gradual slopes. Study unit 6 had the most variable topography with a large difference in altitude between the south-eastern and north-western parts (Table 2.2).

2.4.2 Drainage

The Sweet Bushveld (Van Rooyen & Bredenkamp 1996), which coincides with the Arid Sweet Bushveld (Acocks 1988), drains into the Limpopo river system and is located in the Limpopo basin and along its tributaries (Van Rooyen & Bredenkamp 1996).

The Brak River, which has an extensive drainage system with alluvial deposits and riparian vegetation, bisected study unit 5. Study units 1, 2 and 3 had less well developed drainage lines. Weakly defined watercourses facilitated drainage at study units 4, 6, 7 and 8.

Table 2.1 Identification, geographical positions and sizes (ha) of the game fenced areas of the study units.

Study unit	**Farm/reserve name (deeds office registration)**	**Geographical position**		**Game fenced area (ha)**
1	Alwyn (MR 225)	28° 45' E	22° 42' S	1 080.6**
2	Bonteberg (MR 177)	28° 40' E	22° 36' S	868.5*
3	Canterbury (MR 254) Donkerhoek (MR 224)	28° 44' E	22° 43' S	1 070.0**
4	Flurian Nature Reserve	29° 42' E	23° 10' S	865.0**
5	Langjan Nature Reserve	29° 14' E	22° 50' S	4 587.5**
6	Bleshoenderpan (MR 211)	28° 56' E	22° 34' S	750.0*
7	Oeferman (MR 241)	28° 31' E	22° 42' S	1 792.9*
8	Rondom Fraai (MR 235)	28° 38' E	22° 44' S	1 379.6*
	Total			**12 394.1**

* Area according to registered title deeds

** Game fenced area determined by electronic planimeter

Table 2.2 Range in height above sea level (m) of study units.

Study unit	**Height above sea level (m)**
1	700-760
2	700-740
3	720-780
4	920-980
5	760-820
6	680-840
7	780-880
8	780-840

2.5 GEOLOGY AND SOILS

The geology of the study units consisted predominantly of gneiss and sand of the Quaternary System (Geological survey 2000). Basalt covered the northern part of study unit 5. Quartzite was present in the eastern parts of study unit 6 (Botha undated; Geological Survey 2000).

According to the Geographical Information System (GIS) of the Directorate Resource Technology of the Northern Province Department of Agriculture, soils to the west of the study area are mainly red, massive or weak structured, with a high base status or are less developed. The latter soils often overlay hard or weathering rock with lime present in part. Diverse soils also occur in the study area. Study unit 4 is situated in an area characterised by red, yellow and greyish soils with a high base status. Extensive areas of study unit 5 consist of sand of the Quaternary System (Botha undated).

2.6 CLIMATE

2.6.1 Rainfall

2.6.1.1 LONG-TERM RAINFALL PATTERNS

Official long-term rainfall data was not available for individual study units. Statistics of five official weather stations located in the study area (Figure 2.1) were thus used to obtain an estimation of the rainfall patterns of the study area. Climatic data was obtained from the South African Weather Service[1]. The mean long-term annual (January-December) rainfall is summarised in Table 2.3. A general decline in mean annual rainfall is evident from the south-east to the north-west of the study area, although localised variation confounds the predictability of such a gradient.

Rainfall data from the Mara weather station (1936-1999) is included here to illustrate the monthly distribution of the rainfall in the study area (Figure 2.2). Rainfall occurs mainly during the hot summer months with more than 76 % of the total received from November

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[1] South African Weather Service, Private Bag X097, Pretoria, 0001

Table 2.3 Long term annual rainfall (January-December) of the De Gracht (climn 0763675), Groendraai (climn 0763313), Mara (climn 0722099), Saamboubrug (climn 0763124) and Stolzenfels (climn 0763743) weather stations.

Weather station	**Period**	**Mean (mm)**
De Gracht	1934-1973	370.9
Groendraai	1949-1979	416.8
Mara	1936-1999	442.7
Saamboubrug	1963-1999	338.1
Stolzenfels	1949-1999	328.9

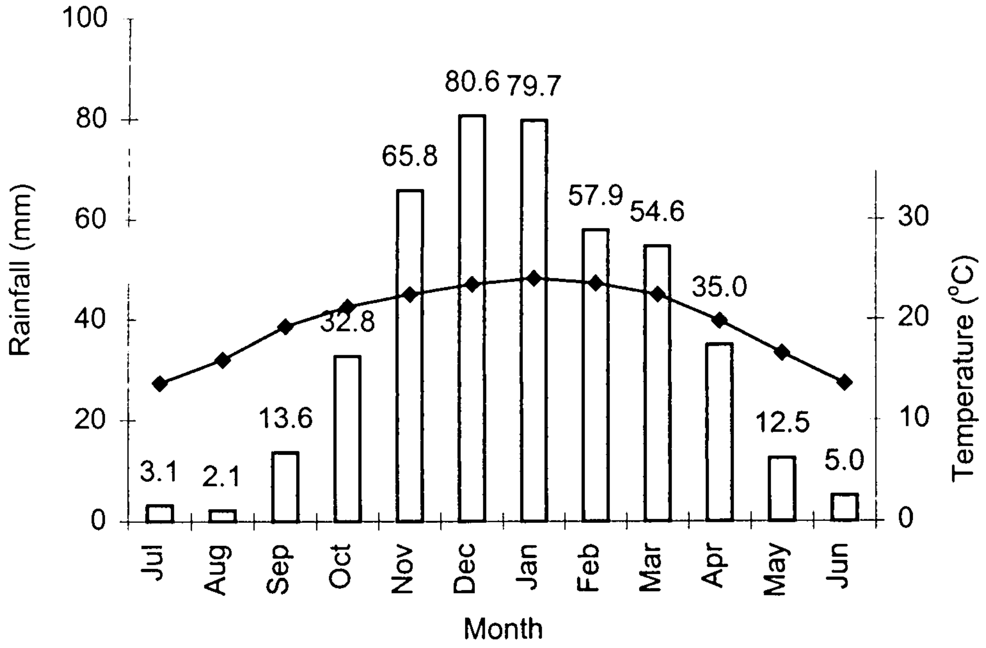

Figure 2.2 The mean monthly rainfall (1936 - 1999) (bars) and mean daily temperature (1960-1999) (line) measured at the Mara weather station.

to March inclusive. The highest mean annual rainfall is received during December (80.6 mm) and January (79.7 mm) (Figure 2.2).

2.6.1.2 RAINFALL DURING THE TRIAL PERIOD

Monthly rainfall was measured at the study units and neighbouring farms from January 1997 to December 1999. Precipitation was measured using ordinary cone-shaped rain gauges, with the exception of study unit 5 where a standard brass rain gauge was used. Rainfall data were available for study units 4, 5, 6, 7 and 8, while data of adjacent farms had to be used in the case of study units 1, 2, and 3.

The monthly rainfall received from January 1997 to December 1999 are presented in Figure 2.3. The mean monthly rainfall calculated for the closest official weather station to a particular study unit is also shown for reference purposes (Figure 2.3).

Rainfall received during the 1997/98 rainfall season was below the long term mean of proximate official weather stations, in spite of a good start during the new season (Figure 2.3). Rainfall received during the 1998/99 rainfall season was in general average to above average (Figure 2.3). The distribution of rainfall over the 1998/99 rainfall season was, however, not typical, and below average rains were received during the latter half of the 1998/99 rainfall season (Figure 2.3). Rainfall was measured during July at study units 4, 5 and 6 during the 1999 dry season. Study unit 4 was the only study unit where rainfall was measured during September 1999. October and November 1999 were generally characterised by above average rainfall (Figure 2.3).

2.6.2 Temperatures

Temperature records were available for only the Mara weather station (1960-1999) and are further discussed to obtain an approximation of the range and seasonal patterns of temperature fluctuations of the study area. Mean daily temperatures peaked in January and reached a low during June (Figure 2.2). The mean daily minimum and maximum temperatures were 18.1^{0}C and 30.3^{0}C and 4.7^{0}C and 22.6^{0}C for December and June respectively. The absolute minimum and maximum temperatures recorded over the period 1960-1999 were –4.2^{0}C and 42.3^{0}C respectively.

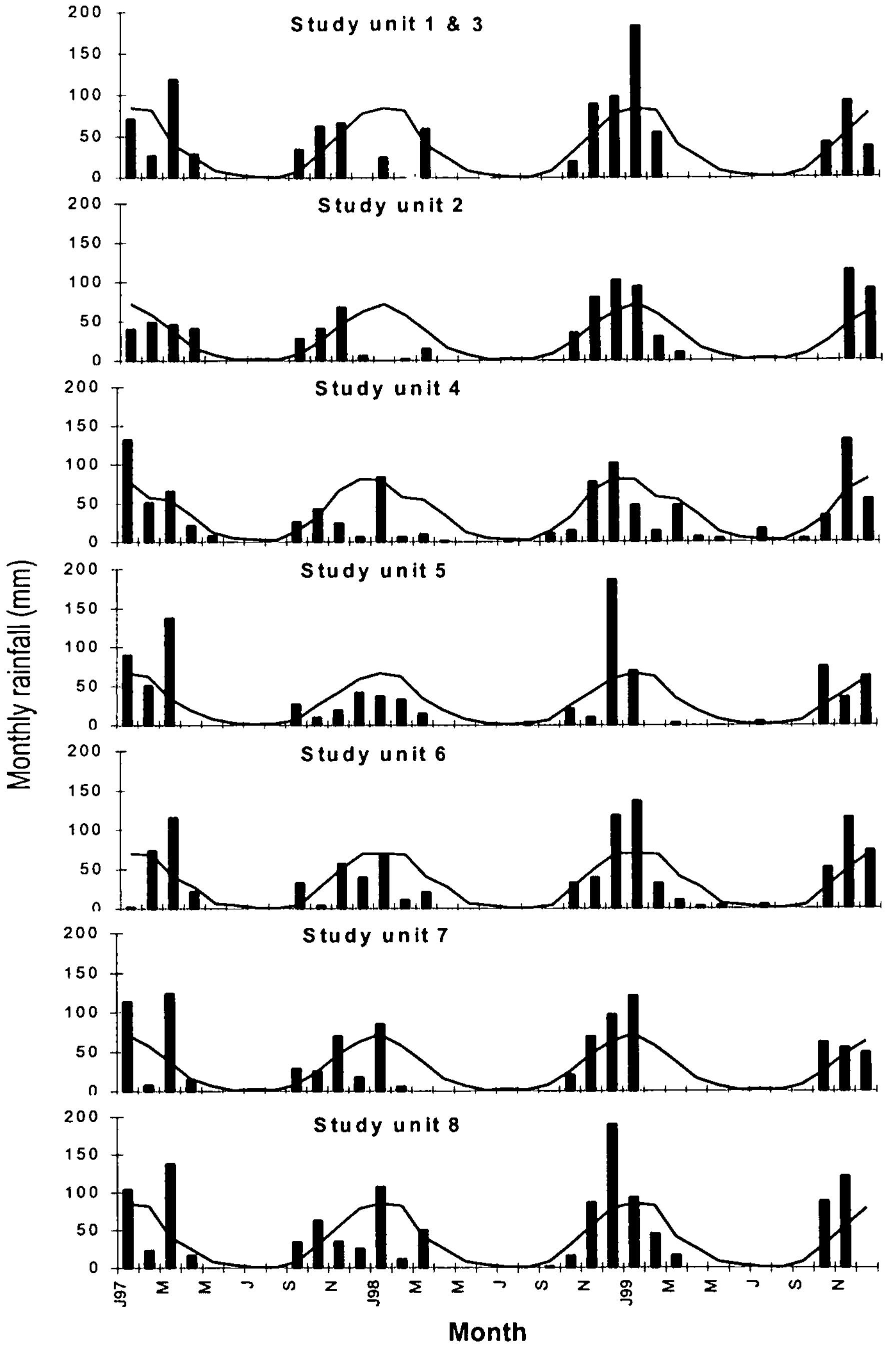

Figure 2.3 Monthly rainfall from January 1997 to December 1999 (bars). Rainfall records of study units 1, 2 and 3 represent records of adjacent farms. Rainfall amounts of study units 4, 5, 6, 7 and 8 represent records measured at the respective study units. Lines represent long-term means for official weather stations (Table 2.3) closest to the study units.

2.6.3 Seasons

Three seasons were identified from the seasonal precipitation and temperature patterns (Figure 2.2). The seasons, arbitrarily chosen, consisted of a wet hot (WH) season from November to the end of April, a dry cool (DC) season over the months of May, June and July, and a dry hot (DH) season from August to the end of October.

2.7 VEGETATION

The vegetation is characterised as a savanna with a well developed woody stratum. The horizontal arrangement of the woody stratum includes open to closed woodland and the vertical structure is mainly low and short (Edwards 1983). Floristically, the study units were located in the Arid Sweet Bushveld (Acocks 1988), or in the Sweet Bushveld as described by Van Rooyen & Bredenkamp (1996).

Woody species that occurred at most of the study units include *Acacia nigrescens, A. tortilis, Dichrostachys cinerea, Combretum apiculatum, C. hereroense* and various *Commiphora* and *Grewia* species. The herbaceous layer was dominated by *Enneapogon cenchroides, Melinis repens, Urochloa mosambicensis, Tricholaena monachne* and species of the *Aristida* and *Eragrostis* genera. Forb species commonly encountered were *Dicoma tomentosa, Monechma divaricatum, Hermstaedtia odorata* and *Tephrosia purpurea.* Abandoned lands in the study area were typically colonised by *Dichrostachys cinerea* and *Acacia tortilis.*

CHAPTER 3

IDENTIFICATION OF HOMOGENEOUS VEGETATION UNITS

3.1 INTRODUCTION

Substantial variation in species composition, production and seasonal availability of the woody layer has been described for different plant communities in the same area (Novellie 1983; Dekker & Smit 1996). This variation can be expected to impact on the utilisation patterns of browse resources by browsers and thus also on the population dynamics of the browsers. Study units were therefore stratified into homogeneous vegetation units according to physiographical and physiognomical differences. The physiography of an area refers to the morphology of the terrain and is determined by differences in topography, slope and aspect (Dekker 1996). The physiography affects the growth conditions for plants and consequently influences their distribution patterns. The physiognomy of an area refers to the growth-form of the vegetation (Kent & Coker 1996).

The objectives of this investigation were:

I. to identify and demarcate homogeneous vegetation units,
II. to determine the sizes of homogeneous vegetation units, and
III. to determine the floristic similarity between homogeneous vegetation units and study units.

3.2 PROCEDURE

3.2.1 Demarcation of homogeneous vegetation units

Study units were stratified into physiographic-physionomic homogeneous units with the aid of black and white stereo-aerial photographs (e.g. Bredenkamp, Deutschländer, & Theron 1993; Bredenkamp & Deutschländer 1995). 1:50 000 scale photographs were used after Dekker & Van Rooyen (1995) and Brown & Bezuidenhout (2000).

Physiographic-physionomic homogeneous units were confirmed and boundaries realigned during field trips.

3.2.2 Size of homogeneous vegetation units

The sizes of homogeneous vegetation units were determined with the aid of an electronic planimeter (Dekker 1996). The relative sizes of homogeneous vegetation units were calculated from three repetitive readings. Relative homogeneous vegetation unit sizes were corrected for actual study unit size (Table 2.1).

3.2.3 Floristic similarity of homogeneous vegetation units

The physiographic-physionomic homogeneous units were floristically classified in order to compare study units on grounds of the similarity in plant species composition. A Two Way INdicator SPecies ANalysis (TWINSPAN) (Hill 1979) was conducted on the quantitative floristic data set (Chapters 4 and 5). The data set consisted of leaf production (dry mass) at peak biomass of woody species and standing crop (dry mass) estimates of herbaceous species (Chapters 4 & 5).

3.3 RESULTS AND DISCUSSION

3.3.1 Homogeneous vegetation unit location and sizes

The limits and location of homogeneous vegetation units are depicted in Figure 3.1. The number of homogeneous units per study unit ranged from three to eight with a mean of 4.9 homogeneous vegetation units per study unit. Homogeneous vegetation unit size varied from 59.2 to 1 810.4 ha with a mean of 317.8 ha per study unit. Table 3.1 summarises the range in homogeneous unit size of the study units.

3.3.2 Floristic similarity

The floristic classification of the homogeneous vegetation units across the study units facilitated a description of the similarity between study unit plant species composition.

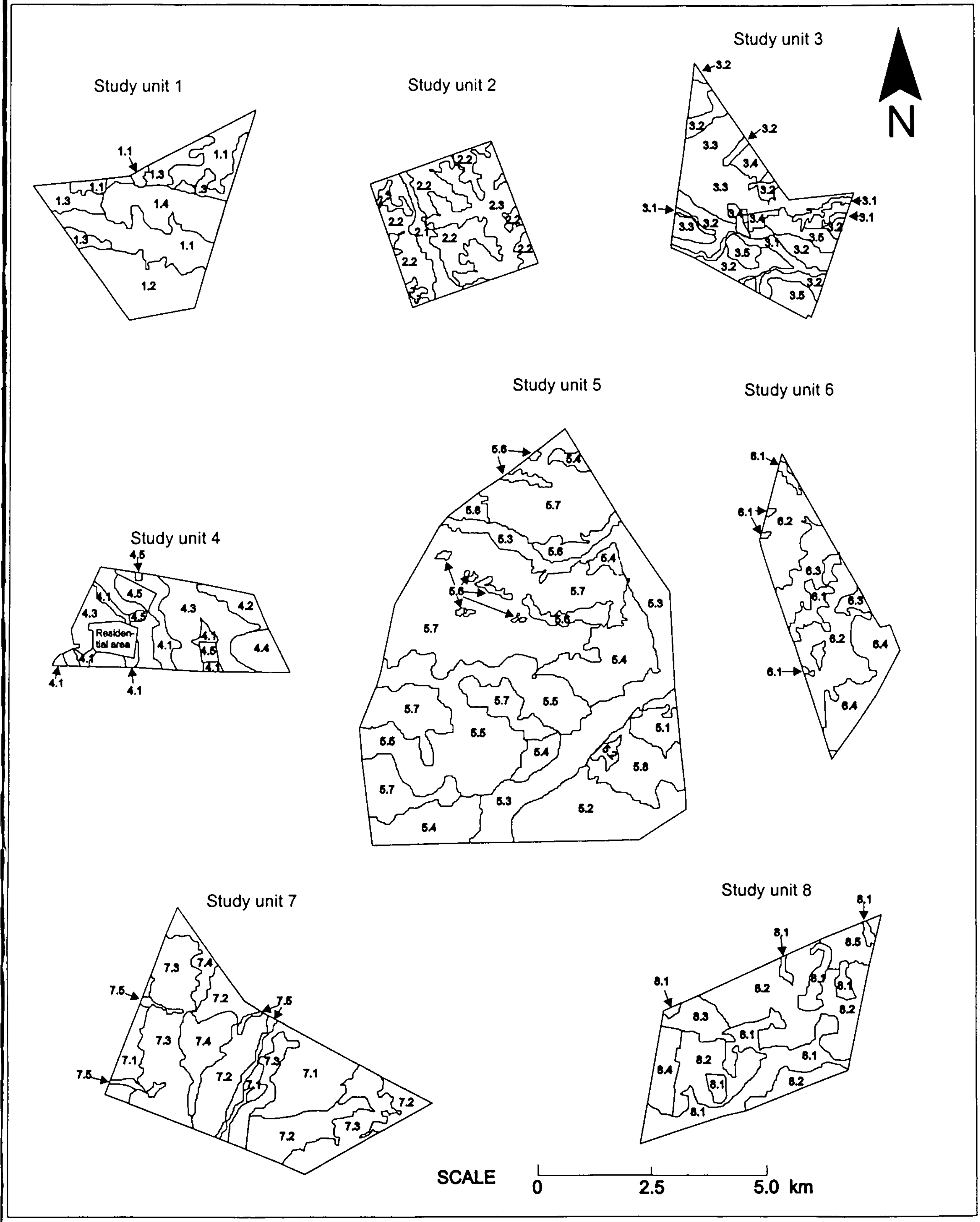

Figure 3.1 The spatial layout of homogeneous vegetation units in the study units redrawn from aerial photographs. The spatial arrangement of the study units to each other is not according to scale.

Table 3.1 The number, range and mean sizes of homogeneous vegetation units per study unit.

Study units	**Number of vegetation units**	**Size (ha)**		
		minimum	**maximum**	**mean**
1	4	220.1	383.5	270.2
2	3	88.3	431.4	289.5
3	5	70.2	395.5	214.0
4	5	75.9	364.3	173.0
5	8	73.5	1 810.4	573.4
6	4	67.8	370.3	187.5
7	5	59.2	639.4	358.6
8	5	73.7	727.9	275.9

Classifying the homogeneous vegetation units floristically instead of calculating a single similarity index for the study units, e.g. that employed by Snyman (1989) to describe the floristic similarity of seven study units, also facilitated the identification of homogeneous areas which were floristically different from other homogeneous vegetation units. These areas might be important from an utilisation point of view due to their distinctive species composition.

The TWINSPAN classification divides homogeneous vegetation units 5.1, 5.2, 5.5 and 5.8 and homogeneous vegetation units 4.1 and 4.5 from other homogeneous vegetation units at the first level of classification (Figure 3.2). Aforementioned homogeneous units of study unit 5, which associated with a sandy substrate, are further separated from those of study unit 4 at the second level of classification. Substantial areas of study unit 1 (homogeneous vegetation units 1.1, 1.3 and 1.4), study unit 3 (homogeneous vegetation units 3.2-3.5) and study unit 8 (homogeneous vegetation units 8.1-8.3 and 8.5) are floristically similar at the third level of classification (Figure 3.2). Likewise homogeneous vegetation units 5.4, 5.6 and 5.7 of study unit 5, 6.1-6.4 of study unit 6 and 7.2, 7.3 and 7.5 of study unit 7 are also floristically similar (Figure 3.2). The largest part of study unit 4 (homogeneous vegetation units 4.2-4.4) is separated from other study units at the second level of classification.

It is concluded that study units 1, 3 and 8 are floristically similar. The non-sand areas of study unit 5, study units 6 and 7 are also similar. Floristically study unit 2 is not grouped with a particular study unit, although floristically corresponding elements are shared with other study units. According to the classification, study unit 4 is floristically the most dissimilar compared to other study units. The sandy areas of study unit 5 are also floristically different compared to other homogeneous vegetation units.

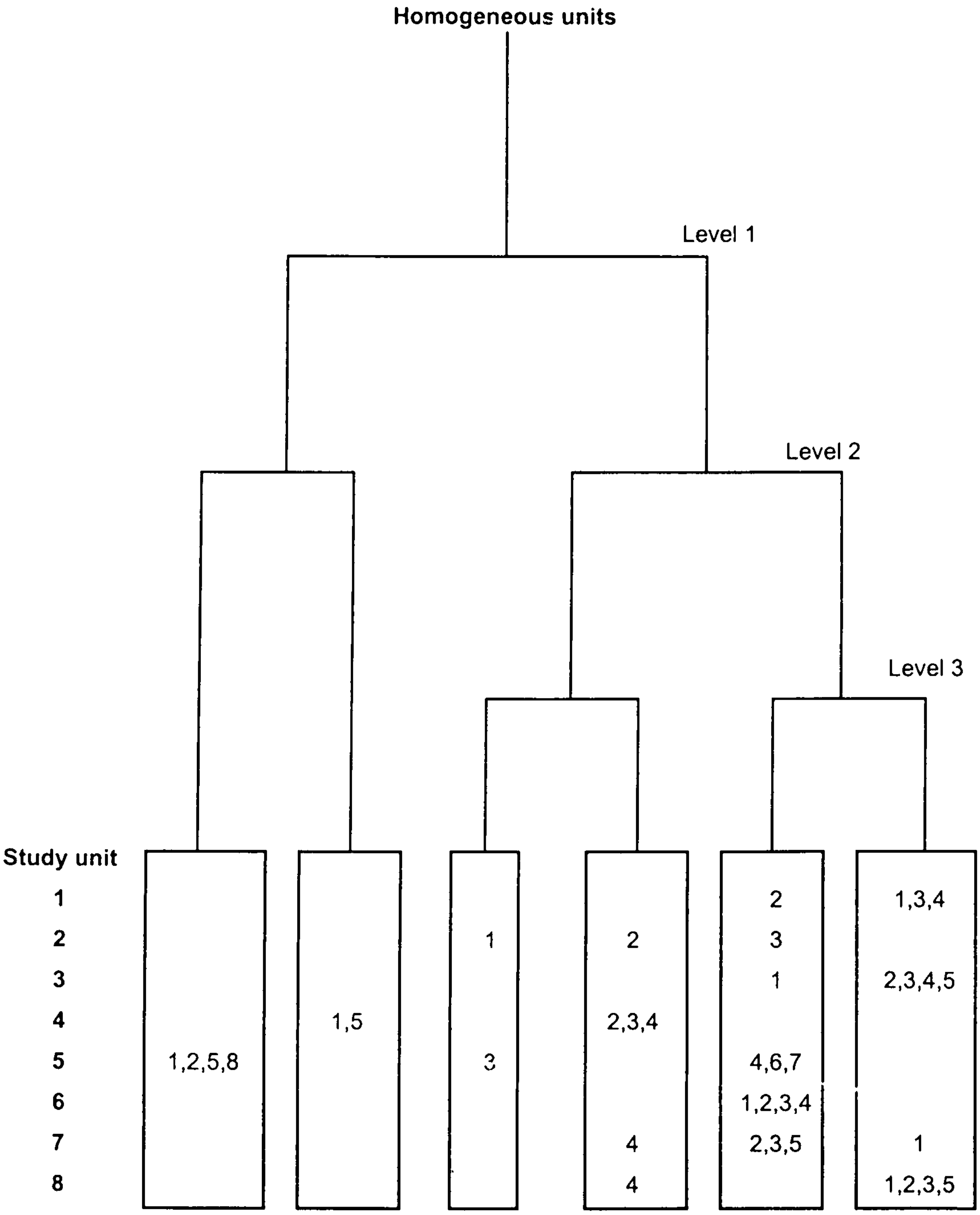

Figure 3.2 A dendrogram illustrating the floristic classification (TWINSPAN) of the homogeneous vegetation units. Homogeneous vegetation units with a similar species composition are vertically arranged.

CHAPTER 4

WOODY BROWSE RESOURCES

4.1 INTRODUCTION

The leaves and shoots of woody plants are the most important components utilised by browsing ungulates (Walker 1980) although fruits and pods (Walker 1980; Owen-Smith 1997; Melville, Cauldwell & Bothma 1999) and flowers (Owen-Smith 1997; Melville *et al.* 1999) are also utilised. The utilisation of browse is influenced, among other factors, by the variation in seasonal availability of browse (Grossman 1994; Dekker & Smit 1996), different browsing heights of animals (Du Toit 1990) and by the complex interaction between browsers and their food supply which is mediated by the chemical and physical attributes of the plants and co-adaptations of the browsing animals (Owen-Smith & Cooper 1987; Cooper, Owen-Smith & Bryant 1988; Bryant, Provenza, Pastor, Reichardt, Clausen & Du Toit 1991b; Bryant, Reichardt & Clausen 1992; Owen-Smith, Robbins, Hagerman 1993; Owen-Smith 1993c).

Plant parts of woody species are differentially accepted by browsers (Haschick & Kerley 1997a; Bryant *et al.* 1991b, Bryant *et al.* 1992, Owen-Smith 1993c). The browser acceptability of a woody species encompasses not only the intrinsic factors of the forage itself but also the circumstances in which the forage is presented to the animal (Meissner, Zacharias & O'Reagain 1999). Palatable species remain acceptable as long as the leaves are retained, while unpalatable species are only consumed when other browse resources are depleted (Owen-Smith & Cooper 1987). The determination of species selection by herbivores should therefore be assessed at peak biomass when all potential woody browse are available. In the study area, it was assumed to coincide with the late wet season before leaf fall of the deciduous species commenced.

The objectives of this study were:

(i) to classify woody species according to browser acceptability, the presence and absence of physical deterrents and the seasonal availability of foliage, and
(ii) to quantify and describe the woody foliage resources within the study units.

4.2 LITERATURE REVIEW

The acceptability of woody plant-parts by browsing ungulates is influenced by nutritional, anti-nutritional and physical factors which differ between different ungulate species and over the seasonal cycle (Owen-Smith 1993c; Haschick & Kerley 1997a). The selection of species by browsers is seldom governed by a single factor but rather by interrelations between chemical factors as well as physical features of plants (Haschick & Kerley 1997b). Nutritional factors which are positively related to plant species or plant-part acceptance by browsing ungulates include: digestibility, soluble carbohydrate content (sugars and starches), the availability of minerals such as phosphorous and magnesium, water content and the presence of aromatic substances (Novellie 1983; Cooper *et al.* 1988; Haschick & Kerley 1997a). Factors negatively associated with browser acceptability include; fibre content, condensed tannin concentration (variable) and the presence of saponins (Novellie 1983; Cooper & Owen-Smith 1985; Cooper *et al.* 1988). Of these factors, the effect of chemical deterrents and the physical attributes of plants (e.g. thorns and spines) have received considerable attention as factors influencing the utilisation of browse by browsing ungulates. These factors will be discussed in the southern African savanna context.

4.2.1 Chemical deterrents of woody plants

Woody plants have relatively high levels of secondary metabolites compared to graminoids (Bernays, Cooper Driver & Bilgener 1989; Bryant *et al.* 1992). This is probably a more important cause of selective feeding by browsers than nutrient or energy content (Palo & Robbins 1991 cited by Bryant *et al.* 1992).

A wide variety of secondary metabolites, which affect the selection of woody plants by mammals, exist (Bryant, Heitkonig, Kuropat & Owen-Smith 1991a; Bryant *et al.* 1992). Secondary metabolites are divided into nitrogen based and carbon based compounds. The type and level of chemical defence depends on the growth and photosynthetic limitations imposed by the environment (Coley, Bryant & Chapin 1985; Bryant *et al.* 1991a; Bryant *et al.* 1991b). Nitrogen based secondary metabolites are more prominent in light limited environments, e.g. forests, where photosynthetic rates are retarded. In nutrient limited soils, plant growth tends to be more restricted by low availability of nutrients than by photosynthetic rates, with the subsequent accumulation of carbohydrates not used in normal growth processes. These surplus carbohydrates are thus available for the synthesis of carbon based metabolites (Coley 1988, Bryant *et al.* 1991b). Woody species associated with nutrient poor soils are generally high in secondary metabolites (condensed tannins) (Owen-Smith & Cooper 1987), although exceptions do exist (Scogings 1998). Scogings (1998) postulated that the investment in chemical deterrents is a function of growth limitation, which is only partly influenced by resource availability. The response of woody plants to water limitation is less clear. An increase in carbon based secondary metabolites usually take place under mild water stress while severe water stress mostly causes lower concentrations (Bryant *et al.* 1991b).

In southern African savanna, which is characterised by growth limitations imposed by nutrient and/or water stress rather than light limitation, research has focused on carbon based secondary metabolites, and tannins in particular. Tannins are high molecular weight polyphenols capable of precipitating proteins and are relatively immobile and apparently metabolically inactive in plants (Coley 1988; Bernays *et al.* 1989; Bryant *et al.* 1991b). Two main classes of tannins are recognised on the basis of their effect on the digestion processes of animals (Bernays *et al.* 1989). Hydrolysable tannins apparently inactivate the digestive enzymes of insect herbivores, but is less effective against mammalian herbivores (Owen-Smith 1993c). Condensed tannins, the most common tannins in vascular plants (Bernays *et al.* 1989), apparently attach to the cellulose and fibre-bound proteins of plant's cell walls, and thereby affect microbial action negatively. In ruminants, retarded microbial action relates to reduced protein and carbohydrate availability in the rumen, although greater post-ruminal digestion and nitrogen absorption may take place (Zucker 1983; Bernays *et al.* 1989). Support is mounting for animals regulating their intake of secondary metabolites such as tannins by a process of post-ingested learning, probably regulated by internal malaise caused by tannins (Du Toit, Provenza & Nastis 1991; Bryant *et al.* 1991b). Condensed tannin concentration of some woody species has been negatively correlated with acceptability ratings of giraffe (Furstenburg & Van Hoven 1993) and kudu during the wet season (Cooper & Owen-Smith 1985) and positively or insignificantly correlated for impala, goats and bushbuck (Cooper & Owen-Smith 1985; Haschick & Kerley 1997b). Browsing ruminants evidently respond to the relative balance in nutrients such as protein content and anti-nutrients such as condensed tannins, instead of to a single chemical factor (Cooper & Owen-Smith 1985; Cooper *et al.* 1988). The inability of giraffe and kudu to tolerate high condensed tannin concentrations, while Boer goats and impala are apparently less affected, has been attributed to the greater dependency of giraffe and kudu on woody browse while impala and goats supplement their diet with substantial amounts of graminoids (Cooper & Owen-Smith 1985).

Evergreen woody species which have long leaf lifetimes often invest in immobile secondary metabolites such as tannins (Coley *et al.* 1985; Coley 1988; Owen-Smith 1993c). The immobile tannin compounds require large initial construction costs, which cannot be reclaimed upon leaf senescence and consequently is more cost effective in long lived leaves (Coley *et al.* 1985; Coley 1988).

Browsers have apparently evolved physiological mechanisms to counter the negative effects of secondary metabolites. Adaptations of browser species to cope with toxic or digesting inhibiting secondary plant metabolites include large parotid glands and adapted livers (Owen-Smith 1997). Kudu have normal sized parotid glands (Robbins, Spalinger & Van Hoven 1995), and probably rely more on detoxification than on the neutralising of secondary metabolites (Owen-Smith 1997). Owen-Smith (1997) concluded that large salivary glands are prominent among forest duikers and giraffe, which are able to consume unripe fruit, rich in astringent tannins. The capacity of detoxification by browsers is limited and intake of toxic substances needs to be regulated to avoid toxic levels (Bryant *et al.* 1991b). Bryant *et al.* (1991b) indicated that browsers usually starve before toxic levels of secondary-metabolite containing browse are ingested. It also follows that chemical-defended species might be intensely browsed provided that the detoxification ability of browsers is not exceeded (Bryant *et al.* 1991b). This might have a bearing on the utilisation of scarce species.

Short-term variation in tannin concentration has been ascribed to browsing by giraffe and the day-night cycle (Furstenburg & Van Hoven 1993). Condensed tannin concentrations have also shown unexplained monthly variation in a number of species at Nylsvley (Owen-Smith 1993c). Owen-Smith (1993c), in his review of browse-browser interactions, concluded that the chemical analysis used and the way concentrations were expressed might have confounded the interpretation of these variations. He proposed that woody species most likely to show increased tannin levels after being browsed, are fast-growing plants on fertile soils. These species are mostly deciduous and would remain leafless during droughts. Evergreen species that are generally high in condensed tannins will thus remain as the principal woody food source available to browsers. The subsequent loss in animal condition and eventually mortalities may be attributed to the effect of the inherent high condensed tannin content of ingested evergreen browse and not to the increased tannin concentration of woody species brought about by browsing (Owen-Smith 1993c).

Contradicting chemical responses of woody plants to utilisation have been reported. An experiment simulating insect defoliation of fast growing, palatable species, such as *Grewia flavescens, Acacia tortilis* and *Dichrostachys cinerea,* has shown an increase in total phenol and condensed tannin concentrations and a reduction in nitrogen and phosphorous concentrations (Bryant *et al.* 1991a). This contrasts with the findings of Du Toit, Bryant & Frisby (1990) who demonstrated that heavily browsed *Acacia nigrescens* trees are associated with lower tannin concentration and increased nutrient levels relative to lightly browsed control trees. This anomaly might, however, be related to the period and level of herbivory. Scogings (1998) postulated that fast growing, palatable species should react variably to short-term herbivory while decreased chemical defences should apply to prolonged, frequent browsing. In slow growing unpalatable species, such as *Burkea africana, Ochna pulcra* and *Euclea natalensis*, the response to simulated insect defoliation results in increased nutrient levels and lower leaf phenol and condensed tannin concentrations (Bryant *et al.* 1991a; Scogings 1998).

4.2.2 Spinescens and intake of browse

Spinescens generally limits food intake rate and has been demonstrated to lower the intake rate of bushbuck (Haschick & Kerley 1997b) and goats (Cooper & Owen-Smith 1986; Gowda 1996; Haschick & Kerley 1997b) in thorn removal experiments. The consumption of woody foliage by kudu, impala and goats has been estimated to be only 1-3 % of the peak leaf biomass for spinescent species, compared to 12-18 % for palatable, deciduous species over the seasonal cycle (Owen-Smith & Cooper 1987).

Kudu, which often include shoot-ends of unarmed species in their diet, reduce their bite size by plucking mostly single leaves of spinescent woody species (Cooper & Owen-Smith 1986). Kudu are apparently unable to compensate for the reduced bite size by increasing their bite rate (Cooper & Owen-Smith 1986). Impala, which have narrower muzzles, have a relative bite size which is less restricted than for kudu, and in general intake rates exceed the estimated daily intake requirements (Cooper & Owen-Smith 1986). Intake rate has been significantly correlated with the acceptability of spinescent species up to a threshold of 2 g minute^{-1} for the larger kudu but is insignificant for impala and goats. Of the spinescent species, hook-thorned species deterred goats and impala more effectively than straight spines or thorns (Cooper & Owen-Smith 1986). Kudu are apparently less affected by hooked thorns while robust straight thorns or spines apparently reduce bite rate, and hence intake rate, more effectively (Cooper & Owen-Smith 1986). The intake of browse by giraffe is apparently minimally affected by thorns (Pellew 1984), although branches with the thorns removed were more often fed on and sustained relatively more damage than control branches in an experiment (Milewski, Young & Madden 1991).

4.3 PROCEDURE

4.3.1 Leaf dry mass estimates

Woody measurements were conducted in randomly placed transects, 4 m x 50 m (200 m^2) in size after Dekker & Smit (1996). A total of 176 transects were completed in the study area. These were placed within the study units according to the number of homogeneous vegetation units identified per study unit (Chapter 3). Table 4.1 indicates the number of transects allocated per study unit and the mean number of transects allocated per homogenous vegetation unit. Transects were orientated with the long axes in a north-south direction. In drainage systems, transects were placed perpendicular to water flow. Disturbances, such as roads and fences, were avoided by placing transects further than 50 m away. The spatial canopies of all rooted, live woody plants encountered within the transects were measured as described by Smit (1989a, 1996) and Smit & Rethman (2000). Canopy measurements were used to calculate the spatial canopy volume that is related to leaf volume and leaf dry mass (Smit 1994; Smit &

Table 4.1 The number of homogeneous vegetation units, the number of transects per homogeneous vegetation unit and the total number of transects per study unit used for the survey of the woody layer (BECVOL).

Study unit	Number of homogeneous vegetation units	Transects per homogeneous vegetation unit	Number of transects
1	4	4.0	16
2	3	4.0	12
3	5	4.0	20
4	5	4.0	20
5	8	6.3	50
6	4	4.5	18
7	5	4.2	21
8	5	3.8	19
Total	**39**	**-**	**176**

Rethman 2000). The measurements of spatial canopies consisted of the following: (1) maximum tree height; (2) height where the maximum canopy diameter occurs; (3) height of first leaves or potential leaf bearing stems; (4) maximum canopy diameter and (5) the base diameter of the foliage at the height of the first leaves. Additional measurements were also recorded in cases where canopies at the maximum canopy diameter and base horizontal plane did not resemble a circle. In these cases, the diameter perpendicular to measurements (4) and (5) were also recorded. The canopies of multi-stemmed species, e.g. *Grewia* species, were treated as single canopies while integrated canopies of different species were measured separately. The following robust forbs were also included in the woody survey: *Solanum gigantium, Psiadia punctulata* and *Vernonia cinerascens*. The woody, tall structure render these species unsuitable for assessment by the double sampling technique that was employed to quantify the herbaceous layer (Chapter 5).

Leaf DM estimates per species per transect were obtained by a modified version of the quantitative descriptive technique of Smit (1989a,b) as described by Smit (1994). This technique estimates the leaf dry mass and leaf volume at peak biomass, based on the relationship between a woody plant's spatial canopy volume and actual leaf dry mass and leaf volume (Smit & Rethman 2000). The technique was incorporated into the BECVOL-model (Biomass Estimates from Canopy VOLume) (Smit 1994) and incorporates regression equations for harvested microphyllous and broad-leaved woody species. Apart from leaf DM production and leaf volume estimates, the BECVOL-model also stratified the leaf DM production into different height strata: below 1.5 m, below 2 m and below 5 m respectively, according to the mean browsing heights of browsers. The height of 1.5 m represents the mean browsing height of impala and Boer goats and 2 m and 5 m the mean browsing heights of kudu and giraffe respectively (Smit 1994). The total leaf production of woody species per study unit was calculated from the leaf production of homogenous vegetation units.

The shrub *Grewia subspathulata* is considered to be a hybrid between *G. monticola* and *G. bicolor,* with morphological features of both species (Coates Palgrave 1996). Individuals that could not be clearly identified as either *G. monticola* or *G. bicolor* in the field were recorded as *G. subspathulata.*

The survey of the woody layer was conducted from January to June 1999.

4.3.2 Sample size

The leaf dry mass production below a height of 2 m was determined per species from ten randomly placed transects in homogeneous vegetation unit 5.5 and 5.7 respectively. Precision was indexed by calculating the Czenkanowski's similarity coefficient which gives a measure of the floristic similarity between two data sets (Kent & Coker 1996; Hardy & Walker 1991; Dekker, Kirkman & Du Plessis 2001). A coefficient value of 0 (0 %) indicates zero similarity while a coefficient value of 1 (100 %) indicates complete similarity. Data used in the analysis consisted of the leaf DM production (< 2 m height) per species for woody plants rooted in one or more transects per homogeneous vegetation unit.

Bootstrapping provides a convenient way to calculate the precision of ecologically meaningful parameters such as similarity indices (Dixon 1993). The bootstrapping procedure as proposed by Dixon (1993) was applied per homogenous vegetation unit and involved the following steps:

(i) The Czenkanowski's coefficient was calculated for the leaf production data of two randomly selected transects from the data bank of ten transects.
(ii) Step (i) was repeated 200 times by replacing the data after calculation and randomly selecting two different transects from the data bank per cycle.
(iii) The same procedure as described above was executed for two sets of data, consisting of the production data of two transects combined. This was repeated 200 times. Data was replaced after calculations.
(iv) Step (iii) was repeated for three, four and five transects combined.
(v) Mean similarity (%) was plotted against the number of transects.

4.3.3 Utilisation frequencies of woody species

Plant based utilisation frequencies, the relative number of utilised plants to unused plants, were calculated for abundant woody species in the study area at the end of the growing season (April-May 1999). Utilisation frequencies were recorded in 1 600 m^2 –

2 000 m^2 belt transects. The larger transects (2 000 m^2) were used to compensate for the lower number of observations in low woody-density plots. Two transects were conducted per study unit, which were randomly placed in different homogeneous vegetation units. All woody canopies taller than 0.8 m were assessed within transects from a fixed point per plant. The assessment was restricted to the 0.8 - 2 m above ground horizontal stratum, which is assumed to represent the preferred browsing height of kudu. The following utilisation categories were noted per plant: (1) not utilised; (2) only leaves utilised; (3) shoots (including leaves) utilised and (4) extensively utilised. Category (3) was allocated if a definite cut surface of the shoot-end as caused by large browsers was observed. Category (4) was allocated to cases where more than half of the shoot-ends in the canopy observation area was assessed as utilised.

4.3.4 Dry season leaf retention

Subjective observations of the leaf phenology of woody species were recorded over the dry seasonal cycle of 1999. Species were classified according to the availability of green foliage recorded at seven regular time intervals from May 1999 to December 1999 in the study units. Green foliage was considered available if it was estimated that more than half of the individuals of a species across study units still had green foliage. Woody species were classified into five leaf retention classes. Retention class 1 species displayed early deciduousness while class 5 species, the 'evergreen' species, retained at least some green foliage throughout the dry season of 1999. Classes 2-4 were allocated to species displaying leaf retention periods falling between class 1 and class 5 species.

4.4 STATISTICAL ANALYSIS

The Chi-square test was applied to test for significant differences in the utilisation frequencies of woody species in the study area.

Simple regression analysis and stepwise variable selection analysis (Statgraphics 1991) were applied to determine if the frequency of woody plant use per study unit was related to the stocking rates of different browsing ungulate species. Mean utilisation frequency per study unit was calculated from the utilisation frequencies of all woody plants observed in the two transects conducted per study unit. For the purpose of this analysis, the stocking rate was expressed as the woody leaf DM production (< 2 m height) available per browser unit (BU) for the different browsing species that occurred in the study area. Browser units were calculated per study unit from the helicopter counted game numbers and the relative energy consumption of the different browsing species corrected for the grass: browse proportion in the diet (Chapter 6).

The leaf: shoot utilisation ratios of unarmed and spinescent species were analysed in order to test the hypothesis that unarmed species suffer more damage to leaf-supporting shoot-ends than spinescent species. The ratios were not normally distributed and the Mann-Whitney U Test was applied to test for significant median leaf: shoot utilisation ratio differences.

4.5 RESULTS AND DISCUSSION

4.5.1 Optimum sample level and precision

The relationship between precision and increasing sample size is often curvilinear (Westfall, Van Staden & Panagos 1987; Hardy & Walker 1991; Stuart-Hill 1995). It follows that an increase in sample size, thus sampling effort, beyond an inflection point results only in a marginal improvement in precision. The relationship between sample size and precision as indexed by floristic similarity in leaf production is displayed in Figure 4.1. For the two areas surveyed, an inflection point in the relationship between similarity and number of transects occurred between a sampling effort of 2 and 3 transects. This means that sampling beyond 3 transects per homogenous vegetation unit improves the precision in terms of the floristic similarity in leaf production only marginally. The progressive improvement in similarity (mean % of the homogeneous vegetation units) relative to the previous sample size was as follows: 1 – 2 transects = 12.0 %, 2 – 3 transects = 6.2 %, 3 - 4 transects = 3.8 % and 4 - 5 transects = 3.6 % improvement (Figure 4.1). It is concluded that a sample size of 3 transects per homogeneous vegetation unit provides the most efficient effort to precision ratio under the study conditions. The mean similarity (n=200), if the data of three transects were combined, amounted to 45.4 and 49.4 % for homogeneous vegetation unit 5.5 and 5.7

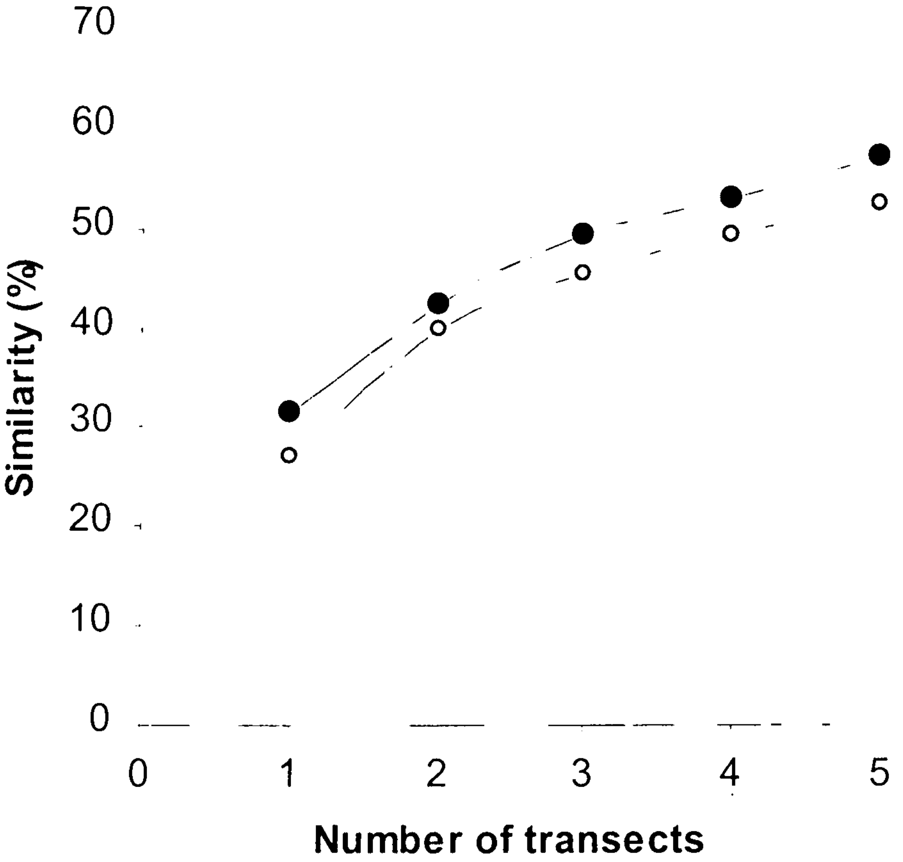

Figure 4.1 Relationship between mean similarity (%) in foliage DM contribution of woody species and the number of transects involved. Closed circles represent data from homogeneous vegetation unit 5.7 and open circles data from homogeneous vegetation unit 5.5.

respectively. If four transects were combined, similarity increased to 49.4 and 53.0 % for the homogeneous vegetation units respectively (Figure 4.1).

4.5.2 Leaf production

The total leaf DM production per study unit ranged from 522.3 kg ha^{-1} to 1 268.3 kg ha^{-1} with a mean of 926.7 kg ha^{-1} (Figure 4.2). The leaf DM production up to a height of 5 m ranged from 517.2 kg ha^{-1} to 1 230.5 kg ha^{-1} (mean 873.3 kg ha^{-1}) and contributed between 92.4 % and 99.0 % of the total leaf DM production. The leaf DM production up to a height of 2 m ranged from 362.1 kg ha^{-1} to 695.1 kg ha^{-1} (mean 504.8 kg ha^{-1}). This stratum contributed between 38.7 % and 74.2 % of the total leaf DM production. The leaf DM production of the shrub layer, 0-1.5 m stratum, ranged from 260.7 kg ha^{-1} to 507.1 kg ha^{-1} (mean 374.7 kg ha^{-1}) and contributed between 25.8 % and 56.0 % of the total leaf DM production (Figure 4.2). Variation in the leaf DM production of the different height strata was the lowest (<2 fold) for the shrub layer (0-1.5 m) and increased progressively in higher strata (Figure 4.2).

The 0 - 2 m height stratum was assumed to coincide with the browsing height of kudu (Wentzel 1990), and are consequently elaborated on here. General floristic patterns in terms of leaf DM production across study units were in order of importance: Tiliaceae (*Grewia* spp.), Combretaceae (*Combretum* spp. and *Terminalia* spp.), Burseraceae (*Commiphora* spp.) and Mimosaceae (*Acacia* spp., *Albizia* spp. and *Dichrostachys cinerea*). Prominent species, contributing five percent or more on average across study units, consisted *of Grewia monticola, G. bicolor, Terminalia prunioides, G. flavescens, Combretum apiculatum* and *Dichrostachys cinerea* (Table 4.2).

4.5.3 Acceptability

The Chi-square test, applied to test for variation between species, indicated that species were selectively utilised (n=30, P<0.001). Woody species were arbitrarily classified as follows: utilisation frequency values < 0.5 as 'avoided', 0.5 - 0.75 as 'intermediate acceptable' and species with utilisation frequencies > 0.75 as 'highly acceptable'. Unarmed species showing high utilisation frequencies (> 0.75) consisted of *Maerua parvifolia, Spirostachys africana, Boscia albitrunca, Cordia monoica, Combretum*

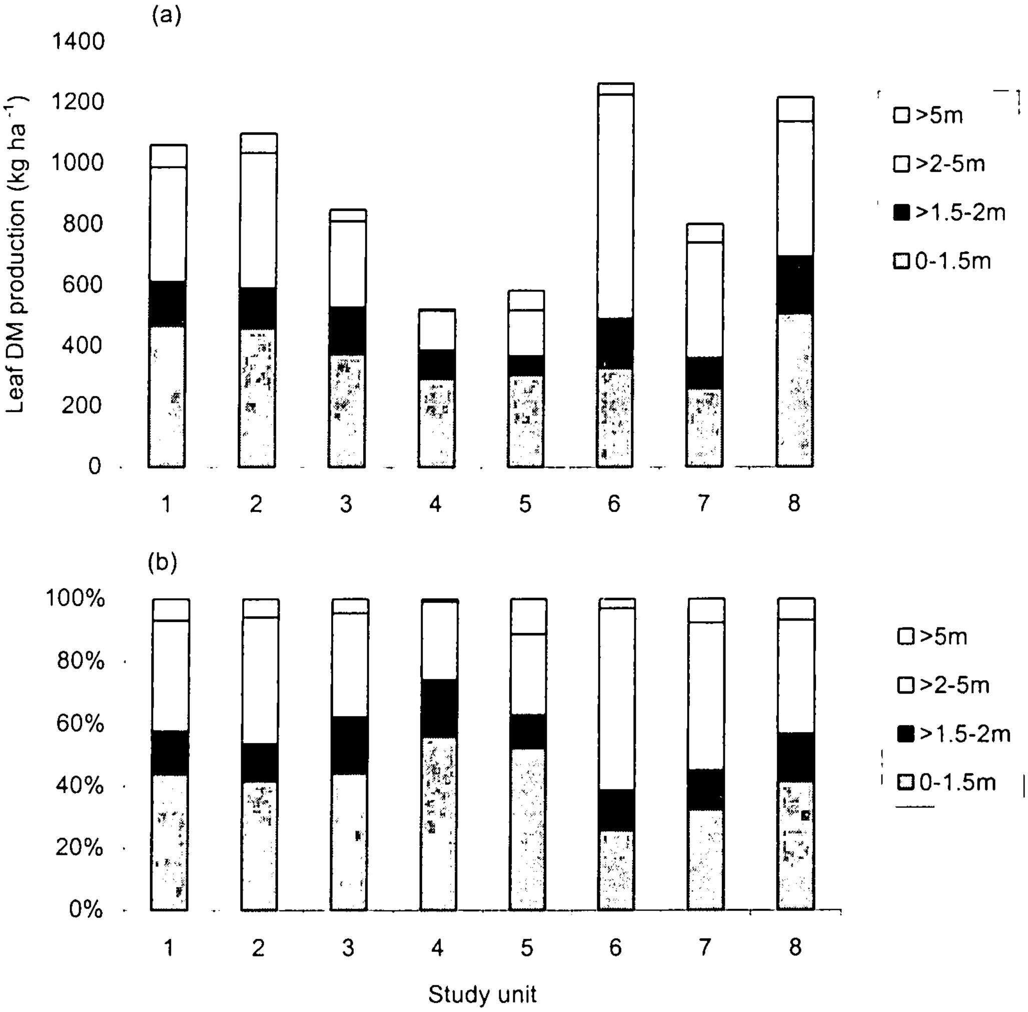

Figure 4.2 A comparison of study units in terms of (a) the leaf DM production of the different height strata and (b) the relative contribution of the leaf DM production of the different height strata.

Table 4.2 Leaf DM production (kg ha^{-1}) below 2 m of woody species per study unit.

Species	**Study units** **1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**Mean**
Grewia monticola	99.2	124.2	110.2	70.7	22.5	64.0	61.6	129.8	**85.3**
Grewia bicolor	127.1	104.5	61.6	53.3	33.0	68.7	29.4	93.3	**71.4**
Terminalia prunioides	136.4	70.0	102.4	0.0	44.4	54.3	84.4	30.6	**65.3**
Grewia flavescens	41.7	14.1	49.7	5.4	36.7	23.9	11.1	204.6	**48.4**
Combretum apiculatum	46.9	59.1	40.6	20.6	1.8	18.5	15.2	53.0	**32.0**
Dichrostachys cinerea	8.4	37.6	51.7	17.9	8.6	2.1	19.0	65.3	**26.3**
Commiphora mollis	15.2	47.6	10.2	3.6	1.4	12.9	27.9	30.1	**18.6**
Acacia tortilis	4.4	17.5	12.0	64.0	22.2	1.8	12.6	6.5	**17.6**
Commiphora pyracanthoides	44.7	12.5	12.6	36.8	22.9	5.7	4.1	0.5	**17.5**
Grewia flava	18.3	8.9	19.7	31.1	25.0	8.5	14.6	2.6	**16.1**
Grewia subspathulata	21.8	27.6	6.1	9.4	10.3	7.5	16.4	26.2	**15.7**
Commiphora marlothii	0.0	0.0	0.0	0.0	0.0	100.8	0.0	0.0	**12.6**
Cordia monoica	6.0	0.0	13.3	0.0	4.9	40.1	0.0	2.0	**8.3**
Acacia nebrownii	0.0	35.9	0.0	0.0	16.9	0.0	0.0	0.0	**6.6**
Commiphora glandulosa	7.3	7.6	16.7	7.6	1.4	4.4	3.2	1.7	**6.2**
Acacia mellifera	0.0	6.3	0.0	0.0	39.5	0.0	3.7	0.0	**6.2**
Acacia nigrescens	7.6	8.3	6.8	0.0	1.0	2.7	6.3	1.8	**4.3**
Cissus cornifolia	0.3	0.0	0.7	0.0	0.0	0.0	9.3	23.3	**4.2**
Commiphora africana	4.2	0.4	0.2	16.1	1.7	6.1	2.5	0.2	**3.9**
Acacia erubescens	6.6	0.0	6.3	0.0	0.0	11.9	0.6	1.6	**3.4**
Grewia villosa	4.8	2.1	1.1	0.0	8.7	3.1	0.9	2.9	**2.9**
Commiphora viminea	0.0	0.0	0.0	0.0	0.0	23.3	0.0	0.0	**2.9**
Maerua parvifolia	5.7	0.9	0.4	0.0	4.2	0.7	8.2	0.0	**2.5**
Ehretia rigida	0.4	0.0	0.8	13.3	1.4	0.2	3.0	0.0	**2.4**
Lannea schweinfurthii	0.3	0.3	0.0	0.0	0.0	1.3	4.2	13.2	**2.4**
Acacia grandicornuta	0.0	0.0	0.5	0.0	5.1	0.7	12.4	0.0	**2.3**
Rhigozum zambesiacum	0.0	0.0	0.0	0.0	18.1	0.0	0.0	0.0	**2.3**
Boscia albitrunca	0.3	0.3	0.2	14.1	0.4	0.0	0.1	0.0	**1.9**
Phaeoptilum spinosum	0.0	5.1	0.0	1.5	8.5	0.0	0.0	0.0	**1.9**
Acacia senegal var. *leiorhachis*	0.0	0.0	0.0	0.0	0.0	13.4	1.2	0.0	**1.8**
Acacia nilotica	0.0	0.0	0.0	13.2	0.0	0.0	0.0	0.0	**1.7**
Vernonia cinerascens	0.0	0.2	0.0	0.0	5.7	2.9	0.0	0.0	**1.1**
Solanum gigantium	1.2	0.0	0.0	0.0	3.2	0.7	3.2	0.0	**1.0**
Sterculia rogersii	0.1	0.0	0.0	0.0	1.1	3.9	2.5	0.0	**0.9**
Ochna inermis	0.0	0.0	0.0	0.0	0.0	5.3	1.7	0.0	**0.9**
Canthium setiflorum	0.0	0.0	0.0	6.3	0.0	0.0	0.0	0.0	**0.8**
Sclerocarya birrea	0.0	0.0	0.8	0.0	0.6	0.0	2.0	0.2	**0.4**
Asparagus species	0.9	0.0	0.2	0.9	0.3	0.0	0.0	1.1	**0.4**
Salvadora australis	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	**0.4**
Albizia harveyi	0.0	0.0	0.6	0.0	0.0	0.0	0.0	2.5	**0.4**
Plectroniela armata	0.0	0.0	0.0	0.0	2.6	0.0	0.0	0.0	**0.3**
Ximenia americana	0.0	0.2	0.6	0.0	0.6	0.0	0.0	0.9	**0.3**

Table 4.2 (Continue).

Species	Study units								
	1	2	3	4	5	6	7	8	Mean
Gymnosporia buxifolia	0.0	0.0	0.6	0.0	0.9	0.0	0.4	0.0	**0.2**
Combretum mossambicensis	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**0.2**
Flueggea virosa	0.0	0.0	1.0	0.0	0.1	0.0	0.3	0.3	**0.2**
Psiadia punctulata	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**0.2**
Markhamia acuminata	1.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4	**0.2**
Strychnos madagascariensis	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	**0.2**
Bauhinia petersiana	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	**0.2**
Anisotes rogersii	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	**0.1**
Euclea natalensis	0.2	0.0	0.8	0.0	0.1	0.0	0.0	0.0	**0.1**
Gymnosporia senegalensis	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	**0.1**
Ehretia amoena	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.8	**0.1**
Euclea divinorum	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	**0.1**
Terminalia sericea	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	**0.1**
Acacia permixta	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	**0.1**
Acacia erioloba	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	**0.1**
Ziziphus mucronata	0.0	0.3	0.0	0.4	0.0	0.0	0.0	0.0	**0.1**
Diospyros lycioides	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	**0.1**
Albizia brevifolia	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	**0.1**
Albizia anthelmintica	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	**0.1**
Vangueria infausta	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	**0.1**
Spirostachys africana	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	**0.1**
Ozoroa species	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	**0.0**
Rhus guensis	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	**0.0**
Lonchocarpus capassa	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	**0.0**
Ormocarpum trichocarpum	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	**0.0**
Catophractes alexandri	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	**0.0**
Schotia brachypetala	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	**0.0**
Combretum imberbe	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	**0.0**
Total	**614.3**	**591.6**	**529.1**	**387.6**	**367.8**	**491.2**	**362.1**	**695.1**	**-**

mossambicense, Ehretia rigida, Terminalia prunioides, Cissus cornifolia, Ochna inermis, Combretum apiculatum and *Grewia flavescens* (Table 4.3). Species showing intermediate utilisation values (0.5 - 0.75) comprised of *Solanum gigantium* (robust forb), *Canthium setiflorum, Commiphora mollis* and *Grewia flava.* The shrub species, *Grewia bicolor, G. monticola* and the robust forb, *Psiadia punctulata,* had low utilisation frequency values (< 0.5) (Table 4.3). Species with fewer than 20 observations in total were classified according to wet season acceptance values derived for kudu in the Kruger National Park (Novellie 1983) and Nylsvley (Owen-Smith & Cooper 1987; Owen-Smith 1993; Owen-Smith *et al.* 1993). The work of Taylor & Walker (1978) and the species review of Walker (1980) were also consulted (Appendix A).

A positive relationship between the stocking rate of browsers and the utilisation frequency of woody plants in an area is to be expected. Woody plants in areas that support large numbers of browsing herbivores would be frequently utilised compared to woody plants in areas that support low numbers of browsing herbivores, where the woody vegetation would be infrequently utilised. Relationships between the utilisation frequency of all woody plants and stocking rates of browsing ungulate species in the study units were, however, insignificant ($P>0.05$). Significant relationships were established if the contribution of the species classified as 'avoided' (Appendix A) in both utilisation frequency and stocking rate calculations were excluded from the calculations. A significant, negative relationship was established for total browser stocking rate ($r=-0.88$, $P<0.05$) (Figure 4.3a). Single browsing ungulate species were not significantly related, but a combination of the stocking rates for kudu and eland was significant ($r=-0.79$, $P<0.05$) (Figure 4.3b). A stepwise variable selection analysis selected only kudu ($P<0.05$) and eland ($P<0.05$) stocking rate variables ($r^2=0.86$). This suggests that kudu and eland are mainly responsible for the observed utilisation patterns of the highly acceptable and intermediate acceptable woody species in the study area. This is to be expected, as the utilisation assessment is restricted to the preferred browsing height of kudu (Du Toit 1990), and probably also eland. Kudu attained the highest stocking rates (BU 100 ha^{-1}) of the browsing ungulate species in the study area and the observed utilisation patterns probably reflect their preferences the closest (Chapter 6).

Table 4.3 Plant based frequency of utilisation of physically armed and unarmed woody species and the ratio of observations where only leaves were utilised to observations where shoot-ends were utilised (values in brackets indicate one standard deviation calculated between study units).

Class	**Species**	**(n)**	**Utilisation frequency**	**Leaves : Shoot-ends**
Armed	*Plectroniella armata*	20	0.90	0.06
	Commiphora africana	29	0.79 (0.42)	0.21
	*Phaeoptilum spinosum**	65	0.75 (0.03)	0.11
	Asparagus spp.	25	0.72 (0.49)	0.20
	Acacia erubescens	76	0.67 (0.15)	0.70
	Commiphora pyracanthoides	152	0.66 (0.13)	1.08
	Acacia grandicornuta	46	0.65 (0.40)	2.00
	*Dichrostachys cinerea**	197	0 63 (0.18)	0.66
	Acacia nebrownii	57	0.61 (0.34)	0.35
	Acacia tortilis	127	0.59 (0.14)	2.04
	Acacia mellifera	39	0.56 (0.36)	2.14
	Acacia nigrescens	95	0.38 (0.35)	0.33
Unarmed	*Maerua parvifolia**	56	1.00 (0.0)	0.04
	*Spirostachys africana**	21	0.95	0.22
	*Boscia albitrunca***	37	0.95 (0.02)	0.09
	*Cordia monoica**	50	0.92 (0.05)	0.08
	*Combretum mossambicense***	20	0.90 (0.07)	0.19
	*Ehretia rigida***	96	0.89 (0.10)	0.12
	*Terminalia prunioides**	370	0.85 (0.10)	0.11
	Cissus cornifolia	20	0.85 (0.25)	0.13
	Ochna inermis	33	0.85	0.33
	*Combretum apiculatum**	315	0.83 (0.10)	0.03
	*Grewia flavescens**	239	0.78 (0.13)	0.02
	Solanum gigantium	35	0.71 (0.25)	0.19
	Canthium setiflorum	20	0.70 (0.28)	0.17
	Commiphora mollis	45	0.64 (0.35)	0.00
	Grewia flava	215	0.56 (0.23)	0.22
	Grewia bicolor	439	0.48 (0.20)	0.09
	Grewia monticola	623	0.48 (0.25)	0.11
	Psiadia punctulata	66	0.11	0.00

* Occasionally heavily utilised

** Frequently heavily utilised

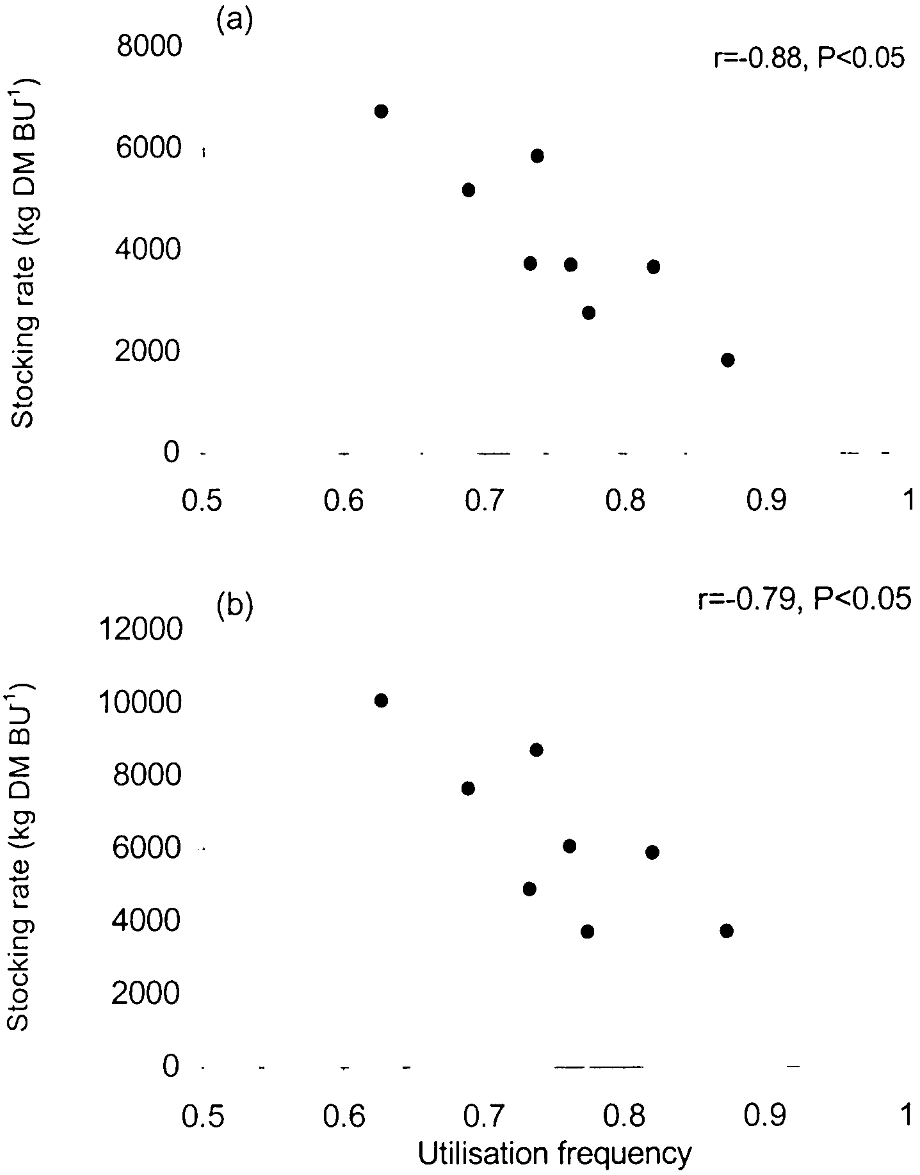

Figure 4.3 The relationships between (a) total browser stocking rate in terms of leaf DM production of the highly acceptable and intermediate acceptable species per browser unit (BU_{total}) and the utilisation frequency of highly acceptable and intermediate acceptable woody species and (b) the combined stocking rate of kudu and eland in terms of leaf DM production of the highly acceptable and intermediate acceptable species per browser unit ($BU_{kudu} + BU_{eland}$) and the utilisation frequency of highly acceptable and intermediate acceptable woody species in the study area.

The plant based acceptability ratings of this study are consistent with the wet season ratings based on direct observation of tamed kudu at Nylsvley (Owen-Smith & Cooper 1987). Common species to both studies are *Grewia flavescens* classified as preferred, *Acacia* species as intermediate to moderately acceptable, and *G. monticola* and *G. bicolor* as avoided. The only species with contradicting acceptability ratings is *Dichrostachys cinerea*, which was favoured at Nylsvley (Owen-Smith & Cooper 1987) and in the Kruger National Park (Owen-Smith & Novellie 1982). In this study it is assessed as intermediate acceptable, and occasionally heavily utilised (Table 4.3).

Woody plant families follow distinctive patterns in phenolic chemistry. This might influence the acceptability of a species by browsers (Owen-Smith 1993c). The highest leaf concentration of condensed tannins were recorded in species in the Caesalpiniaceae (*Schotia brachypetala, Burkea africana*), Anacardiaceae (*Ozoroa paniculosa, Sclerocarya birrea*) and Ebenaceae (*Euclea* spp.) families. This pattern was especially evident for evergreen species. Species of the Combretaceae are generally high in total phenolic substances but low in condensed tannin concentrations. *Combretum hereroense* was an exception. Both *C. mossambicense* and *C. apiculatum* had high acceptance values in this investigation. Species that were palatable in spite of high-condensed tannin concentrations were *Lannea schweinfurthii* (Anacardiaceae) and *Gymnosporia buxifolia* (Celastraceae). These exceptions, coupled with examples of species that are unpalatable despite of low leaf phenolic contents, suggests the presence of unidentified chemical deterrents (Owen-Smith 1993c). Species of the Mimosaceae and Papilionaceae families generally have low levels of phenolics, with the exception of *Acacia nilotica* and *A. karroo* (Owen-Smith 1993c).

Of the spinescent species, members of the Mimosaceae family showed utilisation values < 0.75 in this study. This is consistent with the findings of Owen-Smith & Cooper (1987) who assessed *Acacia* spp. as intermediately to moderately acceptable by kudu in their study. The shrub species *Plectroniella armata, Commiphora africana* and *Phaeoptilum spinosum*, though armed with spines, were frequently accepted (utilisation values > 0.75). In the cases of *Plectroniella armata* and *Commiphora africana,* this might be linked to the comparatively large leaf size, which allows high intake rates compared to the fine leaves of *Acacia* species.

According to a Mann-Whitney U Test (Statgraphics 1991) spinescent species had a highly significant ($P<0.001$) higher median leaf: shoot ratio than unarmed species ($Z = -3.30$, $n=30$), indicating that unarmed species suffered more frequent damage to shoot-ends than did spinescent species. This observation supports the view of Novellie (1983) and Cooper & Owen-Smith (1986) that larger browsers such as kudu include shoot-ends when browsing on unarmed plants and plucks mainly single leaves from spinescent plants. The BECVOL-model estimates only the foliage production of woody plants, thus underestimates the contribution of shoot-ends to the diet of browsing ungulate species such as kudu. The inclusion of the supporting stem material by browsing kudu can be substantial, and Owen-Smith & Cooper (1989) estimated that stem material contributes up to 20 % of the woody DM ingested by kudu at Nylsvley.

Taylor & Walker (1978) and Novellie (1983) reported on a high utilisation of scarce species by browsing ungulates. This was also observed in the study area where utilisation frequencies > 0.9 were calculated for scarce unarmed species. These species contributed on average less than one percent of the total foliage production (< 2 m height), and included *Maerua parvifolia, Spirostachys africana, Boscia albitrunca, Cordia monoica* and *Combretum mossambicense.* Individuals of these species were also hedged (shrubs) or showed a distinctive browse line (trees) (Table 4.3). This pattern did not hold for all scarce species as some species were allocated intermediate and low acceptance ratings in spite of their scarcity.

The woody species *Terminalia prunioides, Combretum apiculatum* and *Grewia flavescens* were all abundant (Table 4.2), showed high utilisation frequencies (Table 4.3) and had either single leaves or leaf clusters which are thought to facilitate high intake rates. Browse of these species probably constitutes the staple diet of kudu during the wet season in the study area. Species classified as staple diet species at Nylsvley consist of *Grewia flavescens, Vitex rehmannii, Dichrostachys cinerea, Diospyros lycioides, Combretum zeyheri* and *Combretum molle* (Owen-Smith & Cooper 1989), and *Acacia nigrescens, Combretum apiculatum* and *Combretum hereroense* in the Kruger National Park (Novellie 1983).

The leaf DM production (< 2 m height) of the different acceptability classes per study unit is displayed in Figure 4.4. The leaf DM production of species for which no acceptability

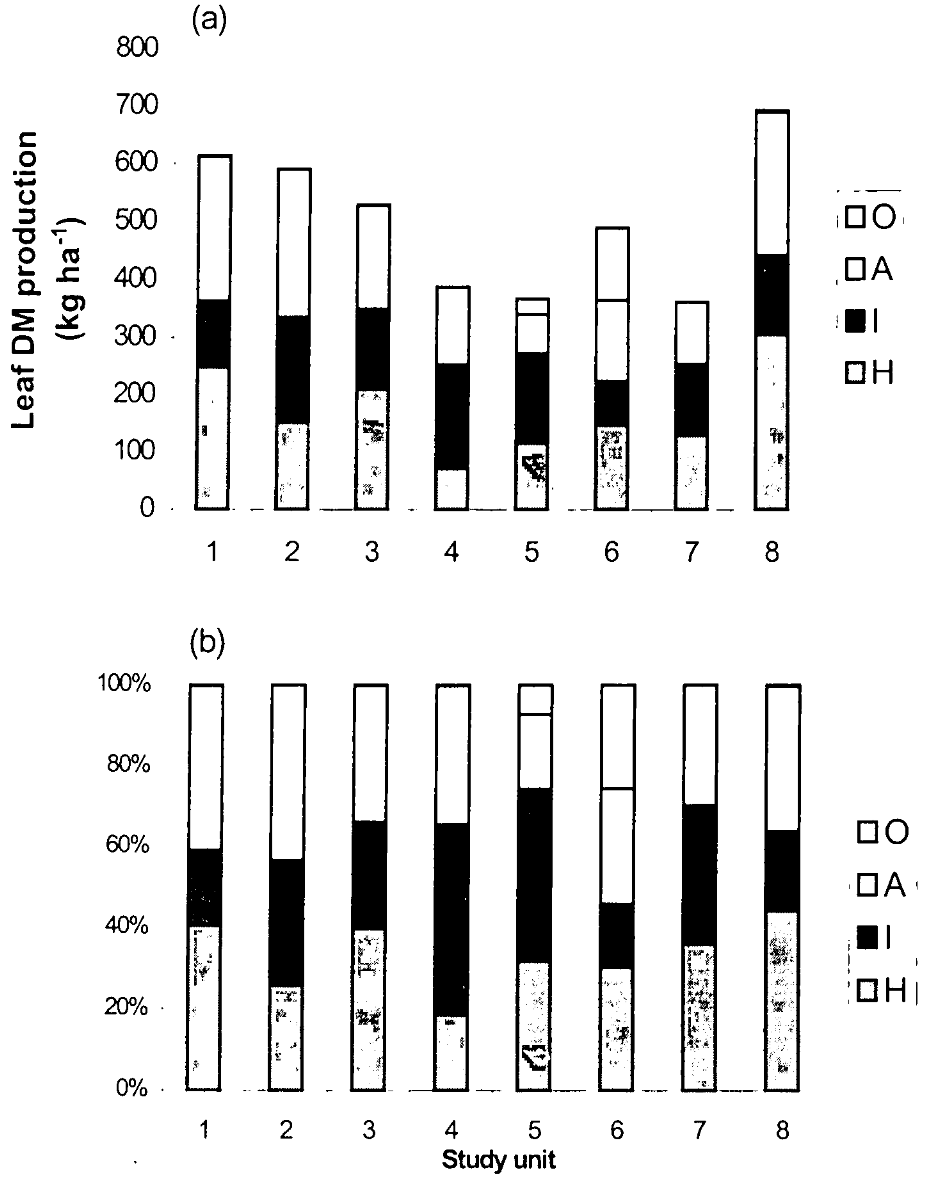

Figure 4.4 A comparison of study units in terms of (a) the leaf DM production (<2 m height) of the acceptability classes and (b) the relative contribution of the leaf DM production of the acceptability classes (H – highly acceptable class, I – intermediate acceptable class, A – avoided class, O – other species for which no acceptability ratings exist).

ratings existed amounted to 7.3 % and 25.6 % of the total (< 2 m height) at study units 5 and 6 respectively (Figure 4.4). Species with no acceptability ratings, which contributed substantially to the leaf DM production below 2 m height at these study units, included *Rhigozum zambesiacum* at study unit 5 and *Commiphora marlothii* and *C. viminea* at study unit 6. Study units 1, 2 and 8 were associated with a relatively large contribution (35.9 – 43.3 %) of 'avoided' species (Figure 4.4). This was linked to the relatively high contribution of the *Grewia bicolor, G. monticola* and *G. subspathulata* species in these study units (Table 4.2). Conversely, study units associated with a relative low leaf DM production (< 2 m height), study units 4, 5 and 7, tend to have a relatively high contribution of species classified as intermediate acceptable. Species that were particularly abundant at these study units relative to other study units were *Commiphora pyracanthoides*, *Grewia flava* and *Acacia tortilis* (Table 4.2).

4.5.4 Spinescent and unarmed classes

The leaf DM production of unarmed species (< 2 m height) ranged between 216.9 kg ha^{-1} and 618.1 kg ha^{-1} (mean 407.5 kg ha^{-1}). The leaf DM production of the spinescent component (< 2 m height) was substantially lower, and ranged between 44.4 kg ha^{-1} and 150.9 kg ha^{-1} (mean 97.3 kg ha^{-1}) between study units. It contributed between 9.0 % and 41.0 % of the total leaf DM production of the study units (mean 21.0 %) (Figure 4.5b).

Study units differed in terms of the composition of the spinescent and unarmed classes' leaf DM production. Study units 4 and 5 had, in absolute (kg ha^{-1}) and relative (%) terms, the lowest unarmed leaf DM production values (Figure 4.5a & b). This was mainly due to the low total leaf DM production (387.6 kg ha^{-1} and 367.8 kg ha^{-1} respectively) and the relatively high contribution of the spinescent component to the total leaf DM production (38.9 % and 41.0 % for study unit 4 and 5 respectively). These study units had low leaf DM production values for *Grewia bicolor, G. monticola* and *G. subspathulata* (unarmed), but high leaf DM production values for *Acacia tortilis* (study unit 4), *A. mellifera* and *Rhigozum zambesiacum* (study unit 5) in comparison to the other study units (Table 4.2).

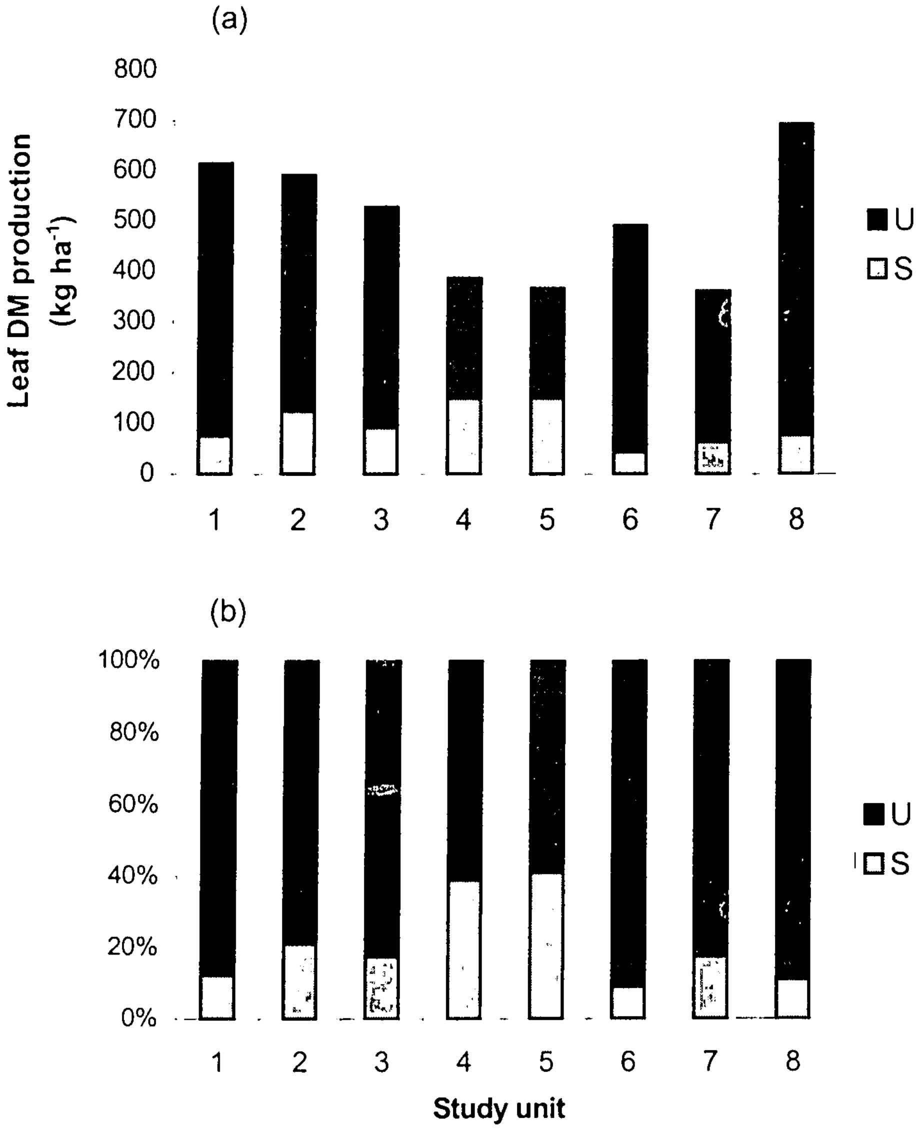

Figure 4.5 A comparison of study units in terms of (a) the leaf DM production (< 2 m height) of the spinescent and unarmed classes and (b) the relative contribution of the leaf DM production of the spinescent and unarmed classes (S – spinescent component, U – unarmed component).

4.5.5 Leaf retention classes

The mean leaf DM production (< 2 m height) and standard deviation values (n=8) of the different leaf retention classes were as follows: leaf retention class 1 = 91±37 kg ha^{-1}; leaf retention class 2 = 32±27 kg ha^{-1}; leaf retention class 3 = 357±134 kg ha^{-1}; leaf retention class 4 = 19±20 kg ha^{-1} and leaf retention class 5 = 6±5 kg ha^{-1} (Figure 4.6).

The high leaf DM production of leaf retention class 1 species (160.5 kg ha^{-1}) at study unit 6 was linked to the contribution of *Commiphora* species, which contributed 92 % of the leaf retention class 1 DM production at this study unit (Table 4.2). The relatively low leaf retention class 1 DM production, estimated at study unit 5, was related to the comparatively low leaf DM production of *Dichrostachys cinerea* at this study unit (Table 4.2). The comparatively high leaf DM production of leaf retention class 2 species at study units 5 and 6 (77.5 kg ha^{-1} and 69.1 kg ha^{-1} respectively) was related to the leaf production of *Acacia mellifera* and *Rhigozum zambesiacum* at study unit 5 and the leaf DM production of *Acacia erubescens, A. senegal* var. *leiorhachis* and *Cordia monoica* at study unit 6. Variation in the estimated leaf retention class 3 DM production between study units was largely due to differences in the contribution of *Combretum apiculatum* and *Grewia* species. These species contributed substantially to the leaf DM production of study units 1, 2, 3 and 8 compared to low estimates at study units 4 – 7 (Table 4.2). *Acacia tortilis* dominated the leaf retention class 4 DM production, which attained relatively high values of 64.0 kg ha^{-1} and 22.2 kg ha^{-1} at study unit 4 and 5 respectively (Table 4.2). The leaf retention class 5 DM production contributed on average only 1.3 % of the total leaf DM production below 2 m (Figure 4.6). *Boscia albitrunca* and *Maerua parvifolia* dominated this retention class in terms of DM leaf production. The leaf DM production of *Boscia albitrunca* was relatively high at study unit 4 (14.1 kg ha^{-1}) while the leaf DM production of *Maerua parvifolia* was estimated at 5.7 kg ha^{-1}, 4.2 kg ha^{-1} and 8.2 kg ha^{-1} for study units 1, 5 and 7 respectively (Table 4.2).

The phenological classification of woody species was made according to the retention period of green foliage. Leaves were, however, retained after senescence in species such as *Combretum apiculatum* and various *Grewia* species. Dry leaves retained on plants are continuously available to kudu, which make limited use of fallen leaf litter

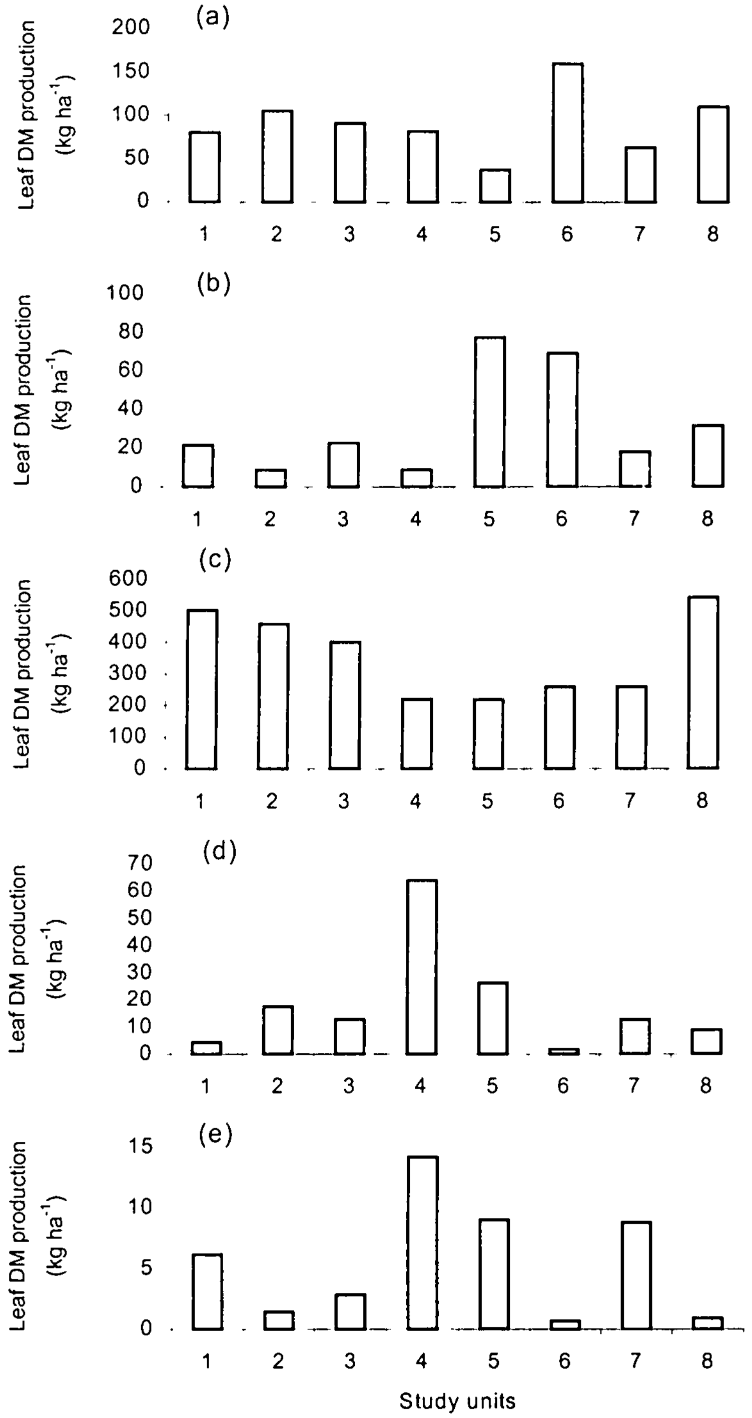

Figure 4.6 Comparison of study units in terms of the leaf DM production of the (a) leaf retention class 1 species, (b) leaf retention class 2 species, (c) leaf retention class 3 species, (d) leaf retention class 4 species and (e) leaf retention class 5 species.

(Owen-Smith & Cooper 1985, 1987). Leaf phenology differences have been demonstrated to vary between plant communities (Dekker & Smit 1996). In this study, deciduous species such as *Grewia* species, which occurred in drainage systems, often displayed extended leaf retention compared to individuals of the same species occurring on evidently drier soils (personal observation). Variation in leaf retention period might also have been influenced by local spatial rainfall differences resulting in soil moisture differences.

Figure 4.7 represents a schematic outlay of the seasonal availability of leaf DM (< 2 m height). The leaf DM production of the spinescent and unarmed classes was calculated per acceptability class per retention class (Appendix A). The gradual decline in foliage availability as the dry season progressed was shown by the consecutive elimination of the contribution of the respective classes in the reverse order of leaf retention period (leaf retention class 1 first eliminated). The decline in leaf DM production per study unit was subsequently related to the wet hot (WH) (leaf DM production at peak biomass), dry cool (DC) and dry hot (DH) seasons. According to Figure 4.7, study units followed a similar seasonal pattern in foliage availability. Peak leaf DM production was attained during the wet hot season and woody leaf resources declined during the dry cool season. The lower limit was reached before leaf flush at the end of the dry hot season.

4.5.6 Other components

Plant parts such as fruits and pods are opportunistically utilised by browsing ungulates (Walker 1980; Owen-Smith 1997). During the study period, fruit bearing of woody species were generally insignificant, with the exception of *Terminalia prunioides*, which fruited profusely. Pods of *T. prunioides* were found in the rumens of two kudu females shot during the dry season of 1999 at study unit 6 (N. van Wyk, personal communication[2]). *Grewia* species, notably *G. flavescens,* also produced fruit, but less profusely.

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[2] Mr. N. van Wyk, P.O. Box 141, Muldersdrift, 1747, Republic of South Africa

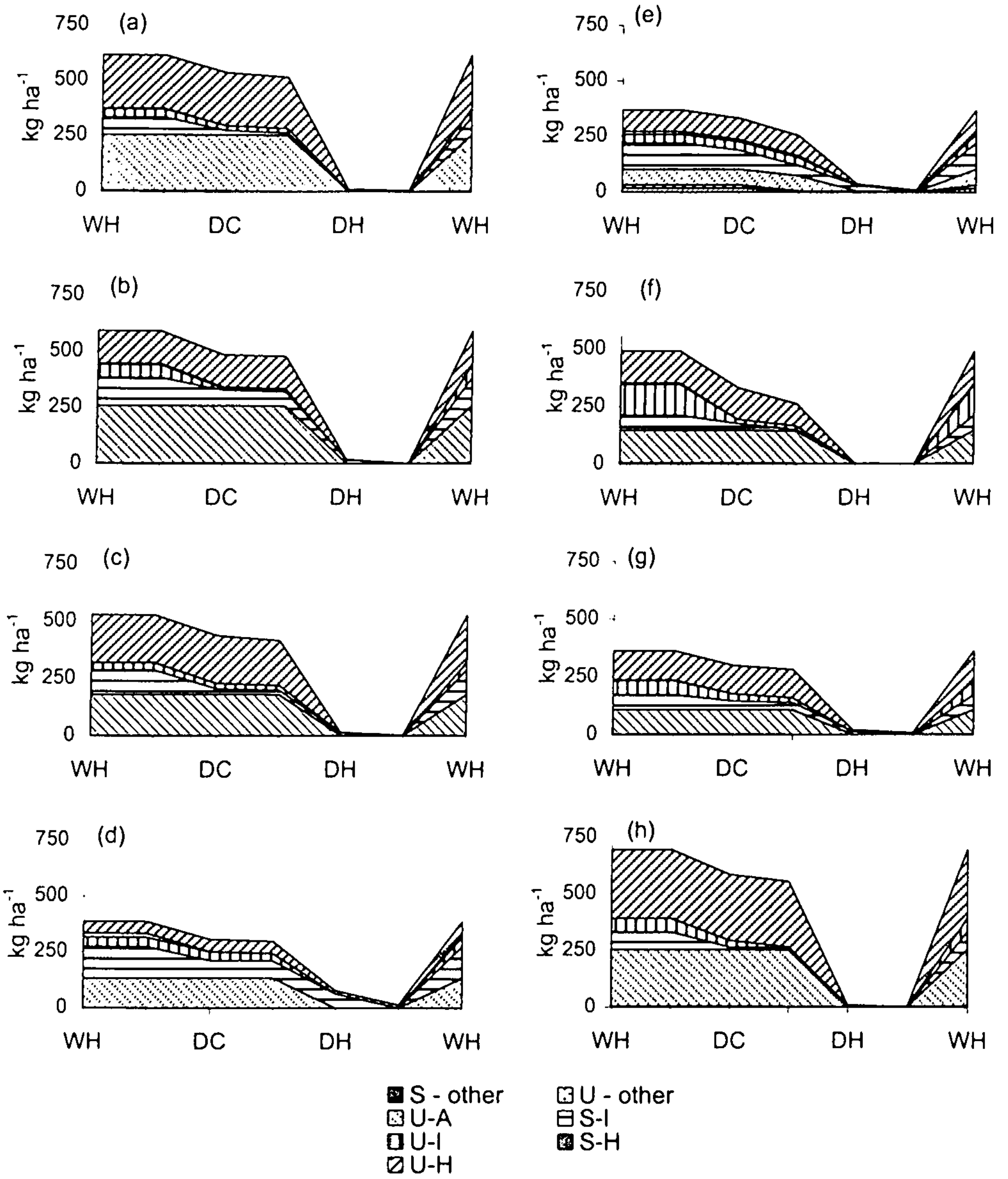

Figure 4.7 Schematic outlay illustrating the decline in leaf DM availability of functional groups during the dry season for (a) study unit 1, (b) study unit 2, (c) study unit 3, (d) study unit 4, (e) study unit 5, (f) study unit 6, (g) study unit 7 and (h) study unit 8 (U-H = unarmed, highly acceptable, U-I = unarmed, intermediate acceptable, U-A = unarmed, avoided, S-H = spinescent, highly acceptable, S-I = spinescent, intermediate acceptable, S - other = spinescent, no acceptability rating and U-other = unarmed, no acceptability rating. WH = wet hot season, DC = dry cool season and DH = dry hot season).

4.6 CONCLUSIONS

The following conclusions were drawn from this investigation:

(i) Considerable variation was evident between study units in terms of leaf DM production. Variation in leaf DM production was the highest in higher strata and tended to decrease in lower strata. The lowest variation was evident for the 0-1.5 m stratum. Kudu are thought to be food-limited (Owen-Smith & Cooper 1985; Novellie 1992; Grossman 1994). This suggests that kudu carrying capacity estimates should be based on the availability of food resources and also confounds the establishment of general carrying capacity norms for the study area.

(ii) Plant based frequency of utilisation showed significant ($P<0.001$) variation between species. Acceptance ratings allocated to species on grounds of the utilisation frequencies observed in the study area compared favourably with animal based rainfall season acceptability ratings for kudu elsewhere. The stocking rates of kudu and eland combined explained the most variation in the utilisation frequencies of the acceptable species at study units. This suggests that the observed utilisation patterns reflect that of large browser species in the study area.

(iii) Spinescent species showed mostly intermediate utilisation frequencies probably as a result of the restrictive effect of spines and thorns on the intake rate of a relatively large browser species such as kudu and eland. Unarmed species were differentially utilised by browsers and suffered significantly ($P<0.001$) greater damage to shoot-ends than spinescent species.

(iv) In terms of leaf production, unarmed species dominated the study area.

(v) Most scarce, unarmed species had high utilisation frequencies and were often heavily browsed. This might affect the survival chances of these species in the long-term and selective over-browsing might even have caused the low density of these species. This has a bearing on the sustainable utilisation of browse resources and needs further investigation.

(vi) The study area was characterised by a marked decline in the availability of green foliage as the dry season progressed and the lowest leaf DM availability is reached during the dry hot season. A marked difference in the seasonal availability of foliage was evident between study units. Study units 4 and 5, and to some extent study unit 7, had high leaf DM production values for the retention classes 4 and 5. This indicates that green foliage was more available over the dry season at these study units compared to other study units. Owen-Smith & Cooper (1985) and Grossman (1994) postulated that foliage availability during the dry season is the most limiting for kudu in deciduous savanna. This suggests that areas with higher dry seasonal resource availability will be able to support a higher kudu density than areas with low dry seasonal resources. This might be of importance in calculating optimal kudu stocking rates.

CHAPTER 5

THE HERBACEOUS LAYER

5.1 INTRODUCTION

Certain forb species contribute substantially to the diet of kudu (Conybeare 1975; Novellie 1983; Owen-Smith & Cooper 1989) and other browsing ungulate species, e.g. eland (Kerr, Wilson & Roth 1970) and impala (Cooper 1982). Forbs are also regarded as a high quality diet component and are thought to play an important role in the population dynamics of kudu (Owen-Smith & Cooper 1989).

Owen-Smith (1997) defined forbs as dicotyledonous herbs. For purposes of this study, forbs constitute non-graminoid herbaceous species, and thus also include monocotyledonous species (e.g. Commelinaceae).

The objectives of this investigation were:

(i) to estimate the standing crop of the grass component and individual forb species at study units, and
(ii) to determine if forb species were differentially utilised by browsing ungulates in the study area.

5.2 LITERATURE REVIEW

Kudu are primarily browsers and grass usually constitutes an insignificant part of their diet (Wilson 1965; Jarman 1971; Owen-Smith 1997). Only small quantities of grass are consumed by kudu during the wet season at Nylsvley (Owen-Smith & Cooper 1985; 1989) and in Zambia (Wilson 1965), and only the green flush following a burn in the Kruger National Park (Novellie 1983). Kudu in the sandy areas of the Hwange National Park appear to consume a higher percentage of grass (Conybeare 1975). Impala, a mixed feeder, allocates between 55 % and 80 % of their annual feeding time to grass consumption (Owen-Smith & Cooper 1985; Meissner, Pieterse & Potgieter 1996), while grass made up 70 % in impala faeces over the seasonal cycle (Skinner, Monro &

Zimmerman 1984). Gemsbok devoted 83 % of the annual feeding time to grass consumption in Kenya (Field 1975). In the Kalahari Gemsbok Park, gemsbok's grass intake ranged from 89 % in the wet season to 76 % in the dry season (Skinner & Smithers 1990). Eland have been established as versatile mixed feeders with a tendency to browse (Owen-Smith 1997). Grass constitutes 6-7 % (Kerr *et al.* 1965), 20.7 % (Field 1975) and 23.5 % (Van Zyl 1965) of the annual diet of eland in savanna areas as determined by various techniques. In browse limited environments, such as open woodlands and grasslands, grass consumption is notably higher (Lamprey 1963 cited by Kerr *et al.* 1965). Interpretation of the relative composition of food items is often confounded by the technique used. For example, diet composition estimates based on feeding time observations are partial to the relative intake rates of food items (Novellie 1983) while faecal-based estimates are influenced by the relative digestion rate of food items (Du Plessis & Skinner 1987).

Browsing ungulates vary grass intake according to season. The relative consumption of grass in the diet of mixed feeders tends to decrease as the dry season progresses (Dunham 1982; Nge'the & Box 1976, Buys 1990; Fabricius & Mentis 1990; Meissner *et al.* 1996; Owen-Smith 1997), probably corresponding to the greater nutritional decline in grass compared to browse during the dry season (Buys 1990; Owen-Smith 1994).

Forbs contribute substantially to the diet of various browsing ungulate species. Forbs constitute 19 % of the year round feeding time of kudu at Nylsvley and up to 60 % of the late wet season feeding time in the Kruger National Park (Novellie 1983). Impala devote only 9 % of their year-round feeding time to forbs at Nylsvley (Owen-Smith & Cooper 1989). Approximately 10 % of the feeding time of eland are allocated to forbs in the Zimbabwean lowveld (Kerr *et al.* 1970). Giraffe, in contrast, feed almost exclusively on woody species (Hall-Martin & Basson 1975; Sauer, Theron & Skinner 1977; Pellew 1984; Oates 1972; Sauer 1983; Hall-Martin 1974a, 1974b; Kok & Opperman 1980; Owen-Smith 1997). Browsing ungulates, e.g. eland and kudu, consume forbs mainly during the wet season and the importance of forbs in the diet declines as the dry season progresses (Kerr *et al.* 1970; Owen-Smith & Cooper 1989). An exception is noted by Novellie (1983) for the Kruger National Park where kudu feed predominantly from the herbaceous layer, presumably on forbs, on a year round basis with the exception of the pre-rain flush when woody species are favoured. The latter case might be related to the high availability of forbs in this area (Novellie 1983).

Forbs are regarded as a high quality diet component (Owen-Smith & Novellie 1982; Novellie 1983; Owen-Smith, Novellie & Cooper 1983; Owen-Smith & Cooper 1989). The availability of forbs may have significant consequences for the population dynamics of kudu by supplying the increased nutritional demands of breeding females during the late pregnancy and early lactation period (Owen-Smith & Cooper 1989).

Owen-Smith & Cooper (1989) noted that kudu tend to select forb species with soft stems, e.g. *Justicia* and *Commelina* species, while impala apparently favour more robust forbs, e.g. *Waltheria indica*.

5.3 PROCEDURE

5.3.1 Standing crop

The dry-weight-rank method, proposed by t'Mannetjie & Haydock (1963) and modified by Jones & Hargreaves (1979) and Barnes, Odendaal & Beukes (1982), was combined with the double sampling yield technique (Reich, Bonham & Remington 1993 cited by Kirkman, Engelbrecht & Cockcroft 1994) in order to determine the simultaneous standing crops of grass and forb species within each homogeneous vegetation unit. The dry-weight-rank method involves the following basic steps as outlined by Kirkman *et al.* (1994): (i) The representative placement of quadrats in the area to be surveyed. (ii) The allocation of three ranks according to the estimated dry mass contribution of the most important herbaceous species per quadrat (more than one rank is allocated to dominant species, and if species appear to have equal DM yields, ranks are shared). (iii) The relative dry mass contribution of the important species per quadrat is calculated by multiplying the first (highest contribution), second and third ranks by 8.04, 2.41 and 1.00 percent respectively. Multipliers of shared ranks are divided. (iv) Quadrats are weighted according to the quadrat's dry mass contribution. In estimating the standing crop of quadrats in heterogeneous herbaceous swards, Kirkman *et al.* (1994) recommend the double sampling technique (Reich *et al.* 1993 cited by Kirkman *et al.* 1994). This technique involves the visual estimation of the standing crop of quadrats on a suitable scale (e.g. 1-10). The standing crop of a proportion of quadrats is harvested and a simple regression established between estimated and corresponding actual DM values of the harvested quadrats. Quadrat yields are subsequently predicted from the regression equation (Kirkman *et al.* 1994).

In this study, a sampling intensity of 100 quadrats, 0.25 m^2 (0.5 x 0.5 m) in size, was allocated per homogeneous vegetation unit. This is in accordance with the sampling intensity and quadrat size recommended for use in the Arid Sweet Bushveld (Dekker, Kirkman & Du Plessis 2001). Of the 100 quadrats allocated per homogeneous vegetation unit, the herbaceous standing crop of 10 quadrats (10%) were harvested with shears at ground level. The harvested quadrats covered a range of estimated DM yields to facilitate regression analysis. The harvested herbaceous material was kept in paper bags, dried to constant mass at 70°C and the DM determined to the nearest 0.1 g. Calculations were executed with the aid of the computer procedures compiled by Kirkman, Engelbrecht, Cockcroft & Swanepoel (undated).

The grass and forb standing crops of study units were calculated from homogeneous vegetation unit standing crop estimates corrected for homogeneous vegetation unit size.

The herbaceous surveys were done between April 1999 to June 1999.

5.3.2 Utilisation frequencies

Forb utilisation frequencies were determined at woody utilisation sample sites (Chapter 4). Fifty 0.25 m^2 quadrats were used per sample site. All forb plants within quadrats were recorded as either being utilised (plant parts missing) or not utilised. Only aboveground terminal plant-parts were considered.

5.4 STATISTICAL ANALYSIS

Simple least square regressions between actual (harvested) and estimated quadrat DM values were established per study unit and DM yields of quadrats predicted from these relationships (Table 5.1). Correlation coefficients (r) ranged from 0.92 and 0.96 ($p<0.001$) between study units (Table 5.1).

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Table 5.1 The relationships (least square fit, power function) between actual (y) and estimated (x) herbaceous standing crop (DM) for study units (the number of quadrates involved (n) and correlation coefficients (r) are also indicated).

Study unit	**$y=bx^c$**		**n**	**r**
	b ($y=bx^c$)	**c** ($y=bx^c$)		
1	1.0504	1.9045	40	0.95
2	0.9578	1.8973	30	0.95
3	1.2129	1.7484	50	0.93
4	2.5058	1.7915	50	0.92
5	0.3265	2.5484	40	0.95
6	0.9075	2.3149	80	0.96
7	0.7829	2 2454	50	0.92
8	1.2575	1.8613	50	0.94

The Chi-square test was applied to test for significant differences in the utilisation frequencies of forb species. All observations across study units were totalled per species. Only species with more than 50 observations were considered.

A stepwise variable selection analysis (Statgraphics 1991) was conducted to determine whether relations exist between the frequency of forb plant use (dependent variable) and browsing ungulate stocking rates (independent variables) between study units. Forb utilisation frequencies represent the total number of plants assessed to be utilised relative to the total number of plants observed per study unit. Stocking rates were calculated from the population sizes of browsing ungulate species as determined by helicopter game census and corrected for metabolic rate and diet composition differences (Chapter 6). For the purposes of this investigation, stocking rates were expressed as the forb standing crop available per browser unit (BU) of the different browsing species. It is reasoned that a significant positive relationship between the stocking rate of a browser species and the utilisation frequencies of forb species across study units would suggest that the observed variation in use of forbs might be largely due to the browsing of that species, thus represent to some degree the utilisation pattern of that species. This would facilitate the classification of forb species into acceptability classes.

5.5 RESULTS AND DISCUSSION

5.5.1 Forb standing crop

Forb standing crop ranged from 82.8 to 375.5 kg DM ha^{-1} (mean 213.5 kg DM ha^{-1}) between study units (Figure 5.1). The forb standing crop at Nylsvley is estimated at approximately 10 kg DM ha^{-1} (Owen-Smith 1994) and ranges between 10.5 and 83.3 kg DM ha^{-1} between different plant communities in the Mopani Veld (Dekker (1996). These values contrast with the high forb standing crop of 425 kg DM ha^{-1} estimated in the knobthorn veld of the Kruger National Park (Novellie 1983).

A small number of species dominated the forb standing crop at the study units. Of the total number of forb species, 9.2 % contributed more than 65 % of the total standing crop on average. These species consisted of *Dicoma tomentosa, Monechma divaricatum,*

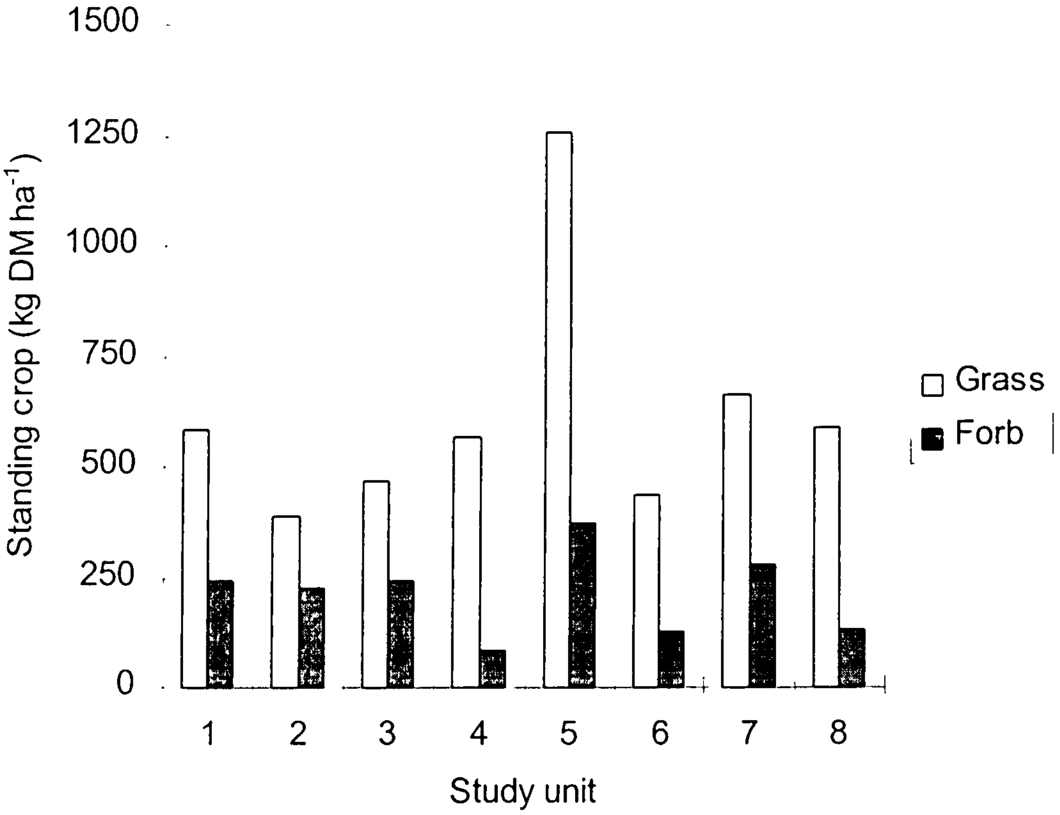

Figure 5.1 The standing crop (kg DM ha^{-1}) of the forb and grass components of the herbaceous layer of study units.

Hermstaedtia odorata, Tephrosia purpurea, Gisekia africana, Heliotropium steudneri, Tribulus terrestris, a *Limeum* species and *Achyranthes aspera* (Table 5.2).

5.5.2 Grass standing crop

The grass standing crop of study units ranged from 390.5 to 1 257.3 kg DM ha^{-1} (mean 620.1 kg DM ha^{-1}) (Figure 5.1). The grass standing crop exceeded that of forbs at all study units by a factor ranging from 1.7 to 6.9 (mean 3.3).

5.5.3 Use of forbs

The observed damage to terminal plant parts of forb species were not in relation to the species' respective abundance values (X^2=287, p<0.001, d.f.=21). Species with frequency values >0.50 consisted of *Phyllanthus maderaspatensis, Tephrosia purpurea, Gisekia africana, Phyllanthus niruri* and *Hermannia boraginiflora* (Table 5.3). Species with frequency values between 0.35 (included) and 0.5 consisted of the following species; *Abitulon grandiflorum, Kohautia cynanchica, Monechma divaricatum, Tribulus terrestris, Tricliceras glanduliferum, Heliotropium steudneri, Leucas glabrata* and *Ocimum canum.* Species with frequency values <0.35 were *Hibiscus micranthus, Hermstaedtia odorata, Chamaesyce neopolycnemoides, Asparagus setaceus, Evolvulus alsinoides* and *Dicoma tomentosa* (Table 5.3).

Relationships established between the frequency of damage to forb plants and the stocking rates (kg forb DM BU^{-1}) of impala, kudu, eland, gemsbuck and giraffe were insignificant (P>0.05). Differences between forb species in terms of frequency of utilisation can subsequently not be interpreted to be caused by the selective browsing of the animals included in the analysis. Plant based estimates of browse utilisation are insensitive regarding the type of animal accountable for the observed damage (Rutherford 1979). Other herbivores, apart from larger browsing ungulates, might also have utilised forbs in the study area, e.g. insects, rodents, small antelope and grazing ungulate species. With the woody survey observations of woody plants were restricted to the stratum above the reaching height of small antelope species such as duiker and steenbok.

Table 5.2 Estimated standing crop (kg DM ha^{-1}) of forb species per study unit.

	Study units								
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**Mean**
Dicoma tomentosa	127.2	111.5	118.7	3.4	0.4	6.7	138.6	30.6	**67.2**
Monechma divaricatum	22.1	31.4	19.8	0.0	15.8	33.3	11.1	25.3	**19.8**
Hermbstaedtia odorata	0.0	0.0	0.0	0.6	52.2	9.4	27.2	1.4	**11.4**
Tephrosia purpurea	0.5	1.9	1.1	3.5	46.1	8.2	20.4	3.9	**10.7**
Gisekia africana	0.0	0.7	0.0	0.1	70.1	1.2	1.8	0.0	**9.3**
Heliotropium steudneri	8.6	17.1	19.4	0.5	0.0	8.0	2.8	11.2	**8.5**
Tribulus terrestris	3.3	4.1	0.7	0.0	48.5	2.4	0.9	0.4	**7.5**
Limeum sp.	0.7	0.0	0.0	0.0	53.9	0.0	0.0	0.0	**6.8**
Achyranthes aspera var. *sicula*	15.4	3.7	2.4	0.0	3.5	15.0	1.3	5.4	**5.8**
Commelina spp.	8.7	1.6	11.8	9.5	7.1	0.0	3.1	0.5	**5.3**
Neuracanthus africanus	0.0	0.0	0.0	0.0	0.1	12.8	22.1	0.0	**4.4**
Priva africana	0.0	0.1	24.6	0.0	0.4	2.4	0.0	0.1	**3.4**
Indigofera heterotricha	0.0	0.0	0.0	0.0	26.8	0.0	0.0	0.0	**3.4**
Creepers	4.8	11.9	1.0	2.1	5.0	1.3	0.3	0.2	**3.3**
Sericorema remotiflora	5.5	0.0	0.0	19.7	0.0	0.0	0.3	0.0	**3.2**
Tricliceras glanduliferum	1.7	7.2	1.0	15.4	0.0	0.0	0.0	0.4	**3.2**
Phyllanthus sp.	1.8	3.4	2.3	0.5	0.1	5.4	4.7	3.8	**2.7**
Evolvulus alsinoides	3.3	4.4	4.3	0.5	1.0	1.7	4.0	2.5	**2.7**
Kohautia cynanchica	0.0	4.3	3.9	6.0	1.1	0.0	0.0	2.5	**2.2**
Hybanthus enneaspermus	1.1	1.8	4.8	0.0	0.8	0.0	1.6	7.6	**2.2**
Ocimum sp.	1.8	0.8	0.0	0.0	0.0	1.6	0.0	9.6	**1.7**
Leucas sexdentata	7.9	0.0	0.2	0.1	2.3	2.5	0.0	0.0	**1.6**
Orthosiphon sp.	2.0	0.0	1.7	1.6	0.0	0.1	1.5	4.5	**1.4**
Hermannia boraginiflora	3.4	0.2	3.1	0.1	0.0	0.2	0.6	3.3	**1.4**
Leucas glabrata	2.1	3.7	0.0	0.2	0.0	4.5	0.1	0.0	**1.3**
Abitulon grandiflorum	3.5	2.9	0.8	0.0	0.0	1.6	0.2	0.0	**1.1**
Sedges	0.7	0.0	1.1	0.3	2.4	0.0	0.0	4.5	**1.1**
Ptycholobium contortum	0.0	0.0	0.0	0.7	1.5	0.0	6.0	0.0	**1.0**
Calostephane divaricata	6.3	0.2	1.6	0.0	0.0	0.0	0.0	0.0	**1.0**
Cleome angustifolia	1.8	0.2	0.0	0.3	4.0	1.1	0.6	0.0	**1.0**
Sesamum triphyllum	0.6	0.0	6.8	0.0	0.7	0.0	0.0	0.0	**1.0**
Hibiscus micranthus	1.6	0.7	0.5	0.5	1.9	0.1	2.3	0.0	**1.0**
Asparagus setaceus	1.3	0.2	0.8	0.0	1.0	1.8	1.6	0.0	**0.9**
Barleria lancifolia	1.0	0.0	0.1	0.0	5.1	0.0	0.4	0.0	**0.8**
Seddera suffruticosa	0.0	0.0	0.0	0.0	2.0	1.4	3.2	0.0	**0.8**
Euphorbia sp.	0.0	0.0	0.0	6.5	0.0	0.0	0.0	0.0	**0.8**
Indigofera nebrowniana	0.7	2.8	0.0	0.0	0.9	0.9	0.9	0.0	**0.8**
Commicarpus fallacissimus	0.0	0.0	0.1	0.0	1.6	0.0	4.4	0.0	**0.8**
Melhania rehmannii	2.7	1.5	0.2	0.0	0.0	0.4	1.1	0.1	**0.7**
Ocimum canum	0.0	0.0	0.7	2.3	0.0	0.0	2.1	0.1	**0.7**
Geigeria burkei	0.0	0.1	1.3	0.8	0.1	0.0	2.7	0.2	**0.6**
Ipomoea magnusiana	0.0	0.0	0.0	0.0	4.4	0.0	0.0	0.0	**0.6**
Petalidium aromaticum	0.3	0.0	0.0	0.0	0.8	0.0	2.8	0.0	**0.5**
Pupalia lappacea	0.0	2.3	0.2	0.0	1.3	0.0	0.0	0.0	**0.5**
Justicia protracta ssp. *Rhodesiana*	0.0	0.0	0.0	0.1	0.4	0.2	2.9	0.0	**0.5**
Phyllanthus maderaspatensis	0.0	1.9	0.0	1.2	0.2	0.0	0.0	0.2	**0.4**

Table 5.2 (Continue).

	Study units								
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**Mean**
Dicerocaryum eriocarpum	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	**0.4**
Indigofera trita	0.0	0.0	0.0	0.9	0.0	0.0	2.2	0.0	**0.4**
Cardiospermum halicacabum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	**0.4**
Monechma debile	0.2	0.0	0.6	0.0	0.0	0.0	0.2	1.9	**0.4**
Blepharis aspera	0.0	1.9	0.0	0.0	0.6	0.0	0.2	0.0	**0.3**
Rhynchosia totta	0.0	0.0	0.0	0.0	2.2	0.2	0.0	0.0	**0.3**
Amaranthus schinzianus	0.5	0.6	0.0	0.0	0.2	1.1	0.0	0.0	**0.3**
Chamaesyce neopolycnemoides	0.3	0.0	0.2	0.1	0.6	0.0	0.8	0.1	**0.3**
Pavonia burchellii	0.1	0.0	0.1	0.0	1.3	0.3	0.0	0.0	**0.2**
Solanum coccineum	0.2	0.0	0.0	1.4	0.0	0.0	0.0	0.0	**0.2**
Rhynchosia pentheri	0.0	0.0	0.0	0.0	0.1	0.0	1.3	0.0	**0.2**
Jatropha sp.	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	**0.2**
Boerhavia sp.	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.2	**0.2**
Abutilon austro-africanum	0.0	0.0	0.4	0.0	0.5	0.2	0.0	0.0	**0.1**
Aptosimum lineare	0.0	0.0	0.2	0.0	0.0	0.0	0.1	0.8	**0.1**
Limeum sulcatum	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.6	**0.1**
Rhinacanthus xerophilus	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	**0.1**
Indigofera circinatum	0.0	0.0	0.0	0.2	0.3	0.0	0.0	0.0	**0.1**
Barleria senensis	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	**0.1**
Megalochlamys kenyensis	0.0	0.0	0.0	0.0	0.1	0.1	0.3	0.0	**0.1**
Geigeria acaulis	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**0.0**
Lantana rugosa	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	**0.0**
Senna italica	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	**0.0**
Other	0.5	0.8	4.9	2.0	1.8	0.0	0.9	5.5	**2.1**
Total	**244.0**	**226.0**	**243.2**	**82.8**	**375.5**	**126.2**	**279.6**	**130.7**	-

Table 5.3 The number of observations and utilisation frequencies of abundant forb species (values in brackets indicate SD).

Species	Number of observations	Utilisation frequency
Phyllanthus maderaspatensis	391	0.63(0.31)
Tephrosia purpurea	194	0.63(0.09)
Gisekia africana	149	0.52(0.32)
Phyllanthus niruri	126	0.51(0.35)
Hermannia boraginiflora	63	0.51(0.24)
Abutilon grandiflorum	128	0.47(0.36)
Kohautia cynanchica	78	0.46(0.01)
Monechma divaricatum	643	0.44(0.12)
Tribulus terrestris	103	0.44(0.20)
Tricliceras glanduliferum	97	0.41(0.24)
Heliotropium steudneri	274	0.41(0.22)
Leucas glabrata	50	0.38(0.52)
Ocimum canum	107	0.35(0.36)
Hibiscus micranthus	72	0.33(0.35)
Hermstaedtia odorata	292	0.33(0.31)
Chamaesyce neopolycnemoides	109	0.29(0.36)
Asparagus setaceus	62	0.19(0.25)
Evolvulus alsinoides	487	0.18(0.15)
Ocimum sp.	113	0.17(0.40)
Dicoma tomentosa	345	0.15(0.14)

Preference ratings should reflect the usage of resources in relation to its availability (Johnson 1980). The differential sizes of forb plants were not taken into account as utilisation frequencies were expressed as the number of plants utilised relative to the number of plants surveyed. Larger plants of selected for species would consequently stand an increased chance of being utilised compared to smaller plants. By observing only a sector of the woody canopy, this problem was avoided in the woody utilisation survey.

5.6 CONCLUSIONS

From this investigation the following conclusions were drawn:

I. The forb standing crop constituted a substantial, but subdominant component of the herbaceous layer at study units. Considerable variation in standing crop was evident between study units.

II. Forb species were differentially utilised in the study area. Relationships between the frequency of damage to forb plants and stocking rates (kg forb DM BU^{-1}) of browsing ungulate species in the study area were, however, insignificant ($P>0.05$). It was concluded that the observed differences in forb species' utilisation frequencies probably did not reflect the utilisation patterns of browsing ungulate species in the study area.

CHAPTER 6

LARGE HERBIVORE NUMBERS, BIOMASS AND STOCKING RATES

6.1 INTRODUCTION

Helicopter surveys have been widely used in enumerating large ungulate species in South Africa (Snyman 1989; Peel 1990; Van Hensbergen, Berry & Juritz 1996; Reilly & Emslie 1998), and are probably the most appropriate census technique in open savanna areas (Bothma, Peel, Pettit & Grossman 1990).

The stocking rate of an area is defined as the number of animals that are allocated to an unit area of land for a specific period of time (Morris, Hardy & Bartholomew 1999) and gives a measure of the impact of the animal component on its food resources. The relative energy consumption per unit livemass provides a convenient index for interspecies comparisons (Mentis 1977, 1978; Meissner 1982; Dekker 1997; Owen-Smith 1999). Relative energy consumption, however, does not necessarily reflect an animals' impact on the forage resource (Peel, Pauw & Snyman 1991b; Hardy 1996; Dekker 1997; Peel, Biggs & Zacharias 1998) although it provides a more accurate estimate than biomass (Mentis 1978). The clear distinction among African ruminants, regarding the graminoid-browse proportion in the diet (Hofmann & Steward 1972; Hofmann 1989; Owen-Smith 1997), necessitates its separate consideration in calculating stocking rates (Dekker 1997).

Biomass has been extensively used in expressing stocking rates in Africa (e.g. Coe, Cumming & Phillipson 1976; East 1984). It has been calculated in order to compare stocking rates of other areas to that of the present study.

The objectives of this investigation were:

(i) to estimate large ungulate species' population sizes at study units,
(ii) to calculate the large herbivore biomass of study units, and
(iii) to calculate grazing and browsing stocking rates expressed as Large Stock Units and Browser Units per unit area.

6.2 PROCEDURE

6.2.1 Game census

Game animal numbers were determined by total helicopter counts in the study units. Game censuses were conducted at the end of August 1999, in the early morning and afternoon. Censuses were done systematically in an east-west direction, starting in either the north or south on 330 m spaced flight paths. The mean height above ground was approximately 40 m but varied according to the terrain and tree structure. The counting team consisted of the pilot and a recorder in the front and two observers in the rear. The recorder also acted as observer to the front while the rear observers counted all animals in a 165 m wide strip to the left and right of the flight path respectively. The pilot also assisted in counting when not otherwise occupied. Both rear counters and the recorder had previous experience of aerial counting. The door at the recorder's side, as well as the rear doors, were removed to enhance visibility while counting. Study units were counted continuously, with the exception of study unit 5 (Langjan Nature Reserve) which was counted in two successive sessions on the same day.

Navigation of the aircraft was facilitated by a Global Positioning System coupled to a Laptop computer in the aircraft. The computer program actively showed the position of the helicopter in relation to gridlines corresponding to vertically projected lines spaced 330 m apart on the ground. The actual flight path flown was also indicated on the computer screen.

Game numbers were recorded on prepared maps of the study units. The maps showed conspicuous landmarks such as roads, hilltops, windmills and buildings in relation to the assumed flight plan. Double counts, the recounting of counted game that ran onto uncounted transects, were minimised by referring back to game herd sizes recorded on their approximate positions on the prepared maps. Elusive gregarious game species such as impala, and to a lesser extent kudu, were flushed from hiding in order to facilitate accurate counting.

Kudu were allocated to three categories according to sex and age to facilitate accurate estimates of the impact on food resources. The 'male' category was allocated to animals that were positively identified as such. The 'juvenile' category was allocated to animals presumably born in 1999. In southern Africa, kudu are typically seasonal breeders and most calves are born from January to March (Simpson 1968; Skinner & Huntley 1971; Owen-Smith 1984). The 'female and yearling' category included all animals not allocated to the former classes and consisted of females and yearlings of both sexes. Yearling male's horns are still inconspicuous (Simpson 1966), at least when seen from the helicopter.

6.2.2 Cattle numbers

Cattle were present at study unit 1, 3 and 7 during the dry season of 1999. Owners stated the number of animals per age and sex class at the time of the helicopter game count.

6.2.3 Stocking rates

6.2.3.1 BIOMASS

The biomass of large animals at study units was calculated from game and cattle numbers multiplied by the mean mass of an individual in a population or animal class (Table 6.1). Kudu biomass was calculated from total kudu numbers multiplied by a mean mass of 140 kg after Dekker (1996).

6.2.3.2 RELATIVE METABOLISABLE ENERGY CONSUMPTION

6.2.3.2.1 Game

The metabolic mass ($W^{0.75}$) of a representative individual (mean mass) in a population was used to equate animals of different sizes on the basis of their relative metabolisable energy requirements (Mentis 1977, 1978; Dekker 1997; Owen-Smith 1999). Stocking rates were expressed in Large Stock Units (LSU) (grazing component) and Browser Units (BU) (browsing component) after Peel *et al.* (1991b) and Dekker (1997). A LSU is defined as the metabolic equivalent of a steer or grazing animal with a mass of 450 kg.

Table 6.1 The mean mass (kg), diet composition and calculated LSU animal^{-1} and BU animal^{-1} for large herbivore species.

Species / animal class	**Mass (kg)**	**% grass**	**% browse (< 2 m)**	**LSU animal^{-1}**	**BU animal^{-1}**
Grazers					
Blesbok	61[2]	100	0	0.22	0.00
Blue wildebeest	182[1]	100	0	0.51	0.00
Burchell's zebra	216[1]	100	0	0.58	0.00
Cattle: bull	600[3]	100	0	1.38[3]	0.00
Cattle: heifer/ox	350[3]	100	0	0.90[3]	0.00
Cattle: dry cow	525[3]	100	0	1.21[3]	0.00
Cattle: cow with calf	525[3]	100	0	1.55[3]	0.00
Ostrich	110[3]	100	0	0.35	0.00
Red hartebeest	120[2]	100	0	0.37	0.00
Warthog	30[1]	100	0	0.13	0.00
Waterbuck	205[1]	100	0	0.55	0.00
Mixed feeders					
Eland	460[2]	30	70	0.30	1.71
Gemsbok	210[2]	70	30	0.40	0.41
Impala	41[1]	50	50	0.08	0.20
Browsers					
Giraffe	828[2]	0	33	0.00	1.25
Kudu	140[4]	0	100	0.00	1.00
Kudu: bull	240[3]	0	100	0.00	1.50
Kudu: cows and sub-adults	160[3]	0	100	0.00	1.11
Kudu: juveniles	55[3]	0	100	0.00	0.50

[1] Mean mass of individual in population (Bothma, Van Rooyen & Du Toit 1995)

[2] Mean mass of adult female (Bothma *et al.* 1995)

[3] Meissner *et al.* (1983)

[4] Dekker (1996)

Dekker (1997) proposed a Grazer Unit (GU), defined as the metabolic equivalent of a grazing animal with a mass of 180 kg. Preference was given to expressing stocking rates in terms of LSU instead of GU per unit area due to the wider use of the former unit which enables easy comparisons between areas. A BU is taken as the metabolic equivalent of a kudu with a live mass of 140 kg (Dekker 1996, 1997; Peel *et al.* 1991b). Mixed feeders were apportioned both a LSU and BU value according to the relative grass: browse composition in the diet (Table 6.1). The diet composition of game species is after Dekker (1996; 1997) and Peel *et al.* (1991b).

Because of the vertical arrangement of woody browse, the spatial availability of browse to browsing ungulate species is restricted to their respective reaching heights. As kudu form the focal study animal, only the spatial overlap in browse use of other browsing species with kudu were considered in calculating their stocking rates. It was assumed that kudu eland, impala and gemsbok browse below a height of 2 m. This assumption is based on mean rather than on maximum values as individuals of eland and kudu are able to utilise browse higher than 2 m by pulling down or breaking of higher branches (Kerr *et al.* 1970; Dayton 1978; Rutherford 1979; Styles 1993 cited by Smit 1994). Impala and gemsbok, because of their smaller size, are thought to feed exclusively below 2 m height (Du Toit 1990; Dayton 1978; Dekker 1997). Giraffe on the other hand are able to utilise browse strata above that of kudu, e.g. Du Toit (1990). However, the feeding stratification between giraffe and other browsers is not complete, and overlap does occur. Several South African studies on the feeding ecology of giraffe have reported on the approximate percentage of the feeding time spent below a height of 2 m, e.g. 10 % in the Kruger National Park (Du Toit 1990), 17 % in the Jack Scott Nature Reserve (Van Aarde & Skinner 1975), 33 % in the Koos Meintjies Nature Reserve (Sauer *et al.* 1977) and 45 % in the Willem Prinsloo Nature Reserve (Kok & Opperman 1980). The feeding height of browsers is influenced by, among other factors, the production of browse at different height strata (Du Toit 1990). This was thought to explain the relative large allocation of feeding time spent at lower browse strata reflecting the large proportion of browse available in lower strata in the preferred habitat of giraffe at the Willem Prinsloo Nature Reserve (Kok & Opperman 1980). In this study the study area is characterised by a relatively well-developed shrub layer (Chapter 4). Giraffe here will probably spent substantial time feeding at lower browse strata. In calculating giraffe stocking rates, a value of 33 % of the total browse intake from below a height of 2 m was therefore assumed.

The LSU per animal for different grazer and mixed feeder species was calculated as:

$$\frac{(\text{Mean body mass})^{0.75} \times (\%\ \text{grass in diet})}{450^{0.75}}$$

The BU per animal for different browser and mixed feeder species or kudu class was calculated as:

$$\frac{(\text{Mean body mass})^{0.75} \times (\%\ \text{browse below 2 m height in diet})}{140^{0.75}}$$

The mean population masses of species or class of animal and the composition of the diet in terms of percentage grass and browse used to calculate the LSU and BU per species or animal class are summarised in Table 6.1.

Two different kudu stocking rates were calculated per study unit using the above equation. For purposes of comparing the total stocking rates of browsing ungulate species in study units, kudu stocking rates were calculated from total kudu numbers. A mean mass of 140 kg was assumed for an individual in a population after Dekker (1996). To represent the impact of kudu on their food resources more accurately for the purpose of relating kudu faecal nitrogen and browse availability (Chapter 8), kudu stocking rates were calculated per animal class (bulls, cows and sub-adults and juveniles) (Table 6.2). The mean masses used to calculate the mean BU per animal class were: bulls 240 kg, cows and sub-adults 160 kg and juveniles 55 kg after Meissner (1983) (Table 6.2).

6.2.3.2.2 Cattle

Cattle stocking rates were calculated from reported numbers for different age and sex classes using LSU equivalents for medium sized grazing cattle (Meissner, Hofmeyer, Van Rensburg & Pienaar 1983). These values also incorporate the increased energy

Table 6.2 Game population sizes as determined by helicopter count for study units at the end of the 1999 dry season.

Species	**Study units**							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Grazers								
Blesbok		3						5
Blue wildebeest	10		9		55	9	35	22
Burchell's zebra			9	29	23	16	8	8
Ostrich				14	91			
Red hartebeest			8		16		13	11
Warthog	13	29	21	45	111	2	54	38
Waterbuck	3	5	17	15	98			3
Mixed feeders								
Eland	6		11		56	6	5	10
Gemsbok	10	1	28		115	3	11	7
Impala	101	79	123	48	133	188	183	136
Browsers								
Giraffe			2	3	42	6		
Kudu: bull	8	2	15	11	21	3	22	9
Kudu: cows and juveniles	24	23	17	27	71	24	60	21
Kudu: calves	5	10	3	2	15	8	30	14
Kudu: total	37	35	35	40	107	35	112	44

requirements per unit livemass of reproductive and productive animals (Meissner *et al.* 1983).

6.3 RESULTS AND DISCUSSION

6.3.1 Game numbers

The population size of the larger ungulate species determined by helicopter censuses at the end of the dry season of 1999, are summarised in Table 6.2. Species that occurred consistently in the study units were warthog, impala and kudu. Of all the species counted, impala were the most abundant, followed by kudu. Other large browsing ungulate species encountered, though not persistent, were eland, gemsbok and giraffe (Table 6.2).

The precision with which game population sizes are determined is often of greater importance than the accuracy thereof (Bothma 1995; Eiselen 1994). Precision gives a measure of the level at which population changes can be detected (Reilly & Emslie 1998). This was deemed of particular importance in this study where study unit game population sizes were to be compared. Reilly & Emslie (1998) expressed precision as the power to detect a 20 % population change from four standardised helicopter counts conducted on four consecutive days. The power to detect a population change was the highest for kudu at 80 %, meaning that repeated counts of kudu showed the least variation. The counts for other species were less precise: 53 % for zebra, 44% for wildebeest and 37 % for impala (Reilly & Emslie 1998). The kudu precision obtained above contrasts with an experiment repeated at the Suikerbosrand Nature Reserve where consecutive counts were highly variable (Reilly & Haskins 1999). These differences between study sites could probably be related to the low kudu density at the Suikerbosrand Nature Reserve (the mean kudu density calculated for four aerial counts was 0.32 kudu 100 ha^{-1}). Other species occurring at low densities also had low precision values at Suikerbosrand Nature Reserve (Reilly & Haskins 1999), a tendency also noted by Eiselen (1994) for rare species in the Kruger National Park. In the light of the relative abundance of kudu and impala, the most abundant browsing species in the study units (Table 6.2), precision was unlikely to be impaired by low density of these species.

Aerial counts, including helicopter counts which are considered to be more accurate than fixed-wing aircraft counts, usually result in underestimates of most species (Bothma *et al.* 1990, Van Hensbergen *et al.* 1996). The accuracy of helicopter counted kudu and impala is estimated at 56 % and 63 % respectively of a drive count (control) (Bothma *et al.* 1990). A kudu helicopter count in the Northern Cape Province yielded 27 % of a determined population (Van Hensbergen *et al.* 1996). Bothma *et al.* (1990) attributed the low accuracy of their kudu count to poor sightability of the fawn-grey coloured kudu against a greyish background of the granitic derived soils in that area. As soils in this study area are mostly red (Chapter 2), this would probably only lessen the sightability of the reddish upper parts of impala (Skinner & Smithers 1990). The low accuracy of the kudu count reported by Van Hensbergen *et al.* (1996) can be related to the wide transects used, 800 m as opposed to 330 m used in this study. They conclude that narrower transects improve both accuracy and precision, provided that double counts are eliminated from total counts.

6.3.2 Cattle numbers

The numbers of different cattle classes that were present at study units 1, 3 and 7 at the end of the dry season of 1999 are summarised in Table 6.3.

6.3.3 Biomass

The calculated biomass of large animals in the study units is presented in Table 6.4. Kudu attained the highest mean biomass (612.0 kg km^{-2}) followed by cattle (only occurring at three study units) (430.5 kg km^{-2}), impala (428.0 kg km^{-2}) and eland (264.9 kg km^{-2}). Of the browsing guild, kudu biomass ranged from 375.5 to 922.0 kg km^{-2} and impala from 118.9 to 1 027.7 kg km^{-2}. Eland and giraffe, while not occurring at certain study units, reached maximum calculated biomass amounts of 561.5 and 758.1 kg km^{-2} respectively.

The biomass - long term rainfall regression of Coe *et al.* (1976) has been suggested as a crude guideline in stocking arid and semi-arid wildlife areas (Du Toit 1995; Peel *et al.* 1998). The regression calculated by Coe *et al.* (1976) is based on the empirically

Table 6.3 Cattle numbers according to animal class present at study units at the end of the 1999 dry season.

Animal class	**Study units**		
	1	**3**	**7**
Bull	1	1	1
Cows: lactating	12	6	11
Cows: dry	10	8	25
Heifers / oxen	6	9	0

Table 6.4 Calculated biomass (kg km^{-2}) of large ungulate species occurring at study units.

Species	**Study units**								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**Mean**
Blesbok	0.0	21.1	0.0	0.0	0.0	0.0	0.0	22.1	**5.4**
Blue wildebeest	168.4	0.0	153.1	0.0	218.2	218.4	355.3	290.2	**175.5**
Burchell's zebra	0.0	0.0	181.7	724.2	108.3	460.8	96.4	125.3	**212.1**
Cattle	1 318.7	0.0	1 037.4	0.0	0.0	0.0	1 087.6	0.0	**430.5**
Eland	255.4	0.0	472.9	0.0	561.5	368.0	128.3	333.4	**264.9**
Gemsbok	194.3	24.2	549.5	0.0	526.4	84.0	128.8	106.6	**201.7**
Giraffe	0.0	0.0	154.8	287.2	758.1	662.4	0.0	0.0	**232.8**
Impala	383.2	372.9	471.3	227.5	118.9	1 027.7	418.5	404.2	**428.0**
Kudu	479.4	564.2	457.9	647.4	326.5	653.3	874.6	446.5	**556.2**
Ostrich	0.0	0.0	0.0	178.0	218.2	0.0	0.0	0.0	**49.5**
Red hartebeest	0.0	0.0	89.7	0.0	41.9	0.0	87.0	95.7	**39.3**
Warthog	36.1	100.2	58.9	156.1	72.6	8.0	90.4	82.6	**75.6**
Waterbuck	56.9	118.0	325.7	355.5	437.9	0.0	0.0	44.6	**167.3**
Total	**2 892.4**	**1 200.6**	**3 952.9**	**2 575.9**	**3 388.5**	**3 482.6**	**3 266.9**	**1 951.2**	**2 838.8**

derived relationship between mean annual rainfall and large herbivore biomass of 12 wildlife and pastoral areas in east and southern Africa. The relationship holds for areas with a mean annual rainfall of up to 700 mm (Coe *et al.* 1976). The regression equation is:

$$\textbf{Large herbivore biomass (kg km}^{-2}\textbf{)} = 8.684 \pm 2.28 * \textbf{(Annual rainfall in mm)} - 1\,205.9 \pm 156.6$$

In this study, large herbivore biomass was predicted from the regression equation (Coe *et al.* 1976) using long term annual rainfall records of proximate official weather stations (Table 2.3). The predicted mean, upper and lower limits (Coe *et al.* 1976) were compared to the actual biomass calculated for study units (Figure 6.1). According to Figure 6.1, study units were stocked substantially higher than the mean predicted values of Coe *et al.* (1976), with the exception of study units 2, 4 and 8 which were stocked at lower rates. Factors which probably contributed to the relatively high biomass of the study units include: (i) the generally lower animal unit mass used by Coe *et al.* (1976) than that indicated by Table 6.1, (ii) different census techniques used, (iii) low large predator density of the study area (personal observation) and (iv) the tendency of confined populations to increase beyond natural densities (Owen-Smith 1982).

The relatively large contribution of browse in relation to grass should probably be reflected in a corresponding shift in favour of browsing animal biomass (Peel *et al.* 1991b), especially in the light of ample evidence for the negative relationship between grass and woody standing crop (Moore & Odendaal 1987; Smit 1994; Smit & Swart 1994). Browser biomass of study units in relation to the bulk and concentrate grazer biomass components was calculated following the classification of Mentis (1988) according to feeding strategy. Browser biomass contributed substantially to the total biomass of study units and in some units approached half of the total large herbivore biomass (Figure 6.2). The relatively high proportion of browser biomass also departed considerably from the recommended composition of 2 Animal Units bulk grazers: 2 Animal Units concentrate grazers: 1 Animal Unit browser proposed by (Mentis 1988) for savanna areas.

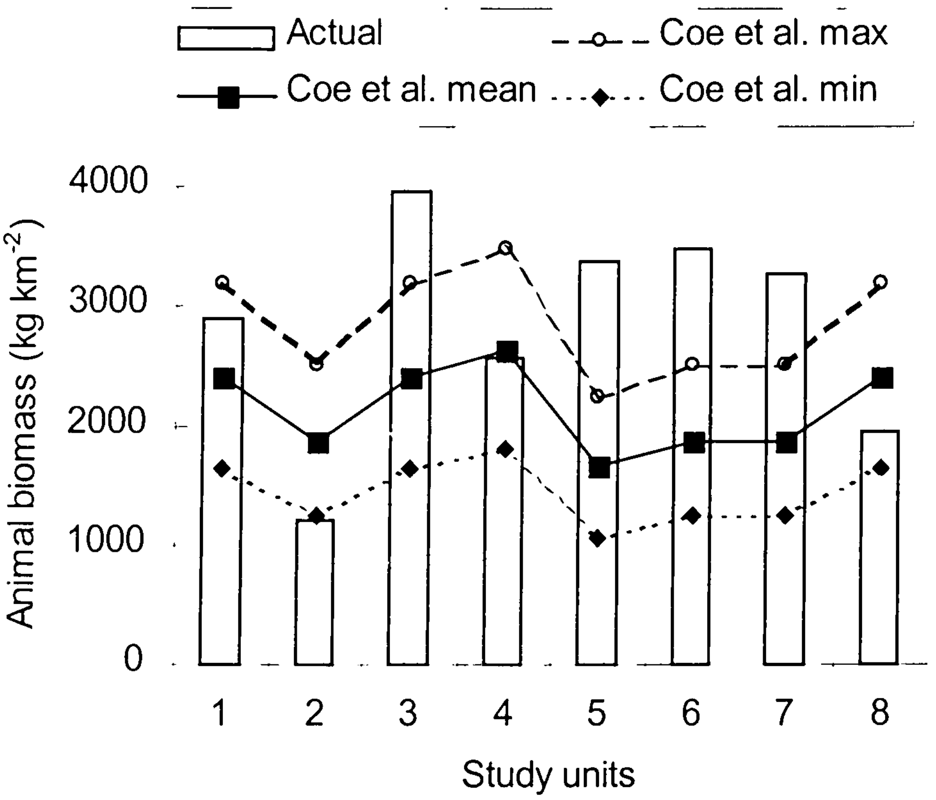

Figure 6.1 The calculated actual animal biomass (histobars) in relation to the predicted animal biomass calculated from Coe *et al.* (1976) (Solid line). Upper and lower limits (Coe *et al.* 1976) are indicated by intermittent lines.

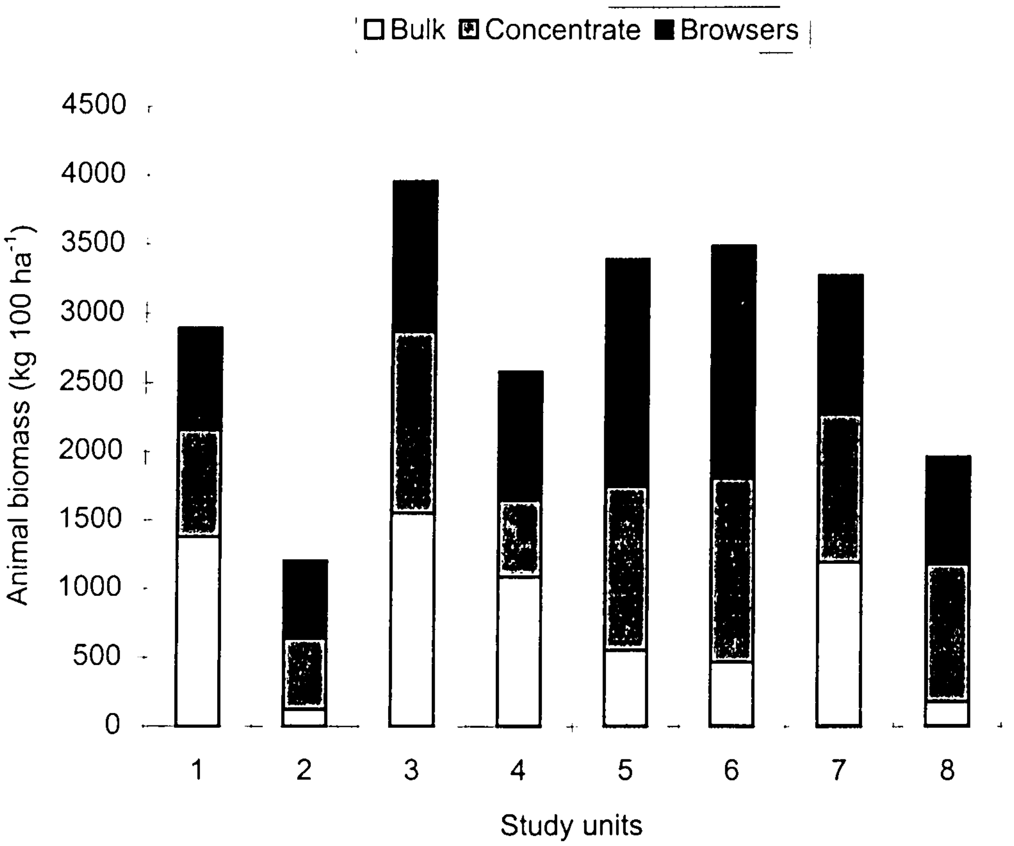

Figure 6.2 Large animal biomass (kg km^2) calculated for study units according to bulk feeder, concentrate feeder and browser biomass.

6.3.4 Stocking rates

Wild ungulate's stocking rates are based on the aerial counts which are reported to represent undercounts in savanna areas (Bothma *et al.* 1990; Van Hensbergen *et al.* 1996). This will result in underestimated stocking rates. As information on the accuracy of helicopter game counts in southern African savanna are scant and are confounded by variation in the techniques used (e.g. strip width, number of observers and time of the year conducted), counted game numbers were not weighted. This should be acknowledged if comparisons are made with related studies and in extrapolating results.

6.3.4.1 GRAZING STOCKING RATES

The grazing stocking rates expressed in LSU 100 ha^{-1}, of different large herbivore species are shown in Table 6.5. Total grazing stocking rates ranged from 1.61 LSU 100 ha^{-1} (62.1 ha LSU^{-1}) for study unit 2 to 7.27 LSU 100 ha^{-1} (13.8 ha LSU^{-1}) for study unit 3. The mean stocking rate was calculated at 4.64 LSU 100 ha^{-1} (21.6 ha LSU^{-1}). The mean grazing stocking rates calculated for these study units were considerably lower than that reported by Peel (1990) for a comparable study in the Mixed Bushveld of the Thabazimbi district. The mean grazing stocking rate calculated for his study units, excluding an ungrazed control, was 9.13 LSU 100 ha^{-1}. The higher stocking rates are probably partially explained by the higher mean rainfall received in his study area.

Grazer stocking rates calculated for this study's units (mean 4.64 LSU 100 ha^{-1}) were mostly stocked lower than the Department of Agriculture's grazing capacity recommendations for the study area. These ranged from 6.7 LSU 100 ha^{-1} in the north-west to 8.3 LSU 100 ha^{-1} in the south-east of the study area (Anonymous 1986). The drought experienced during 1997/98 might have contributed to the lower grazing stocking rates, causing reduced survival and reproduction rates and resulting in the timely removal of animals through management practises.

Table 6.5 The stocking rate (LSU 100 ha^{-1}) of grazing large herbivore species occurring at study units.

Species	**Study unit**							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Grazers								
Blesbok	0.00	0.08	0 00	0.00	0.00	0.00	0.00	0.08
Blue wildebeest	0.47	0.00	0.43	0.00	0.61	0.61	1.00	0.81
Burchell's zebra	0.00	0.00	0.49	1.94	0.29	1.24	0.26	0.34
Cattle	3.47	0.00	2.66	0.00	0.00	0.00	2.72	0.00
Ostrich	0.00	0.00	0.00	0.57	0.69	0.00	0.00	0.00
Red hartebeest	0.00	0.00	0.28	0.00	0.13	0.00	0.27	0.30
Warthog	0.16	0.43	0.26	0.68	0.31	0.03	0.39	0.36
Waterbuck	0.15	0.32	0.87	0.95	1.17	0.00	0.00	0.12
Mixed feeders								
Eland	0.17	0.00	0.31	0.00	0.37	0.24	0.08	0.22
Gemsbok	0.37	0.05	1.05	0.00	1.00	0.16	0.25	0.20
Impala	0.75	0.73	0.92	0.44	0.23	2.01	0.82	0.79
Total LSU 100 ha^{-1}	**5.54**	**1.61**	**7.27**	**4.58**	**4.80**	**4.29**	**5.79**	**3.22**
ha LSU^{-1}	**18.1**	**62.1**	**13.8**	**21.8**	**20.8**	**23.3**	**17.3**	**31.1**

6.3.4.2 BROWSER STOCKING RATES

The total browser stocking rate of the study units ranged between 5.89 and 12.19 BU 100 ha^{-1} (mean 7.78 BU 100 ha^{-1}) (Table 6.6). This represents a higher density than the browser stocking rates calculated over an eight year period by Dekker & Van Wyk (1999) for a game production system in the Mopani Veld north of the Soutpansberg mountain range. Their browser stocking rates were calculated using helicopter counts and the substitution rates proposed by Dekker (1997). Their rates range from 3.3 to 9.7 BU 100 ha^{-1} (mean 6.5 BU 100 ha^{-1}). Browser stocking rates have been recalculated for seven game production units in the Mixed Bushveld by using the helicopter count data of Peel (1990) and the substitution ratios presented earlier in Table 6.1. The browser stocking rates of the seven ranches range from 3.5 to 12.4 BU 100 ha^{-1} (mean 5.9 BU 100 ha^{-1}).

Table 6.6 displays the calculated stocking rates of browsing ungulate species occurring in study units. Of the browsing guild, kudu attained the highest mean browser stocking rate (3.97 BU 100 ha^{-1}), followed by impala (2.08 BU 100 ha^{-1}) and eland (0.98 BU 100 ha^{-1}) (Table 6.6). The total kudu stocking rate is the lowest at study unit 5 (2.33 BU 100 ha^{-1}) and the highest at study unit 7 (6.25 BU 100 ha^{-1}). Giraffe stocking rates, corrected for feeding height stratification, were only significant at study units 5 and 6 which had values of 1.14 and 1.00 BU 100 ha^{-1} respectively (Table 6.6). Of the mixed feeder class, impala had the highest browser stocking rates ranging from 0.58 BU 100 ha^{-1} (study unit 5) to 4.99 BU 100 ha^{-1} (study unit 6). The browser stocking rates of eland reached values of up to 2.09 BU 100 ha^{-1} at study unit 5. Browser stocking rates calculated for gemsbok were generally low, and were only significant at study units 3 and 5, which attained values of 1.06 and 1.02 BU 100 ha^{-1} respectively (Table 6.6).

The mean kudu stocking rate based on class numbers (Table 6.7) were higher (4.23 BU 100 ha^{-1}) than stocking rates based on a mean mass of an individual in a population (3.97 BU 100 ha^{-1}) (Table 6.6). Stocking rates based on the classes were assumed to reflect the impact of kudu on browse resources more accurately than stocking rates based on a mean mass of an individual in a population.

Table 6.6 The stocking rate (BU 100 ha^{-1}) of browsing ungulate species per study unit.

Species		Study units							
		1	2	3	4	5	6	7	8
Browsers									
Giraffe		0.00	0.00	0.23	0.43	1.14	1.00	0.00	0.00
Kudu		3.42	4.03	3.27	4.62	2.33	4.67	6.25	3.19
Mixed feeders									
Eland		0.95	0.00	1.76	0.00	2.09	1.37	0.48	1.24
Gemsbok		0.38	0.05	1.06	0.00	1.02	0.16	0.25	0.21
Impala		1.86	1.81	2.29	1.10	0.58	4.99	2.03	1.96
Total	**BU 100 ha^{-1}**	**6.61**	**5.89**	**8.61**	**6.15**	**7.16**	**12.19**	**9.01**	**6.60**
	ha BU^{-1}	**15.1**	**17.0**	**11.6**	**16.3**	**14.0**	**8.2**	**11.1**	**15.2**

Table 6.7 The stocking rate (BU 100 ha^{-1}) of kudu classes per study unit.

Species		Study units							
		1	2	3	4	5	6	7	8
Kudu: bull		1.11	0.35	2.10	1.91	0.69	0.60	1.84	0.98
Kudu: cows and juveniles		2.45	2.93	1.76	3.45	1.71	3.54	3.70	1.68
Kudu: juveniles		0.23	0.57	0.14	0.11	0.16	0.53	0.83	0.50
Total	**BU 100 ha^{-1}**	**3.79**	**3.85**	**4.00**	**5.47**	**2.56**	**4.67**	**6.37**	**3.16**
	ha BU^{-1}	**26.4**	**26.0**	**25.0**	**18.3**	**39.1**	**21.4**	**15.7**	**31.6**

6.4 CONCLUSIONS

The following general conclusions were evident from this investigation:

I. Impala, kudu and warthog occurred at all study units. Of all the species counted, impala were the most abundant followed by kudu.

II. Of the browsing guild, kudu attained the highest biomass and browser stocking rate estimates.

III. The herbivore biomass calculated from census data in the study area was high in comparison to the biomass predicted from mean annual rainfall (Coe *et al.* 1976).

IV. The mean browsing stocking rate (BU 100 ha^{-1}) calculated was higher than that calculated for a game production system in the Mopani Veld and for game ranches in the Mixed Bushveld. This might point to a high browser capacity of the study area or might indicate that browsers are currently overstocked in the study area.

V. The grazing stocking rates of the study units were in general lower than the recommendations of the Department of Agriculture for the study area. The conservative grazer stocking rates of study units are in line with the recommendation of Peel *et al.* (1991a) who proposed that grazer stocking rates in multi-species systems should be 50 % more conservative than the recommended agricultural stocking rates.

CHAPTER 7

FAECAL NITROGEN AND PHOSPHOROUS IN KUDU

7.1 INTRODUCTION

The nutritional status of an animal is determined by the quality of the diet which affects the survival rate and productivity of ungulates (Wrench, Meissner & Grant 1997). The use of faecal nitrogen (N_f) as an indicator of the nutritional status of ungulates in southern African savanna has been suggested in several studies (Erasmus, Penzhorn & Fairall 1978; Buys 1990; Grant, Meissner & Schultheiss 1995; Wrench, Meissner, Grant & Casey 1996; Wrench *et al.* 1997). Grant *et al.* (1995) recommend that faecal phosphorous (P_f) and N_f should be considered together as their excretion is linked.

The objectives of this investigation were:

I. to determine if kudu faecal N and P concentration were affected by the month in which samples were collected,
II. to determine if faecal N and P concentration were affected by the study unit where samples were collected,
III. to determine if faecal N concentration was related to poor physical condition and mortalities, and
IV. to determine if faecal N and P concentration were affected by the availability of supplementary forage during the dry season.

7.2 PROCEDURE

Faecal samples of kudu were collected at an approximately monthly basis from May 1999 to December 1999 from the study units. Fresh samples, less than 24 hours old, are required (Wrench *et al.* 1996). Thus only droppings still moist at the surface were collected. Samples were collected by locating animals from a vehicle or on foot. If droppings were not found in the vicinity of the first encounter, fleeing animals were tracked. Kudu often release droppings at the first opportunity when on the run. As kudu droppings can be confused with that of juvenile eland and giraffe, care was taken to ensure correct identification by referring to the tracks at the place of the droppings.

Fresh droppings were kept in paper bags and dried at 60 ^{0}C to constant mass. Dried samples were cleaned of soil particles and other debris clinging to the surface. Samples were screened from direct sunlight at all times. Faecal samples were milled in a Tecator mill with a 1 mm sieve attached. The mill was cleaned after each sample to avoid contamination of consecutive samples.

The nitrogen concentration of faecal samples (1 g each) were determined using the Kjeldahl method (AOAC 1984). Faecal N was analysed at the facilities of the Department of Animal Science of the University of the Free State. Samples were pooled for the phosphorous analysis. Pooled samples consisted of samples collected at the same study unit for the same month. Phosphorous concentration was analysed by Technicon Auto Analyzer procedures (Anonymous 1972; Bessinger 1988) after samples were digested by the Nitric-Perchloric Acid Digestion method (Zasoski & Burau 1977). The P analysis was executed by the Institute of Soil, Climate and Water[3] of the Agricultural Research Council.

7.3 STATISTICAL ANALYSIS

Statistical analyses involved a multifactor Analysis of Variance (ANOVA) to test for significant differences between faecal nitrogen and phosphorous concentrations as affected by the month of sampling, the study unit at which samples were collected and the availability of additional forage. A least significant difference (LSD) multiple range test was applied to indicate significant differences. Simple regression analysis was applied to correlate mean monthly N_f values with the pooled P_f values.

Statistical analysis was executed using the Statgraphics (1991) computer program. In the N_f data set, two samples were treated as outliers. These consisted of values that deviated substantially from data for the months June (study unit 2) and November (study unit 8) (Figure 7.1). The distribution of data was tested for normality and variance

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[3] Institute of Soil Climate and Water, Private Bag X79, Pretoria, 0001, Republic of South Africa

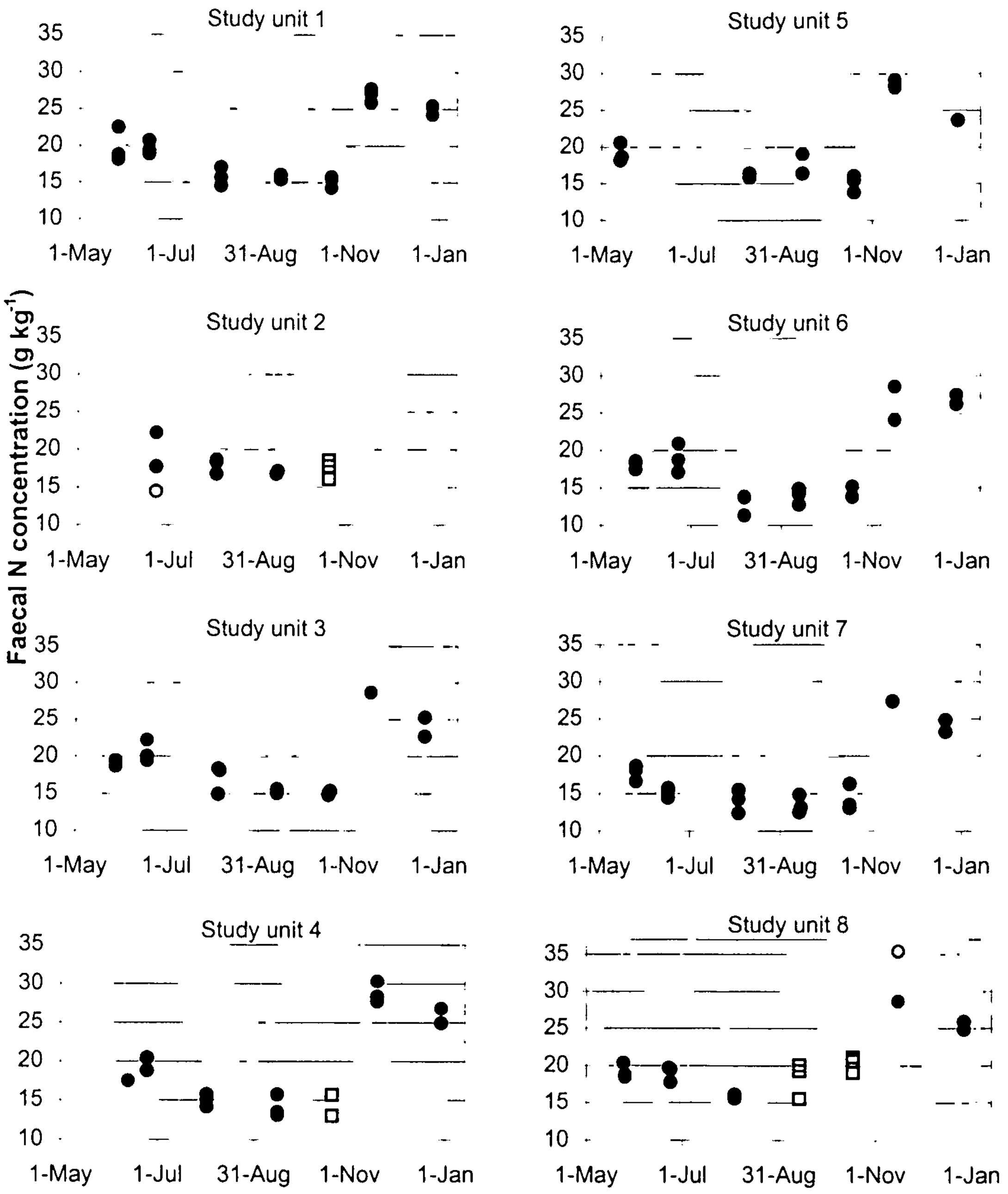

Figure 7.1 Kudu faecal N concentration (g kg^{-1}) values of samples collected at the study units from May 1999 to the end of December 1999. Squares indicate when additional forage in the form of Lucerne hay or concentrated forage were made available to kudu. Open circles indicate outliers.

differences between treatments. The faecal phosphorous data was not normally distributed and was consequently logarithmically transformed.

7.4 RESULTS

7.4.1 Faecal nitrogen

Kudu faecal N was significantly ($P<0.001$) related to the month in which samples were collected (Table 7.1). N_f collected for the months May and June did not differ significantly ($P<0.5$) from each other, nor did samples collected for the months August, September and October (Table 7.1). The N_f concentration of samples collected during November and December were significantly different from each other and the N_f concentration of other months. The N_f concentration followed a distinctive seasonal pattern (Figure 7.1). Faecal N concentrations were consistently low during the dry hot season (August to October), and showed the highest concentration in November. December showed the second highest values, while samples collected during May and June, the cool dry season, fell between the December and hot dry season values (Figure 7.1).

Faecal N concentration was significantly ($P<0.001$) affected by the study unit from which samples were collected (Table 7.1). The N_f concentration of samples collected at study units 4, 6 and 7 were significantly lower than samples collected at study units 2, 3, 5 and 8. Faecal N of samples collected at study unit 1 fall between these extremes but was not significantly different from study unit 4 and study units 2, 3, 5 and 8 (Table 7.1).

Samples that were collected at times when supplementary feeds were available to kudu had a significantly ($P<0.001$) higher N_f concentration than concentrations of samples collected when no supplements were available (Table 7.1).

7.4.2 Faecal phosphorous

Kudu faecal P was significantly ($p<0.001$) related to the month in which samples were collected (Table 7.2). The P_f concentration of samples collected in June, August and September was significantly ($P<0.05$) lower than P_f concentrations collected in May,

Table 7.1 Kudu faecal N as affected by month in which samples were collected, the study unit from which samples were collected and the availability of supplementary forage in the form of Lucerne hay or concentrated feeds as determined by multi-factor analysis of variance.

Month	**n**	**g N kg^{-1} (SE)**	**Study unit**	**n**	**g N kg^{-1} (SE)**	**Availability of supplements**	**n**	**g N kg^{-1} (SE)**
May	17	20.0±0.5^{a}	7	19	19.0±0.4^{c}	No supplements	117	19.6±0.2
June	20	20.0±0.5^{a}	6	19	19.7±0.4^{c}	Supplements	14	21.6±0.5
August	22	16.7±0.4^{b}	4	16	19.8±0.4^{cd}			
September	21	16.4±0.4^{b}	1	19	20.7±0.4^{de}			
October	23	16.1±0.3^{b}	3	17	21.0±0.5^{e}			
November	15	28.7±0.4	5	14	21.1±0.5^{e}			
December	13	26.3±0.5	8	17	21.4±0.4^{e}			
			2	10	21.9±0.5^{e}			
F-ratio=177.886 P<0.0000			F-ratio=6.731 P<0.0000			F-ratio=12.836 P<0.0005		

a,b,c,d,e - N concentrations with the same superscript do not differ significantly.

Table 7.2 Kudu faecal P, logarithmically transformed, as affected by month in which samples were collected, the study unit from which samples were collected and the availability of supplementary forage as determined by multi-factor analysis of variance.

Month	n	log P kg^{-1} (SE)	Study unit	n	log P kg^{-1} (SE)	Availability of supplements	n	log P kg^{-1} (SE)
May	6	0.84±0.11^{b}	1	7	1.00±0.11^{c}	No supplements	47	0.73±0.03
June	7	0.75±0.11^{ab}	2	4	0.86±0.11^{c}	Supplements	4	1.18±0.13
August	8	0.68±0.10^{ab}	3	7	0.91±0.11^{c}			
September	8	0.59±0.09^{a}	4	6	1.10±0.10^{c}			
October	8	0.87±0.08^{b}	5	6	1.02±0.11^{c}			
November	7	1.70±0.10	6	7	1.02±0.11^{c}			
December	7	1.27±0.10	7	7	0.82±0.11^{c}			
			8	7	0.91±0.08^{c}			
F-ratio=24.878 P<0.0000			F-ratio=1.275 P<0.2901			F-ratio=9.875 P<0.0033		

a,b,c - P$_f$ concentrations with the same superscript do not differ significantly.

November and December. The P_f concentrations of samples collected during May and October did not differ significantly. The P_f concentration of samples collected in December and November was significantly ($P<0.5$) different from each other and other samples (Table 7.2). Faecal P concentration also followed a distinctive temporal pattern. Concentrations gradually declined from May to August and reached the lowest point in September. An increase in P_f concentration was evident from September, and reached a peak in November. December concentrations were lower than November values but were higher than those collected in May (Figure 7.2).

No significant differences ($P>0.05$) occurred between the P_f concentrations from the different study units (Table 7.2).

Samples collected where supplementary feeds were available to kudu had a significantly ($P<0.001$) higher P_f concentration than samples collected where no supplements were available (Table 7.2).

7.4.3 Interaction between faecal phosphorous and nitrogen

A significant positive linear relationship ($r=0.84$, $P<0.001$, $n=47$) was established between the P_f (logarithmically transformed) and N_f concentration values (samples collected where supplements were available were omitted) (Figure 7.3). The intercept of the model was also significant ($P<0.001$). The relationship at low and high N concentrations, coinciding with N concentrations for the months September, October and November, was less close than for intermediate N concentrations (May, June and August).

7.5 DISCUSSION

The variation in kudu N_f concentration through the dry season cycle of 1999 resembled the pattern established for kudu on granite derived substrates in the Lowveld of South Africa (Grant, Peel, Zambatis & Van Ryssen 2000) and the calculated diet N of tamed kudu at Nylsvley (Owen-Smith & Cooper 1989). A fundamental difference between these study areas and the present study is that elevated N_f concentrations occur earlier

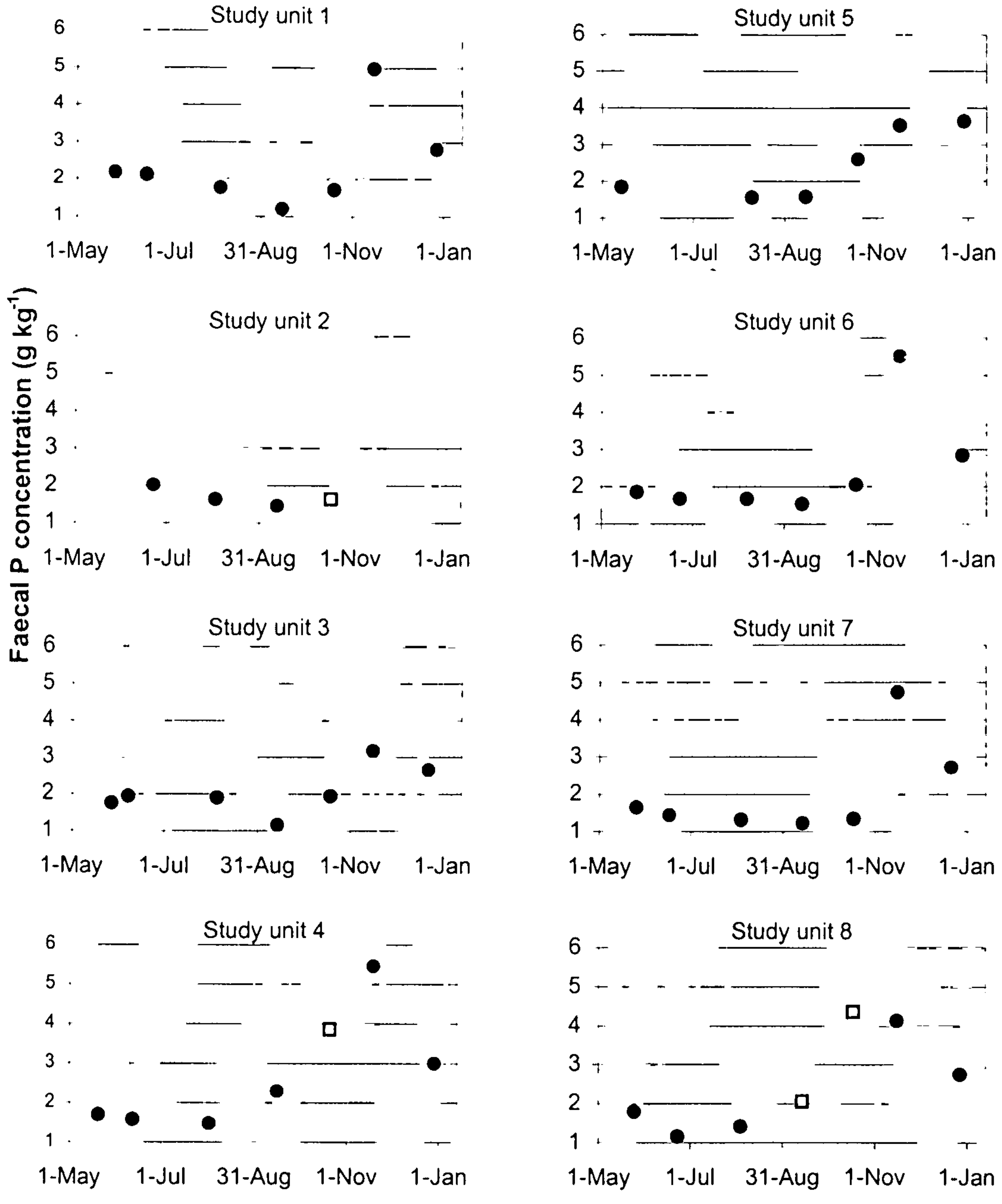

Figure 7.2 Kudu faecal P concentration (g kg^{-1}) values of pooled samples collected at study units from May 1999 to the end of December 1999. Squares indicate when additional forage in the form of Lucerne hay and concentrated forage were made available to kudu.

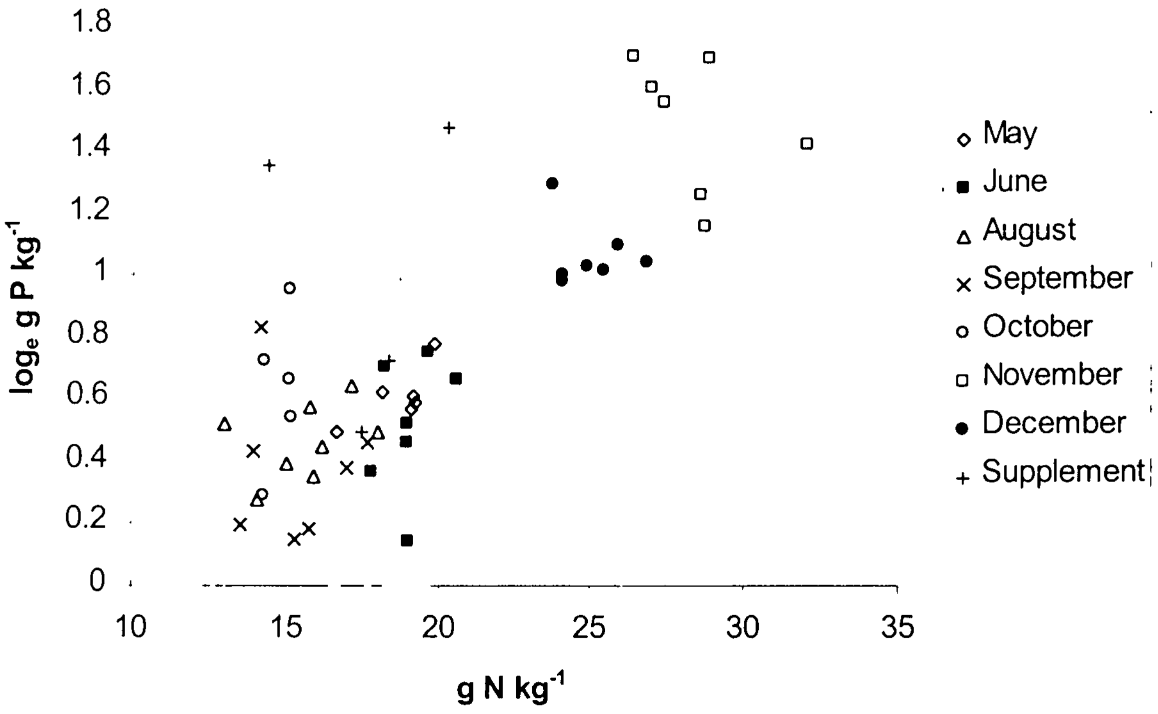

Figure 7.3 The relationship between N_f and P_f for different months of sampling and for samples when supplementary forage was available to kudu at study units.

in the new season compared to peak N_f concentrations observed in the present study. Elevated N_f concentrations in the new season are observed during September at Nylsvley and during October in the Lowveld, but were delayed till November in the study units. Owen-Smith & Cooper (1989) attributed the September peak in diet N to the high N content of new leaves and flowers of early flushing species. With the exception of a few species, mostly associated with drainage lines in the study units, leaf flush coincided with the first rains received in November in the study area. The dry season N_f of Lowveld kudu is also substantially higher than N_f values obtained from the study units, with the exception of September N_f concentrations on basalt in the Lowveld.

Differences between the faecal N concentration of the study units were significant ($P<0.0000$). Mean faecal N can be related to mortalities and physical condition patterns of kudu populations observed during the dry season of 1999. It is notable that the only study units where known mortalities occurred during the dry season of 1999 had low faecal N concentrations for the months August and September (Figure 7.4). At study units 4 and 7, the reported kudu mortalities amounted to 2 and 5 kudu respectively. The mortalities at study unit 4 occurred in spite of additional forage made available after a decline in the physical condition of especially mature male kudu was observed. Although these mortalities probably did not exceed the 'background' mortality rate (disease and accidents) of kudu populations, it appears that these kudu were comparatively worse off than their counterparts in the other study units. It was also evident from the air, at the end of August (game count) and from observations made from the ground during the late dry season, that individuals in study units 4, 6 and 7 were in poor physical condition compared to those in other study units (Figure 7.4). It is possible that mortalities at study unit 6 were to some extent prevented by the heavy losses experienced during the dry season of 1998. These losses could have pre-empted the population of animals with lower survival chances, e.g. older animals (Owen-Smith 1993b). At study unit 4, animals in poor condition consisted mainly of mature males while sub-adults and females were mainly in poor condition at study units 6 and 7. Grant *et al.* (1995) describe a significant positive correlation between the subjectively assessed condition of kudu and impala in the Lowveld, although no significant relationship was found for kudu in a concurrent study (Grant, *et al.* 2000). Samples collected at study units where kudu in poor condition were observed (and mortalities occurred) often had N_f concentrations below 15 g N kg^{-1} (Figure 7.4).

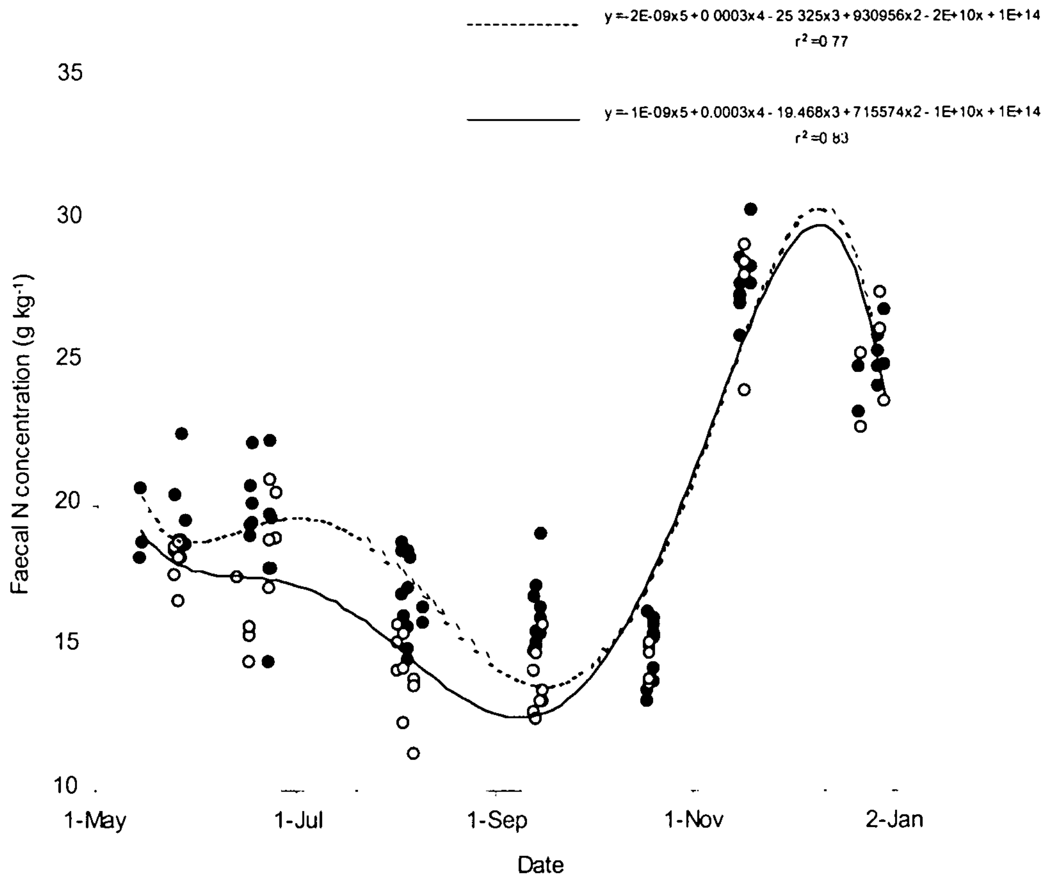

Figure 7.4 A comparison of the kudu faecal N concentration of samples collected in study units where individuals in poor physical condition were observed and some mortalities were reported (open circles) and samples collected in study units where no animals in poor physical condition were observed and no mortalities were reported (closed circles). The intermittent line represents a polynomial function fitted on closed circle data and the smooth line a polynomial function fitted on the open circle data. Samples collected when supplementary forage was available and two outlier data points were omitted.

Kudu P_f concentration at the study units followed the same dry seasonal pattern as the P_f analysed for kudu in the Lowveld (Grant *et al.* 2000), although concentrations were much lower in the study units. The lower P_f concentrations of study units could be explained due to the differences in the analysis. Grant *et al.* (2000) corrected samples for undigested material such as soil and silica, and expressed phosphorous thus in terms of organic matter. Faecal phosphorous values of study units were expressed in terms of dry faecal mass. This affects comparison of the study areas. It is, however, doubtful that the considerable difference between P_f concentration of the study units and that of the Lowveld can be explained only by the effect of inert substances in samples. This needs further investigation as low availability of P has been related to reproduction failure in large herbivore species (Grasman & Hellgren 1993).

The use of faecal N as a predictor of the nutritional status of browsers is reduced by the apparent effect of phenol compounds (tannins) on faecal protein concentration (Hobbs 1987; Wrench *et al.* 1997). Controlled feeding experiments with browsing mammals have established that the intake of phenol containing foodstuffs interferes in the prediction of diet N from faecal N (Mould & Robbins 1981; Sinclair, Krebs & Smith 1982; Wofford, Holechek, Galyean, Wallace & Cardenas 1985). Condensed tannins apparently bind with protein in the digestive tract of the animal and limit the assimilation of protein by the animal. The tannin-bound protein then passes through the digestive tract intact and raises the faecal nitrogen concentration thereby affecting the prediction of diet N from faecal N. It has been argued, however, that under natural feeding conditions browsers avoid foodstuffs high in phenol substances (Leslie & Starkey 1987; Caughley & Sinclair 1994) and that browsers will only consume phenol containing browse when preferred foods become unavailable (Owen-Smith 1993c). Owen-Smith & Cooper (1989) estimated that the concentration of poly-phenols in the diet of kudu increases from 3.3 in the wet season to 6.6 % in the dry season. Condensed tannin concentration varies only between 1.8 and 3.5 %. The peak in condensed tannin content is reached during late September to November when leaves of otherwise unpalatable species are consumed in bulk. In this study, the relationship between N_f and P_f showed larger variances for the months of September, October and November than other sampling months (Figure 7.3). This might be related to the increased intake of phenol containing foodstuffs during these months, although other factors might also be at play. For example, P uptake by plants, and hence P intake by animals, is affected by water stress (Grant *et al.* 2000).

The lower dry season N_f concentrations recorded in this study in comparison to that of Lowveld kudu might be related to the lower availability of crude protein (N) to kudu in the study area or the effect of increased intake of poly-phenols by kudu in dystrophic areas of the Lowveld. Woody species growing in nutrient poor soils, e.g. leached granite derived soils, are generally high in secondary metabolites (condensed tannins) (Owen-Smith & Cooper 1987). In nutrient limited soils, plant growth tends to be more restricted by nutrient limitations than by photosynthesis. This leads to an accumulation of carbohydrates that can be used for the synthesis of carbon based metabolites such as condensed tannins (Coley 1988; Bryant *et al.* 1991b). The soils of the study area are characteristically high in base status (Chapter 2), suggesting that low secondary metabolite concentrations are to be expected.

The feeding of supplements in the form of Lucerne hay (study units 2, 4 and 8) and concentrates (study unit 8) during the dry season was reflected in elevated N_f and P_f concentrations. Lucerne hay is high in crude protein and P (Van der Merwe 1970) while concentrates are formulated to supply game with sufficient N and P amongst other nutrients. The response of N_f and P_f concentration as a result of the high quality supplements points at the sensitivity of the technique as an indicator of nutritional stress in a wild ungulate species such as kudu.

7.6 CONCLUSIONS

The following conclusions were drawn from this investigation:

(i) Faecal N concentration was significantly related to the month of sampling. A general pattern emerged with the lowest N concentrations reached during the dry hot season (August to October) with a peak in November. The December concentration values showed the second highest values and samples collected during May and June intermediate values. The seasonal pattern in N_f resembled that of other deciduous savanna areas, although the new season peak in N_f was delayed relatively to other areas.

(ii) Study units differed significantly in kudu N_f concentration. Low dry hot season N_f concentrations were related to reported mortalities and poor physical condition in kudu.

(iii) Faecal phosphorous was significantly related to the month in which samples were collected but was not affected by the study unit where samples were collected.

(iv) Supplementary feeding significantly raised N_f and P_f values when fed during the dry hot season.

CHAPTER 8

RELATIONSHIPS BETWEEN KUDU FAECAL NITROGEN AND BROWSE RESOURCES

8.1 INTRODUCTION

It has been suggested that the availability of foliage in the dry season regulates kudu populations in deciduous savanna (Owen-Smith & Cooper 1985; Novellie 1992; Grossman 1994). By following the nutritional status of a number of kudu populations over a dry seasonal cycle and relating these to the availability of resources, key factors affecting the nutritional status of kudu can possibly be identified. Faecal nitrogen (N_f) has been suggested as an indicator of the nutritional status of a number of grazer species (Grant *et al.* 1995; Wrench *et al.* 1997) and also in a free ranging browser species (Sinclair *et al.* 1982). In controlled feeding experiments, protein-binding compounds such as condensed tannins have, however, been shown to interfere with the excretion of protein (Sinclair *et al.* 1982; Hobbs 1987; Wrench *et al.* 1997). This affects the reliability of N_f as an indicator of diet quality, and hence the nutritional status of the animals. This still has to be validated for free-ranging browsing animals (Caughley & Sinclair 1994). In addition, kudu tend to avoid condensed tannin-rich components (Cooper & Owen-Smith 1985; Cooper *et al.* 1988). In the current study, populations where mortalities and poor physical condition were observed were associated with relatively low dry season N_f values (Chapter 7). This hints at N_f concentration being a fair index of the nutritional status of kudu under the study conditions.

The objectives of this investigation were to establish the relationship between kudu N_f and the following variables:

I. total woody browse,
II. forb standing crop,
III. grass standing crop,
IV. woody leaf retention classes,
V. woody spinescent and unarmed classes per retention class,
VI. woody acceptability classes per retention class, and

VII. the evapotranspiration potential of the woody component.

8.2 PROCEDURE

8.2.1 Faecal nitrogen (N_f)

The N_f concentration values determined for faecal samples collected during 1999 (Chapter 7) were used for this component of the study. Mean N_f concentrations were calculated per sampling month per study unit. In addition, the mean N_f concentrations were calculated per study unit for the dry cool season (May and June) and for samples collected during the dry hot season (August, September and October). The N_f concentrations of samples collected during these respective periods were not significantly different from each other (Chapter 7). Samples collected when supplementary forage was available to kudu were omitted.

8.2.2 Kudu browser units (BU_{kudu})

Resource variables were expressed as the DM contribution of resource components relative to the BU_{kudu} per study unit. The BU_{kudu} represents the stocking rates calculated from kudu class numbers (Table 6.7).

8.2.3 Herbaceous resource availability

The standing crop estimates of the grass and forb component described in Chapter 5 were used. The herbaceous resources were expressed as standing crop (DM) available per BU_{kudu} for the grass and forb components respectively, per study unit.

8.2.4 Woody resource availability

The woody foliage resources below a height of two metres given in Chapter 4 were used. Woody resource variables were expressed as foliage DM available per BU_{kudu} Woody resources were subjected to different classifications of woody species based on the foliage retention period, rainfall season acceptance and the presence or absence of physical deterrents (Appendix A). Variables used in the analysis consisted of: (i) total foliage DM available per BU_{kudu}, (ii) the respective foliage DM contribution of the five leaf retention classes per BU_{kudu} (Ret_1-Ret_5 BU_{kudu}^{-1}), (iii) the foliage DM contribution of spinescent species per retention class per BU_{kudu} (S_1-S_5 BU_{kudu}^{-1}), (iv) the foliage contribution of unarmed species per retention class per BU_{kudu} (U_1-U_5 BU_{kudu}^{-1}), (v) the foliage contribution of the highly accepted species per retention class per BU_{kudu} (H_1-H_5 BU_{kudu}^{-1}), (vi) the foliage contribution of the intermediate accepted species per retention class per BU_{kudu} (I_1-I_5 BU_{kudu}^{-1}) and (vii) the contribution of the avoided species per retention class per BU_{kudu} (A_1-A_5 BU_{kudu}^{-1}).

8.2.5 Evapotranspiration potential of woody plants

The BECVOL-model estimates the evapotranspiration potential of woody plants based on the relationship between actual leaf volume at peak biomass and the spatial dimensions of tree canopies (Smit 1989a,b). The volume of woody canopies was calculated from seven canopy measurements per woody plant (Chapter 4). The evapotranspiration potential of woody plants is expressed as Evapotranspiration Tree Equivalents (ETTE). An ETTE is quantitatively defined as the equivalent of 500 cm^3 leaf material (Smit 1989a). Study unit ETTE ha^{-1} values were calculated from mean homogeneous vegetation unit values corrected for homogeneous unit size.

8.3 STATISTICAL ANALYSIS

Relationships between chemical and resource data were subjected to regression analysis. The analysis involved simple and multiple regression analysis as well as stepwise variable selection analysis (Statgraphics 1991). For the stepwise variable selection analysis, a confidence level of 95 % and an F-value of 4 (forward selection) were used to determine which variables should be included in the model (Statgraphics 1991). Where browse resource data overlapped as a result of different classifications of the same data, separate analysis were executed on these data sets. In cases where many variables were included in the analysis, variables were tested in different combinations to determine the most important ones. Some components were absent at certain study units, and invariably occurred at low levels where they did occur. Variables with 5 or more zero values were consequently not included in the analysis. These consisted of the U_4 BU_{kudu}^{-1}, H_4 BU_{kudu}^{-1}, I_5 BU_{kudu}^{-1}, A_1 BU_{kudu}^{-1}, A_2 BU_{kudu}^{-1}, A_4 BU_{kudu}^{-1} and A_5 BU_{kudu}^{-1} variables.

Regression analysis was performed on normal and logarithmically (natural) transformed data. Zero data values were replaced by the value 0.1 before transformation (logarithm of 0 can not be calculated). Independent variables selected or significantly related to dependent variables (N_f) were subjected to correlation analysis in order to test for interdependence (Appendix B).

8.4 RESULTS

8.4.1 Transformation of data

The logarithmically transformed browse data, in most cases, resulted in closer relationships than the data not subjected to transformation. An asymmetric relationship was expected where only a part of the data range represents the limited resources. Resource density above an inflection point would not be reflected in an incremental increase in N_f. It is likely, however, that some of the resource data used in the analysis did not include the upper end of the food supply. A linear relationship probably applied under these circumstances. The low number of observations (n=8) made the interpretation of individual variable distribution patterns difficult. It was thus assumed that all food related relationships were best described by logarithmic transformation (Browse resource variables referred to in the text indicate logarithmic transformed data). The ETTE ha^{-1} data represents normal data.

8.4.2 Main forage resource components

Of the main forage resource components available to kudu during the wet season of 1998/99, the best relationships (simple regressions) were evident between woody leaf DM availability per BU_{kudu} and N_f for the DC and DH seasons and the month of November, although these were not significant ($P>0.05$) (Table 8.1). Forb biomass, in conjunction with woody resources, improved the relationship ($P<0.05$) with N_f during the dry hot season (Table 8.1). Grass standing crop was not significantly ($P>0.05$) related to N_f concentration (Table 8.1). The negative relationships established for the December

Table 8.1 Correlation coefficients (r) of simple regressions calculated between mean kudu N_f concentration, collected at study units during the dry cool season, dry hot season, in November and December 1999, and logarithmically transformed woody foliage DM, forb standing crop and grass standing crop available per kudu (kg DM BU_{kudu}^{-1}). Eight observations were involved.

Resource component (kg DM) available per BU_{kudu}	**Correlation coefficient (r)**			
	Dry cool	**Dry hot**	**November**	**December**
Woody leaves	0.62	0.71*	0.51	-0.04
Forb standing crop	0.23	0.61	0.01	-0.78**
Grass standing crop	0.36	0.38	0.33	-0.52
Woody leaves + forb standing crop	0.53	0.76**	0.39	-0.39

*P<0.1, ** P<0.05, ***P<0.001

N_f concentration values, which was significant for the forb component ($P<0.05$), cannot be explained.

8.4.3 Seasonal availability of browse

The relationships (simple regression) between monthly kudu N_f, the temporal availability of woody browse resources (foliage retention classes) and forb standing crop are represented in Figure 8.1. The relationship between N_f and the availability of foliage of the retention class 1 component per BU_{kudu}, as represented by the correlation coefficients, weakened into the dry season but increased in importance in the new rainfall season (November and December 1999). Although not as clear as the case of the retention class 1 variable, the strength of the relationship between N_f and the availability of the leaf retention class 2 component per BU_{kudu} also showed a declining trend towards the end of the dry season. The relationships of both the leaf retention class 3 and 4 variables as well as the forb availability variable showed an initial decline in the relationship with N_f during June and an increase again as the dry season progressed. The relationship between N_f and the availability of evergreen species (leaf retention class 5) increased into the dry season.

A stepwise variable selection analysis selected only the $Ret_3\ BU_{kudu}^{-1}$ and $Ret_4\ BU_{kudu}^{-1}$ variables (Table 8.2).

8.4.4 Seasonal availability of spinescent and unarmed woody components

A stepwise variable selection analysis, where the dry cool season N_f concentration was chosen as the dependent variable, selected only the $S_1\ BU_{kudu}^{-1}$ variable in the model ($r^2=0.35$) (Table 8.3). This component consisted of the species *Commiphora africana, C. glandulosa, C. pyracanthoides* and *Dichrostachys cinerea*. The variation in the dry hot season N_f was best explained by a combination of the $S_3\ BU_{kudu}^{-1}$ and the $U_3\ BU_{kudu}^{-1}$ variables ($r^2=0.92$) (Table 8.3). Simple regression analysis indicated that the $U_3\ BU_{kudu}^{-1}$ variable explained more variance ($r=0.68$, $P=0.06$, d.f.=7) in dry hot season Nf than the $S_3\ BU_{kudu}^{-1}$ variable ($r=0.59$, $P=0.12$, d.f.=7). The U_3 functional group consisted of the following species; *Terminalia prunioides, Combretum apiculatum, Grewia flavescens, G. bicolor, G. monticola, Ehretia rigida, E. amoena, Spirostachys africana* and *Ochna*

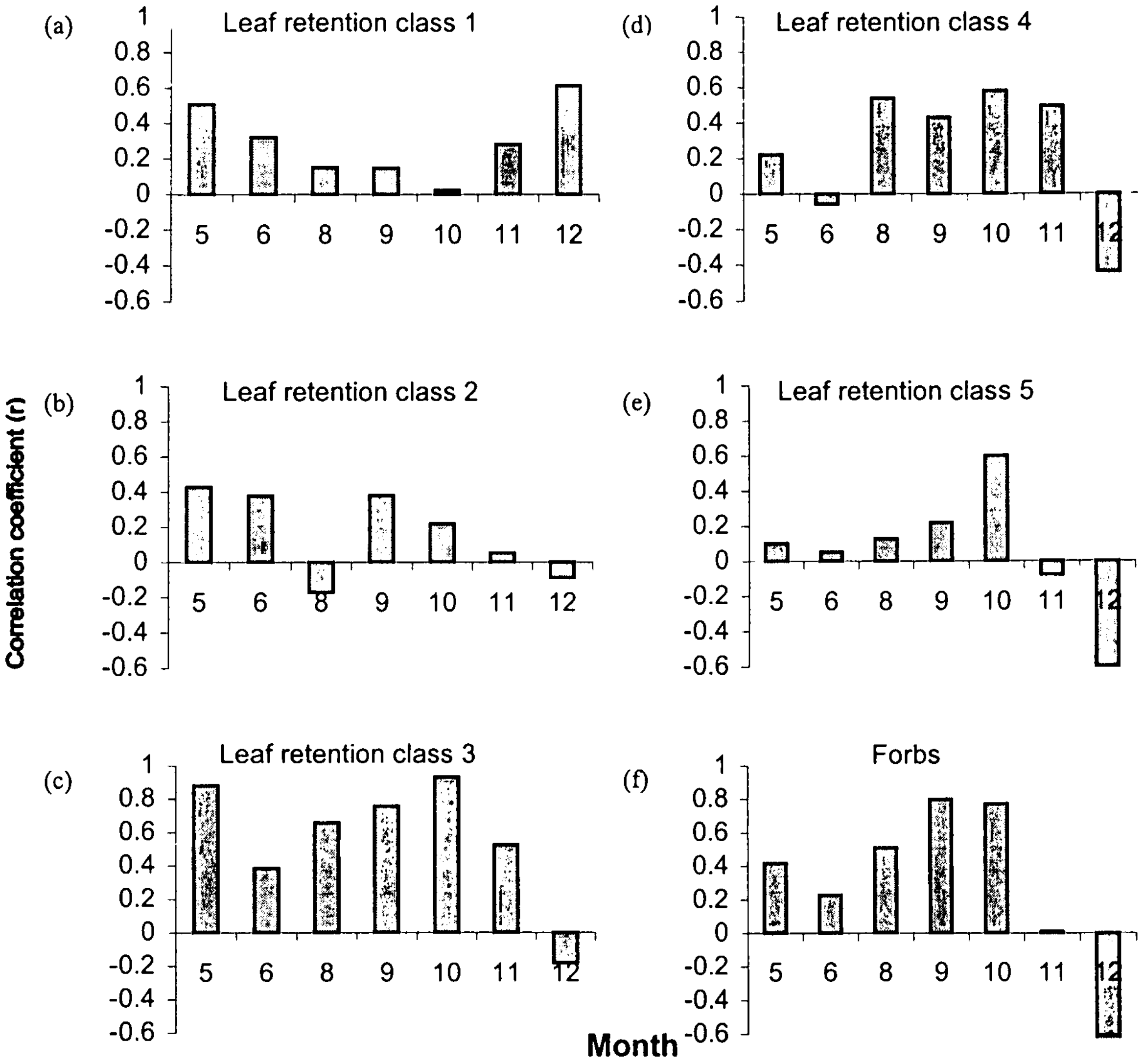

Figure 8.1 Correlation coefficients (r) derived for simple regressions between monthly N_f and (a) leaf retention class 1 DM per BU_{kudu}, (b) leaf retention class 2 DM per BU_{kudu}, (c) leaf retention class 3 DM per BU_{kudu}, (d) leaf retention class 4 DM per BU_{kudu}, (e) leaf retention class 5 DM per BU_{kudu} and (f) the forb standing crop per BU_{kudu}.

Table 8.2 Results of stepwise variable selection analysis involving the five leaf retention classes per BU_{kudu} variables (Ret_1-Ret_5 BU_{kudu}^{-1})and the mean kudu N_f concentrations of the dry cool season, dry hot season, and the months November and December 1999 (dependant variables). Model coefficients derived for resource variables and the constant, number of observations involved and the coefficients of determination (adjusted) are shown. Columns indicate separate analysis. A confidence level of 95 % determined the inclusion of variables in the model.

Resource component (kg DM) available per BU_{kudu}	**Model coefficient**			
	Dry cool	**Dry hot**	**November**	**December**
Ret_3	-	1.77**	-	-
Ret_4	-	0.55*	-	-
Constant	-	-3.62	-	-
r^2	**0.00**	**0.71**	**0.00**	**0.00**
Number of observations (n)	**8**	**8**	**8**	**8**

*P<0.1, ** P<0.05, ***P<0.001

Table 8.3 Results of stepwise variable selection analysis involving the S_1-S_5 BU_{kudu}^{-1} and U_1-U_5 BU_{kudu}^{-1} variables and the mean kudu N_f concentrations of the dry cool season, dry hot season, and the months November and December 1999 (dependant variables). Model coefficients derived for resource variables and the constant, the number of observations involved and the coefficients of determination (adjusted) are shown. Columns indicate separate analysis. A confidence level of 95 % determined the inclusion of variables in the model.

Resource component (kg DM) available per BU_{kudu}	**Model coefficient**			
	Dry cool	**Dry hot**	**November**	**December**
S_1	0.80*	-	-	-
S_3	-	0.79**	-	-
U_3	-	1.77***	-	-
Constant	13.24**	-4.83*	-	-
r^2	**0.35**	**0.92**	**0.00**	**0.00**
Number of observations (n)	**8**	**8**	**8**	**8**

*P<0.1, ** P<0.05, ***P<0.001

inermis. The S_3 group included *Acacia grandicornuta, A. nebrownii, A. nigrescens, A. nilotica, Phaeoptilum spinosum, Ziziphus mucronata* and *Flueggea virosa* (Appendix A).

The November and December N_f values were not explained by any of the spinescent or unarmed variables at a confidence level of 95 %.

8.4.5 Seasonal availability of acceptability classes

Of the acceptability class variables the dry hot season N_f had the highest correlation (r^2=0.72) with a combination of the I_3 BU_{kudu}^{-1} and A_3 BU_{kudu}^{-1} variables (Table 8.4). The variation in dry cool season N_f was not explained by any of the acceptability class variables. However, a model involving the H_2 and H_3 BU_{kudu}^{-1} variables ($P<0.05$) become significant if study unit 4 was omitted from the analysis (Table 8.4). These components consisted of the species *Grewia villosa, Combretum mossambicense, Cordia monoica, Terminalia prunioides, Combretum apiculatum, Grewia flavescens, Ehretia rigida* and *Spirostachys africana*.

The November and December N_f values were not explained by resource components defined by the classification based on acceptability and foliage retention.

8.4.6 Evapotranspiration Tree Equivalents (ETTE ha^{-1})

ETTE ha^{-1} was not significantly related ($P>0.05$) to monthly N_f, dry cool season N_f or dry hot season N_f concentration.

8.5 DISCUSSION

Kudu are largely dependent on woody browse resources during the dry season (Conybeare 1975; Owen-Smith & Cooper 1989). The inclusion of the forb component with the woody component, however, improved the relationship with the dry hot season N_f (Table 8.1). Novellie (1983) indicated that kudu's preference for forbs do not diminish during the dry season in the Kruger National Park. In contrast, forbs are eaten less by kudu in Nylsvley during the dry season (Owen-Smith & Cooper 1985, 1989). It is postulated that kudu favour forbs during the dry season, providing that a high intake rate

Table 8.4 Results of stepwise variable selection analysis involving the H_1-H_5 BU_{kudu}^{-1}, I_1-I_5 BU_{kudu}^{-1} and A_1-A_5 BU_{kudu}^{-1} variables and the mean kudu N_f concentrations of the dry cool season, dry hot season, and the months November and December 1999 (dependant variables). Model coefficients derived for resource variables and the constant, the number of observations involved and the coefficients of determination (adjusted) are shown. Columns indicate separate analysis. A confidence level of 95 % determined the inclusion of variables in the model.

Resource component (kg DM) available per BU_{kudu}	**Model coefficients**			
	Dry cool	**Dry hot**	**November**	**December**
H_2	0.38**	-	-	-
H_3	0.92**	-	-	-
I_3	-	1.06**	-	-
A_3	-	1.94**	-	-
Constant	9.19**	-7.53	-	-
r^2	**0.79**	**0.72**	**0.00**	**0.00**
Number of observations (n)	**7**	**8**	**8**	**8**

*P<0.1, ** P<0.05, ***P<0.001

is maintained. At a low forb standing crop abundance the searching time associated with foraging on sparsely distributed forbs apparently deter kudu from actively selecting this forage component. This restriction is probably overcome in areas where forbs are abundant. Novellie (1983) estimated that the forb standing crop is 425 kg DM ha^{-1} in the Kruger National Park as opposed to only 10 kg DM ha^{-1} at Nylsvley (Owen-Smith 1994). The forb standing crop estimated for the study units was comparatively high (mean 213.5 kg DM ha^{-1}). This would explain why the forb component improved the relationship with the dry hot season N_f (Table 8.1).

Kudu N_f concentration over the dry season is apparently dependent on the relative availability of browse components during this time. The strength of the relationship (correlation coefficient) between monthly N_f and woody components that retained foliage only for a short period into the dry season (retention class 1 and 2) weakened into the dry season (Figure 8.1). On the other hand, an increasing trend was evident for components that retained foliage for longer periods into the dry season (foliage retention classes 3, 4 and 5) (Figure 8.1). The sharp increase in the strength of the relationship with the evergreen component's (Ret_5) foliage availability during the late dry hot season (September and October months) coincided with the time of the year when browse in the study area was at a minimum. The increasing trend in the relationship with the foliage retention class 3 component during the dry hot season might be related to the continued availability of dry leaves on species such as *Combretum apiculatum* and various *Grewia* species. These species contributed substantially to the foliage DM of this class. The phenological classification of woody species was according to the retention period of green foliage, and thus did not account for species that retained dry leaves after leaf colouring. Kudu apparently make little use of fallen leaf litter as a source of food, probably because of the low intake rate associated with eating fallen leaves from the ground (Owen-Smith & Cooper 1985). Dried leaves retained by plants overcome this restriction by offering a relatively higher intake rate. The higher correlation between the new season N_f (November and December N_f respectively) and the foliage availability of the retention class 1 component is probably related to the early foliage-availability of species in this group during the new season. Dekker & Smit (1996) indicate that species such as *Commiphora glandulosa, C. mollis* and *Lannea schweinfurthii* (classified as leaf retention class 1 species in this study), are the first to shed leaves, and also the first to flush during the new season in the Mopani veld. These species apparently flush independently of the first rains and will offer comparatively more foliage to kudu than species dependent on rainfall for new leaf development.

The negative correlation established between most of the browse components and December N_f concentration (Figure 8.1) are hard to explain. Only the Ret_5 BU_{kudu}^{-1} variable is significantly inter-correlated to the Ret_1 BU_{kudu}^{-1} variable ($r=-0.82$, $P<0.05$) (Appendix B), which may explain this variable's negative correlation with the December N_f. Suttie, Goodall, Pennie & Kay (1983) have demonstrated that red deer, which are nutritionally stressed during winter, show compensatory growth during the ensuing summer. It is thus possible that the negative correlation of the December N_f values might be linked to increased protein assimilation efficiency in nutritionally stressed kudu. This will explain why the December correlation coefficients of the leaf retention classes 4 and 5 and the forb component availability per BU_{kudu} approximate the inverse of the late dry hot season values (October) (Figure 8.1). It follows that kudu that are nutritionally stressed because of a short supply of these components during the late dry season will show an increased nutrient assimilation efficiency during the new season in order to restore lost body reserves. This needs, however, to be validated as it might have a bearing on the use of N_f as an indicator of the nutritional status of animals. The generally low correlation coefficients established between browse components and the June N_f concentration, points to the dependency of kudu on a specific resource component at a time that was not delimited by the leaf retention classification followed in this study.

The inclusion of the H_2 and H_3 BU_{kudu}^{-1} variables in the cool dry season model, if study unit 4 is excluded (Figure 8.2), suggests that kudu selected for high quality components at this time. Species such as *Flueggea virosa, Ziziphus mucronata* and *Grewia flavescens* are high in crude protein (Owen-Smith & Novellie 1982; Cooper *et al.* 1988) although *Combretum apiculatum*, which contributed substantially to the H_3 class, has a moderate crude protein content (Novellie 1983; Bonsma 1976; Groenewald, Joubert & Tolken 1967 cited by Meissner, Zacharias & O'Reagain 1999). It is possible that kudu select these components for other reasons than high protein content and that a relationship emerged because of the interrelationship of N content with other nutritional factors. Owen-Smith & Cooper (1989) estimated that the metabolisable energy intake of kudu peak during June. This is partly attributed to an increased intake rate. They

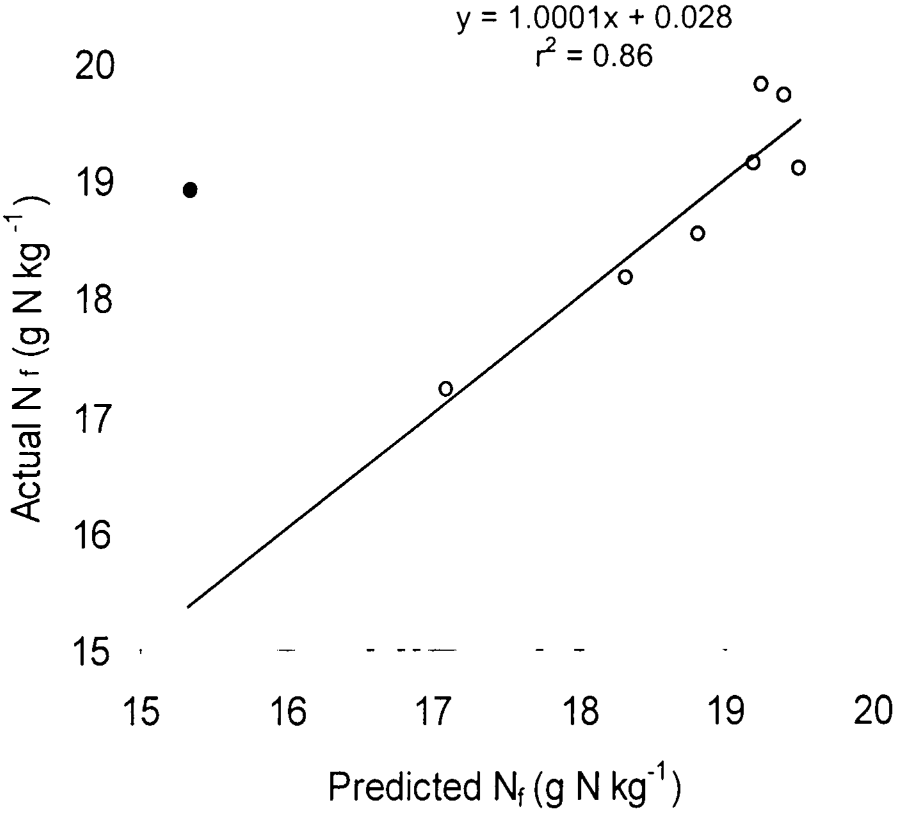

Figure 8.2 Dry cool season N_f concentration in relation to predicted N_f values (circles) calculated form the multiple regression analysis function incorporating the logarithmically transformed H_2 BU_{kudu}^{-1} and H_3 BU_{kudu}^{-1} variables. The closed circle indicates the data point calculated for study unit 4, showing its deviation from the prediction (line).

postulated that this might cause fat deposits that would be needed to bridge the nutritional bottleneck period characteristic of deciduous savanna. This also corresponds with the live mass of kudu bulls and fat deposits on the kidneys, which peak in June at the Langjan Nature Reserve (study unit 5) (Huntley 1971). The dry cool season N_f concentration at study unit 4 was relatively high in spite of the low availability of H_2 and H_3 components. This deviation from the predicted model function (Figure 8.2) derived for the other study units, suggests that kudu substitute these components with other high quality components that are more readily available at study unit 4. Species with high acceptance values that were particularly abundant at study unit 4 included *Commiphora africana, Ehretia rigida* and *Boscia albitrunca*. These species were either absent or occurred at low numbers at other study units. Some spinescent species, e.g. *Acacia tortilis* and *A. nilotica*, regarded as high in quality, were also abundant here relatively to other study units. A simple regression analysis involving all the highly accepted species' foliage contribution per BU_{kudu} was, however, insignificantly ($P>0.05$) related to DC N_f.

Whereas kudu apparently selected for high-quality components during the cool dry season, the dry hot season N_f variation was best explained ($r^2=0.92$) by a combination of the S_3 BU_{kudu}^{-1} and U_3 BU_{kudu}^{-1} variables (Figure 8.3). In the model, both variables were positively correlated with N_f. A model (multiple regression analysis) where the U_3 BU_{kudu}^{-1} variable also included the leaf DM contribution of the U_4 and U_5 groups (U_{3-5} BU_{kudu}^{-1}), explained the same amount of variation ($r^2=0.92$) in dry season N_f. Simple regression analysis established that the U_{3-5} BU_{kudu}^{-1} variable explained more variance ($r=0.69$) in the dry hot season N_f concentration than U_3 BU_{kudu}^{-1} alone ($r=0.68$). This suggests that the availability of the U_4 and U_5 components are also important in explaining dry hot season N_f, although they are not as influential as the foliage availability of the U_3 component which made a larger DM contribution compared to the U_4 and U_5 components. Owen-Smith & Cooper (1989) indicate that the intake rate of food by kudu becomes limiting during the late dry season as the availability of foliage on woody plants decline. Kudu subsequently adapt their feeding strategy in these trying times by striving to maintain a relatively high intake rate rather than selecting high quality components. This would explain why the unarmed group was closer related to the dry hot season N_f than the S_3 BU_{kudu}^{-1} variable in a simple regression analysis. The U_3 group was, however, more available (mean 8 846 kg DM BU_{kudu}^{-1}) than the S_3 group (mean 456

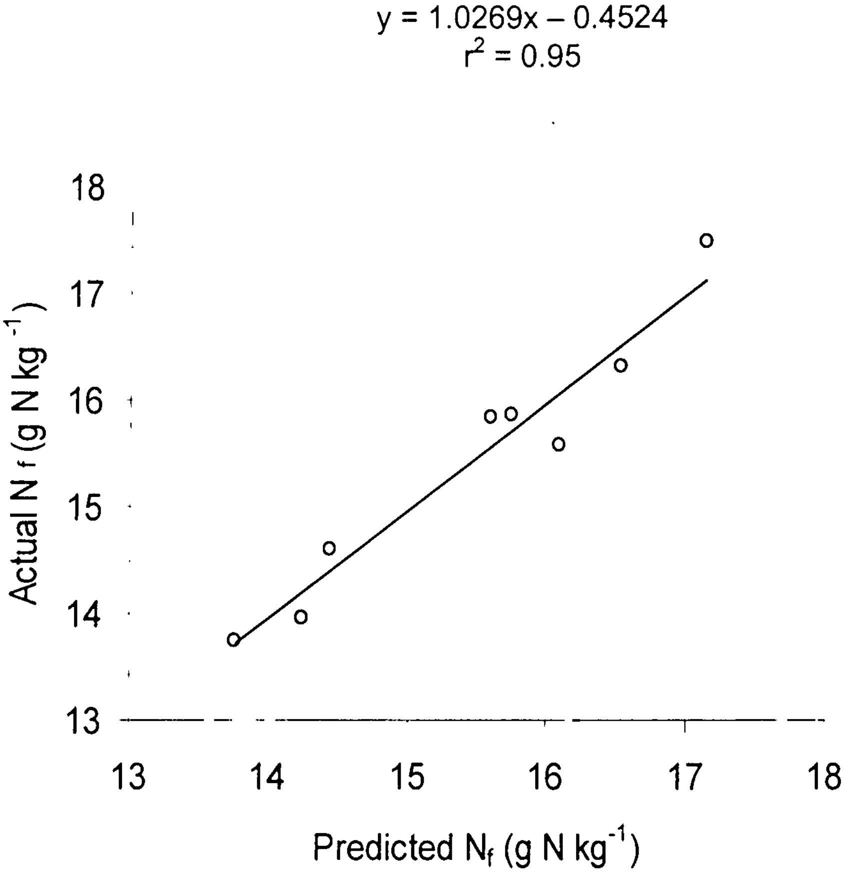

Figure 8.3 Dry hot season N_f concentration in relation to predicted N_f values (circles) calculated form the multiple regression analysis function, incorporating the logarithmically transformed $U_{3\text{-}5}$ BU_{kudu}^{-1} and S_3 BU_{kudu}^{-1} variables.

kg DM BU_{kudu}^{-1}). It is thus significant that the availability of the S_3 group was included in the model, considering the low levels involved.

The species *Grewia bicolor, G. subspathulata* and G. *monticola* consistently dominated the U_3 component of the study units. These species had low plant-based utilisation frequencies compared to other species in this study (Chapter 4). They are avoided by kudu elsewhere (Novellie 1983; Owen-Smith & Cooper 1987). The avoidance of these species seems to be related to the chemical properties of the foliage, as no obvious physical deterrents that might have influenced the acceptance thereof by kudu are apparent. The relationship between diet N and N_f may be modified by the presence of protein binding phenolic compounds (Sinclair *et al.* 1982; Hobbs 1987; Wrench *et al.* 1997). If these species have high protein-binding compound concentrations, then the positive relationships established between N_f and the U_3 BU_{kudu}^{-1} and U_{3-5} BU_{kudu}^{-1} variables might in part be related to the increased excretion of N as a result of the protein-binding effect. This would imply that the capability of secondary metabolites to bind protein is not significantly affected by senescence of the foliage. This was demonstrated in other species (Styles & Skinner 1997). The positive relationship between the availability of the U_3 group and the dry hot season N_f concentration, and the corresponding mortalities and poor condition observed in kudu populations with low dry hot season N_f, suggest that kudu benefited from the availability of these species.

The practical implications of these relationships established between kudu N_f and browse resources will be discussed further in Chapter 10.

8.6 CONCLUSIONS

The following general conclusions were drawn from this study:

(i) Of the main forage components (woody foliage, forb and grass standing crop) the level of woody foliage available per BU_{kudu} was the most related to N_f in kudu. The inclusion of the forb standing crop with woody foliage explained more variation in dry hot season N_f than woody foliage availability alone.

(ii) Kudu N_f was apparently linked to the relative availability of woody foliage and standing crop in the case of the forb component over the dry seasonal cycle.

Browse components that shed leaves early into the dry season became less important in explaining N_f variation as the dry season progressed, while components which became relatively more available as the foliage of other components failed, showed an increased ability to explain N_f variation as the dry season advanced. The forb component apparently also belonged to the latter group.

(iii) Cool dry season N_f variation was the best explained by the foliage availability of certain species with high rainfall season acceptability values. Study unit 4 was atypical in this regard, and deviated substantially from the established relationship. These components were probably substituted by other high quality components at this study unit.

(iv) The dry hot season N_f variation was best explained by a combination of the $U_{3\text{-}5}$ BU_{kudu}^{-1} and the S_3 BU_{kudu}^{-1} variables. The unarmed variable was more important in explaining variation in the dry hot season N_f than the S_3 BU_{kudu}^{-1} variable. This suggested that the availability of especially unarmed components during the late dry season influenced the nutritional status of kudu during the late dry season, although the availability of high quality spinescent components available well into the dry season also affected the nutritional status of kudu at this time.

(v) The evapotranspiration potential of woody plants was apparently not important as a determinant of kudu N_f over the dry seasonal cycle of 1999.

CHAPTER 9

RELATIONS BETWEEN KUDU MORTALITIES, AREA AVAILABLE, KUDU DENSITY AND BROWSE RESOURCES

9.1 INTRODUCTION

During the 1998 dry season severe, localised kudu die-off's were experienced in the study area. Population crashes occurred concurrent with the start of the study and study units were selected to represent a mortality gradient (Chapter 2). This gradient included study units where few deaths were reported and ranged to units where severe losses were experienced.

A relationship between mortalities and resource availability could contribute in identifying food-related determinants affecting kudu survival. This might have a bearing on the optimisation of kudu production in confined areas.

The objective of this investigation was to analyse the relationships between kudu mortalities and the following variables:

(i) total area available to the different populations,
(ii) kudu density before mortalities occurred,
(iii) woody browse available at peak biomass,
(iv) seasonal availability of woody browse,
(v) woody resource components resulting from a functional classification of species according to spinescense and acceptability, and
(vi) the evapotranspiration potential of the woody layer of study units.

9.2 PROCEDURE

9.2.1 Mortality categories

Study units were classified according to the severity of reported kudu mortality. Three categories were evident: (i) study units where few (<3) kudu died; (ii) study units where a moderate number of kudu (3-10) succumbed and (iii) study units where pronounced population crashes (>20 deaths) were reported (Figure 9.1). Accordingly study units 4, 5 and 7 represent the low mortality category (mortality rate 0 – 6 %), study units 1, 2 and 3 the intermediate mortality category (mortality rate 11 – 18 %) and study units 6 and 8 the high mortality category (mortality rate 43 – 45 %).

9.2.2 Study unit size and kudu density

The study unit size (Table 2.1) represents the total area available to the different kudu populations. Kudu densities were calculated from the helicopter game censuses discussed in Chapter 6. The census numbers were adjusted for reported mortality numbers and reductions, e.g. hunting spanning the dry season of 1998 and the time game censuses were conducted. Kudu juveniles counted, which were presumably born during the rainfall season of 1998/99, were omitted.

9.2.3 Browse resources

Woody browse resource variables were expressed as foliage DM available per kudu. The foliage DM below a height of two meters was used (Chapter 4). Kudu numbers used in the calculations represent estimates before the mortalities occurred. The woody foliage resources estimated in the study units (Chapter 4) were subjected to different classifications based on leaf retention period, rainfall season acceptability and the presence or absence of physical deterrents (Appendix A). The following variables were subsequently calculated; (i) total woody foliage DM available per kudu, (ii) the foliage DM contribution of the five leaf retention classes per kudu (Ret_1-Ret_5 $kudu^{-1}$), (iii) the foliage DM contribution of the spinescent species per retention class per kudu (S_1-S_5 $kudu^{-1}$), (iv) the foliage DM contribution of the unarmed species per retention class per kudu (U_1-U_5 $kudu^{-1}$), (v) the foliage DM contribution of the highly acceptable species per retention class per kudu (H_1-H_5 $kudu^{-1}$), (vi) the foliage DM contribution of the intermediate accepted species per retention class per kudu (I_1-I_5 $kudu^{-1}$) and (vii) the foliage DM contribution of the avoided species per retention class per kudu (A_1-A_5 $kudu^{-1}$). No species were allocated to the A_1 and A_4 groups (Appendix A) and these groups were consequently not subjected to analysis.

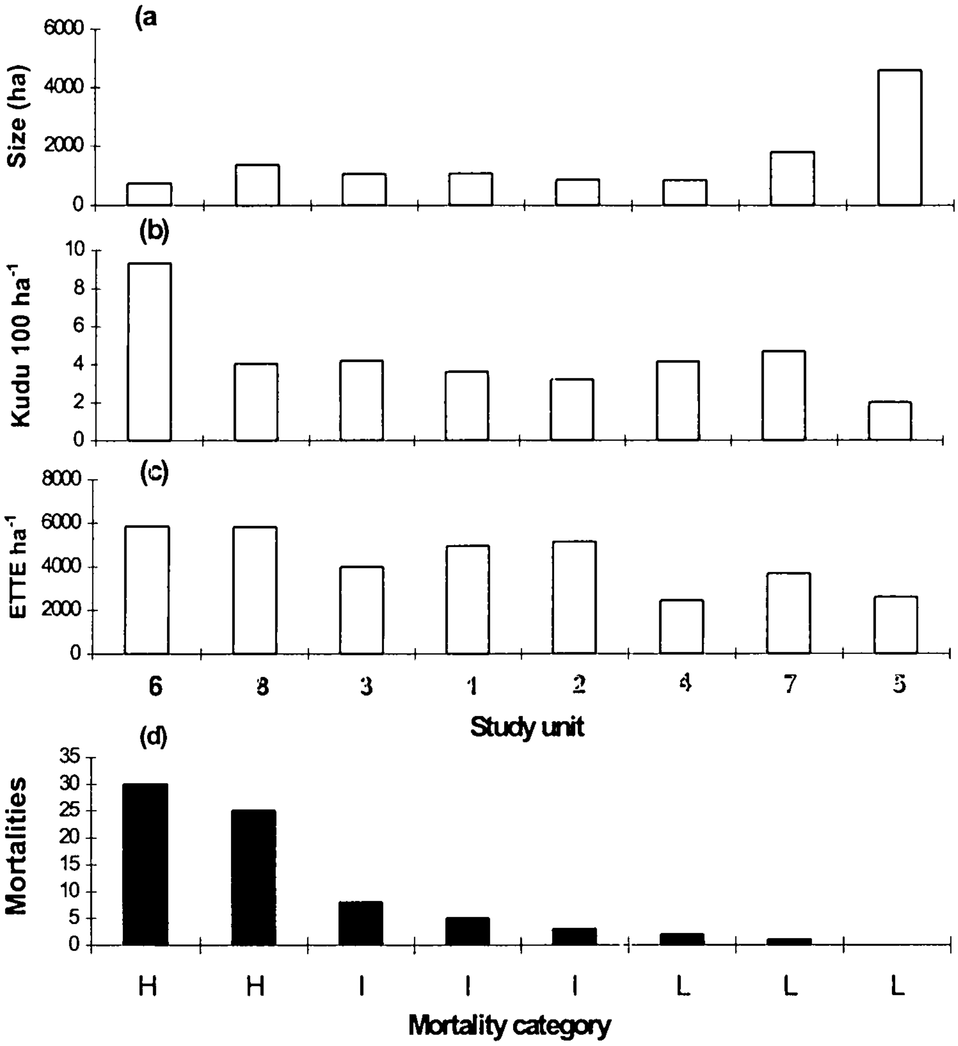

Figure 9.1 Comparison of study units in terms of (a) study unit size, (b) kudu density, (c) ETTE ha^{-1} and (d) kudu mortality category in order to show the relationship between these variables (H-high , I-intermediate, L-low).

9.2.2 Evapotranspiration potential of woody plants

The ETTE ha^{-1} values calculated per study unit were used (Chapter 8).

9.3 STATISTICAL ANALYSIS

One-Way Analysis of Variance (Statgraphics 1991) was applied to the data to test for relationships between mortality category and resource variables. By interpreting Normal Distribution Plots (Statgraphics 1991) variables were tested to assess whether variables could have come from a normal distribution.

Discriminant analysis (Statgraphics 1991) was performed on the data to determine functions consisting of more than one quantitative measurement (resource variables) that would help discriminate between mortality categories (high, intermediate and low mortality). Discriminant analysis, a multivariate technique, is useful to obtain a small number of variables that can be used to discriminate between categories (Statgraphics 1991). Variables used in the analysis consisted of study unit size (ha), kudu density (kudu 100 ha^{-1}), total woody foliage DM available per kudu, and the components resulting from the functional classification and ETTE ha^{-1}. The analysis was executed on both normal and logarithmically (natural) transformed data. As the logarithm of a zero value (e.g. 0 kg leaf DM $kudu^{-1}$) can not be calculated, observations with zero values were replaced with the value 0.1 ($\log_e 0.1 \approx -2.303$). Variables were tested for within group correlation (Discriminant analysis) and correlation between variables (Correlation analysis) (Statgraphics 1991). Multivariate normality was assumed for the data (Hair, Anderson, Tatham & Black 1992).

A significance level of $P<0.05$ was used for the Discriminant functions.

9.4 RESULTS

The logarithmically transformed woody resource variables approximated a normal distribution which was closer than the original data. The transformed woody resource data also resulted in Discriminant functions explaining more variance than the original data and conformed closer to the underlying assumption of equal variances between groups (Statgraphics 1991; Hair *et al.* 1992). Statistics reported on woody resource variables only included those performed on natural logarithmically transformed data. Other variables, ETTE ha^{-1}, study unit size and kudu density, represent data that were not subjected to transformation.

The relationships between study unit size, kudu density, ETTE ha^{-1} and reported kudu mortalities of study units are represented in Figure 9.1. Neither study unit size nor kudu density differed significantly ($P>0.05$) between mortality categories.

The relationships between total woody foliage availability, leaf retention class availability and reported mortalities are represented in Figure 9.2. Total woody foliage available at peak biomass per kudu for mortality categories were not significantly different (F-ratio = 0.775, P=0.51, d.f.=2). Of the retention classes available per kudu, only the Ret_5 $kudu^{-1}$ variable differed significantly ($P<0.01$) between mortality categories (Table 9.1). This variable correlated negatively with the mortality categories. Low levels of this resource component per kudu were associated with increased mortalities, while high levels coincided with few deaths.

Of the spinescent and unarmed classes available per retention class per kudu, only the U_5 $kudu^{-1}$ variable differed significantly between mortality categories at a significance level of $P<0.05$ (Table 9.2, Figure 9.3). Discriminant functions derived for different combinations of the S_3 $kudu^{-1}$, S_4 $kudu^{-1}$ and U_5 $kudu^{-1}$ variables resulted in close relationships (r=0.95-0.98, $P<0.05$) (Table 9.3). The positive correlation (r=0.79, $P<0.05$) between the S_3 $kudu^{-1}$ and S_4 $kudu^{-1}$ variables, however, prevents their inclusion in the same Discriminant analysis (Appendix C) (Hair *et al.* 1992). These groups were subsequently combined to form the S_{3+4} $kudu^{-1}$ group. The combined group was significantly (F-ratio = 5.506, $P<0.1$, d.f.=2) related to mortality category, and contributed to a discriminant function also including the U_5 $kudu^{-1}$ group (r=0.97, $P<0.05$) (Table 9.3). High levels of these components available per kudu were associated with low mortality and low levels with high mortality. The association between S_3 and S_4 groups could be attributed to the similar habitat requirements of the dominant species of these groups.

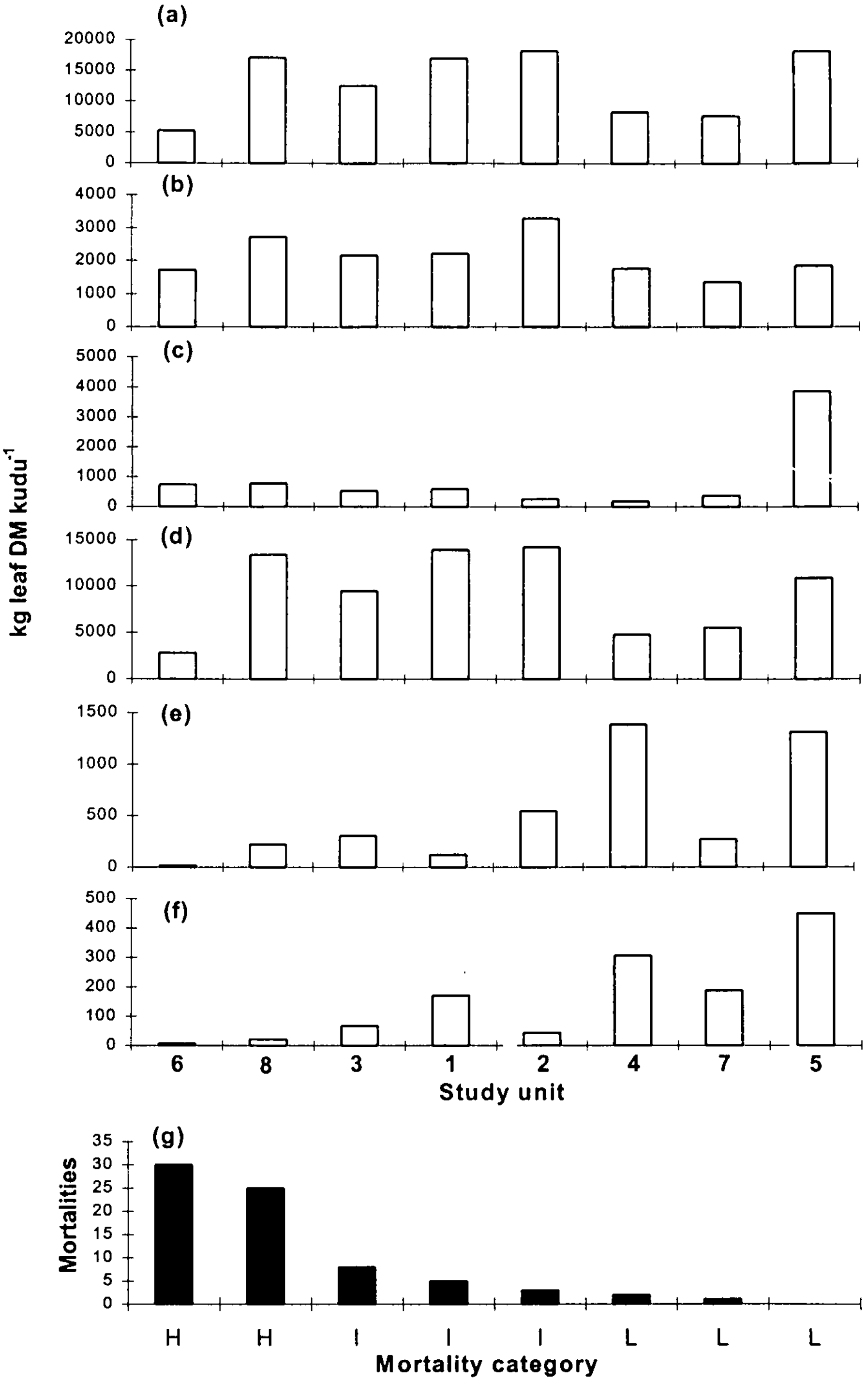

Figure 9.2 Comparison of study units in terms of the (a) total woody browse available per kudu, (b) leaf retention class 1, (c) leaf retention class 2, (d) leaf retention class 3, (e) leaf retention class 4 and (f) leaf retention class 5 available per kudu and (g) mortality category in order to show the relationship between these variables (H-high , I-intermediate, L-low).

Table 9.1 Summary statistics resulting from the One-Way Analysis of Variance for the different leaf retention classes available per kudu (Ret_1-Ret_5 kudu^{-1}). The between-group degrees of freedom, between-group mean squares, F-ratio and significance level are indicated.

Variable (kg DM kudu^{-1})	Between groups		F-ratio	Significance level (P)
	Degrees of freedom	Mean squares		
Ret_1	2	0.139	2.547	0.17
Ret_2	2	0.214	0.197	0.83
Ret_3	2	0.411	1.190	0.38
Ret_4	2	3.744	3.192	0.13
Ret_5	2	6.052	14.941	0.01

Table 9.2 Summary statistics resulting from the One-Way Analysis of Variance for the spinescent woody component availability per retention class per kudu (S_1-S_5 kudu^{-1}) and unarmed component availability per retention class per kudu (U_1-U_5 kudu^{-1}). The between-group degrees of freedom, between-group mean squares, F-ratio and significance level are indicated.

Variable	**Between groups**		**F-ratio**	**Significance**
(kg DM kudu^{-1})	**Degrees of freedom**	**Mean squares**		**level (P)**
U_1	2	1.298	3.411	0.12
U_2	2	0.595	0.807	0.50
U_3	2	0.425	1.293	0.35
U_4	2	1.344	0.090	0.92
U_5	2	15.234	13.676	0.01
S_1	2	0.814	1.125	0.39
S_2	2	0.234	0.076	0.93
S_3	2	4.543	5.372	0.06
S_4	2	4.101	4.112	0.09
S_5	2	2.422	0.266	0.78

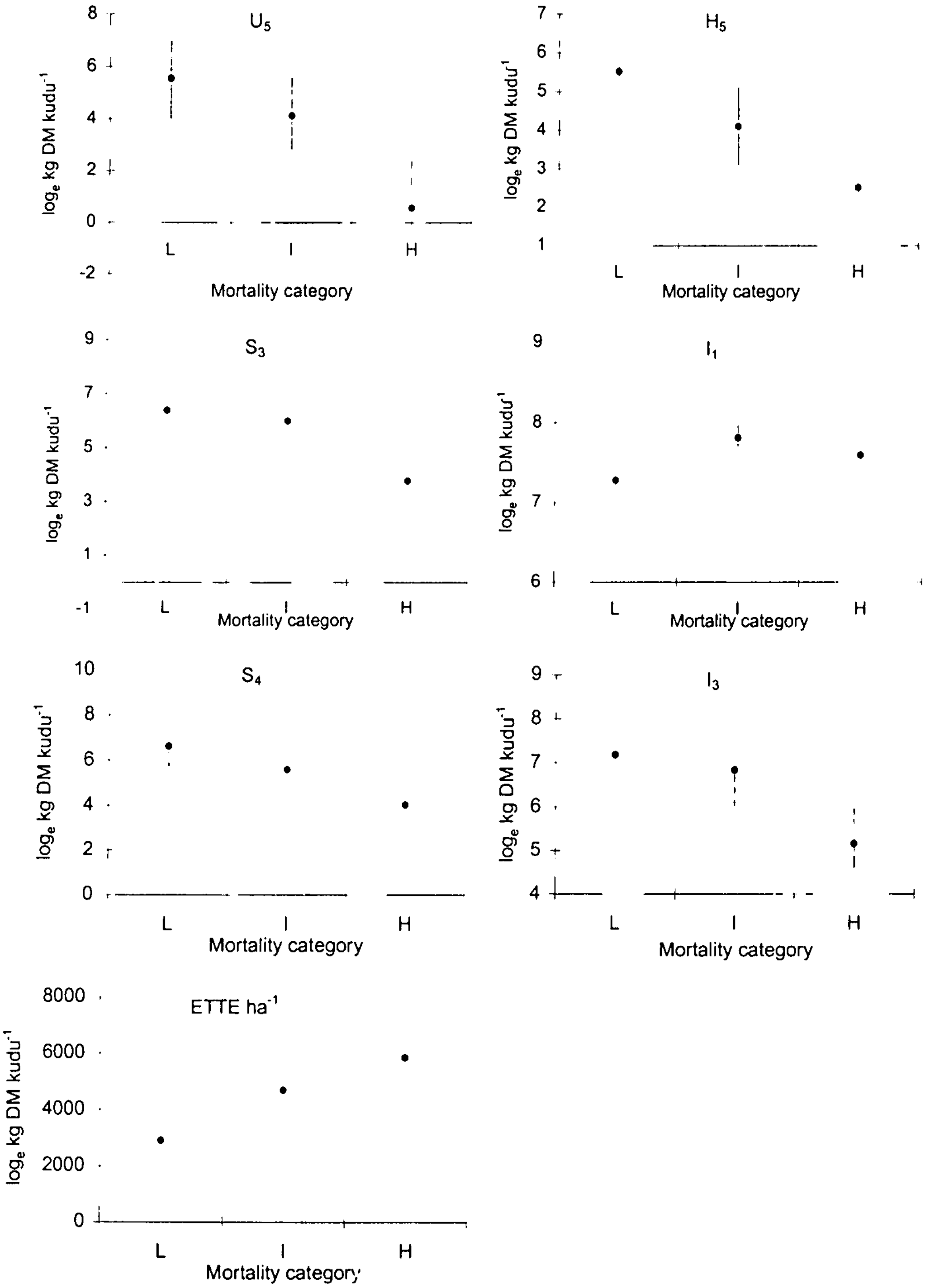

Figure 9.3 Mean values per mortality category for the U_5 group per kudu, S_3 group per kudu, S_4 group per kudu, H_5 group per kudu, I_1 group per kudu, I_3 group per kudu and ETTE ha^{-1}. Bars indicate 95 % confidence intervals. L-low mortality, I-intermediate mortality, H-high mortality).

Table 9.3 Discriminant functions derived for selected variables (significant differences ($P<0.1$) between variables allocated to the mortality categories). The standardised coefficients, canonical correlation coefficients and the significance level are indicated. Only discriminant functions with a significance level below 0.05 (5%) are displayed.

Standardised coefficient							ETTE	Statistic	
S_3	S_4	S_{3+4}	U_5	H_5	I_1	I_3	ha^{-1}	r	P
-0.704			-0.922					0.95	0.03
	-1.170		-1.309					0.98	0.01
-0.124	-1.093		-1.286					0.98	0.04
		-0.994	-1.127					0.97	0.01
	-1.116		-1.270				0.069	0.98	0.02
-0.630							0.932	0.95	0.01
	-0.092						0.959	0.93	0.046
		-0.816	-0.971				0.976	0.98	0.02
			-0.669				0.740	0.95	0.01
				-0.812	0.914	-1.031		0.97	0.03
				-0.818		-0.708		0.95	0.02
				-0.934	0.536			0.93	0.02
					0.974	-1.156		0.94	0.01
				-0.660		-0.518	0.675	0.97	0.04
				-0.673			0.786	0.96	0.02
					0.403		0.931	0.94	0.02
						-0.552	0.834	0.95	0.01

Of the acceptability components per retention class per kudu, only the H_5 kudu^{-1}, I_1 kudu^{-1} and I_3 kudu^{-1} variables varied significantly ($P<0.1$) between mortality categories (Table 9.4, Figure 9.3). Discriminant functions derived for combinations of these variables resulted in significant ($P<0.05$) but generally weaker discriminant functions ($r = 0.93-0.97$) as opposed to discriminant functions derived for the S_3 kudu^{-1}, S_4 kudu^{-1}, S_{3+4} kudu^{-1} and U_5 kudu^{-1} variables ($r = 0.95-0.98$). The function coefficients derived for the I_1 kudu^{-1} variable was consistently opposite in sign compared to the H_5 kudu^{-1}and I_3 kudu^{-1} variables (Table 9.3).

Differences in study unit ETTE ha^{-1} allocated to mortality categories were significant (F-ratio = 16.463, $P<0.01$, d.f. = 2). High ETTE ha^{-1} values were associated with a high incidence of mortality and low ETTE ha^{-1} values with low mortalities (Figure 9.3). The ETTE ha^{-1} also contributed in discriminating between mortality categories in combinations with other variables. Although the within-group correlation was not significant ($P>0.05$), the ETTE ha^{-1} was negatively correlated ($P<0.05$) with the S_4 kudu^{-1}, S_{3+4} kudu^{-1}, U_5 kudu^{-1}, H_5 kudu^{-1}, and I_3 kudu^{-1} variables respectively (Appendix C).

9.5 DISCUSSION

Various assumptions were made that need to be validated. It was assumed that the reported kudu deaths represented actual numbers that died during the dry season of 1998. Bias in the study unit's respective reported mortality is thus possible due to the differential searching effort made to look for carcasses that was applied between study units. This may lead to circularity in the relationship between kudu mortality and kudu density before mortality occurred due to the dependence of kudu density calculations on the stated mortality numbers. For example, a high mortality rate will be reflected in elevated kudu density estimates. By categorising study units into low, intermediate and high mortality categories, which could to some extent be substantiated by carcass remains found during field work and the game censuses, bias as a result of inaccurate mortality numbers was thought to be circumvented to some degree. It was also assumed that the woody browse resources estimated at peak biomass during the 1998/99 rainfall season did not differ significantly from what was available at peak biomass during the wet season of 1997/98. Canopy die-back was observed in a limited

Table 9.4 Summary statistics resulting from the One-Way Analysis of Variance for the highly acceptable component per retention class per kudu (H_1-H_5 kudu^{-1}), intermediate acceptable component per retention class per kudu (I_1-I_5 kudu^{-1}) and avoided component per retention class per kudu (A_1-A_5 kudu^{-1}). The between-group degrees of freedom, between-group mean squares, F-ratio and significance level are indicated. The A_1 kudu^{-1} and A_4 kudu^{-1} variables were not tested because no species were allocated to these groups.

Variable	**Between groups**		**F-ratio**	**Significance**
(kg DM kudu^{-1})	**Degrees of freedom**	**Mean squares**		**Level (P)**
H_1	2	3.413	2.414	0.18
H_2	2	7.95	0.911	0.46
H_3	2	0.584	0.886	0.47
H_4	2	0.595	0.781	0.51
H_5	2	5.497	11.620	0.01
I_1	2	0.212	3.972	0.09
I_2	2	0.834	0.901	0.46
I_3	2	2.669	8.051	0.03
I_4	2	3.744	3.192	0.13
I_5	2	9.329	1.128	0.39
A_2	2	3.897	0.781	0.51
A_3	2	0.541	2.119	0.22
A_5	2	5.746	0.710	0.54

number of woody plants during 1999, a year after the drought, which may have resulted in an under estimation of the resources available during the drought of 1997/98. Localised mortalities were also observed in some species such as *Terminalia prunioides*. The loss in leaf production as a result of canopy die-off, and occasional mortalities, might have been offset by the apparent greater dependence of leaf production on the preceding seasons rainfall rather than on the current season's rainfall found in a dystrophic savanna (Rutherford 1984 cited by Owen-Smith 1990). Of greater importance than differences in foliage production between rainfall seasons might be the changes brought about in leaf phenology and acceptability. The classification of woody species according to acceptability and foliage retention into the dry season was based on observations in 1999, a year after the drought. Novellie (1983) has described year-to-year differences in the acceptability of some species, e.g. *Acacia nigrescens* and *Combretum apiculatum,* which may be attributable to rainfall differences. Water stress, as a result of intra-species competition, has been shown to affect the leaf phenology pattern of a woody species (Smit 1994), and probably alter leaf phenology patterns during droughts (Owen-Smith 1990). It was, however, assumed that the classification of woody species according to dry season leaf retention and acceptance to kudu held across the years in question.

Factors that seem to contribute to kudu population crashes elsewhere include: below average rainfall (Wilson 1970; Van Hoven 1991; Owen-Smith 1993c), overpopulation in confined areas (Wilson 1970), cold weather and frost (Wilson 1970; Simpson 1972; Owen-Smith 1990) and diseases such as pneumonia (Wilson 1970) and anthrax (Owen-Smith 1993c). Keep (1973) noted that overpopulation and cold weather have contributed to a population crash in nyala (*Tragelaphus angasii*), which is closely related to the kudu. The actual cause of death in this case was mostly attributed to anaemia and pneumonia followed by heart failure (Keep 1973). The same pattern has repeated itself at study units 6 and 8 where high mortalities were experienced. A *post mortem* investigation at study unit 8, where 25 kudu reportedly died during the dry season of 1998, established that most kudu that died were emaciated. Kudu deaths generally took place during and after a cold spell were experienced at the end of the 1998 dry season. Pneumonia was also diagnosed in a few cases, although animals where these symptoms were diagnosed apparently succumbed a few days after the cold spell ended (Dr. F. Harris, personal communication[3]).

The availability of food resources at critical times of the year has been shown to be an important population-regulating agent in buffalo (Sinclair 1977), snowshoe hare (Sinclair *et al.* 1982) and reindeer (Skogland 1985). Food resource availability during the dry season has also been suggested to regulate kudu numbers in deciduous savanna (Owen-Smith & Cooper 1985; Novellie 1992; Grossman 1994). This is supported by the close relationship between foliage resources available during the late dry season and kudu mortalities (Tables 9.1-9.3). At times of drought, the dependence of kudu on the limited evergreen and semi-evergreen resource components are accentuated, probably as a result of premature leaf fall of deciduous species (Owen-Smith 1990) and/or nutritional changes (e.g. condensed tannin concentration) brought about by water stress (Van Hoven 1991). Mild water stress is expected to enhance carbon-based defences such as tannins, while severe droughts may facilitate a break down in chemical defences (Bryant *et al.* 1991b). It seems plausible that kudu occurring at high densities relative to key resources will consume these limited resources before the end of the critical period is reached. The lack of food subsequently causes the rapid loss of body reserves as kudu starve or have to revert to food items offering a low metabolisable nutrient return. Animals in areas where key resources (nutrients) are less limited will lose body reserves at a slower rate and will be more able to withstand challenging conditions brought about by cold weather, disease, and probably to some extent predation. Wilson (1970) describes a rapid loss in kudu condition during the dry season following below average rainfall conditions that seems to support this hypothesis.

Smit (1994) has established that *Colophospermum mopane* trees occurring at low densities retain leaves longer into the dry season, and new leaves emerge earlier in the new season than trees occurring at high densities. If this pattern holds for other woody species, the critical period will be prolonged due to premature leaf fall with a subsequent increased dependency of kudu on key resources. This might have negative implications for an area's kudu carrying capacity. The significant ($P<0.05$) relationship between ETTE ha^{-1} and kudu mortality category suggests that this might also be of importance in the study area. Confounding the apparent relationship between kudu mortality and

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ETTE ha^{-1} is the significant negative correlation between ETTE ha^{-1} and other variables that were also important in discriminating between mortality categories (Appendix C). It is possible that at high bush densities, growing conditions for evergreen and semi-evergreen species are negatively altered, probably by upsetting the ground-water balance. Whether or not high bush densities raise the dependency of kudu on critical resources by shortening the seasonal availability of foliage as previously suggested or cause low critical resource levels, it is implied that bush density beyond a certain level not only impacts negatively on the grass layer, and thus the grazing capacity (e.g. Moore & Odendaal 1987; Smit 1994; Smit & Swart 1994), but also lowers the ability of an area to sustain browsers such as kudu. This might have relevance on bush control operations and needs further investigation.

The higher canonical correlation coefficients established for combinations of the U_5 $kudu^{-1}$, S_3 $kudu^{-1}$, S_4 $kudu^{-1}$ and S_{3+4} $kudu^{-1}$ variables (r=0.95-0.98) as opposed to combinations of the H_5 $kudu^{-1}$, I_1 $kudu^{-1}$ and I_3 $kudu^{-1}$ (r=0.93-0.97) suggest that the resource components associated with the former variables delineate key resources more accurately. The higher significance level (P=0.01) (Table 9.2) of the U_5 $kudu^{-1}$ variable relative to the S_3 $kudu^{-1}$ and S_4 $kudu^{-1}$ variables further suggests that the availability of U_5 species' foliage was more important in explaining the differences between the mortality categories than foliage availability of the spinescent variables. The U_5 $kudu^{-1}$ variable also attained a higher model coefficient than either the S_3 $kudu^{-1}$ and S_4 $kudu^{-1}$ variables in spite of lower availability levels (Table 9.3). Owen-Smith & Cooper (1989) postulated that the palatable evergreen component plays a crucial role in supplying metabolisable energy during the critical period. The state of body reserves during the critical phase, however, will not only be a function of the rate of condition loss during the critical bottleneck period, but will also be dependant on the body reserves when the animal enters the critical phase. The relationship between kudu mortality and the S_4 $kudu^{-1}$ and S_3 $kudu^{-1}$ variables might be related to the high nutritional value associated with species in these groups. Many species in the S_3 and S_4 groups have a high nutritional value, such as the leaves and pods of *Acacia* species (Owen-Smith & Novellie 1982; Cooper *et al.* 1988; Haschick & Kerley 1997a) or have a high rainfall season acceptance value indicative of a high nutritional value (Novellie 1983). Although the consumption of spinescent species is restricted (Cooper & Owen-Smith 1986; Gowda 1996; Haschick & Kerley 1997b), high levels of these components available per kudu may result in animals entering the critical period in a nutritionally better condition than animals challenged by low levels of these high-quality resources. *Acacia tortilis,* a prominent species of the S_4 class in this study, contributes to the dry season diet of kudu in an agricultural area (Du Plessis & Skinner 1987), is associated with kudu presence in the Northern Cape during the dry season (Fabricius 1994) and is increasingly used by kudu as browse availability declines at Nylsvley (Owen-Smith & Cooper 1987).

The level of critical resources available per animal when mortalities occurred is of practical value. These might be useful in calculating constraints in kudu production systems or assessing the risk associated with keeping kudu populations at a specific stocking rate. This aspect will be discussed further in Chapter 10.

9.6 CONCLUSIONS

The following general conclusions were drawn from this study:

I. The drought conditions experienced during the 1997/98 rainfall season, which coincided with a cold spell experienced at the end of the dry hot season, lowered the survival chances of certain kudu populations in the study area. The coincidence of drought conditions and kudu mortalities points at a positive relationship between rainfall and kudu survival. Owen-Smith (1990) demonstrated such a relationship for two kudu populations in the Kruger National Park. This might be of value to predict a kudu population's survival chances from current rainfall and should be investigated.

II. Of all the variables investigated, the lack of available browse was the most closely related to the kudu mortalities. Low resource availability per animal coincided with high mortalities and conversely high resource availability with low mortalities. This supports the postulation that kudu populations are regulated by dry season resources and might be of value in assessing the suitability of an area as kudu habitat and in calculating appropriate stocking rates.

III. Of the browse components accessible during the dry season, the unarmed components were more closely related to mortalities than spinescent components. This suggests that the availability of unarmed components was more important for kudu survival than spinescent components.

IV. The evapotranspiration potential of the woody component apparently also affected the survival chances of kudu under the prevailing study conditions. High ETTE ha^{-1} values were associated with high mortalities and low ETTE ha^{-1} values with low mortalities. The close correlation of ETTE ha^{-1} with other important variables is perplexing in its interpretation as a determinant of kudu mortalities within the study area.

CHAPTER 10

CONCLUSIONS AND APPLICATION

10.1 INTRODUCTION

The approach taken by this study and methodology applied imposed certain limitations on the interpretation of the results. The study involved mainly the interpretation of correlates between variables. Correlation between variables cannot be used to interpret that a variable unconditionally causes the variation in another (Snyman 1989). For example, it cannot be concluded without doubt that kudu were dying in certain study units *because* low resource levels per animal existed at that time. Results may also have been biased by the low number of observations used (n=8) and the limited precision involved in the measurements, e.g. game censuses and vegetation surveys. Furthermore, although study units were restricted to the Arid Sweet Bushveld (Acocks 1988), which is situated in a relatively homogeneous climatic zone, notable differences in soils, vegetation and previous land-use were evident between study units.

Considering these constraints, results of a study of this nature cannot be conclusive. Results could, however, be useful in formulating theories and for constructing models that can be tested in controlled experiments or by using independent data in the field.

This chapter aimed at integrating the results obtained in previous chapters. This was used to:

I. Formulate a conceptual model as to how kudu populations in the study area were regulated.
II. Propose practical management considerations for kudu production in the study area.
III. Recommend future research fields.

10.2 DISCUSSION

10.2.1 Population regulation

The growth rate of a population is a function of both the mortality rate and the fecundity rate (Caughley & Sinclair 1994). Owen-Smith (1990) suggests that a process of post conception survival controls the reproductive success in kudu. This contrasts with other species such as giraffe (Hall-Martin, Skinner & Van Dyk 1975) and bontebok (Novellie 1986), where factors influencing the conception rate apparently exert an overriding effect on the lamb and calf crop. There appears to be a link between the adult nutritional status, reproductive success and survival rate in kudu, at least for the juvenile, yearling and old female classes. Owen-Smith (1990) recorded that about 50 % of mortalities in juvenile kudu occur prior to the nutritional bottleneck period. He linked this to the dependence of calf survival on maternal nutritional status. The nutritional status of females probably controls foetal growth during the late pregnancy phase or influences milk production during lactation which determines post-natal growth. Calves subjected to sub-optimum growth conditions will have a lower survival rate than calves developing and growing under optimal conditions. Owen-Smith (1990) further demonstrated that the survival rates of juveniles, yearlings and old females are affected by both recent rainfall and kudu biomass, although the importance of these variables in explaining variation in survival rate differs between the lasses. The prime-aged female class (3-7 years of age) appears to be highly resistant to the effects of food limitations when indexed by kudu biomass and rainfall. Males apparently follow the same survivorship curve as females in so far that prime aged males have a higher survival rate than juvenile or old animals (Owen-Smith 1993b). A fundamental difference between the kudu sexes is that the prime-aged period only extends to an age of about four years in males compared to about seven years in females. In males the body reserves are apparently minimally affected during the breeding season (Huntley 1971). Rivalry among kudu bulls is also less fierce than in other species and probably explains little of the increased mortality rate observed in adult kudu males compared to females (Owen-Smith 1993b).

Sinclair (1977) postulated that food limitations, which are reflected in the nutritional status of a buffalo population, control the population's susceptibility to fatal diseases. In his study, animals apparently seldom die as a direct result of starvation. The same mechanism probably applies to kudu. That is that the nutritional status of an animal largely determines its susceptibility to primary killing agents such as exposure during adverse weather conditions, certain diseases and even predation. Animals associated with a low nutritional status will thus stand an increased chance of dying of exposure or falling ill compared to those animals in good condition. The most likely time for a browser's nutritional status to be at it's lowest is during the late dry season, defined as the critical period in this study, when browse resource availability is at its lowest. This is supported by the low N_f concentration found at this time in the study area (Chapter 7) and in the KNP (Grant *et al.* 1995; Grant *et al.* 2000), and which coincides with the low estimates of protein and energy intake of kudu in a deciduous savanna (Owen-Smith & Cooper 1989). Mortalities in kudu also peak during the late-winter, dry-spring period, indicating that this is the most stressful time of the year (Hirst 1969 cited by Delany & Happold 1979). Many reports have suggested that mortalities in kudu are associated with cold weather spells experienced during the critical period (Wilson 1979; Simpson 1972; Owen-Smith 1990). This implies that kudu are not exposed to a constant threat level and that a kudu's survival chances will also be affected by external factors such as weather conditions.

The dynamic process whereby kudu populations are apparently regulated is explained in the schematic illustration portrayed in Figure 10.1, which shows the relationship between the nutritional status of kudu and their apparent susceptibility to primary killing agents during the critical period. Line A-B represents the nutritional status of a kudu population and line C-D the level of threat, e.g. physical exposure to cold weather and diseases, to which the kudu population is exposed to at a specific point in time. The C-D line is not static but varies according to local conditions such as the occurrence of cold weather spells resulting in challenging physical conditions. It follows that animals associated with a poor nutritional status will not necessarily die, but that such animals will stand a higher chance of dying as a result of the imposed threat. The vertical distance between the nutritional status line (A-B) and the level of threat (C-D) gives an indication of the survival chances of a kudu population, although this will depend on the age and sex structure of a population. The survival chances of juveniles are relatively low but improve gradually until an age of approximately two years is reached (Owen-Smith 1993b). Up to three years of age, the survival chances of both sexes are comparable, but pronounced differences became apparent thereafter. After three years of age the survival rate of

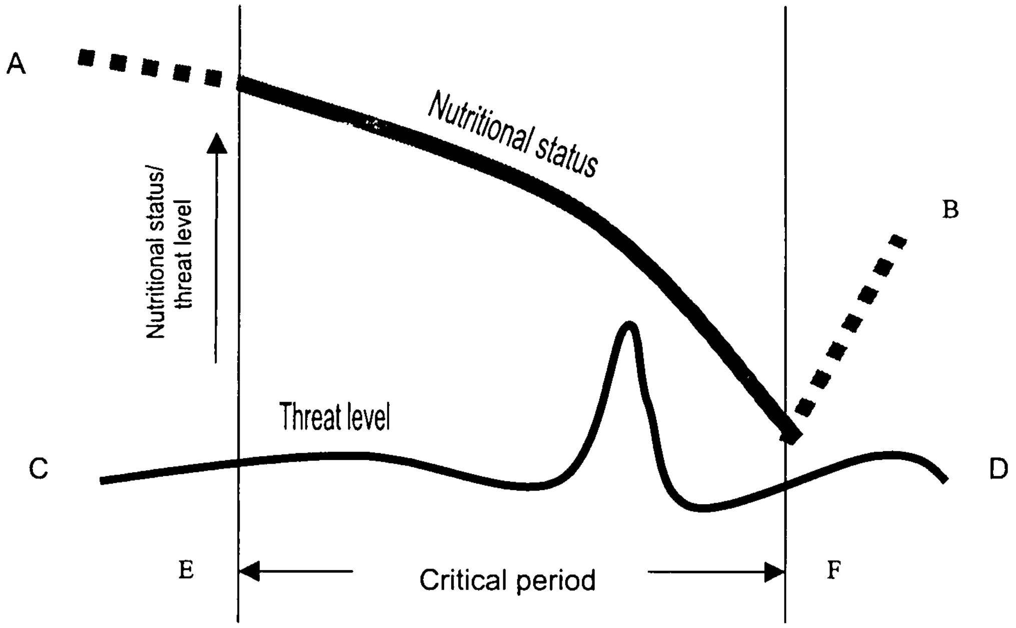

Figure 10.1 A schematic outlay to illustrate the hypothetical mechanism whereby kudu populations are regulated in deciduous savanna. The A-B line represents the nutritional status of a kudu population over the dry seasonal cycle. The C-D line represents the primary killing agents such as exposure to unfavourable weather conditions and certain diseases. The vertical distance between the A-B and C-D lines represents the survival chances of a kudu population. The critical period when browse resources are at a minimum is represented by the horizontal distance between points E and F on the graph.

kudu males progressively declines with increasing age. This contrasts sharply with female animals whose survival only starts to decline after an age of about six years. The decline in survival rate over time is also steeper for males than for females. The senescent period in males commences at about six years of age, but only at 11 years of age for females. Owen-Smith (1993b) found that the oldest male and female in his study was respectively nine and 14 years old.

The relationships established in Chapters 8 and 9 suggest that kudu are regulated mainly by the availability of browse resources during the dry season. Whereas the availability of the evergreen component was apparently crucial for kudu survival in the dry season of 1998, it was of less importance during the dry season of 1999. The drought conditions, which were experienced in 1998, might have accounted for the greater dependency of kudu on critical resources at that time. Owen-Smith (1990) speculated that below average rainfall might result in premature leaf senescence in deciduous species. This will have the effect that the critical period will be relatively prolonged and the dependency of kudu on critical resources increased. This is illustrated in Figure 10.2a. Line A-B_1 represents the nutritional status of a kudu population that has more abundant food available during the critical period compared to a population challenged by a shortage of food (represented by line A-B_2) at the time. The population represented by line A-B_2 stands an increased chance of succumbing if the 'threat level' should intensify. The critical period might also be accentuated if negative changes in the quality of the food supply should occur, e.g. water stress resulting in increased condensed tannin concentration (Van Hoven 1991). Mild water stress is thought to result in an increased carbon-based secondary metabolite concentration. Severe water stress, however, will probably cause a breakdown in chemical defences (Bryant *et al.* 1992).

The nutritional status of kudu as indexed by N_f was apparently less dependent on the evergreen component during the dry season of 1999, which was preceded by rainfall approaching the long term mean in the study area. This suggests that, although the evergreen component is still important in bridging the late dry season under normal rainfall conditions, the period of dependency thereon is of short duration due to the

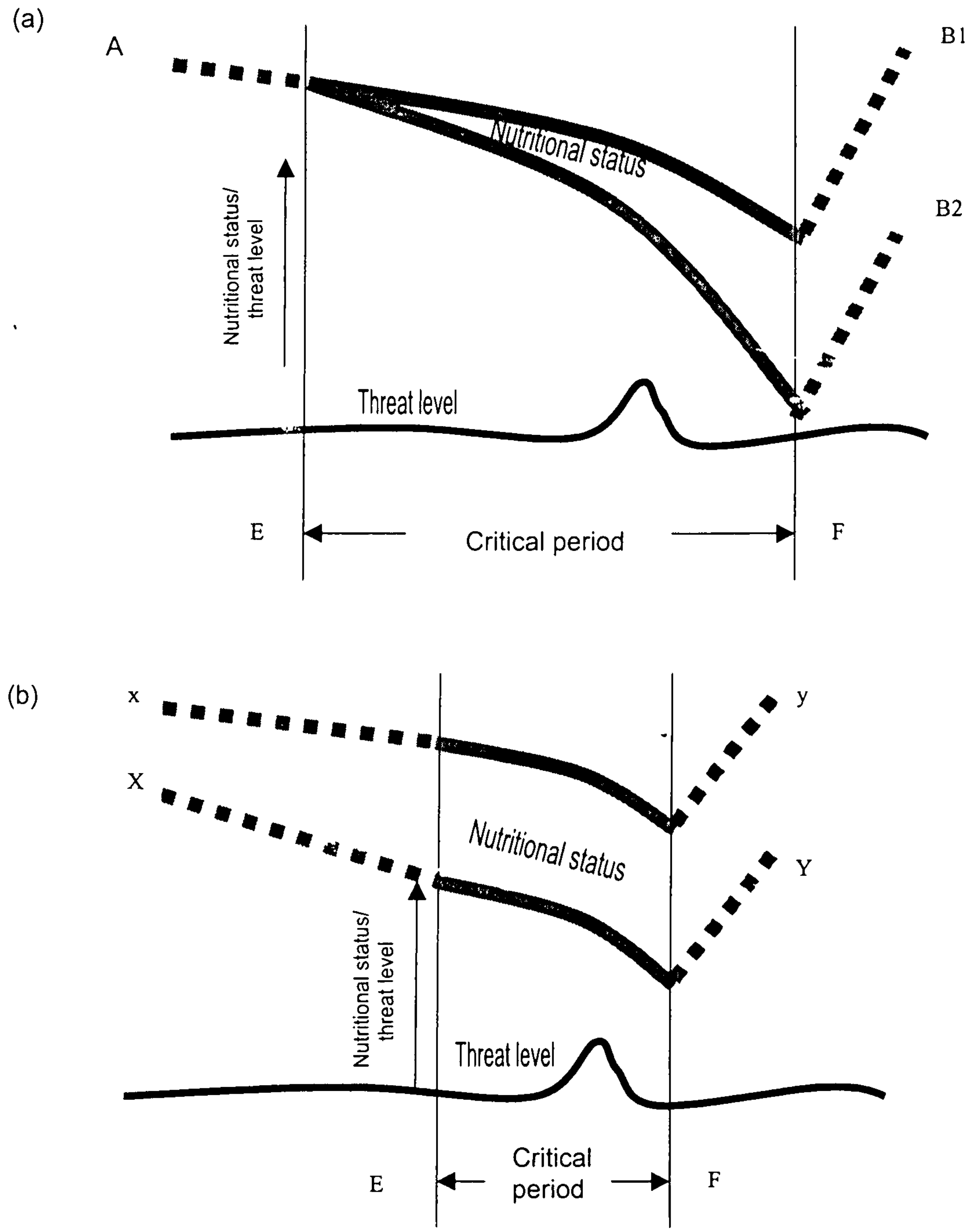

Figure 10.2 A schematic outlay to illustrate the hypothetical mechanism whereby kudu populations are regulated in order to portray; (a) differences in the availability of the critical resources exist and (b) different levels of resource availability when entering the critical period exist. The critical period in the case of (a) is longer than in the case of (b) and represents a normal and below average rainfall season respectively.

extended availability of other browse resources late into the dry season. The availability of browse resources with an extended foliage availability is subsequently more important in explaining the dry season N_f concentration than is the availability of critical resources. This is illustrated in Figure 10.2b, where the nutritional status of a hypothetical kudu population exposed to a high availability of browse resources when entering the short critical period (line x-y) results in a higher nutritional status during the critical period than a population exposed to a lower availability of these resources (line X-Y).

Occurrences such as frost and fire might also impact on the availability and quality of browse resources during the dry season. It is possible that these occurrences might affect population dynamics in the same way that water stress apparently modifies the duration of the critical period and/or impacts on the availability or quality of critical resources.

10.2.2 Practical application

If the mechanism proposed above is indeed the mechanism whereby kudu populations are regulated in the study area, how can this be used to manage confined kudu? A pertinent question concerning wildlife management is how many animals to allow in an area (stocking rate) in order to reach a specific objective, e.g. to optimise animal production, although other factors such as the manipulation of sex ratios and age structures are also important. Seen from a wildlife manager's point of view, the 'threat' level in Figure 10.1 is to a large degree uncontrollable or impractical to control. On the other hand, the nutritional status of kudu can be manipulated to some extent, e.g. by regulating the stocking rate, and hence the availability of limiting resources, or by strategic forage supplementation. The relationships established between kudu mortalities during a drought and the availability of browse resources and kudu N_f over the dry seasonal cycle with the availability of browse resources, suggest that kudu carrying capacity estimates should be based on browse resources which retains foliage well into the dry season.

A deterministic model aiming at predicting the nutritional status of kudu during the dry hot season, as represented by N_f, has been constructed. A prerequisite of a model is that it should be simple and understandable (Starfield & Bleloch 1991). In Chapter 8, it was proposed that the availability of the U_3 and S_3 components were the most limiting for kudu during the dry hot season. The relationship with N_f was not lessened by the inclusion of the foliage contribution of the U_4 and U_5 groups to that of the U_3 group (U_{3-5}). This is convenient if the model is to be extended to areas with a different species composition, as it will be easier to eliminate early deciduous species instead of identifying only the narrowly defined U_3 species group. For that same reason, the S_3 group is also expanded to embrace the foliage contribution of the S_4 and S_5 groups (S_{3-5}). Due to the complicated calculations imposed by the logarithmically transformed resource data, the multiple regression models are not usable (Table 8.4). Original (untransformed) data has, consequently, been used in order to calculate a nutritional status index (NSI). By relating the NSI values to actual dry hot season N_f concentration values, the closest fit has been established by differential weighting of input variables. The model resulting in the closest correlation ($r=0.91$, $P<0.05$, $n=8$) (Figure 10.3) between the calculated nutritional status index and actual dry hot season N_f is described by the following equation:

$$\text{NSI} = U_{3\text{-}5}\ \text{BU}_{\text{kudu}}^{-1} + 5^{*}S_{3\text{-}5}\ \text{BU}_{\text{kudu}}^{-1} \ldots\ldots\ldots\ldots\ldots(1)$$

Where:

NSI = nutritional status index

$U_{3\text{-}5}$ = the foliage dry mass contribution (<2 m height) of unarmed species of leaf retention classes 3-5.

$S_{3\text{-}5}$ = the foliage dry mass contribution (<2 m height) of spinescent species of leaf retention classes 3-5.

The unarmed component used in equation (1) includes the foliage contribution of the U_3, U_4 and U_5 species, but excludes the contribution of the U_1 and U_2 species (Appendix A). The spinescent component consists of the foliage contribution of the S_3, S_4 and S_5 species and excludes the contribution of the early deciduous S_1 and S_2 species (Appendix A). This equation may be useful in obtaining an estimation of the nutritional status index (NSI) of a kudu population of a known size under the same conditions as in the study.

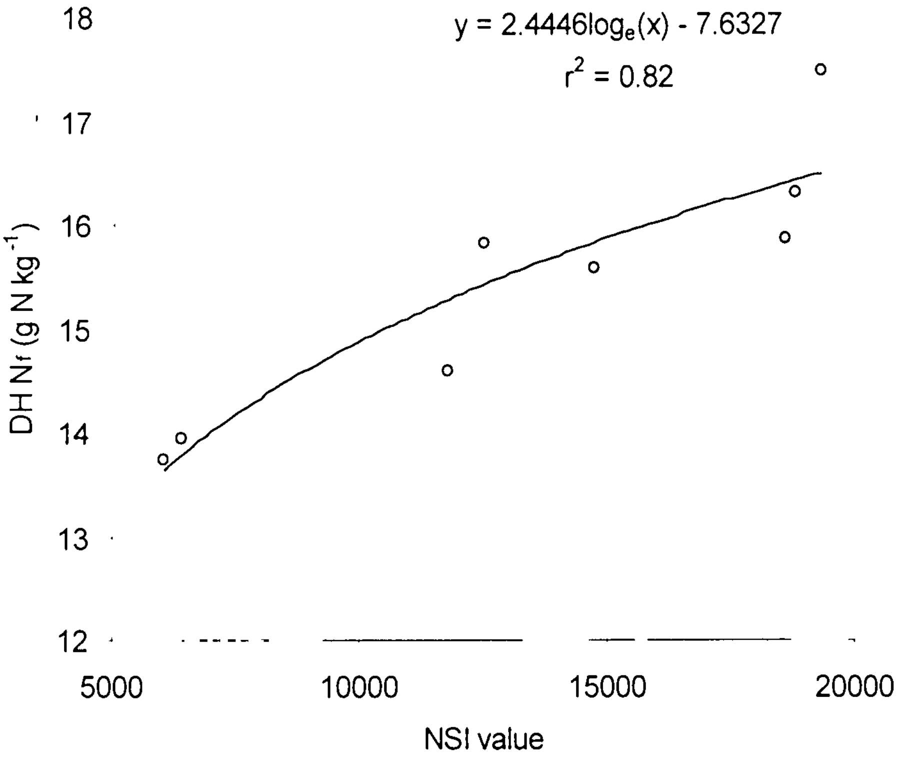

Figure 10.3 The relationship between the nutritional status index (NSI) calculated from browse resource availability and actual dry hot season faecal nitrogen concentration (NSI calculated using equation (1)).

Equation (1) has been rewritten in order to obtain an estimate of the number of kudu browser units for a specified NSI value if the resource variables are known:

$$BU_{kudu} = (U_{3\text{-}5} + 5{*}S_{3\text{-}5})/NSI \ldots\ldots\ldots (2)$$

Equation (2) might be useful in predicting the kudu stocking rate for a specified NSI value from quantitative measurements of the woody vegetation of an area. Different management objectives for an area will prescribe what nutritional status level applies for a population. These might vary from a light stocking rate, which will theoretically result in optimal conditions for individual growth, e.g. trophy animal production, to cases where the objective is to optimise production, e.g. optimum biomass or numbers (Jones & Sandland 1974; Mentis 1984; Trollope 1990). In the latter case, a higher stocking rate will apply. In the study area populations with a dry hot season N_f value below 15 g N kg DM^{-1} showed signs of visible condition loss during the 1999 dry season, and were the only areas where mortalities were reported at that time. Faecal N concentrations below which weight loss takes place in other mammals include; 12 g N kg DM^{-1} for snowshoe hare (Sinclair *et al.* 1982), 16 g N kg DM^{-1} for elk (Gates & Hudson 1981). For southern African grazers, the threshold value has been calculated as 14 g N kg DM^{-1} (Wrench *et al.* 1997).

The carrying capacity in arid and semi-arid environments varies considerably from year to year (Danckwerts & Tainton 1996). Under these circumstances, the carrying capacity of an area is probably the best represented by a range bound by an upper and lower limit. The carrying capacity of an area fluctuates between these limits according to local conditions (Peel *et al.* 1998). It has previously been proposed that kudu might be limited by different components in average and dry years. This suggests that areas will vary, not only in their respective ability to sustain animals in an average year, but also in times of drought. This implies that certain areas may experience a steeper decline in carrying capacity across the same rainfall gradient. Accepting that the availability of the evergreen component is indicative of the lower limit of an area's carrying capacity, the risk attached to keeping a population at a specific stocking rate if below average rainfall conditions occur can be calculated. The resource availability levels calculated for the different mortality categories might be useful in this regard, and are summarised in

Table 10.1. A high risk status will be associated with a shortage in evergreen foliage available to kudu, while a low risk status will apply to areas where the evergreen component occurs in abundance relative to kudu numbers.

It is reasoned that the optimal production (Maximum Sustained Yield) will be realised at a nutritional status level above the threshold N_f value of 15 g N kg DM^{-1}. Assuming that a dry hot season N_f value of 15.5 g N kg DM^{-1} signifies optimal stocking rates in an average rainfall year, optimal stocking rates can be recalculated for study units from resource data. The corresponding NSI value for a dry hot season N_f concentration of 15.5 g N kg DM^{-1} was calculated from the regression equation established between dry hot season N_f and NSI and equals 12 929 (Figure 10.3). Stocking rates were calculated using equation (2) and the sizes of the respective study units. Table 10.2 shows the predicted optimal stocking rates (ha BU_{kudu}^{-1} and BU_{kudu} 100 ha^{-1}) for an average rainfall season for the study units. According to Table 10.2 study unit 2 has the highest (5.8 BU_{kudu} 100 ha^{-1}) and study unit 6 the lowest (2.2 BU_{kudu} 100 ha^{-1}) stocking rates (mean 4.0 BU_{kudu} 100 ha^{-1}). The risk attached to keeping populations at these stocking rates in times of drought is also indicated. Evergreen availability levels < 55 kg $kudu^{-1}$ have been arbitrarily chosen to represent high risk levels. Levels exceeding 200 kg $kudu^{-1}$ indicate low risk and values between 55 to 200 kg $kudu^{-1}$ have been interpreted to indicate intermediate risk levels.

Different management strategies are proposed to cope with the year to year variation in forage resources: (i) Conservative stocking, aimed at supplying a stable forage supply. This would, for the most part, be at sub-optimum stocking rates with consequent losses in production per unit area or unit resource. A shortage might still arise during the driest years (Danckwerts & Tainton 1996). (ii) Adapting stocking rates according to local conditions with the view of following changes in carrying capacity. This option might be constrained, especially where a high risk of die-off's exists, by practical limitations associated with destocking and marketing game animals. Restocking following adverse periods may also prove uneconomical. (iii) Another option is to accumulate fodder, which is used in dry years to bridge temporary forage shortages. The economy of supplementation will determine this option's viability. None of the options listed above are likely to meet expectations entirely on its own and a combination of these options might be more practical (Danckwerts & Tainton 1996).

Table 10.1 The availability of evergreen foliage per kudu per mortality category (range indicated in brackets).

Mortality category	kg Evergreen foliage kudu^{-1}
Low	314(187-448)
Intermediate	93(43-170)
High	14(7-22)

Table 10.2 Predicted optimum kudu stocking rates for an average rainy season (350 mm –450 mm per annum) for study units. It was assumed that a dry hot season N_f concentration value of 15.5 g N kg^{-1} represents optimal nutritional conditions. The availability of evergreen foliage per animal for the calculated optimal stocking rate is also calculated, and the risk of severe population die-off's, should adverse conditions prevail, indicated. An evergreen availability level of > 200 kg DM BU_{kudu}^{-1} was considered as having a low risk and levels < 55 kg DM BU_{kudu}^{-1} as high risk. Availability levels falling between said levels are considered intermediate-risk areas.

Study unit	Study unit size (ha)	$U_{3\text{-}5}$ study unit^{-1} (kg)	$S_{3\text{-}5}$ study unit^{-1} (kg)	BU_{kudu} study unit^{-1}	Stocking rate		Evergreen study unit^{-1} (kg)	Evergreen BU_{kudu}^{-1} (kg BU_{kudu}^{-1})	Risk Category
					ha BU_{kudu}^{-1}	BU_{kudu} 100 ha^{-1}			
1	1 080.6	541 263	12 954	46.9	23.1	4.3	6 646	132	Intermediate
2	868.5	355 905	58 473	50.1	17.3	5.8	1 198	22	High
3	1 070.0	421 160	23 105	41.5	25.8	3.9	3 014	67	Intermediate
4	865.0	188 527	68 470	41.1	21.1	4.7	12 224	276	Low
5	4 587.5	898 621	263 130	171.3	26.8	3.7	41 229	223	Low
6	750.0	192 295	3 852	16.4	45.8	2.2	488	28	High
7	1 792.9	446 190	57 538	56.8	31.6	3.2	15 721	257	Low
8	1 379.6	749 631	12 998	63.0	21.9	4.6	1 219	18	High
Mean	**1 549.3**	**474 199**	**62 565**	**60.9**	**26.7**	**4.0**	**10 217**	**138**	-

According to Table 10.2 study units 4, 5 and 7 fall within the low risk category and study units 1 and 3 in the intermediate risk category. Study units 2, 6 and 8 fall within the high-risk category, necessitating substantial reductions in stocking rate if rainfall deficiencies occur in order to avoid the possibility that large-scale die-off's occur. Owen-Smith (1990) demonstrated that kudu survival rate is linearly related to a ratio of rainfall to kudu biomass in two areas in the KNP. It follows that if only 50 % of the long term mean rainfall is received, the stocking rate should be halved to keep the survival rate constant. If it is accepted that the intermediate-risk category represent conditions in the KNP, then intermediate–risk areas should ideally destock in direct proportion to the relative reduction in rainfall. Low-risk areas are buffered against fluctuations caused in the dry season food supply, necessitating less severe stocking rate adjustments than would apply for intermediate-risk areas. The high-risk category, however, would have to destock at an even faster rate than the intermediate risk category. Marketing and logistic constraints pose a limit to the number of animals that can be captured or culled in order to reduce numbers in overstocked areas. This can be avoided or minimised by adhering to below-optimal stocking rates.

Study units which fall in the high-risk category (large–scale kudu mortalities during droughts) are associated with a lower diversity in terms of species composition (Figure 3.2). Conversely study units 4 and 5, assessed as low-risk areas, include areas that were floristically classified as dissimilar at the first level of the TWINSPAN classification indicating high diversity (Figure 3.2). In the study area, the number of homogeneous vegetation units identified per study unit also tends to be positively related to the size of study units. Lower species composition diversity relates to an increased chance that critical resource species are not present, which will be reflected in wider seasonal and yearly fluctuations in the food supply of kudu. This supports the view of Trollope (1990) and Bothma (1995) that management intensity should scale with area-size.

In conclusion, the considerable variation in the calculated kudu stocking rates, which ranged from 2.2 to 5.8 BU_{kudu} 100 ha^{-1}, confounds the formulation of general norms for the study area. It seems therefore appropriate that kudu stocking rates in semi-arid savanna should be based on resource availability during the nutritional bottleneck period and that stocking rates should be adjusted for the effect of rainfall on resource availability/quality.

10.3 FUTURE RESEARCH

The following fields need further investigation in the context of this study:

I. The effect of inter-species competition between browsing animals was not investigated in this study. Kudu dominated the browsing community in terms of biomass and Browse Units (Chapter 6), which might have lessened the effect of inter-species competition on kudu dynamics. It is however perceived that other browsing animals did interact with kudu, especially during periods of resource restriction such as the dry season and during the drought year of 1997/1998 (Caughley & Sinclair 1994).

II. The approach followed in this study focussed on the response of kudu on varying levels of forage resource availability. The impact of kudu on its forage resource base was consequently not considered. This will have a bearing on the sustainability of present land-use practices.

III. The mechanism whereby rainfall and its distribution within seasons influence the phenology and quality of woody foliage as a source of food has received scant attention in the southern African context. This seems especially relevant as the seasonal availability of foliage was identified as the most limiting factor in this study. Owen-Smith (1990) established significant relationships between kudu survival rate and rainfall, and hints that this acts through the seasonal availability of forage resources.

SUMMARY

A comparative study was conducted in order to investigate the relationship between forage availability and parameters of kudu populations thought to have a bearing on kudu carrying capacity in a semi-arid savanna. This involved eight game-fenced study units. The leaf production and standing crop of woody and forb species were determined. Woody species were classified according to rainfall season acceptance to browsers, the presence and absence of physical deterrents and foliage retention period into the dry season. Ungulate densities were determined during the late dry season of 1999 by helicopter census.

The leaf dry mass production below a height of 2 m, the mean browsing height of kudu, ranged from 362 kg ha^{-1} to 695 kg ha^{-1} (mean = 516 kg ha^{-1}) between study units. The forb standing crop (dry mass) ranged from 83 kg ha^{-1} to 376 kg ha^{-1} (mean = 214 kg ha^{-1}) between study units.

Large-scale kudu mortalities were reported in the dry season of 1998 in the study area. Below average rainfall received during the preceding rainfall season probably contributed to these mortalities, which were further aggravated by a prolonged cold spell experienced at the time. The lack of late dry season woody foliage was significantly related to mortalities. Relationships between kudu mortalities and kudu density or study unit size were insignificant.

Kudu faecal nitrogen concentration was determined at regular time intervals during the dry season of 1999. This was preceded by a normal rainfall season. Kudu faecal nitrogen concentration declined during the dry season and reached a minimum during the dry hot season (August – October). Kudu faecal nitrogen concentration peaked during the month of November. Mortalities and poor physical condition of kudu populations were linked to low dry hot season kudu faecal nitrogen concentrations. Variation in kudu faecal nitrogen concentration was significantly explained by the availability of woody species' foliage, excluding the contribution of early deciduous species.

It is hypothesised that kudu survival is largely dependent on the nutritional status of the animals. Animals with a low nutritional status are more susceptible to diseases and the effect of physical exposure during adverse weather. The nutritional status of kudu populations is apparently dependent on the availability of dry season foliage resources, which is again dependent on the preceding rainy season's rainfall. During droughts, forage resources available during the late dry season, the critical period, are important. During average rainfall years, kudu appear to be less dependent on critical resources, and the availability of dry season resources before the critical period is entered becomes increasingly important.

Different strategies to optimise kudu production, given the variation in forage resources between years, are discussed. It is proposed that kudu carrying capacity in semi-arid savanna is based on the availability of forage resources during the dry season, taking into account the effect of rainfall on resource availability/quality.

Key words: acceptability, availability, browser, critical resources, dry season, nutritional status, phenology, spinescens, stocking rate, rainfall

OPSOMMING

'n Vergelykende studie is uitgevoer met die doel om die verwantskap tussen voedsel beskikbaarheid en parameters van koedoebevolkings, wat moontlik betrekking op koedoedrakrag het, te ondersoek in 'n semi-ariede savanna. Agt wildwerendomheinde studie-eenhede is betrokke by die studie. Die blaar en bogrondse produksie van onderskeidelik die houtagtige en kruid spesies is bepaal. Houtagtige plantsoorte is geklassifiseer volgens reënseisoen-aanvaarbaarheid deur blaarvreterwild, doringagtigheid en die bladhoudendheid tydens die droëseisoen. Hoefdierdigtheid is tydens die laat droëseisoen van 1999 met 'n helikoptersensus bepaal.

Die droëmassa van blare onder 2 m hoogte, die gemiddelde weihoogte van koedoes, het van 362 kg ha^{-1} tot 695 kg ha^{-1} (gemiddeld = 516 kg ha^{-1}) tussen studie-eenhede gewissel. Kruid staande-oes (droëmassa) het van 83 kg ha^{-1} tot 376 kg ha^{-1} (gemiddeld = 214 kg ha^{-1} kg ha) tussen studie-eenhede gewissel.

Grootskaalse koedoevrektes is gedurende die droë seisoen van 1998 in die studiegebied aangemeld. Onder-gemiddelde reënval wat gedurende die voorafgaande reënseisoen ontvang is, het moontlik tot die vrektes bygedrae wat verder vererger is deur 'n langdurige koue gedurende die tyd. Die tekort aan laat-droëseisoen blaarvoedsel was betekenisvol gekorreleer met vrektes. Verwanskappe tussen koedoevrektes en koedoedigtheid of studie-eenheid grootte was nie betekenisvol nie.

Koedoe-misstikstof konsentrasie is op gereelde tye tydens die 1999 droë seisoen bepaal. Dit is voorafgegaan deur 'n normale reënseisoen. Koedoe-misstikstof konsentrasie daal gedurende die droë seisoen en bereik 'n laagtepunt gedurende die droë warm seisoen (Augustus – Oktober). 'n Hoogtepunt in misstikstof is tydens November gevind. Vrektes en swak liggaamstoestand in koedoepopulasies is verbind met lae misstikstof konsentrasies tydens die droë, warm seisoen. Variasie in misstikstof konsentrasie is betekenisvol verklaar deur die blaarbeskikbaarheid van houtagtige spesies wat die bydrae van vroegbladwisselende spesies uitsluit.

Dit word hipoteties gestel dat koedoe-oorlewing grootliks afhang van diere se voedingstatus. Diere met 'n lae voedingstatus is meer vatbaar vir sekere siektes en die

effek van blootstelling tydens ongure weer. Die voedingstatus van koedoebevolkings blyk afhanklik te wees van die beskikbaarheid van blaarvoedsel tydens die droëseisoen wat weer afhanklik is van die afgelope reënseisoen se reënval. Tydens droogtes is veral die beskikbaarheid van voedselhulpbronne tydens die laat droëseisoen, die kritieke periode, belangrik. Gedurende normale reënval jare blyk koedoes minder afhanklik van die beskikbaarheid van blare tydens die kritieke periode te wees en word die beskikbaarheid van droë-seisoen voedselhulpbronne voordat die kritieke periode binnegegaan word, toenemend belangrik.

Verskillende strategieë om koedoeproduksie te optimiseer, gegewe die wisseling in voedselhulpbronne tussen jare, word bespreek. Dit word voorgestel dat koedoedrakrag gegrond word op die beskikbaarheid van voedselhulpbronne gedurende die droëseisoen met inagneming van die invloed van reënval op blaarvoedselbeskikbaarheid.

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Appendix A. Two-way classification of woody species according to acceptability to browsing ungulates and the leaf retention period into the dry season (species in bold denotes classification based on utilisation frequencies while superscript following species names denote citation authority).

Deterrence class	**Acceptability class**	**Leaf retention class**				
		1	**2**	**3**	**4**	**5**
Unarmed	**Highly acceptable**	*Lannea schweinfurthii*^{3,5}	***Grewia villosa*** ***Combretum mossambicensis*** ***Cordia monoica***	***Terminalia prunioides*** ***Combretum apiculatum*** ***Grewia flavescens*** ***Ehretia rigida*** ***Spirostachys africana***	*Combretum hereoense*^{2,4,6}	***Boscia albitrunca*** ***Maerua parvifolia*** *Schotia brachypetala*^{5} *Diospyros lycioides*^{1} *Lonchocarpus capassa*^{3,5,6}
	Intermediate acceptable	*Sterculia rogersii* ***Commiphora mollis***	*Sclerocarya birrea*^{5,6} ***Cissus cornifolia*** ***Canthium setiflorum***	***Solanum gigantium*** ***Ochna inermis*** *Ormocarpum trichocarpum*^{3} ***Grewia flava*** *Vernonia cinerascens*	*Albizia harveyi*^{5} *Combretum imberbe*^{3,5}	
	Avoided		*Terminalia sericea*^{1}	***Grewia bicolor*** ***Grewia monticola*** *Grewia subspathulata*		*Euclea divinorum*^{3} *Euclea natalensis*^{1} ***Psiadia punctulata***
	Unknown	*Commiphora viminea* *Commiphora marlothii*	*Albizia* spp. *Bauhinia petersiana* *Vangueria infausta* ***Markhamia acuminata***	*Anisotes rogersii* *Ozoroa* sp. *Strychnos madagascariensis* *Ehretia amoena*	*Salvadora australis*	*Boscia foetida*
Spinescent	**Highly acceptable**	***Commiphora africana***	***Plectroniela armata***	***Phaeoptilum spinosum*** *Ziziphus mucronata*^{1} *Securinega virosa*^{6}		
	Intermediate acceptable	***Dichrostachys cinerea*** ***Commiphora pyracanthoides*** *Commiphora glandulosa*^{3}	***Acacia erubescens*** ***Acacia mellifera*** *Acacia permixta* *Acacia senegal* var. *leiorhachis*	***Acacia grandicornuta*** ***Acacia nebrownii*** ***Acacia nigrescens*** *Acacia nilotica*^{1,4}	*Acacia erioloba*^{5} ***Acacia tortilis***	*Gymnosporia buxifolia*^{5}
	Unknown		*Rhigosum zambesiacum* *Catophractus alexandri*			*Rhus guensis* *Ximenia americana* *Gymnosporia senegalensis* *Balanites pedicellaris*

[1] Owen-Smith & Cooper (1987) [2] Owen-Smith (1993) [3] Taylor & Walker (1978)

[4] Owen-Smith *et al.* (1993) [5] Walker (1980) [6] Novellie (1983)

Appendix B. Complete correlation matrix indicating Pearson's correlation coefficients (r), sample sizes (in parentheses) and significance levels (P) for forage availability variables (logarithmically transformed) related to kudu faecal nitrogen at study units (Chapter 8). Variable names are explained under sub-heading 8.2.4. and is expressed as the resource level (DM) available per kudu Browser Unit.

	WOOD BU-1	FORB BU-1	BROWSE BU-1	GRASS BU-1	Ret1 BU-1	Ret2 BU-1
WOOD BU-1	1.0000 (8) .0000	.4635 (8) .2473	.9092 (8) .0017	.4258 (8) .2929	.6975 (8) .0544	.4503 (8) .2629
FORB BU-1	.4635 (8) .2473	1.0000 (8) .0000	.7849 (8) .0210	.7194 (8) .0443	-.1565 (8) .7113	.5384 (8) .1686
BROWSE BU-1	.9092 (8) .0017	.7849 (8) .0210	1.0000 (8) .0000	.6733 (8) .0672	.3998 (8) .3264	.5940 (8) .1205
GRASS BU-1	.4258 (8) .2929	.7194 (8) .0443	.6733 (8) .0672	1.0000 (8) .0000	-.1932 (8) .6466	.7017 (8) .0524
Ret1 BU-1	.6975 (8) .0544	-.1565 (8) .7113	.3998 (8) .3264	-.1932 (8) .6466	1.0000 (8) .0000	.2469 (8) .5555
Ret2 BU-1	.4503 (8) .2629	.5384 (8) .1686	.5940 (8) .1205	.7017 (8) .0524	.2469 (8) .5555	1.0000 (8) .0000
Ret3 BU-1	.9600 (8) .0002	.4901 (8) .2176	.8831 (8) .0036	.3265 (8) .4299	.6032 (8) .1134	.2791 (8) .5033
Ret4 BU-1	-.0222 (8) .9584	.1662 (8) .6941	.0907 (8) .8308	.4374 (8) .2785	-.4233 (8) .2960	-.2237 (8) .5943
Ret5 BU-1	-.3173 (8) .4437	.2714 (8) .5156	-.0771 (8) .8559	.4842 (8) .2241	-.8221 (8) .0123	-.1158 (8) .7847
S1 BU-1	.6555 (8) .0776	.2816 (8) .4993	.5900 (8) .1236	.4001 (8) .3261	.1831 (8) .6644	-.0669 (8) .8749
S2 BU-1	.2602 (8) .5337	.7409 (8) .0355	.5291 (8) .1775	.5731 (8) .1375	.0283 (8) .9470	.7911 (8) .0194
S3 BU-1	-.0702 (8) .8688	.5380 (8) .1690	.1974 (8) .6394	.3519 (8) .3926	-.4753 (8) .2339	-.1497 (8) .7234
S4 BU-1	-.0867 (8) .8382	.1453 (8) .7313	.0321 (8) .9399	.3882 (8) .3419	-.4653 (8) .2453	-.2766 (8) .5072

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                    Ret3 BU-1  Ret4 BU-1  Ret5 BU-1    S1 BU-1      S2 BU-1      S3 BU-1
WOOD BU-1             .9600     -.0222     -.3173      .6555        .2602       -.0702
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .0002      .9584      .4437      .0776        .5337        .8688

FORB BU-1             .4901      .1662      .2714      .2816        .7409        .5380
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .2176      .6941      .5156      .4993        .0355        .1690

BROWSE BU-1           .8831      .0907     -.0771      .5900        .5291        .1974
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .0036      .8308      .8559      .1236        .1775        .6394

GRASS BU-1            .3265      .4374      .4842      .4001        .5731        .3519
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .4299      .2785      .2241      .3261        .1375        .3926

Ret1 BU-1             .6032     -.4233     -.8221      .1831        .0283       -.4753
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .1134      .2960      .0123      .6644        .9470        .2339

Ret2 BU-1             .2791     -.2237     -.1158     -.0669        .7911       -.1497
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .5033      .5943      .7847      .8749        .0194        .7234

Ret3 BU-1            1.0000     -.0303     -.2804      .6965        .1368       -.0466
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .0000      .9432      .5012      .0550        .7468        .9128

Ret4 BU-1            -.0303     1.0000      .6532      .5996       -.1851        .6418
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .9432      .0000      .0790      .1161        .6607        .0862

Ret5 BU-1            -.2804      .6532     1.0000      .2842       -.0044        .5312
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .5012      .0790      .0000      .4951        .9918        .1755

S1 BU-1               .6965      .5996      .2842     1.0000       -.2366        .1970
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .0550      .1161      .4951      .0000        .5727        .6401

S2 BU-1               .1368     -.1851     -.0044     -.2366       1.0000        .3323
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .7468      .6607      .9918      .5727        .0000        .4212

S3 BU-1              -.0466      .6418      .5312      .1970        .3323       1.0000
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .9128      .0862      .1755      .6401        .4212        .0000

S4 BU-1              -.0905      .9948      .6810      .5574       -.1869        .6818
                    (    8)    (    8)    (    8)    (    8)      (    8)      (    8)
                      .8313      .0000      .0630      .1512        .6577        .0625

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                  S4 BU-1    S5 BU-1    U1 BU-1    U2 BU-1    U3 BU-1    U5 BU-1
WOOD BU-1         -.0867      .2300      .2484      .3348      .9522     -.5615
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .8382      .5836      .5531      .4176      .0003      .1476

FORB BU-1          .1453      .5712     -.2766      .1508      .4305      .1498
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .7313      .1392      .5072      .7214      .2871      .7233

BROWSE BU-1        .0321      .4527      .0167      .3336      .8483     -.3322
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .9399      .2600      .9688      .4194      .0078      .4214

GRASS BU-1         .3882      .5561     -.5766      .4400      .2699      .1081
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .3419      .1523      .1346      .2753      .5180      .7988

Ret1 BU-1         -.4653     -.2082      .7483      .3091      .6403     -.7657
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .2453      .6207      .0327      .4564      .0872      .0268

Ret2 BU-1         -.2766      .2560      .0229      .8424      .2692     -.2338
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .5072      .5405      .9571      .0087      .5192      .5773

Ret3 BU-1         -.0905      .2575      .2557      .1982      .9952     -.5415
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .8313      .5380      .5411      .6381      .0000      .1657

Ret4 BU-1          .9948      .5863     -.7744     -.3966     -.0957      .3333
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .0000      .1266      .0241      .3307      .8216      .4198

Ret5 BU-1          .6810      .1980     -.9684     -.2013     -.3257      .7943
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .0630      .6384      .0001      .6326      .4312      .0185

S1 BU-1            .5574      .3984     -.3611     -.0792      .6746     -.1384
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .1512      .3282      .3795      .8521      .0665      .7439

S2 BU-1           -.1869      .2072     -.0264      .3917      .0936      .1604
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .6577      .6225      .9505      .3372      .8255      .7044

S3 BU-1            .6818      .3903     -.5417     -.6217     -.1377      .5988
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .0625      .3391      .1655      .0998      .7451      .1168

S4 BU-1           1.0000      .5341     -.7894     -.4596     -.1568      .4120
                 (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                   .0000      .1727      .0198      .2520      .7107      .3104

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                 H1 BU-1    H2 BU-1    H3 BU-1    H5 BU-1    I1 BU-1    I2 BU-1
WOOD BU-1        -.1092      .5841      .8742     -.3589      .7218      .3420
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .7969      .1284      .0045      .3826      .0432      .4069

FORB BU-1        -.4809      .6564      .6048      .1497     -.0445      .5016
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .2277      .0771      .1122      .7234      .9166      .2054

BROWSE BU-1      -.2530      .6978      .8778     -.1597      .4632      .5236
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .5454      .0543      .0042      .7056      .2478      .1830

GRASS BU-1        .0980      .3436      .3636      .4151     -.1695      .8278
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .8174      .4047      .3759      .3064      .6883      .0112

Ret1 BU-1         .0058      .4330      .5017     -.8116      .9892      .0456
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .9890      .2839      .2052      .0144      .0000      .9146

Ret2 BU-1         .0862      .7654      .4322     -.2001      .2880      .9014
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .8392      .0269      .2849      .6347      .4891      .0022

Ret3 BU-1        -.1910      .5396      .9359     -.3201      .6358      .1755
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .6504      .1675      .0006      .4396      .0902      .6777

Ret4 BU-1        -.0975     -.5353     -.1999      .6088     -.4497      .0631
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .8183      .1715      .6351      .1092      .2635      .8820

Ret5 BU-1         .0349     -.4100     -.3116      .9708     -.8262      .0517
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .9347      .3131      .4524      .0001      .0115      .9033

S1 BU-1          -.1424     -.0814      .5088      .2250      .1659     -.0146
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .7365      .8480      .1978      .5921      .6946      .9726

S2 BU-1          -.3179      .7733      .2747     -.0999      .1335      .6583
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .4429      .0244      .5103      .8140      .7526      .0760

S3 BU-1          -.4612     -.1341     -.1441      .4952     -.4064      .0078
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .2500      .7515      .7336      .2121      .3178      .9854

S4 BU-1          -.1302     -.5697     -.2661      .6389     -.4878      .0000
                (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                  .7586      .1404      .5241      .0882      .2201     1.0000

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                    I3 BU-1     I4 BU-1     A3 BU-1
WOOD BU-1           -.1725      -.0223       .8765
                   (    8)     (    8)     (    8)
                     .6829       .9583       .0043

FORB BU-1            .4814       .1660       .1584
                   (    8)     (    8)     (    8)
                     .2272       .6944       .7080

BROWSE BU-1          .0959       .0906       .6596
                   (    8)     (    8)     (    8)
                     .8212       .8310       .0751

GRASS BU-1           .3437       .4376      -.0033
                   (    8)     (    8)     (    8)
                     .4046       .2783       .9938

Ret1 BU-1           -.4752      -.4234       .7470
                   (    8)     (    8)     (    8)
                     .2340       .2959       .0332

Ret2 BU-1            .0005      -.2237       .0103
                   (    8)     (    8)     (    8)
                     .9991       .5943       .9807

Ret3 BU-1           -.2148      -.0305       .9213
                   (    8)     (    8)     (    8)
                     .6094       .9429       .0011

Ret4 BU-1            .4859      1.0000      -.1192
                   (    8)     (    8)     (    8)
                     .2222       .0000       .7785

Ret5 BU-1            .5792       .6533      -.4299
                   (    8)     (    8)     (    8)
                     .1325       .0790       .2877

S1 BU-1              .0314       .5993       .6494
                   (    8)     (    8)     (    8)
                     .9412       .1163       .0814

S2 BU-1              .4950      -.1851      -.1230
                   (    8)     (    8)     (    8)
                     .2123       .6607       .7717

S3 BU-1              .9034       .6420      -.1707
                   (    8)     (    8)     (    8)
                     .0021       .0861       .6861

S4 BU-1              .5451       .9948      -.1628
                   (    8)     (    8)     (    8)
                     .1623       .0000       .7001

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             WOOD BU-1  FORB BU-1  BROWSE BU-1 GRASS BU-1 Ret1 BU-1  Ret2 BU-1
S5 BU-1          .2300      .5712      .4527      .5561     -.2082      .2560
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .5836      .1392      .2600      .1523      .6207      .5405

U1 BU-1          .2484     -.2766      .0167     -.5766      .7483      .0229
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .5531      .5072      .9688      .1346      .0327      .9571

U2 BU-1          .3348      .1508      .3336      .4400      .3091      .8424
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .4176      .7214      .4194      .2753      .4564      .0087

U3 BU-1          .9522      .4305      .8483      .2699      .6403      .2692
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .0003      .2871      .0078      .5180      .0872      .5192

U5 BU-1         -.5615      .1498     -.3322      .1081     -.7657     -.2338
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .1476      .7233      .4214      .7988      .0268      .5773

H1 BU-1         -.1092     -.4809     -.2530      .0980      .0058      .0862
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .7969      .2277      .5454      .8174      .9890      .8392

H2 BU-1          .5841      .6564      .6978      .3436      .4330      .7654
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .1284      .0771      .0543      .4047      .2839      .0269

H3 BU-1          .8742      .6048      .8778      .3636      .5017      .4322
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .0045      .1122      .0042      .3759      .2052      .2849

H5 BU-1         -.3589      .1497     -.1597      .4151     -.8116     -.2001
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .3826      .7234      .7056      .3064      .0144      .6347

I1 BU-1          .7218     -.0445      .4632     -.1695      .9892      .2880
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .0432      .9166      .2478      .6883      .0000      .4891

I2 BU-1          .3420      .5016      .5236      .8278      .0456      .9014
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .4069      .2054      .1830      .0112      .9146      .0022

I3 BU-1         -.1725      .4814      .0959      .3437     -.4752      .0005
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .6829      .2272      .8212      .4046      .2340      .9991

I4 BU-1         -.0223      .1660      .0906      .4376     -.4234     -.2237
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .9583      .6944      .8310      .2783      .2959      .5943

A3 BU-1          .8765      .1584      .6596     -.0033      .7470      .0103
            (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                 .0043      .7080      .0751      .9938      .0332      .9807

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             Ret3 BU-1  Ret4 BU-1  Ret5 BU-1   S1 BU-1    S2 BU-1    S3 BU-1
S5 BU-1        .2575      .5863      .1980      .3984      .2072      .3903
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .5380      .1266      .6384      .3282      .6225      .3391

U1 BU-1        .2557     -.7744     -.9684     -.3611     -.0264     -.5417
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .5411      .0241      .0001      .3795      .9505      .1655

U2 BU-1        .1982     -.3966     -.2013     -.0792      .3917     -.6217
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .6381      .3307      .6326      .8521      .3372      .0998

U3 BU-1        .9952     -.0957     -.3257      .6746      .0936     -.1377
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0000      .8216      .4312      .0665      .8255      .7451

U5 BU-1       -.5415      .3333      .7943     -.1384      .1604      .5988
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .1657      .4198      .0185      .7439      .7044      .1168

H1 BU-1       -.1910     -.0975      .0349     -.1424     -.3179     -.4612
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .6504      .8183      .9347      .7365      .4429      .2500

H2 BU-1        .5396     -.5353     -.4100     -.0814      .7733     -.1341
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .1675      .1715      .3131      .8480      .0244      .7515

H3 BU-1        .9359     -.1999     -.3116      .5088      .2747     -.1441
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0006      .6351      .4524      .1978      .5103      .7336

H5 BU-1       -.3201      .6088      .9708      .2250     -.0999      .4952
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .4396      .1092      .0001      .5921      .8140      .2121

I1 BU-1        .6358     -.4497     -.8262      .1659      .1335     -.4064
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0902      .2635      .0115      .6946      .7526      .3178

I2 BU-1        .1755      .0631      .0517     -.0146      .6583      .0078
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .6777      .8820      .9033      .9726      .0760      .9854

I3 BU-1       -.2148      .4859      .5792      .0314      .4950      .9034
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .6094      .2222      .1325      .9412      .2123      .0021

I4 BU-1       -.0305     1.0000      .6533      .5993     -.1851      .6420
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .9429      .0000      .0790      .1163      .6607      .0861

A3 BU-1        .9213     -.1192     -.4299      .6494     -.1230     -.1707
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0011      .7785      .2877      .0814      .7717      .6861

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              S4 BU-1    S5 BU-1    U1 BU-1    U2 BU-1    U3 BU-1    U5 BU-1
S5 BU-1        .5341     1.0000     -.3440      .0535      .2050     -.1674
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .1727      .0000      .4041      .8998      .6263      .6919

U1 BU-1       -.7894     -.3440     1.0000      .1313      .3069     -.7067
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0198      .4041      .0000      .7567      .4596      .0500

U2 BU-1       -.4596      .0535      .1313     1.0000      .2370     -.4014
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .2520      .8998      .7567      .0000      .5720      .3243

U3 BU-1       -.1568      .2050      .3069      .2370     1.0000     -.5804
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .7107      .6263      .4596      .5720      .0000      .1315

U5 BU-1        .4120     -.1674     -.7067     -.4014     -.5804     1.0000
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .3104      .6919      .0500      .3243      .1315      .0000

H1 BU-1       -.1302     -.3560     -.0201      .3322     -.1644     -.2052
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .7586      .3867      .9623      .4214      .6972      .6259

H2 BU-1       -.5697      .1472       4082      .5839      .5422     -.3331
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .1404      .7279      .3153      .1286      .1651      .4201

H3 BU-1       -.2661      .3439      .3054      .3731      .9387     -.5680
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .5241      .4042      .4620      .3627      .0005      .1419

H5 BU-1        .6389      .0598     -.9138     -.2623     -.3629      .7724
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0882      .8881      .0015      .5303      .3770      .0247

I1 BU-1       -.4878     -.1689      .7590      .2974      .6677     -.7300
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .2201      .6892      .0290      .4744      .0704      .0398

I2 BU-1        .0000      .4402     -.1705      .7083      .1435     -.2166
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
              1.0000      .2750      .6865      .0493      .7347      .6064

I3 BU-1        .5451      .1526     -.5815     -.4462     -.2928      .7881
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .1623      .7184      .1306      .2678      .4815      .0202

I4 BU-1        .9948      .5859     -.7744     -.3967     -.0959      .3333
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0000      .1269      .0241      .3305      .8213      .4198

A3 BU-1       -.1628     -.0249      .4261      .0265      .9354     -.5802
              (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .7001      .9534      .2925      .9503      .0006      .1316

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              H1 BU-1     H2 BU-1     H3 BU-1     H5 BU-1     I1 BU-1     I2 BU-1
S5 BU-1       -.3560       .1472       .3439       .0598      -.1689       .4402
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .3867       .7279       .4042       .8881       .6892       .2750

U1 BU-1       -.0201       .4082       .3054      -.9138       .7590      -.1705
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .9623       .3153       .4620       .0015       .0290       .6865

U2 BU-1        .3322       .5839       .3731      -.2623       .2974       .7083
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .4214       .1286       .3627       .5303       .4744       .0493

U3 BU-1       -.1644       .5422       .9387      -.3629       .6677       .1435
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .6972       .1651       .0005       .3770       .0704       .7347

U5 BU-1       -.2052      -.3331      -.5680       .7724      -.7300      -.2166
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .6259       .4201       .1419       .0247       .0398       .6064

H1 BU-1       1.0000      -.3301      -.2281       .2141      -.1141       .2895
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .0000       .4246       .5869       .6107       .7878       .4867

H2 BU-1       -.3301      1.0000       .7204      -.5110       .5318       .5046
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .4246       .0000       .0438       .1956       .1749       .2022

H3 BU-1       -.2281       .7204      1.0000      -.3804       .5556       .2989
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .5869       .0438       .0000       .3526       .1528       .4721

H5 BU-1        .2141      -.5110      -.3804      1.0000      -.8363       .0126
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .6107       .1956       .3526       .0000       .0097       .9764

I1 BU-1       -.1141       .5318       .5556      -.8363      1.0000       .0557
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .7878       .1749       .1528       .0097       .0000       .8958

I2 BU-1        .2895       .5046       .2989       .0126       .0557      1.0000
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .4867       .2022       .4721       .9764       .8958       .0000

I3 BU-1       -.4608      -.0508      -.2964       .5205      -.3995       .0382
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .2505       .9050       .4759       .1860       .3269       .9285

I4 BU-1       -.0967      -.5356      -.2001       .6091      -.4499       .0634
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .8198       .1713       .6347       .1090       .2633       .8815

A3 BU-1       -.1208       .3359       .7749      -.4204       .7520      -.1217
             (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
               .7757       .4160       .0239       .2996       .0314       .7741
-----------------------------------------------------------------------------------
```

```
-----------------------------------------------
                   I3 BU-1      I4 BU-1      A3 BU-1
S5 BU-1              .1526        .5859       -.0249
                   (    8)      (    8)      (    8)
                     .7184        .1269        .9534

U1 BU-1            -.5815       -.7744         .4261
                   (    8)      (    8)      (    8)
                     .1306        .0241        .2925

U2 BU-1            -.4462       -.3967         .0265
                   (    8)      (    8)      (    8)
                     .2678        .3305        .9503

U3 BU-1            -.2928       -.0959         .9354
                   (    8)      (    8)      (    8)
                     .4815        .8213        .0006

U5 BU-1              .7881        .3333       -.5802
                   (    8)      (    8)      (    8)
                     .0202        .4198        .1316

H1 BU-1            -.4608       -.0967       -.1208
                   (    8)      (    8)      (    8)
                     .2505        .8198        .7757

H2 BU-1            -.0508       -.5356         .3359
                   (    8)      (    8)      (    8)
                     .9050        .1713        .4160

H3 BU-1            -.2964       -.2001         .7749
                   (    8)      (    8)      (    8)
                     .4759        .6347        .0239

H5 BU-1              .5205        .6091       -.4204
                   (    8)      (    8)      (    8)
                     .1860        .1090        .2996

I1 BU-1            -.3995       -.4499         .7520
                   (    8)      (    8)      (    8)
                     .3269        .2633        .0314

I2 BU-1              .0382        .0634       -.1217
                   (    8)      (    8)      (    8)
                     .9285        .8815        .7741

I3 BU-1             1.0000        .4859       -.3236
                   (    8)      (    8)      (    8)
                     .0000        .2222        .4343

I4 BU-1              .4859       1.0000       -.1194
                   (    8)      (    8)      (    8)
                     .2222        .0000        .7783

A3 BU-1            -.3236       -.1194        1.0000
                   (    8)      (    8)      (    8)
                     .4343        .7783        .0000
```

Appendix C. Complete correlation matrix indicating Pearson's correlation coefficients (r), sample sizes (in parentheses) and significance levels (P) for forage availability variables (logarithmically transformed) related to kudu mortalities at study units (Chapter 9). Variable names are explained under sub-heading 9.2.3. and is expressed as the resource level (DM) available per kudu.

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              WOOD BU-1  Ret1 BU-1  Ret2 BU-1  Ret3 BU-1  Ret4 BU-1  Ret5 BU-1
WOOD BU-1       1.0000     .7106      .3137      .9767      .4778      .2964
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .0000     .0482      .4492      .0000      .2312      .4760

Ret1 BU-1        .7106    1.0000     -.1074      .7216      .1014     -.3297
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .0482     .0000      .8002      .0433      .8111      .4251

Ret2 BU-1        .3137    -.1074     1.0000      .1967     -.0169      .1032
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .4492     .8002      .0000      .6405      .9683      .8079

Ret3 BU-1        .9767     .7216      .1967     1.0000      .3932      .2419
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .0000     .0433      .6405      .0000      .3352      .5638

Ret4 BU-1        .4778     .1014     -.0169      .3932     1.0000      .7691
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .2312     .8111      .9683      .3352      .0000      .0257

Ret5 BU-1        .2964    -.3297      .1032      .2419      .7691     1.0000
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .4760     .4251      .8079      .5638      .0257      .0000

S1 BU-1          .8393     .5196      .0034      .8198      .7659      .5716
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .0092     .1869      .9937      .0127      .0267      .1388

S2 BU-1          .2691    -.0841      .8063      .1669     -.0006      .1601
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .5193     .8431      .0156      .6929      .9989      .7049

S3 BU-1          .4773     .1046      .0699      .4095      .7624      .6932
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .2317     .8053      .8693      .3137      .0278      .0566

S4 BU-1          .4424     .0726     -.0560      .3598      .9965      .7893
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .2724     .8643      .8952      .3813      .0000      .0198

S5 BU-1          .4857     .1330      .4262      .4428      .6050      .2953
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .2224     .7536      .2924      .2719      .1120      .4776

U1 BU-1         -.1436     .4023     -.3255     -.0167     -.6835     -.8426
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .7343     .3232      .4314      .9688      .0617      .0086

U2 BU-1          .0487    -.2890      .7997     -.0045     -.2452     -.0258
               (    8)   (    8)    (    8)    (    8)    (    8)    (    8)
                 .9089     .4876      .0172      .9916      .5583      .9517

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              S1 BU-1    S2 BU-1    S3 BU-1    S4 BU-1    S5 BU-1    U1 BU-1
WOOD BU-1      .8393      .2691      .4773      .4424      .4857     -.1436
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0092      .5193      .2317      .2724      .2224      .7343

Ret1 BU-1      .5196     -.0841      .1046      .0726      .1330      .4023
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .1869      .8431      .8053      .8643      .7536      .3232

Ret2 BU-1      .0034      .8063      .0699     -.0560      .4262     -.3255
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .9937      .0156      .8693      .8952      .2924      .4314

Ret3 BU-1      .8198      .1669      .4095      .3598      .4428     -.0167
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0127      .6929      .3137      .3813      .2719      .9688

Ret4 BU-1      .7659     -.0006      .7624      .9965      .6050     -.6835
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0267      .9989      .0278      .0000      .1120      .0617

Ret5 BU-1      .5716      .1601      .6932      .7893      .2953     -.8426
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .1388      .7049      .0566      .0198      .4776      .0086

S1 BU-1       1.0000     -.0905      .5142      .7424      .4738     -.4479
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0000      .8312      .1923      .0349      .2357      .2658

S2 BU-1       -.0905     1.0000      .4300      .0032      .3237     -.1821
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .8312      .0000      .2877      .9939      .4341      .6660

S3 BU-1        .5142      .4300     1.0000      .7908      .4629     -.4131
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .1923      .2877      .0000      .0195      .2480      .3091

S4 BU-1        .7424      .0032      .7908     1.0000      .5631     -.6859
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .0349      .9939      .0195      .0000      .1462      .0604

S5 BU-1        .4738      .3237      .4629      .5631     1.0000     -.2780
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .2357      .4341      .2480      .1462      .0000      .5050

U1 BU-1       -.4479     -.1821     -.4131     -.6859     -.2780     1.0000
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .2658      .6660      .3091      .0604      .5050      .0000

U2 BU-1       -.1009      .3527     -.4345     -.2967      .2017     -.2954
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
               .8121      .3914      .2821      .4755      .6320      .4776

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Appendix C.

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                      U2 BU-1     U3 BU-1     U5 BU-1     H1 BU-1     H2 BU-1     H3 BU-1
WOOD BU-1               .0487       .9605      -.0280      -.1680       .3263       .8775
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .9089       .0001       .9475       .6909       .4303       .0042

Ret1 BU-1              -.2890       .7349      -.4608      -.2939       .2188       .5969
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .4876       .0378       .2505       .4798       .6026       .1182

Ret2 BU-1               .7997       .1742      -.0468      -.0119       .7072       .3768
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .0172       .6799       .9124       .9777       .0498       .3575

Ret3 BU-1              -.0045       .9958      -.0759      -.2056       .3292       .9279
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .9916       .0000       .8582       .6253       .4260       .0009

Ret4 BU-1              -.2452       .3321       .4938       .0447      -.4652       .1410
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .5583       .4215       .2136       .9163       .2455       .7391

Ret5 BU-1              -.0258       .1903       .8337       .1706      -.3450       .0782
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .9517       .6518       .0101       .6863       .4026       .8539

S1 BU-1                -.1009       .8030       .1974      -.0654      -.1537       .6143
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .8121       .0164       .6394       .8778       .7163       .1052

S2 BU-1                 .3527       .1186       .2813      -.3545       .7245       .2858
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .3914       .7798       .4997       .3890       .0421       .4926

S3 BU-1                -.4345       .3300       .6909      -.2444      -.1133       .2083
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .2821       .4247       .0578       .5597       .7894       .6206

S4 BU-1                -.2967       .2968       .5536       .0220      -.4891       .0978
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .4755       .4753       .1546       .9588       .2187       .8179

S5 BU-1                 .2017       .4008      -.0369      -.2694       .1859       .4824
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .6320       .3252       .9309       .5188       .6594       .2260

U1 BU-1                -.2954       .0254      -.6506      -.2432       .3097       .1162
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .4776       .9525       .0807       .5617       .4553       .7841

U2 BU-1                1.0000       .0198      -.2668       .2315       .5196       .2428
                     (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                        .0000       .9629       .5230       .5812       .1869       .5623

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                   H5 BU-1     I1 BU-1     I2 BU-1     I3 BU-1     I4 BU-1     A3 BU-1
WOOD BU-1           .2602       .7072       .3562       .3323       .4777       .8835
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .5337       .0498       .3865       .4213       .2312       .0036

Ret1 BU-1         -.3285        .9767      -.1417      -.0729       .1014       .8495
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .4269       .0000       .7378       .8638       .8113       .0076

Ret2 BU-1           .0240      -.0145       .8921       .1340      -.0169      -.1137
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .9550       .9727       .0029       .7518       .9684       .7887

Ret3 BU-1           .2097       .7219       .2229       .2438       .3931       .9325
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .6182       .0432       .5956       .5606       .3354       .0007

Ret4 BU-1           .7401       .0219       .2891       .6784      1.0000       .3068
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .0358       .9590       .4874       .0644       .0000       .4598

Ret5 BU-1           .9809      -.3636       .2988       .7476       .7692       .0969
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .0000       .3760       .4721       .0330       .0257       .8194

S1 BU-1             .5311       .4471       .1451       .3985       .7657       .7861
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .1756       .2668       .7317       .3282       .0268       .0207

S2 BU-1             .0809       .0788       .6598       .5186      -.0006      -.1000
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .8490       .8529       .0750       .1879       .9989       .8138

S3 BU-1             .6709       .1370       .2612       .9503       .7625       .2973
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .0686       .7463       .5321       .0003       .0278       .4745

S4 BU-1             .7621      -.0017       .2437       .7202       .9965       .2839
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .0279       .9969       .5608       .0439       .0000       .4956

S5 BU-1             .1880       .1592       .5923       .3085       .6047       .1925
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .6557       .7066       .1219       .4573       .1123       .6479

U1 BU-1           -.7923        .4513      -.4528      -.5433      -.6834       .1464
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .0190       .2616       .2599       .1640       .0617       .7295

U2 BU-1           -.0912       -.2564       .6602      -.3453      -.2453      -.2445
                  (    8)     (    8)     (    8)     (    8)     (    8)     (    8)
                    .8300       .5399       .0748       .4022       .5582       .5596

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Appendix C.

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                 ETTE ha-1
WOOD BU-1            .0110
                   (    8)
                     .9794

Ret1 BU-1            .4904
                   (    8)
                     .2173

Ret2 BU-1           -.0750
                   (    8)
                     .8599

Ret3 BU-1            .1070
                   (    8)
                     .8008

Ret4 BU-1           -.7781
                   (    8)
                     .0230

Ret5 BU-1           -.8736
                   (    8)
                     .0046

S1 BU-1             -.3612
                   (    8)
                     .3794

S2 BU-1             -.1245
                   (    8)
                     .7689

S3 BU-1             -.6062
                   (    8)
                     .1111

S4 BU-1             -.8019
                   (    8)
                     .0167

S5 BU-1             -.3589
                   (    8)
                     .3826

U1 BU-1              .8940
                   (    8)
                     .0027

U2 BU-1              .0373
                   (    8)
                     .9302
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Appendix C.

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            WOOD BU-1  Ret1 BU-1  Ret2 BU-1  Ret3 BU-1  Ret4 BU-1  Ret5 BU-1
U3 BU-1         .9605      .7349      .1742      .9958      .3321      .1903
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .0001      .0378      .6799      .0000      .4215      .6518

U5 BU-1        -.0280     -.4608     -.0468     -.0759      .4938      .8337
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .9475      .2505      .9124      .8582      .2136      .0101

H1 BU-1        -.1680     -.2939     -.0119     -.2056      .0447      .1706
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .6909      .4798      .9777      .6253      .9163      .6863

H2 BU-1         .3263      .2188      .7072      .3292     -.4652     -.3450
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .4303      .6026      .0498      .4260      .2455      .4026

H3 BU-1         .8775      .5969      .3768      .9279      .1410      .0782
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .0042      .1182      .3575      .0009      .7391      .8539

H5 BU-1         .2602     -.3285      .0240      .2097      .7401      .9809
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .5337      .4269      .9550      .6182      .0358      .0000

I1 BU-1         .7072      .9767     -.0145      .7219      .0219     -.3636
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .0498      .0000      .9727      .0432      .9590      .3760

I2 BU-1         .3562     -.1417      .8921      .2229      .2891      .2988
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .3865      .7378      .0029      .5956      .4874      .4721

I3 BU-1         .3323     -.0729      .1340      .2438      .6784      .7476
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .4213      .8638      .7518      .5606      .0644      .0330

I4 BU-1         .4777      .1014     -.0169      .3931     1.0000      .7692
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .2312      .8113      .9684      .3354      .0000      .0257

A3 BU-1         .8835      .8495     -.1137      .9325      .3068      .0969
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .0036      .0076      .7887      .0007      .4598      .8194

ETTE ha-1       .0110      .4904     -.0750      .1070     -.7781     -.8736
             (    8)    (    8)    (    8)    (    8)    (    8)    (    8)
                .9794      .2173      .8599      .8008      .0230      .0046

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Appendix C.

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                      S1 BU-1      S2 BU-1      S3 BU-1      S4 BU-1      S5 BU-1      U1 BU-1
U3 BU-1                 .8030        .1186        .3300        .2968        .4008        .0254
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .0164        .7798        .4247        .4753        .3252        .9525

U5 BU-1                 .1974        .2813        .6909        .5536       -.0369       -.6506
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .6394        .4997        .0578        .1546        .9309        .0807

H1 BU-1                -.0654       -.3545       -.2444        .0220       -.2694       -.2432
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .8778        .3890        .5597        .9588        .5188        .5617

H2 BU-1                -.1537        .7245       -.1133       -.4891        .1859        .3097
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .7163        .0421        .7894        .2187        .6594        .4553

H3 BU-1                 .6143        .2858        .2083        .0978        .4824        .1162
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .1052        .4926        .6206        .8179        .2260        .7841

H5 BU-1                 .5311        .0809        .6709        .7621        .1880       -.7923
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .1756        .8490        .0686        .0279        .6557        .0190

I1 BU-1                 .4471        .0788        .1370       -.0017        .1592        .4513
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .2668        .8529        .7463        .9969        .7066        .2616

I2 BU-1                 .1451        .6598        .2612        .2437        .5923       -.4528
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .7317        .0750        .5321        .5608        .1219        .2599

I3 BU-1                 .3985        .5186        .9503        .7202        .3085       -.5433
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .3282        .1879        .0003        .0439        .4573        .1640

I4 BU-1                 .7657       -.0006        .7625        .9965        .6047       -.6834
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .0268        .9989        .0278        .0000        .1123        .0617

A3 BU-1                 .7861       -.1000        .2973        .2839        .1925        .1464
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .0207        .8138        .4745        .4956        .6479        .7295

ETTE ha-1              -.3612       -.1245       -.6062       -.8019       -.3589        .8940
                      (    8)      (    8)      (    8)      (    8)      (    8)      (    8)
                        .3794        .7689        .1111        .0167        .3826        .0027

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Appendix C.

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                 U2 BU-1    U3 BU-1    U5 BU-1    H1 BU-1    H2 BU-1    H3 BU-1
U3 BU-1            .0198     1.0000     -.1309     -.2019      .3424      .9380
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .9629      .0000      .7573      .6316      .4064      .0006

U5 BU-1           -.2668     -.1309     1.0000     -.0672     -.2963     -.2322
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .5230      .7573      .0000      .8744      .4761      .5800

H1 BU-1            .2315     -.2019     -.0672     1.0000     -.4526     -.2637
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .5812      .6316      .8744      .0000      .2602      .5280

H2 BU-1            .5196      .3424     -.2963     -.4526     1.0000      .5879
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .1869      .4064      .4761      .2602      .0000      .1253

H3 BU-1            .2428      .9380     -.2322     -.2637      .5879     1.0000
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .5623      .0006      .5800      .5280      .1253      .0000

H5 BU-1           -.0912      .1585      .8181      .3165     -.4318      .0218
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .8300      .7078      .0131      .4450      .2854      .9591

I1 BU-1           -.2564      .7329     -.4277     -.4525      .3856      .6434
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .5399      .0386      .2906      .2603      .3455      .0852

I2 BU-1            .6602      .1786      .0183      .2526      .3997      .3178
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .0748      .6723      .9658      .5461      .3265      .4430

I3 BU-1           -.3453      .1657      .8440     -.2696     -.0894      .0551
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .4022      .6949      .0084      .5184      .8333      .8970

I4 BU-1           -.2453      .3320      .4938      .0454     -.4654      .1408
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .5582      .4217      .2136      .9149      .2452      .7394

A3 BU-1           -.2445      .9425     -.1484     -.1810      .1427      .7929
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .5596      .0005      .7259      .6680      .7361      .0189

ETTE ha-1          .0373      .1661     -.7905     -.0771      .4768      .2668
                 (    8)   (    8)   (    8)   (    8)   (    8)   (    8)
                   .9302      .6942      .0195      .8560      .2323      .5230

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Appendix C.

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               H5 BU-1    I1 BU-1    I2 BU-1    I3 BU-1    I4 BU-1    A3 BU-1
U3 BU-1         .1585      .7329      .1786      .1657      .3320      .9425
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .7078      .0386      .6723      .6949      .4217      .0005

U5 BU-1         .8181     -.4277      .0183      .8440      .4938     -.1484
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .0131      .2906      .9658      .0084      .2136      .7259

H1 BU-1         .3165     -.4525      .2526     -.2696      .0454     -.1810
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .4450      .2603      .5461      .5184      .9149      .6680

H2 BU-1        -.4318      .3856      .3997     -.0894     -.4654      .1427
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .2854      .3455      .3265      .8333      .2452      .7361

H3 BU-1         .0218      .6434      .3178      .0551      .1408      .7929
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .9591      .0852      .4430      .8970      .7394      .0189

H5 BU-1        1.0000     -.3866      .2636      .7102      .7403      .1002
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .0000      .3441      .5281      .0484      .0357      .8134

I1 BU-1        -.3866     1.0000     -.1162     -.0179      .0217      .8151
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .3441      .0000      .7840      .9665      .9593      .0137

I2 BU-1         .2636     -.1162     1.0000      .2419      .2894     -.0929
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .5281      .7840      .0000      .5639      .4870      .8267

I3 BU-1         .7102     -.0179      .2419     1.0000      .6784      .1241
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .0484      .9665      .5639      .0000      .0644      .7696

I4 BU-1         .7403      .0217      .2894      .6784     1.0000      .3068
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .0357      .9593      .4870      .0644      .0000      .4598

A3 BU-1         .1002      .8151     -.0929      .1241      .3068     1.0000
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .8134      .0137      .8267      .7696      .4598      .0000

ETTE ha-1      -.8231      .5225     -.2725     -.7011     -.7780      .2444
               (   8)     (   8)     (   8)     (   8)     (   8)     (   8)
                .0121      .1840      .5138      .0527      .0230      .5597

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                ETTE ha-1
U3 BU-1            .1661
                 (    8)
                   .6942

U5 BU-1           -.7905
                 (    8)
                   .0195

H1 BU-1           -.0771
                 (    8)
                   .8560

H2 BU-1            .4768
                 (    8)
                   .2323

H3 BU-1            .2668
                 (    8)
                   .5230

H5 BU-1           -.8231
                 (    8)
                   .0121

I1 BU-1            .5225
                 (    8)
                   .1840

I2 BU-1           -.2725
                 (    8)
                   .5138

I3 BU-1           -.7011
                 (    8)
                   .0527

I4 BU-1           -.7780
                 (    8)
                   .0230

A3 BU-1            .2444
                 (    8)
                   .5597

ETTE ha-1         1.0000
                 (    8)
                   .0000

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