RESOURCE OVERLAP WITHIN A GUILD OF BROWSING UNGULATES IN A SOUTH AFRICAN SAVANNA

by

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ABSTRACT

Food selection by free-ranging black rhinoceros, eland, giraffe and kudu as well as the utilisation of vegetation types by the latter three browsers were investigated over an entire seasonal cycle, from June 1998 to July 1999, at Weenen Nature Reserve, KwaZulu-Natal. The study was aimed at determining the extent of resource overlap within this browser guild. Feeding habits of eland, giraffe and kudu were studied by direct observations, while a plant-based technique was used for black rhinoceros. Dung counts were conducted to monitor selection for vegetation types. Overlap was estimated by measuring the similarities in resource utilisation patterns.

Giraffe were exclusively browsers, feeding mostly on woody foliage, over the complete seasonal cycle. The bulk of the annual diet of kudu also consisted of woody browse, although forbs were important and their use increased from early summer to winter. The annual diet of eland consisted of approximately equal proportions of grass and browse, with pods making up almost a third of the diet. Similar to kudu, forbs were more prominent in the winter diet, while grass use decreased. During winter, overlap in forage types generally increased and was considerable because the browsers did not resort to distinct forage 'refuges'. Overlap in the utilisation of woody plant species, however, decreased as animals diversified their diets. Nonetheless, overlap was extensive, primarily owing to the mutual utilisation of *Acacia karroo* and *Acacia nilotica.*

The quantity of woody foliage decreased during winter, as indicated by phenological differences, but numerous individual plants still carried leaves. Based on current evidence, food quality was assumed to decline. Under prevailing conditions, eland, giraffe and black rhinoceros suffered no mortalities indicating that they were not food limited, possibly owing to the nutritional advantages conferred by their large body size, and that competition among them was unlikely. By comparison, kudu mortalities were great which may signify that they were constrained by food supply and that the larger browsers exerted a pronounced competitive effect on them.

Based on the current study it is hypothesised that during periods of resource scarcity the abundance of high quality foods are limited and if interspecific competition does prevail, which will further limit the availability of these resources, it is the smaller bodied herbivores that will be most affected and suffer the greatest mortalities. Consequences of competitive interactions among these browsers have important management implications, especially in small reserves, which are a key stone for the conservation of mammalian herbivores.

DECLARATION

I, Lorene Breebaart, declare that the research reported in this thesis is the result of my own investigations, except where acknowledged. It has not, in its entirety or in part, been submitted previously for any degree or examination at any other university.

8th day of December 2000

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INTRODUCTION

INTRODUCTION

A striking feature of African herbivore communities is the relatively large number of species with similar ecological requirements that often coexist in the same area (Leuthold 1978). Lamprey (1963) used the term ecological separation to explain how such a diversity of large (> 5 kg) herbivores may coexist in an ecosystem. Although studies in Africa (Lamprey 1963; Gwynne & Bell 1968; Jarman 1971; Ferrar & Walker 1974; Leuthold 1978; Kelso 1986; Du Toit 1988, 1990; Fritz *et al.* 1996; Dekker *et al.* 1996) have demonstrated ecological separation, they have also shown there is extensive overlap in resource use among large mammalian herbivores.

Ecological separation is usually studied between sympatric members of a group of species having some general similarity in their trophic roles (Schoener 1986). Such a group is called a 'guild', originally defined by Root (1967) as a group of "species that exploit the same class of resources in a similar way". In African savanna systems, studies of ecological separation or overlap have largely concentrated on grazer species (reviewed in Sinclair & Norton-Griffiths 1979). By comparison, the current level of knowledge on the occurrence of resource overlap among large browsing herbivores in southern African is limited (Lamprey 1963; Jarman 1971; Ferrar & Walker 1974; Leuthold 1978; Du Toit 1988, 1990; Fritz *et al.* 1996; Dekker *et al.* 1996). Further investigations are clearly required if the management of wildlife areas is to be placed on an ecologically sound basis. This study was, therefore, restricted to black rhinoceros (*Diceros bicornis* Linnaeus 1758), giraffe (*Giraffa camelopardis* Linnaeus 1758), greater kudu (*Tragelaphus strepsiceros* Pallas 1766) and eland (*Taurotragus orynx* Pallas 1766) whose primary food resource consist of the foliage of dicotyledonous plants (trees, shrubs, and / or forbs) (Lamprey 1963; Wilson 1965; Goddard 1968, 1970; Kerr *et al.* 1970; Jarman 1971; Joubert & Eloff 1971; Hofmann & Stewart 1972; Leuthold & Leuthold 1972; Oates 1972; Hall-Martin 1974a; Conybeare 1975; Field 1975; Stephens 1975; Mukinya 1977; Sauer *et al.* 1977; Leuthold 1978; Owen-Smith 1979, 1982; Hall-Martin *et al.* 1982; Novellie 1983; Hansen *et al.* 1984; Pellew 1984a; Owen-Smith & Cooper 1985, 1989; Kelso 1986; Du Toit 1988; Buys 1990; Skinner & Smithers 1990; Emslie & Adcock 1993; Oloo *et al.* 1994; Owen-Smith 1997).

Principal factors contributing to ecological separation are considered to be a preference for grass or browse, differences in body size (McNaughton & Georgiadis 1986) and differences in habitat use (Lamprey 1963). Early studies, particularly by Lamprey (1963), demonstrated that different proportions of grass and browse in the diets of grazers, mixed feeders and browsers contributed to ecological separation. Similarly, Du Toit (1988) found that the grass:browse ratio in the diets of coexisting browsers differed. Owing to the fact that body size determines metabolic costs and digestive efficiency, different sized herbivores, both grazers (Gwynne & Bell 1968) and browsers (McNaughton & Georgiadis 1986; Du Toit 1988), may partition available food according to its nutritional quality. Differential use of food may also be achieved by different browser species, because of body-size differences, feeding at different levels in the vegetation (Lamprey 1963; Leuthold 1978; Du Toit 1988, 1990). Herbivores are not evenly distributed in an area while foraging, but rather favour certain habitat types over others (Hirst 1975). Therefore, ecological separation may be achieved by different species utilising different habitats at the same time or the same habitat at different times (Lamprey 1963).

Interspecific competition is considered an important process driving patterns of ecological separation (Schoener 1974, 1986; Leuthold 1978; McNaughton & Georgiadis 1986; Manley *et al.* 1993). However, other factors such as predation and migration may also contribute to ecological separation (Sinclair & Norton-Griffiths 1982; Schluter 1984; Sinclair 1985). The most direct way of assessing the significance of interspecific competition is by experimentally manipulating potentially competing populations (Schoener 1983). Unfortunately, experimental manipulations of wild ungulate populations are difficult to achieve. In addition, data on the prevalence of interspecific competition are generated very slowly, vegetation changes must be monitored, and predation and disease need to be determined both before and after removals (Wiens 1989). An alternative approach, which is commonly employed in field studies, is to measure the degree of overlap in resource use between coexisting species (Schoener 1974, 1986; Sale 1974; Hurlbert 1978; Abrams 1980) and to compare the extent of overlap during periods of low and high resource availability (Gordon & Illius 1989). The competition theory predicts that during periods of resource scarcity, directional selection may favour trophic phenotypes which use resources most effectively and consequently, overlap during lean times is often less as species specialise (Schoener 1982, 1986).

If the utilisation of resources is similar between species, as indicated by overlap, then interspecific competition can occur only if the sizes of the populations are limited by the amount of available resources (Sale 1974; Hurlbert 1978;Abrams 1980; Lawlor 1980; Krebs 1999). The most common resources considered in overlap studies are food and space (habitat) (Schoener 1974) which are interdependent, because habitat choices by large mammalian herbivores are associated with food abundance and quality (McNaughton & Georgiadis 1986; Fritz *et al.* 1996). In arid and semi-arid environments, ungulates commonly experience considerable seasonal variation in resources (Illius & O'Connor 2000). During the season of active plant growth, large mammalian herbivores may be surrounded by an abundance of potential food. However, during the dry season food availability decreases drastically in both quantity and quality (Owen-Smith 1982; Sauer *et al.* 1982; Pellew 1984b; Cooper *et al.* 1988). Current evidence indicates that during periods of resource scarcity, such as the dry season or during drought years, grazer and browser populations are controlled by food supply (Novellie 1986; Fryxell 1987; Sinclair & Norton-Griffiths 1982; Owen-Smith 1990).

Predators have the potential to regulate populations independently of resource availability (Mentis 1978) and, therefore, confound results of either overlap or experimental studies. Similarly, seasonal movements, especially migration, may buffer a population against seasonal variability by allowing a dry-season refuge to herbivores (Illius & O'Connor 2000) and result in separation between herbivore populations without competition (Sinclair & Norton-Griffiths 1982). The absence of predators and migration would, therefore, result in more robust conclusions about interspecific competition. In small reserves, such as Weenen Nature Reserve, usually with an absence of migration and predation, populations are also more likely to be close to the carrying capacity of the area, and hence regulated through food resources, than in large open systems (Owen-Smith 1989, 1990). In addition, small reserves typically offer a restricted number of habitat or vegetation types for which animals could select. Therefore, the potential for interspecific competition may be intensified (Ferrar & Walker 1974).

In southern Africa, small reserves are a keystone for the conservation of large mammals whose management should be based on an understanding of mechanisms allowing these species to coexist. Thus, a study on the degree of resource overlap between browsing ungulates in such a confined area has important management considerations. This study, therefore, endeavoured to provide a more sound understanding of potential competitive interactions among browsing ungulates under prevailing circumstances typical of small reserves that should contribute to improved management of the conservation of large mammalian herbivores.

AIM AND OBJECTIVES

The aim of this study was to determine the extent of and seasonal variation in overlap, in terms of food and habitat selection, by free-ranging black rhinoceros, eland, giraffe and greater kudu (henceforth kudu) over a complete seasonal cycle (June 1998 - July 1999). Based on current understanding, the objectives of the study were to test the hypotheses that ecological separation is achieved by coexisting species:

- consuming different proportions of grass and browse (Lamprey 1963; McNaughton & Georgiadis 1986);
- utilising different plant species (Lamprey 1963; Schoener 1974);
- feeding at different levels in the vegetation (Lamprey 1963; Du Toit 1988, 1990); and
- utilising different habitats during the same season or the same habitat during different seasons (Lamprey 1963).

Assuming that interspecific competition is the process driving the above patterns of ecological separation, then it was predicted that resource overlap should decrease during the 'lean' season (Schoener 1982, 1986), i.e., winter. This was expected to be achieved by:

- the browsers specialising in their diets as well as habitats (Schoener 1982, 1986);
- each browser making use of a distinct food type, i.e., refuge (Jarman 1971);
- the browsers utilising different sizes of food (Schoener 1986);
- there being a clear stratification in feeding heights (Du Toit 1988, 1990); and
- the different browsers utilising different vegetation types (Lamprey 1963).

Seasonal changes in the abundance and quality of food necessitates animals to make modifications to their feeding behaviour so they can meet their metabolic requirements (Owen-Smith 1979). If grass was utilised, its contribution to the diet was expected to decrease during winter (Kerr *et al.* 1970; Field 1975; Jankowitz 1982 in Owen-Smith 1997; Kelso 1986; Buys 1990) owing to a decline in its quality (Field 1975; Buys 1990). Owing primarily to a decrease in food supply of deciduous species during winter, broadleaved or evergreen species were expected to become more abundant in the diet (Owen-Smith 1979).

The following questions, concerning the seasonal use of food and habitats by the guild of browsers, were addressed:

- What is the diet composition, in terms of forage types and woody plant species, of each browser and how does it change over time?
- What is the degree of dietary overlap, in terms of diet composition and feeding height, among the guild of browsers and how does this vary across seasons?
- Which vegetation types are utilised by each browser and when are they used?
- Do browsers utilise the same vegetation type/s and if so, to what degree?

Throughout this study, the emphasis was on present-day interactions between species, rather than on an evolutionary approach of resource partitioning, which is the result of past competitive pressures. The ecosystem of Weenen Nature Reserve bears little resemblance to conditions under which the browser species would have been selected in terms of acquiring attributes relevant to foraging ecology. Firstly, the spacial scale of this system (*ca* 3 150 ha) is minuscule compared with the former ranges of some of these species when unrestricted in there movement. For example, in Kruger National Park kudu female groups (averaging 6 adults) had home ranges of 300 to 2 500 ha, while males moved over a larger home range of up to 5 000 ha. In East Africa the home ranges of giraffe females and males were 8 500 ha and 6 200 ha, respectively (Skinner & Smithers 1990), but home ranges of females in Tsavo National Park, Kenya, were up to 48 000 ha (Owen-Smith 1988). Average home range size of female black rhinoceros ranged from 7 600 ha on the Serengeti plains, Tanzania (Frame 1980), to 670 ha in Hluhluwe Game Reserve, South Africa (Owen-Smith 1988). Home ranges of male black rhinoceros tend to be smaller than those of females, although a maximum home range of 13 3000 ha was recorded in the Serengeti (Frame 1980). Secondly, the past distribution of giraffe indicates that they never occurred in KwaZulu-Natal (Goodman & Tomkinson 1987). Lastly, most of the vegetation of Weenen Nature Reserve was derived from abandoned cultivated lands.

Although this study focused on present-day interactions, I also investigated the extent of past competition by comparing consumer preferences as suggested by Lawlor (1980). I, therefore, also addressed the following questions:

- What are the preferences of each animal species for woody plant species and how do they change over time?
- What are the preferences for feeding heights, when consuming woody plant species, and how do they change over time?

- Among the browsers, how similar are the preferences for woody plant species and browsing heights?

LITERATURE REVIEW

INTRODUCTION

This section sets out to give a literature review of the topics applicable to the current study. Firstly, there are a number of approaches for assessing and quantifying diet composition and habitat utilisation, calculating food and habitat preferences, and estimating the degree of overlap and resource partitioning between pairs of species. Associated with each of these methods are a number of advantages and disadvantages which have stimulated discussion as to which is the most useful. An overview and critical evaluation of these methods are presented with specific reference to large herbivores. Secondly, the controversy as to what overlap indices convey about competition is discussed. Thirdly, an overview of prevailing concepts of ecological separation is presented. Lastly, a brief description of what is currently known about the browser species under consideration and the extent of overlap between them is given.

DIET COMPOSITION

ASSESSING DIET COMPOSITION

There are three main groups of methods by which diet composition and food utilization of browsers can be estimated, namely: (1) analysis of ingesta or faeces of animals; (2) direct observations of feeding (animal-based methods); and (3) the measurement of previously browsed vegetation (plant-based methods) (Barnes 1976).

Faecal and Ingesta Analysis

Microscopic examination of plant residues recovered from oesophageal fistulae, stomach contents and faeces are three common methods for determining food utilisation of large herbivores (McInnes *et al.* 1983). Oesophageal fistulation is one approach used to study the diet composition of captive ungulates (Wickstrom *et al.* 1984) but has not been extensively used with wild herbivores (McInnes *et al.* 1983). This method necessitates a considerable amount of veterinary care and a great deal of handling, which non-domestic animals may not tolerate or survive (Monro 1982). Two additional problems with fistulation are: plant fragments found in oesophageal extrusa represent the diet of the animal for only that length of time during which the fistula sample is being collected; and the feeding behaviour of fistulated individuals may differ from that of intact animals (McInnes *et al.* 1983).

Examination of rumen contents is used frequently for determining the diet of large, free-ranging animals (Lewis 1994). The main limitation of this technique is that it requires capturing or killing of animals (McInnes *et al.* 1983) which precludes large sample sizes (Lewis 1994). Monro (1982) states this to be the most fundamental sampling error in analysis of rumen contents.

A popular technique used to define the diets of wild animals is the examination of faecal material. Advantages of this method include: it does not interfere with the normal feeding habits of the animal; it is the only feasible procedure to use when studying secretive or endangered species where direct observations or rumen collections cannot be conducted; it does not require the capture or killing of animals (McInnes *et al.* 1983); faeces are easily obtained; and large amounts of material can be collected (Monro 1982). Faecal samples also represent a longer feeding interval than samples from oesophageal fistulation or rumen contents (Lewis 1994).

The analysis of herbivore faeces and ingesta are subject to various limitations owing to errors involved in sampling and identification of materials (Goddard 1968). Faecal and ingesta material are usually sieved to remove the smallest particles. As a consequence, the sieved material is unlikely to contain as much of the dietary spectrum as unsieved material (Monro 1982). Lewis (1994) found that sieving resulted in a loss of finely chewed or partially digested particles. As a result, the unsieved material contained fragments of plants which were not observed in the sieved material (Lewis 1994).

Examination of stomach contents and faeces may give biased estimates of diets owing to differential digestibility, ease of identification and turnover rate among different dietary components (Lewis 1994). In comparing four methods used to determine the diets of large herbivores, McInnes *et al.* (1983) detected a consistent disappearance of forbs as they passed through the digestive tract. Lower percentages of forbs were contained in the faeces than in the rumen, and in the rumen than in the oesophagus. The result was that rumen and faecal analysis overestimated less digestible portions of the diet while underestimating more digestible portions. Lewis (1994) also found that identification of easily digested forbs was greater in rumen than in faecal samples. He concluded that the problems of differential digestibility and ease of identification tended to be more pronounced in faecal than in rumen analyses.

Three factors involved in epidermal identification can seriously affect the estimation of diet composition. The first of these is that a substantial amount of material may not be identifiable. If one chooses sampling techniques with the least bias (e.g., not sieving out the smallest fragments) then difficulties are experienced with identification (Monro 1982). Lewis (1994) detected a high proportion of unidentifiable material in unsieved samples which was not found in sieved samples. The second factor affecting results is that some species and plant parts are more easily identified than others. Consequently, the former tends to be recorded disproportionately more often than the latter. Lastly, results are complicated by mis-identification, since the epidermis of some species are very similar in appearance (Monro 1982).

Although microscopic analysis of faeces, rumen contents and oesophageal extrusa is subject to various limitations and is not quantitative, it has the potential for providing useful and, in the case of faecal samples, easily obtainable qualitative information. It may indicate the monocot:dicot ratio (Monro 1982) or proportion of woody to leaf material in the diet, compositional change over seasons, and additional items in the diet, such as fruit and flowers.

Animal-based Methods

Direct observations of kudu (Owen-Smith 1979, 1994; Cooper 1985; Owen-Smith & Cooper 1985, 1987a, 1987b, 1989; Cooper & Owen-Smith 1986; Du Toit 1988, 1990), giraffe (Jarman 1971; Leuthold & Leuthold 1972; Oates 1972; Leuthold 1978; Pellew 1984a; Du Toit 1988, 1990) and other browsers (Jarman 1971; Dunham 1980; Monro 1982; Du Toit 1988, 1990; Haschick & Kerley 1997) have been successfully employed. These studies were conducted in relatively open habitats where visibility was good or by using tame animals in small enclosures.

To permit close-range observations, tame animals have been used for feeding studies (Dunham 1980; Monro 1982; Cooper 1985; Owen-Smith & Cooper 1989; Owen-Smith 1994; Haschick & Kerley 1997). An assumption of these studies is that feeding habits of tame individuals are similar to those of wild animals. This has been suggested as not being so (Leuthold 1970). Apart from this, all studies on tame animals are subject to a number of flaws. These include the use of too few animals, their restriction to only a small area of their natural range, their removal from possible influences of other animals in a herd, and the short duration of the studies. The time, effort and capital involved in rearing and taming these animals is also considerable (Monro 1982).

The main disadvantages of direct observation methods include the following. (1) Animals may be difficult to find and hence a large amount of time is spent searching for them. (2) Observers may cause a change in animal behaviour, thus introducing a bias in observations. (3) Animals browse during the night and this is usually unaccounted for by direct observation. If a change in the utilisation pattern occurs during diurnal and nocturnal feeding, a direct observation technique is likely to be far more biased than a plant-based technique. (4) Vegetation may obscure feeding animals (Kotze & Zacharias 1993) and thus observations are interrupted temporarily, whenever the animal gets out of sight. (5) Food items taken at ground level often cannot be recognised or identified and are, therefore, under represented in the data collected (Leuthold 1970). (6) It is not always possible to ascertain which part of a particular plant is being eaten. (7) Observations are usually conducted some distance from the feeding animal, making accurate recordings difficult.

As a result of the above shortcomings of direct observations it is impossible to obtain a complete quantitative record of the food utilised within a given period of time. Nevertheless, the method yields useful information, if applied for a sufficient length of time and in different vegetation types (Leuthold 1970).

Plant-based Methods

Plant measurements are complementary and supplementary to animal-based methods for assessing diet composition and food preferences. In situations where several animal species feed at the same time on a particular vegetation, plant measurements cannot usually be used on their own to estimate browse utilisation by individual species (Barnes 1976). However, where an animal's feeding manner is distinct, such as black rhinoceros' bite, then a plant-based approach, without the use of direct techniques, can be used (Emslie & Adcock 1993; Kotze & Zacharias 1993; Oloo *et al.* 1994).

Plant-based methods are particularly useful in densely vegetated areas, where the animal of interest is difficult to find, or is potentially dangerous to track. Studies of black rhinoceros using direct observations (Goddard 1968, 1970; Mukinya 1977) have been carried out in relatively open habitats where visibility was good. However, direct observations have been found to be unsuitable for black rhinoceros feeding in densely vegetated areas (Emslie & Adcock 1993; Kotze & Zacharias 1993; Oloo *et al.* 1994), even with the use of a radio-tracking device (Emslie & Adcock 1993). This is mainly owing to the difficulty in finding black rhinoceros and vegetation obscuring feeding animals (Kotze & Zacharias 1993).

Emslie and Adcock (1993) reviewed alternative approaches for assessing the diet of black rhinoceros. The conclusions reached were that plant-based methods (1) eliminate most of the serious biases associated with direct observation methods or dung analysis, (2) had potentially greater return per unit effort than direct observation methods or dung analysis, and (3) enabled the size of the browsed plants and their settings to be quantified, unlike faecal analysis.

Although plant-based methods appear to have a number of advantages over direct observation techniques, it is important that some of the limitations of this technique, in particular for black rhinoceros, are recognised. (1) The method can be used on its own only where a single animal species feeds on a particular vegetation (Barnes 1976) or where an animal has a unique and recognisable way of feeding. (2) Kudu, giraffe and black rhinoceros may browse non-thorny or non-spinescent species by running their lips over the twigs (Joubert & Eloff 1971) or pluck leaves from a plant without biting off actual twigs (pers. obs). Consequently, browse offtake from species browsed in this manner will be underestimated. (3) Forbs, succulents and plant species with fine stems cannot be considered in assessing the diet of black rhinoceros as they are not browsed in the characteristic manner (Kotze & Zacharias 1993). (4) It is impossible to judge, by looking at a utilised plant, exactly when it was eaten. Judging the age of bites is of relevance when comparing seasonal changes in diet composition. This problem is not overcome by using direct observations in combination with a plant-based technique. Where a plant has been previously utilised, it is extremely difficult, if not impossible, to judge which twigs were browsed by the observed animal.

QUANTIFYING DIET COMPOSITION

Diet composition may be quantified using the following procedures: (a) frequency of utilisation, i.e., the number of instances a plant species is utilised or the number of individual plants of a species utilised, (b) time spent feeding on each plant species, (c) counting the number of bites taken, and (d) estimating the actual or relative amounts of browse removed from each plant species. Clearly, the latter procedure can only be determined using a plant-based method, while direct observations are required for the second- and third-mentioned techniques.

Frequency of Utilisation

The frequency method is one of the easiest and most simple procedures to conduct and because the results are counts not estimates they can be analysed statistically. The main drawback of this approach is that it does not represent actual quantities ingested (Leuthold 1970, 1978). However, the frequency method does provide an indication of the relative importance of the various plant species in the diet (Goddard 1970).

The frequency with which a plant is utilised may be determined using direct observations or a plant-based approach. For example, Oates (1972), Leuthold (1978) and Owen-Smith and Cooper (1987a, 1987b) used direct observations while Joubert and Eloff (1971) used a twig-count method for quantifying the diet composition of large herbivores. Although the plant-based technique used by Joubert and Eloff (1971) does not give a precise measure of the volume consumed it may give a closer estimate of the relative quantities ingested and is an improvement on simply recording whether individual plants have been browsed or not.

Feeding Time

Similar to frequency of utilisation, feeding time may not accurately reflect the relative quantities of each plant species eaten (Leuthold 1970; Jarman 1971; Owen-Smith & Cooper 1985). Nonetheless, Jarman (1971) maintained that the amount of time spent feeding on a plant species must be related to the value of food obtained from it. He argued that it would be maladaptive for an animal to devote a disproportionate amount of feeding time to an unrewarding plant when more valuable foods were available.

In Owen-Smith's earlier studies (see Owen-Smith 1979), he reasoned that feeding time would be a closer measure of quantity of food intake than number of bites taken. Bite size varied widely, depending on what was being eaten, and was difficult to measure accurately under field conditions. Owen-Smith and Cooper (1985) used feeding time for comparing consumption of vegetation components among kudu, impala and goats. Although they recognised that feeding time may differ from the relative quantities eaten, they concluded that biases should be similar for the species investigated, and should not change the conclusions drawn (Owen-Smith & Cooper 1985).

Both the frequency of utilisation and feeding time methods have drawbacks. For example, a common but small plant, of which only a few bites are taken at a time, may be over represented among the frequency data, but under-recorded in the time data, relative to the actual amount consumed. Conversely, a rare but highly preferred species, or one in which the leaves are not easily available (e.g. because of thorns), is likely to be over recorded by feeding time, but under recorded by the frequency method (Leuthold 1970).

Enumeration of Bites

It has been proposed that counting the number of bites taken by an animal on a particular plant will give a more accurate estimation of the amount of browse consumed, than either the frequency or feeding time procedures. This is based on the assumption that the quantity of browse removed with each bite by a particular animal species remains constant. However, bite size varies widely according to the particular plant species (Owen-Smith 1982; Koerth & Struth 1991) and plant part eaten (Dunham 1980), to the type of bite (Cooper & Owen-Smith 1986; Haschick & Kerley 1997) and to the individual animal, because intake rates are also influenced by anatomical features of the feeding animal, such as body size (Owen-Smith 1982).

As a result of the variability of bite size, a precise measure of the amount of browse consumed cannot be achieved by counting the number of bites taken from a plant. In addition, it is difficult to enumerate bites, especially when herbaceous plants are eaten (Owen-Smith & Cooper 1989).

Amount or Volume of Browse Consumed

Plant-based methods involve the estimation of the relative or actual amounts of plant material removed by animals. Certain plant dimensions, such as stem circumference or height of plant, are of little value in estimating browse utilisation because these dimensions change only slightly or not at all, with the removal of plant material by browsers. However, where very heavy browsing and damage is involved, volume or area of the canopy may be used. Usually, plant-based methods involving the measurement of twigs and leaves are used for estimating the quantity of browse ingested. Measurements may be made before and after browsing (difference technique) or after browsing only (post-browse technique) (Barnes 1976).

Intake is the result of the time and rate of eating. Eating rate depends on number and size of bites which are functions of both the food and animal (Allden & Whittaker 1970). As a consequence, another approach used for determining the amount of material consumed is to estimate bite size and bite rate. Direct observations are used to count number of bites and time spent feeding, while bite sizes are determined using a plant-based approach.

Difference Techniques

In order to use a difference technique one must know the amount of edible material present at a given time because the quantity of browse consumed is estimated as the difference between the amount on offer and the amount left uneaten. Most of these methods involve intensive sampling, such as counting branches and leaves per branch before and after browsing, and have been used with domestic stock in more controlled environments (see Barnes 1976) or in experimental feeding trials where bite size and intake rate are estimated.

Twig length (mm) measured before and after browsing may offer a practical means for detecting trends in utilization (Hobson 1988). However, Aucamp (1979) warns that twig length is not directly proportional to mass and should not be used as an absolute measure of utilization.

Photographic techniques have been used for estimating browse removal. This involves taking photographs of the vegetation with a grid in the immediate background or projecting slides onto a grid-marked screen. The number of grids obscured by plant material are then counted. Counts before and after browsing give a measure of utilisation. Linear regressions, relating the number of squares intercepted to the actual plant mass, are then developed (Barnes 1976). These techniques are appropriate for long-term browse utilisation assessments and where a single animal species utilises a particular vegetation type.

Post-browse Techniques

Measurements made after browsing usually involve techniques which relate twig number and / or twig dimensions to browse utilisation (Barnes 1976). Shafer (1963) developed the twig-count method where counts of twigs of “average browsing diameter” were converted to a twig mass. Average browsing diameter at point of browsing (DPB) was determined at the start of the study by measuring the diameter of twigs that were browsed. Twigs of each species having a diameter equal to the mean DPB for the species were collected and oven-dried to obtain an average mass. Total mass of plants utilised was the product of the number of utilised twigs for a species and average twig mass for that species. This method is largely non-destructive and because results are counts not estimates, they can be analysed statistically. In addition, the twig-count method gave estimates which were in agreement with those obtained by clipping and weighing but could be done in about a quarter of the time (Shafer 1963).

The clip-and-weigh method may be used for assessing browse intake (Basile & Hutchings 1966; Telfer 1969; Barnes 1976). Twigs of various diameters are clipped, oven-dried and weighed and regressions, which relate twig diameter to twig mass, are derived for each plant species under consideration. Browse utilization is then assessed by measuring the diameter at the severed ends of browsed twigs and, from the regressions, estimating the mass of material removed (Barnes 1976). The clip-and-weigh method has several disadvantages. It is destructive, labourious and time consuming. Not all plant species utilised are considered, because regression methods usually involve evaluating key plant species only. The mass obtained using the regression equations are only reliable within the range of diameters occurring in the sample from which the regressions were constructed (Telfer 1969). A further disadvantage of regression techniques is that the relationship is usually only applicable to localised sites. Basile and Hutchings (1966) found that regressions for any one species may differ significantly between sites or locations, between plants subjected to different abiotic factors and between different parts of the plant crown. Additional factors affecting twig mass include the time of year twigs are collected and the composition of the twigs, i.e., whether they are composed entirely of new growth or of wood of several years (Telfer 1969).

Emslie and Adcock (1993) developed a new volumetric woody browse measure called the 'browse bottle', which was also successfully used by Kotze and Zacharias (1993) in a study of black rhinoceros in Itala Game Reserve, South Africa. Browse offtake was estimated visually by comparing the diameter of browsed twigs with unbrowsed branches of the same diameter on the same tree (or neighbouring tree of the same species and similar height) and estimating the amount of browse on the equivalent unbrowsed twig, in standardized browse volumes. A browse volume is the amount of plant material needed to fill a one litre bottle. The 'browse bottle' method allows for all utilised species to be measured. It is a non-destructive and more time efficient approach than clipping and weighing. This plant-based technique may not give a precise measure of the volume consumed but it is an improvement on simply recording whether individual plants have been browsed or not (Kotze & Zacharias 1993). However, direct visual estimation is generally regarded as an unsatisfactory method because of its unrepeatability and difficulty in analysing the data statistically (Shafer 1963). Nonetheless, Rutherford (1979) indicated the value of visual estimation, provided regular checks are made of the actual volume to minimise bias.

The above techniques are applicable only where twigs and leaves are eaten together. Post-browse techniques have the advantage of only requiring one sample as apposed to two for sampling before and after browsing. The time and effort in locating, marking and pre-measuring shrubs is eliminated by using a post-browse technique rather than a difference approach (Barnes 1976).

Bite Size and Intake Rate

Rate of eating, which is dependent on the number and size of bites, and time spent feeding determine the amount of food consumed by an animal (Allden & Whittaker 1970). The difficulty in recording bite size (mg/bite) and bite rate (bites/min) has resulted in few data being available for African ungulates. Studies of large Africa herbivores that have recorded bite sizes and bite rates have been performed on tame animals (Dunham 1980; Monro 1982; Cooper 1985; Owen-Smith & Cooper 1989; Owen-Smith 1994; Haschick & Kerley 1997) allowing close-range observations. Some of these studies (Dunham 1980; Haschick & Kerley 1997) also involve experimental feeding trials.

Bite sizes and bite rates achieved by impala feeding on woody plant species were recorded by Dunham (1980). Feeding trials were conducted on tame impala in small enclosures. Branches of known mass of woody plant species were offered to the impala. The time that the impala spent feeding on each species and the number of bites taken were recorded. The mass of each branch eaten was the difference between its initial mass and its mass after the experimental trial. Mean bite size was found to be positively correlated with mean leaf mass while mean bite rate was negatively correlated with mean bite size.

Monro (1982) conducted feeding studies on tame impala at Nylsvley Nature Reserve, South Africa. Bite rate on different plant species was found by noting the total number of bites and the total length of feeding bouts. Bite size was estimated by hand plucking 50-100 simulated bites from the relevant species. The author admits that the bite counting-bite simulation method was inaccurate for calculating intake. He suggested that the bite simulation method could be improved by attempting to measure the amount of material removed in a bite and then accurately simulating this by clipping with scissors rather than hand plucking. He does not, however, give any suggestions as to how one would attempt to measure the amount of material removed with each bite.

Eating rates (mg/min) obtained by tame kudu for key plant species were measured as the product of bite size and biting rate (Cooper 1985; Owen-Smith & Cooper 1989; Owen-Smith 1994). Bite sizes were estimated visually by recording the number of leaves plucked per bite and estimating the leaf:stem ratio ingested. Samples of leaves were weighed to determine mean leaf mass for the main woody species. Owen-Smith and Cooper (1989) acknowledged that data were the least reliable for eating rates, since bite size varied widely and was difficult to estimate in the field.

The size of the bite cropped is determined by the interaction between the geometry of the animals mouth (Illius & Gordon 1987) and the geometric arrangement of plant tissue in space (Laca *et al.* 1992). Intake rate by herbivores is influenced by plant morphological features that include: plant size, growth form, presence of structural defences, leaf toughness and fibrousness (Owen-Smith 1982; Koerth & Struth 1991). Bite size, therefore, differs considerably according to the particular plant species and plant part eaten. Dunham (1980) found that mean bite size and mean intake rate of tame impala differed overall by 8- and 7-fold, respectively, when feeding on ten woody plant species. *Acacia* and *Dichrostachys* species offered much smaller bite sizes relative to other plant species. This was owing to the presence of thorns and small leaf size of these two species (Dunham 1980). Cooper and Owen-Smith (1986) and Haschick and Kerley (1997) have also shown that spinescence restricts bite size. Although *Capparis tomentosa* has thorns, leaf size is much greater than for *Acacia* and *Dichrostachys* species and as a result bite size was two and a half times larger (Dunham 1980).

In a feeding trial of herbivores, Gross *et al.* (1993) found that differences in bite size were imposed by changing plant height and density in patches. A 10-fold or greater difference in mass between the smallest and largest bites taken by each herbivore species was recorded as a result. In addition, a positive linear relationship between bite size and plant size existed.

Intake rates from a particular plant species will be influenced by anatomical features of the feeding animal such as body size, mouth and tooth dimensions, stomach structure and digestive capabilities (Owen-Smith 1982). Not only do intake rates and bite sizes vary among animal species, but also among individuals of a particular animal species. This is mainly as a result of the type of bite taken. In studies involving kudu (Cooper & Owen-Smith 1986) and bushbuck (Haschick & Kerley 1997) the authors classified bites into cheek, front and single bites. Bites were further classified into large and small bites (Cooper & Owen-Smith 1986). Shipley and Spalinger (1992) measured intake rate of moose, caribou and white-tailed deer feeding on a single plant species, red maple. Intake rate of each animal species increased 2- to 10- fold as a result of increasing bite size.

Although intake rate is assumed to give reliable estimates of actual amount of browse removed, Koerth and Struth (1991) found this relationship to be weak. Intake rate by tame white-tailed deer was poorly correlated with preference indices based on weight of forage removed and amount of time spent browsing. However, preference indices based on weight of forage removed and time spent browsing were significantly positively related (Koerth and Struth 1991).

A summary of the drawbacks and benefits of the various methods for assessing and quantifying diet composition follows. Food consumption data may be obtained by the analysis of faeces and ingesta, direct observations or plant-based methods. Estimates based on gut contents and faeces are biased by differential rates of digestion for different food types (Ambrose & DeNiro 1986), though can provide some useful information about the diets of animals (Monro 1982). Faecal analysis tends to be less accurate than ingesta analysis because differential digestion is more pronounced (Lewis 1994) and, being purely qualitative, it has more limited application than ingesta analysis (Monro 1982). Fistulation gives a relatively precise picture of food consumption (McInnes *et al.* 1983), but this technique cannot be used for free-ranging wild animals (Ambrose & DeNiro 1986).

Plant-based techniques appear to have a number of advantages over direct observations and are especially applicable where vegetation is dense, animals may be difficult to find or are not accustomed to vehicles. However, plant-based methods are based on previously browsed material and thus estimating the amount of browse removed may be inaccurate. Direct observations can be made with minimal equipment where animals are accustomed to vehicles or can be followed on foot. The return per unit effort, however, is considerably low (Emslie & Adcock 1993) and visual observations are notoriously imprecise (Ambrose & DeNiro 1986).

The frequency with which a plant is consumed, time spent feeding on and the number of bites taken from a plant do not give a precise measure of the amount of browse ingested by an animal. Plant-based difference techniques usually involve intensive sampling and tend to be used in more controlled situations. The twig count, regression and Emslie and Adcock's 'browse bottle' methods are only applicable where twigs and leaves are eaten together. Bite size and intake rate are subject to a number of shortcomings. The size of the bite cropped and the rate of food intake is determined by the interaction between anatomical features of the feeding animal (Illius & Gordon 1987) and plant morphological features (Owen-Smith 1982; Koerth & Struth 1991; Laca *et al.* 1992). As a result bite size and intake rate vary widely, not only among animal species but also among individuals of a species. Bites are difficult to enumerate in the field (Owen-Smith & Cooper 1989) and thus many studies have involved tame animals or experimental feeding trials.

FOOD PREFERENCES

To classify plant species in terms of their value as food resources for large herbivores some measure of relative preferences for them is required (Owen-Smith & Cooper 1987a). Studies evaluating resource use but not availability result in inferences about utilisation not preference (Thomas & Taylor 1990). The measurement of food preference thus requires a comparison of usage and availability of each plant component.

Preference, as defined by Johnson (1980), is the likelihood that a resource will be chosen if offered on an equal basis with others. Studies under controlled, experimental conditions typically follow this definition of preference. Under field conditions relative availabilities usually differ (Thomas & Taylor 1990) and hence Johnson's (1980) definition of preference is not applicable to most field studies. Petrides (1975), on the other hand, defined food preference as the extent to which a food is consumed in relation to its availability. This definition is thus more suited to field studies of selectivity (Thomas & Taylor 1990).

The decision about the array of components actually deemed available to the animal under study, is a central shortcoming of comparing usage and availability data for determining preference. Firstly, sampling procedures used to determine availability may not faithfully reflect the true availabilities to the animal (Johnson 1980). Resource availability should be seen as the quantity accessible to the animal during the period of time that the resource is utilised (Barnes 1976; Owen-Smith & Cooper 1987a). However, when availabilities are estimated at the feeding site (i.e., third-order selection), the conclusions drawn may not hold at larger scales (Johnson 1980; Thomas & Taylor 1990). On the other hand, Owen-Smith and Cooper (1987a) state that sampling errors involved in estimating availability independently of feeding observations do not reflect preferences accurately.

Secondly, the amount of browse available to animals is influenced by the following factors: density of woody plants, amount of leaf material within reach of an animal, species composition of woody vegetation, palatability and digestibility and the growth potential of woody species (Aucamp 1979; Pauw 1988). Further-more, McNaughton and Georgiadis (1986) caution that estimates of food availability based on crude standing crop or other techniques that ignore food quality and defensive chemistry may be misleadingly high. It is difficult to quantify palatability, digestibility (both of which depend on the species of animal) and growth potential and, therefore, in most studies only the first three factors are considered.

Lastly, problems arise in determining what is accessible to the animal under study. For example, Leuthold and Leuthold (1972) observed that giraffe were reluctant to enter dense plant clumps and tended to feed at the edges only. It is, therefore, debatable if plants growing inside the clumps should be considered available (Leuthold & Leuthold 1972).

ASSESSING FOOD AVAILABILITY

Food availability may be assessed using techniques which estimate mass or volume of plant material or by using frequency of occurrence. Plant mass may be estimated by the clip-and-weigh method (Barnes 1976; Rutherford 1979) but the technique is mainly limited to grasslands, forests and monospecific plantations (Rutherford 1979). In deciding whether to employ this technique, homogeneity of the vegetation is likely to be the most important consideration (Rutherford 1979). In addition, this method has been widely recognised as labourious, expensive and destructive (Barnes 1976).

Whole-plant dimensions, such as circumference of the main stem, height and area or volume of the leaf canopy may be used to calculate the amount of available plant material using regression equations (Barnes 1976). Plant height is extensively used to measure phytomass of herbaceous vegetation (Bransby & Tainton 1977; Trollope & Potgieter 1986; Trollope 1990) but has received little attention in shrub vegetation (Hobson 1988). Smit (1989) developed the BECVOL (Biomass Estimates from Canopy VOLume) model which uses different regression equations to estimate leaf dry mass (DM) from canopy volume, for microphyllous and broadleaved tree species. Regressions were developed by harvesting trees to obtain true biomass. In addition to total leaf DM ha^{-1} the model also facilitates stratified estimates of the leaf DM ha^{-1} below 1.5 m, 2.0 m, and 5.0 m. Volume of leaf canopy has shown to give higher correlation coefficients than has either diameter or area (Hobson 1988).

Available plant material may be also determined using a formula, developed by Teague (1989a) to calculate canopy leaf volume. Only browse material below the height reach of the animal under consideration is regarded as available (Teague 1989a). The formula was developed in the False Thornveld of the Eastern Cape, which has relatively homogeneous tree populations with regard to both species diversity and height distribution. The use of this formula is, therefore, not suitable to calculate biomass in heterogeneous tree communities (Smit 1989).

Ocular techniques involve being trained to estimate mass of plant material present. In using this method it is essential that some relation be established between estimated and actual quantities. Estimation methods are usually fast and non-destructive, but the results cannot be analysed statistically (Rutherford 1979). For example, Walker (1976) uses an eight-point scale to rank plants visually according to whichever variable is being measured. The approach is rapid and not labourious but the rank classes are not related to actual values.

The twig-count method, developed by Shafer (1963), may also be used for determining available plant mass per unit area. Twigs of 'average browsing diameter' were converted to a twig mass. To obtain an estimate of mass per unit area, twig mass was multiplied by a count of twigs taken on a series of plots. Compared with the clip-and weigh technique, the twig-count method is largely non-destructive and rapid, although almost as accurate (Shafer 1963).

Availability may also be assessed using techniques which involve parameters which are not closely related to quantities of food, such as frequency of occurrence. Frequency of occurrence is, however, partly dependent on the density and pattern of vegetation and is affected by quadrat size. In addition, the connection between a frequency value and yield of browse material is ambiguous (Barnes 1976). Although this is the case, frequency of occurrence is one of the most common parameters used in field studies (Leuthold & Leuthold 1972; Oates 1972; Loutit *et al.* 1987; Owen-Smith & Cooper 1987a). The number of plants available to giraffe in Tsavo National Park, Kenya, were recorded but this technique was found inadequate for plant species that formed dense clumps because giraffe were reluctant to enter such clumps and tended to feed at the edges only (Leuthold & Leuthold 1972).

Large herbivores generally consume only a small fraction of the vegetation components that they could eat. Thus assessments of food availability by direct measurements on vegetation could be a poor reflection of food availability as experienced by the animal (Owen-Smith 1979). Owen-Smith (1979) thus proposed an index of feeding efficiency which could be used as an indicator of available food. Accepted food abundance (AFA) was expressed in terms of the feeding time achieved per unit distance. Results confirmed the proposed index reflected both the habitat and seasonal differences in food availability. The higher the AFA value, the longer the animal fed per unit distance, concluding that there was more food available in that habitat.

Ideally, one ought to know the exact qualitative and quantitative composition for the entire study area, in order to determine which plant species are preferred and which are rejected. However, a complete analysis can rarely, if ever, be achieved (Leuthold 1970).

FOOD PREFERENCE INDICES

Preferences are usually expressed as an index and calculated as the quotient of the proportion of a species in the diet and the proportion occurrence of that species in the environment (Johnson 1980). Those species that are proportionally more abundant in the diet than in the environment are regarded as favoured, while those less abundant are regarded as rejected or avoided (Owen-Smith & Cooper 1987a).

Comparing usage and availability, for determining preference, is subject to two flaws. Firstly, the decision as to which components are actually available to the animal (Johnson 1980; Owen-Smith & Cooper 1987a). Secondly, the components deemed available depend upon the scale of selection being considered (Johnson 1980). In the first case, when available food includes mostly unimportant items measured in the habitat, other items will be given a higher rating. Comparing food use within home ranges or at feeding sites may be misleading. Johnson (1980) points out that one may claim that a food item is avoided because only 50 % of the animals consumption consisted of that item, whereas it made up 90 % of the items available at the feeding site. However, the very fact that the animal has chosen that site may be because that food item is available there. Contrary to this, Owen-Smith and Cooper (1987a) caution that sampling errors involved in estimating availability independently of feeding observations do not reflect preferences accurately. Clearly, there are drawbacks to whichever scale of selection is considered. Nonetheless, it must still be taken into account that studies at third-order selection (i.e., feeding site) may result in inferences that do not hold at larger scales (Thomas & Taylor 1990).

Ivlev's preference index (Ivlev 1961 in Alldredge & Ratti 1986) is the ratio of the proportion of a species in a diet and the proportion of that species available in the environment. Thus a species that is consumed in the same proportion as the proportion of that species on offer has a preference index of 1.0. An index value greater than or less than one 1.0 will, respectively, indicate species that are selected as a preferred and those which are avoided or neglected (Petrides 1975). This preference index is also known as the forage ratio (FR) (Owen-Smith & Cooper 1987a).

The forage ratio is the most widely used index (Owen-Smith & Cooper 1987a). Proportional utilisation and availability may be based on various quantities or simply frequency of utilisation or occurrence. For example, preferences of giraffe in the Serengeti National Park, Tanzania, were calculated by dividing the proportion of time spent feeding on a plant species by the proportion of that species available in total biomass (Pellew 1984a). Similarly, Owen-Smith and Cooper (1985) related percentage time spent browsing to percentage available mass for determining the food preferences of kudus, impalas and goats. Food preferences of black rhinoceros in Itala Game Reserve, South Africa, were determined as the ratio of standard browse volumes utilised and the amount of browse on offer. For estimating the amount of browse on offer, each plant species was assigned a semi-quantitative abundance value based on its frequency of occurrence (Kotze & Zacharias 1993).

Oates (1972) assessed the food preferences of giraffe in the Transvaal Lowveld Mopane Woodland, South Africa. The preference rating for each species was calculated as the ratio of percentage frequency of the species taken by giraffe and the percentage frequency occurrence of the species in the environment. Leuthold and Leuthold (1972), in studying the food habits of giraffe, and Loutit *et al.* (1987), in a study of black rhinoceros in Namibia, also used frequency of utilisation and occurrence to determine preferred species.

Johnson (1980) suggested that rank orders of usage and availability should be compared to circumvent difficulties in deciding what food types are available to the animal of consideration. Food types are ranked in order of preference and not classified into preferred and rejected categories. The rank order preference method is relatively insensitive to the inclusion or exclusion of doubtful components and results are less subjective (Johnson 1980). A drawback of Johnson's method is it requires that individual animals are identified and studied. In many studies it is not possible to monitor the feeding of individuals (Lechowicz 1982).

Owen-Smith and Cooper (1987a) derived two acceptability indices in assessing food preferences of kudu. The two accessibility indices reflect the likelihood of an animal feeding on a species when that species is available nearby. The indices differ in assumptions about what constitutes an offering. The plant-based acceptance of a species was calculated as the total number of individual plants of the species eaten, divided by the number of individual plants of that species encountered within neck reach. The site-based acceptance of a species was calculated from all-day observations as the number of 30-minute intervals during which the species was eaten divided by the number of 30-minute intervals during which the species was present within 10 m of the kudu. A definite distinction between favoured and neglected plant species eaten by kudu was revealed by site-based acceptances. However, plant-based acceptances did not show such a clear-cut pattern. This was owing to the fact that successive plants of a species encountered do not in general represent independent offerings, especially if plants are clumped.

The plant- and site-based acceptability indices derived by Owen-Smith and Cooper (1987a) were compared with other measures of preference. Forage ratios related the proportion of total consumption of each species to its relative available biomass. The ratios did not indicate the clear-cut distinction that site-based acceptances showed. This was largely because of the sampling errors involved in estimating availability independently of feeding observations. Rank orders of preference showed little consistency, as species within the favoured and neglected categories did not differ significantly in acceptability (Owen-Smith & Cooper 1987a).

The plant-based acceptance index differs from the forage ratio in two important aspects. The plant-based acceptance index is based on usage and availability data that are collected concurrently and along the same feeding path. The forage ratio compares proportional usage of a food item with proportional availability of that item in the environment. This entails separate sampling of usage and availability at different times over different areas (Du Toit 1988), leading to sampling errors (Owen-Smith & Cooper 1987a). An added advantage of the plant-based acceptance index is that availability is only recorded when the animal of interest is actually feeding, which provides an accurate reflection of the animal's feeding choice. However, relative plant abundance along the feeding path could be used in calculating forage ratios (Owen-Smith & Cooper 1987a), thereby eliminating the two disadvantages mentioned here. A disadvantage of the plant-based index is that the determination of whether a species is neglected or preferred is arbitrary.

Lechowicz (1982) reviewed seven preference or electivity indices, namely Ivlev's electivity index, the forage ratio, Jacob's modified electivity index, Jacob's modified forage ratio, Strauss' linear index, Chesson's alpha index, and Vanderploeg and Scavia's electivity index. The following criteria were used to compare and evaluate the indices: random model, symmetry, range of index values, linearity, robustness, statistical testability and stability. Lechowicz concluded that no index ideally satisfied all these criteria, but that the Vanderploeg and Scavia's electivity provided the single most useful preference index. Ivlev's electivity index, the forage ratio, Jacob's modified electivity and Strauss' linear index are inappropriate for comparison of preferences derived from samples differing in relative abundances.

Although studies evaluating resource use, but not availability, result in inferences about utilisation not preference (Thomas & Taylor 1990) percentage utilization of a given food has been used as a measure of preference. In other words, preference is determined using utilization only and not expressed as a ratio of what is on offer. Food preferences of black rhinoceros in Etosha, South West Africa were determined by counting the number of twigs browsed per plant (Joubert & Eloff 1971). Species that were heavily utilised were expressed as a percentage of the total number of heavily utilised plants and this percentage was then used to express preference. Species that were most heavily browsed were thus most preferred. Mukinya (1977) used the frequency with which a species was utilised to express preference. The species with the highest frequency in the diet was assumed to be the most preferred.

While recording the time spent feeding on each plant species may not represent actual quantities ingested (Leuthold 1970) it may be used as an indicator of preference (Owen-Smith & Cooper 1987a; Koerth & Struth 1991). In a feeding study of kudu, Owen-Smith and Cooper (1987a) found that kudu tended to feed longer on favoured species than on neglected species. The findings, therefore, indicated that feeding durations and acceptance frequencies were inter-correlated (Owen-Smith & Cooper 1987a). Similar results were found by Koerth and Struth (1991). Preference indices based on weight of forage removed and time spent browsing, by tame white-tailed deer, were significantly positively related. This indicated that the two techniques closely agreed in species ranking. Interestingly, intake rate by deer was poorly correlated with preference indices based on weight of forage removed and amount of time spent browsing (Koerth and Struth 1991). Owen-Smith and Cooper (1987a) compared feeding durations to site-based acceptances. Feeding durations showed distinct groupings of species similar to that revealed by site-based acceptances. This indicated that acceptance frequencies and feeding durations were inter-correlated. Durations were longer on high-acceptability species than on low-acceptability species.

Where preferences are assessed using techniques which involve parameters which cannot be closely related to quantities of food, the values should not be accepted at face value without considering the implications inherent in the unit of measurement. Frequency of occurrence, for example, is dependent partly on the density of plants and partly on the pattern of vegetation and is affected by sample quadrat size (Barnes 1976).

HABITAT UTILISATION

This section is, firstly, concerned with giving an overview of methods for determining the utilisation of habitats by large mammalian herbivores within a given area. Secondly, a method used for determining preferences of habitats or vegetation types, which was not covered under food preferences, is reviewed.

ASSESSING THE UTILISATION OF HABITATS

Populations of animals are surveyed to measure habitat use, obtain trend and distribution data and estimate population densities (Rowland *et al.* 1984). Surveys may be conducted either by counting the animals themselves or by counting signs of their presence, such as dung pellets (Johnson & Jarman 1987), burrows and latrine pits (Putman 1984). Many animals are difficult to see and count consistently, and surveys based on counts of signs may often be necessary (Johnson & Jarman 1987).

Aerial surveys are widely used, but may be of limited value, depending upon visibility, topography and distribution of animals (Jachmann & Bell 1979). Foot surveys, applied to small areas (< 500 km^2) and using line-transects, show little bias when carefully designed. Vehicle surveys are limited by the available road system and when used to count a species with a clumped distribution may give results that can be used as a reliable estimator of relative abundance, but may be of poor accuracy (Jachmann 1991).

Differential distribution of dung between habitats has been used to establish patterns of habitat use (Andrew & Lange 1986; Novellie & Winkler 1993; Lehmkuhl *et al.* 1994) and is commonly used for wildlife, for example elephants (Jachmann & Bell 1979; Jachmann 1991), kangaroos (Andrew & Lange 1986; Johnson & Jarman 1987) and deer (Bailey & Putman 1981). A study of zebra in the Mountain Zebra National Park, South Africa, demonstrated there was a high correlation between total sighting frequency of zebras and pellet counts and between the sightings of feeding zebras and pellet-group counts (Novellie & Winkler 1993). Lange (1983) also found that cattle presence was highly correlated with dung-pat density. However, a study of mule deer indicated that pellet-group densities may not correctly predict use of habitats (Collins & Urness 1981). The dung-count technique and its deficiencies have been extensively discussed (Putman 1984; Rowland *et al.* 1984). One of the main assumptions of this technique is that average deposition rates within individual habitats (Collins & Urness 1981) and among seasons are similar (Rowland *et al.* 1984). In other words, one assumes that defecation rates remain constant. Seasonal shifts in defecation rates as well as differences in pellet deposition between sexes and ages have, however, been reported (Rowland *et al.* 1984).

There are a number of arguments for using counts of pellet-groups rather than individual pellets. The assumption that all pellet-groups are independent (which is necessary if one is to assign confidence limits to estimates of density) should cause less distortion than the assumption that all individual pellets are independent. A group of pellets lasts longer than most individual pellets and an individual pellet is more easily missed by a surveyor than a group of pellets. This could cause counts of individual pellets to return lower estimates of animal density than do counts of pellet-groups (Johnson & Jarman 1987).

There are also problems with counting pellet-groups. An animal which spends long periods feeding on the same spot may drop two or more defecations in one place and these may be wrongly counted as one group. Animals that tend to produce several defecations in fairly quick succession, will increase the chance of underestimation of groups (Hill 1978). Animals might scatter pellet-groups by walking through them and thereby inflate estimates of density. Both effects should be detectable by comparing the number of pellets produced per defecation, when these are observed directly, with the sizes of groups of fresh pellets counted on the ground. In the first situation, the number of pellets per group on the ground would be greater than the average dropped per defecation; in the second case, groups of pellets counted on the ground would be unexpectedly small (Johnson & Jarman 1987).

In order for pellet-group counts to be reliable indices of habitat use, it is critical to account for pellet-group persistence (Putman 1984; Rowland *et al.* 1984; Johnson & Jarman 1987; Lehmkuhl *et al.* 1994). Rate of disappearance can be measured at trials established at the initial survey, to give an unbiased estimate of pellet deposition rates (Lehmkuhl *et al.* 1994). In their study, conducted in Australia, Johnson and Jarman (1987) found that pellets disappeared quickly during warm, moist conditions, but survived well in cold, dry conditions. The same pattern of pellet degradation was found by Lehmkuhl *et al.* (1994) where the most rapid decay occurred during the wet, warm period.

HABITAT PREFERENCE INDICES

Preference for a resource component is determined by comparing its relative use to its relative availability (Barnes 1976). In the case of habitat preferences, availability is usually determined by calculating the area of each habitat, which is commonly derived from aerial photographs or maps (Thomas & Taylor 1990).

Various procedures have been devised for determining the preference for a component (see Krebs 1999). Three methods, which are commonly reported in the literature, are reviewed. Ivlev's preference index (Ivlev 1961 in Alldredge & Ratti 1986) is calculated as the proportional of a component divided by its proportional availability. Johnson (1980) proposed a technique, based on ranking components by usage and availability (see *Food Preference Indices*). The Chi-square goodness-of-fit test is often used to determine whether there is a significant difference between expected utilisation of habitats and observed use (Byers *et al.* 1984; Alldredge & Ratti 1986, 1992; Thomas & Taylor 1990). In conjunction with the chi-square test, Neu *et al.* (1974) and Byers *et al.* (1984) suggested a statistical technique to determine which habitats are used more or less frequently than expected by calculating simultaneous Bonferroni confidence intervals. The application of the Chi-square goodness-of-fit test and Neu-Byers method involves comparing the observed counts in each habitat with the counts expected if each habitat is used in proportion to its availability (Alldredge & Ratti 1986, 1992).

Choosing among the above methods depends on how the data were collected. Firstly, estimating resource use may or may not include identifying individual animals (Thomas & Taylor 1990). The Neu-Byers method and Ivlev's preference index do not require that individuals be identified; i.e., usage is measured across all animals for each habitat. Johnson's ranking method, on the other hand, necessitates information on usage of habitats for each animal considered individually (Alldredge & Ratti 1986). Secondly, resource availabilities may either be treated as known, for example by measuring availability from aerial photographs or maps, or estimated, using point, plot or transect sampling methods. Sampling methods give an error which precludes the use of the Chi-square test and associated Neu-Byers method because these methods require the assumption that availabilities are treated as known constants (Thomas & Taylor 1990; Alldredge & Ratti 1992). Ivlev's preference index is not constrained by this assumption, but is of limited value because it does not use a statistical test (Alldredge & Ratti 1986).

RESOURCE OVERLAP AND PARTITIONING

Measures of similarity or overlap are often considered to be synonymous with measures of resource partitioning [also referred to as *niche* overlap by Hurlbert (1978) and Krebs (1999)]. As a result, some measures of similarity are identical to those measuring resource partitioning (Krebs 1999). However, indices vary considerably in their basic characteristics (Linton *et al.* 1981) and confusion in deciding which index to use is largely owing to what the researcher is attempting to measure (Krebs 1999). If one is attempting to determine the degree that two species share a common resource, then similarity indices and overlap measures, which ignore resource availabilities, are appropriate (Lawlor 1980). Resource partitioning methods, on the other hand, are related to past competition and should include the relative resource abundances (Schoener 1974; Hurlbert 1978; Lawlor 1980) and their variation (Hurlbert 1978).

MEASURES OF OVERLAP OR SIMILARITY

When patterns of resource usage are similar between two animal species then these species may be considered as having a high degree of "overlap"; species with dissimilar resource usage patterns are regarded as having low overlap. The affinity between species is estimated by the use of similarity or overlap indices (Ludwig & Reynolds 1988). More than two dozen measures of similarity exist (Krebs 1999) and these may be classified as distance measures, association measures, correlation coefficients or information measures (Ludwig & Reynolds 1988).

Distance measures are actually estimates of dissimilarity; if a distance coefficient is zero, then communities are identical (Krebs 1999). Krebs (1999) reviewed several similarity measures and concluded that distance coefficients were not independent of proportional differences between samples, an undesirable trait, but correlation coefficients were. An undesirable attribute of correlation coefficients was that they were strongly affected by sample size. Percentage Similarity (PS), also known as Schoener's (1968) index, was relatively unaffected by sample size and species richness, and was independent of proportional differences between samples. Horn's index was relatively unaffected by sample size, but it was not as robust as Morisita's index. Krebs (1999) recommended the Morisita's index as the best overall measure of similarity.

The utility of four overlap indices, namely Percentage Similarity (or Schoener's index), Horn's index, modified Morisita's index and Pianka's index, were reviewed by Linton *et al.* (1981). The area in common between two resource utilisation distributions were compared by calculating true overlaps for various sample sizes and number of resource states by randomisation procedures. True overlap was then compared with the estimated overlap for each of the four indices. The authors found that Pianka's and the modified Morisita's indices gave almost identical results. Percentage Similarity estimated overlap accurately when true overlaps were between 7 and 85 %, while the three other indices were poor estimators of overlap in this range. Horn's index consistently over-estimated overlap by approximately 50 %, while Morisita and Pianka's indices tended to underestimate overlap by about 15 %. With real overlaps ranging from 85 to 90 %, all four indices had similar accuracy. All indices gave poor estimates of overlap when true overlap was less than 7 %. In conclusion, only Percentage Similarity accurately estimated overlap over the majority of range of overlaps (Linton *et al.* 1981). The authors suggest that both the Percentage Similarity method and Pianka's index should be calculated and if estimated overlap values are less than 80 for Percentage Similarity and less than 0.92 for Pianka's index, then Percentage Similarity is the most appropriate measure. If the opposite occurs, i.e., PS > 80 and Pianka's index > 0.92, then Pianka's index should be used.

Although Wolda (1981 in Krebs 1999) recommended Morisita index as a measure of similarity he also stated that Percentage Similarity is one of the best and most simple indices available. From the work conducted by Linton *et al.* (1981) it is clear that Percentage Similarity is a more accurate measure of overlap than Horn, Morisita and Pianka indices, especially when true overlap ranges between 7 % and 85 %.

When two resource states are investigated, the question arises as to how one determines total resource overlap. Unfortunately, May (1975) discussed this in terms of the competition coefficient, α_{ij}. He suggested that if the utilisation functions on resource dimensions (states) are independent, then the total competition coefficient (i.e., total overlap) should be calculated as the product of the individual one-dimensional coefficients. According to May (1975) food size and feeding height are independent resource dimensions. When two resource dimensions are clearly not independent, for example food type and feeding place, then the summation of one-dimensional coefficients will indicate true total overlap. If various resource dimensions are not strongly interdependent, then summation of coefficients can give a significant overestimate of total resource overlap, while multiplication (product α) tends to under estimate the degree of resource overlap. The decision of whether the summation or product of one-dimensional coefficients gives a better estimate of the total competition coefficient rests on the ecologists' intuition about a particular situation (May 1975).

MEASURES OF RESOURCE PARTITIONING

Measures for determining the degree of resource partitioning among coexisting herbivores should include not only the proportions of utilisation but also the relative resource abundances (Schoener 1974; Hurlbert 1978; Lawlor 1980). This is because the proportion of a food type in the diet of the consumer depends on, firstly, the availability of that food type in the environment and, secondly, the consumer's preference or electivity for that food type (Lawlor 1980). Lawlor (1980) proposed that consumer preferences are more likely to reflect evolutionary changes and thus be a better measure of past competitive pressures.

Lawlor's index measures the similarity between consumers based on their preferences. His index is identical to Pianka's index, except that proportions of utilisation have been replaced by electivities. Hurlbert (1978) defined resource overlap as "the degree to which the frequency of encounter between two species is higher or lower than it would be if each species utilised each resource state in proportion to its abundance". Because Hurlbert's index takes the abundance of resources into account it is appropriate as a measure of resource partitioning. Therefore, if the diets of two species are identical in two separate cases but each species utilises a certain resource more intensely in one case than the other, then resource partitioning should be less in the first case than the second. Hurlbert's index is 1.0 when both species utilise each resource state in proportion to its abundance, and it is 0 when no resources are shared by the two species. When both species use certain resource states more intensely than others and the preferences of the two species for resources tend to coincide, then the index is greater than 1.0 (Hurlbert 1978).

RESOURCE PARTITIONING, OVERLAP AND COMPETITION

It has been proposed that differential use of resources promotes ecological separation which, in turn, reduces interspecific competition between species with similar ecological requirements (Leuthold 1978; Manley *et al.* 1993). A need to quantify the degree of resource partitioning or overlap has led to numerous proposed indices each with their own advantages and drawbacks. Not only is there confusion in deciding which index to use (as discussed above) but controversy as to what these indices convey about competition.

Resource partitioning indices, which compare consumer preferences, reflect evolutionary interactions and are thus concerned with past competitive pressures (Lawlor 1980). Measures of overlap or similarity, on the other hand, represent current ecological interactions and, therefore, pertain to present-day competition. Although it is recognised that overlap indices are not true measures of the intensity of competition, they do give an indication of approximate competition (Lawlor 1980; Schoener 1982, 1986), but only if the resources considered are in short supply such that the sizes of the populations are limited by the amount of available resource (Sale 1974; Hurlbert 1978; Abrams 1980; Lawlor 1980; Krebs 1999).

Relating current interspecific competition with the observed degree of overlap between species must be done with caution. Firstly, the particular resources being studied may not be limiting and species may overlap with no competition (Hulbert 1978; Abrams 1980; Lawlor 1980; Krebs

1999). Secondly, although considerable overlap for certain limiting resources may exist between species, these species may separate ecologically in another way, which has not been investigated in the study, and so reduce the extent of competition (Wiens 1989). Lastly, the selective pressure, promoting ecological separation, may not be competition but rather predation or migration (Sinclair & Norton-Griffiths 1982; Sinclair 1985). In small reserves, with an absence of predators and restricted seasonal movements, the potential for competition is, however, more likely (Ferrar & Walker 1974).

Zero or little overlap does not mean that interspecific competition may be absent. In order to avoid competitors, animals may alter their utilisation of resources (Abrams 1980). Low current overlap may be the result of extensive past competition (Hulbert 1978; Lawlor 1980).

ECOLOGICAL SEPARATION

The principal issue of intra-guild studies is to examine the different ways species in the same community utilise resources. The extent to which ecological separation or resource partitioning results from pressures, evolutionary or otherwise, to avoid interspecific competition has been a subject of debate (Schoener 1982, 1986). The view that interspecific competition plays a dominant role in structuring communities was first fostered by the competitive exclusion principal which states that if two species compete for the same limiting resources, then one of the species will be driven to extinction (Begon *et al.* 1990).

The most direct way of assessing the significance of interspecific competition is by experimentally manipulating potentially competing populations (Schoener 1983). Such experiments are, however, extremely difficult to achieve (Wiens 1989). The alternative, is to measure the degree of overlap in resource use between coexisting species and to infer the presence or absence of interspecific competition (Schoener 1974, 1986; Sale 1974; Hurlbert 1978; Abrams 1980).

For competition to occur animals must be at densities where the available resources limit the size of populations (Sale 1974; Hurlbert 1978; Abrams 1980; Lawlor 1980; Krebs 1999). Food is considered to be the ultimate resource limiting animal populations and is more likely to occur in reserves with a high density and diversity of herbivores, lack of predation and migration (Ferrar & Walker 1974; Owen-Smith 1990). Evidence in support of resource limitation is provided by an increase in mortalities and decrease in fecundity (MacNally 1983). Studies have shown that during the dry season or during drought years, herbivore populations are regulated through food resources (Fryxell 1987; Sinclair & Norton-Griffiths 1982; Owen-Smith 1990).

There are two schools of thought concerning how animals should respond to changes in food abundance. The competition theory speculates that animals should specialise during times of resource scarcity, i.e., diversity in diets should decrease, and thus overlap and the potential for competition between species should also decline (Schoener 1982, 1986). The optimal foraging model, on the other hand, predicts the opposite. When food is limited animals should expand their diet and, therefore, dietary diversity and overlap should increase (MacArthur & Pianka 1966; Pyke *et al.* 1977).

Numerous studies have shown that during periods of resource scarcity, overlap between similar coexisting species decreased (Schoener 1982; Wiens 1989). Dietary overlap between large mammalian herbivores in the woodlands around Lake Kariba, Zimbabwe, decreased during the early dry season because each animal made use of different food types, i.e., refuges (Jarman 1971). The use of different feeding levels has been suggested as a mechanism reducing overlap among browsing species, especially when these animals differ in body size (Lamprey 1963; Leuthold 1978; McNaughton & Georgiadis 1986; Du Toit 1988, 1990). Du Toit (1990) tested this hypothesis by comparing feedings heights of giraffe, kudu, impala and steenbok. His study showed that despite clear stratification in the mean feeding heights among these browsers, there was considerable overlap among kudu, impala and steenbok. Only giraffe appeared to be separated from the other species in terms of feeding height, yet they did feed at lower levels, so even this separation was not complete. In Tsavo National Park, Kenya, giraffe fed at higher levels during the dry than wet season (Leuthold & Leuthold 1972; Leuthold 1978) and this change in feeding behaviour was interpreted as a means of reducing overlap with smaller browsers, in particular lesser kudu (*Tragelaphus imberbis* Blyth 1869) and black rhinoceros (Leuthold 1978). In a similar manner to feeding heights, animals species of different size may decrease the extent of overlap among them by utilising different sizes of food (Schoener 1986). Large herbivores may also be separated spatially by feeding in different habitats during the same season (Lamprey 1963; Leuthold 1978). The above mentioned strategies can thus be predicted to occur during periods of resource scarcity, on the assumption that interspecific competition is the process shaping communities.

Differences in body size are regarded as a factor contributing to ecological separation (McNaughton & Georgiadis 1986). Body size determines metabolic costs and digestive efficiency and as a result small ungulates are more limited by food quality and large ungulates by food quantity (Murray & Illius 1996). Large body size bestows a number of nutritional advantages, particularly during the dry season. Large herbivores can subsist on a lower quality diet than smaller animals because of their lower mass-specific metabolic rates (Owen-Smith 1988). However, large herbivores are constrained because they need to satisfy higher absolute energy costs (McNaughton & Georgiadis 1986). They do select high quality diet items (Owen-Smith 1988), but because these are too rare to satisfy their energy demands, especially during the dry season, large herbivores are forced to expand their diets to include lower quality, but more abundant plant material (McNaughton & Georgiadis 1986). For this reason, though, large animals can survive longer on a submaintenance diet than smaller animals. In addition, large herbivores loose condition more slowly on a starvation diet than do smaller animals because of their ability to store greater fat reserves (Owen-Smith 1988). Although small browsers, because of their mouth structure, can select a higher quality diet they are constrained because they have higher specific metabolic costs than do large animals and therefore require high quality foods to meet their energy requirements (McNaughton & Georgiadis 1986). Apart from the nutritional advantages, large browsers can also utilise a food resource that is inaccessible to smaller browsers. Large herbivores, particularly those exceeding a body mass of 1 000 kg, thus appear to have an advantage over small herbivores during the dry season when food quality declines (Owen-Smith 1988).

BROWSERS AT WEENEN

The species considered during this study, namely greater kudu, giraffe, black rhinoceros and eland, depend primarily on the foliage of dicotyledonous plants, both woody (trees and shrubs) and herbaceous (forbs). A brief overview of each browser is given followed by what is currently known about the extent of overlap in resource use between them.

KUDU

Greater kudu males stand approximately 1.4 m at the shoulder and have an average mass of 224 kg and maximum mass of about 260 kg. Females are smaller with a shoulder height of about 1.25 m and an average mass of 155 kg (Skinner & Smithers 1990).

In Botswana, Namibia, Mozambique and Zimbabwe kudu are distributed widely. In South Africa their distributional range is mainly limited to the Northern and Eastern Cape and Northern Province, having disappeared from parts of KwaZulu-Natal (Skinner & Smithers 1990).

Kudu are found in savanna woodlands and do not occur in desert, forest (Skinner & Smithers 1990) or open areas (Ferrar & Walker 1974; Skinner & Smithers 1990). In Kruger National Park (Du Toit 1988) and Zimbabwe (Skinner & Smithers 1990) kudu selected riparian woodlands and thickets along drainage lines during the late dry season.

Kudu are primarily browsers utilising very little grass (Wilson 1965; Jarman 1971; Hofmann & Stewart 1972; Conybeare 1975; Owen-Smith 1979, 1982; Novellie 1983; Owen-Smith & Cooper 1985, 1989; Kelso 1986; Du Toit 1988). Freshly sprouted grass tends to be preferred by kudu and hence grass consumption is mainly restricted to the wet season (Wilson 1965; Conybeare 1975; Novellie 1983; Owen-Smith & Cooper 1985; Du Toit 1988; Kelso 1986). Forbs are an important component of the diet of kudu (Novellie 1983; Kelso 1986), particularly during the rainy season (Jarman 1971; Conybeare 1975; Du Toit 1988; Owen-Smith & Cooper 1989). A wide variety of woody plants are utilised by kudu and staple species are from the families Combretaceae (*Combretum* species), Mimosaceae (*Acacia* species, *Dichrostachys*), Rhamnaceae (*Ziziphus*) and Tiliaceae (*Grewia* species) (Owen-Smith 1985).

GIRAFFE

The average height of a giraffe male is about 5.2 m, while females are slightly shorter at approximately 4.6 m. Average shoulder height of males and females are 3.0 m and 2.7 m, respectively. Male giraffe have an average mass of 1 191 kg compared with 828 kg for females (Skinner & Smithers 1990).

The current distribution of giraffe, from north-eastern South Africa to West Africa, is patchy and discontinuous (Skinner & Smithers 1990). Although giraffe have been introduced into KwaZulu-Natal, they did not formally occur here (Goodman & Tomkinson 1987).

Giraffe occur in a wide variety of savanna habitats, ranging from scrub to woodlands. They do not occur in forests (Skinner & Smithers 1990) and generally avoid open habitats (Leuthold 1978; Pellew 1984a; Young & Isbell 1991; Dekker *et al.* 1996; Ginnett & Demment 1997). During the dry season giraffe commonly make use of riparian vegetation (Hall-Martin 1974b; Leuthold 1978; Pellew 1984a; Du Toit 1988; Ginnett & Demment 1997).

Giraffe are predominantly browsers (Leuthold & Leuthold 1972; Oates 1972; Hall-Martin 1974a; Stephens 1975; Sauer *et al.* 1977; Leuthold 1978; Hansen *et al.* 1984; Pellew 1984a; Du Toit 1988; Skinner & Smithers 1990) and will occasionally utilise forbs (Lamprey 1963; Pellew 1984a) and grasses (Lamprey 1963; Smithers 1971 in Oates 1972; Oates 1972; Hall-Martin 1974a; Sauer *et al.* 1977; Hansen *et al.* 1984; Skinner & Smithers 1990). *Acacia* species feature predominantly in the diet of giraffe (Hall-Martin 1974a; Hall-Martin & Basson 1975; Stephens 1975; Van Aarde & Skinner 1975; Hansen *et al.* 1984; Pellew 1984a; Owen-Smith 1985), but numerous other species are utilised, such as *Euclea* sp., *C. mopane*, *Maytenus* sp., *Schotia brachypetala*, *Diospyros* sp., *Albizia harveyi* (Hall-Martin & Basson 1975), *Olea* sp. (Hansen *et al.* 1984) and *Combretum* species (Sauer *et al.* 1982).

ELAND

Eland are the largest of the African antelope, adult males standing approximately 1.7 m at the shoulder and having an average mass of 650 kg (range 425-840 kg). Females are smaller with a shoulder height of about 1.5 m and a mass of up to about 460 kg (Skinner & Smithers 1990).

They have a wide distribution in southern Africa, but in South Africa are confined to Kruger National Park and adjacent areas, and mainly the Drakensberg foothills in KwaZulu-Natal. The habitats utilised by eland range from semi-desert scrub to montane grassland. Eland avoid forests and extensive short grass plains (Skinner & Smithers 1990). They tend to show a preference for closed rather than open woodlands (Ferrar & Walker 1974; Kelso 1986; Fabricius & Mentis 1990; Dekker *et al.* 1996), although Lamprey (1963) observed the opposite.

Eland are classified as mixed feeders (Skinner & Smithers 1990; Owen-Smith 1997) and vary their feeding habits to suit prevailing circumstances. Grass use declines while the utilisation of browse increases during the dry season (Kerr *et al.* 1970; Field 1975; Jankowitz 1982 in Owen-Smith 1997; Kelso 1986; Buys 1990; Skinner & Smithers 1990). They tend to make limited use of forbs (Lamprey 1963; Kelso 1986; Kerr *et al.* 1970). Eland utilise a variety of woody plant species, including those of the genera *Acacia, Dichrostachys, Colophospermum, Grewia, Euclea, Combretum* and *Diospyros* (Kerr *et al.* 1970; Field 1975; Nge'the & Box 1976; Lightfoot & Posselt 1977; Owen-Smith 1985; Kelso 1986; Buys 1990).

BLACK RHINOCEROS

Black rhinoceros stand about 1.6 m at the shoulder (Skinner & Smithers 1990) and the mass of males ranges between 708 kg and 1 022 kg. Females are somewhat larger, having a mass of between 718 kg and 1 132 kg (Owen-Smith 1988).

The former distributional range of black rhinoceros in the southern African subregion has been drastically reduced not only within the past 350 years, but three decades. The resulting distribution of black rhinoceros is scattered and discontinuous, mainly confined to National Parks and reserves of South Africa, Namibia and Zimbabwe (Skinner & Smithers 1990).

Black rhinoceros occur within a wide range of habitats, from forests to scrub and savanna woodlands, but are not usually found in open country (Skinner & Smithers 1990). They prefer dense thornveld, especially where bush encroachment is in its early stages and tend to avoid feeding in tall grass (Emslie & Adcock 1993). Owing to the fact that black rhinoceros are dependent on water they are seldom found more than 15 km from it (Skinner & Smithers 1990).

The diet of black rhinoceros consists mainly of browse (Jarman 1971; Joubert & Eloff 1971; Leuthold 1978; Skinner & Smithers 1990; Oloo *et al.* 1994), grass is rarely consumed (Goddard 1968, 1970; Mukinya 1977; Hall-Martin *et al.* 1982). The proportion of forbs in the diet of black rhinoceros varies, depending on area and season (Emslie & Adcock 1993). Woody plants in their diet consist predominantly of *Acacia* species (Goddard 1968; Emslie & Adcock 1993; Kotze & Zacharias 1993; Oloo *et al.* 1994), but succulents are also important, particularly during the dry season (Goddard 1968; Jarman 1971; Hall-Martin *et al.* 1982; Loutit *et al.* 1987; Oloo *et al.* 1994; Dudley 1997).

OVERLAP IN RESOURCE USE BETWEEN BROWSER PAIRS

Several studies (Lamprey 1963; Jarman 1971; Leuthold 1978; Kelso 1986; Du Toit 1988, 1990; Dekker *et al.* 1996) have investigated the extent of ecological separation among the browsers considered in the current study. Rather than showing a clear separation in resources utilised by these herbivores, there was extensive overlap. The findings of these studies are reviewed.

Kudu and Eland

Lamprey (1963) documented the diets and habitat selection of numerous herbivores, including eland, lesser kudu, giraffe and black rhinoceros, in Tarangire Game Reserve, Tanzania. Diets were described in terms of the proportional utilisation of grasses, sedges, herbs, shrubs, trees. Dietary overlap was considerable between eland and lesser kudu, mainly owing to the large inclusion of monocotyledons in both diets, 70 % and 67 %, respectively. Overlap in the use of vegetation types was, however, relatively low, lesser kudu preferring more dense areas which were little utilised by eland. Similarly, eland and greater kudu were never associated with each other in any of the plant communities in a Mopani veld in South Africa, over an entire seasonal cycle (Dekker *et al.* 1996). Eland tended to occur in short closed (150 - 300 trees ha $^{-1}$) woodlands where the grass layer was lightly utilised, while greater kudu selected low closed woodlands or thickets and areas with moderate rock cover (1 - 30 %) and a grass layer that was lightly or unutilised. In Pilansberg National Park, South Africa, eland and greater kudu frequently used the same habitat types and also had a great degree of overlap in the use of food resources (Kelso 1986). They made use of similar woody plant species and both tended to utilise thorn thickets during the dry season.

Kudu and Giraffe

In Tanzania, the diets of lesser kudu and giraffe appeared to be relatively dissimilar because giraffe rarely made use of grasses (< 1 %) (Lamprey 1963). However, 33 % of the diet of lesser kudu consisted of woody foliage, so over a third of their diets were similar. Overlap in vegetation types utilised was great, because both made use of dense and open *Commiphora* woodlands. Giraffe did, however, utilise *Acacia tortilis* woodlands, which lesser kudu did not. Contrary to Lamprey's findings, Leuthold (1978) found that the winter diets of lesser kudu and giraffe overlapped considerably (Pianka's index: 0.98). Similarly, overlap in habitats was extensive (Pianka's index: 0.97), both species preferring densely wooded vegetation types and avoiding open woodland. Differential use of feeding heights (Pianka's index: 0.51) reduced the total overlap, but this was still substantial (Pianka's index: 0.48), because 37 % of giraffe browsing was below 2 m. Similar observations were made by Du Toit (1988) in Kruger National Park, South Africa. Dietary overlap between greater kudu and giraffe was considerable, even during the late dry season (PS: 50.5). Feeding at different heights contributed to resource partitioning between these two browsers, but giraffe browsing was not restricted to levels beyond the reach of greater kudu, so separation was not complete. Giraffe and kudu also had similar winter preferences for habitats, particularly riverine vegetation (Du Toit 1988). Unlike the above studies, giraffe and greater kudu in Mopane veld showed distinct differences in the vegetation types utilised (Dekker *et al.* 1996).

Kudu and Black Rhinoceros

Studies investigating resource overlap between kudu and black rhinoceros showed there was extensive overlap in their diets (Lamprey 1963; Jarman 1971; Leuthold 1978) and in habitats utilised (Lamprey 1963; Leuthold 1978). Black rhinoceros in Tanzania included a large amount of monocotyledons (38 %) in their diet (Lamprey 1963), which was unusual compared with other studies (Goddard 1968, 1970; Jarman 1971; Joubert & Eloff 1971; Mukinya 1977; Leuthold 1978; Hall-Martin *et al.* 1982; Skinner & Smithers 1990; Oloo *et al.* 1994). Owing to the fact that lesser kudu also made substantial use of grass (67 %), the resulting overlap was considerable. Lesser kudu and black rhinoceros both made use of dense and open *Commiphora* woodlands and avoided open and bare *Acacia tortilis* woodlands, hence habitat overlap was also great (Lamprey 1963). Black rhinoceros and lesser kudu and in Tsavo East National Park, Kenya, had similar diets (Pianka's index: 0.61) and fed at the same heights (Pianka's index: 1.0) (Leuthold 1978). Habitat selection by lesser kudu and black rhinoceros was almost identical (Pianka's index: 0.93), both species preferring dense woodlands. Total overlap was, therefore, extensive (Pianka's index: 0.57). Jarman (1971) assessed the diets of greater kudu and black rhinoceros in the woodlands around Lake Kariba, Zimbabwe, and found that they were relatively similar during the wet season (PS: 39.0), early dry season (PS: 26.8) and late dry season (PS: 38.2). He concluded that ecological separation, through diets, was not complete but suggested that differential use of habitats, before the valley was flooded, would have reduced resource overlap.

Eland and Black Rhinoceros

The diets of eland and black rhinoceros in Tanzania were extremely similar, mainly because both species made substantial use of grasses, 70 % and 36 %, respectively (Lamprey 1963). The use of herbs by eland (9 %) and black rhinoceros (9 %) also contributed to the great dietary overlap observed. Overlap in habitats was, however, low, because black rhinoceros tended to utilise dense woodlands, which eland mostly avoided.

Giraffe and Black Rhinoceros

In Tarangire Game Reserve, dietary overlap between giraffe and black rhinoceros appeared to be great, because the majority of their diets consisted of woody browse, 99 % and 62 %, respectively (Lamprey 1963). Their diets differed, though, owing to the fact that giraffe made extensive use of trees (86 %), while black rhinoceros favoured shrubs (41 %). In addition, they apparently fed at different heights, thus further reducing dietary overlap. Both species utilised dense and open *Commiphora* woodlands, but giraffe exploited *Acacia tortilis* woodlands, which black rhinoceros rarely used, so overlap in habitats was relatively low. Contrary to this, Leuthold (1978) found that black rhinoceros and giraffe, in Tsavo East National Park, had a great degree of overlap in habitats utilised (Pianka's index: 0.89), both preferring dense woodlands. Overlap in diets (Pianka's index: 0.47) and feeding heights (Pianka's index: 0.51) were also similar, yet total overlap was relatively low (Pianka's index: 0.21).

Giraffe and Eland

Lamprey (1963) found that the diets of eland and giraffe were dissimilar, because eland included a large proportion of monocotyledons in their diet (70 %) while giraffe mainly fed on dicotyledons, especially trees. Although eland and giraffe utilised open habitats, eland avoided dense woodlands which giraffe appeared to prefer and, therefore, habitat overlap was low. Similarly, eland and giraffe in Mopane veld were spatially separated by utilising different vegetation types (Dekker *et al.* 1996).

STUDY AREA

INTRODUCTION

Weenen Nature Reserve (WNR) was proclaimed in 1975. Prior to this, the land was a labour tenant farm and crop and goat farming were extensively practised. In 1948 the Department of Agriculture expropriated the land because it was severely eroded owing ostensibly to overgrazing and poor cultivation practices. Over the following 27 years extensive reclamation work, using retaining walls, gabions, rock packs and brush packing was conducted in some areas of WNR in order to combat soil erosion. These measures have largely proven successful[1]. The reserve is currently managed by KwaZulu-Natal Nature Conservation Service (KZNNCS).

LOCATION AND SIZE

The reserve is situated between 28°49′- 28°56′ S and 29°57′-30°03′ E. WNR is approximately 25 km north-east of Escourt and 8 km west of Weenen, in KwaZulu-Natal (Fig. 1). Weenen Nature Reserve is fenced and comprises 4 923 ha in total. A wilderness area to the south (Bushmans section, Fig. 1), which is closed to the public, is approximately 1 100 ha in size. A western section of WNR, known as Makhwezi (*ca* 660 ha), is only accessible to four-wheel drive vehicles. The effective size of the study area was, therefore, 3 153 ha.

TOPOGRAPHY AND GEOLOGY

Weenen Nature Reserve is situated on the Draycott plain and altitude varies from approximately 940 m in the north to 1 220 m in the Umthunzini hills, dropping to 900 m along the Bushmans River in the south (Fig. 1). The topography in northern and central regions is undulating while the southern and eastern regions are steep rocky slopes. The Bushmans, Nyandu, uNothongo rivers drain the reserve and flow into the Tugela River.

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[1] Visitor's Guide: Weenen Nature Reserve. Printed by KwaZulu-Natal Nature Conservation Service, Pietermaritzburg.

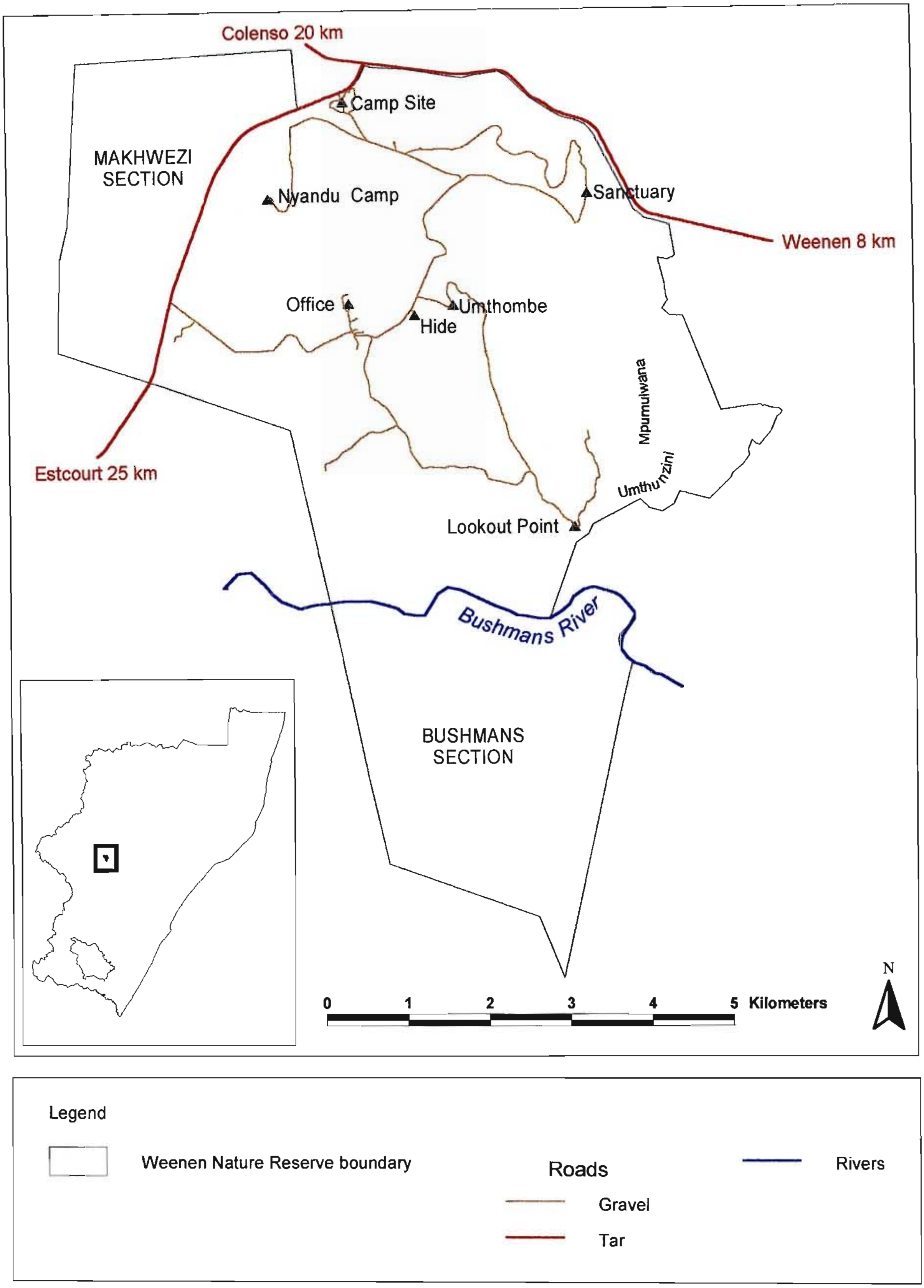

Figure 1. Locality of Weenen Nature Reserve within KwaZulu-Natal, South Africa, and the study area (excluding Bushmans and Makhwezi sections) within the reserve.

The reserve is underlain by shale, mudstone and sandstone of the Beaufort Series (Escourt and Adelaide Formations) but many dolerite outcrops occur throughout the reserve. The majority of the area is characterised by shallow (< 300 mm) Mispah (mostly on shale) and Shortlands (on dolerite) soil forms. These soils are extremely susceptible to erosion, mainly owing to their shallow depth. In addition, Valsrivier (a duplex soil form), which chiefly occurs in the western part of the reserve, is among the most prone to water erosion. Therefore, it is not surprising that overstocking in the past resulted in severe erosion (Hughes 1989).

CLIMATE

At WNR summer months, September to April, are hot with daily temperatures averaging 28°C, but reaching a daily maximum of 37°C during January. Daily winter temperatures average 10°C, but often fall below 0°C. Frost is common although snow is seldom recorded.

The reserve is situated in the summer rainfall area, with a hot and humid wet season and a cool to cold dry season. Rainfall is erratic, the annual rainfall, measured at WNR, ranged from 489 mm to 1 039 mm with a mean of 732.3 mm for 1981 - 1999. Rain is also strongly seasonal, 93 % falling during the summer months. The peak in the wet season usually occurs in January, with a mean monthly rainfall of 147.6 mm (Fig. 2). The dry season stretches from May to August, with June and July being the driest months (mean monthly rainfall of 10.9 mm and 10.6 mm, respectively).

During the study period, June 1998 to July 1999, monthly rainfall peaked during November (Fig. 2). With the exception of November, total rainfall for the months from June 1998 to May 1999 were well below the monthly means, with the result that the dry season in 1998 extended from April to the beginning of November.

Annual rainfall fluctuations for the period 1990 to 1999, reveal that 1990, 1994 and, in particular, 1992 and 1999 were dry years, annual precipitation being well below the mean (1981 - 1999) (Fig. 3). This was primarily owing to the fact that, during these years, rainfall was below the mean for early summer (September - November: 195.8 mm) and late summer (December - April: 486.3 mm), rather than winter (May - August: 50.2 mm).

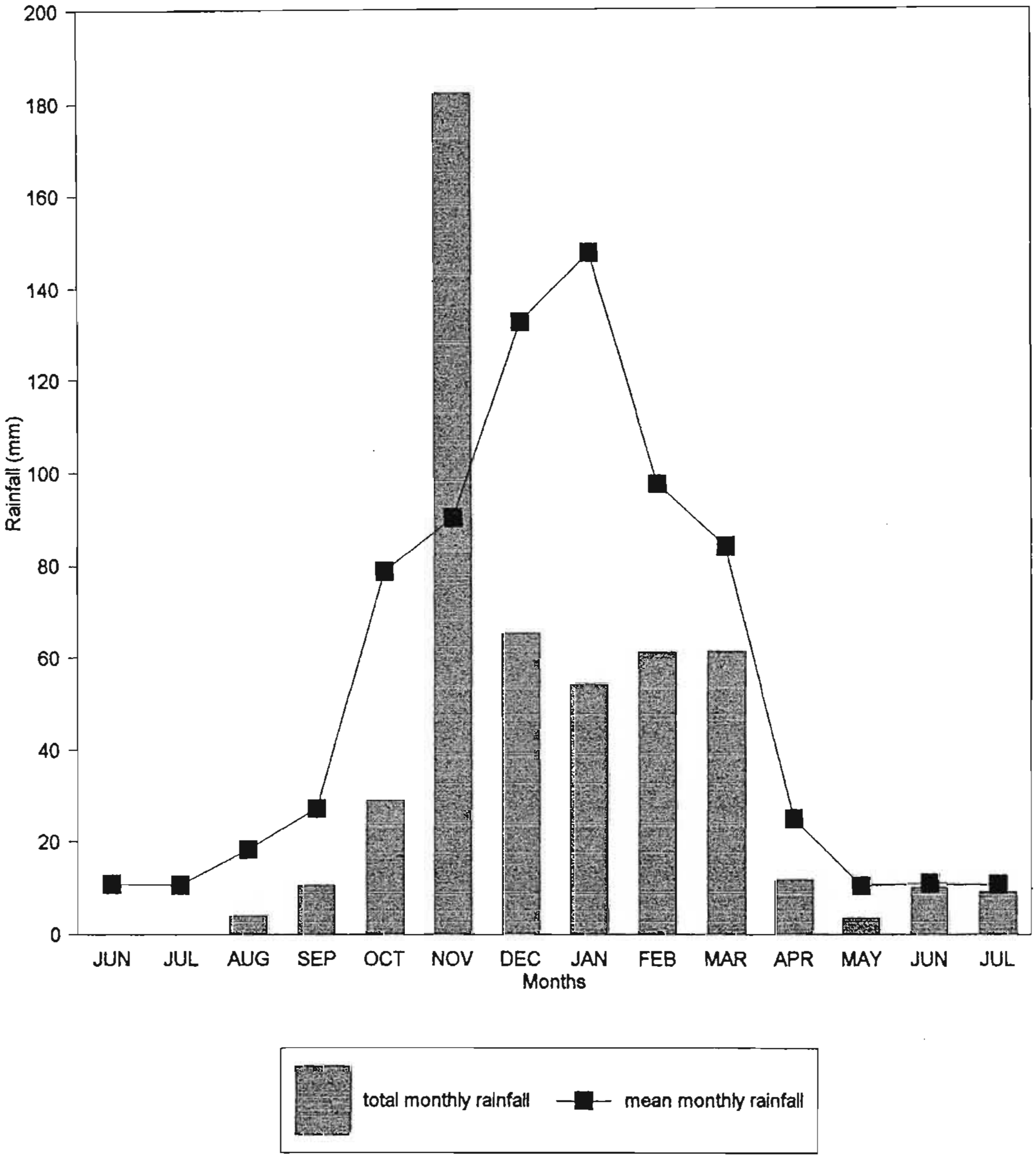

Figure 2. Total monthly rainfall from June 1998 to July 1999 and mean monthly rainfall (1981 - 1999) at Weenen Nature Reserve.

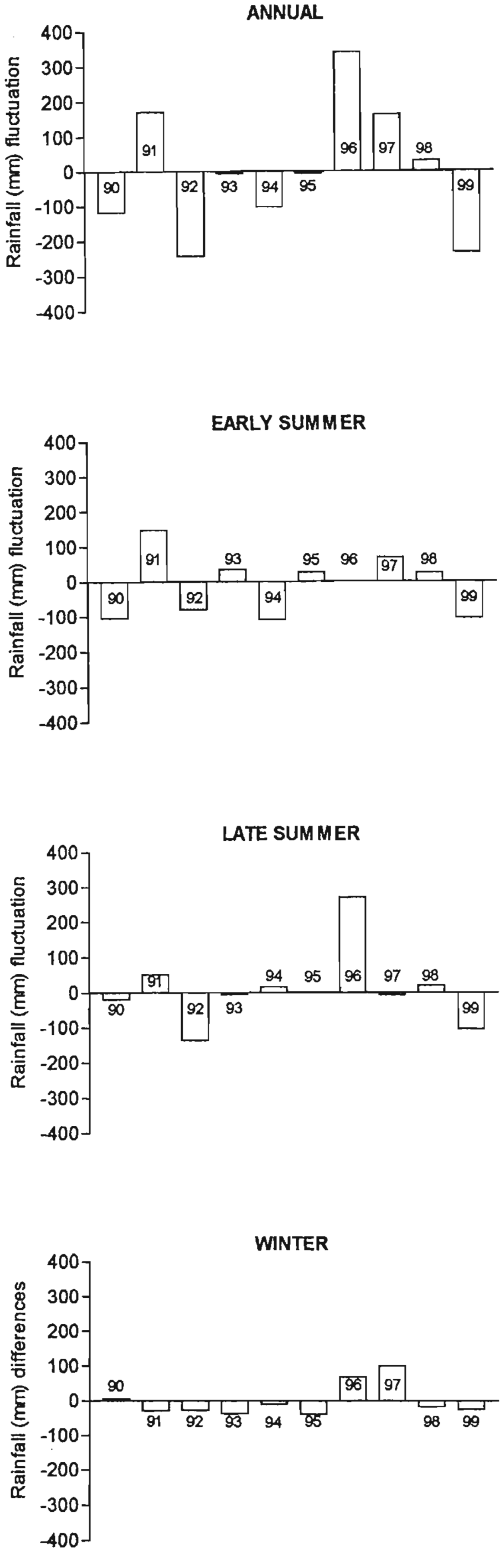

Figure 3. 10 year (1990 - 1999) fluctuations about the mean annual, early summer (September - November), late summer (December - April) and winter (May - August) rainfall at Weenen Nature Reserve.

FAUNA

The reserve supports a diversity of large mammal species, including black rhinoceros (9), giraffe (60), kudu (180), eland (80), white rhinoceros (38), red hartebeest (130) and zebra (150). Sixteen roan antelope were introduced into the reserve in 1988. Impala and warthog are not intentionally stocked, because they tend to over utilise specific areas which can lead to soil erosion, but have moved into WNR from neighbouring farms. Resident predators are essentially absent, although hyaena do move through the reserve.

The population dynamics of black rhinoceros, giraffe, kudu and eland were investigated from data provided by KZNNCS. Population numbers are estimates not counts and must thus be regarded with caution. The numbers of large herbivores are actively controlled, either through culling or live removals and these figures are reliable. Mortalities include those where the cause was poor body condition, malnutrition or unknown and exclude deaths by injury, snares or predation. The objective was to determine if the herbivore populations are regulated by food supply which was indirectly assessed by relating mortalities to rainfall. There is evidence to suggest that during periods of low rainfall, such as the dry season or particularly dry years, animal populations are regulated by the amount of available food (Novellie 1986; Fryxell 1987; Sinclair & Norton-Griffiths 1982; Owen-Smith 1990). The phenology of plants, especially deciduous trees, in the reserve was strongly associated with rainfall and temperature (pers. obs.). During May, deciduous plants started shedding their leaves, marking the commencement of winter. As temperatures started to rise again and the first rain for the season fell, plants began flushing new leaves. This denoted the onset of early summer. The majority of deciduous trees and shrubs were completely leaved out by December, indicating the beginning of late summer.

The black rhinoceros population has declined steadily from 1993 to the present, because individuals have either been translocated (Fig. 4a) or have died as a result of injuries sustained during fighting. The aggressive behaviour among males may indicate an imbalance in the sex ratio of the population and / or territorial conflict owing to overlapping home ranges. If the former is true, this may reflect that the number of black rhinoceros at WNR are restricted by social behaviour rather than food. However, if the latter is valid, this may indicate that food is limiting the black rhinoceros population.

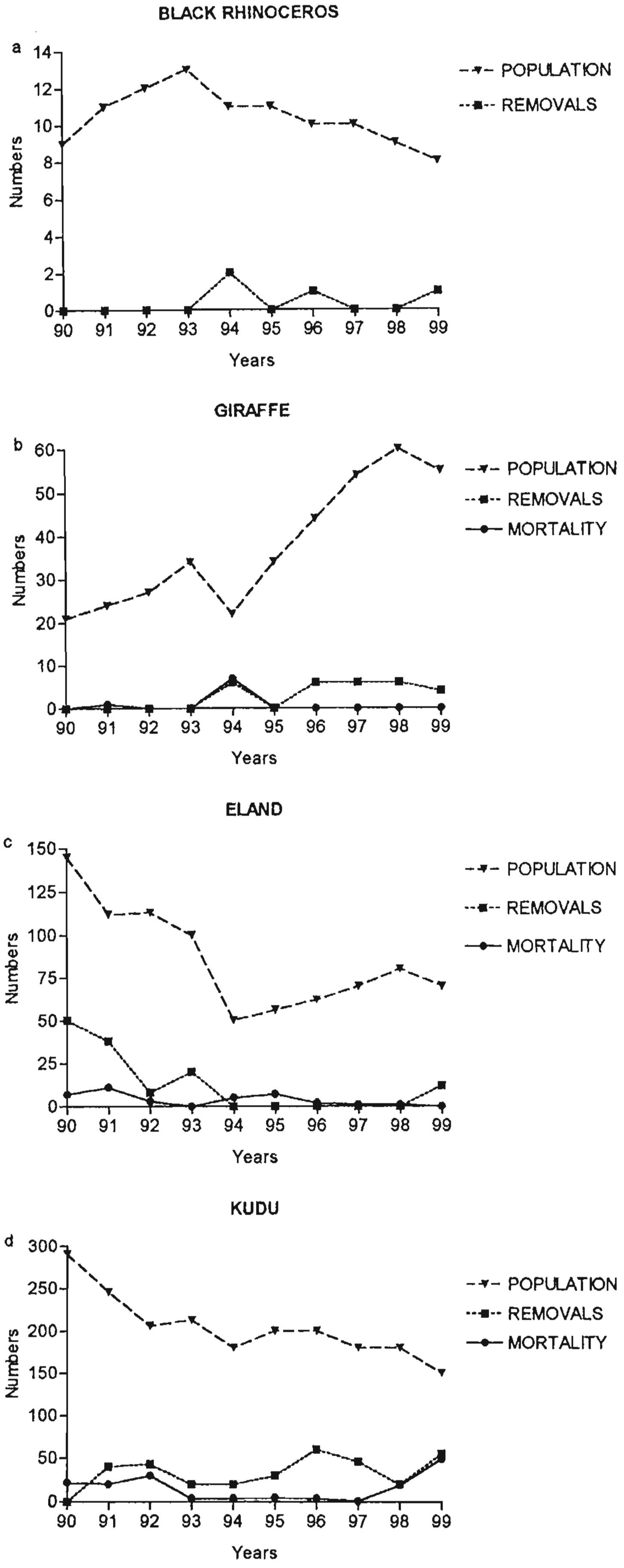

Figure 4. Population dynamics of (a) black rhinoceros, (b) giraffe, (c) eland and (d) kudu from 1990 to 1999, at Weenen Nature Reserve.

Giraffe numbers have increased from an estimate of 21 individuals in 1990 to 55 in 1999, despite mortalities and removals (Fig. 4). The greatest mortalities (21 %) occurred in 1994, even though 18 % of the population was removed. There were apparently no mortalities in 1999 and only six individuals were removed, but the giraffe population declined, owing ostensibly to low birth rates. Total annual rainfall during 1994 and 1999 were well below the annual mean (Fig. 3). Great mortalities and poor reproductive performance may, therefore, be related to a decline in food abundance during dry years. However, 1992 was also a particularly dry year which did not appear to negatively effect the giraffe population.

The number of eland at WNR was at its lowest during 1994, particularly because 18 % of the population was removed in 1993 (Fig. 4). Twelve individuals (approximately 15 %) were removed during 1999, contributing to a decline in the population. The substantial removal of animals during these years appeared to decrease the probability of mortalities during the dry years of 1994 and 1999 (Fig. 3). In 1995, 14 % of the eland population died (Fig. 4) as a result of poor body condition, malnutrition or unknown causes, and no animals were removed. Annual rainfall in 1995 was only slightly below the mean (Fig. 3). However, the low rainfall during 1994 could have contributed to the relatively high mortalities experienced in the succeeding year. A decline in food abundance during dry years may lead to increased mortalities of eland, although this pattern is not very clear.

The kudu population has decreased over the past 10 years, from an estimated 291 to 150 individuals in 1999 (Fig. 4). During 1992, 12 % of the kudu population died and 17.5 % were removed. Mortalities were more pronounced during 1999 (27.2 %), despite extensive removals (30.5 %). Not only were 1992 and 1999 extremely dry years, but both early and late summer rainfall was below average (Fig. 3). Kudu at WNR, therefore, suffer the greatest mortalities during extended dry periods which may be related to a limited food supply.

VEGETATION

INTRODUCTION

Weenen Nature Reserve is located within the northern variation of Valley Bushveld Veld Type (Acocks 1953). Edwards (1967) described the area as an *Acacia karroo* - *Acacia nilotica* thornveld which has invaded the grasslands. Three bioresource groups, namely Dry Tall Grassveld (13), Mixed Thornveld (18) and Valley Bushveld (21) (Camp 1999a) are found within WNR. The dry Tall Grassveld is characteristically sparse, encroached by woody species and is found on old lands dominated by *Hyparrhenia hirta* (Hurt & Camp 1999a). Various *Acacia* species, especially *A. karroo* and *A. nilotica*, and broadleaved species, such as *Euclea crispa, Euclea racemosa, Olea europaea, Ozoroa paniculosa, Premna mooiensis,* and *Vitex rehmannii* are found in Mixed Thornveld. In some areas, usually disturbed sites, *A. karroo* and *A. nilotica* have increased in abundance (Camp 1999b). The Valley Bushveld typically occurs in hot valleys of large rivers and is characterized by broad-leaved thickets of the evergreen species and contains *Euphorbia* species (Hurt & Camp 1999b). Nomenclature follows Arnold and de Wet (1993).

In June 1998 I undertook to identify and describe the woody vegetation of the savanna system contained within Weenen Nature Reserve, based on data collected prior to the current study. One of the aims of this study was to determine habitat selection of the browsers concerned. Therefore, it was necessary to describe the species composition of woody vegetation types at a spatial scale relevant to large mammalian browsers. Habitat types were considered to be distinct woody plant communities.

VEGETATION SAMPLING

A total of 102 transects were randomly placed throughout the reserve and sampled by various students. The data base is, therefore, amalgamated. Sampling of the vegetation was conducted from April 1996 to March 1998 using 50 m transects of variable width. Transect width was governed by density of woody vegetation with an aim of including at least 15 individuals of the most common woody plant species (Taylor & Walker 1978). All woody plants (≥ 0.5 m in height) rooted within the transect were identified to species and height of tree canopy was measured.

VEGETATION CLASSIFICATION

The woody species-by-site data were ordinated by correspondence analysis (CA) using the CANOCO package (Ter Braak & Šmilauer 1998). Two outlier samples were identified by the CA ordination and excluded from further analyses. The woody density data were analysed using Two-Way Indicator Analysis (TWINSPAN; Hill 1979) to obtain a classification of vegetation types. Four pseudo-species cut levels for the density data were equivalent to 0, 100, 1 000 and 10 000 individuals per hectare.

VEGETATION DESCRIPTION

The TWINSPAN classification identified six vegetation types at various hierarchical levels from the density data. Owing to the fact that, firstly, most communities at WNR are species poor and, secondly, two species, namely *Acacia karroo* and *Acacia nilotica*, are common and widespread throughout the reserve, the analysis required some refinement. Based on identifiable homogenous units on 1:10 000 orthophotographs (1989) and familiarity with the vegetation of the study area, transects at the third level were rearranged. The six vegetation types of WNR are illustrated (Fig. 5) and each described in turn (Table 1). See Appendix 1 for revised names of vegetation types as in forthcoming publication.

Thornveld

The Thornveld vegetation type is extensive and occurs mainly in the northern and western regions of the study area. The flat regions of this vegetation type have a history of extensive cultivation, which, together with shallow, shale soils, have resulted in severe soil erosion (Hughes 1989). Reclamation efforts have not been successful in some of these areas, with grass production still poor so that no more than four controlled burns have taken place here over the past 30 years. The moderate slopes of Thornveld were not cultivated, hence are not extensively eroded, so that burning in these areas has been more frequent, between five and 13 burns in 30 years.

Thornveld is represented by few plant species and is dominated by *A. karroo*, *Acacia tortilis* and *A. nilotica*, with occasional tall *Acacia robusta* and *Acacia sieberiana*. In many areas there are dense monospecific stands of relatively short (≤ 2 m) *Acacia* species. Uncommon species include *Coddia rudis*, *Dichrostachys cinerea*, *Diospyros lycioides*, *Maytenus heterophylla* and *Rhus pentheri*.

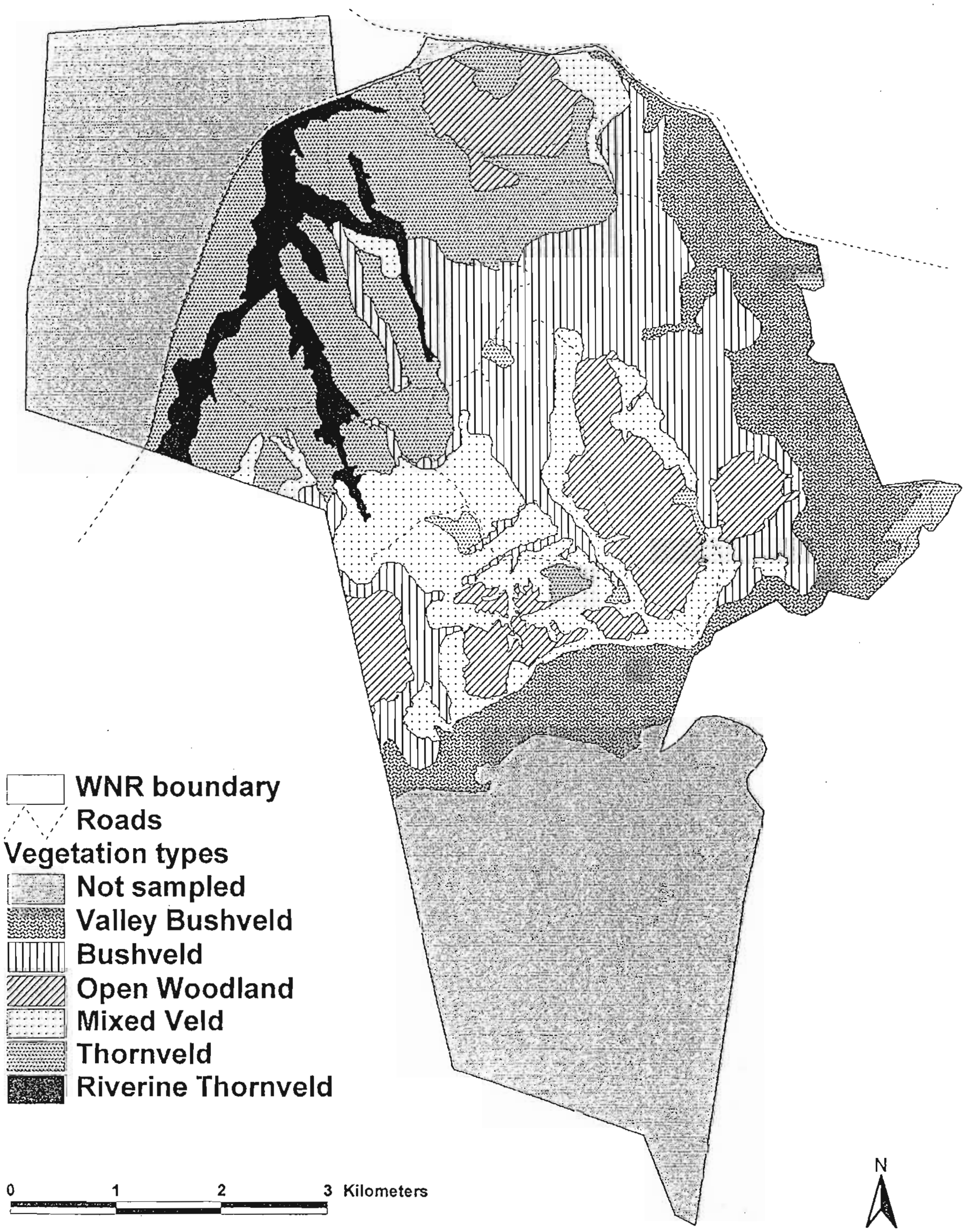

Figure 5. Vegetation types identified within the study area of Weenen Nature Reserve.

Table 1. The mean absolute density (individuals per hectare) of each woody plant species in each vegetation type. No entry denotes zero

Plant species	Vegetation types																	
	Thornveld			**Open Woodland**			**Riverine Thornveld**			**Mixed Veld**			**Bushveld**			**Valley Bushveld**		
	$n = 16$			$n = 9$			$n = 5$			$n = 20$			$n = 35$			$n = 15$		
	mean	max	% freq	mean	max	% freq	mean	max	% freq	mean	max	% freq	mean	max	% freq	mean	max	% freq
Acacia nilotica	293	677	94	185	520	100	70	120	80	241	1360	95	166	513	97	63	680	27
Acacia tortilis	452	1615	94	10	40	44	414	660	100	59	520	37	25	320	40	64	400	33
Acacia karroo	598	3040	94	647	2280	89	325	893	80	255	1360	84	157	1633	77	143	1250	40
Acacia sieberiana	4	40	13	72	383	78				1	18	5	< 1	13	3	3	40	7
Boscia albitrunca							68	281	60	4	80	5				2	35	7
Clausena anisata							4	20	20							3	40	7
Dais cotinifolia										8	155	5	5	148	6	3	40	7
Rhus dentata	3	20	19	< 1	3	11				54	246	68	31	400	49			
Rhus rehmanniana	10	86	25	< 1	1	11	50	156	40	101	600	74	73	520	63	52	360	20
Vitex rehmannii							20	100	20	152	900	47	118	1280	60	66	320	47
Brachylaena sp.										6	120	5						
Maytenus senegalensis										2	40	5	23	760	6			
Ozoroa paniculosa										11	133	21	28	200	37	8	120	7
Ziziphus mucronata	2	20	13	< 1	3	11	24	63	60	29	133	47	46	800	46	38	370	27
Euclea crispa	6	40	19	< 1	1	11	16	80	20	66	260	95	152	1360	74	40	370	27
Buddleja salviifolia													1	40	3			
Diospyros whyteana													1	40	3			
Euphorbia ingens													1	31	3			
Ximenia caffra													1	16	6			
Spirostachys africana													< 1	17	3			
Canthium ciliatum													1	40	6	5	80	7
Clerodendrum glabrum													3	62	9	5	80	7
Opuntia ficus-indica	1	13	6							4	80	5				11	160	7
Aloe ferox										1	13	5	1	20	3			
Pleurostylia capensis										1	20	5				3	40	7
Cussonia spicata										6	67	21	7	160	14	8	80	13
Trimeria trinervis													1	20	6	21	320	7
Oleo europaea													1	18	3	23	185	27
Dichrostachys cinerea	15	100	38	9	40	22				15	120	32	6	86	20	34	160	33
Pappea capensis	1	20	6							14	280	5	1	40	6	41	154	40
Ehretia rigida																64	308	47
Schotia brachypetala				1	6	11				2	20	11	5	48	20	67	333	53
Tarchonanthus camphoratus										9	80	16	38	1280	9	69	833	27
Zanthoxylum capense										1	19	5	5	80	6	70	923	20
Euclea racemosa										12	240	5				80	556	47
Dalbergia obovata													3	120	3	106	615	40
Acacia robusta	9	100	13				52	260	20	30	240	21	20	320	23	113	923	27
Premna mooiensis										6	40	16	3	50	6	115	417	73
Acacia caffra	1	13	6							122	702	74	86	720	77	135	1320	33
Rhoicissus tridentata										20	140	37	27	400	29	136	741	53
Celtis africana				< 1	3	11				2	40	5	18	320	9	162	1231	20
Berchemia zeyheri													1	27	3	166	1111	33
Hippobromus pauciflorus													6	143	9	190	2769	20
Maytenus undata													2	71	3	204	1667	33
Rhus pentheri	18	80	38	< 1	3	11	91	357	60	97	1200	26	45	320	40	237	972	87
Grewia occidentalis	3	40	6							6	40	16	2	40	6	263	926	80
Brachylaena elliptica													7	145	11	290	2400	53
Acacia ataxacantha										56	720	16	7	240	3	297	1920	40
Maytenus heterophylla	39	214	44	1	6	22	96	167	80	86	440	89	124	657	83	311	1077	87
Vepris lanceolata										3	20	16	4	67	11	333	4000	47
Diospyros lycioides	19	120	25							27	380	26	18	400	14	337	4462	20
Dombeya cymosa										4	80	5				509	3760	40
Coddia rudis	41	280	31				195	357	80	114	1200	37	43	480	31	751	2593	73
Calpurnia aurea							7	36	20	56	440	37	159	1080	71	1615	5625	80
Grewia flava																2	35	7
Cnestis polyphylla																3	40	7
Dovyalis zeyheri																3	40	7
Heteromorpha trifoliata																3	40	7
Croton gratissimus																5	80	7
Greyia sutherlandii																5	80	7
Rhus lucida																8	120	7
Vitellariopsis dispar																9	89	13
Commiphora harveyi																11	160	7
Cassine transvaalensis																11	80	13
Scutia myrtina																13	154	13
Brachylaena ilicifolia																40	561	13
Ptaeroxylon obliquum																43	560	13
Ficus thonningii																43	640	7
Scolopia zeyheri																44	417	13
Tapiphyllum parvifolium																51	769	7
Combretum erthrophyllum																75	1120	7
Allophylus africanus																78	400	33
Monanthotaxis caffra																110	1444	13

n = total number of transects

Open Woodland

The Open Woodland vegetation type occurs on old cultivated lands on relatively flat topography. Such sites are found in the northern and central regions, and along the western boundary of the reserve. This vegetation type is characterized by shallow Mispah soils, underlain by shale (Hughes 1989). Over the past 30 years, these areas have been burnt between five and 13 times.

This vegetation type is low in species richness and is characterized by a low density of tall (>5 m) *A. sieberiana* and a greater density of short (≤ 2 m) *A. karroo* and *A. nilotica* trees. Invasion by *A. karroo* is occurring and most individuals of this species are restricted in height as a result of fire. *A. tortilis* and *D. cinerea* are uncommon while *E. crispa, M. heterophylla, R. pentheri* and *Rhus rehmanniana* are rare.

Riverine Thornveld

Riverine Thornveld is found along the Nyandu River and its tributaries, in the eastern part of the reserve. The predominant soil is an association of 60 % Oakleaf and 40 % Valsrivier. Soils are generally deeper (300 mm - >1 000 mm) than in other areas of the reserve (Hughes 1989). Erosion is severe in the area where the Nyandu crosses the south-eastern border of the reserve and, as a result, no burns have been carried out in this section. Between one and nine burns have been conducted in the remaining areas of this vegetation type over the past 30 years. Sections of the Riverine Thornveld were extensively cultivated in the past.

The Riverine Thornveld is a closed, species poor woodland dominated by *A. tortilis* and tall (> 4 m) *A. karroo* trees. *Acacia nilotica, Boscia albitrunca* and *A. robusta* are relatively common while *Ziziphus mucronata* occurs occasionally. The understorey is dominated by *C. rudis, M. heterophylla* and *R. pentheri* as well as the forb *Peristrophe cernua.* Other woody species include *R. rehmanniana, E. crispa* and *Calpurnia aurea.*

Mixed Veld

Mixed Veld typically occurs on gradual slopes or in proximity to drainage lines, adjacent to Bushveld and Thornveld or Open Woodland, mainly in the southern - central regions of WNR. In the past, only small areas of Mixed Veld were cultivated, though not extensively. Both shale and dolerite soils were found in this vegetation type. Shallow (< 300 mm) Mispah soils were found throughout Mixed Veld, but there were isolated patches of Shortlands and Glencoe soils. The latter soil form develops in areas where the shale parent material has become impregnated with iron, usually from surrounding dolerite (Hughes 1989). Between five and 13 controlled burns have been carried out in this vegetation type over the past 30 years.

Mixed Veld is a transition between Bushveld and Thornveld and, therefore, plant species common to both vegetation types are found here. Compared with Thornveld, Open Woodland and Riverine Thornveld, Mixed Veld has a high diversity of plant species. A medium density of broadleaved and microphyllous trees (≤ 4 m) characterize the Mixed Veld. *Acacia karroo* and *A. nilotica* dominate this vegetation type, but *V. rehmannii, Acacia caffra, C. rudis, R. rehmanniana, R. pentheri* and *M. heterophylla* are also common. Rare species include *E. crispa, A. tortilis, Acacia ataxacantha, C. aurea* and *Rhus dentata.*

Bushveld

The majority of the Bushveld vegetation type occurs on hill slopes in the central region of the study area and along drainage lines in the east. The main soil form is Shortlands and dolerite rocks are abundant (Hughes 1989). Only isolated patches of this vegetation type were cultivated, but old stone kraals and homesteads are common throughout. Most areas of Bushveld have been burnt between five and nine times, while in small areas fires have been more frequent (10-13) over the past 30 years.

Bushveld can be described as a relatively species rich, medium to dense low (≤ 5 m) woodland. Although microphyllous species, such as *A. nilotica* and *A. karroo* are prevalent, broadleaved plant species are typical of this vegetation type. These include *C. rudis, E. crispa, M. heterophylla* and *R. rehmanniana.* Other species include *A. caffra, R. dentata, Ziziphus mucronata, R. pentheri* and *C. rudis.* Although not common, *Buddleja saligna, Diospyros whyteana, Spirostachys africana* and *Ximenia caffra* appear to be unique to this vegetation type.

Valley Bushveld

The Valley Bushveld vegetation type is found on the eastern and southern facing slopes of the Umthunzini hills and within the uNothongo valley. This area was not cultivated in the past and shallow (< 300 mm) Mispah and Shortland soils predominate (Hughes 1989). Over the past 30 years fires have been relatively infrequent (1-9).

This species rich vegetation type is characterized by a dense woody growth of broadleaved trees (< 10 m) and shrubs (< 3 m). There is a high diversity of plants and common woody species include *C. aurea*, *C. rudis*, *Dombeya cymosa*, *D. lycioides*, *Vepris lanceolata*, *M. heterophylla*, *A. ataxacantha*, *Brachylaena elliptica*, *Grewia occidentalis* and *R. pentheri*. Numerous species, such as *Monanthotaxis caffra*, *Allophylus africanus*, *Ficus thonningii* and *Tapiphyllum parvifolium*, appear to be unique, although uncommon, to Valley Bushveld.

FEEDING PATTERNS

INTRODUCTION

Successful management of areas of natural vegetation depends on a knowledge of the composition of the vegetation, the extent to which it is being used, and changes which take place in response to differential use by herbivores (Walker 1976). Estimates of the amounts of woody browse consumed contributes useful information in rating the relative importance of plant species as mammalian food sources and can provide a basis for deciding if the browsing capacity of an area is being exceeded (Telfer 1969). Comparison of herbivore food selection is of value to management in situations were these species share the same range (Novellie 1978).

Where species coexist, despite similar ecological requirements, they may do so through resource partitioning (Leuthold 1978; Manley *et al.* 1993). Resource partitioning is defined as the differential use of resources, such as food and space, by organisms (Schoener 1974; Begon *et al.* 1990; Krebs 1999). Ecological separation, by resource partitioning, of large mammalian herbivores in Africa is mainly owing to the selection of distinct diets and differential occupation of habitat types (Jarman 1971). In this chapter I consider the selection of diets by a guild of browsers and aim to determine the extent and seasonal variation of resource overlap among members of this guild.

DIET COMPOSITION

Diet choice by mammalian herbivores is a multi-decision process requiring perception of morphological and qualitative characteristics of the plant. On every encounter with a potential food item the animal has to decide if the plant is suitable as food or not (Palo *et al.* 1992). Selection of plant species by animals is influenced by a number of factors. Olfactory cues most likely play an important role in selection of food by herbivores. However, other sensory cues, such as taste and vision, may also be important. Furthermore, selection may be influenced by learning, accessibility and availability of specific food items (Sauer *et al.* 1982). What an animal chooses to eat will alter as the relative quantities and qualities of the items change (Pellew 1984a). Nutritional requirements of the animal will also influence diet composition, in terms of plant species selected (Sauer *et al.* 1982). In addition, large differences in nutritional qualities of available food items among seasons, species and plant parts of the same species have been demonstrated (Pellew 1984a). Dietary selection thus involves the selection of taxonomic class (grass or browse), plant species, individuals of a species and plant part (Coleman *et al.* 1989).

Herbivores may be ordered along a grazer-to-browser continuum, with grazers, feeding exclusively on grasses, and browsers, clumped at the opposite extreme. Those species which consume varying proportions of grass and browse are termed mixed feeders (McNaughton & Georgiadis 1986). Kudu, giraffe and black rhinoceros are regarded as browsers, while eland are considered mixed feeders (Skinner & Smithers 1990), although the gut structure of eland resembles browsers (McNaughton & Georgiadis 1986). Preference for grass or browse is considered a principal factor contributing to resource partitioning among African herbivores (McNaughton & Georgiadis 1986).

Schoener (1974) reviewed 81 studies of resource partitioning and found that 78 % of the groups of species were separated by food. Therefore, different animal species utilise different plant species or the same plant species, but to varying degrees. Diet relations among species are complicated by the fact that diets may change as resource abundance and availability vary in both space and time (Wiens 1989).

SPECIES RICHNESS AND DIETARY DIVERSITY

Some animals are more specialised than others and this may be quantified by measures of species richness and dietary diversity (Krebs 1999). Diversity is comprised of two distinct components: (1) the total number of items in the diet (richness) and (2) evenness (how the abundance data are distributed among the items) (Ludwig & Reynolds 1988). A low diversity indicates that utilisation among resources is not evenly spread (Zar 1996).

According to the competition theory, animals should specialise during the lean season and thus dietary diversity should decrease. During the 'fat' season, as resources become more abundant, animals should expand their diets and diversity in diets increase (Schoener 1982, 1986). Contrary to this, the optimal foraging model predicts that when food is limited, dietary diversity should increase as animals expand their diet (MacArthur & Pianka 1966; Pyke *et al.* 1977).

DIETARY PREFERENCES

Preference, as defined by Johnson (1980), is the likelihood that a resource will be chosen if offered on an equal basis with others. Studies under controlled, experimental conditions typically follow this definition of preference. Under field conditions relative availabilities usually differ (Thomas & Taylor 1990) and hence Johnson's (1980) definition of preference is not applicable to most field studies. Petrides (1975) defines preference as the extent to which a component is utilised in relation to its availability. This definition is thus more suited to field studies of selectivity. Preference is not synonymous with selection, which is the process in which an animal chooses a resource (Johnson 1980), irrespective of its availability. Studies evaluating resource use but not availability, therefore, result in inferences about utilisation not preference (Thomas & Taylor 1990). The measurement of preference thus requires a comparison of usage and availability of each plant component.

Preferences for plant species are generally determined in order to classify plant species in terms of their value as food resources for large herbivores (Owen-Smith & Cooper 1987a). In addition, Lawlor (1980) states that consumer preferences may be used as a measure of past competition.

RESOURCE OVERLAP

Species having similar patterns of resource usage may be considered to have a great degree of overlap, while those species with dissimilar usage patterns are regarded as having low overlap (Ludwig and Reynolds 1988). An increase in resource overlap is often associated with an increase resource abundance (fat season) (Schoener 1982, 1986; Gordon & Illius 1989). Overlap during lean times is often less as species specialise (Schoener 1982, 1986). Although inferring interspecific competition from patterns of resource overlap is controversial (Sale 1974; Hulbert 1978; Abrams 1980; Lawlor 1980; Schoener 1982, 1986; Wiens 1989; Krebs 1999), the general pattern of decreasing resource overlap during periods of resource scarcity is widespread among many similar species (Schoener 1982; Wiens 1989).

During the dry or cold season, when many plants become dormant, food availability decreases drastically in both quantity and quality (Owen-Smith 1982). Studies have indicated that resource limitation is not likely to occur continually, but during punctuated periods of a populations existence, such as during dry spell in the wet season (Owen-Smith 1990), during the dry season (Fryxell 1987; Sinclair & Norton-Griffiths 1982; Owen-Smith 1990) and during drought years (Novellie 1986; Fryxell 1987).

Similarity measures which do not take resource availabilities into account simply tell us the degree to which two species are similar (Sale 1974; Ludwig & Reynolds 1988). Overlap measures do not, therefore, represent the intensity of competition (Sale 1974; Hulbert 1978) but they do give

give an indication of approximate competition (Lawlor 1980; Schoener 1982, 1986), provided resources are limiting (Sale 1974; Hulbert 1978; Ludwig & Reynolds 1988; Krebs 1999). Alternatively, measures of similarity which are independent of resource abundance may in fact indicate evolutionary divergence of resource utilisation patterns, owing to past competitive pressures (Lawlor 1980). The stronger these past interactions, the smaller the observed degree of overlap (Hulbert 1978).

Diet choice involves the selection of plant species, plant parts and feeding height and thus one must look at all levels of resource selection in order to assess the degree of overlap among browsers. Differential selection at any level might render overlap at another level inconsequential (Coleman *et al.* 1989).

ECOLOGICAL SEPARATION

Ecological separation may explain how species coexist, despite similar ecological requirements (Leuthold 1978; Manley *et al.* 1993). The major selective force causing this differential use of resources is considered to be competition, although other processes, such as predation, facilitation (Schoener 1974, 1986; Sinclair 1985), disease (Sinclair & Norton-Griffiths 1982; Sinclair 1985) and migration (Murray & Illius 1996), may also lead to the partitioning of resources.

Amongst African ungulates, ecological separation has been described in terms of habitat choice (Lamprey 1963; Ferrar & Walker 1974; Dekker *et al.* 1996; Fritz *et al.* 1996), plant species eaten (Jarman 1971; Leuthold 1978), plant part eaten (Gwynne & Bell 1968) and feeding height (Leuthold 1978; Du Toit 1988, 1990). The underlying assumption of these studies was that ecological separation was the result of interspecific competition. Furthermore, a number of field manipulation studies have demonstrated that competition, either by territorial aggression or exploitation, was the principal mechanism causing ecological separation (Schoener 1986). However, predation may be as important as interspecific competition in structuring a guild of grazers in the Serengeti-Mara region in East Africa (Sinclair & Norton-Griffiths 1982; Sinclair 1985). Sinclair (1985), found that facilitation, within the Serengeti-Mara grazer guild, may be the process regulating the kongoni population, although interspecific competition and predation may also play a role. Differences in behaviour, anatomy, metabolism and reproduction between migrant and resident ungulates may also contribute to ecological separation (Murray & Illius 1996).

The essence of this section was to determine the similarities in resource utilisation patterns among the browser species investigated. However, before focussing on this issue it was first necessary to quantify the relative use of vegetation components by each browser species. I aimed to verify that different proportions of grass and browse are consumed by coexisting species. Diet composition, in terms of woody plant species, was hypothesized to differ among coexisting browsers. Selection of woody plant species was expected to change with regards to food abundance and, therefore, I also investigated changes in the availability of woody forage. Species richness and dietary diversity were investigated to test if both richness and diversity decreased during the lean, winter period. This was followed by examining the average height at which browsers feed to determine if animals of different size feed at different feeding levels. I then examined dietary overlap, in terms of diet composition and feeding heights. Following the conventional theory of competitive exclusion, dietary overlap among the four browser species was expected to be minimized during the lean dry season. The next section aimed to determine food and feeding height preferences of each browser studied, by comparing resource use to resource availability. Lastly, resource partitioning among the guild of browsers was examined, by comparing similarities in dietary preference.

METHODOLOGY - DATA COLLECTION

DIET COMPOSITION

Diet selection by free-ranging black rhinoceros, giraffe, kudu and eland was recorded through a complete seasonal cycle. Sampling was conducted from June 1998 to July 1999, to ensure a repetition of sampling during the dry season. The dry season is considered to be ecologically more important, as the potential for competition over food is greatest during this period (Leuthold 1978). Selection was conducted at the patch and feeding station levels. A feeding station was defined as an area that was grazed or browsed without the animal taking a step (Coleman *et al.* 1989) and a patch was regarded as a series of feeding stations over the distance the focal animal was observed.

The different methods used were considered in terms of the species studied, available manpower and budget constraints for sampling. On account of the areas occupied by black rhinoceros in Weenen Nature Reserve being densely vegetated, it was concluded that direct observations would be unsuitable. A plant-based approach was thus chosen for assessing browse utilization by black rhinoceros. The method relies on the characteristic manner in which black rhinoceros browse, biting off mainly large twigs with a 'pruning shear'- like action (Joubert & Eloff 1971).

Both direct observations and a plant-based method were initially intended to be used for the other browsers considered in the study. One cannot distinguish among the bites of kudu, eland and giraffe and, therefore, direct observations of these animals would need to precede a plant-based technique. A pilot study indicated that a plant-based technique was not feasible. Where a plant had been previously utilised it was found to be impossible to judge which twigs were browsed by the observed animal. In addition, kudu, eland and giraffe were observed to browse non-thorny or non-spinescent species by running their lips over the twigs or simply plucking leaves from a plant without biting off actual twigs. Owing to these limitations only direct observations were used for assessing diet selection by giraffe, kudu and eland.

Black Rhinoceros

Random 2.5 m wide belt transects (Kotze & Zacharias 1993) of variable length, located in each vegetation type known to be occupied by rhinoceros, were patrolled on foot. Black rhinoceros tend to remain within a specific home range (Skinner & Smithers 1990) and it was, therefore, considered legitimate to sample only areas known to be occupied by rhinoceros. The lengths of the transects depended on the dimensions of the vegetation type at each sampling location. The location of each transect was accurately marked on 1:10 000 orthophotos and the position of the start and end of each transect recorded. Note was made of whether the area where black rhinoceros browsed was burnt or not. If burnt, the date of the burn was obtained from KZNNCS records.

The plant-based technique precluded recording the use of fruit, flowers and plant species with fine stems (grasses, creepers, most forbs and certain succulents) by black rhinoceros because they are not browsed in the characteristic manner. All plants rooted within the transect were inspected for evidence of black rhinoceros utilization. If the least doubt existed as to whether a particular plant had been browsed by black rhinoceros or not, it was ignored. Only recently browsed plants were recorded as utilised. This ensured that browse utilization was measured for a specific season and sampling did not overlap among seasons. The age of bites was judged, using degree of discolouration and decomposition of the end of browsed branches, by personal observation and the assistance of a game guard familiar with the feeding habits of black rhinoceros.

For each plant, within the transect, utilised by black rhinoceros, plant species and plant part were recorded. Plant parts were classified as leaves (new or old) and / or shoots. A precise measure of plant height and feeding height was made. Where black rhinoceros broke branches to feed, the feeding height was recorded as the original height at which the forage would have been prior to being broken.

Diet composition of black rhinoceros was quantified using three methods: the number of individuals of a plant species utilised (hereafter termed frequency), enumeration of twigs browsed, i.e., counting the number of freshly browsed stem tips on a particular plant, and amount of browse removed. To measure the amount of browse removed the 'browse bottle' technique developed by Emslie and Adcock (1993) was used because it has a number of advantages over the regression method (see *Literature Review*). Although regression methods are likely to be more accurate and precise than the 'browse bottle' method, the non-destructive, more time efficient technique was preferred. For each twig utilised the amount of material removed was measured in standardized browse volumes (SBV's) using photographic standards. Browse offtake was estimated by comparing the diameter of browsed twigs at the point of browsing with unbrowsed branches of the same diameter on the same tree (or neighbouring tree of the same species and similar height) and visually estimating the amount of browse in SBV's on the equivalent unbrowsed twig.

Other Browsers

A pilot study indicated that feeding observations could be made from a vehicle, because animals within the study area are habituated to vehicles. However, animals were too wary to allow long observation periods. Diet description was, therefore, based mainly on instantaneous feeding observations.

The road network of Weenen Nature Reserve was regularly patrolled by vehicle. The entire road network was patrolled on each observation day. Survey routes were used independently of animal occupancy and varied daily to avoid introducing systematic time-of-day effects. The road network in the study area is not designed to sample vegetation types in proportion to their area of occurrence and thus survey routes may be biased. This was minimised as far as possible by determining the area sampled for each vegetation type and correcting for under-sampling in follow up surveys. The area sampled was calculated by multiplying mean visibility, measured with a range finder, and distance covered by road, recorded to the closest 50 m. If a vegetation type was found to be under sampled then the section of road, for that vegetation type, was traversed proportionately more often.

A pilot study revealed that observations over complete days (i.e., from dawn to dusk) were profitless as animals were observed not to be actively feeding during the warmer hours of the day. Patrols, during winter, were conducted from 7-12 am and from 2-5 pm. During the remainder of the year, observations were conducted from 6-11 am and from 3-6 pm.

Observations were made with the aid of 7 × 50 binoculars. Only feeding animals were observed. If a browser was not feeding, but involved in another activity, such as moving towards water, resting or ruminating, it was watched for 10 minutes. If it did not feed during this time period then no record was made. If an animal had commenced feeding before it was observed, then it would not constitute a feeding event. If a herd of animals was encountered, the individual which could be most clearly viewed was selected as the focal animal. The date, time and duration of the observation was recorded. The location of the feeding individual was accurately marked on 1:10 000 orthophotos and co-ordinates recorded.

All woody plants eaten were identified to species level. If grasses and forbs (including creepers) could not be identified then they were recorded as categories. Grasses consisted of all graminoids; forbs and creepers of all soft-stemmed dicotyledons. Plant height for each plant eaten was precisely measured. Plant parts of woody species eaten were classified according to leaves (old / new), shoots, fruit or flowers. Feeding height was recorded by measuring the height above ground at which an animal browsed. All feeding heights utilised during a single feeding event were noted. Where kudu, eland or giraffe broke branches to feed, the feeding height was taken as the original height at which the forage would have been prior to being broken.

Two methods were used to quantify diet composition of eland, giraffe and kudu: the number of feeding events (henceforth termed frequency), and time spent feeding on each plant species. Each instance in which a focal animal fed on an individual woody plant was recorded as one feeding event. If an animal browsed on three separate individuals of a woody species, this was counted as three separate events for that plant species. If two individuals fed simultaneously on the same plant, only the focal animal's feeding would constitute an event. If an animal returned to a plant, that it had previously browsed, this was not regarded as a separate, independent feeding event. Herbaceous plants grow in close proximity to each other and, therefore, it was found to be impossible to consider feeding events on individual plants. Thus, where grasses and forbs (including creepers) were eaten, this was regarded as a single feeding event, irrespective of the number of plants utilised.

Feeding time was recorded with a stop watch. Each feeding event included the time between when the focal animal took its first bite from a particular woody plant and when the animal swallowed its last bolus, before moving on and switching to feeding on a different plant. Feeding time, therefore, included the time spent biting off and chewing food items. If an animal returned to a plant this was not regarded as a separate, independent feeding event, and its feeding time was simply added to the first record for that individual plant. If the focal animal fed on herbaceous plants, i.e., grasses, forbs or creepers, the feeding time included the total time that the animal's nose was in the sward. Such records did not, therefore, constitute feeding events on individual plants. Feeding may be interrupted by short spells of other activities such as grooming, resting or ruminating. These interruptions were not included in the calculation of feeding durations.

AVAILABLE BROWSE

Available browse was estimated during the course of the dietary assessment. A sample of available food items was taken at each feeding site. This was done, firstly, to reduce sampling errors usually associated with estimating availability independently of feeding records (Owen-Smith & Cooper 1987a) and, secondly, to maximise sampling efficiency. Here, available browse refers only to woody plant species, because it is difficult to quantify the availability of forbs and grasses.

Available browse was defined as the total plant material (leaves, twigs, flowers and fruit) of all woody plant species accessible to the focal animal while feeding. It was, therefore, necessary to define the maximum height and neck reach of each animal species and to estimate the amount of edible material within these levels. The extreme foliage and shoot densities of certain shrubs and trees can impede access to the centre of the plant (Pellew 1983) but this restriction was not included in the methods for estimating available browse. No qualitative restriction was incorporated to account for preference by the ungulates. The assessment of available browse is thus likely to result in an over-estimate of the actual quantity of edible material present (Pellew 1983; McNaughton & Georgiadis 1986).

Black Rhinoceros

For each woody plant species utilised within the dietary-assessment transect, browse availability was estimated in a circle of 2 m radius around the trunk of the plant. The radius was dependent on the neck reach of black rhinoceros, which was assumed to extend 1 m on either side of its foot placement. If a plant was rooted in the circle but browse material was above the maximum height reach of rhinoceros, i.e., 2.0 m, then that plant was not considered available. Each available woody plant was recorded in terms of plant species, and plant height and height to bottom of the canopy were precisely measured. Available leaf material was visually rated as a percentage of the estimated potential maximum that could be borne by an individual plant. The percentage classes were: 0 %, 1-10 %, 11-25 %, 26-50 %, 51-75 %, 76-90 %, 91-99 % and 100 % (Walker 1976).

The amount of available browse was determined using the total number of plants (i.e., frequency of occurrence) and in SBV's using photographic standards. The techniques were chosen to yield data most comparable with other dietary studies of large herbivores and proved satisfactory in a pilot study.

Other Browsers

Similar to black rhinoceros, available browse was assessed using frequency of occurrence and amount of browse in SBV's. Both methods proved adequate in a pilot study. The techniques used for estimating available browse were based on the method of Owen-Smith and Cooper (1987a). Their approach is especially advantageous as it eliminates the use of time-consuming vegetation surveys for estimating browse availability. During the feeding observations the foraging path of the focal animal as well as the plants browsed were noted. At the end of the observation period, a string was laid along the foraging path. The string was subsequently followed and each woody plant species within neck reach of the animal, rooted on either side of the string, was enumerated and the amount of browse visually estimated in SBV's. It was assumed that a kudu and eland's neck reach extends 0.5 m on either side of its hoof placement; lateral neck reach for giraffe was considered to be 2 m. If a plant was within neck reach, but plant material was above maximum height reach, then the plant was not recorded as available. Maximum height reach was assumed to be 2.5 m for kudu and eland bulls; 2 m for kudu and eland cows; and 5.5 m and 5 m for giraffe bulls and cows, respectively. Each available woody plant was recorded in terms of plant species. Plant height and height of canopy bottom were precisely measured. The following classes were used, 0 %, 1-10 %, 11-25 %, 26-50 %, 51-75 %, 76-90 %, 91-99 % and 100 % (Walker 1976), to visually rate available leaf, fruit and flowers as a percentage of the estimated potential maximum that could be borne by an individual plant. If the animal's foraging path could not be accurately located or only a single plant was fed on, then availability was assessed within a circle around the stem of the plant fed on, with the radius dependent on the appropriate neck reach of the animal.

Sample size necessitated pooling monthly data into seasons which were considered biologically realistic. However, it must be recognised that browse availability within seasons may vary considerably. Data were divided into three seasonal periods: winter (May - August); early summer (September - November) and late summer (December - April). The delineation of seasons was based on the phenology of deciduous trees, which form the bulk of the study area's vegetation (Table 1). The commencement of winter was marked by trees shedding their leaves. The flush of new leaves denoted the onset of early summer while the start of late summer was indicated by the majority of trees being in full leaf (pers. obs).

PHENOLOGY OF AVAILABLE WOODY PLANT SPECIES

The phenology of available woody plant species was investigated. Available woody plants included those fed on at the time of sampling, irrespective of plant part. When grasses and forbs were eaten, woody species within neck reach of the animal were treated as available.

For each woody plant species available to each browser during each season, the proportion of individuals whose flowers, fruit and foliage was visually rated as a percentage class of the estimated potential maximum that could be borne by an individual plant was determined. Original data were reclassified into the following percentage classes: 0 %, 1-25 %, 26-50 %, 51-75 % and 76-100 %. Statistical tests for determining seasonal differences were considered inappropriate.

DIET COMPOSITION

A single feeding observation included either a single feeding event or a number of events over the time an animal was observed. Feeding events were thus not always independent of each other because successive plants do not represent independent offerings. However, on average a substantial proportion (36 %, 40 % and 50 % for giraffe, kudu and eland, respectively) of events were independent, i.e., one plant eaten per observation (Appendix 2). If successive plants of different species are considered independent (Owen-Smith & Cooper 1987a) then the use of all feeding events does not greatly violate the assumption of independence (Appendix 2).

For analysing feeding patterns, forage types were identified and the proportional contribution of each was measured. A forage type was defined as a class of food items for which it may be assumed there is less variability in quality within a class than among classes (Du Toit 1988). Herbaceous forage types were classified into two categories: grasses and forbs (including creepers). Woody forage types were categorised by three classes of plant part: shoots and / or leaves (hereafter termed woody forage), flowers and fruit. Woody plant species were also investigated separately and included those fed on at the time of sampling, irrespective of plant part. Seasonal data for each browser were pooled to represent the annual feeding patterns of that browser species. Although seasons were not sampled equally, the pooled data were considered as good an estimate of the annual feeding patterns as possible.

For examining the relation between the different methods used for assessing the diets of the browsers, linear correlations were performed separately on the data for each browser species for each season and all seasons combined (annual). Linear correlations were selected based on visual examination of relevant scatter plots. All zero pairs were excluded from the analyses.

The diets of the browser species considered were compared by grouping woody plant species into two classes, namely, microphyllous and broadleaved plants. *Acacia* species and *Dichrostachys cinerea* were regarded as microphyllous and all other species were treated as broadleaved plants. This grouping was required to ensure that average expected frequencies were at least 6.0 (Roscoe & Byars 1971). A log-likelihood test or, where zero values in the data set, chi-square (χ^2) (Zar 1996) was employed separately for each season and all seasons combined (annual) for determining if proportions of microphyllous and broadleaved plants were dependent on animal species.

The diet of each browser was also examined separately. For determining if proportions of microphyllous and broadleaved plants were independent of season a log-likelihood test or, where zero values in the data set, χ^2 was employed separately for each animal species.

In order to test if woody plant species were utilised with equal frequency by a browser, a goodness-of-fit test was conducted separately on the annual, early summer, late summer and winter data for each browser species. Goodness-of-fit tests were applied only if data fitted both the Roscoe and Byars (1971) and Koehler and Larntz (1980) guidelines. If found to be false ($P < 0.05$) then simultaneous confidence intervals were constructed using the Bonferroni method (Neu *et al.* 1974; Byers *et* *al.* 1984). By this method one can be at least 100 (1 - α) % confident that the intervals contain their respective true proportions, p_i:

$$p_i \pm Z_{\alpha/2k} \sqrt{p_i \, (1-p_i)/n}$$

where $Z_{\alpha/2k}$ is the upper standard normal table value corresponding to a probability tail area of $\alpha/2k$ (in this case $\alpha = 0.05$); k is the number of categories tested (Byers *et al.* 1984) and n is the total number of plants utilised over all woody plant species. Owing to the fact that several parameters are estimated simultaneously the level of significance requires the $\alpha/2k$ adjustment (Neu *et al.* 1974). Bonferroni confidence intervals were constructed for investigating which plant species were utilised differently from each other. Any estimate that falls within the confidence interval for species j is an estimate of the population proportion of species j (p_{ij}). Similarly, any estimate that falls within the confidence interval for species k is an estimate of the population proportion of that species (p_{ik}). Thus, any degree of overlap in the confidence intervals of p_{ij} and p_{ik} would imply that the two proportions are not significantly different at the set level of confidence[2].

The Bonferroni method assumes that sample size (n) is sufficiently large so a normal distribution approximation to the binomial distribution is valid. Therefore, confidence intervals were considered accurate only when np_i and $n(1 - p_i)$ were both ≥ 5 (Alldredge & Ratti 1986).

SPECIES RICHNESS, DIETARY DIVERSITY AND EVENNESS

A measure of species richness is the total number of species present in the diet (S), but S depends on sample size (n). Margalef and Menhinick indices (reviewed by Ludwig & Reynolds 1988) presuppose that a functional relation exists between S and n. These indices should only be used if their underlying functional relations hold (Ludwig & Reynolds 1988). This is not the case in the current study and rarely so in practice (Ludwig & Reynolds 1988). As a result, species richness was measured as the total number of woody plant species present in the diet. A log-likelihood goodness-of-fit test was used to evaluate if the annual number of woody plant species in the diet were equal among the four browsers. In addition, the data for each browser were investigated separately, by employing goodness-of-fit tests, to determine if the number of woody plant species utilised by an animal species were equal among seasons.

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Diversity in forage types for the annual and seasonal diets of eland, kudu and giraffe was calculated using the Shannon-Wiener diversity index, H', (Pielou 1977):

$$H' = -\Sigma\ (p_i \log p_i)$$

where p_i is the proportion of feeding events allocated to the ith resource included in the diet. Similarly, annual and seasonal dietary diversity *(H')*, based on woody plant species, for each browser was estimated. The value of H' is zero if and only if there is one component in the diet and H' is maximum ($H_{\max}$) only when all components in the diet are represented by the same number of individuals (Ludwig & Reynolds 1988). Maximum diversity ($H_{\max}$) for a data set consisting of k categories is:

$$H_{\max} = \log k$$

The smaller the difference between H' and $H_{\max}$ for a data set, the closer the observed diversity is to maximum diversity. The Shannon-Wiener index should be viewed as a measure of 'uncertainty'. If dietary diversity is great, then there should be much uncertainty in predicting which food item would be selected at random. However, where the bulk of data occurs in only a few categories diversity would be low and one would be relatively certain of being able to predict which food item would be selected at random. Unfortunately, H' is known to be an underestimate of the dietary diversity in a sampled population, but this bias decreases with increasing sample size (Zar 1996).

Hutcheson's (1970 in Zar 1996) two-sample t-test was used for determining if annual diversity in woody plant items was equal among browsers. This test was specifically proposed, by Hutcheson, for assessing if Shannon-Wiener diversity indices are equal between two samples. The t-test was performed for each combination of browser pairs (i.e., eland-kudu, giraffe-kudu, kudu-black rhinoceros, eland-giraffe, eland-black rhinoceros and giraffe-black rhinoceros). Hutcheson's t-test was also conducted separately for each browser to test if diversity indices were equal among seasons. Thus, the test was employed for each combination of seasons, i.e., early summer - late summer, early summer-winter and late summer-winter.

Diversity indices incorporate both species richness and evenness into a single value. The value of the diversity index on its own makes it impossible to say what the relative importance of species richness and evenness is (Ludwig & Reynolds 1988). Therefore, the modified Hill's ratio (*HR*)

(Alatalo 1981) was employed as a measure of evenness:

$$HR = \frac{(1/\lambda) - 1}{e^{H'} - 1}$$

where H' is Shannon-Wiener diversity index (defined above) and λ (Simpson's index) is:

$$\lambda = \Sigma \, p_i^2$$

where p_i is the proportional abundance of the i-th species (Ludwig & Reynolds 1988). Evenness (*HR*) of forage types and woody plant species was calculated. The modified Hill's ratio approaches zero as a single species becomes more and more dominant. The ratio tends to be relatively unaffected by species richness and sample size, and is one of the most interpretable evenness measures (Alatalo 1981).

FEEDING HEIGHT

Linear correlations were performed separately on each browser species data for each season and all seasons combined (annual) for examining the relation between the different methods used for quantifying feeding height utilisation. Linear correlations were selected based on visual examination of relevant scatter plots. All zero pairs were excluded from the analyses.

Utilisation of feeding heights was examined by considering the use of, firstly, all forage types and, secondly, woody plant species only. In both instances feeding heights were grouped into the following height classes: 0-0.5 m, 0.6-1.0 m, 1.1-1.5 m, 1.6-2.0 m, 2.1-2.5 m, 2.6-3.0 m, 3.1-3.5 m, 3.6-4.0 m, 4.1-4.5 m, 4.6-5.0 m and 5.1-5.5 m. For each browser the proportional utilisation of each height class was determined and 95 % Bonferroni confidence intervals constructed.

Average feeding height was calculated for each browser during each season and all seasons combined (annual) by:

$$Average\ feeding\ height = \Sigma p_i \ h_i$$

where p_i is the proportional utilisation in the i-th feeding height class and h_i is the median height above ground (in metres) of the i-th feeding height class in question (Du Toit 1990).

DIETARY OVERLAP

Ecological similarity was assessed by estimating the degree of resource overlap among the guild of browsers studied. Dietary overlap between species pairs was calculated separately for each season as well as the entire seasonal cycle. Similarity measures are descriptive coefficients and do not estimate some statistical parameter (Krebs 1999). Therefore, statistical testing of these indices is meaningless.

Diet Composition Overlap

Overlap in diets, based on all forage types, was estimated for browser pairs eland-kudu, eland-giraffe and giraffe-kudu. Similarities in the utilisation of woody plant species was also assessed for each combination of browser pairs i.e., eland-kudu, eland-giraffe, eland-black rhinoceros, giraffe-kudu, giraffe-black rhinoceros and kudu-black rhinoceros.

Following recommendations by Linton *et al.* (1981) both Percentage Similarity and Pianka's overlap index were used for assessing diet overlap between pairs of browsers. Percentage Similarity (PS) was calculated for each combination of browser pairs by:

$$PS = \Sigma \; minimum \; [\, j_i, \; k_i]$$

where j_i and k_i denote the percentage allocation of feeding to the ith food item by browsers j and k, respectively. PS is given by the sum of all the lowest values from each pair of percentages and values range from 0 (no overlap) to 100 (total overlap). Pianka's overlap index (O_{jk}) was calculated for each combination of browser pairs by:

$$O_{jk} = \frac{\Sigma P_{ij} \; P_{ik}}{\sqrt{\Sigma P_{ij}^2 \; \Sigma P_{ik}^2}}$$

where P_{ij} and P_{ik} are the relative proportions of the i-th resource utilised by the j-th and k-th species, respectively. Overlap values range from 0 (no resources used in common) to 1.0 (complete overlap).

Feeding Height Overlap

Overlap in the utilisation of feeding height classes was estimated by considering the utilisation of, firstly, all forage types and, secondly, woody plant species only. Overlap was calculated for each combination of browser pairs, as defined above, by both the Percentage Similarity and Pianka's overlap index methods.

Total Dietary Overlap

Total overlap in diets was estimated, firstly, in terms of all forage types and, secondly, woody plant species only. Using the results obtained for overlap in diets and overlap in feeding heights, total dietary overlap was calculated by multiplying the two separate measures. PS values were scaled to proportions before multiplication. Multiplication of the two measures ("product α" May 1975) assumes that the resource dimensions are independent of each other. Although this is questionable, total interdependence is even more unlikely in this case.

DIETARY PREFERENCES

Dietary preferences of the guild of browsers studied were determined by comparing the utilisation and availability of only woody plant species. Preferences for forage types were not determined. When grasses and forbs were eaten, woody species within neck reach of the animal were treated as available. Available woody plants included those fed on at the time of sampling, irrespective of plant part. Preferences were estimated for all seasons combined (annual). To accommodate seasonal variations in feeding selection, all preferences were also calculated separately for each season.

Food Preferences

The relation between the two methods used to determine available browse, i.e., frequency of occurrence and amount of browse in standard browse volumes, was examined by linear correlation. Correlations were performed separately on the data for each browser species for each season and all seasons combined (annual). Linear correlations were selected based on visual examination of relevant scatter plots. All zero pairs were excluded from the analyses.

For comparing if the availability of woody plant species was the same among browsers during each season, plant species were first grouped into two classes, namely, microphyllous and broadleaved plants (as defined above). This grouping was required to ensure that average expected frequencies were at least 6.0 (Roscoe & Byars 1971). Log-likelihood tests were then employed to determine if availability was independent of animal species.

For evaluating if a browser used available woody plant species in proportion to their occurrence, simultaneous Bonferroni confidence intervals (Neu *et al.* 1974; Byers *et al.* 1984) were constructed for the observed proportions of utilisation of a plant species, p_i. Expected utilisation, p_{io}, corresponded to the relative availability of that plant species. Being a pair-wise comparisons, if the expected proportion of usage does not lie within the confidence interval of p_i, one may conclude that expected and actual utilisation are significantly different (Byers *et al.* 1984). Woody plant species whose confidence intervals were less or greater than expected were, respectively, judged as neglected or preferred. Where there was no significant difference between actual and expected utilisation, the species was treated as neutrally selected. Both 90 % and 95 % confidence intervals were constructed, but were considered accurate only when np_i and $n(1 - p_i)$ were both ≥ 5 (Alldredge & Ratti 1986). Byers *et al.* (1984) point out that a chi-square or log-likelihood test does not have to be conducted in order for the Bonferroni probability statements to hold.

Use of the Bonferroni method assumes that availabilities are known constants, i.e., measured without error, not estimated quantities (Thomas & Taylor 1990; Alldredge & Ratti 1992). However, available browse is always estimated and can never be treated as known. The methods used for assessing availability are considered as good an estimate as possible.

Preferences of the guild of browsers studied were also determined using Ivlev's forage ratio (1961 in Alldredge & Ratti 1986). For each browser studied, the forage ratio of a woody plant species was calculated as the proportion of a species eaten divided by the proportion of that species available. Plant species that yielded a forage ratio greater than 1.0 were regarded as positively selected (preferred or favoured). Those that yielded a ratio less than 1.0 were assumed to be selected against (avoided or neglected). Only forage ratios calculated for species which were encountered frequently, i.e., ≥ 5 on an annual basis, were considered accurate.

The relation between utilisation of a species and its forage ratio (FR) value was examined using linear correlations. Utilisation refers to the average time spent feeding on a species by eland, kudu and giraffe and the average number of twigs browsed per species by black rhinoceros. Correlations were performed separately for each season and for all seasons combined (annual) for each browser species, but only for woody plant species encountered frequently (≥ 5 on an annual basis). Linear correlations were selected based on visual examination of relevant scatter plots. All zero pairs were excluded from the analyses.

Feeding Height Preferences

The frequency of each height class available to each browser was determined. The feeding height classes treated as available depended on the maximum height reach of the animal under consideration. Feeding height preferences were estimated using the forage ratio method, as described above, under the same conditions. Here the emphasis was on which feeding height classes the relevant animal preferred, irrespective of woody plant species.

RESOURCE PARTITIONING

Resource partitioning was examined by comparing preferences for woody plant species of two animal species. Similarity (S_{jk}) between resource use patterns of browser types j and k were calculated by:

$$S_{jk} = \frac{\Sigma a_{ij}\ a_{ik}}{\sqrt{\Sigma a_{ij}^2\ \Sigma a_{ik}^2}}$$

where a_{ij} and a_{ik} are the preferences of the i-th resource utilised by the j-th and k-th species, respectively (Lawlor 1980). Preferences (a_{ij} and a_{ik}) were defined as forage ratios.

Similarities in preference, based on diet composition and feeding height classes, were estimated for each combination of browser pairs for each season and all seasons combined. Using these results, total dietary resource partitioning was estimated by multiplying the two separate measures ("product α" May 1975). As with overlap indices, statistical testing of these measures is meaningless.

RESULTS

PHENOLOGY OF AVAILABLE WOODY PLANT SPECIES

The phenology of woody plant species available to each browser during each season is presented. Fruit and flowers of woody plants available to kudu, eland and giraffe are presented briefly. The availability of fruit and flowers was not estimated for black rhinoceros, because their use could not be assessed owing to the method used. The availability of leaves of all plant species are depicted separately for each animal species, but only the three most commonly utilised species and at least one broadleaved species are illustrated.

Fruit and Flowers

None of the individual plants available to eland carried flowers during any of the seasons. Although scarce, flowers of individual plants available to kudu and giraffe were, on average, more prominent during early than late summer, and none where available during winter. Only 6.6 % of *Acacia nilotica* plants available to kudu had flowers during late summer compared with 18.0 % during early summer. Individual plants of *Acacia caffra* available to kudu carried flowers only during early summer (5.5 %), while 1.4 % of plants of *Acacia karroo* had flowers in late summer but not in early summer. Although only 2.1 % and 1.8 % of individuals of *A. karroo* available to giraffe carried flowers during early and late summer, respectively, 20.5 % of plants of *A. caffra* had flowers during early summer compared with none during late summer. Individual plants of *A. nilotica* available to giraffe carried flowers only during late summer (6.7 %).

Fruit of woody plant species were available to kudu, eland and giraffe during all three seasons, but to varying degrees. Trees available to kudu carried, on average, more fruit during late summer and winter than early summer. Only 16.7 % of individuals of *Acacia sieberiana* bore fruit during early summer compared with 33.3 % during late summer and 61.5 % during winter. Similarly, of the *A. nilotica* plants available to kudu, 19.8 % and 21.3 % carried fruit during late and early summer, respectively, compared with 37.5 % during winter. The number of plants of *Acacia tortilis* which bore fruit was approximately equal during early summer and winter, 21.2 % and 26.2 % respectively, but more during late summer (66.7 %). More plants of *A. nilotica* bore fruit during winter (37.5 %) compared with early (21.2 %) and late summer (26.2 %).

Of the plants available to eland while feeding, only *A. sieberiana* bore fruit. More individuals of *A. sieberiana* carried fruit during early summer (38.7 %) compared with winter (25.0 %), while none bore fruit during late summer.

On average, more trees available to giraffe bore fruit during early summer and winter than late summer. The number of *A. caffra* plants available to giraffe which bore fruit was approximately equal during early summer and winter, 53.8 % and 47.2 % respectively, but less during late summer (9.3 %). More individuals of *A. sieberiana* bore fruit during winter (64.5 %) than early (22.2 %) and late summer (4.5 %). More plants of *A. karroo, A. tortilis* and *Acacia robusta* bore fruit during early summer, 29.1 %, 10.0 % and 22.2 %, respectively, than during late summer (3.1 %, 5.9 % and 9.1 %, respectively) and winter (0 %, 5.9 % and 3.61 %, respectively). The number of plants of *A. nilotica* which bore fruit was approximately equal during late summer (19.7 %) and winter (15.1 %) but less during early summer (10.2 %). The fruit of *Maytenus heterophylla* was available only during early summer, with 30.8 % of individuals bearing fruit.

Leaves

During late summer all individual plants available to kudu (Table 2), eland (Table 3) and black rhinoceros (Table 5) carried leaves. Only 1 % of plants available to giraffe were without leaves during late summer, which included *A. karroo, A. nilotica* and *A. tortilis* (Table 4). Contrary to the definition of late summer, i.e, majority of trees in full leaf, an average of only 31 % of available trees carried at least 75 % foliage during this season. Reasons for this situation are unclear but may be a combined effect of herbivory and early leaf fall. In addition, available plants represent those at each feeding site and do not include all plants within the study site.

Of the plants available to kudu and giraffe during early summer, the bulk carried some leaf material, 89.4 % and 95.7 %, respectively (Tables 2 & 4). With the exception of *Vitex rehmannii*, all species without leaves were of the genus *Acacia*. During early summer, the proportion of leafless individual plants available to eland and black rhinoceros was exceptionally great, 47.6 % and 53.0 %, respectively (Tables 3 & 5). This was primarily owing to the fact that these two browsers frequently fed in recently burnt areas. Plant species without leaves included *A. karroo, A. nilotica, A. sieberiana, Calpurnia aurea* and *Rhus pentheri. Acacia caffra* was the first to flush new leaves in September and, where available, most individuals had some leaf material (Tables 2, 4 & 5).

Slightly more individual plants available to kudu and giraffe did not have leaves during winter (22.8 % and 16.8 %, respectively) compared with early summer (10.6 % and 4.3 %, respectively) (Tables 2 & 4). By comparison, the proportion of individual plants available to black rhinoceros that retained leaves, was greater in winter (67.9 %) than early summer (47.0 %) (Table 5). All *Acacia* species, except *Acacia ataxacantha*, had some leafless individuals while this was also true for numerous broadleaved species. The majority (81.5 %) of plants available to eland did not retain foliage during winter (Tables 3), as a result of leaf fall and burning. Apart from eland, the above indicates the unusual situation of deciduous species still retaining leaves during winter.

Of the plant species available to kudu, only *A. karroo, A. nilotica, C. aurea* and *R.. pentheri* are illustrated (Fig. 6). For all four plant species the number of individuals in each percentage class was relatively even during early summer compared with the other two seasons. During late summer the majority (> 70 %) of the plants of *A. karroo, A. nilotica* and *C. aurea* had more than 75 % of their potential maximum foliage, whereas during winter more than 70 % of individuals of these three species retained less than 26 % of their total leaf material. The majority of the individuals of *Rhus pentheri* clearly had more leaf material available during winter than the other three woody plant species.

Table 2. The proportion of individuals of a woody plant species available to kudu whose foliage was visually rated as a percentage class of the potential maximum that could be borne by an individual plant, as determined for early summer, late summer and winter

EARLY SUMMER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia caffra	18	0.056	0.333	0.056	0.000	0.556
Acacia karroo	197	0.173	0.305	0.081	0.193	0.249
Acacia nilotica	61	0.131	0.311	0.115	0.246	0.197
Acacia robusta	4	0.000	0.000	0.250	0.500	0.250
Acacia sieberiana	18	0.333	0.278	0.056	0.167	0.167
Acacia tortilis	14	0.429	0.286	0.071	0.143	0.071
Buddleja saligna	1	0.000	0.000	0.000	0.000	1.000
Calpurnia aurea	56	0.071	0.304	0.161	0.054	0.411
Coddia rudis	6	0.000	0.167	0.000	0.000	0.833
Diospyros lycioides	9	0.000	0.889	0.111	0.000	0.000
Diospyros whyteana	1	0.000	1.000	0.000	0.000	0.000
Euclea crispa	34	0.000	0.176	0.000	0.059	0.765
Euclea racemosa	1	0.000	0.000	0.000	0.000	1.000
Grewia occidentalis	1	0.000	1.000	0.000	0.000	0.000
Maytenus heterophylla	29	0.000	0.207	0.000	0.310	0.483
Oleo europaea	2	0.000	0.000	0.000	1.000	0.000
Orthosiphon labiatus	1	0.000	0.000	0.000	1.000	0.000
Ozoroa paniculosa	2	0.000	0.500	0.500	0.000	0.000
Premna mooiensis	7	0.000	0.143	0.000	0.000	0.857
Rhus lucida	1	0.000	1.000	0.000	0.000	0.000
Rhus pentheri	43	0.000	0.209	0.186	0.163	0.442
Rhus rehmanniana	11	0.000	0.182	0.545	0.273	0.000
Vepris lanceolata	6	0.000	0.000	0.000	1.000	0.000
Vitex rehmannii	42	0.048	0.310	0.119	0.333	0.190
Ziziphus mucronata	10	0.000	0.100	0.000	0.000	0.900

LATE SUMMER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia ataxacantha	1	0.000	0.000	0.000	0.000	1.000
Acacia caffra	15	0.000	0.000	0.133	0.133	0.733
Acacia karroo	140	0.000	0.036	0.107	0.121	0.736
Acacia nilotica	91	0.000	0.022	0.044	0.099	0.835
Acacia robusta	6	0.000	0.000	0.333	0.167	0.500
Acacia sieberiana	24	0.000	0.000	0.208	0.000	0.792
Acacia tortilis	18	0.000	0.000	0.222	0.000	0.778
Acalypha glabrata	5	0.000	0.000	0.000	0.000	1.000
Berchemia zeyheri	2	0.000	0.000	0.000	0.000	1.000
Brachylaena discolor	1	0.000	0.000	0.000	0.000	1.000
Brachylaena elliptica	3	0.000	0.000	0.000	0.000	1.000
Calpurnia aurea	73	0.000	0.055	0.082	0.055	0.808
Coddia rudis	16	0.000	0.000	0.000	0.063	0.938
Dais cotinifolia	3	0.000	0.222	0.000	0.222	0.556
Dichrostachys cinerea	9	0.000	0.000	0.000	0.000	1.000
Euclea crispa	11	0.000	0.000	0.000	0.091	0.909
Grewia occidentalis	1	0.000	1.000	0.000	0.000	0.000
Jasminum multipartitum	1	0.000	0.000	0.000	0.000	1.000

Table 2 continued

LATE SUMMER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Maytenus heterophylla	14	0.000	0.000	0.071	0.000	0.929
Nuxia congesta	1	0.000	0.000	1.000	0.000	0.000
Oleo europaea	1	0.000	0.000	0.000	0.000	1.000
Premna mooiensis	5	0.000	0.000	0.600	0.400	0.000
Rhus dentata	2	0.000	0.000	0.000	0.000	1.000
Rhus pentheri	8	0.000	0.000	0.000	0.625	0.375
Rhus rehmanniana	7	0.000	0.000	0.000	0.429	0.571
Vepris lanceolata	1	0.000	0.000	0.000	1.000	0.000
Vitellariopsis dispar	2	0.000	0.000	0.000	0.000	1.000
Vitex rehmannii	14	0.000	0.000	0.071	0.286	0.643
Ximenia caffra	2	0.000	0.000	0.000	0.500	0.500
Ziziphus mucronata	1	0.000	0.000	0.000	0.000	1.000

WINTER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia karroo	60	0.267	0.583	0.083	0.033	0.033
Acacia nilotica	48	0.188	0.521	0.188	0.063	0.042
Acacia robusta	5	0.800	0.000	0.000	0.200	0.000
Acacia sieberiana	13	0.538	0.154	0.154	0.154	0.000
Acacia tortilis	42	0.143	0.405	0.190	0.190	0.071
Boscia albitrunca	1	0.000	0.000	0.000	0.000	1.000
Brachylaena discolor	1	0.000	1.000	0.000	0.000	0.000
Brachylaena elliptica	6	0.000	0.333	0.000	0.167	0.500
Buddleja saligna	1	0.000	0.000	0.000	0.000	1.000
Calpurnia aurea	128	0.422	0.555	0.000	0.023	0.000
Canthium mundianum	4	0.000	0.000	0.250	0.000	0.750
Coddia rudis	36	0.278	0.417	0.056	0.139	0.111
Cussonia spicata	1	0.000	1.000	0.000	0.000	0.000
Dais cotinifolia	15	0.867	0.133	0.000	0.000	0.000
Diospyros lycioides	3	0.000	1.000	0.000	0.000	0.000
Euclea crispa	43	0.116	0.070	0.047	0.186	0.581
Grewia occidentalis	7	0.286	0.429	0.286	0.000	0.000
Hippobromus pauciflorus	3	0.000	0.333	0.000	0.333	0.333
Maytenus heterophylla	50	0.000	0.300	0.160	0.260	0.280
Oleo europaea	6	0.000	0.000	0.000	0.000	1.000
Orthosiphon labiatus	18	0.278	0.722	0.000	0.000	0.000
Ozoroa paniculosa	1	0.000	0.000	0.000	0.000	1.000
Premna mooiensis	1	0.000	1.000	0.000	0.000	0.000
Rhus pentheri	49	0.000	0.286	0.224	0.163	0.327
Rhus rehmanniana	5	0.000	0.600	0.000	0.400	0.000
Schotia brachypetala	2	0.000	0.000	0.000	0.500	0.500
Spirostachys africana	1	0.000	0.000	0.000	1.000	0.000
Tarchonanthus camphoratus	6	0.000	0.167	0.000	0.333	0.500
Vitellariopsis dispar	1	0.000	1.000	0.000	0.000	0.000
Vitex rehmannii	33	0.121	0.576	0.091	0.030	0.182
Ximenia caffra	3	0.000	0.667	0.333	0.000	0.000
Ziziphus mucronata	1	0.000	0.000	1.000	0.000	0.000

Table 3. The proportion of individuals of a woody plant species available to eland whose foliage was visually rated as a percentage class of the potential maximum that could be borne by an individual plant, as determined for early summer, late summer and winter

EARLY SUMMER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia caffra	1	0.000	0.000	0.000	1.000	0.000
Acacia karroo	83	0.530	0.301	0.012	0.072	0.084
Acacia nilotica	24	0.375	0.167	0.083	0.125	0.250
Acacia sieberiana	31	0.548	0.323	0.032	0.065	0.032
Acacia tortilis	2	0.000	0.000	0.500	0.500	0.000
Calpurnia aurea	1	0.000	0.000	1.000	0.000	0.000
Euclea crispa	3	0.000	1.000	0.000	0.000	0.000
Rhus pentheri	2	0.000	0.000	1.000	0.000	0.000

LATE SUMMER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia karroo	8	0.000	0.000	0.125	0.250	0.625
Acacia nilotica	5	0.000	0.000	0.200	0.000	0.800
Acacia sieberiana	2	0.000	0.000	0.000	0.000	1.000
Acacia tortilis	2	0.000	0.000	0.000	0.500	0.500
Calpurnia aurea	2	0.000	0.000	0.000	0.000	1.000

WINTER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia karroo	60	0.833	0.067	0.050	0.033	0.017
Acacia sieberiana	4	0.750	0.250	0.000	0.000	0.000
Maytenus heterophylla	1	0.000	0.000	0.000	1.000	0.000

Table 4. The proportion of individuals of a woody plant species available to giraffe whose foliage was visually rated as a percentage class of the potential maximum that could be borne by an individual plant, as determined for early summer, late summer and winter

EARLY SUMMER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia caffra	39	0.000	0.564	0.128	0.103	0.205
Acacia karroo	289	0.038	0.232	0.239	0.163	0.329
Acacia nilotica	108	0.111	0.296	0.204	0.093	0.296
Acacia robusta	9	0.000	0.000	0.222	0.000	0.778
Acacia sieberiana	42	0.000	0.095	0.262	0.143	0.500
Acacia tortilis	30	0.067	0.333	0.133	0.133	0.333
Calpurnia aurea	6	0.000	1.000	0.000	0.000	0.000
Coddia rudis	3	0.000	0.000	0.000	0.667	0.333
Combretum erythrophyllum	2	0.000	0.000	0.000	0.000	1.000
Cussonia spicata	3	0.000	0.000	0.000	0.667	0.333
Diospyros lycioides	1	0.000	1.000	0.000	0.000	0.000
Euclea crispa	11	0.000	0.182	0.000	0.364	0.455
Euclea racemosa	2	0.000	0.000	0.000	0.000	1.000
Maytenus heterophylla	13	0.000	0.000	0.385	0.077	0.538
Premna mooiensis	3	0.000	0.000	0.333	0.333	0.333
Rhus pentheri	8	0.000	0.250	0.000	0.500	0.250
Rhus rehmanniana	6	0.000	0.500	0.000	0.167	0.333
Schotia brachypetala	1	0.000	0.000	0.000	0.000	1.000
Tarchonanthus camphoratus	2	0.000	0.000	0.000	1.000	0.000
Vitex rehmannii	1	0.000	1.000	0.000	0.000	0.000
Ziziphus mucronata	3	0.000	0.333	0.000	0.000	0.667

LATE SUMMER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia caffra	54	0.000	0.056	0.056	0.130	0.759
Acacia karroo	390	0.005	0.067	0.267	0.221	0.441
Acacia nilotica	239	0.021	0.054	0.096	0.255	0.573
Acacia robusta	11	0.000	0.000	0.000	0.091	0.909
Acacia sieberiana	67	0.000	0.015	0.060	0.134	0.791
Acacia tortilis	56	0.036	0.232	0.161	0.286	0.286
Calpurnia aurea	5	0.000	0.000	0.000	0.200	0.800
Euclea crispa	3	0.000	0.000	0.000	0.000	1.000
Euclea racemosa	1	0.000	0.000	0.000	0.000	1.000
Maytenus heterophylla	21	0.000	0.143	0.190	0.048	0.619
Premna mooiensis	2	0.000	0.000	0.000	0.500	0.500
Rhus pentheri	5	0.000	0.000	0.000	0.000	1.000
Rhus rehmanniana	15	0.000	0.000	0.000	0.133	0.867
Vitex rehmannii	8	0.000	0.000	0.000	0.250	0.750
Ziziphus mucronata	2	0.000	0.000	0.000	0.500	0.500

Table 4 continued

WINTER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia caffra	53	0.094	0.566	0.094	0.226	0.019
Acacia karroo	276	0.225	0.409	0.152	0.185	0.029
Acacia nilotica	185	0.135	0.535	0.081	0.184	0.065
Acacia robusta	28	0.464	0.429	0.107	0.000	0.000
Acacia sieberiana	31	0.194	0.323	0.226	0.194	0.065
Acacia tortilis	34	0.059	0.618	0.265	0.059	0.000
Brachylaena elliptica	1	0.000	0.000	0.000	0.000	1.000
Calpurnia aurea	12	0.667	0.333	0.000	0.000	0.000
Cussonia spicata	5	0.000	0.000	0.000	0.000	1.000
Dalbergia obovata	1	0.000	1.000	0.000	0.000	0.000
Dichrostachys cinerea	3	0.000	0.667	0.333	0.000	0.000
Euclea crispa	35	0.000	0.000	0.029	0.086	0.886
Euclea racemosa	9	0.000	0.000	0.000	0.222	0.778
Grewia occidentalis	1	0.000	1.000	0.000	0.000	0.000
Maytenus heterophylla	23	0.000	0.130	0.174	0.217	0.478
Ozoroa paniculosa	6	0.167	0.000	0.000	0.333	0.500
Rhus pentheri	21	0.000	0.143	0.238	0.238	0.381
Rhus rehmanniana	13	0.000	0.615	0.077	0.077	0.231
Tarchonanthus camphoratus	1	0.000	0.000	0.000	0.000	1.000
Vitex rehmannii	20	0.300	0.650	0.050	0.000	0.000
Ziziphus mucronata	5	0.000	1.000	0.000	0.000	0.000

Table 5. The proportion of individuals of a woody plant species available to black rhinoceros whose foliage was visually rated as a percentage class of the potential maximum that could be borne by an individual plant, as determined for early summer, late summer and winter

EARLY SUMMER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia caffra	3	0.000	0.000	0.000	0.000	1.000
Acacia karroo	209	0.569	0.268	0.038	0.029	0.096
Acacia nilotica	133	0.481	0.226	0.023	0.053	0.218
Acacia robusta	7	0.143	0.143	0.429	0.143	0.143
Acacia sieberiana	5	1.000	0.000	0.000	0.000	0.000
Acacia tortilis	117	0.718	0.197	0.009	0.051	0.026
Brachylaena elliptica	3	0.333	0.667	0.000	0.000	0.000
Calpurnia aurea	8	0.250	0.375	0.000	0.000	0.375
Dais cotinifolia	2	0.500	0.000	0.000	0.000	0.500
Dichrostachys cinerea	4	0.750	0.250	0.000	0.000	0.000
Diospyros lycioides	2	0.000	0.000	0.000	1.000	0.000
Euclea crispa	4	0.000	0.250	0.500	0.000	0.250
Maytenus heterophylla	7	0.000	0.429	0.286	0.143	0.143
Oleo europaea	1	0.000	0.000	0.000	0.000	1.000
Rhus lucida	1	0.000	1.000	0.000	0.000	0.000
Rhus pentheri	11	0.182	0.636	0.000	0.000	0.182
Rhus rehmanniana	1	0.000	0.000	1.000	0.000	0.000
Vitex rehmannii	9	0.000	0.111	0.333	0.333	0.222
Ziziphus mucronata	2	0.000	0.000	0.000	0.500	0.500

LATE SUMMER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia caffra	27	0.000	0.000	0.148	0.000	0.852
Acacia karroo	169	0.000	0.018	0.006	0.059	0.917
Acacia nilotica	64	0.000	0.031	0.063	0.109	0.797
Acacia robusta	12	0.000	0.000	0.000	0.083	0.917
Acacia sieberiana	6	0.000	0.000	0.000	0.000	1.000
Acacia tortilis	167	0.000	0.012	0.018	0.078	0.892
Brachylaena elliptica	5	0.000	0.000	0.200	0.400	0.400
Calpurnia aurea	4	0.000	0.000	0.000	0.000	1.000
Coddia rudis	23	0.000	0.000	0.000	0.000	1.000
Dichrostachys cinerea	5	0.000	0.000	0.200	0.400	0.400
Euclea crispa	1	0.000	0.000	0.000	0.000	1.000
Maytenus heterophylla	24	0.000	0.042	0.125	0.083	0.750
Oleo europaea	1	0.000	0.000	0.000	0.000	1.000
Premna mooiensis	3	0.000	0.000	0.667	0.000	0.333
Rhus pentheri	26	0.000	0.000	0.077	0.231	0.692
Tarchonanthus camphoratus	2	0.000	0.000	0.000	0.500	0.500
Vitex rehmannii	15	0.000	0.000	0.000	0.000	1.000
Ziziphus mucronata	3	0.000	0.000	0.000	0.000	1.000

Table 5 continued

WINTER

Plant species	Sample size	Percentage class				
		0	1 - 25	26 - 50	51 - 75	75 - 100
Acacia ataxacantha	3	0.000	1.000	0.000	0.000	0.000
Acacia caffra	17	0.294	0.529	0.059	0.118	0.000
Acacia karroo	368	0.386	0.443	0.139	0.022	0.011
Acacia nilotica	109	0.431	0.523	0.037	0.000	0.009
Acacia robusta	13	0.154	0.385	0.462	0.000	0.000
Acacia sieberiana	1	1.000	0.000	0.000	0.000	0.000
Acacia tortilis	111	0.288	0.387	0.135	0.081	0.108
Brachylaena elliptica	7	0.000	0.571	0.429	0.000	0.000
Brachylaena ilicifolia	3	0.000	1.000	0.000	0.000	0.000
Calpurnia aurea	58	0.603	0.362	0.034	0.000	0.000
Coddia rudis	124	0.476	0.460	0.032	0.032	0.000
Dais cotinifolia	19	1.000	0.000	0.000	0.000	0.000
Dichrostachys cinerea	14	0.357	0.571	0.000	0.071	0.000
Diospyros whyteana	3	0.000	1.000	0.000	0.000	0.000
Euclea crispa	34	0.059	0.088	0.000	0.265	0.588
Euclea racemosa	5	0.000	0.000	0.000	0.000	1.000
Grewia occidentalis	14	0.357	0.571	0.071	0.000	0.000
Hippobromus pauciflorus	4	0.000	1.000	0.000	0.000	0.000
Maytenus heterophylla	44	0.023	0.568	0.068	0.182	0.159
Oleo europaea	2	0.000	0.000	0.000	0.000	1.000
Orthosiphon labiatus	5	0.000	0.800	0.000	0.200	0.000
Ozoroa paniculosa	1	0.000	1.000	0.000	0.000	0.000
Rhus pentheri	108	0.046	0.648	0.194	0.074	0.037
Rhus rehmanniana	2	0.000	1.000	0.000	0.000	0.000
Schotia brachypetala	1	0.000	1.000	0.000	0.000	0.000
Scolopia zeyheri	4	0.500	0.000	0.000	0.000	0.500
Tarchonanthus camphoratus	6	0.167	0.833	0.000	0.000	0.000
Vitex rehmannii	50	0.000	0.920	0.080	0.000	0.000
Ziziphus mucronata	8	0.375	0.500	0.000	0.125	0.000

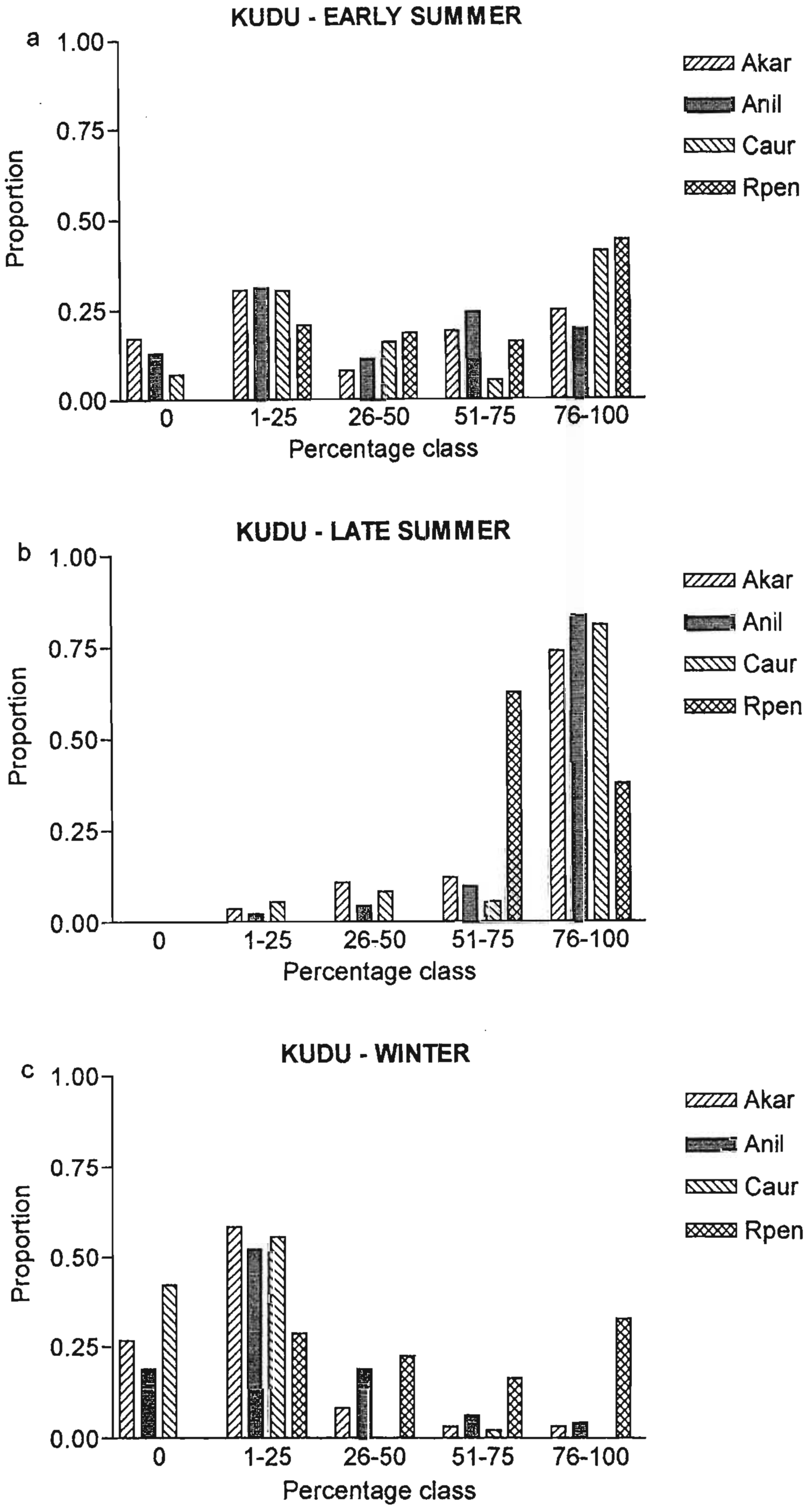


Figure 6. The proportion of individuals of *Acacia karroo* (Akar), *Acacia nilotica* (Anil), *Calpurnia aurea* (Caur) and *Rhus pentheri* (Rpen) available to kudu whose foliage was visually estimated as a percentage class of the potential maximum that could be borne by an individual plant, as determined for (a) early summer, (b) late summer and (c) winter.

The seasonal variation of leaves of *A. karroo*, *A. nilotica*, *A. sieberiana* and *C. aurea* available to eland indicates (Fig. 7) that during early summer, the two individuals of *C. aurea* had between 26% and 50 % of their potential maximum foliage, while for *A. karroo*, *A. nilotica* and *A. sieberiana* the number of plants in each percentage class was relatively even. At least 60 % of plants of each species had more than 75 % of total leaf present during late summer, whereas during winter the majority of plants of *A. karroo* and *A. sieberiana* retained no leaf material.

Of the plant species available to giraffe, only *A. karroo*, *A. nilotica*, *A. sieberiana* and *M. heterophylla* are illustrated (Fig. 8). All plants of *M. heterophylla* and the bulk of individuals of *A. karroo*, *A. nilotica* and *A. sieberiana* had more than 25 % of their potential maximum foliage during early summer. During late summer, 79 % and 62 % of *A. sieberiana* and *M. heterophylla* plants, respectively, had more than 75 % of total leaf material. The majority of *A. karroo* (63 %) and *A. nilotica* (80 %), during this season, retained at least 50 % of their maximum potential foliage. The number of *A. karroo*, *A. nilotica* and *A. sieberiana* plants without leaves during winter was greater than the other two seasons, yet at least a third of the plants retained at least 25 % of total foliage. During winter, all plants of *M. heterophylla* carried leaf, most of which had more than 75 % of total leaf material.

The proportion of leafless individual plants of *A. karroo*, *A. nilotica* and *A. tortilis* available to black rhinoceros during early summer was great (Fig. 9), mainly as a result of the plants being burnt. Nevertheless, numerous plants of these species still retained more than 50 % of total leaf material. During late summer the majority of *A. karroo*, *A. nilotica* and *A. tortilis* plants, and all individuals of *Coddia rudis* had at least 75 % of total leaf present. The bulk of plants of these four species retained less than 25 % of total leaf material during winter.

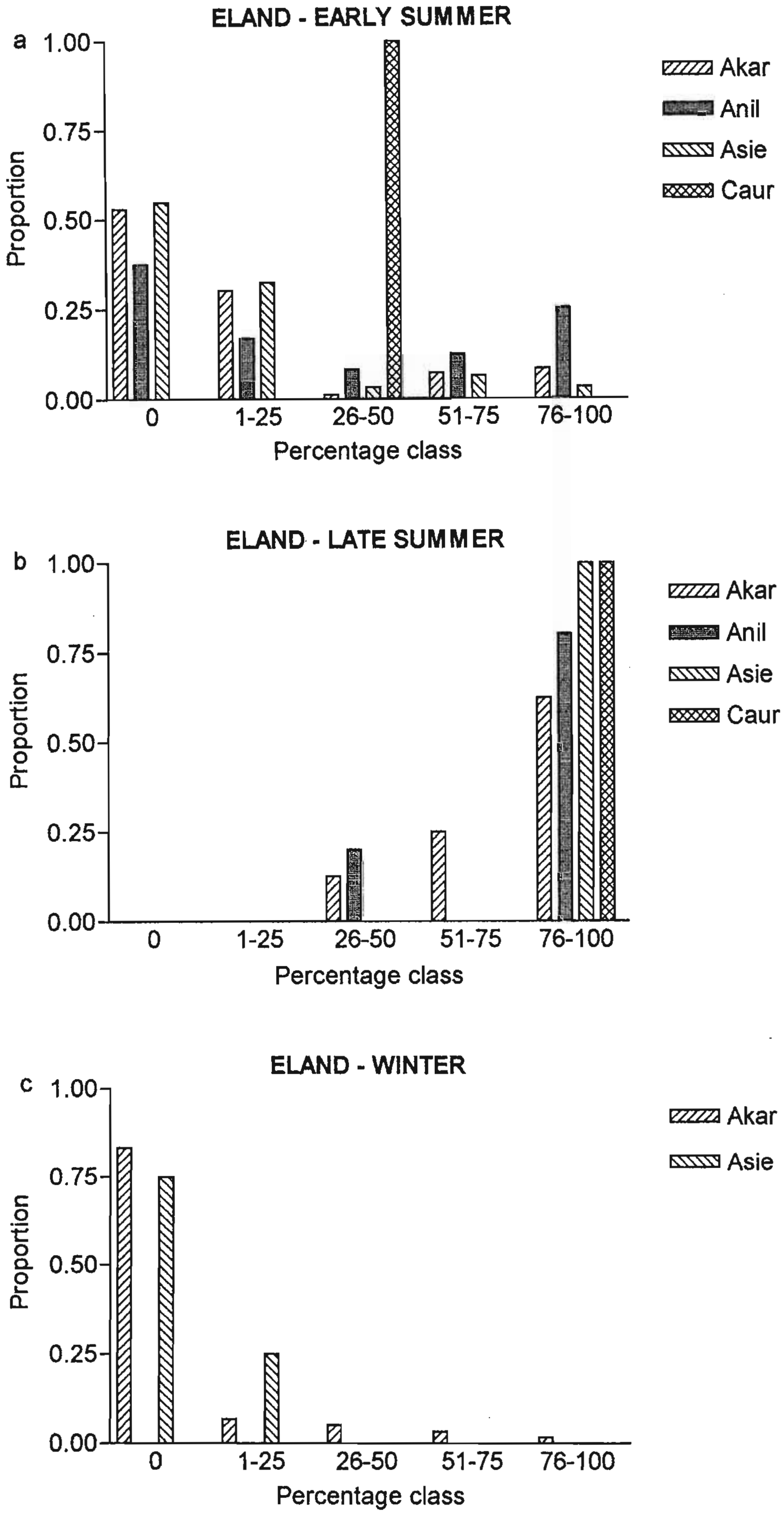


Figure 7. The proportion of individuals of *Acacia karroo* (Akar), *Acacia nilotica* (Anil), *Acacia sieberiana* (Asie) and *Calpurnia aurea* (Caur) available to eland whose foliage was visually estimated as a percentage class of the potential maximum that could be borne by an individual plant, as determined for (a) early summer, (b) late summer and (c) winter.

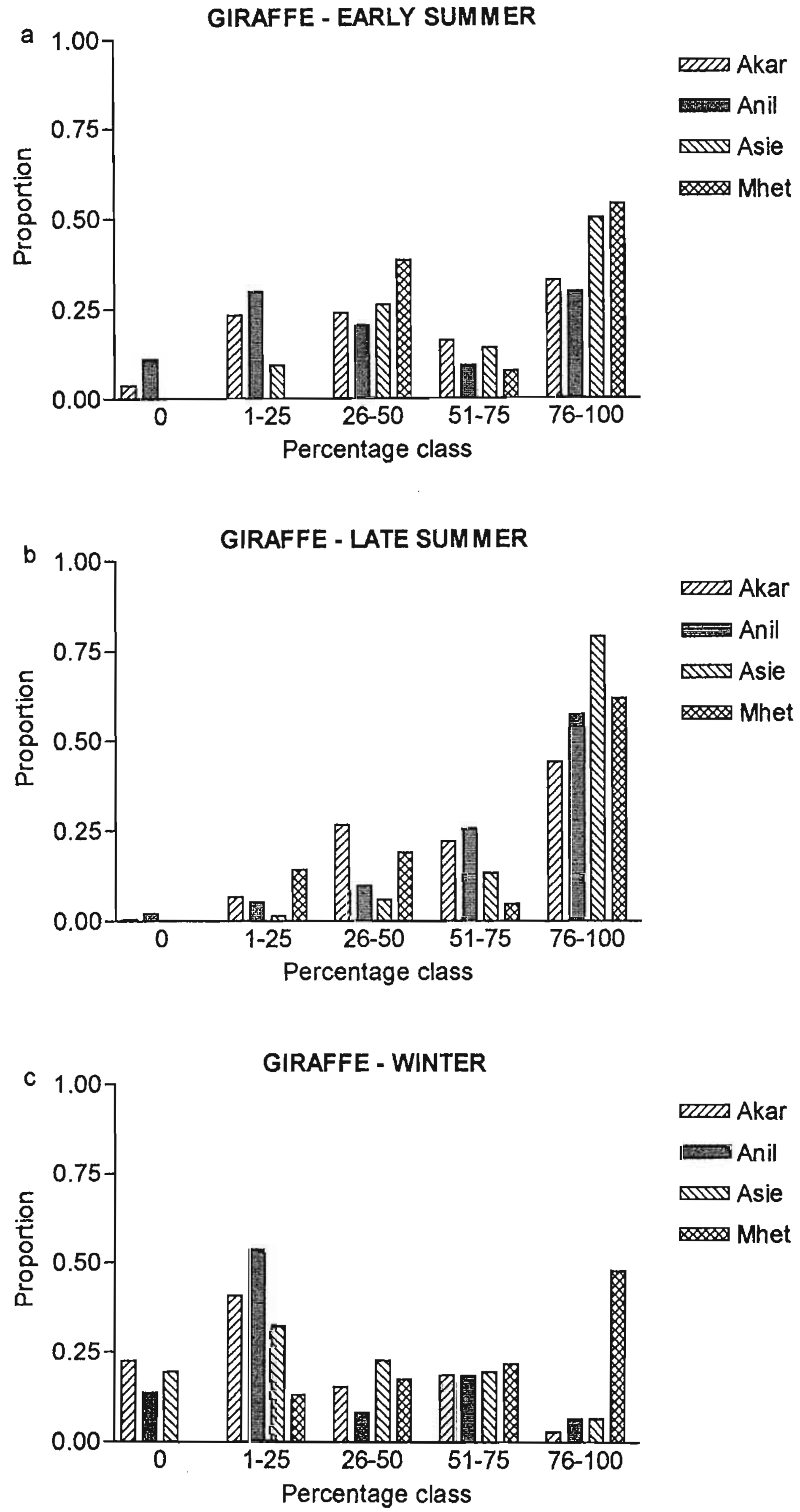


Figure 8. The proportion of individuals of *Acacia karroo* (Akar), *Acacia nilotica* (Anil), *Acacia sieberiana* (Asie) and *Maytenus heterophylla* (Mhet) available to giraffe whose foliage was visually estimated as a percentage class of the potential maximum that could be borne by an individual plant, as determined for (a) early summer, (b) late summer and (c) winter.

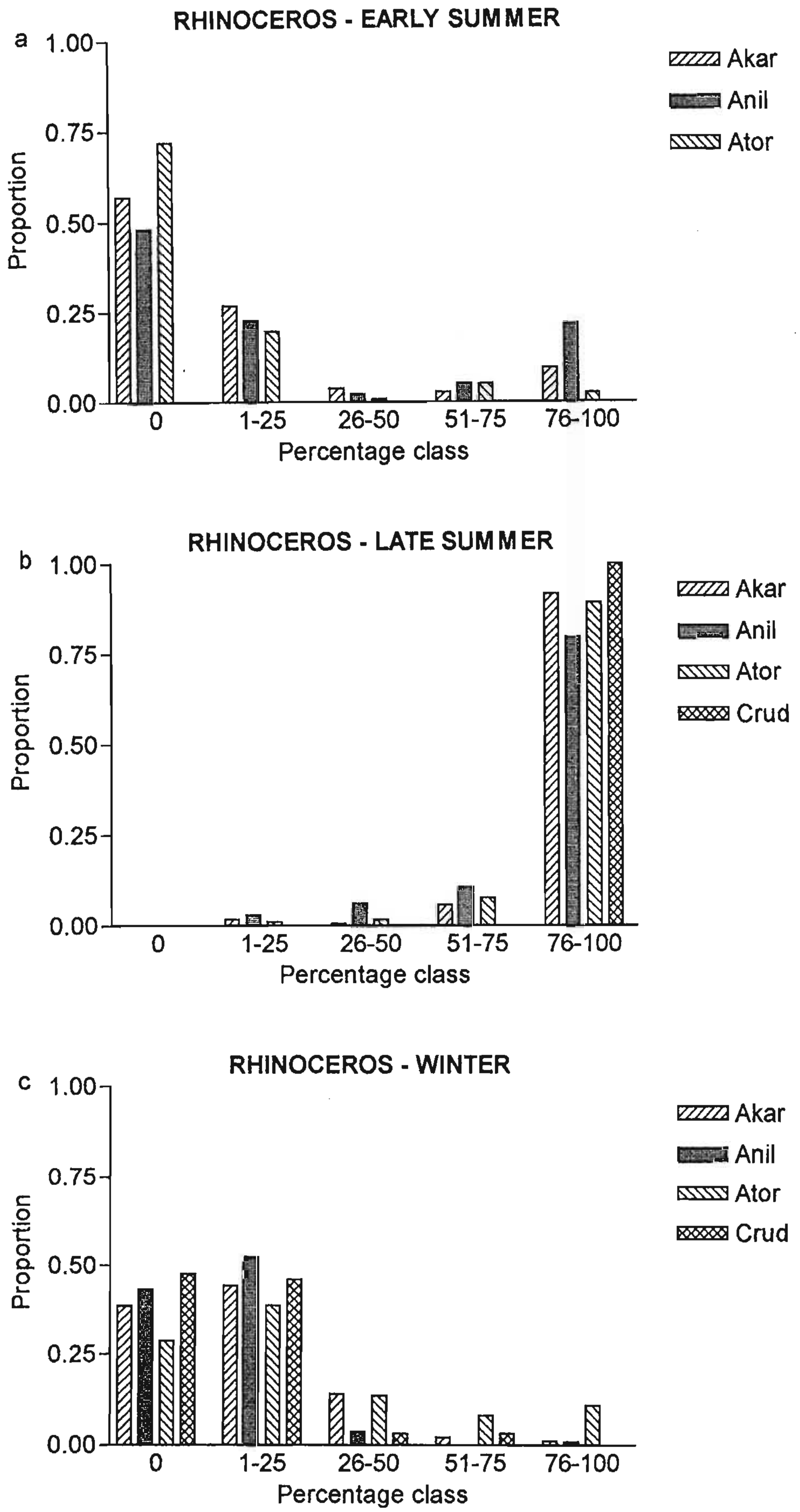


Figure 9. The proportion of individuals of *Acacia karroo* (Akar), *Acacia nilotica* (Anil), *Acacia tortilis* (Atort) and *Coddia rudis* (Crud) available to black rhinoceros whose foliage was visually estimated as a percentage class of the potential maximum that could be borne by an individual plant, as determined for (a) early summer, (b) late summer and (c) winter.

DIET COMPOSITION

Dietary assessment data were collected over 825 hours with a total of 4 360 km driven. Black rhinoceros data were collected from 115 transects. The results of diet composition are presented, firstly in terms of forage types, for eland, kudu and giraffe, and secondly, based on woody plant species alone, for all the browsers studied. Dietary findings of eland are based on limited feeding events (132) and must therefore be regarded with caution.

Forage Types

The two indices of forage type use, frequency (i.e., total number of feeding events) and feeding time, were significantly positively correlated for the kudu data for each season and all seasons combined (Table 6). However, significant correlations were not obtained for giraffe because they utilised a limited number of forage types (Table 7). Correlations were also not significant for the eland data (Table 6). Eland utilised grasses, forbs, pods and flowers relatively frequently (Table 7) and in each case this was regarded as a single feeding event, irrespective of the number of plants or items utilised. By comparison, feeding time represented the time over which all individual plants or items were eaten during a single event. As a consequence, the proportion of time spent feeding was greater than the proportion of feeding events on these forage types. It was, therefore, concluded that feeding time would give a more accurate account of the contribution of forage types to the diets than the number of feeding events (frequency). Diet composition was thus expressed in terms of the proportional distribution of feeding time among forage types.

Table 6. Correlation coefficients for the relation between the methods frequency and feeding time used for quantifying the diet composition, in terms of forage types, of kudu, eland and giraffe

Animal species	Values of r^1 and degrees of freedom (df)			
	Annual	Early summer	Late summer	Winter
Kudu	0.9825**	0.9971**	0.9719*	0.9704*
	(3)	(2)	(2)	(2)
Eland	0.0000	0.4000	1.0000	na
	(2)	(2)	(1)	-
Giraffe	1.0000	na	0.8600	na
	(1)	-	(1)	-

[1] Pearson's product-moment correlation coefficient for kudu. Spearman's rank correlation coefficient for eland and giraffe

* $P < 0.05$, ** $P < 0.005$; na - not applicable as too few paired samples

Although the method used for assessing the diet of black rhinoceros precluded recording the use of plant species with fine stems as well as fruit and flowers, black rhinoceros did consume the robust exotic forb *Datura stramonium*. This was the only forb recorded as utilised by black rhinoceros and it contributed less than 2 % to the annual diet.

On an annual basis, kudu clearly allocate less time to feeding on grass than eland (Table 7). Grass seemed more prominent in the diet of kudu during early summer, when they were observed grazing newly sprouted grass, in either burnt or unburnt areas. Utilisation of this forage type by eland was more pronounced during late summer. During winter and early summer, eland fed almost exclusively on newly sprouted burnt grass. Giraffe were never observed utilising grass.

Table 7. Annual and seasonal diet composition of kudu, eland and giraffe measured in terms of percentage allocation of feeding time to each forage type

Animal species	Time period	Forage types				
		Grass	Forbs	Fruit	Flowers	Woody forage
Kudu	Annual (*n* = 835)	2.6	28.0	5.9	0.1	63.4
	Early summer (*n* = 318)	6.2	15.1	7.2	0	71.5
	Late summer (*n* = 228)	0.2	33.8	0	0.6	65.4
	Winter (*n* = 289)	0.7	36.9	8.5	0	53.9
Eland	Annual (*n* = 132)	49.0	8.2	26.6	0	16.2
	Early summer (*n* = 77)	50.4	2.7	35.0	0	11.9
	Late summer (*n* = 26)	72.4	17.8	0	0	9.8
	Winter (*n* = 29)	25.0	20.6	16.8	0	37.6
Giraffe	Annual (*n* = 830)	0	0	2.0	0.4	97.6
	Early summer (*n* = 271)	0	0	0	0	100.0
	Late summer (*n* = 319)	0	0	2.6	1.0	96.4
	Winter (*n* = 240)	0	0	3.0	0	97.0

n - number of feeding events

Kudu were recorded to spend more time feeding on forbs than eland, over the entire seasonal cycle (Table 7). The proportion of forbs in the diets of both animals appeared to increase from early to late summer and reach a peak during winter. During winter, when most deciduous trees had shed their leaves, kudu were seen eating wilted and dried *Peristrophe cernua*, a sprawling perennial forb (Pooley 1998). The majority of forbs eaten by eland were *Helichrysum* species. Forbs were not recorded being utilised by giraffe.

Eland seemed to be more dependent on fruit than kudu and giraffe, on an annual basis (Table 7). Fruit was particularly conspicuous in the diet of eland during early summer. Similar to kudu, this forage type was not recorded as utilised by eland during late summer. Kudu were observed consuming the fruit (pods) of *Acacia nilotica*, *Acacia sieberiana* and *Acacia tortilis*, while eland fed on pods of only *A. sieberiana.* During winter, giraffe utilised *Acacia caffra* and *A. nilotica* pods. Pods of *A. nilotica* and *A. sieberiana* were eaten by giraffe during late summer.

Total annual feeding time allocated to flowers by kudu and giraffe was less than 1 % (Table 7). Both kudu and giraffe utilised this vegetation component only during late summer and fed on flowers of *Acacia karroo*. Eland were not observed utilising this forage type.

Woody plant forage (leaves and / or twigs) comprised a large portion of the annual diet of giraffe, compared with kudu and eland (Table 7). During early summer, when deciduous trees started to flush, giraffe utilised only this forage type. Similarly, kudu allocated more time to woody forage during early summer. The greatest proportion of eland's feeding time devoted to woody forage was during winter. All three browsers were observed consuming branches without leaves during winter and early summer. Over the entire seasonal cycle, bare branches constituted only 1.5 % and 3.8 % of woody forage of the diets of giraffe and kudu, respectively. Eland were recorded to spend the most time feeding on branches without leaves (11.3 % of woody forage) compared with giraffe or kudu.

The prediction that coexisting species utilise different proportions of grass and browse was generally met. Grass constituted a large percentage of the diet of eland, compared with kudu and giraffe. Although the diets of giraffe and kudu appeared similar, in terms of the proportion of browse, giraffe were never observed utilising grass or forbs.

Woody Plant Species

The two indices of woody species use, frequency and feeding time, were significantly positively correlated for each season and all seasons combined (annual) for kudu and giraffe (Table 8). There were no significant linear correlations for the eland data owing to the unsatisfactorily small paired samples ($n = 4$). Only two woody plant species were utilised by eland during winter and, therefore, no correlation could be performed. The three methods used for assessing the diet of black rhinoceros (frequency, number of twigs browsed and standard browse volumes) were significantly positively correlated with each other for each season and all seasons combined.

Table 8. Correlation coefficients for the relation between the various methods used for quantifying the diet composition, in terms of woody plant species, of kudu, eland, giraffe and black rhinoceros

Animal species	Values of r^1 and degrees of freedom (df)			
	Annual	Early summer	Late summer	Winter
Kudu[2]	0.9940 ***	0.9789 ***	0.9799 ***	0.9378 ***
	(39)	(16)	(21)	(26)
Eland[2]	0.8000	0.8000	0.7716	na
	(2)	(2)	(2)	-
Giraffe[2]	0.9773 ***	0.9883 ***	0.9511 ***	0.9480 ***
	(18)	(14)	(10)	(13)
Black rhinoceros				
frequency vs twigs	0.9801 ***	0.9798 ***	0.9845 ***	0.9623 ***
	(26)	(13)	(13)	(22)
frequency vs SBV	0.9779 ***	0.9829 ***	0.9964 ***	0.9078 ***
SBV vs twigs	0.9829 ***	0.9763 ***	0.9870 ***	0.9584 ***

[1] Pearson's product-moment correlation coefficient for kudu, giraffe and black rhinoceros. Spearman's rank correlation coefficient for eland

[2] Correlations for the methods frequency and feeding time

*** P < 0.0001; na - not applicable as too few paired samples

On account of the indices of use being significantly correlated in all but three instances, it was concluded that the frequency data for each browser would be employed to describe diet composition, based on the utilisation of woody plant species. Diet composition was thus expressed in terms of the proportional distribution of the number of plants per woody plant species utilised by each browser. Discrepancies among methods were identified and those noted for black rhinoceros were compared with only the twig count method.

Proportions of microphyllous and broadleaved plants in the diets were dependent on animal species during early summer ($G = 140.549$, $df = 3$, $P < 0.001$), late summer ($G = 75.581$, $df = 3$, $P < 0.001$), winter ($\chi^2 = 205.546$, $df = 3$, $P < 0.001$) and all seasons combined ($G = 359.358$, $df = 3$, $P < 0.001$). In other words, diet composition, in terms of the proportions of broadleaved and microphyllous plants, differed among the coexisting browsers for each season and all seasons combined. During early summer and winter, kudu utilised microphyllous plants to a lesser degree than the other browsers, while this was true for eland during late summer (Table 9).

Table 9. Annual and seasonal percentages of microphyllous plants in the diets of kudu, eland, giraffe and black rhinoceros

Animal species	Time period			
	Annual	Early summer	Late summer	Winter
Kudu	54.1	62.7*	69.9	28.7*
Black rhinoceros	76.7	95.2	85.8	59.9
Giraffe*	94.0	91.5	96.9	92.9
Eland*	95.5	97.7	60.0	100.0

* *Acacia* species only

The proportions of microphyllous and broadleaved plants in the diet were dependent on seasons for kudu ($G = 80.093$, $df = 2$, $P < 0.001$), black rhinoceros ($G = 186.954$, $df = 2$, $P < 0.001$), giraffe ($G = 8.697$, $df = 2$, $0.010 < P < 0.025$) and eland ($\chi^2 = 16.416$, $df = 2$, $P < 0.001$). There was a distinct shift in the diets of kudu and black rhinoceros from predominantly microphyllous plants during early and late summer to broadleaved plant species during winter (Table 9). Giraffe utilised more broadleaved species during winter and early summer than late summer, while eland utilised less microphyllous woody plants during late summer than early summer and winter.

Kudu

Over the entire seasonal cycle, kudu utilised a wide variety of woody plant species (Fig. 10a). These species were utilised to varying degrees, as indicated by a goodness-of-fit test ($G = 1524.056$, $df = 40$, $P < 0.001$) and 95 % Bonferroni confidence intervals. Broadleaved plants were relatively common in the annual diet of kudu. Although *Acacia karroo* (26.2 %) appeared to be the most utilised species it did not differ significantly from *Calpurnia aurea* (16.9 %). *Calpurnia aurea* was utilised more often ($P < 0.05$) than the other species in the diet, except *Acacia nilotica* (14.5 %). Utilisation of *Rhus pentheri* (5.5 %), *Acacia sieberiana* (4.6 %), *Maytenus heterophylla* (4.4 %), *Vitex rehmannii* (4.3 %), *Acacia tortilis* (3.8 %), *Acacia caffra* (3.3 %), *Rhus rehmanniana* (1.8 %), *Coddia rudis* (1.5 %), *Dais cotinifolia* (1.5 %), *Acacia robusta* (1.4 %), *Euclea crispa* (1.2 %) and *Premna mooiensis* (1.1 %) was not different ($P > 0.05$). However, *P. mooiensis* was utilised significantly less than *R. pentheri*. The remaining 25 species each contributed less than 1 % to the annual diet of kudu and Bonferroni confidence intervals were not considered accurate for these species. There was little discrepancy between the two methods used for quantifying the annual diet of kudu (Fig. 11a).

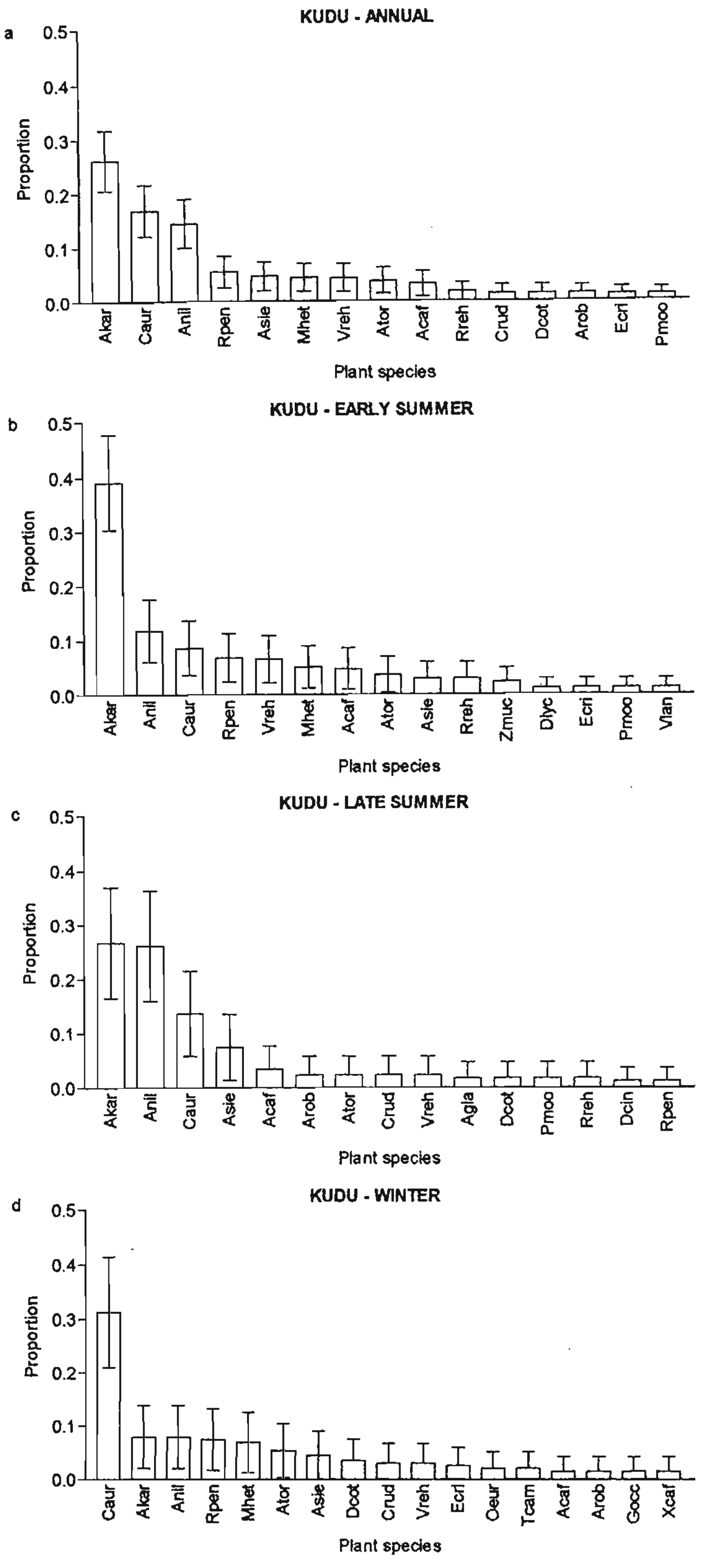


Figure 10. Relative frequency of woody plant species utilised (and 95 % Bonferroni confidence intervals) by kudu for (a) whole year, (b) early summer, (c) late summer and (d) winter. Species contributing less than 1 % to the diet are not included. Key to species: Acaf = *Acacia caffra*, Akar = *Acacia karroo*, Anil = *Acacia nilotica*, Arob = *Acacia robusta*, Asie = *Acacia sieberiana*, Ator = *Acacia tortilis*, Agla = *Acalypha glabrata*, Caur = *Calpurnia aurea*, Crod = *Coddia rudis*, Dcin = *Dichrostachys cinerea*, Dcot = *Dais cotinifolia*, Dlyc = *Diospyros lycioides*, Ecri = *Euclea crispa*, Gocc = *Grewia occidentalis*, Mhet = *Maytenus heterophylla*, Oeur = *Olea europaea*, Pmoo = *Premna mooiensis*, Rpen = *Rhus petheri*, Rreh = *Rhus rehmanniana*, Tcam = *Tarchonanthus camphoratus*, Vlan = *Vepris lanceolata*, Vreh = *Vitex rehmannii*, Xcaf = *Ximenia caffra*, Zmuc = *Ziziphus mucronata*.

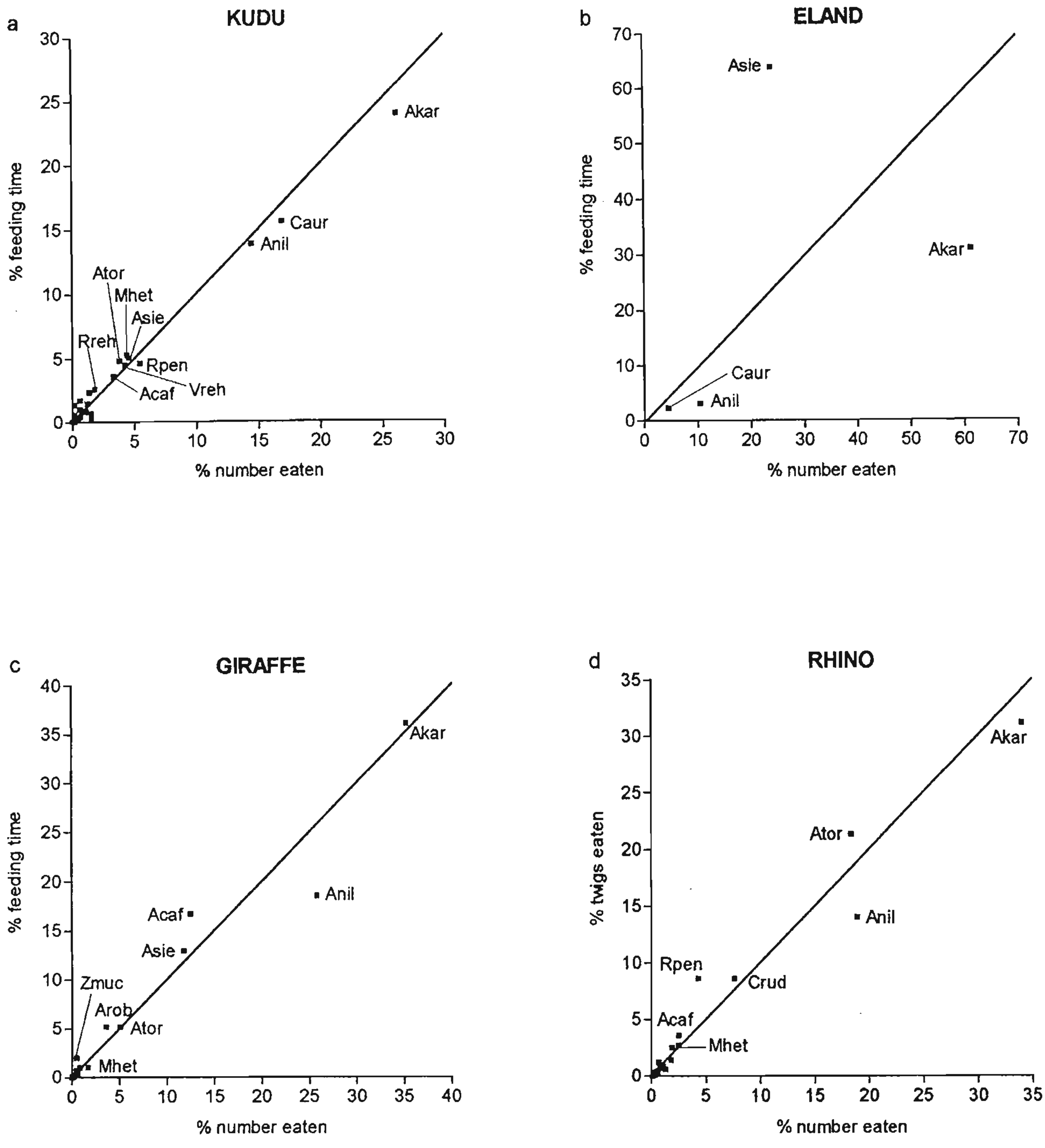


Figure 11. Comparison between relative contributions of various woody plant species to the annual diets of (a) kudu, (b) eland,(c) giraffe and (d) black rhinoceros, in terms of feeding time or number of twigs browsed, and frequency of utilisation. The solid line indicates a correlation of 1.0. Key to species: Acaf = *Acacia caffra*, Akar = *Acacia karroo*, Anil = *Acacia nilotica*, Arob = *Acacia robusta*, Asie = *Acacia sieberiana*, Ator = *Acacia tortilis*, Caur = *Calpurnia aurea*, Crod = *Coddia rudis*, Mhet = *Maytenus heterophylla*, Rpen = *Rhus petheri*, Rreh = *Rhus rehmanniana*, Zmuc = *Ziziphus mucronata*.

During early summer, woody plant species were not equally utilised by kudu (G = 399.172, df = 17, P < 0.001) (Fig. 10b) and Bonferroni confidence intervals (95 %) revealed that *A. karroo* (39.1 %) was the principal species in the early summer diet. There were no differences (P > 0.05) in utilisation of *A. nilotica* (11.8 %), *C. aurea* (8.6 %), *R. pentheri* (6.8 %), *V. rehmannii* (6.5 %), *M. heterophylla* (5.0 %), *A. caffra* (4.7 %) and *A. tortilis* (3.6 %). However, *R. rehmanniana* (2.9 %), *A. sieberiana* (2.9 %) and *Ziziphus mucronata* (2.2 %) were utilised significantly less than only *A. karroo* and *A. nilotica.* The contribution of each remaining species was less than 2 % and confidence intervals were not judged as accurate for these species. The scatter plot of the early summer data illustrated that kudu spent less time feeding on *A. nilotica* and *C. aurea* and more on *V. rehmannii*, *A. tortilis* and *R. rehmanniana* than expected.

Woody plant species were not equally utilised by kudu during late summer (G = 314.842, df = 22, P < 0.001) (Fig. 10c) as confirmed by 95 % Bonferroni confidence intervals. *Acacia karroo* (26.7 %) and *A. nilotica* (26.1 %) were utilised significantly more often than the remaining species, except *C. aurea* (13.6 %). There were no differences (P > 0.05) in utilisation of *C. aurea*, *A. sieberiana* (7.4 %) and *A. caffra* (3.4 %). Confidence intervals could not be regarded as accurate for the remaining species, which were eaten infrequently (< 3 %). Examination of the relevant scatter plot revealed that kudu spent less time browsing *A. karroo* and more time browsing *C. aurea* than expected.

Utilisation of woody plant species by kudu was not uniform during winter (G = 291.794, df = 27, P < 0.001) (Fig. 10d). Confidence intervals (95 %) indicated that *C. aurea* (31.2 %), regarded as a broadleaved species in this study, was the most utilised. This species was considered important to kudu during this period. *Acacia karroo* (7.9 %), *A. nilotica* (7.9 %), *R. pentheri* (7.4 %), *M. heterophylla* (6.9 %), *A. tortilis* (5.4 %), *A. sieberiana* (4.5 %), *D. cotinifolia* (3.5 %), *C. rudis* (3.0 %), *V. rehmannii* (3.0 %) and *E. crispa* (2.5 %) were not utilised significantly differently from each other. The remainder of the species contributed less than 2.5 % to the winter diet and Bonferroni confidence intervals were not considered accurate for these species. Visual inspection of the scatter plot for the winter data showed that kudu allocated less time to feeding on *C. aurea* than expected, similar to early summer. Kudu also spent less time feeding on *R. pentheri* and more on *M. heterophylla* than expected.

Eland

Eland were observed utilising only four woody plant species over the entire seasonal cycle (Fig. 12a). The relative frequency of use among these species was not uniform (G = 49.405, df = 3 P < 0.001) and Bonferroni confidence intervals (95 %) showed that *A. karroo* (61.2 %) was the most utilised species. Utilisation of *A. sieberiana* (23.9 %) and *A. nilotica* (10.4 %) did not differ significantly from each other. Although it appeared that *A. sieberiana* was utilised more than *C. aurea* (4.5 %), Bonferroni confidence intervals were not regarded as accurate for *C. aurea*. Eland spent more time browsing *A. sieberiana* and less time browsing *A. karroo* and *A. nilotica* than expected, on an annual basis (Fig. 11b).

During early summer, eland did not utilise woody plant species equally (Fig. 12b), as indicated by a goodness-of-fit test (G = 27.159, df = 3, P < 0.001) and 95 % Bonferroni confidence intervals. Utilisation of *A. karroo* (51.2 %) and *A. sieberiana* (32.6 %) was not significantly different. *Acacia karroo* was, however, utilised to a greater extent than *A. nilotica* (13.9 %) during this season. *Calpurnia aurea* (2.3 %) appeared to be eaten less than *A. karroo* and *A. sieberiana*, but confidence intervals were not judged as accurate. The relevant scatter plot illustrated that eland allocated more time to *A. sieberiana* and less to the remaining species than expected.

A goodness-of-fit test was not performed on the late summer data because the guidelines proposed by Roscoe and Byars (1971) and Koehler and Larntz (1980) were not met. Woody plant species were utilised too infrequently to construct accurate Bonferroni confidence intervals. However, it appeared that the majority of the late summer diet consisted of *C. aurea* (40.0 %) (Fig. 12c).

The remaining three species contributed equally (20 %) to the diet. This differed from the results obtained with feeding time, where more time was devoted to *A. karroo* (31.8 %) than *A. nilotica* (6.7 %) and *A. sieberiana* (1.9 %). Sample size for this season was exceptionally small ($n = 5$) and these results must therefore be regarded with caution.

During winter, eland utilised *A. karroo* (94.7 %) significantly more than *A. sieberiana* (5.3 %) ($G_c = 15.844$, df = 1, P < 0.001). During this season, eland restricted their woody browse intake to these two species, feeding mainly on recently burnt plants.

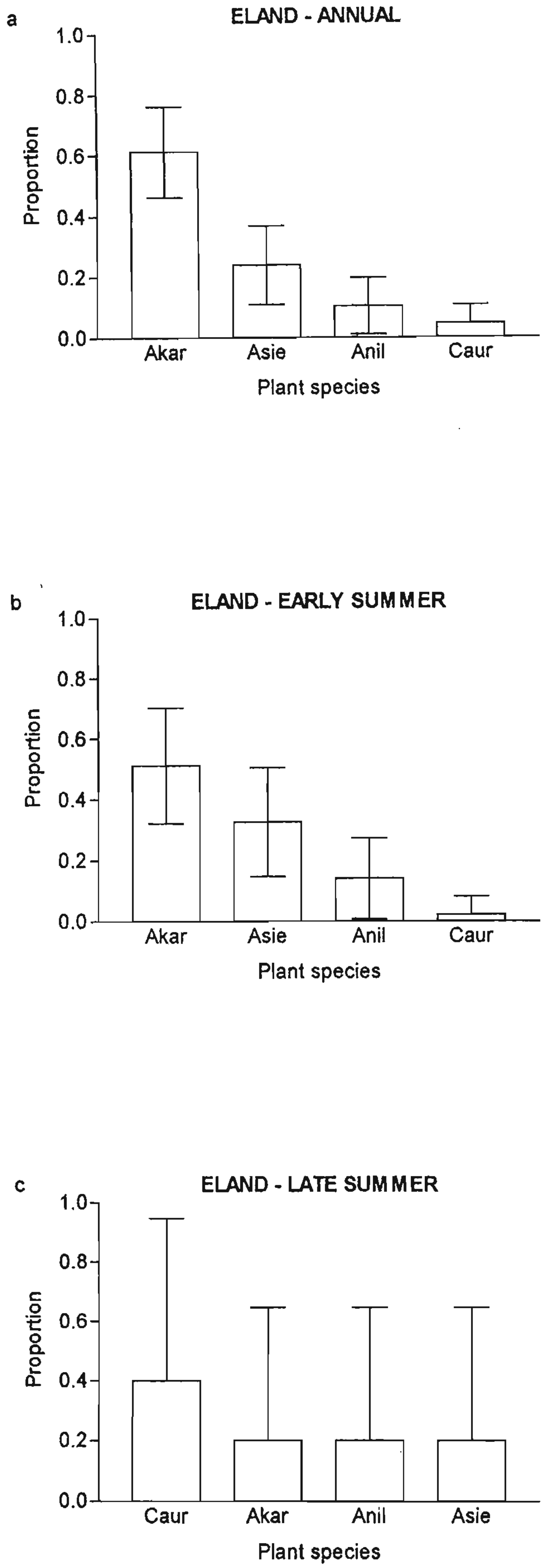


Figure 12. Relative frequency of woody plant species utilised (and 95 % Bonferroni confidence intervals) by eland for (a) whole year, (b) early summer and (c) late summer. Winter data not included as only two species, namely *Acacia karroo* and *Acacia sieberiana*, were utilised. Key to species: Akar = *Acacia karroo*, Anil = *Acacia nilotica*, Asie = *Acacia sieberiana*, Caur = *Calpurnia aurea*.

Giraffe

Giraffe utilised a total of 20 woody plant species to varying degrees as indicated by a goodness-of-fit test ($G = 1974.80$, $df = 19$, $P < 0.001$) and supported by 95 % Bonferroni confidence intervals. *Acacia* species were prominent in the annual diet of giraffe (Fig. 13a). *Acacia karroo* (35.2 %) and *A. nilotica* (25.8 %) were the most ($P < 0.05$) utilised species. There was no significant difference in utilisation between *A. caffra* (12.5 %) and *A. sieberiana* (11.8 %), but both were utilised more ($P < 0.05$) than the remaining species. Utilisation of *A. tortilis* (5.1 %), *A. robusta* (3.6 %) and *M. heterophylla* (1.7 %) was not significantly different. *Cussonia spicata* (0.8 %), *P. mooiensis* (0.6 %) and *R. rehmanniana* (0.6 %) were not ($P > 0.05$) utilised differently from each other, but all were utilised significantly less than *A. tortilis*. The remaining species each contributed little (≤ 0.05 %) to giraffe's diet and confidence intervals were not regarded as accurate for these species. Giraffe devoted less time to *A. nilotica* and more to *A. caffra* than expected (Fig. 11c). Although *Z. mucronata* was eaten infrequently (0.5 %), it constituted 2.0 % of giraffe's annual feeding time.

During early summer, giraffe did not utilise woody plant species with equal frequency ($G = 581.318$, $df = 15$, $P < 0.001$) and Bonferroni confidence intervals (95 %) demonstrated that *A. karroo* (49.1 %) was the species most utilised by giraffe (Fig. 13b). There were no significant differences in the use of *A. nilotica* (15.1 %), *A. sieberiana* (11.8 %) and *A. caffra* (10.0 %), but *A. nilotica* was eaten more frequently than the remaining species. Utilisation of *A. sieberiana* was not ($P > 0.05$) different from *A. tortilis* (3.3 %) but did differ significantly from *M. heterophylla* (2.6 %) as well as the remainder of species in the diet. *Acacia tortilis*, *M. heterophylla* and *A. robusta* (2.2 %) were not ($P > 0.05$) utilised differently. Bonferroni confidence intervals were not considered accurate for the remaining species, which contributed less than 2 % to the diet. The scatter plot for this season revealed that giraffe allocated more time to *A. sieberiana* and less to *A. nilotica* than expected. Similar to the annual diet, *Z. mucronata* (0.7 %) was eaten infrequently, but for longer than expected.

Woody plant species were not utilised equally by giraffe during late summer ($G = 486.251$, $df = 11$, $P < 0.001$) as confirmed by 95 % Bonferroni confidence intervals. *Acacia nilotica* (31.7 %) and *A. karroo* (28.2 %) were the most utilised species but did not differ significantly from each other (Fig. 13c). There were no ($P > 0.05$) differences in utilisation of *A. sieberiana* (13.8 %), *A. caffra* (12.2 %) and *A. tortilis* (7.8 %). The former two species were eaten significantly more frequently than *A. robusta* (3.1 %). The remaining species were eaten infrequently (< 1 %) and confidence intervals were not considered accurate for these species. Similar to early summer, giraffe allocated less feeding time to *A. nilotica* and more to *Z. mucronata* than expected. *Acacia caffra* and *A. tortilis* also contributed more feeding time to the late summer diet than expected, as deduced from the relevant scatter plot.

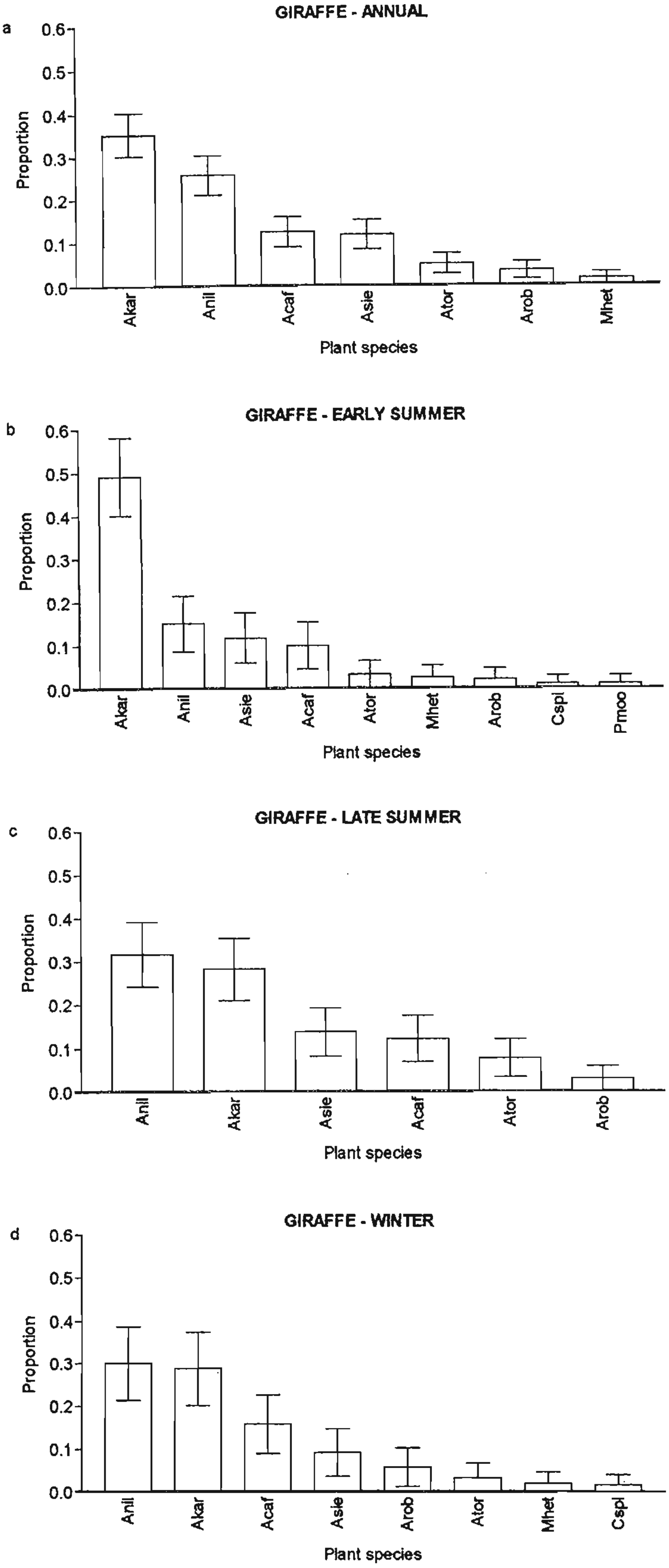


Figure 13. Relative frequency of woody plant species utilised (and 95 % Bonferroni confidence intervals) by giraffe for (a) whole year, (b) early summer, (c) late summer and (d) winter. Species contributing less than 1 % to the diet are not included. Key to species: Acaf = *Acacia caffra*, Akar = *Acacia karroo*, Anil = *Acacia nilotica*, Arob = *Acacia robusta*, Asie = *Acacia sieberiana*, Ator = *Acacia tortilis*, Cspi = *Cussonia spicata*, Mhet = *Maytenus heterophylla*, Pmoo = *Premna mooiensis*.

During winter, woody plant species were not equally utilised by giraffe (G = 418.888, df = 14, P < 0.001) (Fig. 13d). Bonferroni confidence intervals (95 %) demonstrated that *A. nilotica* (30.0 %) and *A. karroo* (28.8 %) were utilised more (P < 0.05) than the remaining species in the diet, except *A. caffra* (15.8 %). Utilisation of *A. caffra*, *A. sieberiana* (9.2 %) and *A. robusta* (5.8 %) was not significantly different. However, giraffe utilised *A. caffra* more (P < 0.05) than the remaining species. There were no significant differences in the use of *A. sieberiana*, *A. robusta*, *A. tortilis* (3.3 %) and *M. heterophylla* (2.1 %). Bonferroni confidence intervals were not considered accurate for the remaining species, which were eaten infrequently (< 2 %). The scatter plot indicated that giraffe allocated less time to *A. nilotica* than expected, similar to early and late summer. More time was spent browsing *A. caffra* than expected, which was similar to late summer. More time was also allocated to *A. robusta* and less to *A. tortilis* and *M. heterophylla* than expected.

Black Rhinoceros

Black rhinoceros consumed a total of 28 woody plant species but to different intensities (G = 2988.518, df = 27, P < 0.001) and Bonferroni confidence intervals (95 %) indicated that *A. karroo* (34.0 %) was the most utilised species, on an annual basis (Fig. 14a). Utilisation of *A. nilotica* (18.9 %) and *A. tortilis* (18.3 %) was not significantly different, but both species were utilised more frequently (P < 0.05) than the remaining species. *Coddia rudis* (7.6 %), did not differ significantly from *R. pentheri* (4.3 %), but was eaten more often (P < 0.05) than the remainder of species. The contribution of *R. pentheri* to the annual diet of black rhinoceros did not (P > 0.05) differ from *A. caffra* (2.5 %), *M. heterophylla* (2.5 %), *C. aurea* (1.9 %) and *D. cotinifolia* (1.8 %). However, *R. pentheri* was utilised significantly more frequently than both *Dichrostachys cinerea* (1.3 %) and *V. rehmannii* (1.1 %). Each of the remaining species contributed less than 1 % to the diet of black rhinoceros. Over the entire seasonal cycle, black rhinoceros browsed more twigs of *A. tortilis* and *R. pentheri* and less of *A. nilotica* than expected (Fig. 11d).

Woody plants were not equally utilised by black rhinoceros during early summer (G = 937.028, df = 14, P < 0.001) as substantiated by 95 % Bonferroni confidence intervals (Fig. 14b). Utilisation of *A. karroo* (37.4 %), *A. nilotica* (29.0 %) and *A. tortilis* (26.1 %) was not significantly different. However, all three species were eaten more often (P < 0.05) than *A. sieberiana* (1.3 %) and the remaining species, although confidence intervals were not regarded as accurate in the latter case.

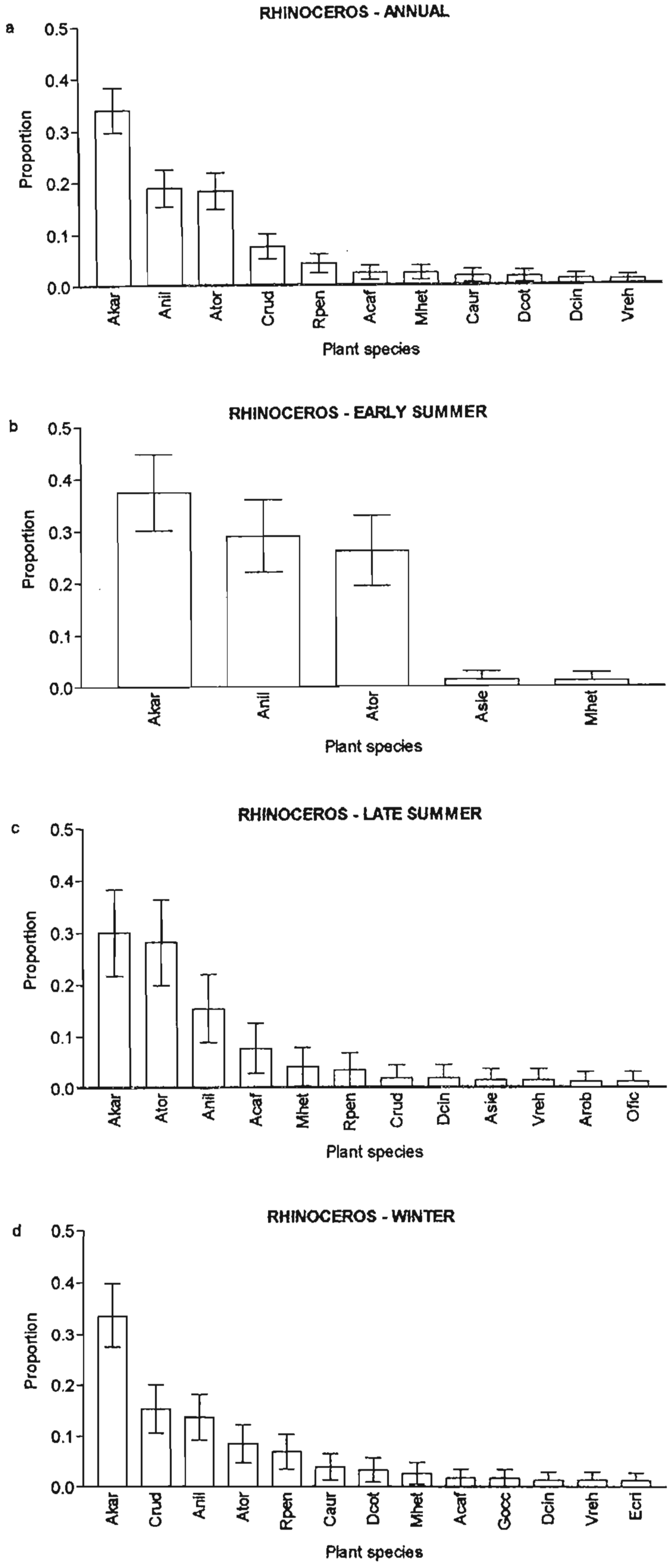


Figure 14. Relative frequency of woody plant species utilised (and 95 % Bonferroni confidence intervals) by black rhinoceros for (a) whole year, (b) early summer, (c) late summer and (d) winter. Species contributing less than 1 % to the diet are not included. Key to species: Acaf = *Acacia caffra*, Akar = *Acacia karroo*, Anil = *Acacia nilotica*, Arob = *Acacia robusta*, Asie = *Acacia sieberiana*, Ator = *Acacia tortilis*, Caur = *Calpurnia aurea*, Crod = *Coddia rudis*, Dcin = *Dichrostachys cinerea*, Dcot = *Dais cotinifolia*, Ecri = *Euclea crispa*, Gocc = *Grewia occidentalis*, Mhet = *Maytenus heterophylla*, Ofic = *Opuntia ficus-indica*, Rpen = *Rhus petheri*, Vreh = *Vitex rehmannii*.

The scatter plot showed that the proportion of twigs browsed was greater for *A. tortilis, A. sieberiana* and *M. heterophylla* and less for *A. nilotica* than expected. Although black rhinoceros did not utilise *E. ingens* often (0.8 %) and the number of twigs utilised were less than expected, the proportion of material consumed in SBV's (7.3 %) was greater than expected. If one considers the growth form of this species, then the potential amount of plant material (in SBV's) on one branch far exceeds that of other woody species.

Black rhinoceros did not utilise woody plant species uniformly during late summer ($G = 403.027$, $df = 14$, $P < 0.001$) (Fig. 14c) which was supported by Bonferroni confidence intervals (95 %). *Acacia karroo* (30.0 %) and *A. tortilis* (28.1 %) were not utilised significantly differently from each other, nor *A. nilotica* (15.4 %), but both were eaten more often ($P < 0.05$) than the remaining species. There were no significant differences in utilisation of *A. caffra, M. heterophylla* (4.2 %), *R. pentheri* (3.5 %), *C. rudis* (1.9 %) and *D. cinerea* (1.9 %). The remaining species were eaten infrequently (< 2 %) and confidence intervals were not judged as accurate. Examination of the scatter plot indicated that the number of twigs browsed was greater for *A. tortilis* and *R. pentheri* and less for *A. nilotica* than expected.

During winter, utilisation of woody plant species by black rhinoceros was not uniform as demonstrated by a goodness-of-fit test ($G = 1078.864$, $df = 23$, $P < 0.001$) and 95 % Bonferroni confidence intervals. Broadleaved plant species contributed substantially to the diet during winter although *A. karroo* (33.6 %) was the principal species ($P < 0.05$) (Fig. 14d). While utilisation of *C. rudis* (15.3 %), *A. nilotica* (13.7 %) and *A. tortilis* (8.5 %) was not significantly different, *C. rudis* was utilised more than the remaining species in the winter diet. Utilisation of *Acacia nilotica* and *A. tortilis* did not ($P > 0.05$) differ from *R. pentheri* (7.0 %), but *A. nilotica* was eaten more frequently($P < 0.05$) than the rest of the species. Both *A. tortilis* and *R. pentheri* were not utilised significantly different from *C aurea* (4.0 %), *D. cotinifolia* (3.4 %) and *M. heterophylla* (2.7 %). *Rhus pentheri* did also not differ to *A. caffra* (1.8 %), *Grewia occidentalis* (1.8 %) but was eaten more frequently than *D. cinerea* (1.4 %), *V. rehmannii* (1.4 %) and *E. crispa* (1.3 %). Bonferroni confidence intervals were not considered accurate for the remaining species which contributed less than 1 % to the diet. Similar to early and late summer, black rhinoceros browsed less twigs of *A. nilotica* and more of *R. pentheri* than expected, as deduced from the scatter plot. Although *E. ingens* was utilised infrequently (0.4 %), it was regarded as an important species during the dry season owing to its high moisture content. *Coddia rudis* as well as *R. pentheri* were also considered important to black rhinoceros during this period.

Among the four browsers, over the entire seasonal cycle, there was a general pattern of *A. karroo* being the most utilised woody plant species. *Acacia nilotica* was also prominent in the annual diets of all browsers, especially giraffe. During winter, the most utilised woody plant species by eland and black rhinoceros was *A. karroo*, while *C. aurea* was most frequently eaten by kudu during this season. Giraffe did not concentrate its feeding on one particular woody plant species during winter, rather three species, namely *A. nilotica*, *A. karroo* and *A. caffra*, made up the bulk of the diet.

SPECIES RICHNESS, DIETARY DIVERSITY AND EVENNESS

Forage Types

On an annual basis, kudu utilised all five categories of forage types, eland four and giraffe three (Table 10). Throughout the seasonal cycle giraffe were not observed consuming grass or forbs while eland were never seen utilising flowers (Table 7).

Annual forage-type diversity (H') was greater for eland than kudu or giraffe (Table 10). In other words, there is a great degree of uncertainty in predicting which forage type would be utilised by eland at random. This, in turn, implies that forage types were more evenly utilised by eland compared with the other two browsers. This result was substantiated by the relatively great evenness value and small difference between maximum and observed diversity for eland (Table 10). The relatively low diversity and evenness indices, and large difference between maximum and observed H' values for giraffe indicated that they were inclined to specialise on one forage type. This was evident by the great proportion of time spent browsing woody forage (Table 7).

Between kudu and eland there was a common pattern of diversity decreasing from early to late summer and then increasing and reaching a peak during winter (Table 10). The relatively great diversity values estimated for eland and kudu during winter suggests that utilisation of forage types was even. This was supported by the greater evenness values and smaller differences between maximum and observed diversity values during this season for these two browsers. For giraffe, the Shannon-Wiener index was zero in early summer because only one forage type was utilised. Diversity appeared to be greatest during late summer, but the evenness index value and difference between maximum and observed values of H' indicated that diversity was in fact greater in winter than late summer. This last conclusion does not, however, seem reasonable, because only two forage types were utilised during winter and to considerably varying degrees (Table 7).

Table 10. Forage-type richness (*S*)[1], diversity (*H'*)[2], maximum diversity (H'_{max}) and evenness (*HR*)[3] for the annual and seasonal diets of kudu, eland and giraffe

Animal species	Time period	Indices			
		Richness (*S*)	Diversity (*H'*)	Maximum diversity (H'_{max})	Evenness (*HR*)
Kudu	Annual	5	0.397	0.699	2.183
	Early summer	4	0.385	0.602	1.792
	Late summer	4	0.299	0.602	2.425
	Winter	4	0.400	0.602	2.652
Eland	Annual	4	0.522	0.602	2.784
	Early summer	4	0.462	0.602	2.648
	Late summer	3	0.334	0.447	1.938
	Winter	4	0.582	0.602	3.347
Giraffe	Annual	3	0.054	0.477	0.893
	Early summer	1	0.000	0.000	-
	Late summer	3	0.077	0.477	0.939
	Winter	2	0.058	0.301	1.035

[1] Number of woody plant species

[2] Shannon-Wiener diversity index

[3] Modified Hill's Ratio

Contrary to expectation, eland and kudu at Weenen Nature Reserve did not tend to specialise during the lean dry period. Giraffe, on the other hand, concentrated their feeding time on woody plant forage over all three seasons.

Woody Plant Species

The four browsers did not utilise an equal number of woody plant species over the entire seasonal cycle (G = 36.823, df = 3, P < 0.001). Kudu utilised a relatively great number of species followed by black rhinoceros, giraffe and eland (Table 11). The number of woody plant species utilised among the three seasons was not significantly different for kudu (G = 2.191, df = 2, 0.25 < P < 0.50), eland (G = 0.874, df = 2, 0.50 < P < 0.75), giraffe (G = 0.620, df = 2, 0.50 < P < 0.75) and black rhinoceros ($G = 2.869$, $df = 2$, $0.10 < P < 0.25$). The prediction that species richness should decrease during the dry winter season as animals tend to specialise was, therefore, not met.

Table 11. Species richness (*S*) [1], dietary diversity (*H'*) [2], maximum diversity (H'_{max}) and evenness (*HR*) [3] for the annual and seasonal diets of kudu, eland and giraffe, based on woody plant species

Animal species	Time period	Indices			
		Richness (*S*)	Diversity (*H'*)	Maximum diversity (H'_{max})	Evenness (*HR*)
Kudu	Annual	41	1.109	1.613	3.265
	Early summer	18	0.945	1.255	2.686
	Late summer	23	0.973	1.362	2.995
	Winter	28	1.134	1.447	3.154
Eland	Annual	4	0.422	0.602	2.250
	Early summer	4	0.465	0.602	2.668
	Late summer	4	0.579	0.602	3.282
	Winter	2	0.090	0.301	1.182
Giraffe	Annual	20	0.784	1.301	2.904
	Early summer	16	0.738	1.204	2.238
	Late summer	12	0.748	1.079	3.164
	Winter	15	0.797	1.176	3.058
Rhinoceros	Annual	28	0.901	1.447	2.829
	Early summer	15	0.629	1.176	2.761
	Late summer	15	0.840	1.176	2.985
	Winter	24	0.959	1.380	2.990

[1] Number of forage types utilised

[2] Shannon-Wiener diversity index

[3] Modified Hill's Ratio

For each combination of browser pairs there was a significant difference between annual diversity index values (Table 12). Annual dietary diversity appeared to be greater for kudu and black rhinoceros than giraffe or eland (Table 11). Similarly, dietary evenness and species richness seemed greatest for kudu and least for eland compared with black rhinoceros or giraffe. The relatively low diversity and evenness values for the diet of eland reflected that utilisation was not as evenly spread among woody plant species as that for the other browsers. Throughout the seasonal cycle, only one species, *Acacia karroo*, was dominant in the diet of eland (Fig. 12a), thus supporting the above conclusion. The differences between maximum diversity and observed diversity, however, contradict these results. Calculated diversity was closer to maximum diversity for eland (Table 11) compared with the other browsers, suggesting that dietary diversity was in fact greater for eland, probably owing to the low species richness, than the other browsers. The large difference between maximum and observed diversity for black rhinoceros implies that diversity was lowest for this browser compared with eland, kudu and giraffe.

Table 12. Hutcheson's *t* values for the comparison of Shannon-Wiener diversity indices between browser pairs. Shannon-Wiener indices calculated for the annual diet, of each browser, in terms of the number of woody plant species eaten

	Browser pair [1]					
	E/K	E/G	E/BR	G/K	K/BR	G/BR
Calculated *t* value	-14.663 ***	-7.964 ***	-10.712 ***	12.034 ***	7.787 ***	-5.244 ***
Calculated degrees of freedom	112	90	89	1261	1305	1935

[1] E, eland; K, kudu; G, giraffe; BR, black rhinoceros

*** P < 0.001

Dietary diversity for kudu was not different between early and late summer (t = -0.580, df = 361, 0.20 < P < 0.50). However, diversity indices were dissimilar between early summer and winter (t = -4.033, df = 428, P < 0.001) and between late summer and winter (t = -2.999, df = 369, P < 0.005). Diversity was, therefore, greatest during winter (Table 11) which was supported by the relatively great evenness value and small difference between maximum and observed diversity.

Diversity values for the diet of black rhinoceros were significantly different for all combinations of seasons (early summer-late summer: t = -5.807, df = 549, P < 0.001; early summer-winter: t = -10.552, df = 864, P < 0.001; late summer-winter: t = -3.382, df = 559, P < 0.001). Although diversity appeared to be greatest in winter, compared with the other two seasons, the difference between maximum and calculated diversity was smallest for late summer (Table 11), implying that diversity was in fact greater for late summer. Contrary to expectation, diversity was not lowest during winter, but early summer.

Dietary diversity for eland was not significantly different between early and late summer (t = -1.474, df = 9, 0.10 < P < 0.20) but was different between early summer and winter (t = 4.957, df = 34, P < 0.001) and late summer and winter (t = 5.309, df = 15, P < 0.001). Unlike kudu and black rhinoceros, dietary diversity and evenness were minimal during winter (Table 11), suggesting that eland tended to specialise during this season, as expected. Only two woody plant species were utilised during winter and a substantial portion of the winter diet was allocated to *A. karroo* (94.7 %), thus supporting the above conclusion.

Diversity values for giraffe were not significantly different for all combinations of seasons (early summer-late summer: $t = -0.260$, df = 475, $P > 0.50$; early summer-winter: $t = -1.392$, df = 507, $0.10 < P < 0.20$; late summer-winter: $t = -1.418$, df = 473, $0.10 < P < 0.20$). However, the relatively large difference between maximum and calculated diversity values for early summer implied that diversity was in fact lowest for this season, which was supported by the comparatively low evenness value (Table 11). This suggests an uneven utilisation of woody plant species during early summer, which was clearly demonstrated by *A. karroo* being the principal species (Fig. 13b) in the diet during this season. Similar to kudu and black rhinoceros, diversity was, therefore, not at a minimum during winter, contrary to expectation.

No patterns existed between species richness, evenness and diversity in forage types and woody plant species. The prediction that animals should specialise during the lean, winter period was only met for eland, when woody plant species were assessed.

FEEDING HEIGHT

Results of feeding heights are presented, firstly, when all forage types were assessed, from which black rhinoceros are excluded, owing to the limitations imposed by the plant-based method. Secondly, results for all the browsers studied are presented when only woody plant species were considered.

Forage Types

The two methods used for determining the utilisation of feeding heights, frequency and feeding time, were significantly positively correlated for kudu and giraffe for each season and all seasons combined (Table 13). For eland, significant correlations were obtained for early summer, late summer and all seasons combined, but not for winter. It was concluded that frequency data would be employed to describe feeding height utilisation because indices of use were significantly correlated in all instances, except one. Feeding height was thus expressed as the proportional distribution of the number of times a forage height class was utilised.

Table 13. Correlation coefficients for the relation between methods frequency and feeding time used for quantifying feeding height utilisation by kudu, eland and giraffe when all forage types were analysed

Animal species	Values of r^1 and degrees of freedom (df)			
	Annual	Early summer	Late summer	Winter
Kudu	0.9147***	0.8589***	0.8678***	0.8907***
	(24)	(24)	(23)	(24)
Eland	0.8522***	0.9497***	0.7563*	0.1273
	(16)	(12)	(6)	(11)
Giraffe	0.9735***	0.9544***	0.9397***	0.9528***
	(44)	(30)	(34)	(37)

[1] Pearson's product-moment correlation coefficient for kudu and giraffe. Spearman's rank correlation coefficient for eland

* $P < 0.05$, *** $P < 0.0001$

Over the entire seasonal cycle, when the utilisation of all forage types were assessed, 72.7 % of giraffe feeding occurred above the height reach of eland and kudu (i.e., 2.5 m) (Fig. 15). Only 3.1 % of kudu feeding was at the height range 2.1-2.5 m which was utilised relatively frequently by giraffe (12.1 %) and not by eland. However, kudu allocated 96.9 % of feeding below 2.1 m which was utilised completely by eland. The majority of feeding by eland occurred below 0.6 m (68.7 %) but this still constituted a large portion of kudu's feeding (33.4 %). Although giraffe are assumed to generally feed at high levels (Du Toit 1990), 15.2 % of giraffe feeding occurred below 2.1 m.

Eland restricted their feeding to below 1.6 m during early and late summer (Fig. 15). This height range was utilised substantially by kudu during both the early (76.7 %) and late (73.3 %) summer periods. Giraffe allocated only 3.9 % and 7.5 % of their feeding to this height range during early and late summer, respectively. Although a considerable amount (> 20 %) of feeding by giraffe and kudu occurred between 1.6 and 2.5 m during both seasons, giraffe allocated the majority of their feeding above this height range.

All feeding by eland occurred below 2.1 m during winter. During this season, kudu allocated almost all of their feeding to this height range (98.1 %). Giraffe generally fed at greater heights, allocating 77.3 % of their feeding to levels above 2.6 m (Fig. 15) and 12.1 % to heights below 2.1 m.

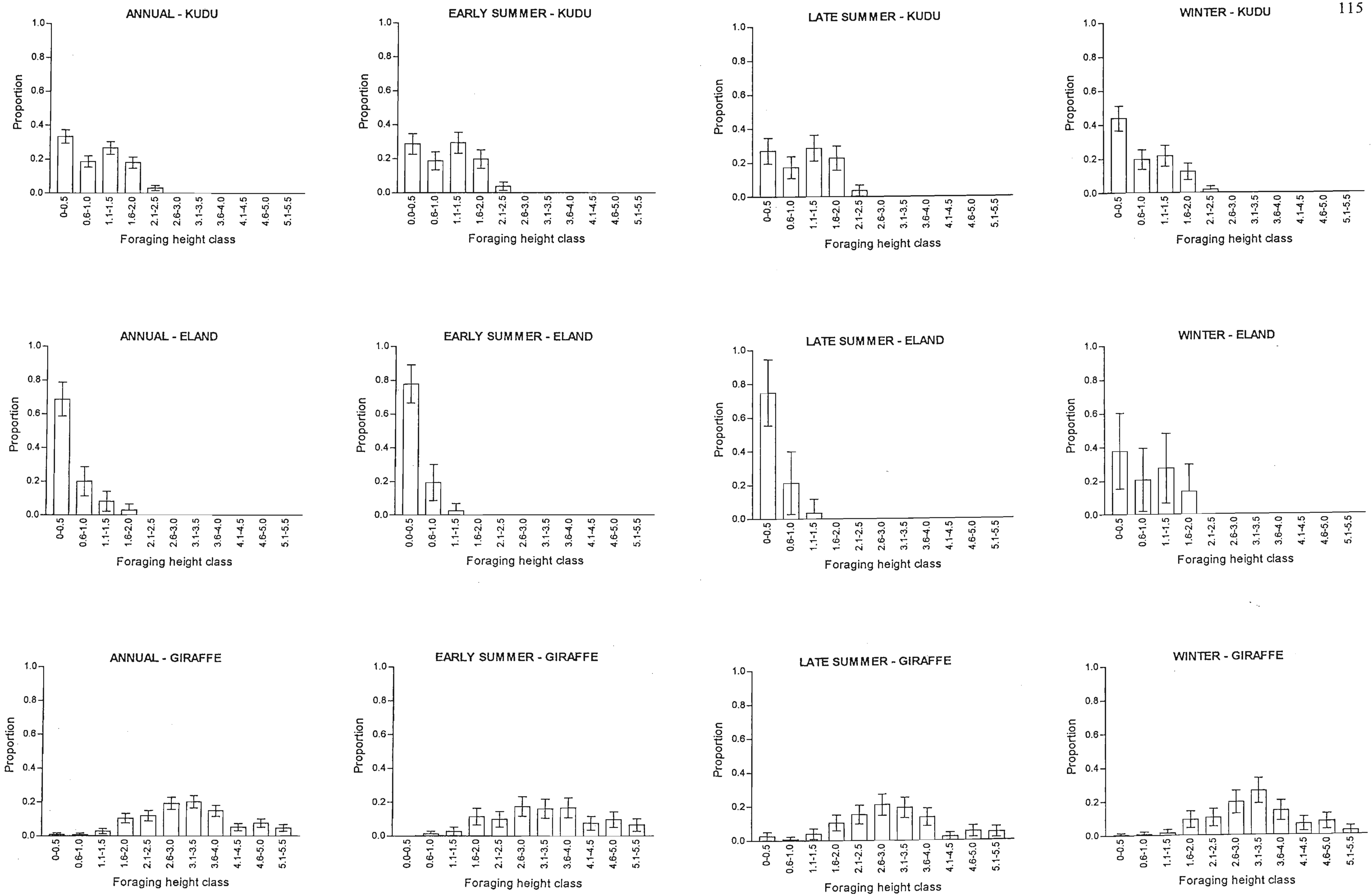


Figure 15. Relative frequency of feeding height classes utilised (and 95 % Bonferroni confidence intervals) by kudu, eland and giraffe for the whole year, early summer, late summer and winter, considering all forage types.

There appeared to be a clear stratification in average feeding heights among eland (0.49 m), kudu (0.98 m) and giraffe (3.15 m) on an annual basis as well as during early and late summer (Fig. 16a). However, during winter the average feeding height of eland increased, reflecting the increased use of woody forage and decreased use of grass during this season (Table 7) while that for kudu decreased (Fig. 16a), which was attributed to the increased use of forbs and fallen pods and decreased use of woody forage during winter (Table 7). Thus, during winter only giraffe appeared to be separated from kudu and eland in terms of average feeding height (Fig. 16a).

Woody Plant Species

When considering the utilisation of woody plant species by kudu and giraffe, the two methods used for determining the utilisation of browsing heights, frequency and feeding time, were significantly positively correlated for each season and all seasons combined (Table 14). For eland, significant correlations were obtained for early summer and all seasons combined, but not for winter. A linear correlation (parametric or non-parametric) could not be performed for late summer because a different feeding height was only utilised once. The three methods used for assessing browsing height utilisation by black rhinoceros (frequency, number of twigs browsed and standard browse volumes) were significantly positively correlated with each other for each season and all seasons combined. It was therefore concluded that frequency data would be used to describe the utilisation of feeding heights because indices of use were significantly correlated in all instances, except two. Browsing heights of woody plant species was thus expressed as the proportional distribution of the number of times a forage height class was utilised.

When assessing the utilisation of woody plant species, feeding heights utilised by giraffe were the same as when all plants were considered, because giraffe were never observed utilising herbaceous plants (forbs or grass) or pods on the ground. On an annual basis, only 15.2 % of giraffe browsing occurred below 2 m (Fig. 17). Kudu allocated 96.1 % and black rhinoceros 99.4% of browsing to this height range, which was utilised completely by eland. Although it was assumed that black rhinoceros could not browse above 2.0 m, 0.6 % of their feeding occurred within the 2.1-3.0 m height class. Within this range, black rhinoceros broke branches to feed. The maximum browsing height recorded for black rhinoceros was 2.1 m during early summer and 2.8 m during winter.

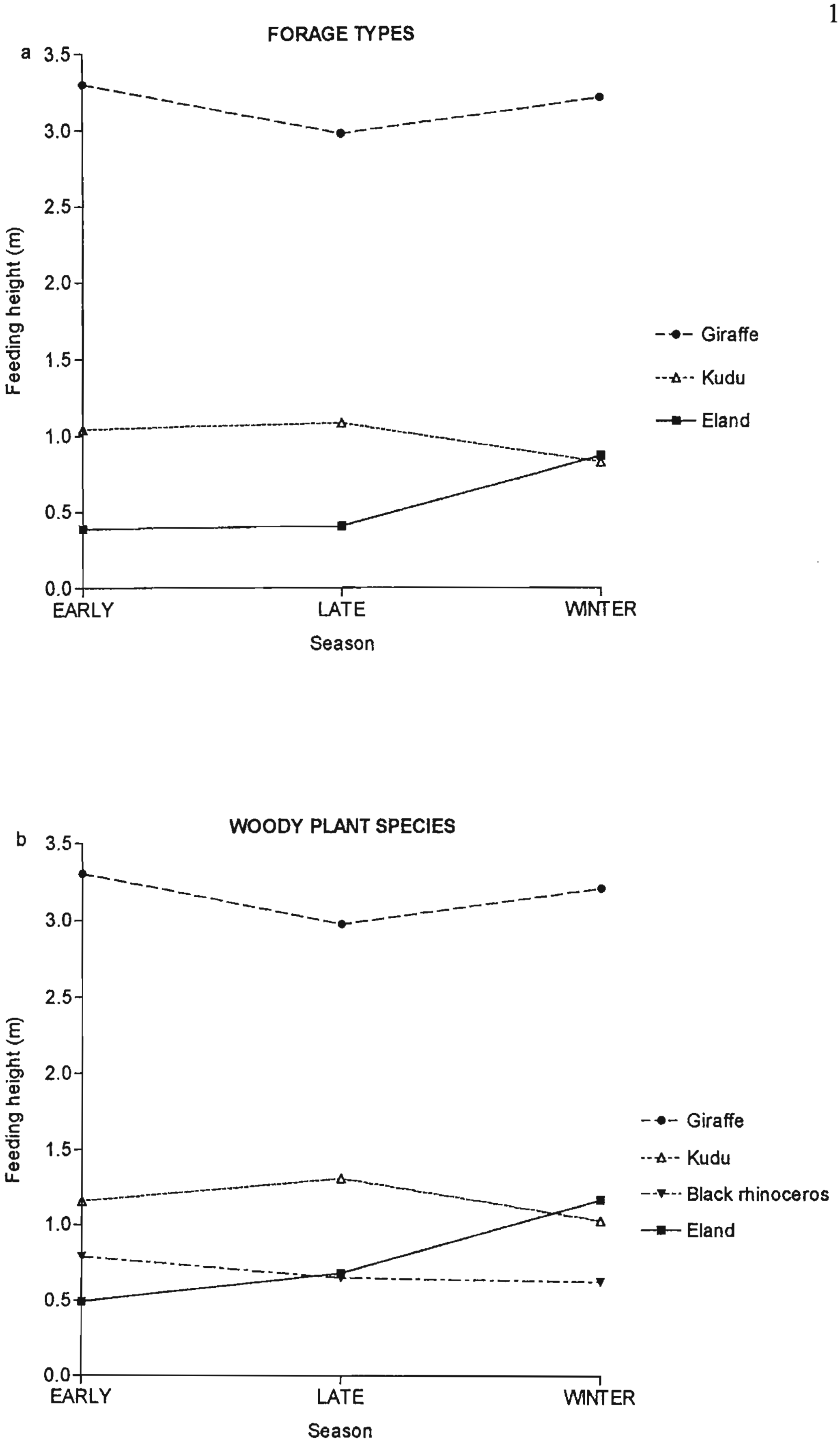


Figure 16. Average feeding height based on (a) all forage types and (b) woody plant species for early summer (EARLY), late summer (LATE) and winter.

Table 14.Correlation coefficients for the relation between the various methods used for quantifying browsing height utilisation by kudu, eland, giraffe and black rhinoceros when only woody plant species were analysed

Animal species	Values of *r*[1] and degrees of freedom (df)			
	Annual	Early summer	Late summer	Winter
Kudu[2]	0.8737***	0.8584***	0.8585***	0.7610***
	(24)	(24)	(23)	(24)
Eland[2]	0.6702**	0.6833**	na	0.0424
	(16)	(12)	(2)	(8)
Giraffe[2]	0.9735***	0.9544***	0.9397***	0.9528***
	(44)	(30)	(34)	(37)
Black rhinoceros				
frequency vs twigs	0.9812***	0.9810***	0.9675***	0.9755***
	(26)	(16)	(19)	(26)
frequency vs SBV	0.9782***	0.8614***	0.9777***	0.9501***
SBV vs twigs	0.9742***	0.8942***	0.9716***	0.9611***

[1] Pearson's product-moment correlation coefficient for kudu, giraffe and black rhinoceros. Spearman's rank correlation coefficient for eland

[2] Correlations for the methods frequency and feeding time

*** $P < 0.0001$; na - not applicable

During early and late summer, eland restricted their browsing to below 1.6 m (Fig. 17). Giraffe made little (< 8 %) use of browsing at this height range during both seasons. Kudu and black rhinoceros, on the other hand, allocated the majority (> 65 %) of their feeding to this height range during the early and late summer months. A considerable amount (> 20 %) of browsing by kudu and giraffe occurred between 1.6 m and 2.5 m during both seasons, but this height range was utilised little (< 3 %) by black rhinoceros. More than 66 % of giraffe browsing occurred above the height reach of the eland, kudu and black rhinoceros during both early and late summer.

The majority of browsing by kudu and black rhinoceros occurred below 2.1 m during winter (≥ 97 %) (Fig. 17). This height range was utilised completely by eland and to some degree by giraffe (12.1 %) during this season. Kudu did not browse above 2.5 m, while black rhinoceros allocated 1.3 % of their feeding to the 2.1-3.0 m height range. Similar to the other two seasons, the majority of giraffe browsing occurred above the height reach of the other three browsers.

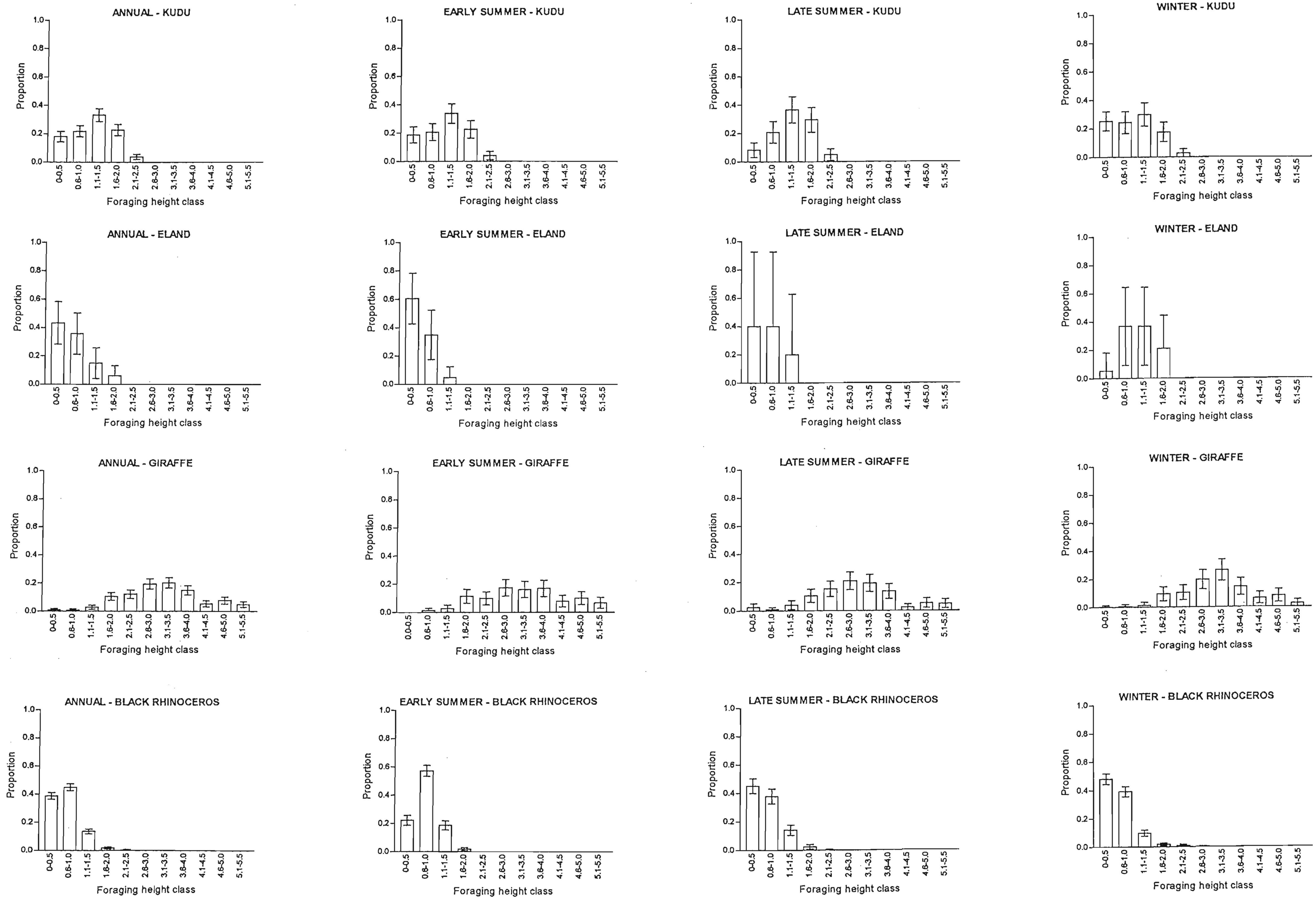


Figure 17. Relative frequency of feeding height classes utilised (and 95 % Bonferroni confidence intervals) by kudu, eland, giraffe and black rhinoceros for the whole year, early summer, late summer and winter, considering woody plant species.

On an annual basis, there appeared to be a clear stratification in average browsing heights between giraffe (3.15 m) and the others browsers, and between kudu (1.15 m) and black rhinoceros (0.68 m). The average feeding height of giraffe was greater than that of the other browsers during all three seasons, while there was a marked difference in average browsing heights of kudu and black rhinoceros only during late summer (Fig. 16b). The difference in average annual browsing height between eland (0.97 m) and black rhinoceros, and between eland and kudu were relatively small. However, the average feeding heights of eland and black rhinoceros were relatively dissimilar during winter, while this was true for eland and kudu during early and late summer (Fig. 16b). Average feeding heights of the browsers did not seem to differ remarkably among seasons, except for eland. During early summer, fallen pods constituted a large portion of their diet (Table 7), thus the relatively low average feeding height (Fig. 16b).

DIETARY OVERLAP

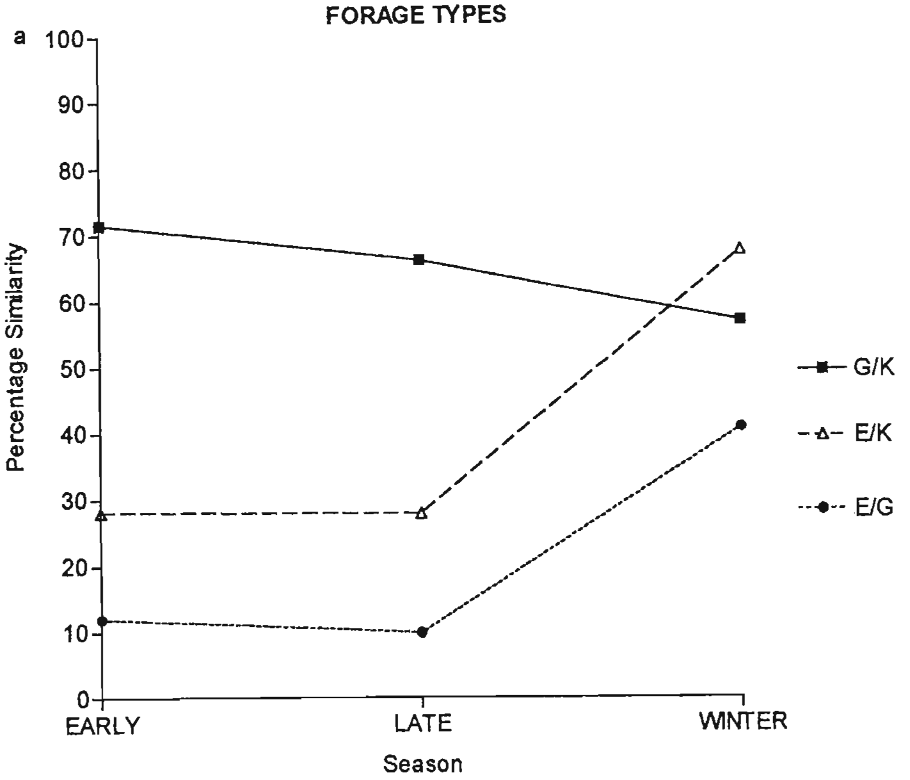
Diet Composition Overlap

Examination of calculated overlap values revealed that all PS values were less than 80 %. Only 8.3 % of Pianka's overlap index values were greater than 0.92. Therefore, the PS method was considered a more accurate measure of true overlap (see Linton *et al.* 1981) than Pianka's method. In addition, highly significant correlations between the two overlap indices for all forage types (Pearson's $r = 0.9712$, $df = 7$, $P < 0.0001$) and woody plant species (Pearson's $r = 0.8272$, $df = 16$, $P < 0.0001$) were obtained and, thus, only the results for PS are presented and discussed. (See Appendix 3 and 4 for Pianka's overlap index values.)

Forage Types

Annual overlap was great between giraffe and kudu (65.5 %), both of which depend heavily on woody forage (Table 7). Annual forage type utilisation between eland and kudu was also similar (32.9 %), mainly owing to the use of woody plant forage (Table 7). Despite the absence of grass in the diet of giraffe, overlap between eland and giraffe was still regarded as extensive (18.2 %).

Overlap between giraffe and kudu decreased during the dry season (Fig. 18a), as expected, but was still considerable (56.8 %). This decrease in overlap was owing to a decrease in woody forage utilisation by kudu during winter (Table 7). Between the eland-giraffe and eland-kudu pairs, maximum overlap was during winter (Fig. 18a), contrary to expectation, mainly because eland made more use of woody plant forage during winter than in the other two seasons (Table 7).



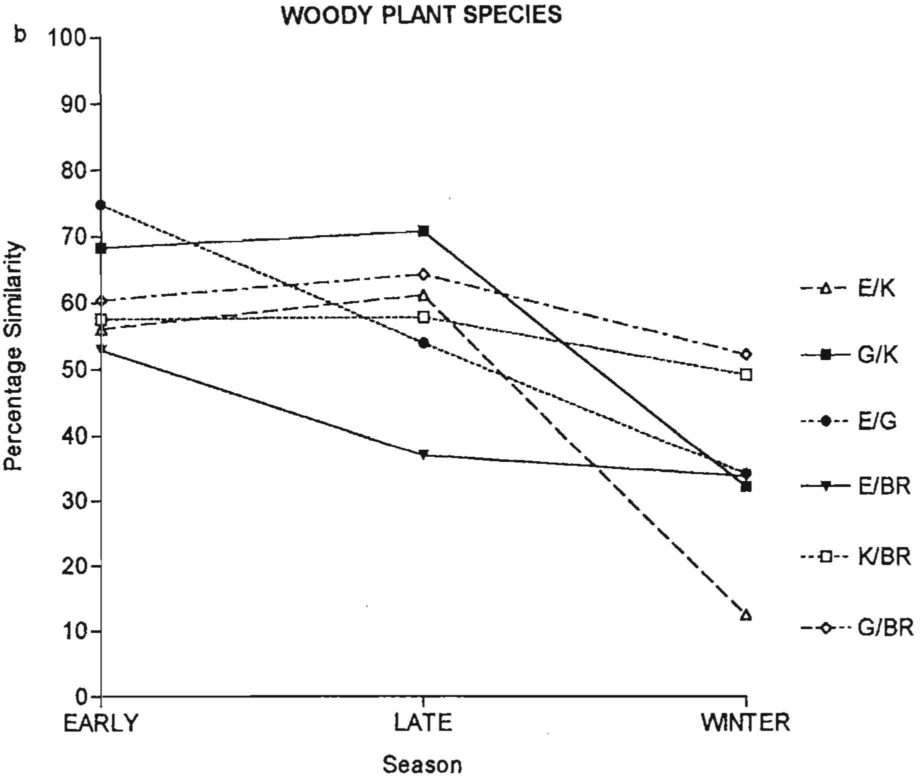


Figure 18. Overlap in diets based on the utilisation of (a) all forage types and (b) woody plant species for early summer (EARLY), late summer (LATE) and winter. BR = black rhinoceros, E = eland, G = giraffe, K = kudu.

Woody Plant Species

Annual similarities in the utilisation of woody plant species was substantial among the four browser species, all of which relied heavily on *Acacia karroo* and *Acacia nilotica* (Figures 10a, 12a, 13a, 14a). Percentage similarity values were slightly lower between eland and kudu (45.7 %) and eland and black rhinoceros (47.2 %) than that for the eland-giraffe (57.4 %), giraffe-kudu (59.2 %), kudu-black rhinoceros (64.9 %) and giraffe-black rhinoceros (65.3 %) pairs.

Seasonal dietary overlap decreased during winter for all combinations of browser pairs (Fig. 18b). These results, therefore, meet the prediction of overlap being at a minimum during the dry season. However, during this period PS values between all species pairs, except eland-kudu, ranged from 32 to 52 % indicating that utilisation of woody plant species was not considerably different. Overlap between eland and kudu was relatively small (12.4 %) during this season with only *A. karroo* and *Acacia sieberiana* being common to both diets.

Diets of all browsers appeared to be extremely similar, whether all forage types or only woody plant species were assessed. In general, overlap seemed lower during winter, but was still regarded as considerable.

Feeding Height Overlap

Only 11.1 % of all calculated PS values were greater than 80 %. Similarly, 11.1 % of Pianka's overlap index values were greater than 0.92. Results obtained by the PS method were, therefore, regarded to be a more accurate measure of true overlap than Pianka's method. On account of highly significant correlations between the two overlap indices for all forage types (Pearson's $r = 0.9826$, $df = 7$, $P < 0.0001$) and woody plant species (Pearson's $r = 0.9938$, $df = 16$, $P < 0.0001$) only the results for PS are presented and discussed. (See Appendix 5 and 6 for Pianka's overlap index.)

Forage Types

On an annual basis, extensive overlap in feeding heights between eland and kudu existed (63.3 %). The majority of overlap occurred within the 0-0.5 m height range (Fig. 15) owing to the utilisation of herbaceous plants and fallen pods by both species (Table 7). Kudu and giraffe also fed at similar heights (18.3 %), particularly within the 1.6-2.0 m height class (Fig. 15). By comparison, overlap between eland and giraffe was relatively small (7.7 %), but was still considered substantial.

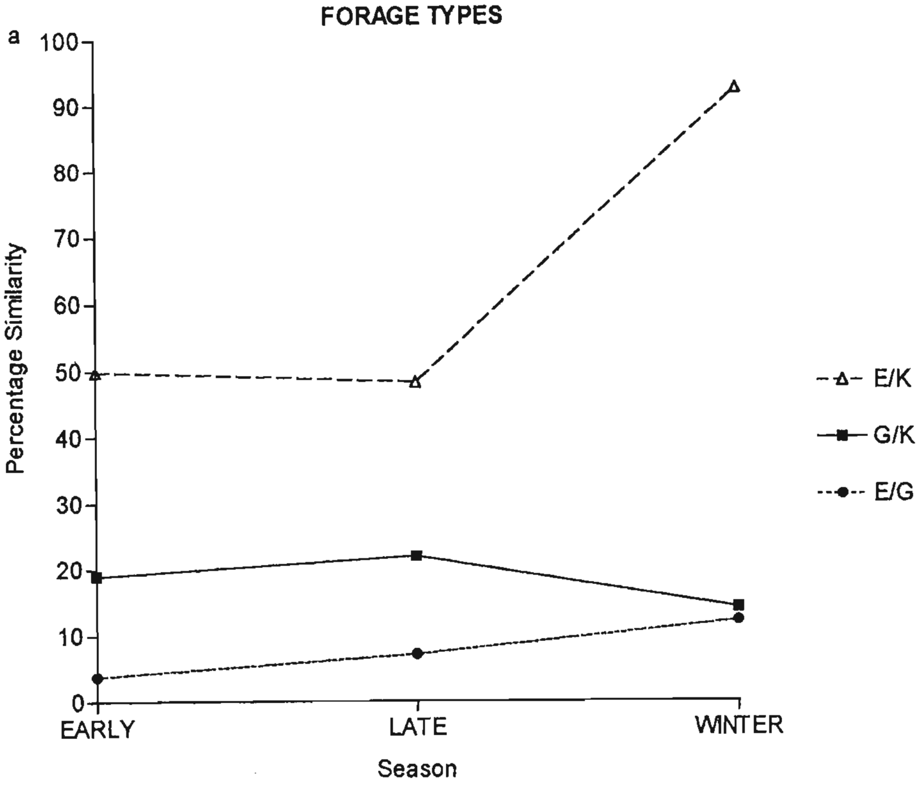
Although overlap between kudu and giraffe decreased during winter (Fig. 19a), as expected, it was still considerable (14.0 %). Contrary to expectation, overlap was at a maximum for the eland-giraffe and eland-kudu pairs during winter. The 1.6-2.0 m height class was utilised by eland during winter, but not the other two seasons (Fig. 15), hence the increased overlap with kudu and giraffe during this season.

Woody Plant Species

Over the entire seasonal cycle, browsing heights were similar between the pairs kudu-black rhinoceros (56.0 %), eland-kudu (60.9 %) and eland-black rhinoceros (90.1 %), in particular. The majority of overlap among these three browser pairs occurred within the height range 0-1.0 m. By comparison, overlap in feeding heights of woody plant species was relatively small for all browsers paired with giraffe (giraffe-black rhinoceros - 7.2 %, eland-giraffe - 10.7 %, giraffe-kudu - 19.1 %). Giraffe allocated most of their browsing to levels beyond the height ranges accessible to the other three browsers (Fig. 17).

The prediction that overlap should be lowest during the dry winter period was only met for three browser pairs (eland-black rhinoceros, giraffe-kudu, giraffe-black rhinoceros) (Fig. 19b). Contrary to expectation, overlap in browsing heights increased during winter between the eland-kudu and eland-giraffe pairs. Even though overlap among the browsers paired with giraffe appeared to be low, compared with the other browser pairs, it was still regarded as extensive. During winter, overlap among browsers paired with giraffe was greatest within the 1.6-2.0 m height class. Between eland and kudu the majority of overlap during winter occurred in the height range 1.1-1.5 m, while between pairs eland-black rhinoceros and kudu-black rhinoceros maximal overlap was in the 0.6-1.0 m height class.

During winter, there was substantial overlap among all browsers (Fig. 19b), despite the distinct stratification in average feeding heights between giraffe and the other browsers (Fig 16b). Thus, although giraffe appeared to be separated from the other species, in terms of feeding height, giraffe did feed within the height range of eland, kudu and black rhinoceros, so separation was not complete.



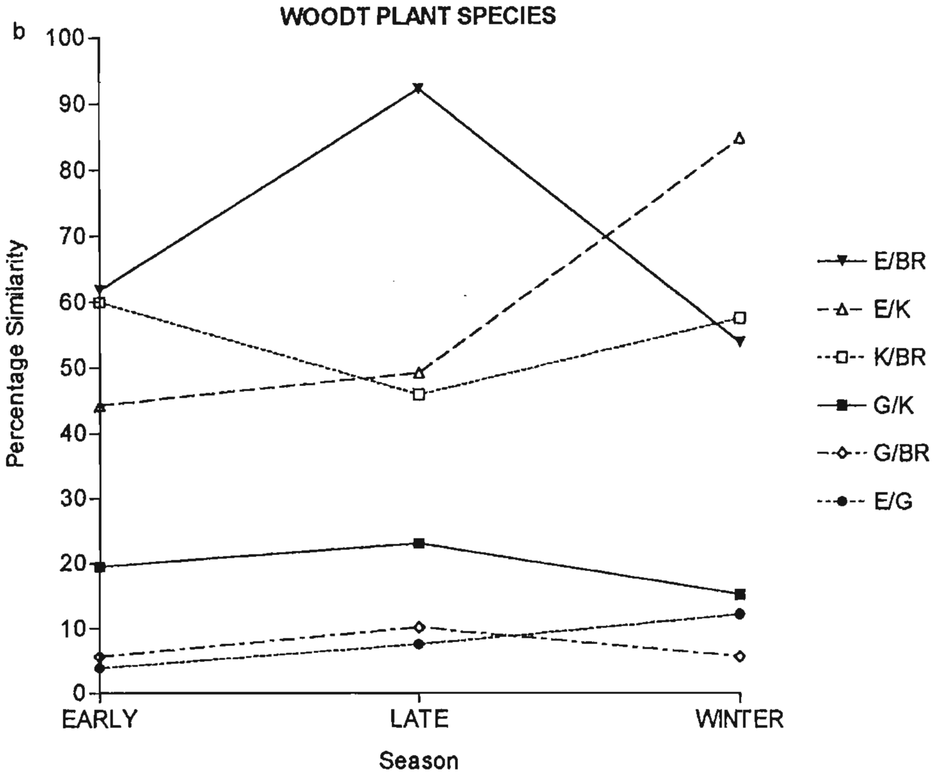


Figure 19. Overlap in feeding heights based on the utilisation of (a) all forage types and (b) woody plant species for early summer (EARLY), late summer (LATE) and winter. BR = black rhinoceros, E = eland, G = giraffe, K = kudu.

Total Dietary Overlap

All calculated values of total dietary overlap were well below 80 % and 0.92. Following the guideline of Linton *et al.* (1981), the PS method was judged to be a more accurate measure of true overlap than Pianka's method. In addition, correlations between the two overlap indices were highly significant for all forage types (Pearson's r = 0.9965, df = 10, P < 0.0001) and woody plant species (Pearson's r = 0.9480, df = 22, P < 0.0001) and, therefore, only the results for PS are presented and discussed. (See Appendix 7 and 8 for Pianka's overlap index values.)

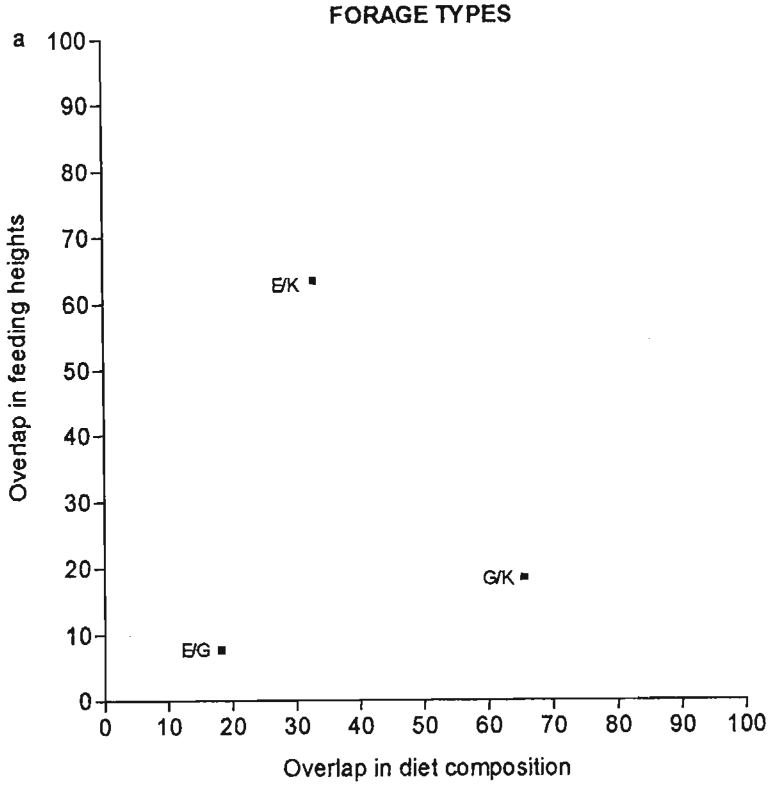
Forage Types

Over the entire seasonal cycle, total dietary overlap, in terms of forage types, was great between eland and kudu (20.8 %), mainly owing to similarities in feeding heights (Fig. 20a). Although giraffe and kudu tended to feed at relatively different heights, both browsers relied heavily on woody forage (Table 7), thus total annual dietary overlap was conspicuous (12.0 %). Total overlap was small for the eland-giraffe pair (1.4 %) mainly because giraffe allocated most of its feeding to heights beyond the reach of eland (Fig. 20a) and did not utilise grass.

As expected, total dietary overlap decreased during winter between giraffe and kudu (Fig. 21a). Overlap between eland and kudu increased substantially during the dry winter period, contrary to expectation, mainly owing to extremely similar feeding heights during this period. Similarly, total overlap was at a maximum for the eland-giraffe pair during winter. Although the prediction of a decrease in resource overlap during winter was generally not met, it is more important to look at the degree of overlap between browsers during this period. Overlap between eland and giraffe was considered relatively small (4.9 %), whereas the feeding patterns of giraffe and kudu (8.0 %), and eland and kudu (62.1 %), in particular, were regarded as similar during this period.

Woody Plant Species

Total annual dietary overlap, based on utilisation of woody plant species, was relatively low for browsers paired with giraffe (giraffe-black rhinoceros - 4.7 %, eland-giraffe - 6.1 %, giraffe-kudu - 11.3 %). Although the diets were similar among these browsers, browsing heights were relatively different (Fig. 20b). Feeding patterns were very similar between eland and black rhinoceros (42.5 %), largely owing to comparable browsing heights. Substantial overlap between the eland-kudu (27.8 %) and kudu-black rhinoceros (36.4 %) pairs was attributed to similarities in the utilisation of woody plant species as well as browsing heights.



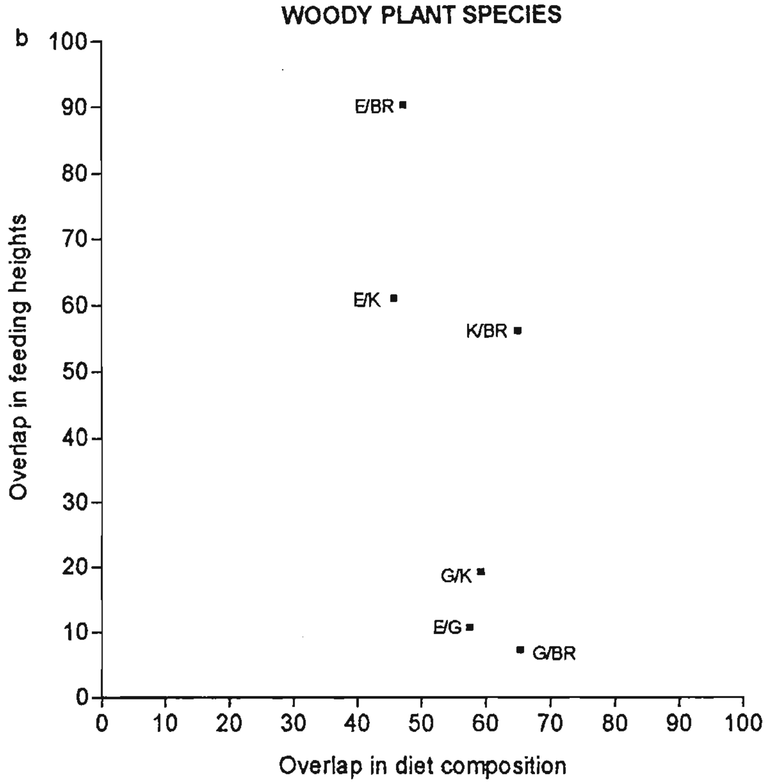
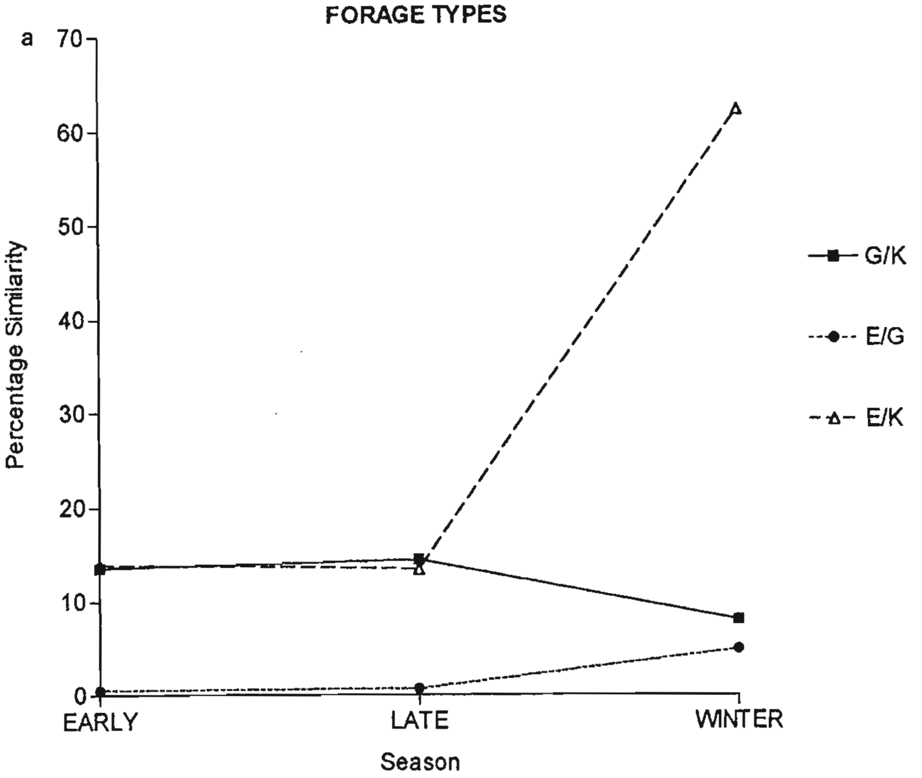


Figure 20. A comparison between annual overlap in diet composition and feeding height based on the utilisation of (a) all forage types and (b) woody plant species. BR = black rhinoceros, E = eland, G = giraffe, K = kudu.



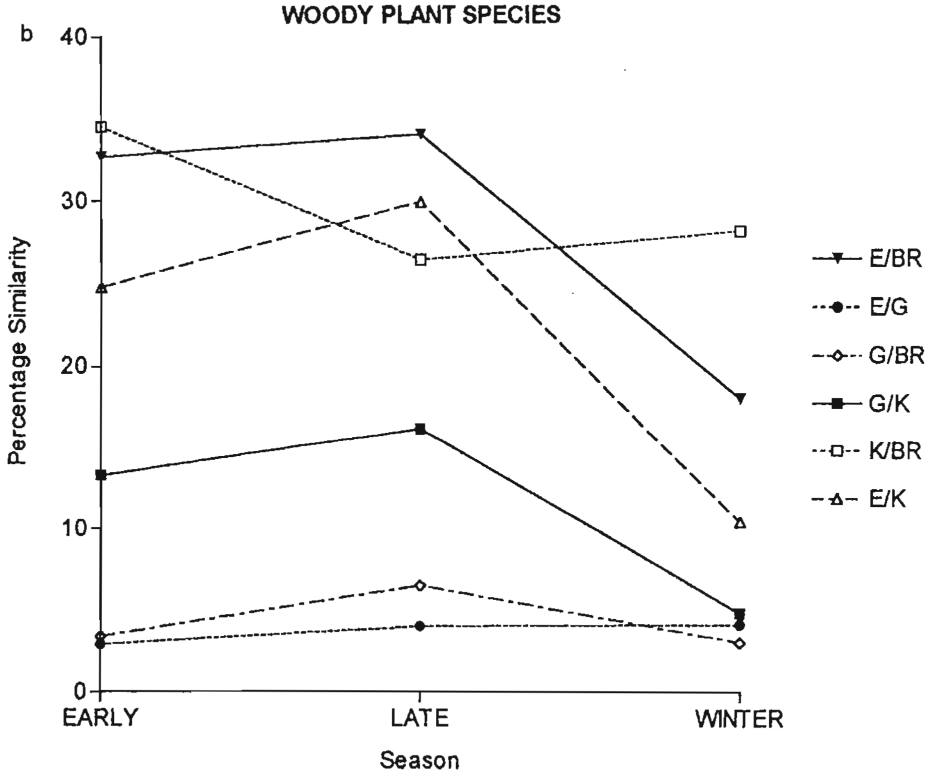


Figure 21. Total dietary overlap as a product of diet composition and feeding height based on the utilisation of (a) all forage types and (b) woody plant species for early summer (EARLY), late summer (LATE) and winter. BR = black rhinoceros, E = eland, G = giraffe, K = kudu.

On a seasonal basis, total dietary overlap decreased during winter, as expected, for four of the browser pairs (Fig. 21b). Similarities between the eland-giraffe and kudu-black rhinoceros pairs, however, increased during the dry season. Total dietary overlaps, during this period, were judged to be relatively low for those species paired with giraffe. In conclusion, it would appear that browser pairs eland-kudu, eland-black rhinoceros and, in particular, kudu-black rhinoceros did not utilise food resources considerably differently during winter. Owing to the great conservation status of black rhinoceros, the extensive overlap of black rhinoceros with eland and kudu, at WNR, is a consideration for management.

DIETARY PREFERENCES

Preference is a measure of the extent to which a food is consumed in relation to its availability (Petrides 1975) and is not synonymous with selection, which does not take availability into account. The preferences of the four browsers, at Weenen Nature Reserve, for woody plant species and browsing heights are presented.

Food Preferences

The two indices used for assessing available browse, frequency of occurrence and amount of browse in standard browse volumes, were significantly positively correlated for each season and all seasons combined for kudu, giraffe and black rhinoceros (Table 15). Correlations were significant for eland for the early summer and annual data, but not for the winter data, owing to the small sample size ($n = 3$). No monotonic relation existed for eland for the late summer data and therefore no correlation could be performed. All correlations, except two, were significant and thus it was concluded that frequency of occurrence would provide a realistic estimate of availability and be used to determine preference ratings for individual woody plant species.

Available proportions of microphyllous and broadleaved plants were dependent on animal species for early summer ($G = 293.805$, $df = 3$, $P < 0.001$), late summer ($G = 195.576$, $df = 3$, $P < 0.001$), winter ($G = 420.280$, $df = 3$, $P < 0.001$) and all seasons combined ($G = 832.925$, $df = 3$, $P < 0.001$). Available woody plant species could thus not be pooled and preferences of each browser were based on woody plant species available to that animal species.

Table 15. Correlation coefficients for the relation between the two methods[1] used for quantifying the amount of browse available to kudu, eland, giraffe and black rhinoceros

Animal species	Values of r^2 and degrees of freedom (df)			
	Annual	Early summer	Late summer	Winter
Kudu	0.9435 ***	0.9802 ***	0.9795 ***	0.7362 ***
	(44)	(23)	(30)	(32)
Eland	0.9197 ***	0.9757 ***	na	0.1667[3]
	(7)	(7)	(3)	(1)
Giraffe	0.8221 ***	0.9973 ***	0.7443 ***	0.9262 ***
	(24)	(19)	(13)	(19)
Black rhinoceros	0.9685 ***	0.9574 ***	0.9825 ***	0.9730 ***
	(32)	(18)	(17)	(28)

[1] Correlations for the methods frequency and standard browse volume (SBV)

[2] Pearson's product-moment correlation coefficient, except eland winter data

[3] Spearman's rank correlation coefficient

*** $P < 0.001$; na - not applicable

A total of nine woody plant species were recorded as available to eland, followed by 26 to giraffe, 34 to black rhinoceros and 46 to kudu. Although not all available species were eaten, they were still regarded as potential food items. Only 95 % Bonferroni confidence intervals are presented because in all instances, except one, results did not change for intervals constructed at 90 %. Only forage ratios (FR) calculated for species which were encountered frequently, i.e., ≥ 5 on an annual basis, were judged to be accurate, but this meant that preferences for rare species could not be reliably assessed.

Kudu

Bonferroni confidence intervals demonstrated that, on an annual basis, kudu did not utilise any woody plant species significantly more than expected and therefore none were judged as preferred (Table 16). However, *Coddia rudis* and, especially, *Euclea crispa* were considered neglected. Although it appeared that kudu neglected *Orthosiphon labiatus*, confidence intervals were not regarded as accurate. Contrary to these results, FR values revealed that kudu were selective feeders. Throughout the entire seasonal cycle, *Tarchonanthus camphoratus* attained the greatest FR value followed by *Acalypha glabrata, Acacia robusta* and *Ximenia caffra.* With the exception of *A. robusta*, these species were regarded as broadleaved plants and relatively uncommon. Species judged as strongly neglected included *Brachylaena elliptica*, *C. rudis*, *E. crispa* and *O. labiatus*. Woody plant species available, but not recorded as utilised, were *Diospyros whyteana,*

Table 16. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by kudu for all seasons combined

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	**0.026**	**0.033**	**0.010** ≤ P ≤ **0.057**	1.293
Acacia karroo	**0.239**	**0.262**	**0.205** ≤ P ≤ **0.318**	1.095
Acacia nilotica	**0.120**	**0.145**	**0.099** ≤ P ≤ **0.190**	1.201
Acacia robusta	**0.009**	**0.014**	**-0.001** ≤ P ≤ **0.029**	1.517
Acacia sieberiana	**0.033**	**0.046**	**0.019** ≤ P ≤ **0.073**	1.379
Acacia tortilis	**0.045**	**0.038**	**0.013** ≤ P ≤ **0.063**	0.854
Acalypha glabrata	0.003	0.005	-0.004 ≤ P ≤ 0.013	1.517
Brachylaena elliptica	0.005	0.003	-0.004 ≤ P ≤ 0.010	0.562
Calpurnia aurea	**0.155**	**0.169**	**0.121** ≤ P ≤ **0.217**	1.092
Coddia rudis	**0.035**	**0.015**	**-0.001** ≤ P ≤ **0.031**	0.436
Dais cotinifolia	**0.014**	**0.015**	**-0.001** ≤ P ≤ **0.031**	1.053
Diospyros lycioides	0.007	0.005	-0.004 ≤ P ≤ 0.013	0.632
Euclea crispa	**0.053**	**0.012**	**-0.002** ≤ P ≤ **0.026**	0.230
Grewia occidentalis	0.005	0.006	-0.004 ≤ P ≤ 0.016	1.124
Maytenus heterophylla	**0.056**	**0.044**	**0.018** ≤ P ≤ **0.071**	0.788
Olea europaea	0.005	0.006	-0.004 ≤ P ≤ 0.016	1.124
Orthosiphon labiatus	0.011	0.002	-0.003 ≤ P ≤ 0.007	0.133
Premna mooiensis	**0.008**	**0.011**	**-0.003** ≤ P ≤ **0.024**	1.361
Rhus pentheri	**0.060**	**0.055**	**0.025** ≤ P ≤ **0.084**	0.910
Rhus rehmanniana	**0.014**	**0.018**	**0.001** ≤ P ≤ **0.036**	1.319
Tarchonanthus camphoratus	0.004	0.006	-0.004 ≤ P ≤ 0.016	1.685
Vepris lanceolata	0.004	0.005	-0.004 ≤ P ≤ 0.013	1.083
Vitex rehmannii	**0.054**	**0.043**	**0.017** ≤ P ≤ **0.069**	0.795
Ximenia caffra	0.003	0.005	-0.004 ≤ P ≤ 0.013	1.517
Ziziphus mucronata	**0.007**	**0.009**	**-0.003** ≤ P ≤ **0.021**	1.264
Acacia ataxacantha	0.002	0.002	-0.003 ≤ P ≤ 0.007	0.843
Berchemia zeyheri	0.001	0.002	-0.003 ≤ P ≤ 0.007	1.264
Boscia albitrunca	0.001	0.002	-0.003 ≤ P ≤ 0.007	2.528
Brachylaena discolor	0.001	0.002	-0.003 ≤ P ≤ 0.007	1.264
Buddleja saligna	0.001	0.002	-0.003 ≤ P ≤ 0.007	1.264
Canthium mundianum	0.002	0.003	-0.004 ≤ P ≤ 0.010	1.264
Cussonia spicata	0.001	0.002	-0.003 ≤ P ≤ 0.007	2.528
Dichrostachys cinerea	0.002	0.003	-0.004 ≤ P ≤ 0.010	1.685
Diospyros whyteana	0.001	0.000	na	0.000
Euclea racemosa	0.001	0.002	-0.003 ≤ P ≤ 0.007	2.528
Euphorbia tirucalli	0.001	0.002	-0.003 ≤ P ≤ 0.007	2.528
Hippobromus pauciflorus	0.002	0.000	na	0.000
Jasminum multipartitum	0.001	0.002	-0.003 ≤ P ≤ 0.007	2.528
Nuxia congesta	0.001	0.002	-0.003 ≤ P ≤ 0.007	2.528
Opuntia ficus-indica	0.001	0.002	-0.003 ≤ P ≤ 0.007	2.528
Ozoroa paniculosa	0.002	0.003	-0.004 ≤ P ≤ 0.010	1.685
Rhus dentata	0.001	0.000	na	0.000
Rhus lucida	0.001	0.000	na	0.000
Schotia brachypetala	0.001	0.003	-0.004 ≤ P ≤ 0.010	2.528
Spirostachys africana	0.001	0.000	na	0.000
Vitellariopsis dispar	0.002	0.002	-0.003 ≤ P ≤ 0.007	0.843

[1] where $\alpha = 0.05$, $k = 46$, $Z_{\alpha/2k} = 3.30$, $n = 657$

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable

Hippobromus pauciflorus, *Rhus dentata*, *R. lucida* and *Spirostachys africana*. Preferences (FR's) and average feeding times were not correlated (Spearman's $r = 0.1802$, $df = 23$, $P < 0.200$).

During early summer, expected proportions of usage, p_{io}, for all species, except *E. crispa*, lay within the confidence intervals for p_i (Table 17) and, therefore, it was concluded that kudu were not selective during this season. Kudu appeared to neglect *E. crispa*, but confidence intervals were not considered accurate. Contrary to these results, FR values indicated that *Rhus rehmanniana*, a broadleaved species, *Acacia caffra* and *Acacia tortilis* were strongly preferred during early summer. *Euclea crispa* was the only species considered to be strongly neglected. There was no correlation between forage ratios and average feeding times (Spearman's $r = 0.1122$, $df = 14$, $P < 0.400$).

Table 17. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by kudu during early summer

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	**0.031**	**0.047**	**0.007** ≤ P ≤ **0.086**	1.488
Acacia karroo	**0.343**	**0.391**	**0.300** ≤ P ≤ **0.482**	1.140
Acacia nilotica	**0.106**	**0.118**	**0.058** ≤ P ≤ **0.179**	1.115
Acacia robusta	0.007	0.007	-0.009 ≤ P ≤ 0.023	1.030
Acacia sieberiana	**0.031**	**0.029**	**-0.002** ≤ P ≤ **0.060**	0.916
Acacia tortilis	**0.024**	**0.036**	**0.001** ≤ P ≤ **0.071**	1.472
Calpurnia aurea	**0.097**	**0.086**	**0.034** ≤ P ≤ **0.138**	0.883
Coddia rudis	0.010	0.000	na	0.000
Diospyros lycioides	0.016	0.011	-0.008 ≤ P ≤ 0.030	0.687
Euclea crispa	0.059	0.011	-0.008 ≤ P ≤ 0.030	0.182
Grewia occidentalis	0.002	0.000	na	0.000
Maytenus heterophylla	**0.050**	**0.050**	**0.009** ≤ P ≤ **0.091**	0.995
Olea europaea	0.003	0.000	na	0.000
Orthosiphon labiatus	0.002	0.000	na	0.000
Premna mooiensis	0.012	0.011	-0.008 ≤ P ≤ 0.030	0.883
Rhus pentheri	**0.075**	**0.068**	**0.021** ≤ P ≤ **0.115**	0.911
Rhus rehmanniana	**0.019**	**0.029**	**-0.002** ≤ P ≤ **0.060**	1.499
Vepris lanceolata	0.010	0.011	-0.008 ≤ P ≤ 0.030	1.030
Vitex rehmannii	**0.073**	**0.065**	**0.019** ≤ P ≤ **0.110**	0.833
Ziziphus mucronata	**0.017**	**0.022**	**-0.006** ≤ P ≤ **0.049**	1.237
Buddleja saligna	0.002	0.000	na	0.000
Diospyros whyteana	0.002	0.000	na	0.000
Euclea racemosa	0.002	0.004	-0.008 ≤ P ≤ 0.015	2.061
Ozoroa paniculosa	0.003	0.007	-0.009 ≤ P ≤ 0.023	2.061
Rhus lucida	0.002	0.000	na	0.000

[1] where $\alpha = 0.05$, $k = 25$, $Z_{\alpha/2k} = 3.10$, $n = 276$

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable

During late summer, kudu tended to be non-selective, as illustrated by Bonferroni confidence intervals (Table 18). Although it appeared that *Maytenus heterophylla* was neglected, this species was utilised too infrequently to construct accurate confidence intervals. Forage ratios showed that *Grewia occidentalis* appeared to be the most preferred species, during late summer. This may be as a result of a sampling error, because only one individual of this species was recorded as available during this season. *Acacia robusta*, *A. glabrata*, *Premna mooiensis* and *Acacia sieberiana* also attained FR values greater than 1.4 and were therefore clearly favoured. The only species rated as strongly neglected was *M. heterophylla*. The correlation between preferences and average feeding times was significant (Spearman's r = 0.5670, df = 14, P < 0.020). In other words, feeding durations were generally longer on preferred species (e.g. *A. robusta*) than on neglected species.

Bonferroni confidence intervals showed that kudu neglected *E. crispa* during winter (Table 19). It appeared that kudu also selected against *O. labiatus*, but confidence intervals were not judged as accurate. No species were regarded as favoured by kudu during this season when confidence intervals were set at 95 %. However, 90 % confidence intervals indicated that *C. aurea* (0.215-0.409) was favoured. Examination of FR values revealed that, during the dry season, broadleaved species were generally preferred. *Premna mooiensis* and *X. caffra* were strongly favoured followed by *A. sieberiana*, *Olea europaea*, *T. camphoratus*, *A. robusta* and *Calpurnia aurea*. Species that were obviously neglected (FR < 0.6) were *E. crispa*, as during early summer, *C. rudis*, *O. labiatus* and *Vitex rehmannii*. Average feeding times and preferences were not correlated (Spearman's r = 0.0426, df = 19, P < 0.500).

Table 18. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by kudu during late summer

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	**0.031**	**0.034**	**-0.009** ≤ P ≤ **0.078**	1.091
Acacia karroo	**0.292**	**0.267**	**0.161** ≤ P ≤ **0.373**	0.916
Acacia nilotica	**0.190**	**0.261**	**0.156** ≤ P ≤ **0.367**	1.379
Acacia robusta	0.013	0.023	-0.013 ≤ P ≤ 0.058	1.818
Acacia sieberiana	**0.050**	**0.074**	**0.011** ≤ P ≤ **0.137**	1.477
Acacia tortilis	0.038	0.023	-0.013 ≤ P ≤ 0.058	0.606
Acalypha glabrata	0.010	0.017	-0.014 ≤ P ≤ 0.048	1.636
Brachylaena elliptica	0.006	0.000	na	0.000
Calpurnia aurea	**0.152**	**0.136**	**0.054** ≤ P ≤ **0.219**	0.897
Coddia rudis	0.033	0.023	-0.013 ≤ P ≤ 0.058	0.682
Dais cotinifolia	0.019	0.017	-0.014 ≤ P ≤ 0.048	0.909
Euclea crispa	0.023	0.000	na	0.000
Grewia occidentalis	0.002	0.006	-0.012 ≤ P ≤ 0.024	2.727
Maytenus heterophylla	0.029	0.006	-0.012 ≤ P ≤ 0.024	0.195
Olea europaea	0.002	0.000	na	0.000
Premna mooiensis	0.010	0.017	-0.014 ≤ P ≤ 0.048	1.636
Rhus pentheri	0.017	0.011	-0.014 ≤ P ≤ 0.037	0.682
Rhus rehmanniana	0.015	0.017	-0.014 ≤ P ≤ 0.048	1.169
Vepris lanceolata	0.002	0.000	na	0.000
Vitex rehmannii	0.029	0.023	-0.013 ≤ P ≤ 0.058	0.779
Ximenia caffra	0.004	0.000	na	0.000
Ziziphus mucronata	0.002	0.000	na	0.000
Acacia ataxacantha	0.002	0.006	-0.012 ≤ P ≤ 0.024	2.727
Berchemia zeyheri	0.004	0.006	-0.012 ≤ P ≤ 0.024	1.364
Brachylaena discolor	0.002	0.000	na	0.000
Dichrostachys cinerea	0.006	0.011	-0.014 ≤ P ≤ 0.037	1.818
Euphorbia tirucalli	0.002	0.006	-0.012 ≤ P ≤ 0.024	2.727
Jasminum multipartitum	0.002	0.006	-0.012 ≤ P ≤ 0.024	2.727
Nuxia congesta	0.002	0.006	-0.012 ≤ P ≤ 0.024	2.727
Opuntia ficus-indica	0.002	0.006	-0.012 ≤ P ≤ 0.024	2.727
Rhus dentata	0.004	0.000	na	0.000
Vitellariopsis dispar	0.004	0.000	na	0.000

[1] where $\alpha = 0.05$, $k = 32$, $Z_{\alpha/2k} = 3.18$, $n = 176$

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable

Table 19. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by kudu during winter

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	0.017	0.015	-0.012 ≤ P ≤ 0.042	0.900
Acacia karroo	**0.099**	**0.079**	**0.018 ≤ P ≤ 0.140**	0.800
Acacia nilotica	**0.079**	**0.079**	**0.018 ≤ P ≤ 0.140**	1.000
Acacia robusta	0.008	0.015	-0.012 ≤ P ≤ 0.042	1.800
Acacia sieberiana	**0.021**	**0.045**	**-0.002 ≤ P ≤ 0.091**	2.077
Acacia tortilis	**0.069**	**0.054**	**0.003 ≤ P ≤ 0.106**	0.786
Brachylaena elliptica	0.010	0.010	-0.012 ≤ P ≤ 0.032	1.000
Calpurnia aurea	**0.211**	**0.312**	**0.207 ≤ P ≤ 0.417**	1.477
Coddia rudis	**0.059**	**0.030**	**-0.009 ≤ P ≤ 0.068**	0.500
Dais cotinifolia	**0.025**	**0.035**	**-0.007 ≤ P ≤ 0.076**	1.400
Diospyros lycioides	0.005	0.000	na	0.000
Euclea crispa	**0.071**	**0.025**	**-0.010 ≤ P ≤ 0.060**	0.349
Grewia occidentalis	0.012	0.015	-0.012 ≤ P ≤ 0.042	1.286
Maytenus heterophylla	**0.083**	**0.069**	**0.012 ≤ P ≤ 0.127**	0.840
Olea europaea	0.010	0.020	-0.012 ≤ P ≤ 0.051	2.000
Orthosiphon labiatus	0.030	0.005	-0.011 ≤ P ≤ 0.021	0.167
Premna mooiensis	0.002	0.005	-0.011 ≤ P ≤ 0.021	3.000
Rhus pentheri	**0.081**	**0.074**	**0.015 ≤ P ≤ 0.133**	0.918
Rhus rehmanniana	0.008	0.005	-0.011 ≤ P ≤ 0.021	0.600
Tarchonanthus camphoratus	0.010	0.020	-0.012 ≤ P ≤ 0.051	2.000
Vitex rehmannii	**0.054**	**0.030**	**-0.009 ≤ P ≤ 0.068**	0.545
Ximenia caffra	0.005	0.015	-0.012 ≤ P ≤ 0.042	3.000
Ziziphus mucronata	0.002	0.000	na	0.000
Acacia ataxacantha	0.003	0.000	na	0.000
Boscia albitrunca	0.002	0.005	-0.011 ≤ P ≤ 0.021	3.000
Brachylaena discolor	0.002	0.005	-0.011 ≤ P ≤ 0.021	3.000
Buddleja saligna	0.002	0.005	-0.011 ≤ P ≤ 0.021	3.000
Canthium mundianum	0.007	0.010	-0.012 ≤ P ≤ 0.032	1.500
Cussonia spicata	0.002	0.005	-0.011 ≤ P ≤ 0.021	3.000
Hippobromus pauciflorus	0.005	0.000	na	0.000
Ozoroa paniculosa	0.002	0.000	na	0.000
Schotia brachypetala	0.003	0.010	-0.012 ≤ P ≤ 0.032	3.000
Spirostachys africana	0.002	0.000	na	0.000
Vitellariopsis dispar	0.002	0.005	-0.011 ≤ P ≤ 0.021	3.000

[1] where $\alpha = 0.05$, $k = 34$, $Z_{\alpha/2k} = 3.21$, $n = 202$.

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable.

Eland

With the exception of *C. aurea*, all woody plant species utilised by eland were microphyllous and regarded as common. Over the entire seasonal cycle, eland utilised only three species frequently enough to construct accurate Bonferroni confidence intervals (Table 20). Eland showed no positive or negative selection for woody plant species, because expected utilisation for all species fell within the confidence intervals. However, FR values demonstrated that *A. sieberiana* was preferred, while *A. karroo* and *A. nilotica* were regarded as neutrally selected. Although *C. aurea* appears to be preferred it's FR value was not considered accurate. More than half of the woody species available were not recorded as utilised. There was a perfect positive correlation between forage ratios and average feeding times, although not significant (Spearman's $r = 1.0000$, $df = 1$, $P < 0.200$) owing to the small sample size. This indicated that feeding durations were longer on preferred species than on neutrally selected species.

Table 20. Simultaneous confidence intervals, using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by eland for all seasons combined

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia karroo	**0.654**	**0.612**	**0.447** ≤ P ≤ **0.777**	0.936
Acacia nilotica	**0.126**	**0.104**	**0.001** ≤ P ≤ **0.208**	0.832
Acacia sieberiana	**0.160**	**0.239**	**0.095** ≤ P ≤ **0.383**	1.491
Acacia caffra	0.004	0.000	na	0.000
Acacia tortilis	0.017	0.000	na	0.000
Calpurnia aurea	0.013	0.045	-0.025 ≤ P ≤ 0.115	3.448
Euclea crispa	0.013	0.000	na	0.000
Maytenus heterophylla	0.004	0.000	na	0.000
Rhus pentheri	0.009	0.000	na	0.000

[1] where $\alpha = 0.05$, $k = 9$, $Z_{\alpha/2k} = 2.77$, $n = 67$.

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable.

During early summer, eland did not select for or against any of the woody plant species (Table 21) as indicated by Bonferroni confidence intervals. However, *A. sieberiana* attained FR values greater than 1.0 and was, therefore, regarded as favoured. *Acacia karroo* and *Acacia nilotica* were neutrally selected. Average browsing time was longer for *A. sieberiana* than *A. karroo* and *A. nilotica*, although the positive correlation between forage ratios and preferences was not significant (Spearman's $r = 1.0000$, $df = 1$, $P < 0.200$) because of the small data set.

Table 21. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by eland during early summer

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia karroo	**0.565**	**0.512**	**0.302** $\leq P \leq$ **0.721**	0.906
Acacia nilotica	**0.163**	**0.140**	**-0.006** $\leq P \leq$ **0.285**	0.854
Acacia sieberiana	**0.211**	**0.326**	**0.129** $\leq P \leq$ **0.522**	1.544
Acacia caffra	0.007	0.000	na	0.000
Acacia tortilis	0.014	0.000	na	0.000
Calpurnia aurea	0.007	0.023	-0.040 $\leq P \leq$ 0.087	3.426
Euclea crispa	0.020	0.000	na	0.000
Rhus pentheri	0.014	0.000	na	0.000

[1] where $\alpha = 0.05$, $k = 8$, $Z_{\alpha/2k} = 2.75$, $n = 43$.

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable.

Sample size was extremely small for both late summer ($n = 5$) and winter ($n = 19$). During these two seasons, woody species were utilised too infrequently to construct accurate confidence intervals. Similar to early summer, *A. sieberiana* was regarded as preferred during late summer. *Acacia nilotica* was neutrally selected while *A. karroo* was considered neglected (Table 22). Average feeding durations were shorter on *A. sieberiana* and longer on the other two species, but the correlation was not significant (Spearman's r = - 1.0000, df = 1, P < 0.200). During winter, eland showed neither a preference for or against *A. karroo* and *A. nilotica*. No correlation was constructed for the winter data because only two woody plant species were utilised. Although *M. heterophylla* was available during winter it was not utilised.

Table 22. Forage ratios (FR) for utilisation of woody plant species by eland during late summer and winter

Plant species	Season	
	Late summer	Winter
Acacia karroo	0.475	1.026
Acacia nilotica	0.760	-
Acacia sieberiana	1.900	0.855
Acacia tortilis	0.000	-
Calpurnia aurea	3.800	-
Maytenus heterophylla	-	0.000

Species under line: availability ≥ 5 (based on annual)

Giraffe

Bonferroni confidence intervals illustrated that, over the entire seasonal cycle, giraffe did not prefer any woody plant species (Table 23). However, *R. rehmanniana* and, especially, *A. karroo* were selected against. It appeared that *E. crispa*, *Rhus pentheri* and *V. rehmannii* were also neglected but the guidelines proposed by Alldredge and Ratti (1986) were not met. Similar to kudu, giraffe seemed to be selective feeders when examining FR values. On an annual basis, *P. mooiensis*, an uncommon broadleaved species, appeared to be the most preferred plant. In fact, each individual of this species recorded as available to giraffe was utilised. *Cussonia spicata*, *A. caffra*, *A. sieberiana* and *A. robusta* were also highly favoured. Species considered strongly neglected (FR < 0.6) were *E. crispa*, *R. pentheri* and *V. rehmannii*, similar to Bonferroni results, as well as *Ozoroa paniculosa* and *R. rehmanniana*. Six species were not recorded as utilised by giraffe, although available. Average feeding times and preferences were correlated (Spearman's $r = 0.5382$, $df = 14$, $P < 0.020$) indicating a general pattern of feeding durations being longer on preferred species than on neglected species.

Table 23. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by giraffe for all seasons combined

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	**0.066**	**0.125**	**0.090** ≤ P ≤ **0.161**	1.909
Acacia karroo	**0.429**	**0.352**	**0.300** ≤ P ≤ **0.403**	0.819
Acacia nilotica	**0.239**	**0.258**	**0.211** ≤ P ≤ **0.305**	1.078
Acacia robusta	**0.022**	**0.036**	**0.016** ≤ P ≤ **0.056**	1.675
Acacia sieberiana	0.063	0.118	0.083 ≤ P ≤ **0.153**	1.876
Acacia tortilis	**0.054**	**0.051**	**0.027** ≤ P ≤ **0.074**	0.938
Calpurnia aurea	0.010	0.000	na	0.000
Cussonia spicata	**0.004**	**0.008**	**-0.001** ≤ P ≤ **0.018**	2.342
Euclea crispa	0.022	0.001	-0.003 ≤ P ≤ 0.005	0.055
Euclea racemosa	0.005	0.005	-0.003 ≤ P ≤ 0.012	0.893
Maytenus heterophylla	**0.026**	**0.017**	**0.003** ≤ P ≤ **0.031**	0.658
Ozoroa paniculosa	0.003	0.001	-0.003 ≤ P ≤ 0.005	0.447
Premna mooiensis	**0.002**	**0.006**	**-0.002** ≤ P ≤ **0.014**	2.680
Rhus pentheri	0.015	0.004	-0.003 ≤ P ≤ 0.010	0.236
Rhus rehmanniana	**0.015**	**0.006**	**-0.002** ≤ P ≤ **0.014**	0.394
Vitex rehmannii	0.013	0.002	-0.003 ≤ P ≤ 0.008	0.185
Ziziphus mucronata	0.004	0.005	-0.003 ≤ P ≤ 0.012	1.072
Brachylaena elliptica	0.000	0.000	na	0.000
Clerodendrum glabrum	0.001	0.001	-0.003 ≤ P ≤ 0.005	0.893
Combretum erythrophyllum	0.001	0.001	-0.003 ≤ P ≤ 0.005	1.340
Dalbergia obovata	0.000	0.001	-0.003 ≤ P ≤ 0.005	2.680
Dichrostachys cinerea	0.001	0.000	na	0.000
Diospyros lycioides	0.000	0.000	na	0.000
Grewia occidentalis	0.000	0.000	na	0.000
Schotia brachypetala	0.000	0.001	-0.003 ≤ P ≤ 0.005	2.680
Tarchonanthus camphoratus	0.001	0.000	na	0.000

[1] where $\alpha = 0.05$, $k = 26$, $Z_{\alpha/2k} = 3.10$, $n = 830$.

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable.

During early summer, giraffe did not select for or against any woody plant species, as demonstrated by Bonferroni confidence intervals (Table 24). However, FR values indicated that three broadleaved species, namely *C. spicata*, *Euclea racemosa* and *P. mooiensis*, were clearly preferred. Species also regarded as strongly favoured were *A. sieberiana*, *A. caffra*, *A. robusta* and *Ziziphus mucronata*. The only species rated as neglected (FR < 0.6) was *R. pentheri*. Forage ratios and average feeding times were not correlated during this season (Spearman's r = 0.3126, df = 11, P < 0.200).

Table 24. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by giraffe during early summer

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	**0.067**	**0.100**	**0.044 ≤ P ≤ 0.155**	1.487
Acacia karroo	**0.497**	**0.491**	**0.398 ≤ P ≤ 0.583**	0.988
Acacia nilotica	**0.186**	**0.151**	**0.085 ≤ P ≤ 0.217**	0.815
Acacia robusta	**0.015**	**0.022**	**-0.005 ≤ P ≤ 0.049**	1.432
Acacia sieberiana	**0.072**	**0.118**	**0.058 ≤ P ≤ 0.178**	1.636
Acacia tortilis	**0.052**	**0.033**	**0.000 ≤ P ≤ 0.066**	0.644
Calpurnia aurea	0.010	0.000	na	0.000
Cussonia spicata	0.005	0.011	-0.008 ≤ P ≤ 0.030	2.148
Euclea crispa	0.019	0.000	na	0.000
Euclea racemosa	0.003	0.007	-0.008 ≤ P ≤ 0.023	2.148
Maytenus heterophylla	**0.022**	**0.026**	**-0.003 ≤ P ≤ 0.055**	1.156
Premna mooiensis	0.005	0.011	-0.008 ≤ P ≤ 0.030	2.148
Rhus pentheri	0.014	0.004	-0.008 ≤ P ≤ 0.015	0.268
Rhus rehmanniana	0.010	0.007	-0.008 ≤ P ≤ 0.023	0.716
Vitex rehmannii	0.002	0.000	na	0.000
Ziziphus mucronata	0.005	0.007	-0.008 ≤ P ≤ 0.023	1.432
Clerodendrum glabrum	0.005	0.004	-0.008 ≤ P ≤ 0.015	0.716
Combretum erythrophyllum	0.003	0.004	-0.008 ≤ P ≤ 0.015	1.074
Diospyros lycioides	0.002	0.000	na	0.000
Schotia brachypetala	0.002	0.004	-0.008 ≤ P ≤ 0.015	2.148
Tarchonanthus camphoratus	0.003	0.000	na	0.000

[1] where $\alpha = 0.05$, $k = 21$, $Z_{\alpha/2k} = 3.04$, $n = 271$.

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable.

As indicated by Bonferroni confidence intervals, giraffe were relatively selective during late summer (Table 25). *Acacia caffra* and *A. sieberiana* were considered favoured, with giraffe selecting more strongly for the former than the latter, while *A. karroo* was neglected. Similar to kudu, giraffe appeared to neglect *M. heterophylla* but this species was utilised too infrequently to construct reliable confidence intervals. Forage ratios demonstrated that *P. mooiensis*, *Z. mucronata* and *A. robusta* were strongly preferred, followed by *A. caffra* and *A. sieberiana*. During late summer, species judged as highly neglected (FR < 0.6) were *R. pentheri*, similar to early summer, *M. heterophylla*, *R. rehmanniana* and *V. rehmannii*. There was no correlation between average feeding times and preferences (Spearman's r = 0.1331, df = 10, P < 0.400).

Table 25. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by giraffe during late summer

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	**0.061**	**0.122**	**0.069** ≤ P ≤ **0.176**	1.990
Acacia karroo	**0.444**	**0.282**	**0.208** ≤ P ≤ **0.356**	0.636
Acacia nilotica	**0.272**	**0.317**	**0.240** ≤ P ≤ **0.393**	1.164
Acacia robusta	**0.013**	**0.031**	**0.003** ≤ P ≤ **0.060**	2.505
Acacia sieberiana	**0.076**	**0.138**	**0.081** ≤ P ≤ **0.194**	1.810
Acacia tortilis	**0.064**	**0.078**	**0.034** ≤ P ≤ **0.122**	1.230
Calpurnia aurea	0.006	0.000	na	0.000
Euclea crispa	0.003	0.000	na	0.000
Euclea racemosa	0.001	0.000	na	0.000
Maytenus heterophylla	0.024	0.006	-0.007 ≤ P ≤ 0.019	0.262
Premna mooiensis	0.002	0.006	-0.007 ≤ P ≤ 0.019	2.755
Rhus pentheri	0.006	0.003	-0.006 ≤ P ≤ 0.012	0.551
Rhus rehmanniana	0.017	0.006	-0.007 ≤ P ≤ 0.019	0.367
Vitex rehmannii	0.009	0.003	-0.006 ≤ P ≤ 0.012	0.344
Ziziphus mucronata	0.002	0.006	-0.007 ≤ P ≤ 0.019	2.755

[1] where $\alpha = 0.05$, k = 15, $Z_{\alpha/2k} = 2.93$, n = 319.

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; na - not applicable.

Giraffe were generally non-selective feeders during winter, as demonstrated by Bonferroni confidence intervals (Table 26). However, *A. caffra* was strongly preferred during this season. It appeared that giraffe neglected *E. crispa*, *R. pentheri* and *V. rehmannii* but confidence intervals were not considered accurate. Examination of FR values indicated that giraffe showed a preference for fewer species during winter than the other two seasons. Interestingly, during winter only one broadleaved species, *C. spicata*, was preferred. Other plant species strongly favoured by giraffe during this season were *A. caffra*, *A. sieberiana* and *A. robusta*. Species considered clearly neglected were *E. crispa*, *O. paniculosa*, *R. pentheri*, *R. rehmanniana* and *V. rehmannii*. The latter three species were also selected against during late summer, while *R. pentheri* was also neglected during early summer. The correlation between forage types and average feeding times was significant (Spearman's r = 0.7407, df = 14, P < 0.002). In other words, feeding durations were generally shorter on neglected species than on preferred species.

Table 26. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by giraffe during winter

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	**0.069**	**0.158**	**0.087** $\le P \le$ **0.230**	2.279
Acacia karroo	**0.362**	**0.288**	**0.199** $\le P \le$ **0.376**	0.795
Acacia nilotica	**0.242**	**0.300**	**0.210** $\le P \le$ **0.390**	1.237
Acacia robusta	**0.037**	**0.058**	**0.012** $\le P \le$ **0.104**	1.590
Acacia sieberiana	**0.041**	**0.092**	**0.035** $\le P \le$ **0.148**	2.256
Acacia tortilis	**0.045**	**0.033**	**-0.002** $\le P \le$ **0.069**	0.748
Calpurnia aurea	0.016	0.000	na	0.000
Cussonia spicata	0.007	0.017	-0.008 $\le P \le$ 0.042	2.543
Euclea crispa	0.046	0.004	-0.008 $\le P \le$ 0.017	0.091
Euclea racemosa	0.012	0.008	-0.010 $\le P \le$ 0.026	0.706
Maytenus heterophylla	**0.030**	**0.021**	**-0.007** $\le P \le$ **0.049**	0.691
Ozoroa paniculosa	0.008	0.004	-0.008 $\le P \le$ 0.017	0.530
Rhus pentheri	0.028	0.004	-0.008 $\le P \le$ 0.017	0.151
Rhus rehmanniana	0.017	0.004	-0.008 $\le P \le$ 0.017	0.245
Vitex rehmannii	0.026	0.004	-0.008 $\le P \le$ 0.017	0.159
Ziziphus mucronata	0.007	0.000	na	0.000
Brachylaena elliptica	0.001	0.000	na	0.000
Dichrostachys cinerea	0.004	0.000	na	0.000
Dalbergia obovata	0.001	0.004	-0.008 $\le P \le$ 0.017	3.179
Grewia occidentalis	0.001	0.000	na	0.000
Tarchonanthus camphoratus	0.001	0.000	na	0.000

[1] where $\alpha = 0.05$, $k = 21$, $Z_{\alpha/2k} = 3.04$, $n = 240$.

Species in bold: $np_i \ge 5$ and $n(1 - p_i) \ge 5$; species above line: availability ≥ 5 (based on annual); na - not applicable.

Black Rhinoceros

As revealed by Bonferroni confidence intervals, black rhinoceros were relatively selective feeders, over the entire seasonal cycle (Table 27), compared with the other browsers studied. Similar to kudu, black rhinoceros selected against *E. crispa* on an annual basis. In addition, *R. pentheri* and, in particular, *V. rehmannii* were neglected. The only preferred species was *A. nilotica*. Examination of FR values indicated that, over the entire seasonal cycle, black rhinoceros appeared to select most strongly for *D. cotinifolia* and *Euphorbia ingens*. All *D. cotinifolia* plants available to black rhinoceros were, in fact, eaten. The same applied to *E. ingens* but this was judged to be as a result of sampling errors. Black rhinoceros also showed a strong preference for *A. sieberiana*, similar to giraffe and eland. Species rated as highly neglected were *A. robusta*, *E. crispa*, *T. camphoratus* and *V. rehmannii*. Six plant species, although available, were not recorded as utilised by black rhinoceros. Preferences and average feeding times were not correlated (Spearman's r = 0.0019, df = 18, P < 0.500).

Table 27. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by black rhinoceros for all seasons combined

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	**0.021**	**0.025**	**0.011** ≤ P ≤ **0.040**	1.199
Acacia karroo	**0.334**	**0.340**	**0.296** ≤ P ≤ **0.384**	1.017
Acacia nilotica	**0.137**	**0.189**	**0.152** ≤ P ≤ **0.225**	1.375
Acacia robusta	**0.014**	**0.008**	**-0.000** ≤ P ≤ **0.017**	0.587
Acacia sieberiana	**0.005**	**0.008**	**-0.000** ≤ P ≤ **0.016**	1.409
Acacia tortilis	**0.177**	**0.183**	**0.147** ≤ P ≤ **0.219**	1.032
Brachylaena elliptica	**0.007**	**0.007**	**-0.001** ≤ P ≤ **0.014**	1.002
Calpurnia aurea	**0.031**	**0.019**	**0.007** ≤ P ≤ **0.032**	0.617
Coddia rudis	**0.066**	**0.076**	**0.051** ≤ P ≤ **0.100**	1.150
Dichrostachys cinerea	**0.010**	**0.013**	**0.002** ≤ P ≤ **0.023**	1.225
Dais cotinifolia	**0.009**	**0.018**	**0.005** ≤ P ≤ **0.030**	1.879
Euclea crispa	**0.017**	**0.006**	**-0.001** ≤ P ≤ **0.013**	0.337
Euclea racemosa	0.002	0.002	-0.002 ≤ P ≤ 0.006	0.752
Euphorbia ingens	**0.002**	**0.004**	**-0.002** ≤ P ≤ **0.010**	1.879
Grewia occidentalis	**0.006**	**0.008**	**-0.000** ≤ P ≤ **0.017**	1.342
Maytenus heterophylla	**0.034**	**0.025**	**0.011** ≤ P ≤ **0.040**	0.752
Orthosiphon labiatus	0.002	0.000	na	0.000
Rhus pentheri	**0.065**	**0.043**	**0.024** ≤ P ≤ **0.062**	0.661
Tarchonanthus camphoratus	0.004	0.001	-0.002 ≤ P ≤ 0.004	0.235
Vitex rehmannii	**0.033**	**0.011**	**0.001** ≤ P ≤ **0.021**	0.330
Ziziphus mucronata	**0.006**	**0.005**	**-0.002** ≤ P ≤ **0.012**	0.867
Acacia ataxacantha	0.001	0.001	-0.002 ≤ P ≤ 0.004	0.626
Brachylaena ilicifolia	0.001	0.000	na	0.000
Diospyros lycioides	0.001	0.000	na	0.000
Diospyros whyteana	0.001	0.000	na	0.000
Hippobromus pauciflorus	0.002	0.001	-0.002 ≤ P ≤ 0.004	0.470
Olea europaea	0.002	0.001	-0.002 ≤ P ≤ 0.004	0.470
Opuntia ficus-indica	0.001	0.003	-0.002 ≤ P ≤ 0.007	1.879
Ozoroa paniculosa	0.000	0.000	na	0.000
Premna mooiensis	0.001	0.001	-0.002 ≤ P ≤ 0.004	0.626
Rhus lucida	0.000	0.001	-0.002 ≤ P ≤ 0.004	1.879
Rhus rehmanniana	0.001	0.000	na	0.000
Schotia brachypetala	0.000	0.001	-0.002 ≤ P ≤ 0.004	1.879
Scolopia zeyheri	0.002	0.003	-0.002 ≤ P ≤ 0.007	1.409

[1] where $\alpha = 0.05$, $k = 34$, $Z_{\alpha/2k} = 3.21$, $n = 1188$.

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable.

Black rhinoceros were not regarded as selective feeders during early summer, because expected utilisation lay within the Bonferroni confidence intervals for all species (Table 28). However, FR values revealed that *A. sieberiana*, *D. cotinifolia* and *E. ingens* were equally preferred while *C. aurea*, *R. pentheri* and *V. rehmannii* were neglected. There was no correlation between average number of twigs browsed and forage ratios during this season (Spearman's r = - 0.0177, df = 12, P < 0.500).

Table 28. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by black rhinoceros during early summer

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	0.006	0.000	na	0.000
Acacia karroo	**0.393**	**0.374**	**0.298** ≤ P ≤ **0.449**	0.951
Acacia nilotica	**0.250**	**0.290**	**0.219** ≤ P ≤ **0.361**	1.161
Acacia robusta	0.013	0.008	-0.006 ≤ P ≤ 0.022	0.613
Acacia sieberiana	**0.009**	**0.013**	**-0.005** ≤ P ≤ **0.031**	1.430
Acacia tortilis	**0.220**	**0.261**	**0.192** ≤ P ≤ **0.329**	1.186
Brachylaena elliptica	0.006	0.005	-0.006 ≤ P ≤ 0.017	0.953
Calpurnia aurea	0.015	0.003	-0.005 ≤ P ≤ 0.011	0.179
Dichrostachys cinerea	0.008	0.005	-0.006 ≤ P ≤ 0.017	0.715
Dais cotinifolia	0.004	0.005	-0.006 ≤ P ≤ 0.017	1.430
Euclea crispa	0.008	0.000	na	0.000
Euphorbia ingens	0.006	0.008	-0.006 ≤ P ≤ 0.022	1.430
Maytenus heterophylla	0.013	0.011	-0.005 ≤ P ≤ 0.027	0.817
Rhus pentheri	0.021	0.008	-0.006 ≤ P ≤ 0.022	0.390
Vitex rehmannii	0.017	0.003	-0.005 ≤ P ≤ 0.011	0.159
Ziziphus mucronata	0.004	0.003	-0.005 ≤ P ≤ 0.011	0.715
Diospyros lycioides	0.004	0.000	na	0.000
Olea europaea	0.002	0.000	na	0.000
Rhus lucida	0.002	0.003	-0.005 ≤ P ≤ 0.011	1.430
Rhus rehmanniana	0.002	0.000	na	0.000

[1] where $\alpha = 0.05$, k = 20, $Z_{\alpha/2k} = 3.02$, n = 372.

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable.

Similar to kudu and eland, black rhinoceros were not selective during late summer, as demonstrated by Bonferroni confidence intervals (Table 29). Forage ratios, on the other hand, indicated that black rhinoceros showed a strong preference for *Dichrostachys cinerea* followed by *A. caffra, A. sieberiana* and *Z. mucronata*. Black rhinoceros clearly neglected *Acacia robusta, C. rudis* and *V. rehmannii.* The correlation between preferences and average number of twigs browsed was not significant (Spearman's r = - 0.3251, df = 11, P < 0.200).

Bonferroni confidence intervals revealed that during winter black rhinoceros neglected *E. crispa* and, in particular, *V. rehmannii* (Table 30) and preferred no species. Examination of FR values, however, showed that *D. cotinifolia* and *E. ingens* were strongly preferred followed by *Grewia occidentalis, A. nilotica* and *C. rudis.* With the exception of *A. nilotica* these are all broadleaved species. During this season, black rhinoceros strongly selected against *E. crispa, T. camphoratus* and *V. rehmannii.* Similar to the other two seasons, average browsing times and preferences were not correlated (Spearman's r = 0.2310, df = 17, P < 0.200).

Table 29. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by black rhinoceros during late summer

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	**0.048**	**0.077**	**0.027** ≤ P ≤ **0.127**	1.595
Acacia karroo	**0.302**	**0.300**	**0.214** ≤ P ≤ **0.386**	0.994
Acacia nilotica	**0.114**	**0.154**	**0.086** ≤ P ≤ **0.221**	1.346
Acacia robusta	0.021	0.012	-0.008 ≤ P ≤ 0.032	0.538
Acacia sieberiana	0.011	0.015	-0.008 ≤ P ≤ 0.038	1.436
Acacia tortilis	**0.298**	**0.281**	**0.197** ≤ P ≤ **0.365**	0.942
Brachylaena elliptica	0.009	0.008	-0.009 ≤ P ≤ 0.024	0.862
Calpurnia aurea	0.007	0.000	na	0.000
Coddia rudis	**0.041**	**0.019**	**-0.006** ≤ P ≤ **0.045**	0.468
Dichrostachys cinerea	**0.009**	**0.019**	**-0.006** ≤ P ≤ **0.045**	2.154
Euclea crispa	0.002	0.000	na	0.000
Maytenus heterophylla	**0.043**	**0.042**	**0.005** ≤ P ≤ **0.080**	0.987
Premna mooiensis	0.005	0.004	-0.008 ≤ P ≤ 0.015	0.718
Rhus pentheri	**0.046**	**0.035**	**0.000** ≤ P ≤ **0.069**	0.746
Tarchonanthus camphoratus	0.004	0.000	na	0.000
Vitex rehmannii	0.027	0.015	-0.008 ≤ P ≤ 0.038	0.574
Ziziphus mucronata	0.005	0.008	-0.009 ≤ P ≤ 0.024	1.436
Olea europaea	0.002	0.000	na	0.000
Opuntia ficus-indica	0.005	0.012	-0.008 ≤ P ≤ 0.032	2.154

[1] where $\alpha = 0.05$, $k = 19$, $Z_{\alpha/2k} = 3.02$, $n = 260$.

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable.

Results obtained using Bonferroni confidence intervals revealed that all browsers were non-selective during early summer. Giraffe appeared to be the only selective feeder during late summer, preferring *A. caffra* and *A. sieberiana* and neglecting *A. karroo*. All browsers, except eland, were selective during winter. During this season, kudu and black rhinoceros both neglected *E. crispa* while black rhinoceros also selected against *V. rehmannii*. Over the winter period, giraffe showed a preference for *A. caffra* while kudu preferred *C. aurea*, but only at the 10 % level. Throughout the seasonal cycle, black rhinoceros favoured *A. nilotica* and neglected *E. crispa, R. pentheri* and *V. rehmannii* while kudu selected against *E. crispa* as well as *C. rudis*. On an annual basis, *A. karroo* and *R. rehmanniana* were neglected by giraffe.

Table 30. Simultaneous confidence intervals using the Bonferroni approach[1] and forage ratio (FR) values for utilisation of woody plant species, p_i, by black rhinoceros during winter

Plant species	Expected proportion of usage, p_{io}	Actual proportion of usage, p_i	Bonferroni intervals for p_i	FR values
Acacia caffra	**0.015**	**0.018**	**0.000** $\leq P \leq$ **0.036**	1.206
Acacia karroo	**0.323**	**0.336**	**0.273** $\leq P \leq$ **0.400**	1.042
Acacia nilotica	**0.096**	**0.137**	**0.091** $\leq P \leq$ **0.183**	1.430
Acacia robusta	0.011	0.007	-0.004 $\leq P \leq$ 0.019	0.631
Acacia sieberiana	0.001	0.000	na	0.000
Acacia tortilis	**0.097**	**0.085**	**0.047** $\leq P \leq$ **0.122**	0.868
Brachylaena elliptica	0.006	0.007	-0.004 $\leq P \leq$ 0.019	1.172
Calpurnia aurea	**0.051**	**0.040**	**0.013** $\leq P \leq$ **0.066**	0.788
Coddia rudis	**0.109**	**0.153**	**0.105** $\leq P \leq$ **0.201**	1.405
Dichrostachys cinerea	**0.012**	**0.014**	**-0.002** $\leq P \leq$ **0.030**	1.172
Dais cotinifolia	**0.017**	**0.034**	**0.010** $\leq P \leq$ **0.059**	2.050
Euclea crispa	**0.030**	**0.013**	**-0.002** $\leq P \leq$ **0.028**	0.422
Euclea racemosa	0.004	0.004	-0.004 $\leq P \leq$ 0.012	0.820
Euphorbia ingens	0.002	0.004	-0.004 $\leq P \leq$ 0.012	2.050
Grewia occidentalis	**0.012**	**0.018**	**0.000** $\leq P \leq$ **0.036**	1.465
Maytenus heterophylla	**0.039**	**0.027**	**0.005** $\leq P \leq$ **0.049**	0.699
Orthosiphon labiatus	0.004	0.000	na	0.000
Rhus pentheri	**0.095**	**0.070**	**0.036** $\leq P \leq$ **0.104**	0.740
Tarchonanthus camphoratus	0.005	0.002	-0.004 $\leq P \leq$ 0.007	0.342
Vitex rehmannii	**0.044**	**0.014**	**-0.002** $\leq P \leq$ **0.030**	0.328
Ziziphus mucronata	0.007	0.005	-0.004 $\leq P \leq$ 0.015	0.769
Acacia ataxacantha	0.003	0.002	-0.004 $\leq P \leq$ 0.007	0.683
Brachylaena ilicifolia	0.003	0.000	na	0.000
Diospyros whyteana	0.003	0.000	na	0.000
Hippobromus pauciflorus	0.004	0.002	-0.004 $\leq P \leq$ 0.007	0.513
Olea europaea	0.002	0.002	-0.004 $\leq P \leq$ 0.007	1.025
Ozoroa paniculosa	0.001	0.000	na	0.000
Rhus rehmanniana	0.002	0.000	na	0.000
Schotia brachypetala	0.001	0.002	-0.004 $\leq P \leq$ 0.007	2.050
Scolopia zeyheri	0.004	0.005	-0.004 $\leq P \leq$ 0.015	1.538

[1] where $\alpha = 0.05$, $k = 30$, $Z_{\alpha/2k} = 3.17$, $n = 556$.

Species in bold: $np_i \geq 5$ and $n(1 - p_i) \geq 5$; species above line: availability ≥ 5 (based on annual); na - not applicable.

As indicated by FR values, eland, giraffe and black rhinoceros showed a strong preference for *A. sieberiana*, during early summer. During this season, both kudu and giraffe strongly favoured *A. caffra*. All four browsers showed a selection for *A. sieberiana* during late summer, but to varying degrees. *Premna mooiensis* and, especially, *A. robusta* were favoured by kudu and giraffe during late summer. During this season, giraffe and black rhinoceros showed a preference for *A. caffra* and *Z. mucronata*. During winter, *A. sieberiana* and *A. robusta* were strongly favoured by kudu and giraffe. Both kudu and black rhinoceros showed a preference for *Dais cotinifolia* during winter. Kudu, giraffe and black rhinoceros neglected *Euclea crispa* and *Vitex rehmannii* during the dry season. Over the entire seasonal cycle, *A. sieberiana* was strongly preferred by eland and black rhinoceros and to a lesser extent by giraffe.

Feeding Height Preferences

On an annual basis, kudu preferred to browse between 1.1 and 2.0 m, because FR values were greatest for this height range (Table 31). The height class selected most strongly against was within the maximum height range of kudu, i.e., 2.1-2.5 m. Eland appeared to be non-selective for feeding heights on an annual basis, as forage ratios were comparable for all the height classes utilised. Giraffe browsed at relatively high levels, strongly favouring a height range of 3.1-3.5 m and strongly neglecting the 0.6-1.0 m height class. Unlike the other browsers, giraffe showed a preference for its maximum height range. Throughout the seasonal cycle, black rhinoceros preferred browsing between 0 and 1.0 m and bowsing heights above 1.5 m were neglected. Although black rhinoceros were observed to browse above 2.0 m (Fig. 17), I considered that the maximum height to which they could browse did not exceed this level. Therefore, feeding heights in excess of 2.0 m were not recorded as available. The maximum browsing height recorded for black rhinoceros in the present study was 2.8 m and I would therefore suggest that future workers should set the maximum height reach of black rhinoceros at 3.0 m.

Table 31. Forage ratio (FR) values for and availability[1] of feeding height classes, considering only woody plant species, for all seasons combined

Height class	Browser species							
	Kudu		Eland		Giraffe		Black rhinoceros	
	FR values	Availability	FR values	Availability	FR values	Availability	FR values	Availability
0.0-0.5 m	0.708	0.256	1.107	0.391	0.188	0.056	1.058	0.367
0.6-1.0 m	0.777	0.281	0.963	0.372	0.089	0.105	1.292	0.348
1.1-1.5 m	1.607	0.207	0.897	0.166	0.233	0.126	0.708	0.193
1.6-2.0 m	1.455	0.157	1.104	0.054	0.750	0.140	0.210	0.092
2.1-2.5 m	0.394	0.099	-	-	0.902	0.134	-	-
2.6-3.0 m	-	-	-	-	1.587	0.122	-	-
3.1-3.5 m	-	-	-	-	2.092	0.097	-	-
3.6-4.0 m	-	-	-	-	1.991	0.075	-	-
4.1-4.5 m	-	-	-	-	0.972	0.056	-	-
4.6-5.0 m	-	-	-	-	1.476	0.052	-	-
5.1-5.5 m	-	-	-	-	1.313	0.037	-	-

[1] Relative frequency of available height classes

During early summer, kudu showed a preference for the height range 1.1-2.0 m and an avoidance for feeding within their maximum height reach (Table 32). Eland and black rhinoceros preferred to browse at lower levels than kudu, during this season. Giraffe generally showed a preference for all height classes above the height reach of eland, kudu and black rhinoceros and selected most strongly for the 3.6-4.0 m height class.

Table 32. Forage ratio (FR) values for and availability[1] of feeding height classes, considering only woody plant species, for early summer

Height class	Browser species							
	Kudu		Eland		Giraffe		Black rhinoceros	
	FR values	Availability	FR values	Availability	FR values	Availability	FR values	Availability
0.0-0.5 m	0.813	0.231	1.483	0.408	0.000	0.018	0.718	0.309
0.6-1.0 m	0.692	0.299	0.886	0.394	0.189	0.063	1.510	0.380
1.1-1.5 m	1.539	0.219	0.364	0.128	0.277	0.098	0.852	0.219
1.6-2.0 m	1.450	0.156	-	0.050	0.943	0.121	0.197	0.092
2.1-2.5 m	0.439	0.094	-	0.021	0.709	0.140	-	-
2.6-3.0 m	-	-	-	-	1.239	0.141	-	-
3.1-3.5 m	-	-	-	-	1.374	0.118	-	-
3.6-4.0 m	-	-	-	-	1.701	0.099	-	-
4.1-4.5 m	-	-	-	-	0.975	0.080	-	-
4.6-5.0 m	-	-	-	-	1.344	0.074	-	-
5.1-5.5 m	-	-	-	-	1.360	0.049	-	-

[1] Relative frequency of available height classes

Kudu preferred to browse between 1.1 and 2.0 m, during late summer (Table 33), similar to early summer (Table 32). During late summer, eland selected for a higher browsing level than during early summer, which was reflected by an increase in average browsing height (Fig. 16b). Giraffe and black rhinoceros showed a preference for a lower height class (Table 33) than during early summer (Table 32). This was also illustrated by a decrease in average browsing heights (Fig. 16b).

Similar to early and late summer, kudu preferred to browse within the height range 1.1-2.0 m, during winter (Table 34). The height ranges favoured by black rhinoceros and giraffe, during this season, were similar to those preferred during the other two seasons. However, giraffe did not prefer the 5.1-5.5 m height class during winter. Eland showed a strong selection for higher browsing levels during winter than the other two seasons. This was displayed by average browsing height being maximum during the dry season (Fig. 16b).

Table 33. Forage ratio (FR) values for and availability[1] of feeding height classes, considering only woody plant species, for late summer

Height class	Browser species							
	Kudu		Eland		Giraffe		Black rhinoceros	
	FR values	Availability	FR values	Availability	FR values	Availability	FR values	Availability
0.0-0.5 m	0.300	0.273	0.853	0.469	0.365	0.070	1.172	0.387
0.6-1.0 m	0.838	0.000	1.422	0.281	0.065	0.131	1.127	0.337
1.1-1.5 m	1.890	0.194	1.280	0.156	0.284	0.140	0.804	0.176
1.6-2.0 m	1.722	0.171	-	0.094	0.682	0.155	0.240	0.101
2.1-2.5 m	0.429	0.115	-	-	1.097	0.140	-	-
2.6-3.0 m	-	-	-	-	1.886	0.112	-	-
3.1-3.5 m	-	-	-	-	2.326	0.083	-	-
3.6-4.0 m	-	-	-	-	2.254	0.061	-	-
4.1-4.5 m	-	-	-	-	0.573	0.040	-	-
4.6-5.0 m	-	-	-	-	1.397	0.039	-	-
5.1-5.5 m	-	-	-	-	1.643	0.029	-	-

[1] Relative frequency of available height classes

Table 34. Forage ratio (FR) values for and availability[1] of feeding height classes, considering only woody plant species, for winter

Height class	Browser species							
	Kudu		Eland		Giraffe		Black rhinoceros	
	FR values	Availability	FR values	Availability	FR values	Availability	FR values	Availability
0.0-0.5 m	0.956	0.265	0.152	0.347	0.051	0.072	1.242	0.387
0.6-1.0 m	0.836	0.292	1.043	0.353	0.064	0.113	1.158	0.338
1.1-1.5 m	1.447	0.206	1.578	0.234	0.107	0.135	0.520	0.187
1.6-2.0 m	1.208	0.146	3.906	0.054	0.665	0.142	0.204	0.088
2.1-2.5 m	0.300	0.090	-	0.012	0.860	0.123	-	-
2.6-3.0 m	-	-	-	-	1.671	0.118	-	-
3.1-3.5 m	-	-	-	-	2.826	0.093	-	-
3.6-4.0 m	-	-	-	-	2.048	0.071	-	-
4.1-4.5 m	-	-	-	-	1.259	0.052	-	-
4.6-5.0 m	-	-	-	-	1.655	0.048	-	-
5.1-5.5 m	-	-	-	-	0.756	0.034	-	-

[1] Relative frequency of available height classes

RESOURCE PARTITIONING

Diet Composition Similarities

Annual similarities, based on preferences for woody plant species, were greater among kudu-black rhinoceros, giraffe-kudu and giraffe-black rhinoceros than among eland-black rhinoceros, eland-kudu and eland-giraffe pairs (Table 35). Among four browser pairs (eland-kudu, kudu-black rhinoceros, eland-black rhinoceros and giraffe-black rhinoceros) there was a common pattern of similarities being least during winter (Fig. 22a), as expected. In other words, resource partitioning was at its greatest among these browser pairs during the dry season, but was incomplete. Contrary to expectation, food preferences between eland and giraffe were most similar during winter and least similar for the giraffe-kudu pair during late summer.

Table 35. Similarity measures, based on woody plant species, calculated by Lawlor's similarity (LS) method for annual food preferences, feeding height preferences and total dietary preferences between species pairs

Similarity measures	Browser pairs[1]					
	E/K	E/G	G/K	E/BR	K/BR	G/BR
Diet composition	0.203	0.168	0.498	0.262	0.531	0.445
Feeding heights	0.918	0.156	0.198	0.880	0.717	0.083
Total	0.186	0.026	0.099	0.231	0.381	0.037

[1] E, eland; K, kudu; G, giraffe; BR, black rhinoceros

Feeding Height Similarities

Throughout the seasonal cycle, preferences for browsing heights were less similar for all browsers paired with giraffe (Table 35) because giraffe preferred to utilise height classes beyond the reach of the other browsers (Table 31). Similarities in preferred browsing heights were great among the pairs eland-kudu, eland-black rhinoceros and kudu-black rhinoceros (Table 35). There was a common pattern of similarities being least during winter among the giraffe-kudu, eland-black rhinoceros and giraffe-black rhinoceros pairs (Fig. 22b), as expected. Resource partitioning, based on browsing heights, was minimal during the lean winter period, contrary to expectation, for the other three browser pairs. Partitioning of the food resource, by differential preferences for feeding heights, was incomplete.

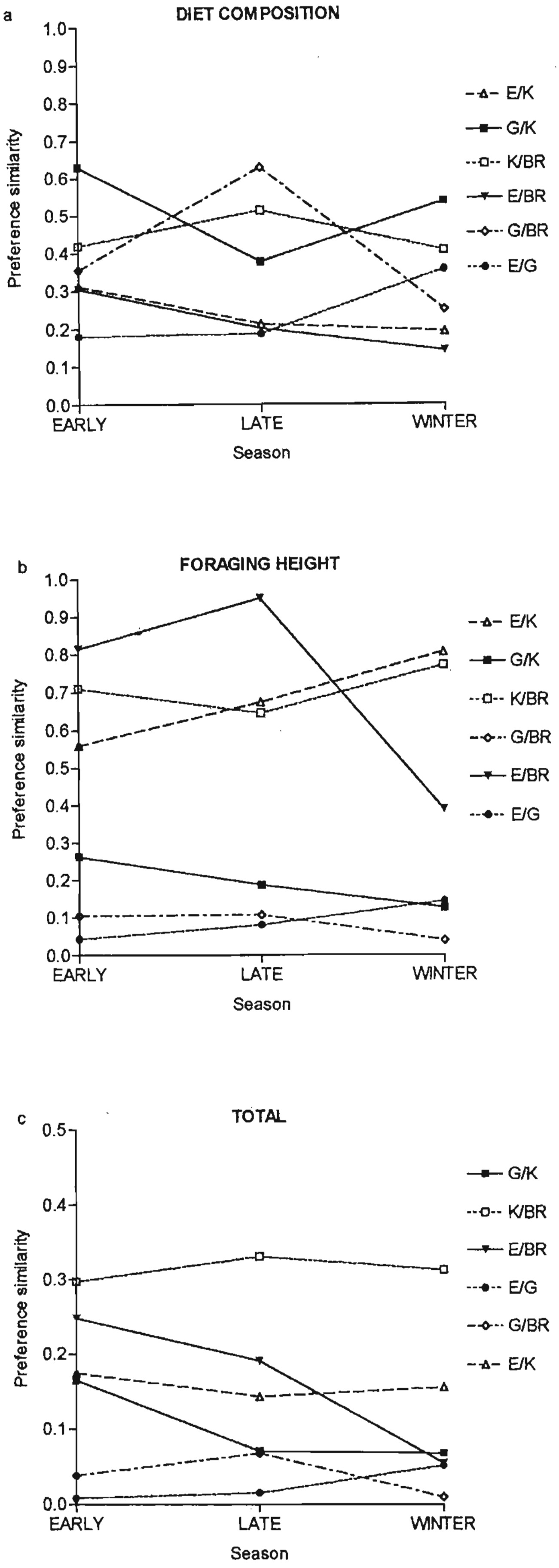


Figure 22. Similarities, based on preferences for woody plant species, in (a) food preference, (b) feeding height preference and (c) total dietary similarities as a product of food and feeding height preferences. Similarities calculated for early summer (EARLY), late summer (LATE) and winter. BR = black rhinoceros, E = eland, G = giraffe, K = kudu.

Total Dietary Similarities

Total dietary similarities were relatively low for all browsers paired with giraffe (Table 35). This was attributed to differences in preferences for browsing heights. Dietary preferences of kudu and black rhinoceros seemed to be most similar. The prediction that the greatest degree of resource partitioning (least similarity) should occur during the dry season was met for browser pairs giraffe-black rhinoceros, eland-black rhinoceros and giraffe-kudu (Fig. 22c). Although this was not the case for the kudu-black rhinoceros and eland-kudu pairs, maximum similarity did not occur during winter between these pairs, but during late and early summer, respectively. More importantly, the degree of resource partitioning during the lean dry period should be investigated. Among all the browser pairs, except eland-kudu and kudu-black rhinoceros, similarity values were less than 0.07 during winter. Even though similarity in preferences was maximal between eland and giraffe during this period, it was still regarded as low. The least extent of resource partitioning, during winter, occurred between kudu and black rhinoceros. For the majority of browser pairs, dietary preferences during winter were judged to be considerably different which implies that resource partitioning does occur.

DISCUSSION

Before turning to the interpretation of results, a number of important issues must be taken into account when comparing the feeding results of the present study. Firstly, the method used for studying the feeding patterns of black rhinoceros was not the same as that for eland, giraffe and kudu. Each procedure has its own drawbacks and as a consequence, diets documented by different methods bear different relations to what the animals actually consume (Wiens 1989). Feeding observations in this study were conducted during the day only and it was assumed that food selection during the day did not differ from that at night. In contrast, the plant-based method accounted for diurnal and nocturnal feeding of black rhinoceros. Secondly, when kudu and eland fed at ground level it was often impossible to identify, by observations from the vehicle, exactly what was being consumed. In these instances, the animals could have been feeding on grasses, forbs, fallen fruit or seedlings of woody plants. Close examination of feeding sites did not solve the problem. Forbs and seedlings are often bitten off at ground level or completely pulled out of the soil (pers obs; Du Toit 1988). In addition, animals may often eat a mixture of plants with one mouthful (Mukinya 1977; Du Toit 1988). Similar problems were encountered by Lamprey (1963), Conybeare (1975), Owen-Smith (1979), Novellie (1983), Du Toit (1988) and Oloo *et al.* (1994).

DIET COMPOSITION

Forage Types

Hofmann and Stewart (1972) and Hofmann (1973) classified eland as intermediate feeders preferring browse, i.e., shrub and tree foliage, and forbs. However, eland utilise varying proportions of grass and browse (McNaughton & Georgiadis 1986; Skinner & Smithers 1990), depending on the availability and protein content of these forage types (Fabricus & Mentis 1990). In the present study, approximately equal proportions of grass and browse were consumed by eland over the entire seasonal cycle. Similar results were obtained for eland in Kenya (Nge'the & Box 1976) and Zimbabwe (Lightfoot & Posselt 1977). In Tanzania, 70 % of the annual diet of eland consisted of grass (Lamprey 1963). Kerr *et al.* (1970), on the other hand, observed that grass was a minor (7 %) component in the diet of eland in Zimbabwe. On an annual basis, grass constituted 16 % of the diet of eland in Bophuthatswana, South Africa (Kelso 1986), and 21 % in Kenya (Field 1975). Despite differences in the annual monocot:dicot ratios in the diet of eland, this study supports what has been found in studies conducted elsewhere of eland: diet composition varies seasonally, with a decrease in grass use and subsequent increase in browse during the dry season. Field (1975) and Buys (1990) found that the proportion of dicotyledons in the diet of eland increased substantially during winter when protein levels in grasses declined. Similarly, eland became almost pure browsers during the dry season in southern Zimbabwe (Kerr *et al.* 1970), Namibia (Jankowitz 1982 in Owen-Smith 1997) and Bophuthatswana, South Africa (Kelso 1986). In the latter three studies, the proportion of grass consumed was related to its availability, which in turn was correlated with rainfall.

Kudu are primarily browsers utilising very little grass (Wilson 1965; Hofmann & Stewart 1972; Conybeare 1975; Owen-Smith 1979, 1982; Novellie 1983; Owen-Smith & Cooper 1985, 1989; Kelso 1986; Du Toit 1988). The small proportion of time kudu allocated to grass during the current study agrees with this general finding. During early summer, the utilisation of grass increased following the first rains of the season, when kudu were recorded grazing newly sprouted grass. The observed rise in grass consumption was also associated with the fact that the majority of burns were carried out during this season. Similar results were obtained for kudu by Novellie (1983) and Owen-Smith and Cooper (1985) where average grass utilisation was low, increased during the wet season and was greatest when kudu grazed the green grass flush on firebreaks. In Kruger National Park (Du Toit 1988) and Pilansberg National Park (Kelso 1986), South Africa, grass constituted less than 2 % of the annual diet of kudu and use was restricted to short periods during the wet season. Wilson (1965) recorded a small amount of green grass, mainly during the rains, in stomach contents of kudu in Zambia. In Wankie National Park, Zimbabwe, Conybeare (1975) observed that the annual diet of kudu consisted of approximately 7 % grass, eaten only during the wet season. Grass use increased substantially during the late wet season (73 %) and the stomach contents of one individual contained 80 % grass. Conybeare (1975) concluded that the amount of grass in the diet appeared to be a function of local conditions.

Giraffe, in the current study, devoted all its feeding time to woody plant species and were never observed utilising grass, forbs or creepers. Similarly, no records were obtained of giraffe consuming grass in Tsavo National Park, Kenya, (Leuthold & Leuthold 1972; Leuthold 1978), Sable Park, Zimbabwe (Stephens 1975), Serengeti National Park, Tanzania (Pellew 1984a) and Kruger National Park (Du Toit 1988) although limited use of forbs and / or creepers were recorded. On rare occasions, giraffe have been observed to eat grass (Lamprey 1963; Smithers

1971 in Oates 1972; Oates 1972; Hall-Martin 1974a; Sauer *et al.* 1977; Hansen *et al.* 1984), when it is green and newly sprouted (Smithers 1971 in Oates 1972) or in areas with sodium-rich soils (Oates 1972).

The method used in this study for assessing the diet composition of black rhinoceros precluded recording the use of plant species with fine stems (grasses, creepers and forbs) as well as fruit and flowers. Therefore, a review of studies where the use of such components could be recorded is necessary in order to compare the utilisation of forage types with eland, kudu and giraffe. Black rhinoceros are browsers, feeding mainly on woody vegetation (Skinner & Smithers 1990), but may utilise grass and forbs. A number of studies have found that grass was either not utilised (Jarman 1971; Joubert & Eloff 1971; Leuthold 1978; Oloo *et al.* 1994) or rarely used by black rhinoceros (Goddard 1968, 1970; Hall-Martin *et al.* 1982). Mukinya (1977) observed that black rhinoceros occasionally take grass together with forbs in the same mouthful. One study indicating a substantial use of grass (36 %) by black rhinoceros was in Tanzania (Lamprey 1963). A common trend among these studies was that the utilisation of grass was greater in the wet than dry season.

In the present study, the prediction that diets of coexisting species should differ in their monocot:dicot ratios was generally met, on an annual basis. Eland utilised a large proportion of grass, while kudu utilised little and giraffe none. Based on the above studies of black rhinoceros, the approximate average utilisation of grass is 5.8 % (n = 8). If this is considered a reliable estimate, then the annual diet of black rhinoceros is very similar to kudu, in terms of the proportion of graminoids and dicotyledons.

Despite differences in the proportional use of monocotyledons by the animal species studied, the proportion of browse in each diet was great. When the browse component is separated into forbs, fruit, flowers and woody forage then some differences are apparent. Forbs formed a large part of the diet of kudu, while utilised little by eland and not at all by giraffe. Other studies have indicated that forbs are an important food source to kudu (Novellie 1983; Kelso 1986), particularly during the wet season (Jarman 1971; Conybeare 1975; Owen-Smith 1979; Du Toit 1988; Owen-Smith & Cooper 1989). Similar to the current study, Lamprey (1963), Kelso (1986) and Kerr *et al.* (1970) observed that eland made limited use of forbs. However, Field (1975) found that forbs made up almost a third of the diet of eland. Numerous studies have shown that giraffe did not utilise forbs (Oates 1972; Leuthold & Leuthold 1972; Hall-Martin 1974a; Sauer *et al.* 1977; Leuthold 1978; Hansen *et al.* 1984; Du Toit 1988) although creepers or vines were occasionally consumed (Leuthold & Leuthold 1972; Leuthold 1978; Du Toit 1988). In Tanzania, Lamprey (1963) and Pellew (1984a) recorded giraffe making limited use of forbs.

The proportion of forbs in the diet of black rhinoceros varies depending on area and season (Emslie & Adcock 1993). In the present study, records were obtained of black rhinoceros consuming *Datura stramonium,* a poisonous exotic forb. Although this forb contributed less than 2 % to the annual diet, every individual of this plant I encountered had been eaten by black rhinoceros. Use of this poisonous plant by black rhinoceros was also recorded by Goddard (1968) and Oloo *et al.* (1994). Forbs contributed relatively little (< 16 %) to the diet of black rhinoceros in Tarangire Game Reserve, Tanzania (Lamprey 1963), Etosha National Park, Namibia (Joubert & Eloff 1971), Tsavo National Park (Leuthold 1978) and Laikipia District, Kenya (Oloo *et al.* 1994). In the Hluhluwe-Umfolozi Complex, South Africa, the proportion of forbs in the diet was 21 % (based on faecal analysis; Emslie & Adcock 1993), in the Masai Mara Game Reserve, Kenya, it was 29 % (Mukinya 1977) and 42 % in Addo Elephant Park, South Africa (Hall-Martin *et al.* 1982). As with grass utilisation, the use of forbs by black rhinoceros was more pronounced during the wet than dry season. A crude average of forb utilisation, based on these studies, is 17.5 % ($n = 7$).

In the current study, eland, kudu and giraffe utilised the fruit (pods) of only *Acacia* species, but to varying degrees. Interestingly, although the pods of *Acacia karroo* were abundantly available, they were not recorded as utilised by any of the browsers. Coe and Coe (1987) state that browsing ungulates prefer indehiscent pods to dehiscent ones and this was generally supported by the current study. Both kudu and giraffe made use of the pods of *Acacia nilotica* and *Acacia sieberiana*, the latter also being used by eland. Kudu also utilised *Acacia tortilis* pods, while giraffe made limited use of the dehiscent pods of *Acacia caffra.* Although pods are considered an important food item for most savanna browsers, particularly during the dry season (Coe & Coe 1987), only eland utilised this forage type substantially. Lightfoot and Posselt (1977) observed eland consuming the pods of *A. sieberiana* as well as *A. karroo*, but no indication of proportional use was given. Pods were consumed by eland only during the dry season in Pilansberg National Park, but contributed little (< 4 %) to the diet (Kelso 1986). In the Kruger National Park less than 4 % of kudu's annual feeding time was devoted to fruit, but during the wet season the fruit of *Sclerocarya birrea* were sought out and avidly consumed (Du Toit 1988). In other studies of kudu fruit also contributed little to the annual diet (Owen-Smith 1979; Owen-

Smith & Cooper 1985; Kelso 1986), although when available they were sought after (Owen-Smith 1979; Owen-Smith & Cooper 1985). Wilson (1965) found the seeds of five *Acacia* species, as well as 11 other woody plants, in the stomach contents of kudu. Giraffe allocated little feeding time to fruit, in the current study. Similar records were obtained in other studies where the fruit of *Acacia* species (Oates 1972; Sauer *et al.* 1977; Pellew 1984a; Du Toit 1988), *Dichrostachys cinerea* (Du Toit 1988), *Combretum* sp. (Oates 1972; Stephens 1975), *Strychnos* sp. (Oates 1972) and *Ximenia caffra* (Stephens 1975) were consumed by giraffe, but only in small proportions.

In the present study, no records were obtained of eland utilising flowers, similar to Kerr *et al.* (1970) and Lightfoot and Posselt (1977). However, in Tanzania the flowers of *Kigelia* were sought after (Lamprey 1963). On only two occasions, in the current study, were kudu and giraffe observed consuming flowers (*A. karroo*). This limited use of flowers by giraffe and kudu was in accordance with studies conducted elsewhere. Flowers made up a small percentage of the diet of giraffe in a Mopane woodland in South Africa (Oates 1972), Sable Park, Zimbabwe (< 0.05 %, Stephens 1975), North-west Province, South Africa (< 0.05 %, Sauer *et al.* 1977) and Serengeti National Park (5 %, Pellew 1984a). When available the flowers of *Acacia nigrescens* were sought after by giraffe in Kruger National Park, forming up to 23.5 % of their monthly diet (Du Toit 1990). Similarly, in a reserve neighbouring Kruger National Park, flowers, particularly *A. nigrescens*, were important for giraffe (Hall-martin 1974a). Owen-Smith (1979), Owen-Smith and Cooper (1985) and Du Toit (1988) observed that although flowers contributed little to the annual diet of kudu, they were avidly eaten when available.

Unfortunately, few data are available for black rhinoceros in terms of fruit and flowers utilised. In Tanzania, flowers (Goddard 1968) and *Kigelia* fruit (Lamprey 1963) made up a small proportion of the diet.

When assessing the utilisation of dicotyledons, the diet of kudu differs from eland and giraffe by the large inclusion of forbs. Pods comprised a large proportion of the diet of eland, but were not extensively utilised by kudu and giraffe. In terms of forage types, the diet of black rhinoceros seems more similar to kudu than eland or giraffe.

Woody Plant Species

When the utilisation of woody plant species was assessed, they included all those fed on, irrespective of plant part. Based on the proportion of microphyllous and broadleaved woody plants, the diets of the four browsers in this study differed over the entire seasonal cycle. However, the principal species in the annual diet of each browser was *A. karroo*, with *A. nilotica* also being prominent, particularly in the diet of giraffe. Eland have been recorded consuming *Acacia* species in other areas but they also utilise a wide variety of other species (Nge'the & Box 1976; Lightfoot & Posselt 1977; Kelso 1986; Buys 1990). Similar results have been obtained in other areas for giraffe (Leuthold & Leuthold 1972; Oates 1972; Hall-Martin 1974a; Hall-Martin & Basson 1975; Stephens 1975; Van Aarde & Skinner 1975 in Sauer *et al.* 1982; Sauer *et al.* 1977; Hansen *et al.* 1984; Pellew 1984a; Du Toit 1988), kudu (Wilson 1965; Owen-Smith 1979; Novellie 1983; Kelso 1986; Owen-Smith & Cooper 1985, 1987a, 1987b, 1989; Du Toit 1988) and black rhinoceros (Goddard 1968, 1970; Joubert & Eloff 1971; Mukinya 1977; Hall-Martin *et al.* 1982; Loutit *et al.* 1987; Emslie & Adcock 1993; Kotze & Zacharias 1993; Oloo *et al.* 1994). According to Owen-Smith (1985), staple browse species in the diet of eland, kudu and giraffe in a broadleaved savanna are from the families Combretaceae (*Combretum* species), Mimosaceae (*Acacia* species, *Dichrostachys*), Rhamnaceae (*Ziziphus*) and Tiliaceae (*Grewia* species). In the current study, giraffe, kudu and black rhinoceros utilised *Ziziphus mucronata*, while *Grewia occidentalis* was also eaten by the latter two browsers. Only giraffe were observed to browse *Combretum erythrophyllum*, possibly because the foliage of this species was beyond the height range of the other browsers.

In savanna woodlands, browsers are affected by changes in the abundance of food supply because of leaf fall of deciduous species (Owen-Smith 1979). Microphyllous woody plant species, such as those of the genera *Acacia* and *Dichrostachys*, are deciduous (Pooley 1993) while numerous broadleaved plants, for example species of *Euclea* and *Rhus*, are considered to be semi-evergreen or evergreen (Owen-Smith & Cooper 1987b; Owen-Smith 1994). A large herbivore, confronted with varying quality and quantity of its food supply, must make suitable modifications to its feeding behaviour in order to maintain a nutrient intake adequate to meet its metabolic requirements (Owen-Smith 1979). It would thus be expected that evergreen or semi-evergreen species become more abundant in the diet during winter.

Seasonal variations in the use of microphyllous and broadleaved woody plants were more apparent in the diet of kudu and black rhinoceros than eland or giraffe in the present study. Black rhinoceros and kudu showed a distinct shift in their diets from predominantly microphyllous plants during summer to broadleaved species during winter. During summer, the principal species in the diet of kudu were *A. karroo*, *A. nilotica* and *Calpurnia aurea*. Most of the plants of these three species available to kudu while feeding had more than 75 % of total leaf present. During the winter months *C. aurea*, considered a broadleaved species in this study, constituted almost a third of the diet of kudu, despite the fact that 42 % of the individual plants bore no leaves. Numerous other broadleaved plants were eaten in small amounts. All individuals of *Maytenus heterophylla* and *Rhus pentheri* carried some leaf material and these species may serve as dry season reserves. A similar seasonal pattern in the diet of kudu was observed in Nylsvley Nature Reserve, South Africa (Owen-Smith 1985). In other studies, reserve species during the dry season included *Croton* sp. (Jarman 1971), *M. heterophylla* and *Euclea divinorum* (Owen-Smith 1979; Novellie 1983), *Euclea crispa* and *Rhus* species (Owen-Smith & Cooper 1985, 1989; Kelso 1986).

In the current study three species, namely *A. karroo*, *A. nilotica* and *A. tortilis*, made up the bulk of the diet of black rhinoceros during all three seasons, but their contribution to the diet decreased from early to late summer and was least during winter. During early summer, the majority of the individuals of these *Acacia* species available to black rhinoceros while feeding carried little ($\leq$ 25 %) or no leaf material. This was because black rhinoceros often fed in recently burnt areas, as observed elsewhere (Emslie & Adcock 1993). A similar situation prevailed during winter, but the lack of foliage was as a result of seasonal leaf loss and burning. Despite the fact that most of the *Acacia* species bore more leaf material during late than early summer, black rhinoceros utilised these species to a lesser degree during the former season. *Coddia rudis* was more prominent in the winter than late summer diet, even though individuals of this species carried less leaf in the former than latter season. Therefore, black rhinoceros did not appear to select species based on the amount of available leaf material, but rather favoured burnt plants. In fact, almost 30 % of the twigs consumed by black rhinoceros in the current study lacked leaves. Being a non-ruminant and of large body size, it can meet its metabolic requirements from such low quality material (Owen-Smith 1988). Although use of *C. rudis*, *Euphorbia ingens* and *R. pentheri* was not restricted to winter, these species were regarded as important plants during the dry months. A common pattern in studies of black rhinoceros was the utilisation of succulents, particularly during the dry season (Goddard 1968; Jarman 1971;

Hall-Martin *et al.* 1982; Loutit *et al.* 1987; Oloo *et al.* 1994; Dudley 1997), which was attributed to their higher moisture content compared with other woody plant species (Goddard 1968; Hall-Martin *et al.* 1982; Loutit *et al.* 1987; Dudley 1997). Other important species in the diet of black rhinoceros during the dry season were *A. tortilis* in Tanzania (Goddard 1968), *Grewia* species (Goddard 1970) and *Euclea* species (Oloo *et al.* 1994) in Kenya, *Boscia* species in Zimbabwe (Jarman 1971) and Namibia (Loutit *et al.* 1987) and *Diospyros* sp. in Zimbabwe (Jarman 1971). These studies suggest that black rhinoceros are selective feeders and modify their diet according to environmental conditions.

In terms of microphyllous and broadleaved woody plants, the diet of eland did not vary remarkably across seasons. Nonetheless, the principal species in the diet were *A. karroo* and *A. sieberiana* during early summer, *C. aurea* in late summer and *A. karroo* during winter. Similar to black rhinoceros, the selection of plant species does not seem to be governed by the availability of green leaf material. During early summer, although a greater proportion of individual plants of *A. nilotica* bore leaves compared with *A. karroo* and *A. sieberiana*, it was eaten less frequently. Despite the fact that *M. heterophylla* carried approximately 60 % of the potential maximum leaf material during winter, it was not eaten. Eland were recorded to utilise only *A. karroo* and *A. sieberiana* during winter, even though the majority of the plants carried no leaf material. The dietary results may not, however, accurately reflect the true diet of eland owing to the limited number of feeding events (132). In other studies (Kerr *et al.* 1970; Field 1975; Lightfoot & Posselt 1977; Buys 1990) the feeding habits of eland appear to be determined by the availability of green plant material. In Mopane (*Colophospermum mopane*) savanna in southern Zimbabwe, eland utilised *C. mopane* and *Grewia* species until mid-winter (Kerr *et al.* 1970). Only when these species dropped their leaves did *E. divinorum* (an evergreen species) become acceptable to eland (Kerr *et al.* 1970), possibly because of its relatively high crude protein levels compared with other species at that time (Lightfoot & Posselt 1977). The use of *E. divinorum* ceased when deciduous species, especially *Combretum apiculatum*, flushed in spring (Kerr *et al.* 1970). A similar change in feeding patterns by eland was observed by Field (1975) and Buys (1990). Although *Grewia tristis* was utilised throughout the year it was important in the diet of eland for two to three months after the rains had ceased. When *G. tristis* lost their leaves eland turned to an evergreen *Combretum* shrub (Field 1975). Buys (1990) found *Diospyros lycioides* to be abundant in eland faeces throughout the year, except mid-winter when *Tarchonanthus camphoratus* occurred in the largest proportions. *Grewia flava* was utilised during each season (Buys 1990). In Pilansberg National Park, eland made less use of broadleaved species during the dry than wet season. *Acacia caffra* and *A. karroo* were important species during both seasons, while *Combretum molle* and *Euclea crispa* were prominent in the diet of eland during the wet and dry season, respectively (Kelso 1986). Although these studies indicate that eland adapt their feeding habits to suit prevailing circumstances this was not particularly evident in this study. This may, however, be because the feeding habits of eland were poorly sampled in the current study.

During the present study, *Acacia* species contributed more than 90 % to the diet of giraffe during all three seasons. The dependency on the genus *Acacia* during winter indicates the unusual situation of deciduous species providing food during the dry season. With the exception of *Acacia robusta*, more than 70 % of the individual plants of all *Acacia* species available to giraffe during winter bore leaves, yet less than 3 % of the material consumed by giraffe consisted of twigs without leaves. It would, therefore, appear that giraffe selected individual plants which provided leaf material. This selection for leaves has been recorded elsewhere (Pellew 1984a; Du Toit 1988). The extensive utilisation of *Acacia* species in southern Africa is not uncommon (Hall-Martin 1974a; Stephens 1975;Van Aarde & Skinner 1975 in Sauer *et al.* 1982; Hansen *et al.* 1984; Owen-Smith 1985). Giraffe in the Timbavati (Hall-Martin 1974a) and Jack Scott Nature Reserve (Van Aarde & Skinner 1975 in Sauer *et al.* 1982), South Africa, fed predominantly on *Acacia senegal* and *A. caffra*, respectively, even during the dry season. However, *C. mopane* was also important to giraffe in the Timbavati (Hall-Martin 1974a). Hansen *et al.* (1984) found that *Acacia* and *Olea* species were most abundant in dung samples during the dry period. In the present study, broadleaved species were slightly more prominent in the diet of giraffe during winter and early summer than late summer. A change in the diet of giraffe from deciduous plants in the wet season to evergreen or semi-evergreen woody species in the dry season has been documented by Leuthold and Leuthold (1972), Hall-Martin and Basson (1975), Leuthold (1978), Sauer *et al.* (1982) and Pellew (1984a). In the Northern Province, South Africa, deciduous plants in the diet of giraffe were replaced by *Euclea undulata*, *C. mopane*, *Maytenus senegalensis*, *Schotia brachypetala* and *Diospyros mespiliformis* (Hall-Martin & Basson 1975). Giraffe, in the Serengeti, switched from feeding on *Acacia* species to *Grewia* species during the dry season (Pellew 1984a).

The selection of woody plant species by the four browsers may have been influenced by fibre (Sauer *et al.* 1982; Pellew 1984a), leaf condensed tannin (Cooper & Owen-Smith 1985; Cooper *et al.* 1988; Du Toit 1988), crude protein (Hall-Martin & Basson 1975; Sauer *et al.* 1982; Pellew

1984a; Du Toit 1988), nitrogen (Sauer *et al.* 1982; Cooper *et al.* 1988; Du Toit 1988), phosphorus (Pellew 1984a; Du Toit 1988), ash (Sauer *et al.* 1982; Hall-Martin & Basson 1975) and potassium (Pellew 1984a) content, and structural defences (Cooper & Owen-Smith 1986; Owen-Smith & Cooper 1987b; Du Toit 1988). However, owing to time and logistic constraints, I was unable to assess the influence of these factors on feeding selection.

THE GUILD AND INTERSPECIFIC COMPETITION

Owing to the fact that direct evidence of interspecific competition could not be obtained from the present study, because experimental manipulations were not conducted, one is forced to infer the presence or absence of competition. The existence of considerable overlap between animal species does not confirm the presence of competition. Furthermore, there is great ambiguity as to what measured resource overlap values actually convey (Sale 1974; Hulbert 1978; Abrams 1980; Lawlor 1980; Schoener 1982, 1986; Wiens 1989; Krebs 1999). This makes it difficult to assess what the extensive dietary overlap values found among browser pairs in the current study suggest in terms of interspecific competition. The approach I used to assess the significance of interspecific competition was to establish whether predictions, relating to competition under conditions of resource limitation, were met.

If interspecific competition is the process driving ecological separation, then dietary diversity and overlap between species was predicted to decrease during the dry season (Schoener 1982, 1986). To avoid or reduce the extent of overlap during this season, the browsers at WNR should each make use of distinct food types, i.e., refuges (Jarman 1971), there should be a clear stratification in feeding heights (Lamprey 1963; Du Toit 1988, 1990) and the browsers should make use of different sizes of food (Schoener 1986). Lastly, for competition to occur it must be shown that the browsers are limited by the amount of available resources (Sale 1974; Hurlbert 1978; Abrams 1980; Lawlor 1980; Krebs 1999). Overlap may also be reduced by different herbivores utilising different habitats (Schoener 1974, 1986). This is discussed under *Selection for Vegetation Types.*

Dietary Diversity and Overlap

The competition theory predicts that animals should specialise during times of resource scarcity, thus diversity in diets should decrease and resource overlap between species should decline (Schoener 1982, 1986). Contrary to this, the optimal foraging theory suggests that when resources become limited animals should expand their diet resulting in an increase in dietary diversity and overlap between species (MacArthur & Pianka 1966; Pyke *et al.* 1977).

Results from the present study, as well as others (Leuthold 1978; Kelso 1986; Du Toit 1988), are not consistently in agreement with the strategies predicted by either the competition theory or optimal foraging theory. However, the two theories need not completely contradict each other or be mutually exclusive. During winter, little other than the woody component was available and animals were thus forced to specialise by concentrating their feeding on this one food type. As a consequence overlap, with regards to forage types, generally increased during the dry season. However, within this one food component, the browsers, with the exception of eland, diversified their diets by increasing the number of woody plant species utilised and overlap between all browser pairs decreased. Animals need to adjust their diets during the dry season in order to meet their nutritional and energy demands (Owen-Smith 1979). Owing to the differences in body size of these browsers, and hence different metabolic costs and digestive efficiency, the available woody food may be partitioned according to its nutritional quality (McNaughton & Georgiadis 1986). It seems likely that nutritional demands decreased the extent of overlap between the browsers at WNR during winter, but not to the extent of complete ecological separation. Overlap between browser pairs was still extensive and, therefore, the potential for interspecific competition still exists.

Overlap Avoidance or Reduction

Jarman (1971) showed that during the early dry season overlap decreased because each animal made use of different food types, i.e., refuges. In the current study, none of the browsers made exclusive use of a particular forage type during the dry period but rather all depended greatly on woody plant species, similar to other studies (Leuthold 1978; Kelso 1986; Du Toit 1988). Eland utilise monocotyledons which kudu, giraffe and black rhinoceros rarely exploit. In this way eland can reduce the degree of overlap with the other browsers on an *annual* basis. However, during winter the proportion of grass in the diet decreased substantially, probably owing to a decline in protein levels (Field 1975; Buys 1990) and, therefore, this forage type does not act as a 'refuge' for eland during winter.

In the present study, black rhinoceros was the only browser observed utilising *E. ingens*. Although the latex produced by most *Euphorbia* species is highly toxic (Coates Palgrave 1992), several other studies have recorded the use of this genus by black rhinoceros (Lydekker 1926 in

Goddard 1968; Van Rensburg 1963 in Dudley 1997; Goddard 1968; Hargreaves 1978 in Dudley 1997; Hall- Martin *et al.* 1982; Loutit *et al.* 1987; Dudley 1997). Black rhinoceros are thus able to utilise plants which, because of formidable chemical defences, cannot be used by other herbivores (Loutit *et al.* 1987). During winter, *E. ingens* was, however, utilised infrequently, contributing less than 1 % to their diet, and thus this species is unlikely to act as a 'refuge' for black rhinoceros.

The use of different feeding levels has been suggested as a mechanism reducing overlap among browsing species, especially when these animals differ in body size (Lamprey 1963; Leuthold 1978; McNaughton & Georgiadis 1986; Du Toit 1988, 1990). In the current study, overlap in browsing heights among black rhinoceros, eland and kudu were extensive, while those for browsers paired with giraffe were relatively small. However, despite clear differences in the average feeding height of giraffe with the other browsers, giraffe browsing was not confined to upper layers of the vegetation, as demonstrated in this study as well as others (Waytt 1969 in Leuthold & Leuthold 1972; Leuthold & Leuthold 1972; Sauer et al. 1977; Leuthold 1978; Pellew 1984a; Du Toit 1988, 1990; Young & Isbell 1991), thus separation was not complete and overlap was not reduced (Du Toit 1990).

Overlap in the utilisation of woody plant species as well as browsing heights was considerable for the eland-black rhinoceros and kudu-black rhinoceros pairs. A possible way to decrease the extent of overlap among these browsers may be to differentiate the food resource based on size (Schoener 1986). Owing to differences in dentition and mouth size, black rhinoceros are capable of utilising far larger twigs than eland or kudu. Joubert and Eloff (1971) found that 10 mm was the maximum twig thickness that black rhinoceros browsed, but in the current study, twigs with a diameter of 30 mm were recorded as utilised by this browser. Eland and kudu consume twigs of very similar diameter, up to 7 mm (Kerr *et al.* 1970; Kelso 1986) and 6 mm (Kelso 1986), respectively. Of course, black rhinoceros also utilise smaller twigs, thereby depleting the resource available to the smaller browsers, so overlap was not reduced.

It is clear from the above discussion, that the browsers at WNR did not resort to any of the predicted strategies in order to avoid or reduce the degree of overlap among them. This suggests that interspecific competition is not the process shaping the feeding habits of these browsers. However, there was a reduction in overlap between browser pairs, not because the browsers specialised but rather diversified their diets with respect to woody plant species. The decrease in overlap during winter may suggest competition between species is likely. Before such conclusive statements can be made, it is necessary to determine if the browsers at WNR are limited by the amount of available food.

Food Limitation

Food, in terms of both quality and quantity, is considered to be the ultimate resource limiting animal populations. However, small herbivores will be more limited by food quality and large herbivores by food quantity (Murray & Illius 1996). For competition to occur resources must be limiting (Hulbert 1978; Abrams 1980; Lawlor 1980; Krebs 1999). In the field this is difficult to establish for certain (Leuthold 1978), but it is generally accepted that in African savannas, food decreases in both quality and quantity during the dry season (Owen-Smith 1982; Sauer *et al.* 1982; Pellew 1984b; Cooper *et al.* 1988) and that this is the most likely period for competition to occur (Schoener 1982, 1986). The majority of the winter diet of each browser consisted of woody plants, thus it was necessary to determine if the browsers are in fact limited by the availability of this food resource. Mortalities, especially where predators are absent, can be used as an indication of food limitation (MacNally 1983).

At WNR, the amount of available woody foliage decreased during winter, as indicated by phenological differences. Although only 18 % of all plants available to eland bore leaves during winter, at least 65 % of the individual plants available to kudu, giraffe and black rhinoceros carried leaf material. Therefore, there appeared to still be a large amount of food available during the dry winter period. However, the quality of available food was unknown but, most likely declined (Owen-Smith 1982; Sauer *et al.* 1982; Cooper *et al.* 1988). Owing to the differences in body size of the browsers studied, the effects of the prevailing conditions at WNR on each browser population is expected to differ.

Mortalities of black rhinoceros at WNR were as a result of injuries sustained during fighting. The black rhinoceros population, therefore, appears to be restricted by social behaviour rather than food. However, if social constraints are the result of territoriality and limited space, this may reflect a food resource limitation. Eland and giraffe did suffer losses during the dry season, but not to the same extent as kudu. For example in 1999, 27 % of the kudu population died but none of the other browsers did. Eland and, particularly, giraffe and black rhinoceros, because of their large body size are able to store greater reserves of fat than smaller animals (Owen-Smith 1988), such as kudu. They can therefore survive longer on a starvation diet than smaller animals (Owen-Smith 1988). In addition, large herbivores can tolerate low quality food (McNaughton & Georgiadis 1986; Owen-Smith 1988). Although food may be in short supply and of poor quality at WNR during winter, most of the individuals of the larger browsers can still meet their energy requirements. Conversely, not all individuals of the kudu population at WNR are meeting their nutritional and energy requirements during winter. Being smaller, kudu require higher quality foods to survive than do the larger browsers. The high mortalities of kudu may be as a consequence of the quality of abundant foods dropping to levels no longer acceptable to kudu and good quality plants being low in abundance. In an African savanna crude protein levels in plants drop by up to 30 % and acceptability of woody plants by kudu was correlated with food value, in terms of protein-tannin content (Cooper *et al.* 1988). Large herbivores remove large quantities of plant material, but because they do select high quality foods when available (Owen-Smith 1988), they may deplete the abundance of good quality food items for smaller herbivores.

Owing to the fact that larger herbivores are able to tolerate poor quality foods and store large fat reserves, they appear to have an advantage over smaller browsers during the dry season. Therefore, larger browsers, particularly giraffe and black rhinoceros, may exert a pronounced competitive effect on a smaller browser, i.e., kudu, under conditions of resource limitation.

SELECTION FOR VEGETATION TYPES

INTRODUCTION

Savanna vegetation in southern Africa is markedly heterogeneous (e.g. Hirst 1975) and herbivores exhibit a correspondingly heterogeneous distribution while feeding because they display varying degrees of habitat selectivity (Jarman 1971; Hirst 1975). Ungulate movements and habitat choices by large herbivores are associated with high quality food (McNaughton & Georgiadis 1986; Fritz *et al.* 1996) rather than with gross vegetation structure *per se* (Ferrar & Walker 1974; McNaughton & Georgiadis 1986). The quantity and quality of available browse for herbivores can be expected to vary among locations depending on species composition because of differences in palatability and accessibility, and edaphic conditions owing to its affect on the nutritive value of plant species (Bell 1982). Habitat quality can, therefore, be expected to affect an individual's ability to survive and reproduce, which means that it is unlikely that evolution will leave habitat selection to chance (Melton 1987).

Differential habitat selection has been proposed as a mechanism contributing to the ecological separation of herbivores (Lamprey 1963; Ferrar & Walker 1974; Schoener 1974, 1986; Leuthold 1978; Manley *et al.* 1993). Schoener (1974) reviewed 81 studies on resource partitioning and found that 90 % of the groups were separated by habitat. Lamprey (1963) found that herbivores in Tarangire Game Reserve, Tanzania, were separated spatially and temporally by either feeding in different habitats during the same season or in the same habitat during different seasons. Of the large herbivores that Leuthold (1978) studied in Tsavo National Park, Kenya, overlap in habitat selection tended to be least for species pairs with great food overlap. A similar finding was reported by Du Toit (1988) where great overlaps in habitat use by giraffe, kudu and impala, particularly during the dry season, were reduced by these animals feeding along distinct foraging paths. However, ecological separation among coexisting herbivores may not always be complete. For example, of the 14 large herbivores studied in Kyle National Park, Zimbabwe, only eight of these species were separated by habitat (Ferrar & Walker 1974). Fritz *et al.* (1996) found that overlap in habitat utilisation as well as diet between impala and kudu was extensive, even during periods of resource scarcity.

The driving force behind habitat partitioning, especially during the dry season, has been considered to be interspecific competition (Schoener 1974, 1986; Leuthold 1978). Although patterns of habitat partitioning have been demonstrated (Lamprey 1963; Ferrar & Walker 1974;

Leuthold 1978; Du Toit 1988; Dekker *et al.* 1996), the assumption that competition is the cause of these patterns has been challenged. Other factors such as predators, parasites, facilitation, topography and proximity to water may influence the use of habitats (McNaughton & Georgiadis 1986). Habitat selection by zebra, Thomson's and Grant's gazelles was strongly influenced by predation while use of habitats by kongoni was attributed to facilitation or interspecific competition with wildebeest, in the Serengeti-Mara region of Tanzania and Kenya (Sinclair 1985). In Kyle National Park herbivore distribution was associated with topographic features, such as slope, degree of rockiness and boulder cover, but distance to water was an irrelevant environmental factor (Ferrar & Walker 1974). Du Toit (1995) suggests that males and females of a particular species may have different foraging patterns, and hence different habitat preferences, because of differences in nutritional requirements.

The habitat of an organism is defined as "the area containing the biotic and abiotic environmental components for the survival of a population of that organism" (Fabricius & Mentis 1990). An homogenous vegetation unit is distinguished by similarities in vegetation structure, species composition, slope, aspect and soil type (Van Rooyen & Theron 1990). Therefore, a vegetation type is considered an appropriate habitat unit for large mammalian herbivores.

The objective of this part of the study was to investigate the spatial and temporal distribution of eland, kudu and giraffe. I aimed to establish whether usage by an animal was differentiated in vegetation types and if this changed over time. For determining if species pairs were associated, I measured how often two species were likely to be found in the same location.

METHODOLOGY - DATA COLLECTION

Direct counts of individuals were not considered possible at Weenen Nature Reserve. Firstly, the road network in the study area is restricted and not designed to sample vegetation types in proportion to their area of occurrence and, thus, road surveys may be biased. Secondly, manpower was limited and foot surveys could not be conducted. It was therefore concluded that a dung count method would be best for estimating the spatial distribution of eland, giraffe and kudu over a complete seasonal cycle. Neither the direct count nor dung count methods could be used for black rhinoceros, owing to rare sightings of this browser and social constraints of dunging by this animal.

The dung survey was based on the assumption that more dung is deposited where an animal spends a greater proportion of its time feeding (see Novellie & Winkler 1993). In order to conduct the dung counts, 8 x 8 m quadrats were used. This quadrat size proved to be adequate in a pilot study and a small quadrat size ensures uniform efficiency of searching. At the start of the study a complete vegetation map of the reserve did not exist and, therefore, permanently marked plots were distributed randomly throughout the reserve, to ensure a complete and unbiased coverage of the study area. The corners of each plot were marked with rock piles and the location of each quadrat was accurately recorded on 1:10 000 orthophotos. All vegetation types, except Valley Bushveld and Riverine Thornveld, contained both burnt and unburnt areas for the 1998 season. Data collection was completed before burning commenced in 1999.

A total of 45 quadrats were cleared of all dung at an initial survey, in June 1998. All quadrats were sampled from July 1998 to end July 1999, at four-week intervals (i.e., a total of 14 surveys). Pellet- groups were counted and removed from each quadrat and special care was taken to record groups which may have settled below the herb layer. To be counted, a group had to contain at least eight pellets similar in size, shape, texture and colour, and for those groups straddling the quadrat boundary only one pellet of the group had to occur in the quadrat. The 'eight-pellet' rule ensured that partly decomposed groups were still counted; it also meant that a group inadequately cleared would not be counted again at the next visit. Pellets were rarely missed on the first count and, if so, then only one or two remnant pellets survived.

Pellet decomposition rates were determined in order to confirm the appropriateness of a count interval of four weeks (28 days). Pellet-disappearance trials were established at the beginning of each season. Fresh pellet-groups (collected immediately they were voided or early in the morning and judged to have been dropped overnight) from each species under consideration were collected and placed in shaded and unshaded sites. A minimum of three pellet-groups were included in each species-by-site trial. Pellet-group decay was sampled on a weekly basis for four weeks noting the percentage disappearance of each pellet-group.

UTILISATION OF VEGETATION TYPES

Initially, the abundance of pellet-groups was to be used for determining the degree of utilisation of a specific vegetation type by the browsers. However, possibly owing to the small populations of animals considered, frequency of sampling and small quadrat size used, the abundance of dung in each quadrat was low. This necessitated the transformation of each data set to a binary variable. The presence (1) or absence (0) of each browser species in each quadrat was thus used as the dependent variable. Logistic regression models (Hosmer & Lemeshow 1989) were fitted to the data, for each animal species, using GENSTAT (GENSTAT 5 Committee 1987). For all models the logit-link function was used. The analyses were performed to investigate how the likelihood of the presence of browsers related to the explanatory factors, vegetation type and season. Data were pooled into six vegetation types, i.e., Valley Bushveld, Bushveld, Thornveld, Riverine Thornveld, Mixed Veld and Open Woodland, and three seasons, namely, winter (May to August), early summer (September to November) and late summer (December to April). A description of each vegetation type is given in the Study Area section (Table 1; See Appendix 1 for revised names of vegetation types).

An advantage of the logistic model is the estimation of odds ratios. An odds ratio(ψ), measures how much more (or less) likely the odds of success of data set 1 is to the odds of success of data set 2 (Hosmer & Lemeshow 1989). For example, how much more or less likely is an animal to visit vegetation type A compared to vegetation type B? This is given by:

$$\psi = \frac{\pi(1)_1 \;/\; [1-\pi(1)_1]}{\pi(1)_2 \;/\; [1-\pi(1)_2]} = \frac{\textit{odds of success - vegetation A}}{\textit{odds of success - vegetation B}}$$

An odds ratio greater than 1 suggests that an animal is more likely to visit vegetation type A than vegetation type B, while an odds ratio less than 1 implies the opposite. A disadvantage of the model is that predicted probabilities are only approximate estimates and, therefore, do not always agree with findings of odds ratios[3]. Confidence intervals ($\alpha = 0.10$) were constructed for each odds ratio and predicted probability. Broader confidence interval estimates were used owing to the nature of the data.

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Predictions of the logistic regression model, in this case, indicate the *probability* of the presence of dung of animal species *x* in vegetation type *y*. Therefore, preference, which is calculated by comparing the proportion of use of a component to its proportional availability, could not be estimated. Although Johnson (1980) compared ranks of habitat use with ranks of habitat availability, his method necessitates information for each animal considered individually (Alldredge & Ratti 1986) and thus could not be used for estimating preference.

ASSOCIATION

For measuring how often two species are likely to be found in the same location, measures of association are recommended (Ludwig & Reynolds 1988). For each season, association between all pair-wise combinations of browser species, i.e., eland-kudu, eland-giraffe and giraffe-kudu, was determined by a chi-square independence test (presence-absence data). If an association was found to exist ($P < 0.10$) then Jaccard's interspecific association index (JI) (Ludwig & Reynolds 1988) was used to test the strength of this relation by:

$$JI = \frac{a}{a+b+c}$$

where a is the number of quadrats where both species occur, b is the number of quadrats where species A occurs, but not B, and c is the number of quadrats where species B occurs, but not A. Jaccard's index ranges from 0, when the two species are never found together, to 1, when both species always occur together. To avoid biased chi-square test statistics, Yates' continuity correction was used when a cell in the 2 x 2 contingency table had an expected frequency < 1 or if more than two cells had expected frequencies < 5 (Ludwig & Reynolds 1988).

RESULTS

In general, vegetation types were sampled in proportion to their area. However, Valley Bushveld and Bushveld were slightly under-sampled. Estimated population sizes in 1998 were 80 eland, 60 giraffe and 180 kudu. Owing to the greater number of kudu it is not surprising that kudu dung was present more frequently (60.4 %) over all counts (quadrats by surveys) compared with eland (13.2 %) and giraffe (13.4 %). When present, the abundance of pellet-groups in each quadrat was low which probably indicates that the 8 m x 8 m quadrats were too small, under the prevailing circumstances. It is recommended that larger quadrats, perhaps 12 m x 12 m, be used in similar situations, but the size would need to be checked in a pilot study.

Pellet-disappearance trials indicated that, on average, at least 10 % of pellets in a group were still present after 28 days during summer (Table 36). During winter, pellets did not decompose rapidly and after four weeks no more than 40 % of each pellet-group had disappeared. Each season-by-site trial for each browser showed that pellets decomposed more rapidly in the shade than in the sun, possibly owing to a higher moisture content in the former than latter site. These results confirm that an interval of 28 days would ensure that pellet-groups had not decomposed completely before the next survey.

Table 36: Range of pellet decomposition (% lost) after 28 days for each species-by-site trial for each season

Animal species	Site	Season		
		Early summer	Late summer	Winter
Eland	Shaded	50 - 70	10 - 45	0 - 40
	Unshaded	15 - 20	0 - 40	0 - 35
Kudu	Shaded	40 - 65	0 - 80	0 - 30
	Unshaded	10 - 20	0 - 40	0 - 20
Giraffe	Shaded	60 - 90	5 - 15	0 - 20
	Unshaded	15 - 20	0	0

UTILISATION OF VEGETATION TYPES

Kudu [reference: Appendix 9 (logistic regression output)]

Disregarding seasons, the likelihood of the presence of kudu differed ($P < 0.001$) among vegetation types. The probability of kudu being present in Mixed Veld and Open Woodland was significantly less than the other vegetation types (Fig. 23a). Although predicted probabilitites did not indicate any further differences among vegetation types, odds ratios showed that kudu were between 1.1 and 3.9 times less likely to visit Thornveld than Riverine Thornveld (Table 37). The odds of kudu being present in Riverine Thornveld was 3.8 and 15.9 times greater than Mixed Veld and Open Woodland, respectively.

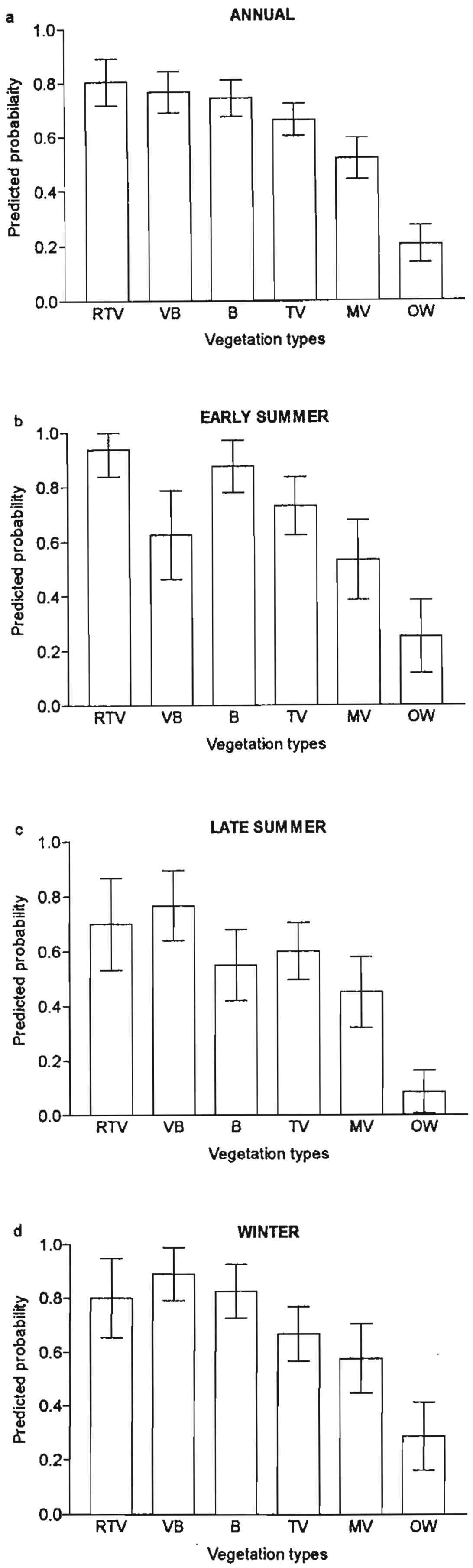

Figure 23. Predicted probabilities and 90 % confidence intervals from logistic regression models of the presence of kudu dung across six vegetation types for (a) whole year, (b) early summer, (c) late summer and (d) winter. Key to vegetation types: B = Bushveld, MV = Mixed Veld, OW = Open Woodland, RTV = Riverine Thornveld, TV = Thornveld, VB = Valley Bushveld.

Table 37: Odd ratios of Riverine Thornveld relative to alternative vegetation types, from a logistic regression model, for kudu

Vegetation type	Odds ratio (ψ)	Confidence intervals (α =0.10)
Valley Bushveld	1.254	0.622 - 2.527
Bushveld	1.429	0.742 - 2.754
Thornveld	2.101	1.135 - 3.884
Mixed Veld	3.808	2.018 - 7.185
Open Woodland	15.954	8.012 - 31.785

There was a weak interaction ($P < 0.13$) between explanatory variables, vegetation type and season. All vegetation types, except Bushveld, were less likely ($P < 0.10$) to be visited than Riverine Thornveld during early summer (Fig. 23b). Kudu were significantly more likely to be present in Bushveld than Mixed Veld, while Open Woodland had the lowest likelihood of the presence of kudu, during this season. During late summer, the probability of kudu being present in Mixed Veld was less ($P < 0.10$) than Valley Bushveld (Fig. 23c). Similar to early summer, the likelihood of kudu visiting Open Woodland was less ($P < 0.10$) than the other vegetation types during late summer (Fig. 23c) and winter (Fig. 23d). There were no significant differences in the likelihood of the presence of kudu among the remaining vegetation types, during winter.

For all vegetation types, except Valley Bushveld and Bushveld, the likelihood of the presence of kudu did not differ significantly across seasons. Valley Bushveld was more likely ($P < 0.01$) to be visited by kudu during winter than early summer (Fig. 23). Kudu were significantly less likely to be present in Bushveld during late summer than the other two seasons.

Eland [reference: Appendix 10 (logistic regression output)]
There were differences ($P < 0.08$) in the likelihood of the presence of eland among vegetation types when ignoring time periods. Eland were less likely ($P < 0.10$) to visit Open Woodland than Mixed Veld and Thornveld, and no further differences in predicted probabilities were found (Fig. 24a). However, odds ratios, comparing Mixed Veld to alternative vegetation types, demonstrated that Bushveld was also less likely ($P < 0.10$) to be visited than Mixed Veld (Table 38).

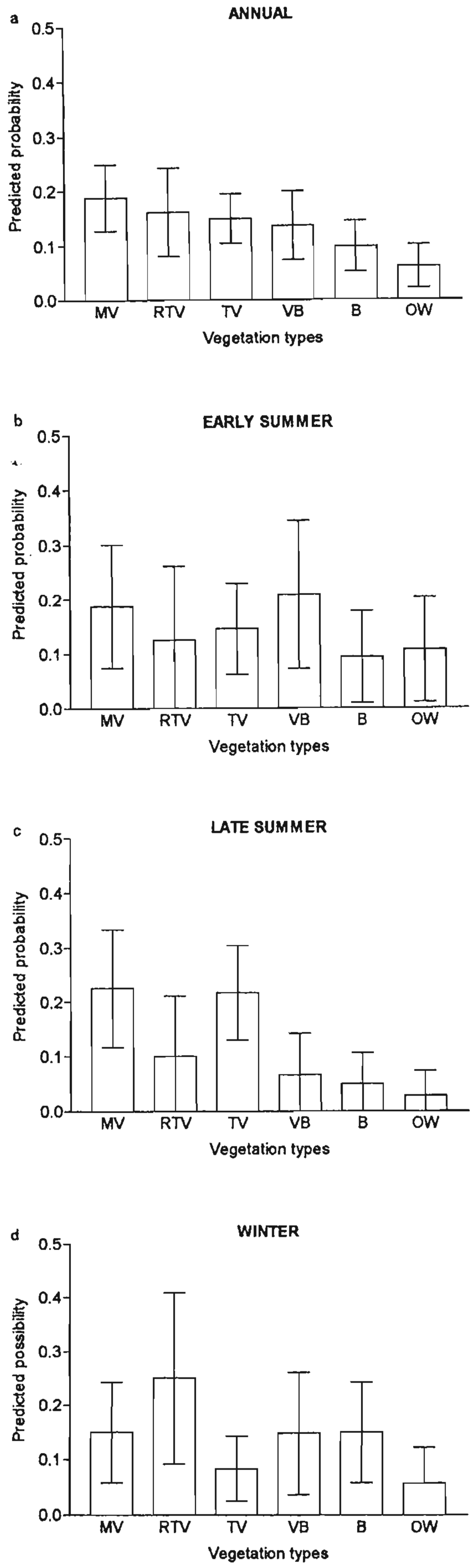

Figure 24. Predicted probabilities and 90 % confidence intervals from logistic regression models of the presence of eland dung across six vegetation types for (a) whole year, (b) early summer, (c) late summer and (d) winter. Key to vegetation types: B = Bushveld, MV = Mixed Veld, OW = Open Woodland, RTV = Riverine Thornveld, TV = Thornveld, VB = Valley Bushveld.

Table 38: Odd ratios of Mixed Veld relative to alternative vegetation types, from a logistic regression model, for eland

Vegetation type	Odds ratio (ψ)	Confidence intervals (α =0.10)
Riverine Thornveld	1.205	0.587 - 2.474
Thornveld	1.320	0.773 - 2.255
Valley Bushveld	1.469	0.756 - 2.852
Bushveld	2.119	1.213 - 3.702
Open Woodland	3.539	1.594 - 7.862

There was a weak, non-significant interaction ($P < 0.23$) between vegetation types and seasons indicating that the likelihood of visitations by eland in various vegetation types was relatively consistent over time. However, during late summer eland were more likely ($P < 0.10$) to be present in Mixed Veld and Thornveld than Bushveld and Open Woodland (Fig. 24c). Across seasons, there were no significant differences in probability of the presence eland among vegetation types (Fig. 24).

Giraffe [reference: Appendix 11 (logistic regression output)]
Giraffe dung was not found in any of the quadrats representing the Valley Bushveld vegetation type for any of the 14 surveys. It was, therefore, concluded that giraffe did not utilise this vegetation type and it was excluded from analyses.

Omitting seasons, there were highly significant differences in the probability of giraffe being present in different vegetation types. Thornveld was more likely ($P < 0.10$) to be visited by giraffe than Open Woodland (Fig. 25a). In addition, giraffe were less probable ($P < 0.10$) to visit Bushveld, Riverine Thornveld and Open Woodland than Mixed Veld. The odds ratios of Mixed Veld relative to the four remaining vegetation types indicated that giraffe were also less likely to visit Thornveld than Mixed Veld (Table 39). Giraffe were 4.5 times more likely to visit Mixed Veld than Open Woodland. The odds of giraffe being present in Riverine Thornveld and Bushveld were, respectively, 3.6 and 2.4 times less than Mixed Veld. In other words, the odds of finding giraffe in Mixed Veld was far more likely than in any other vegetation type.

Table 39: Odd ratios of Mixed Veld relative to alternative vegetation types, from a logistic regression model, for giraffe

Vegetation type	Odds ratio (ψ)	Confidence intervals (α =0.10)
Thornveld	1.675	1.030 - 2.726
Bushveld	2.446	1.357 - 4.405
Riverine Thornveld	3.564	1.524 - 8.333
Open Woodland	4.543	2.179 - 9.434

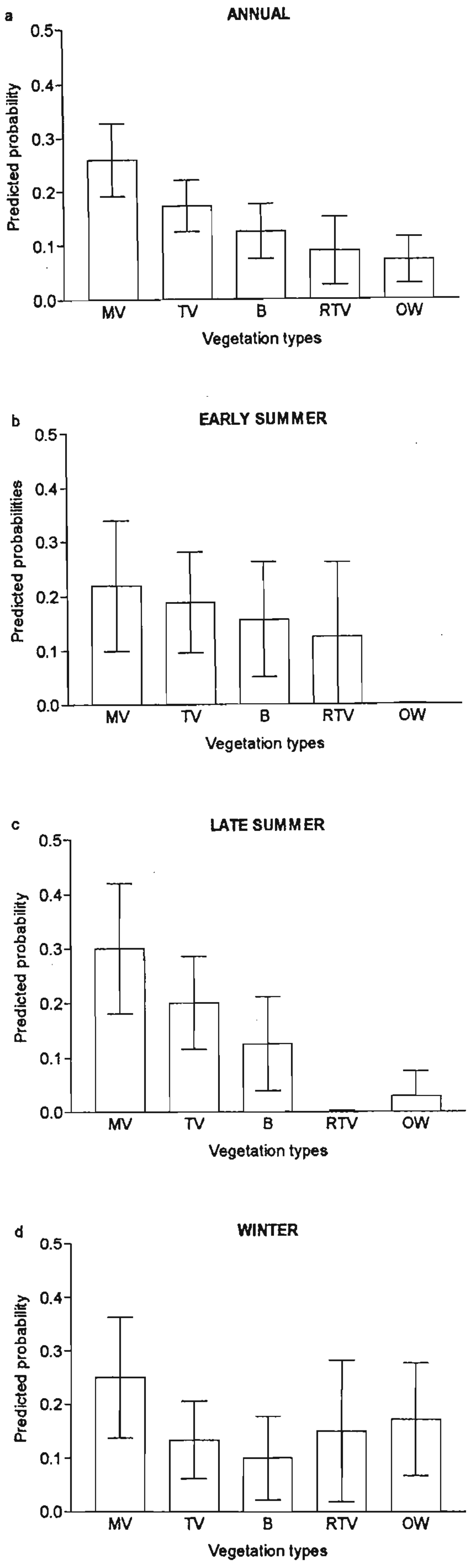

Figure 25. Predicted probabilities and 90 % confidence intervals from logistic regression models of the presence of giraffe dung across five vegetation types for (a) whole year, (b) early summer, (c) late summer and (d) winter. Key to vegetation types: B = Bushveld, MV = Mixed Veld, OW = Open Woodland, RTV = Riverine Thornveld, TV = Thornveld.

There was a strong indication ($P < 0.05$) that the probability of visitations by giraffe in various vegetation types was not consistent over seasons. Open Woodland was less likely ($P < 0.10$) to be visited than all vegetation types, except Riverine Thornveld, during early summer (Fig. 25b). During late summer, the likelihood of the presence of giraffe in both Riverine Thornveld and Open Woodland was less ($P < 0.10$) than Mixed Veld and Thornveld (Fig. 25c). Giraffe were also less likely to visit Riverine Thornveld than Bushveld during this season. During winter, there were no significant differences in the probability of visitations among vegetation types (Fig. 25d).

Across seasons, there were no significant differences in likelihood of the presence of giraffe in Mixed Veld, Thornveld and Bushveld. Giraffe were less likely ($P < 0.10$) to visit Riverine Thornveld during late summer than winter. The probability of giraffe being present in Open Woodland was significantly greater during winter than early summer (Fig. 25).

Ignoring seasons, the likelihood of finding kudu, eland and giraffe in Open Woodland appeared to be less than the other vegetation types, except that differences were not significant for the latter two species. Odds ratios indicated that giraffe were more likely ($P < 0.10$) to be present in Mixed Veld than the other vegetation types (Table 39). Although it appeared that eland were also most likely to visit Mixed Veld, the odds of eland being present in Mixed Veld was only greater than Open Woodland and Bushveld (Table 38). Kudu, on the other hand, were less likely to be present in Mixed Veld than all other vegetation types, except Open Woodland (Fig. 23a).

ASSOCIATION

Tests of independence demonstrated that the three browser species had neither a positive nor negative association with each other during any of the seasons, across all vegetation types (Table 40). However, when each vegetation type was examined separately there was a weak negative association between eland and kudu in Valley Bushveld during winter and late summer, and in Bushveld during winter (Table 41). Although there appeared to be seven other associations between browser pairs, Jaccard's interspecific association index correctly showed no association because the species being compared did not occur together (i.e., $a = 0$).

Table 40. Chi-square test statistic between three browser species across six vegetation types

Browser pair	Season		
	Early summer (N = 180)	Late summer (N = 225)	Winter (N = 222)
Eland-kudu	0.304	1.473	0.091
Eland-giraffe	0.199	0.009	1.373
Giraffe-kudu	0.302	1.380	1.985

where N is the total number of counts (quadrats by surveys)

Table 41. Chi-square test statistic and Jaccard's interspecific association index (in parentheses) for three browser pairs in each vegetation type

Browser pair	Season	Vegetation types[1]					
		VB	B	MV	TV	RTV	OW
Eland-kudu	Early summer	2.038	0.053	0.205	1.033	1.371	0.124
	Late summer	3.198* (0.042)	0.766	1.218	0.016	0.026	4.506** (0.000)
	Winter	3.311* (0.120)	8.152*** (0.083)	0.032	0.027	0.417	2.983* (0.000)
Eland-giraffe	Early summer	na	0.003	0.042	0.107	0.293* (0.000)	na
	Late summer	na	2.707* (0.000)	1.973	0.249	na	10.362*** (0.000)
	Winter	na	2.636	0.000	2.674	3.268* (0.000)	2.652
Giraffe-kudu	Early summer	na	0.142	0.731	0.219	1.371	na
	Late summer	na	1.443	0.943	0.167	na	4.506** (0.000)
	Winter	na	0.618	0.135	0.588	1.985	1.453

[1] VB, Valley Bushveld; B, Bushveld; MV, Mixed Veld; TV, Thornveld; RTV, Riverine Thornveld; OW, Open Woodland

* $P < 0.10$, ** $P < 0.05$, *** $P < 0.005$; na, not applicable as a and $c = 0$

DISCUSSION

UTILISATION OF VEGETATION TYPES

The movement of ungulates and their choice of habitats in which to feed are related to the abundance and quality of food (McNaughton & Georgiadis 1986; Fritz *et al.* 1996) and hence would be expected to correspond with their diets. In some regards this was found to be true.

Over the entire seasonal cycle, all three browsers tended to avoid Open Woodland. This vegetation type occurs on old cultivated lands and is dominated by tall *Acacia sieberiana* and shorter *Acacia karroo* and *Acacia nilotica* trees. It is not surprising there was a small probability of finding kudu in this vegetation type owing to the fact that woody plant species eaten by kudu, such as *Calpurnia aurea, Rhus pentheri, Maytenus heterophylla, Vitex rehmannii* and *Rhus rehmanniana,* were either not found in Open Woodland or were more abundant in other vegetation types. In addition, studies elsewhere have indicated that kudu do not generally prefer open areas (Lamprey 1963; Ferrar & Walker 1974; Leuthold 1978; Du Toit 1988). The fact that giraffe were less likely to visit Open Woodland than Mixed Veld and Thornveld generally corresponded with their diet, which consisted predominantly of *A. karroo* and *A. nilotica* (Fig. 7a). Although these species are abundant in Open Woodland they are also common and widespread throughout the reserve. Even though *A. sieberiana* was eaten relatively frequently by giraffe (12 %) this species is not confined to Open Woodland. The small likelihood of finding giraffe in open areas was also in accordance with most other studies (Leuthold 1978; Pellew 1984a; Young & Isbell 1991; Dekker *et al.* 1996; Ginnett & Demment 1997) although females, usually with young, prefer more open habitats or floodplains (Pellew 1984a; Young & Isbell 1991; Ginnett & Demment 1997). In studies conducted elsewhere, eland showed a preference for closed woodlands (Ferrar & Walker 1974; Kelso 1986; Fabricius & Mentis 1990; Dekker *et al.* 1996) rather than open plant communities, similar to the current study. However, considering that almost a quarter of the annual diet of eland consisted of *A. sieberiana* (Fig. 6a) it is surprising that eland were unlikely to visit Open Woodland.

Kudu showed distinct preferences for certain vegetation types across seasons. Valley Bushveld was more likely to be visited by kudu during winter than early summer. This vegetation type is characterised by broadleaved species, such as *Coddia rudis, Maytenus* species, *R. pentheri, Schotia brachypetala* and *Tarchonanthus camphoratus*, and the increase of broadleaved species in the winter diet of kudu supports this trend. The fact that kudu were more likely to be found in Bushveld during late summer than the other two seasons cannot be readily explained. Microphyllous woody plant species made up 70 % of the diet of kudu during late summer. Although various *Acacia* species do occur in the Bushveld vegetation type, it is dominated by broadleaved species.

Eland were generally non-selective with regard to the use of different vegetation types. During late summer they were, however, more likely to be found in Mixed Veld and Thornveld than Bushveld and Open Woodland. This does not correspond with their diet for this season, given that *C. aurea* was prominent in the diet and is more abundant in Bushveld than Thornveld and Mixed Veld. Similarly, *A. sieberiana* was utilised relatively frequently and, although not confined to Open Woodland, it is most abundant in this vegetation type.

Interestingly, giraffe were more likely to visit Open Woodland during winter than early summer. A possible reason for this could be that the tall *A. sieberiana* trees act as a 'refuge' to giraffe during this period because they are out of the height reach of the other browsers. Although a deciduous species, more than 80 % of the individuals of *A. sieberiana* available to giraffe, while feeding, still retained leaves during winter and formed 9 % of their diet during this season.

A relatively common pattern reported for giraffe is a seasonal movement across the drainage catena, where giraffe tend to frequent riverine vegetation during the dry season (Hall-Martin 1974b; Leuthold 1978; Pellew 1984a; Du Toit 1988; Ginnett & Demment 1997). Although the probability of finding giraffe in Riverine Thornveld during winter was no greater than any of the other vegetation types, giraffe were more likely to be found in Riverine Thornveld during winter than late summer. The majority of the winter diet of giraffe consisted of *A. nilotica* and *A. karroo* (Fig. 7d), despite the fact that 67 % and 63 % of the available individuals, respectively, carried less than 26 % of the potential maximum leaf material. Therefore, giraffe were most likely taking advantage of the prolonged productivity typical of riverine habitats (Pellew 1984a).

The prediction that the different browsers should utilise different vegetation types during winter was not met. All three browsers were least selective for vegetation types during winter than both summer seasons. Similarly, the diets of all browsers, except eland, became more diverse with respect to woody plant species during winter, thereby corresponding well with the pattern of vegetation type utilisation. Overlap in the use of woody plant species decreased for all browser pairs, owing to the diverse range of plants available to them. However, the number of vegetation types available to the browsers at WNR is limited and this decrease in specialisation of vegetation type implies an increase in overlap (Schoener 1982, 1986).

If interspecific competition is the controlling force influencing the use of habitats then it is hypothesised that species should decrease the range of vegetation types utilised. The resulting effect would be a decrease in overlap between species. The opposite is predicted to occur if intraspecific competition is the selective pressure (Sinclair 1985). It would, therefore, appear that intraspecific competition is more important than interspecific competition in influencing the use of habitats among the guild members at WNR. Based on mortality data and results from the dietary study, eland and giraffe do not appear to be limited by food supply and thus interspecific competition between them is unlikely. However, kudu seemed to be constrained by food supply and, if true, then they are likely to experience considerable competition from eland and giraffe.

ASSOCIATION

An association between two species may exist because: (1) of similar abiotic and biotic requirements; (2) both species select or avoid the same habitat or habitat factors; or (3) one or both species have either an attraction or repulsion for the other (Ludwig & Reynolds 1988). A lack of association between species may indicate a balancing of negative and positive forces (Schluter 1984) but may also signify that species do not interact (Ludwig & Reynolds 1988). At WNR, the distributions of eland and giraffe as well as giraffe and kudu were independent of each other, implying that there was no interaction.

Eland and kudu, however, occurred together less often than expected, i.e., a negative association, in two vegetation types. An interaction may be the result of predation (Schluter 1984; Sinclair 1985), facilitation (Sinclair 1985) or competition (MacNally 1983; Sinclair 1985). Predation is discounted, firstly because resident predators are essentially absent from WNR. Secondly, the pressure of predation is most likely to result in a positive association between herbivores, as they stay together for mutual protection (Sinclair 1985).

According to Sinclair (1985) facilitation occurs when one herbivore alters a habitat which is then used sometime later by a second herbivore species. The two species would thus occur together less often than expected. Such a process is known as a grazing succession and has been observed in Serengeti National Park, Tanzania (Bell 1970; Murray & Illius 1996). Lamprey (1963) observed that elephant facilitate the feeding of warthog and black rhinoceros. Both eland and kudu use their horns to break branches on which to feed. Eland are slightly taller than kudu, an adult male standing 1.7 m and 1.4 m at the shoulder, respectively (Skinner & Smithers 1990). Eland are thus able to reach higher than kudu and by breaking branches they may make previously inaccessible food available to kudu. However, considering that in less than five percent of the observations eland and kudu fed in this matter, facilitation is unlikely to be the process responsible for the observed negative association.

A negative interaction between species may be defined as either the active (e.g., territoriality or interference) or passive (e.g., exploitation) denial of access to resources by one species to another (MacNally 1983). Eland and kudu do not defend territories (Smithers & Skinner 1990) and throughout this study I never observed antagonistic behaviour among any of the browsers. Therefore, if competition is the ecological process structuring this herbivore community, then it most likely exploitative. I do not consider interspecific competition to be the cause of the spatial distribution of eland and giraffe, as discussed above. However, kudu may experience considerable competition from the two larger browsers. During winter, kudu included a range of broadleaved species in their diet which eland did not and one would, therefore, not expect eland and kudu to utilise the same vegetation types, during this season. This may be driven by competition, but a negative association may in fact indicate no interaction between species because they have different resource requirements (Schluter 1984).

CONCLUSION

LIMITATIONS OF STUDY

Several shortcomings of this study are recognised. Although examination of the phenology of woody plant species showed a decrease in browse availability, absolute measures of browse biomass would have been preferable. The assessment of available browse is likely to be an over-estimate of the actual quantity of edible material present because no qualitative restriction was incorporated to account for preferences by the browsers (Pellew 1983; McNaughton & Georgiadis 1986). In addition, a precise measure of the amount of food ingested by the animals was not obtained. The dung count method did not prove to be highly successful for assessing the selection of vegetation types, possibly owing to the small quadrat size used and frequency of sampling.

Results from this study can only be applied to WNR or areas of similar vegetation, because the utilisation of habitats and food types by the browsers are specific to the area of study. Whether or not interspecific competition exists among the browsers at WNR cannot be established with absolute certainty because, firstly, we do not know if the animals are in fact resource limited and, secondly, the methods used are not direct measures of competition. Conclusive evidence of competition may be obtained by experimentally manipulating the browser populations, which obviously was not possible in the current study.

INTERSPECIFIC COMPETITION

If interspecific competition is the process shaping the browser guild, then it was expected that overlap between species should decline during the lean season (Schoener 1982, 1986). In terms of forage types, overlap between species generally increased because the browsers concentrated their feeding on the woody component. However, overlap in the utilisation of woody plant species decreased as animals diversified their diets. The expansion of diets, and hence use of habitats, was considered to be driven by each animal's nutritional and energy requirements, rather than competition. Nevertheless, if resources become scarce such that the populations are limited by the amount of available resource, then interspecific competition is highly probable (Sale 1974; Hurlbert 1978; Abrams 1980; Lawlor 1980; Krebs 1999) owing to the extensive overlap, in terms of diets as well as the utilisation of vegetation types, between browsers during the dry season.

Interspecific relations are, however, complex and competition among coexisting species depends not only on the degree of resource overlap (French 1985), but also on forage production, resource abundance and population density (Abrams 1980; French 1985; Du Toit 1990).

Food production was not assessed in the current study, but the availability of woody plant material was investigated. Although this was not a direct measure of the amount of food available, on a mass basis, it did provide an indication of seasonal changes in abundance. Available foliage did decrease during winter, but many plants, even deciduous species, still carried leaves. Despite the fact that the quality of food during this season was not assessed, it is most probable that it did decline (Owen-Smith 1982; Sauer *et al.* 1982; Cooper *et al.* 1988). Under the prevailing conditions at WNR the larger browsers, namely eland, giraffe and black rhinoceros, suffered no mortalities possibly owing to the nutritional advantages conferred by their body size. At the current densities of the browser populations the food resource did not appear to be depleted to such an extent for interspecific competition to either take place or be pronounced among the larger browsers. By comparison, kudu mortalities were great. This may be as a result of kudu not having the nutritional benefits of larger herbivores and that the larger browsers exert a pronounced competitive effect on kudu, if the kudu population is constrained by food supply.

Given the mortalities of kudu, it is highly probable that kudu are feeling the effects of interspecific competition with the other browsers, but the larger browsers do not seem to be negatively influenced by the extensive overlap with kudu. Eland, giraffe and black rhinoceros have an advantage over kudu, simply because they are able to survive on a low quality foods and survive longer on a starvation diet. In addition, giraffe can reach food inaccessible to kudu and thereby expand their food resource base. In a similar way, black rhinoceros can consume far larger twigs than kudu. Black rhinoceros are also able to cope with coarser food material than kudu, because of their simple stomache structure. Thus, if competition between browsers at WNR does occur, the smallest browser, namely kudu, is more likely to be affected.

Mechanisms to reduce the extent of overlap and potential competition between kudu and the other browsers are limited. If giraffe restrict their feeding to beyond the height reach of smaller browsers, the extent of overlap on a long-term basis would not be reduced because the shared browse resource is being depleted, regardless of the height at which plant material is being removed. In a similar way, the degree of overlap between black rhinoceros and kudu would not diminish if black rhinoceros restricted their feeding to large twigs. A study conducted in Botswana revealed that within less than a year shoot length and shoot biomass of *A. tortilis* were significantly less in wildlife areas than in an area with no browsers (Dangerfield *et al.* 1996). Similarly, in Addo Elephant Park, a dense shrub thicket was transformed into open dwarf shrubs within a few years due to intense black rhinoceros browsing (Hall-Martin *et al.* 1982). However, Pellew (1984b) concluded that although giraffe browsing stunted the growth of *A. tortilis* in the Serengeti, there was no *short-term* evidence that it curtailed productivity. Teague and Walker (1988) and Teague (1989b) found that *Acacia karroo* responded positively to defoliation by goats, but also on a short-term basis. After a few years productivity was found to decline at moderate defoliation and mortality increase with heavy defoliations (Teague 1989b). Although giraffe and black rhinoceros will be negatively effected by the reduction in the browse resource, kudu will be most effected because they are unable to access the resources still available to the larger browsers.

On a short-term basis giraffe, by feeding beyond the height reach of smaller browsers, are relatively removed from the extensive overlap and potential competition, but at a longer time scale this may not be true. Only those individual trees which are out of the height reach of smaller browsers are exclusively available to giraffe. However, these trees grow from saplings on which the smaller browsers feed. If this browsing is excessive then regeneration of these trees would be impeded and hence the likelihood of exploitative competition between giraffe and the smaller browsers must be considered (Du Toit 1990). For example, in Tsavo National Park, Leuthold and Leuthold (1972) observed that *Melia* trees were stunted because they were heavily utilised by giraffe and other species, such as lesser kudu.

Weenen Nature Reserve, being relatively small, offers a limited number of vegetation types for which the browsers can select. Thus the degree of overlap could not be reduced by each browser feeding in different habitats during winter. In Tsavo National Park (Leuthold 1978), Kruger National Park, South Africa (Du Toit 1988) and Grove Ranch, Zimbabwe (Fritz *et al.* 1996), selection for habitats was extremely similar between browsers. Du Toit (1988) thus concluded that differential habitat selection promoting ecological separation among a browsing guild may not be as important as previously suggested (e.g. Lamprey 1963). The findings of my study are thus further evidence in support of Du Toit's conviction.

RESOURCE PARTITIONING

Lawlor (1980) suggests that evolutionary divergence of resource use patterns, due to past competitive pressures, will be indicated by differences in preference and that these differences may indicate a low probability of present-day competition. Similarities in preference for woody plant species during the dry season were considerable for all browser pairs, except eland-black rhinoceros and eland-kudu. Based on Lawlor's (1980) concept, past competition between eland and kudu was likely to be intense and present-day competition weak. Eland and black rhinoceros showed little similarity in their preference for woody plant species, yet overlap was relatively great (34 %) which may suggest that competitive pressures in the past were strong and that the great degree of present overlap is permissible because the resources preferred by the two species are not limited. Among the four remaining browser pairs, i.e., giraffe-kudu, kudu-black rhinoceros, eland-giraffe and giraffe-black rhinoceros, past competition may have been slight as indicated by similarities in preference. This, and the fact that overlap among these browser pairs was found to be extensive, suggests that present-day competition may be highly probable. It must be borne in mind that the ecosystem of WNR is inappropriate for investigating evolutionary relationships.

MANAGEMENT RECOMMENDATIONS

Based on the current study it is hypothesised that during periods of resource scarcity the abundance of high quality foods are limited and if interspecific competition does prevail, which will further limit the availability of these resources, it is the smaller bodied herbivores that will be most affected and suffer the greatest mortalities. If true, this has important implications for management.

The following recommendations concerning the management of the four browsers studied are suggested. Controlled burning should be continued to be practised, firstly, because it provides acceptable, palatable grass for eland. Secondly, burning is beneficial to black rhinoceros because long grass, which tends to interfere with their feeding (Emslie & Adcock 1993), is removed. Thirdly, burning maintains the height structure of many woody plant species at levels accessible to browsers. The populations of the larger browser at WNR should not exceed far beyond their current numbers, as the potential for competition at greater densities is highly likely. Mortalities of kudu at WNR are great and thus it is strongly recommended that their numbers be reduced. Owing to the great conservation status of black rhinoceros, the reduction of kudu numbers is also recommended because this will decrease the potential competitive effect of kudu on black rhinoceros.

More robust conclusions about interspecific competition between the browsers will be achieved if changes in the absolute quantity and quality of woody browse is investigated. The total above ground biomass and consumable material available on an individual tree basis may be attained by developing regression equations relating biomass and edible material to various plant dimensions, such as canopy volume. Chemical analysis of browse material for crude protein, fibre, phosphorus and condensed tannin will provide an indication of the quality of browse material. This information can then be used to determine which foods maintain the browser populations, based on their nutritional requirements, and what the abundance of these foods are.

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APPENDICES

Appendix 1. A publication to be submitted to African Journal of Range & Forage Science, entitled Woody vegetation and soil types of Weenen Nature Reserve, KwaZulu-Natal by Breebaart, O'Connor, Hughes & Rushworth, has revised names of the vegetation types in order that they reflect floristic and structure more meaningfully than the names in this thesis.

Table1: Revised names of the six vegetation types of Weenen Nature Reserve, as in publication to be submitted

Current vegetation type names	Revised vegetation type names
Thornveld	*Acacia karroo - Acacia tortilis* Woodland
Open Woodland	*Acacia sieberiana* Open Woodland
Riverine Thornveld	*Acacia tortilis* Riparian Woodland
Mixed Veld	*Acacia karroo - Vitex rehmannii* Woodland
Bushveld	*Calpurnia aurea - Euclea crispa* Woodland
Valley Bushveld	*Coddia rudis - Dombeya cymosa* - Cosed Woodland

Appendix 2: An indication of the independence of feeding events for each animal species per season considering (a) one event per observation and (b) successive individuals of different plant species as a percentage (%) of the total number of feeding events

(a)

Animal species	Early summer			Late summer			Winter			
	Events	Total events	%	Events	Total events	%	Events	Total events	%	mean
Eland	36	77	46.8	18	26	69.2	10	29	34.5	50.2
Kudu	98	318	30.8	110	228	48.2	116	289	40.1	39.7
Giraffe	61	271	22.5	139	319	43.6	98	240	40.8	35.6

(b)

Animal species	Early summer			Late summer			Winter			
	Events	Total events	%	Events	Total events	%	Events	Total events	%	mean
Eland	61	77	79.2	26	26	100.0	10	29	34.5	71.2
Kudu	257	318	80.8	203	228	89.0	244	289	84.4	84.8
Giraffe	183	271	67.5	257	319	80.6	201	240	83.8	77.3

Appendix 3. Annual and seasonal overlap in diets, considering all forage types, between species pairs as calculated by Pianka's overlap index

Time period	Browser pairs		
	Eland-Kudu	Eland-Giraffe	Giraffe-Kudu
Annual	0.378	0.286	0.912
Early summer	0.316	0.190	0.970
Late summer	0.277	0.130	0.888
Winter	0.854	0.727	0.821

Appendix 4. Annual and seasonal overlap in diets, in terms of woody plant species, between species pairs as calculated by Pianka's overlap index

Time period	Browser pairs[1]					
	E/K	E/G	G/K	E/BR	K/BR	G/BR
Annual	0.803	0.857	0.833	0.783	0.835	0.873
Early summer	0.836	0.926	0.938	0.701	0.810	0.817
Late summer	0.805	0.592	0.908	0.394	0.716	0.792
Winter	0.225	0.635	0.347	0.809	0.458	0.759

[1] E, eland; K, kudu; G, giraffe; BR, black rhinoceros

Appendix 5. Annual and seasonal overlap in feeding heights, considering all forage types, between species pairs as calculated by Pianka's overlap index

Time period	Browser pairs		
	Eland-Kudu	Eland-Giraffe	Giraffe-Kudu
Annual	0.814	0.054	0.190
Early summer	0.673	0.011	0.205
Late summer	0.655	0.076	0.269
Winter	0.988	0.094	0.093

Appendix 6. Annual and seasonal overlap in feeding heights, in terms of woody plant species, between species pairs as calculated by Pianka's overlap index

Time period	Browser pairs[1]					
	E/K	E/G	G/K	E/BR	K/BR	G/BR
Annual	0.760	0.084	0.288	0.984	0.724	0.066
Early summer	0.582	0.022	0.234	0.762	0.715	0.061
Late summer	0.603	0.095	0.288	0.990	0.550	0.101
Winter	0.956	0.125	0.144	0.591	0.722	0.037

[1] E, eland; K, kudu; G, giraffe; BR, black rhinoceros

Appendix 7. Annual and seasonal total dietary overlap, as a product of diet composition and feeding height based on the utilisation of all forage types, between species pairs as calculated by Pianka's overlap index

Time period	Browser pairs		
	Eland-Kudu	Eland-Giraffe	Giraffe-Kudu
Annual	0.308	0.015	0.173
Early summer	0.213	0.002	0.199
Late summer	0.181	0.010	0.239
Winter	0.844	0.068	0.076

Appendix 8. Annual and seasonal total dietary overlap, as a product of diet composition and browsing height based on the utilisation of woody plant species, between species pairs as calculated by Pianka's overlap index

Time period	Browser pairs[1]					
	E/K	E/G	G/K	E/BR	K/BR	G/BR
Annual	0.610	0.072	0.240	0.770	0.605	0.058
Early summer	0.487	0.020	0.219	0.534	0.579	0.050
Late summer	0.485	0.056	0.262	0.390	0.394	0.080
Winter	0.215	0.079	0.050	0.478	0.331	0.028

[1] E, eland; K, kudu; G, giraffe; BR, black rhinoceros

Appendix 9: Logistic regression for kudu

Table 9a: Vegetation

```
***** Regression Analysis *****
Response variate: count
Binomial totals: N
Distribution: Binomial
Link function: Logit
Fitted terms: Constant + VEG

*** Summary of analysis ***
                                    mean  deviance      approx
              d.f.     deviance   deviance     ratio      chi pr
Regression      5        100.3     20.052     20.05       <.001
Residual      621        741.4      1.194
Total         626        841.6      1.344


*** Estimates of parameters ***
                                                                       antilog of
                                          estimate       s.e.     t(*)  t pr.    estimate
Constant(Riverine Thornveld - RTV) 1.409          0.336     4.19  <.001      4.0910
Valley Bushveld (VB)                     -0.226          0.426    -0.53  0.596      0.7977
Bushveld (B)                             -0.357          0.399    -0.89  0.371      0.6996
Mixed Veld (MV)                          -1.337          0.386    -3.47  <.001      0.2626
Thornveld (TV)                           -0.742          0.374    -1.99  0.047      0.4760
Open Woodland (OW)                       -2.770          0.419    -6.61  <.001      0.0627

* MESSAGE: s.e.s are based on dispersion parameter with value 1
```

Table 9b: Mean Seasonal Effects

```
***** Regression Analysis *****
Response variate: count
Binomial totals: N
Distribution: Binomial
Link function: Logit
Fitted terms: Constant + VEG + SEASON

*** Summary of analysis ***
                                    mean  deviance      approx
              d.f.     deviance   deviance     ratio      chi pr
Regression      7        114.2     16.318     16.32       <.001
Residual      619        727.4      1.175
Total         626        841.6      1.344
Change         -2        -14.0      6.984      6.98  <.001


*** Estimates of parameters ***
                                                                   antilog of
                              estimate          s.e.      t(*)  t pr.    estimate
Constant(RTV,WINTER)             1.712          0.365      4.69  <.001      5.5400
VB                              -0.220          0.430     -0.51  0.609      0.8023
B                               -0.365          0.403     -0.90  0.366      0.6944
MV                              -1.371          0.390     -3.51  <.001      0.2540
TV                              -0.759          0.377     -2.01  0.044      0.4680
OW                              -2.835          0.424     -6.69  <.001      0.0587
Early summer (EARLY)            -0.052          0.231     -0.23  0.821      0.9492
Late summer (LATE)              -0.714          0.213     -3.35  <.001      0.4898

* MESSAGE: s.e.s are based on dispersion parameter with value 1
```

Table 9c: Season x Vegetation Type Interaction

```
***** Regression Analysis *****
Response variate: count
Binomial totals: N
Distribution: Binomial
Link function: Logit
Fitted terms: Constant + VEG + SEASON + SEASON.VEG

*** Summary of analysis ***
                                        mean  deviance     approx
              d.f.     deviance     deviance     ratio     chi pr
Regression     17         129.4        7.609      7.61      <.001
Residual      609         712.3        1.170
Total         626         841.6        1.344
Change        -10         -15.1        1.513      1.51      0.127


*** Estimates of parameters ***
                                                                     antilog of
                              estimate         s.e.       t(*) t pr.   estimate
Constant                         1.386        0.559       2.48 0.013     4.0000
VB                               0.693        0.829       0.84 0.403     2.0000
B                                0.164        0.697       0.24 0.814     1.1790
MV                              -1.084        0.644      -1.68 0.092     0.3382
TV                              -0.693        0.622      -1.11 0.265     0.5000
OW                              -2.303        0.673      -3.42 <.001     0.1000
EARLY                             1.32         1.16       1.13 0.257     3.7490
LATE                            -0.539        0.742      -0.73 0.468     0.5833
EARLY.VB                         -2.89         1.38      -2.09 0.036     0.0556
EARLY.B                          -0.93         1.35      -0.69 0.492     0.3961
EARLY.MV                         -1.50         1.26      -1.19 0.234     0.2234
EARLY.TV                         -1.02         1.24      -0.83 0.409     0.3591
EARLY.OW                         -1.50         1.30      -1.16 0.247     0.2223
LATE.VB                          -0.35         1.05      -0.33 0.739     0.7041
LATE.B                          -0.811        0.908      -0.89 0.372     0.4444
LATE.MV                          0.036        0.868       0.04 0.967     1.0370
LATE.TV                          0.251        0.834       0.30 0.763     1.2860
LATE.OW                          -0.91         1.03      -0.89 0.375     0.4018

* MESSAGE: s.e.s are based on dispersion parameter with value 1
```

Appendix 10: Logistic regression for eland

Table 10a: vegetation

```
***** Regression Analysis *****
Response variate: count
Binomial totals: N
distribution: Binomial
Link function: Logit
Fitted terms: Constant + VEG

*** Summary of analysis ***
                                     mean     eviance       approx
               d.f.      deviance    deviance    ratio       chi pr
Regression       5          9.9      1.9837      1.98        0.078
Residual       621        480.2     0.7733
Total          626        490.2     0.7830


*** Estimates of parameters ***
                                                                     antilog of
                               estimate         s.e.       t(*)  t pr.   estimate
Constant(Mixed Veld - MV)       -1.466          0.242     -6.07  <.001     0.2308
Valley Bushveld (VB)            -0.384          0.404     -0.95  0.342     0.6809
Bushveld (B)                    -0.751          0.399     -1.88  0.060     0.4719
Thornveld (TV)                  -0.278          0.325     -0.86  0.392     0.7576
Riverine Thornveld (RTV)        -0.187          0.437     -0.43  0.669     0.8298
Open Woodland (OW)              -1.264          0.485     -2.60  0.009     0.2826

* MESSAGE: s.e.s are based on dispersion parameter with value 1
```

Table 10b: Mean Seasonal Effects

```
***** Regression Analysis *****
Response variate: count
Binomial totals: N
Distribution: Binomial
Link function: Logit
Fitted terms: Constant + VEG + SEASON

*** Summary of analysis ***
                                     mean    deviance       approx
               d.f.      deviance    deviance    ratio       chi pr
Regression       7         10.2      1.4636      1.46        0.175
Residual       619        479.9      0.7753
Total          626        490.2      0.7830
Change          -2         -0.3      0.1635      0.16        0.849


*** Estimates of parameters ***
                                                                     antilog of
                               estimate         s.e.       t(*)  t pr.   estimate
Constant(MV,WINTER)             -1.522          0.292     -5.21  <.001     0.2183
VB                              -0.387          0.405     -0.96  0.339     0.6794
B                               -0.751          0.399     -1.88  0.060     0.4717
TV                              -0.278          0.325     -0.86  0.392     0.7574
RTV                             -0.187          0.437     -0.43  0.669     0.8297
OW                              -1.264          0.486     -2.60  0.009     0.2824
Early summer (EARLY)             0.159          0.295      0.54  0.590     1.1720
Late summer (LATE)               0.025          0.286      0.09  0.931     1.0250

* MESSAGE: s.e.s are based on dispersion parameter with value 1
```

Table 10c: Season x Vegetation Type Interaction

```
***** Regression Analysis *****
Response variate: count
Binomial totals: N
Distribution: Binomial
Link function: Logit
Fitted terms: Constant + VEG + SEASON + SEASON.VEG

*** Summary of analysis ***
                                     mean  deviance      approx
              d.f.     deviance  deviance     ratio      chi pr
Regression     17          23.2    1.3666      1.37       0.142
Residual      609         466.9    0.7667
Total         626         490.2    0.7830
Change        -10         -13.0    1.2987      1.30       0.224


*** Estimates of parameters ***
                                                                   antilog of
                              estimate         s.e.      t(*)  t pr.  estimate
Constant(MV,WIINTER             -1.735        0.443     -3.92  <.001    0.1765
VB                              -0.015        0.699     -0.02  0.983    0.9855
B                                0.000        0.626      0.00  1.000    1.0000
TV                              -0.663        0.644     -1.03  0.303    0.5152
RTV                              0.636        0.679      0.94  0.349    1.8890
OW                              -1.069        0.851     -1.26  0.209    0.3434
EARLY                            0.268        0.633      0.42  0.672    1.3080
LATE                             0.498        0.582      0.86  0.392    1.6450
EARLY.VB                         0.146        0.972      0.15  0.881    1.1570
EARLY.B                         -0.802        0.982     -0.82  0.414    0.4483
EARLY.TV                         0.362        0.886      0.41  0.683    1.4360
EARLY.RTV                       -1.120        1.110     -1.00  0.316    0.3277
EARLY.OW                         0.410        1.140      0.36  0.716    1.5140
LATE.VB                         -1.390        1.080     -1.28  0.199    0.2496
LATE.B                          -1.710        1.030     -1.66  0.097    0.1813
LATE.TV                          0.615        0.809      0.76  0.447    1.8490
LATE.RTV                        -1.600        1.080     -1.48  0.138    0.2026
LATE.OW                         -1.220        1.350     -0.90  0.367    0.2957
* MESSAGE: s.e.s are based on dispersion parameter with value 1
```

Appendix 11: Logistic regression for giraffe

Table 11a: Vegetation

```
***** Regression Analysis *****
Response variate: count
Binomial totals: N
Distribution: Binomial
Link function: Logit
Fitted terms: Constant + VEG

*** Summary of analysis ***
                                     mean  deviance      approx
              d.f.      deviance   deviance     ratio      chi pr
Regression      4           17.6     4.4032      4.40       0.001
Residual      541          451.2     0.8340
Total         545          468.8     0.8602

*** Estimates of parameters ***
                                                                     antilog of
                              estimate           s.e.       t(*)  t pr.  estimate
Constant(Mixed Veld - MV)       -1.052          0.215      -4.89  <.001    0.3494
Bushveld (B)                    -0.894          0.358      -2.50  0.012    0.4088
Thornveld (TV)                  -0.516          0.296      -1.74  0.082    0.5971
Riverine Thornveld (RTV)        -1.271          0.516      -2.46  0.014    0.2806
Open Woodland(OW)               -1.513          0.447      -3.38  <.001    0.2201

* MESSAGE: s.e.s are based on dispersion parameter with value 1
```

Table 11b: Mean Seaonal Effects

```
***** Regression Analysis *****
Response variate: count
Binomial totals: N
Distribution: Binomial
Link function: Logit
Fitted terms: Constant + VEG + SEASON

*** Summary of analysis ***
                                     mean  deviance      approx
              d.f.      deviance   deviance     ratio      chi pr
Regression      6           17.7     2.9508      2.95       0.007
Residual      539          451.1     0.8369
Total         545          468.8     0.8602
Change         -2           -0.1     0.0459      0.05       0.955

* MESSAGE: ratios are based on dispersion parameter with value 1

*** Estimates of parameters ***
                                                                     antilog of
                              estimate           s.e.       t(*)  t pr.  estimate
Constant(MV,WINTER)             -1.011          0.267      -3.78  <.001    0.3638
B                               -0.895          0.358      -2.50  0.012    0.4088
TV                              -0.516          0.296      -1.74  0.082    0.5970
RTV                             -1.271          0.516      -2.47  0.014    0.2805
OW                              -1.514          0.447      -3.38  <.001    0.2201
Early summer (EARLY)            -0.092          0.303      -0.30  0.762    0.9122
Late summer (LATE)              -0.040          0.283      -0.14  0.887    0.9606

* MESSAGE: s.e.s are based on dispersion parameter with value 1
```

Table 11c: Season x Vegetation Type Interaction

```
***** Regression Analysis *****
Response variate: count
Binomial totals: N
Distribution: Binomial
Link function: Logit

Fitted terms: Constant + VEG + SEASON + SEASON.VEG

*** Summary of analysis ***
                                        mean  deviance     approx
              d.f.     deviance    deviance     ratio     chi pr
Regression     14         33.8      2.4162      2.42      0.002
Residual      531        435.0      0.8192
Total         545        468.8      0.8602
Change         -8        -16.1      2.0152      2.02      0.041

*** Estimates of parameters ***
                                                                     antilog of
                              estimate         s.e.      t(*)  t pr.   estimate
Constant (MV,WINTER)            -1.099        0.365     -3.01  0.003     0.3333
B                               -1.099        0.641     -1.71  0.087     0.3333
TV                              -0.773        0.527     -1.47  0.142     0.4615
RTV                             -0.636        0.725     -0.88  0.380     0.5294
OW                              -0.477        0.578     -0.82  0.410     0.6207
EARLY                           -0.174        0.562     -0.31  0.757     0.8400
LATE                             0.251        0.502      0.50  0.617     1.2860
EARLY.B                          0.685        0.912      0.75  0.452     1.9840
EARLY.TV                         0.580        0.773      0.75  0.453     1.7860
EARLY.RTV                       -0.040        1.130     -0.03  0.974     0.9637
EARLY.OW                        -6.820        8.340     -0.82  0.414     0.0011
LATE.B                           0.000        0.871      0.00  1.000     1.0000
LATE.TV                          0.234        0.708      0.33  0.741     1.2640
LATE.RTV                        -7.080        9.860     -0.72  0.473     0.0009
LATE.OW                         -2.200        1.220     -1.81  0.071     0.1106
* MESSAGE: s.e.s are based on dispersion parameter with value 1
```