

**THE FEEDING ECOLOGY OF EXTRALIMITAL
NYALA (*TRAGELAPHUS ANGASII*) IN THE ARID MOSAIC THICKET
OF THE SOUTHERN CAPE**

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ABSTRACT

The nyala on Buffelsdrift Private Game Reserve were found to be mainly browsers and made little use of grass during the study period. Browse contributed 87.8% to the annual diet, while grass contributed 12.2%. Only six species formed > 5% of the annual diet. Of these six only three species formed > 10%. They are the shrubs *Acacia karroo*, *Pappea capensis* and *Grewia robusta*. These were followed by the shrub *Portulacaria afra*, the dwarf shrub *Zygophyllum lichtensteinianum* and the grass *Cynodon dactylon* all contributing between 5 - 10%. There were definite seasonal dietary shifts with preference to different plant species. The shift takes place between the wet seasons (winter and spring) and the dry season (summer). Herbaceous species such as *Cynodon dactylon* and *Erharta calycina* were favoured in the winter/wet season. Shrubs such as *P. capensis*, *P. afra* and dwarf shrubs such as *Limeum aethiopicum* and *Z. lichtensteinianum* were favoured during the spring/wet and summer/dry seasons. Nyala habitat use in BPGR differed significantly from expected use when taking the relative area of habitats into consideration. However nyala did not display significantly different habitat preferences between seasons. Male and female nyala displayed differences in foraging behaviour at the plant form, plant species and habitat scale. Males preferred a greater proportion of shrubs and females a greater proportion of dwarf shrubs. Males preferred the shrubs *Pappea capensis* and *Portulacaria afra* the most and females preferred the dwarf shrubs *Limeum aethiopicum* and *Zygophyllum lichtensteinianum* the most. Plant species site availability varied significantly between the sexes, indicating that males and females selected different feeding paths. The difference in their feeding strategy appears to be related to the selection of plants that best satisfy the nutrient requirements of each sex. These findings are in agreement with the results from earlier studies on nyala sexual dimorphism. At the habitat scale females selected more for open dwarf shrubland and males more for densely vegetated habitats. This appears to be as a result of males attempting to maximize their foraging opportunities by selecting areas that offer food in greater quantities. Nyala in BPGR appear to co-exist with kudu and eland through spatial resource partitioning. This is suggested to be due to the influence of body size-gut size relationships on forage selectivity.

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DECLARATION

I, Ryno Cuyler Pienaar with student number 210016736, declare that this thesis is my own, original work and that it has not been submitted for a degree to any other University.



Ryno Cuyler Pienaar.

CHAPTER ONE: INTRODUCTION

1.1 BACKGROUND

Prior to the 1950's, wildlife in South Africa was perceived as a hindrance to the agricultural industry (Bigalke 1950; Carruthers 2008). Since the 1950's private landowners started developing a greater appreciation for wildlife, due to the recognized economic viability of converting from agriculture to game ranching, especially in arid areas (Bigalke and Neitz 1954; Castley *et al.* 2001; Van der Merwe and Saayman 2004; Carruthers 2008; Cousins *et al.* 2010). Today, the economic value of wildlife has dramatically increased (Bond *et al.* 2004; Cloete and Taljaard 2008; Brink *et al.* 2011; Palazy *et al.* 2012) and consequently, the number of private game and nature reserves on private land has increased (Castley *et al.* 2001; Bond *et al.* 2004; Van Niekerk 2004). Private game ranches outnumber formally protected areas in South Africa (Van der Merwe and Saaiman 2004); it is estimated that approximately 80% of natural rangeland is on private land, and therefore privately owned game and nature reserves have an increasing obligation towards conservation (Bond *et al.* 2004; Palmer *et al.* 2006; Cousins *et al.* 2010). Although many conservation objectives are met by these areas (Bond *et al.* 2004; Cousins *et al.* 2010), certain practices such as extralimital species introductions contradict conservation principles (Castley *et al.* 2001; Palmer *et al.* 2006). Private landowners and managers are introducing extralimital mammalian herbivores to enhance faunal diversity and to increase the financial viability of tourism based operations (Castley *et al.* 2001; Bothma 2005).

Nyala (*Tragelaphus angasii*) is a species in high demand as an extralimital introduction in South Africa, due to its adaptability as a species (Hayes 1967; Vincent *et al.* 1968; Keep 1971; Tello and Van Gelder 1975; Anderson 1978; Skinner and Chimimba 2005), its popularity for game viewing and hunting (Bothma 2005; Pfitzer and Kobes 2005; Bothma *et al.* 2010) and consequent economic value for tourism (Bothma 2005; Bothma *et al.* 2010). Nyala are sexually dimorphic, with males being considerably larger than females (Tello and Van Gelder 1975; Skinner and

Chimimba 2005). The male's larger body size and prominent horns make them more valuable to the hunting industry than the smaller females (Bothma *et al.* 2010). Nyala have been introduced into Buffelsdrift Private Game Reserve, in the Arid Mosaic Thicket of the Southern Cape to increase the visibility and diversity of wildlife for tourists on safari.

The only documented study on nyala in an extralimital context was conducted in KwaZulu-Natal by Coates and Downs, (2005) and focused on the status and management of sympatric bushbuck and nyala. No studies on nyala have been done in the Albany Thicket Biome. This study was carried out on the Buffelsdrift Private Game Reserve (BPGR) which is situated in Arid Mosaic Thicket, in the western portion of the Albany Thicket Biome and has the following objectives: (a) to determine the seasonal variation in diet composition of nyala, as well as investigate the influence of nyala's marked sexual dimorphism on their diet composition; (b) to determine the seasonal variation in nyala diet preference, as well as investigate the influence of sexual dimorphism on their diet preference and (c) to determine the seasonal variation in habitat use of nyala and investigate the influence of sexual dimorphism on their habitat use.

1.2 NYALA TAXONOMY

The species was first scientifically described by Gray in 1849 (Tello and Van Gelder, 1975; Skinner and Chimimba 2005). Nyala is a monotypic species of the family Bovidae and the tribe Tragelaphini (Grubb 1993; Estes 1997). Tribal traits consist of a medium to large body, spiralled horns, white vertical stripes and a distinct sexual dimorphism (Skinner and Chimimba 2005). Other species in this tribe include bushbuck (*Tragelaphus scriptus*), mountain nyala (*Tragelaphus buxtoni*), sitatunga (*Tragelaphus speki*), greater kudu (*Tragelaphus strepiceros*), lesser kudu (*Tragelaphus imberbis*), eland (*Taurotragus oryx*), Derby's eland (*Taurotragus derbianus*) and the bongo (*Tragelaphus eurycerus*) (Grubb 1993; Estes 1997; Skinner and Chimimba 2005).

1.3 NYALA DISTRIBUTION

The species has a limited distribution range in the south eastern regions of Africa due to particular habitat requirements (Tello and Van Gelder 1975; Anderson 1978; Van Rooyen 1992; Skinner and Chimimba 2005; Kazembe 2010). Nyala are found naturally throughout Limpopo, Swaziland, the low lying areas of northern and southern Zimbabwe, the low lying areas of Mozambique, the southern regions of Malawi, northern KwaZulu-Natal and north-eastern Mpumalanga (East 1996; Skinner and Chimimba 2005). The species has been studied mainly in KwaZulu-Natal by Anderson (1978; 1979; 1980; 1985), Anderson and Pooley (1977), Van Rooyen (1992), Coates and Downs (2005), Fay and Greeff (1999; 2008) and Kirby (2008); in southern Mozambique by Tello and Van Gelder (1975), in Malawi by Hayes (1967), Mkanda (1996) and Kazembe (2010) and in Zimbabwe by Gandiwa (2013). Nyala have been translocated to various private reserves and wildlife ranches in South Africa (Mills and Hes 1997) and today they occur extraliminally in the Eastern Cape (Van Niekerk 2004), Southern KwaZulu-Natal (Coates and Downs 2005), the North West Province (Castley *et al.* 2001), the Northern Cape (Castley *et al.* 2001) and the Southern Cape. Since nyala are extralimital to the Arid Mosaic Thicket of the Southern Cape (Skead 1987; Skead *et al.* 2007), there is a need for information concerning their feeding ecology in this particular system.

1.4 FEEDING ECOLOGY

Feeding ecology investigates certain processes which determine patterns of resource use by mammalian herbivores in a particular system (Owen-Smith *et al.* 1983; Senft *et al.* 1987; Owen-Smith 2002). The study of a mammalian herbivore's feeding ecology can be defined as the evaluation of the relationship between the mammalian herbivore and its available food supply (Johnson 1980; Owen-Smith *et al.* 1983; Owen-Smith 2002).

The processes that determine the diet of a mammalian herbivore does not occur in a single dimension, but rather in a hierarchy of spatial scales (Senft *et al.* 1987; Kotliar and Wiens 1990; Bailey *et al.* 1996; Wiens 2000; Laca *et al.* 2010; Owen-Smith *et al.* 2010). Senft *et al.* (1987) describes these processes occurring at

community, landscape and regional scales respectively. Community scales refer to the relatively constant assemblages of plant populations that are grouped in combination with soils or patterns of disturbance (Senft *et al.* 1987). Landscape systems are formed by communities clustered in conjunction with geomorphic features and regional systems are large-scale assemblages of landscapes (Senft *et al.* 1987).

Six spatial scales of behavioural mechanisms presented by Bailey *et al.* (1996) will be recognized in this study. These six spatial scales coincide with the hierarchical scales presented by Senft *et al.* (1987). They are as follows: (a) bite, coincides with behaviour occurring at a community scale and is defined as a sequence of head, tongue and jaw movements to achieve foliage intake (Laca *et al.* 1994; Bailey *et al.* 1996); (b) feeding station selection, occurs at community scale and is defined as a collection of plants immediately available to the herbivore (Owen-Smith and Cooper 1987a; Bailey *et al.* 1996); (c) patch selection, occurs at the community and landscape scales and is defined as an assemblage of feeding stations distinguished from others by a break in the foraging sequence when the herbivore moves to a new area (Laca *et al.* 1994; Bailey *et al.* 1996); (d) feeding site selection, occurs at a landscape scale and is defined as a collection of patches in a proximate spatial area that browsers utilize during a feeding session (feeding sessions are separated by a change in behaviour i.e. resting to ruminating to browsing); (e) camp selection, occurs at the landscape and regional scales and is defined as a set of feeding sites that share a common centre of interest where the herbivores drink, rest or seek cover and (f) home range, occurs at a regional scale and is defined as a collection of camps separated by fences, barriers or extent of migration (Bailey *et al.* 1996). The aforementioned behavioural mechanisms will ultimately produce the distribution patterns of the herbivore in its environment (Senft *et al.* 1987; Bailey *et al.* 1996).

Knowledge of herbivore feeding ecology is essential for effective range management (Hanley and Hanley 1982; Holecheck *et al.* 1982; Owen-Smith *et al.* 2010). This information is required in order to: (a) select types of herbivores compatible with the forage resource; (b) to estimate suitable herbivore stocking densities; (c) estimate the outcome of over utilization by different animals; (d) identify the problem species on which to base management and most importantly for this

study; (e) determine the suitability of an exotic mammalian herbivore for a particular range type (Holecheck *et al.* 1982).

In terms of diet selection, herbivores are surrounded by a variety of plants that can be accepted as food (Owen-Smith 1982). However, these potential food items have marked spatial and seasonal differences in their nutritional quality and in their general quantity (Owen-Smith 1982; Owen-Smith and Novellie 1982; McNaughton and Georgiadis 1986; Owen-Smith *et al.* 2010). Hence, herbivores have to select for acceptable food resources from a varying environment in order to meet their nutritional requirements (Hanley 1982; Owen-Smith 1982; McNaughton and Georgiadis 1986; Owen-Smith 1988). My study of nyala feeding ecology is concerned with mechanisms related to the acquisition of food and habitat resources by an extralimital large herbivore in a variable environment. It addresses decisions regarding; (a) where to search and (b) which food types to consume (Schoener 1971; Pyke *et al.* 1977; Owen-Smith *et al.* 1983; Stephens and Krebs 1986; Owen-Smith 2002; Laca *et al.* 2010; Owen-Smith *et al.* 2010).

1.4.1 DIET COMPOSITION

An analysis of diet composition requires the identification of dietary components so that the proportional contribution of each may be measured (Holecheck *et al.* 1982; Du Toit 1988; Holecheck *et al.* 2004). Forage available to herbivores can be categorized into three different groups; (1) plant form (e.g. grasses, succulents, forbs, dwarf shrubs and shrubs), (2) plant parts (e.g. leaves and stems) and (3) plant species (Petrides 1975; Grunow 1980; Everett *et al.* 1991; Watson and Owen-Smith 2000; Venter and Watson 2007). The principal food species of an herbivore in a certain system are those species which it eats in the greatest quantities and preferred food species are those that are consumed in a greater proportion than its representation in the environment (Petrides 1975). A principal food species can also be a preferred food species, but a preferred food species may not necessarily be a principal food species (Petrides 1975; Everett *et al.* 1991). The first research chapter of the thesis will focus on the seasonal variation in proportional use of plant forms and principal plant species by nyala in BPGR.

1.4.2 DIET PREFERENCE

The process of selecting an assortment of food items from the abundance of food resources in the environment is known as diet selection (Westoby 1974; Owen-Smith and Chafota 2012). Herbivores are surrounded by a variety of possible food species while foraging (Westoby 1974; Owen-Smith 1982). However, some plant species are more utilised than others (Owen-Smith 1982; Owen-Smith and Novellie 1982). A mammalian herbivore's preference for certain food items is derived from the level of selection for the food items in a given habitat (Leuthold 1972; Owen-Smith and Cooper 1987a). Selection takes place when a food item is examined by the herbivore and it is accepted or rejected (Westoby 1974; Johnson 1980; Owen-Smith and Cooper 1987a).

Acceptability indices are used to determine the relative probability that a herbivore will consume a particular food (Hobbs and Bowden 1982; Owen-Smith and Cooper 1987a). In order to determine a preference index for individual plant species, the use of each species is related to its availability to the herbivore (Westoby 1974; Petrides 1975; Johnson 1980). In this study the acceptability index of Owen-Smith and Cooper (1987a) is used to assess plant species preference.

Some preferred plant species may be proportionately less available in the environment than its representation in the diet of the herbivore and this preference could result in increased pressure on the selected species, which could lead to local extinction, especially in smaller areas where pressure on the vegetation will be greater due to increasing densities of herbivores (Jacobs 2008). The second research chapter of this thesis will assess the seasonal variation in diet preference of nyala in BPGR.

1.4.3 HABITAT USE

Analysis of how wildlife use habitat is among the most essential aspects of wildlife management (Du Toit 1988; Henley 2001; Olivier 2007; Gandiwa 2013). The ecological management of wildlife populations in a set area without detriment to either habitat or mammalian herbivore depends to a large extent on a thorough understanding of the habitat needs, habitat use and potential interspecific competition among the animal species (Pienaar 1974; Scoggings *et al.* 1990; Fay and Greeff 2008; Ritchie *et al.* 2009). Habitat selection is the process of herbivores occupying and utilising areas which provide the essential resources for survival (Morris 2003; Morrison *et al.* 2006). A preferred habitat type is one that is selected more than is expected from its availability (Neu *et al.* 1974; Garshelis 2000; Manly *et al.* 2003; Alldredge and Griswold 2006).

The selection of habitat may be governed by various factors: (a) the distribution and availability of water (Leuthold 1978; McNaughton and Georgiadis 1986); (b) the extent of interspecific competition (Lamprey 1963; Ferrar and Walker 1974); (c) the distribution and availability of quality forage (Sinclair 1979) as well as the distribution and availability of forage quantity (McNaughton and Georgiadis 1986); (d) predation (Sinclair 1985) and (e) the distribution and availability of shelter (McNaughton and Georgiadis 1986; Ben-Shahar and Skinner 1988; Dekker *et al.* 1996; Dörgeloh 1998). Among these factors, food seems to be the most important in influencing habitat selection among large herbivores (McNaughton 1987). In the third research chapter nyala distribution patterns are related to the geo-physical characteristics in BPGR in order to determine which factors are influencing the selection of their habitat.

1.5 LITERATURE REVIEW

1.5.1 THE GENERAL NYALA DIET

The diets of mammalian herbivores are widely recognized along a browser/grazer continuum based on the proportion of browse or grass in the diet (Hofmann and Stewart 1972; Hofmann 1973; Illius and Gordon 1992; Gordon and Illius 1994;

Robbins *et al.* 1995; Codron *et al.* 2007a; Müller *et al.* 2013). Three guilds are typically described: browsers, grazers and mixed-feeders (Hofmann and Stewart 1972; Jarman 1974; Hofmann 1989; Owen-Smith 1997; Du Toit 2003; Searle and Shipley 2008).

Nyala are medium sized antelope classified as mixed-feeders (Hofmann 1973; Jarman 1974; Hoffmann 1989; Woodall and Skinner 1993; Woodall and Skinner 1994). They select for fresh grass in season and occasionally practice osteophagia (Anderson 1974), but their diet comprises primarily of browse material (Vincent *et al.* 1968; Tello and Van Gelder 1975; Anderson and Pooley 1977; Anderson 1978; Van Rooyen 1992; Botha and Stock 2005; Codron *et al.* 2007a; Kirby *et al.* 2008). Nyala are one of the most sexually dimorphic ruminants in Africa (Skinner and Chimimba 2005; Kirby *et al.* 2008); males have a mean shoulder height of 1.1m and a mean mass of 110 kg, while females have a mean shoulder height of 0.9m and a mean mass of 65kg (Vincent *et al.* 1968; Skinner and Chimimba 2005). In a study conducted by Kirby *et al.* (2008), nyala displayed differences in foraging behaviour between males and females. The differences were suggested to be as a consequence of differing energetic and nutritional demands driven by their marked difference in body size and divergent reproduction strategies (Main *et al.* 1996; Kirby *et al.* 2008). Females tended to select for high quality forage and males for a greater available biomass (Kirby *et al.* 2008). Hence, an investigation of possible feeding effects of nyala in BPGR for conservation management purposes could not be seen as complete if it does not consider the separate diets of both males and females (Kie and Bowyer 1999; Bowyer *et al.* 2001; Stewart *et al.* 2003; Bowyer 2004; Shannon *et al.* 2006). In this study, diet composition, diet preference and habitat use will be investigated for nyala as a species as well as between the sexes.

In the savannas of KwaZulu-Natal, nyala were found to be mostly browsers with grass only being important during the wet season (Anderson and Pooley 1977; Anderson 1978; Van Rooyen 1992; Botha and Stock 2005; Van Eeden 2006; Kirby *et al.* 2008). Findings from Mpumalanga (Codron *et al.* 2007a) and Mozambique (Tello and Van Gelder 1975) support this classification. No studies of nyala diet composition have been conducted in the Albany Thicket Biome and there is thus a gap in our knowledge of how the animal responds to food and habitat resources in this Biome.

1.5.2 DIET COMPOSITION

Several methods have been used to determine plant species composition of ruminant diets: (a) Stomach content analysis (Anderson and Pooley 1977; Van Rooyen 1992; Ley *et al.* 2008) where plant residue recovered from the stomach is microscopically examined to determine plant species composition. (b) Direct observation (Owen-Smith *et al.* 1983; Kirby *et al.* 2008) where visual records of plant selection are made. There are different approaches to direct observation such as (1) the feeding record method (Leuthold 1971; Leuthold and Leuthold 1972), in which each instance of an animal feeding on an individual plant is counted as one food record for that plant species and, (2) the location of feeding sites can be determined through direct observation, but the selected plants are examined after feeding (Watson and Owen-Smith 2000). (c) Indirect observation (Klaus-Hügi *et al.* 1999; Owen-Smith and Chafota 2012) where plants are examined after feeding by a specific herbivore. This differs from the method of Watson and Owen-Smith (2000) in that feeding sites are not selected by direct viewing of feeding, but by analysing dung trials and tracks. (d) Microscopic analysis of faeces (Holecheck and Gross 1982; Alipayo *et al.* 1992) where plant material is identified from faeces under a microscope and (e); esophageal fistulation (Bath *et al.* 1956; Jesson *et al.* 2004) where plant material collected from esophageal fistula is identified.

The feeding record method was ruled out for this study because feeding events on each plant species are counted without considering relative feeding time allocation or plant part separation (Du Toit 1988), making it difficult to determine proportional contributions of different components. Stomach content analysis and esophageal fistulation were also ruled out, because the monetary value of the study population to the tourism based operation eliminated the options of killing or fistulating the animals. Indirect observation was eliminated as an option, because it is subject to sampling error due to the fact that it relies heavily on the level of training of the observer (Klaus-Hügi *et al.* 1999) and it is mostly used only when direct observation proves impractical (Owen-Smith and Chafota 2012).

The majority of diet composition studies in the Albany Thicket Biome made use of microscopic faecal analysis and direct observation techniques. Jacobs (2008) and

and Landman *et al.* (2008) used the presence of plant cuticles in faeces to determine composition. Midgeley (2009) rejected conclusions of the latter method, suggesting that differences in surface to volume ratios and digestibility means that not all plant parts or plant species produce cuticles in equal proportions to the size of the pieces ingested. Haschick and Kerley (1997) used ingested plant biomass in cafeteria style trials to determine proportions of plants in the bushbuck diet. This was done under controlled conditions and thus may not be representative of plant species proportions in the wild.

Direct observation was the method selected for my study. Several other authors employed this method in diet composition of browsing ruminants such as Parker *et al.* (2003), Parker and Bernard (2006) and Cornelius (2010) used direct observation to determine the diet composition of giraffes with apparent success. Parker and Bernard (2006) compared the use of microhistological faecal analysis and direct observation using the interval-scan method (Parker *et al.* 2003). They suggested that direct observation may overestimate the importance of certain food species since the sampling period for direct observations is usually short (3 hours a day in their study). The sampling period for my study is significantly longer (8 hours a day) and may thus be more objective. The use of faecal analysis may overestimate fibrous plant species and underestimate the importance of succulent species due to disparities in digestion of plant species after ingestion (McInnes *et al.* 1983; Parker and Bernard 2006). Both methods may provide accurate results and best results will be obtained by employing both methods concurrently (Parker and Bernard 2006).

Depending on the conditions in the particular study, circumstances exist under which any of the aforementioned methods could yield accurate results (Holecheck *et al.* 1982; McInnes *et al.* 1983; Alipayo *et al.* 1992; Norbury and Sanson 1992). For example, in this study, the study population has become habituated to vehicles. Their docile nature makes it possible to observe the animals from short distances for extended periods of time. Due to these circumstances, the method of direct observation was chosen for this study, which according to Holecheck *et al.* (1982), yields the most accurate results when employed with habituated animals. Simplicity and minor equipment requirements are some of the advantages of this method (Bjugstad *et al.* 1970; Theurer 1970; Theurer *et al.* 1976). Quantitative data from direct observation can be attained from the bite-count and feeding duration

approaches (Bjugstad *et al.* 1970). When the bite-count procedure is employed the number of bites taken from each species, rather than the length of feeding time, is recorded (Reppert 1960; Watson and Owen-Smith 2000). In the feeding duration approach, time spent feeding on each plant species is quantified in order to reflect the proportional significance of the species in the diet (Bjugstad *et al.* 1970; Du Toit 1988). The feeding duration approach was chosen for this study, as focal animals can be observed over short distances for extended periods.

The disadvantages of the feeding duration method include: (a) difficulty in species identification and quantification of how much of a plant species was consumed, mostly due to terrain characteristics; (b) it may be difficult to differentiate between mere nibbling and active feeding; (c) diet selection is a complex behavioural process that is influenced by several factors (Kreuger *et al.* 1974; Senft *et al.* 1987; Owen-Smith *et al.* 2010), thus when using artificially reared and/or maintained animals, important factors such as physiological condition, degree of hunger, topography, other animals present and past utilization history may be overlooked (Holecheck *et al.* 1982). The latter disadvantage is overcome as the nyala in the study area are free roaming wild animals merely habituated to vehicles and all the complex behavioural processes referred to by Kreuger *et al.* (1974), Senft *et al.* (1987) and Owen-Smith *et al.* (2010) still apply. Other factors influencing the accuracy and precision of this method include; (a) the degree of training of the observer; (b) complexity of the plant community present and/or (c) phenological development of individual plants (Holecheck *et al.* 1982).

1.5.3 DIET PREFERENCE

Nyala utilize a large variety of woody plants, forbs and grasses; however they feed selectively preferring a diet of low fibre and high protein (Anderson and Pooley 1977; Anderson 1978; Van Rooyen 1992) in a range of vegetation types within a fairly large home range (Hayes 1967; Anderson 1978; Van Rooyen 1992; Skinner and Chimimba 2005; Kirby *et al.* 2008). Several preference indices have been developed to measure food preference (Ivlev 1961; Jacobs 1974; Petrides 1975; Chesson 1978; Owen-Smith and Cooper 1987a). The forage ratio of Ivlev (1961) and Petrides (1975) has been accepted as the best measure of food preference in the past

(Crawley 1983), however the forage ratio does have two major disadvantages: (a) the index varies irregularly between zero and infinity (Jacobs 1974) and (b) the index is subjected to variations in the relative densities of the food types considered, particularly when feeding considerably reduces the densities of these food types (Jacobs 1974). The electivity index was developed by Ivlev (1961) and the log Q index by Jacobs (1974), in order to deal with the problem of asymmetry. The problem of changes in the relative densities of the food types considered is overcome by the log Q index and the α -index of Chesson (1978).

The forage ratio and variations of the method are all affected by the number of food types considered to be available to the herbivore (Owen-Smith and Cooper 1987a). Johnson (1980) recommends that only the rank order of usage and availability of food types should be compared, since food types can be assessed as preferred or neglected depending on the exclusion or inclusion of other food types in the study (Johnson 1980). Owen-Smith and Cooper (1987a) used acceptability indices to determine the preference of woody species to browsing ruminants. In the analysis of woody species available to kudu; site based acceptance values indicated a difference between accepted and neglected species (Owen-Smith and Cooper 1987a). Acceptance values of the species within the favoured and neglected categories did not differ significantly from each other. Thus the rank order of preference (Johnson 1980), may not be important in these categories (Owen-Smith and Cooper 1987a). The acceptability index of Owen-Smith and Cooper (1987a) was chosen for this study. The motivation for this choice is the advantages of the index, they include; (a) food availability and consumption is measured concurrently; (b) indices are not affected by variations in the relative abundance of food in the environment; (c) indices effectively show the general diet selection pattern of the herbivore; (d) confidence limits around indices can be computed with the use of binomial statistics (Owen-Smith and Cooper 1987a).

1.5.4 HABITAT USE

Nyala have been shown to utilise a wide range of habitats but consistently prefer denser areas offering cover from heat and predation (Hayes 1967; Tello and Van Gelder 1975; Anderson 1978; Anderson 1980; Van Rooyen 1992; Coates and

Downs 2005; Kazembe 2010). A comprehensive study conducted by Tello and Van Gelder (1975), recorded the habitat occupied by nyala in the Zinave National Park in Mozambique over a two year period. In the first year; 40% of the observations were in tree savanna with thickets, 17% were in open tree savanna with thickets, 14% were at the edges of thickets, 5% were in grassland and fewer than 10% were in tree savanna, open tree savanna and woodlands without thickets respectively. In the following year 80% of observations were in tree savanna with thickets and no more than 6% of observations were in any of the other habitats. This preference for thickets was confirmed by later studies (Van Rooyen 1990; Van Eeden 2006; Canter 2008; Kirby *et al.* 2008). In terms of water dependency, nyala have the ability to persist for a number of months without available drinking water (Roberts 1936; Davison 1971), however where water is freely available they will drink approximately once a day during the dry season and less in the wet season as the leaves on which they browse contain more moisture (Tello and Van Gelder 1975; Van Eeden 2006).

Several methods have been developed for the statistical analysis of habitat selection (Morrison *et al.* 2006; Hawthorne *et al.* 2010). According to Manly *et al.* (2003) there are three main designs for determining habitat selection: (1) Habitat use measurements are made at the population level; used habitats, unused habitats or available habitats are sampled for the whole study area and for the collection of all focus animals in the study area. In this design, individual animals are not identified. (2) Individual animals are identified and the use of habitat is measured for each individual, but availability is measured at the population level. (3) Individual animals are identified as in the previous design and at least two from three sets of; used, unused or available habitats are sampled for each individual animal. In this study the first research design was used, because it is inexpensive and allows for more accurate assumptions at the population level (Manly *et al.* 2003).

In terms of statistical methods used in the first research design; chi-squared goodness-of-fit analysis to test for differences between the expected and observed frequency of habitat use followed by Bonferroni confidence intervals to determine preference is a widely accepted method of testing (Neu *et al.* 1974; Byers *et al.* 1984; Manly *et al.* 2003). Other methods in the first design include: (a) multivariate methods of testing for habitat selection such as habitat preference analysis (Johnson 1980), compositional analysis (Aebischer *et al.* 1993), the multiresponse permutation

procedure (Mielke 1986; Alldredge *et al.* 1991) and log-linear models (Heisey 1985; Otis 1997; Otis 1998), logistic regression (Pereira and Itami 1991) and the geometric method (Kincaid and Bryant 1983).

The most important element of habitat use studies is the definition of availability (Mclean *et al.* 1998). This definition is complicated because; (a) if habitats are aggregated, the size of the study area can influence the results of resource selection analyses (Church 1987) and (b) the area considered as available may include habitats that are not actually available to the animal (Johnson 1980). In this study the method of Neu *et al.* (1974) was chosen for nyala as a species, because animals are recorded as a species and not as individuals and when this is the case, it is suggested as the most effective technique to use (Mclean *et al.* 1998).

1.5.5 SEXUAL DIMORPHISM

The evolution of sexual dimorphism in large mammalian herbivores has mainly been attributed to sexual selection and mating strategies (Ruckstuhl and Neuhaus 2000; Stokke and Du Toit 2002). Males have a lower investment in reproduction relative to females and are only limited by the availability of receptive mates, while females are inhibited by the high energetic demands linked to weaning and gestation (Clutton-Brock *et al.* 1982; Clutton-Brock 1989). Consequently females actively select males on the basis of their strength and dominance (Allonzo and Warner 2000). Being larger and stronger thus gives a male a greater chance of reproductive success (McElligot *et al.* 2001).

Sexual differences in habitat and food resource use is an important part of life history strategies of sexually dimorphic ungulates (Clutton-Brock *et al.* 1982, Main *et al.* 1996). Consequently sexual segregation holds important theoretical, management and conservation implications (Shannon *et al.* 2006; Main 2008; Shannon *et al.* 2013). Numerous studies have investigated the possible explanations for sexual segregation in ungulates (Bowyer 2004) however this remains a topic of debate (Main 1998; Main and Coblentz 1990; Mysterud 2000; Mooring and Rominger 2004; Bon *et al.* 2005; Main and Du Toit 2005; Ruckstuhl and Neuhaus 2005; Main 2008; Shannon *et al.* 2013).

Environmental stresses display considerable seasonal fluctuation and these stresses vary greatly between different locations (Main 2008; Owen-Smith *et al.* 2010). Behavioral and physiological responses to specific environmental stresses are the focus for most explanations for sexual segregation (Bowyer 2004; Main 2008). However, due to the variability in environmental pressures between seasons and locations, such explanations cannot serve as an ultimate answer (Ruckstuhl and Neuhaus 2000; Ruckstuhl and Neuhaus 2005; Main 2008; Shannon *et al.* 2013). This is where most of the debate stems from; the fact that authors seek to uncover a single, immediate explanation that completely explains sexual segregation between dimorphic ungulates (Bowyer 2004; Main 2008). Even though the debate continues on what constitutes the best explanation, it is generally accepted that no sole, proximate response is sure to provide a universal explanation (Ruckstuhl and Neuhaus 2000; Main 2008). The most popular general consensus is that multiple environmental and behavioral factors operate together to influence sexual segregation in mammalian herbivores (Main *et al.* 1996; Bleich *et al.* 1997; Ruckstuhl and Neuhaus 2000; Mooring *et al.* 2003; Bonenfant *et al.* 2004; Bon *et al.* 2005; Du Toit 2005; Perez-Barberia *et al.* 2005; Loe *et al.* 2006; Main 2008; Shannon *et al.* 2013).

Sexual segregation hypotheses are grouped into social and ecological explanations; however ecological explanations are suggested to best explain why sexes use different areas and habitats (Main 2008). Although there is still discussion about which hypotheses best explains ecological segregation in dimorphic ungulates, the five leading ecological explanations in order of popularity according to recent authors (Ruckstuhl and Neuhaus 2000; Main 2008) are: (a) the predation risk hypothesis also referred to as the reproductive strategy hypothesis; (b) the forage selection hypothesis; (c) the scramble competition hypothesis; (d) the activity budget hypothesis and; (e) the social preference hypothesis.

If nyala were to segregate between the sexes, the explanation for the segregation is likely to stem from one or a combination of these hypotheses. Here follows a short summary of what these hypotheses predict: The theory behind the predation risk hypothesis is that larger males are less vulnerable to predation than the smaller females and their young (Main *et al.* 1996). Consequently, males take more risks than females by selecting habitats with high food availability, while females firstly

select habitats that are safe from predators and secondly include food in their choice of habitat (Jakimchuk *et al.* 1987; Berger 1991; Young and Isbell 1991).

The forage selection hypothesis also known as the sexual dimorphism-body-size hypothesis predicts that because larger ruminants have a larger rumen and slower passage rate of food than smaller ones (Van Soest, 1994), it may be that between the sexes, larger males have higher absolute metabolic requirements than females and hence they need to ingest more quantity relative to females (Main *et al.* 1996). Females have lower relative absolute food requirements, but higher relative energy requirements due to the energy demands associated with gestation and lactation (Main *et al.* 1996). The sexes then segregate because males have to select for higher quantity and females for higher quality (Main *et al.* 1996).

The scramble competition hypothesis stems from explanations presented in the forage selection hypothesis and it predicts that between sex competition over food and habitat resources leads to sexual segregation (Main *et al.* 1996).

The activity budget hypothesis proposes that sexual differences in body size lead to sexual differences in energetic requirements and digestive efficiencies (Robbins 1993) and consequently to differences in foraging behaviour (Main *et al.* 1996). The activity budget hypothesis is not the same as the forage selection hypothesis, because it proposes differences in activity budgets and movement rates, instead of differences in habitat or food selection to be responsible for sexual segregation (Mooring and Rominger 2004).

The social preference hypothesis predicts that sexual segregation is as a consequence of social preferences among males (Ruckstuhl and Neuhaus 2000). For example, a specimen may prefer to stay in an all-male group to develop fighting skills or as a consequence of being in an inferior breeding condition (Bon 1991; Villaret and Bon 1995).

1.5.6 THE EXTRALIMITAL FACTOR

Herbivores, sexually dimorphic or otherwise can have a negative impact on plant life through herbivory when introduced outside their historical range in South Africa (Spear 2008). Extralimital herbivores may have a number of impacts: (a) potential competition with indigenous herbivores through exploitation and subsequent habitat

degradation; (b) loss of plant species and a decline in plant biomass, specifically amongst the small, endemic succulents and geophytes; (c) introduction of new pathogens and parasites and (d) hybridization with indigenous ungulate species (Castley *et al.* 2001; Kerley *et al.* 2004; Grobler *et al.* 2005a; Spear 2008; Vlok and Coetzee 2008; Cape Nature 2011). Evidence of such impacts exists in several studies: Coates and Downs (2005) suggest competition exists between bushbuck (*Tragelaphus scriptus*) and nyala (*Tragelaphus angasii*), in areas in Kwa-Zulu Natal where nyala occurs extraliminally. Giraffe (*Giraffa camelopardalis*) have significantly changed tree abundance and composition in their extralimital range in Kwa-Zulu Natal (Bond and Loffell 2001) and in the Eastern Cape (Jacobs 2008). Hybridization between blue wildebeest (*Connochaetes taurinus*) and black wildebeest (*Connochaetes gnou*) has been recorded where either of the two species occur extraliminally (Fabricius *et al.* 1988; Grobler *et al.* 2005b). The extralimital introduction of springbok, (*Antidorcas marsupialis*), into areas where bontebok (*Damaliscus pygargus pygargus*) occurs naturally, introduced a lungworm (*Bronchonema magna*), which then infested the bontebok, causing mortality (Meltzer 1993; Spear 2008).

With some extralimital ungulate introductions, the ecological costs such as hybridization and loss of sensitive species through competitive exclusion appear to outweigh the benefits and these ecological costs do not receive the required attention (Castley *et al.* 2001; Kerley *et al.* 2004; Palmer *et al.* 2006; Spear 2008). Nyala did not historically occur in the Southern Cape (Skead 1987; Skead *et al.* 2007) and according to Cape Nature (2011) and Vlok and Coetzee (2008) nyala is not a suitable species for introduction in Arid Mosaic Thicket due to the probability of competition with locally sensitive species such as grey duiker (*Sylvicapra grimmia*), eland (*Taurotragus oryx*) and kudu (*Tragelaphus strepiceros*).

The Thicket Biome is subject to degradation from agriculture and unsustainable game farming (Lechmere-Oertel 2003; Lechmere-Oertel *et al.* 2005). Transformation of thicket in response to herbivory could result in a considerable loss of plant and functional diversity (Stuart-Hill and Aucamp 1993; Kerley *et al.* 1995; Lechmere-Oertel 2003; Lechmere-Oertel *et al.* 2005). The impacts of herbivory on plants range from minor loss of leaf material to death of the plant and plants exposed to intense herbivory may suffer a loss of fitness and a decline in abundance (Wilson 2001;

Kerley *et al.* 2004). Therefore, herbivore feeding preferences could influence the distribution and abundance of plants, as well as the competitive interactions between these plants (Wilson 2001).

Different herbivores have different feeding preferences (Owen-Smith and Novellie 1982; Owen-Smith and Cooper 1987a), thereby impacting on different plant species (Wilson 2001). Herbivores also have different feeding styles and abilities, thereby impacting on different plant parts (Wilson 2001). Browsing ungulates at high densities inhibit seedling establishment and retard regeneration of plants through browsing pressure (Prins and van der Jeugd 1993; Augustine and McNaughton 1998; Cumming and Cumming 2003; Moolman and Cowling 1994; De Ridder 2004) and over utilization of the browsing component alters woody species composition, often with an inclination towards heavily defended and unpalatable species (Hanley 1982; Stuart-Hill 1989a; Bryant *et al.* 1991; Bryant *et al.* 1992; Augustine and McNaughton 1998; Augustine and McNaughton 2004). Abundant medium sized browsers have been shown to have a substantial impact on the woody vegetation recruitment and community dynamics of savanna ecosystems (Prins and Van Der Jeugd 1993). The Albany Thicket Biome has a very high degree of plant endemism and diversity (Jürgens 1997; Cowling and Vlok 2004; Hoare *et al.* 2006) and the addition of an extralimital species to the ecosystem could affect biodiversity and ultimately, ecosystem function (Risser 1995; Simberloff 2005). The animal/plant/animal interactions in Suptropical Thicket are very complex and there is a strong need for further studies on the impacts of browsing species in the biome (Kerley *et al.* 2004), hence this study will provide valuable information regarding the future management of nyala in the region.

When introducing any extralimital mammalian herbivore into a new system, the most important consideration is not whether the area is suitable to sustain the animal, but what the ecological impacts of the extralimital species on the indigenous vegetation could be (Bothma 2004). Thus, irrespective of how well any extralimital herbivore seems to thrive or adapt, it should be kept in mind that the animal did not evolve within the system and thus it is bound to have some impact on plant communities through feeding pressure and on the naturally occurring herbivores through interspecific competition (Pienaar 1974; Fay and Greeff 1999; Vlok and Coetzee 2008; Bothma 2004; Ritchie *et al.* 2009; Richard *et al.* 2012).

CHAPTER 2: STUDY AREA

2.1 LOCATION AND TOPOGRAPHY

Buffelsdrift Private Game Reserve (BPGR), a 1500 ha privately owned reserve is located 7km north of Oudtshoorn in the Little Karoo, Western Cape Province. A drainage valley extending north-east to south-west bisects the reserve longitudinally into a mountainous north and lower lying south. This valley's drainage line used to be a minor tributary of the Grobbelaarsriver, which flows from the Swartberg past the western boundary. The Andrew De Jager dam built in 2003 now intercepts the majority of runoff. The highest point on the property is at 641m and the lowest point is at 400m above sea level.

2.2 GEOMORPHOLOGY

The geology of BPGR falls within the Cape Supergroup and originates from sedimentary deposits between the Cretaceous and the Quaternary periods (Toerien 1979; Norman and Whitfield 2006). These sediments are derived from the Congo, Kansa and Uitenhage groups; the latter is the youngest and includes the prominent Enon formation (Norman and Whitfield 2006). The Cretaceous deposits south of the Swartberg along the Kango-Baviaanskloof Fault were deposited in structural basins and are underlain by Bokkeveld sediments (Trunswell 1977; Toerien 1979). Three distinct formations occur in the study area; Enon conglomerates, Calcrete and Hardpan and Intermediate and low level terrace gravels (Coetzee 2002). The majority of mountainous areas of BPGR consist of Enon conglomerates, which are exposed as hard cliffs at the escarpment (Coetzee 2002). Calcrete deposits occur throughout the low-lying areas to the south of the Enon cliffs and extend through most of the Oudtshoorn area (Toerien 1979; Coetzee 2002). The intermediate and low level terrace gravels area consist of fragments of rocks, sand and gravel which are the deposits of ancient erosion during the Quaternary period (Trunswell 1977; Toerien 1979; Coetzee 2002).

The soils overlying the sediments in the study area are mostly high base status apedal, soils with a medium texture (Ellis and Lambrechts 1986). The soils are

generally shallow (< 400mm) and have high clay content and high pH values (Ellis and Lambrechts 1986; Coetzee 2002). Topsoil layers are high in most plant nutrients particularly potassium (Ellis and Lambrechts 1986; Coetzee 2002).

2.3 CLIMATE AND WEATHER

BPGR is situated in the south facing foothills of the Swartberg Mountains, in a transitional zone between summer and winter rainfall areas (Schulze 1965; Breytenbach 1982). The foothills of the Swartberg receive between 102 - 545 mm of rain per year and frost occurs sporadically (Hoare *et al.* 2006). Rainfall is non-seasonal in this area, with a peak in June/July and September/October and a pronounced low point in December to February (Lubke 1996; Hoare *et al.* 2006). Rainfall is of a cyclonic-orographic nature; therefore BPGR receives most of its rain from rain-bearing south-westerly winds (Schulze 1965). Mean monthly maximum and minimum temperatures for Oudtshoorn are 39.9° C and 4.0° C for February and July respectively (Hoare *et al.* 2006). The area receives more than 80% of the potential solar radiation throughout the year, resulting in high evaporation rates from Nov – March (Schulze and McGee 1978; Cowling *et al.* 1987).

There was no reliable weather data available from BPGR; hence data from the closest reliable site was used in the form of the Oudtshoorn experimental research farm (Agricultural Research Council) (Figure 2.1). Field observations in this study were carried out from May 2012 to April 2013 (rainfall = 260 mm). The study period was divided into three seasons according to the rainfall recorded during the study: (a) the winter/wet season (June - September); (b) the spring/wet season (October - January) and (c) the summer/dry season (February – May). Rainfall over the seasonal cycle was lowest in the Summer/dry season, highest in the winter/wet season and moderate in spring/wet season. The long term annual rainfall recorded for the period 1992–2012 was 243 mm, indicating an above average annual rainfall during the study period.

2.4 WATER SOURCES

There are no perennial water sources in the study area hence BPGR has to rely on the use of artificial water points. There are four artificial water sources on the 1500 ha property (Figure 2.2). The Andrew De Jager dam in the western extreme of the reserve is regulated to have permanent water for aesthetic value and to accommodate hippopotamus (*Hippopotamus amphibious*). The three other considerably smaller water sources are spread across BPGR and are also kept full throughout the year. The reserve receives its water through a canal system originating from the Raubenheimer Dam, the main reservoir for Oudtshoorn. In times of sufficient rainfall, the drainage line of the valley bisecting the reserve flows westwards contributing to the Andrew De Jager dam. In addition there are two small non-perennial dams on the southern boundary of BPGR, holding water only in times of heavy rain.

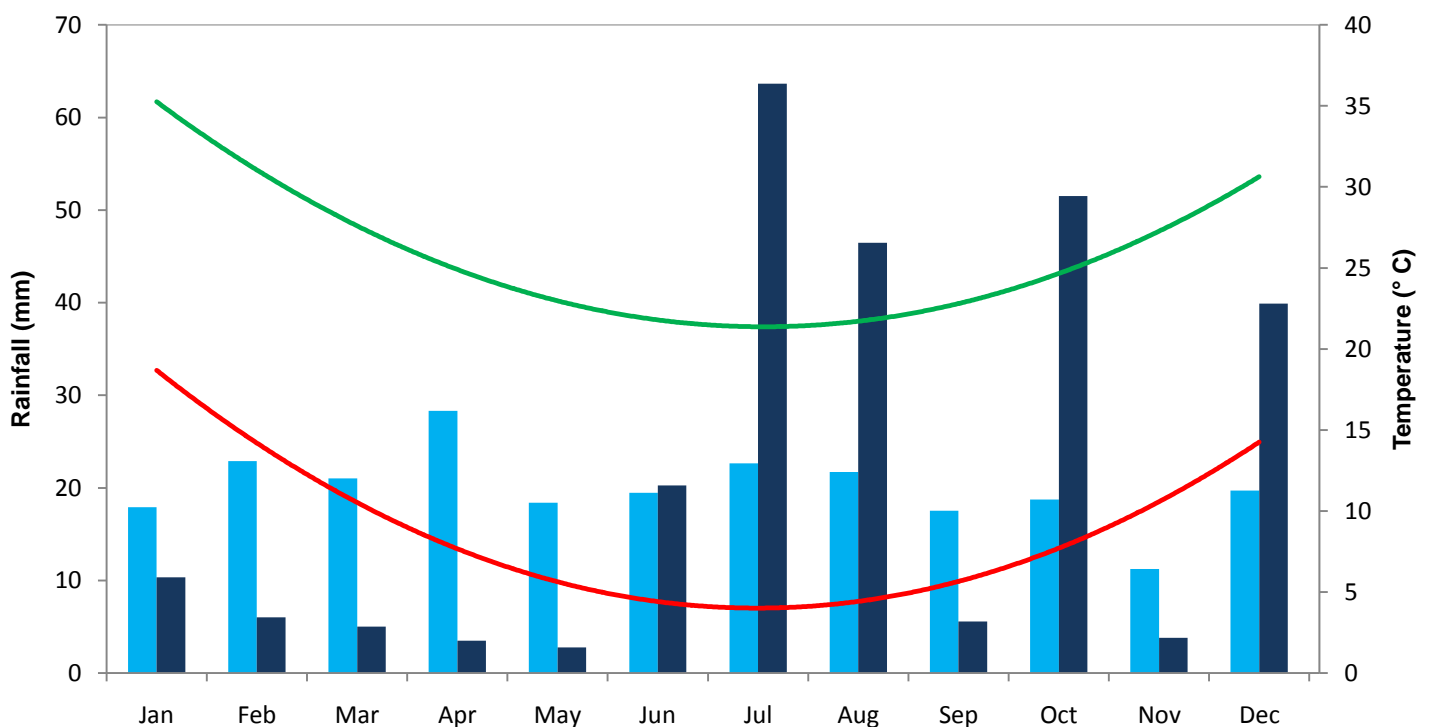


Figure 2.1: Climate diagram for the Oudtshoorn area. The upper line indicates mean daily temperature maxima and the lower line minima for each month (1992 – 2012). Light blue column indicates long term monthly rainfall (1992 – 2012) and dark blue column indicates monthly rainfall for the study period (May 2012 – April 2013) (Agricultural Research Council 2013).

2.5 VEGETATION

The study area is situated in the Albany Thicket Biome, in the eastern region of the Little Karoo (Hoare *et al.* 2006). Arid Mosaic Thicket falls in the western extremes of Albany Thicket, an area with significantly lower rainfall and higher temperatures relative to the eastern parts of the Biome (Vlok *et al.* 2003; Vlok *et al.* 2005). The vegetation of Arid Mosaic Thicket is a combination of Albany Thicket and Succulent Karoo elements (Vlok *et al.* 2003; Vlok *et al.* 2005).

Vlok *et al.* (2005) mapped a total of 56 habitat types, containing 369 vegetation units in the Little Karoo region. A six-tier hierarchical classification system was used in order to document information from a local to a regional scale, they are as follows: (1) ecosystem, (2) biome, (3) habitat type, (4) biogeographical region (formed by local river drainage zone), (5) sector (recognizing local variance of the regional habitat type i.e. floristic components and/or structural differences) and (6) solid versus mosaic vegetation units (Vlok *et al.* 2005). The vegetation in BPGR was consequently classified as Albany Thicket/Succulent Karoo at the biome level. Four major habitat types namely Apronveld, Valley Thicket with Spekboom Mosaics, River and Floodplain and Waboomveld are found in BPGR. These habitat types are all of the mosaic grain type and represent four major sectors: Grootkop, Kruisrivier, Olifants and Mons Ruber (Vlok *et al.* 2005). From this, four unique vegetation units were delineated in the study area; Kruisrivier Spekboom-Pruimveld, Olifants River and floodplain, Mons Ruber Waboomveld and Grootkop Apronveld (Figure 2.2). However, the study area has been subjected to intense utilization by domestic stock in the past, altering available biomass and species composition in some areas (Coetzee 2002). Consequently the Olifants River and floodplain vegetation unit was subdivided into intact and degraded forms, resulting in five relatively homogenous habitat units within the study area.

Due to the changes in nomenclature over time, the most recently available literature was used for plant identification in the form of Vlok and Schutte-Vlok (2010).

i) KRUISRIVIER SPEKBOOM-PRUIMVELD (65.2%)

Dense stands of thicket occur on undulating to steep foothills and in valleys on gravelly sandy soils originated from Enon conglomerates throughout the north-western part of the study area (Coetzee 2002). *Portulacaria afra* is dominant among trees such as: *Carissa haematocarpa*, *Euclea undulata*, *Searsia glauca*, *Gloveria integrifolia*, *Nymania capensis*, *Pappea capensis*, *Grewia robusta* and *Rhigozum obovatum* (Vlok *et al.* 2005). Succulent Karoo communities make up the matrix in which dwarf shrubs such as: *Pteronia incana*, *Galenia africana* and *Eriocephalus ericoides* are abundant (Coetzee 2002; Vlok *et al.* 2005). Grasses include: *Cenchrus ciliaris*, *Ehrharta calycina*, *Panicum coloratum*, *Panicum deustum*, *Sporobolus fimbriatus*, *Eragrostis plana* and *Stipa dregeana*, however they are only abundant after good rain (Vlok *et al.* 2005). Stem- and leaf succulents are abundant and include: *Aloe microstigma*, *Aloe ferox*, *Cotyledon orbiculata*, *Gasteria brachyphylla*, *Pelargonium peltatum*, *Pelargonium tetragonum*, *Quaqua pillansii*, *Ruschia ceresiana*, *Sarcostemma viminale*, *Tylecodon cacalioides* and *Tylecodon paniculatus* (Vlok *et al.* 2005). Abundant geophytes include: *Chlorophytum comosum*, *Dipcadi viride*, *Drimia capensis*, *Hessea stellaris*, *Nerine humilis* and *Ornithogalum graminifolium* (Vlok *et al.* 2005). This habitat unit is classified by Skowno *et al.* (2010) as least threatened, however according to Vlok *et al.* (2005), it is vulnerable to impacts caused by large herbivores, as they fragment the vegetation and cause soil erosion.



Figure 2.2: Habitat units available to nyala in Buffelsdrift Private Game Reserve.

The majority of the vegetation type along the southern boundary has already been transformed due to severe overutilization by domestic stock in the past (Coetzee 2002). It shows accelerated soil erosion, has a typical pseudo savanna appearance and consists of a severely degraded basal layer, mostly represented by pioneering dwarf shrubs such as *Pteronia incana*, *Pteronia pallens*, *Galenia africana*, *Atriplex lindleyi sub inflata* and various pioneering succulents such as *Drosanthemum hispidum*, *Leipoldtia schultzeii*, *Mesembryanthemum guerichianum* and *Mesembryanthemum splendens* (Coetzee 2002; Vlok et al. 2005). The reduced remnants of the original woody thicket tree and shrub component are dominated by: *Pappea capensis*, *Euclea undulata*, *Lycium oxycarpum*, *Lycium ferocissimum*, *Gloveria integrifolia*, *Nymania capensis*, *Grewia robusta* and *Rhigozum obovatum*.

ii) OLIFANTS RIVER AND FLOODPLAIN (9.8%)

Dense stands of *Acacia karroo* occur, along the main drainage lines on deep alluvial soils (Coetzee 2002). This unit occurs within the 1:50 year flood-line and is sporadically submerged during floods (Vlok and Schutte-Vlok 2010). *Acacia karroo* is the dominant among shrubs such as: *Searsia lucida*, *Lycium oxycarpum*, *Portulacaria afra*, *Zygophyllum morgsana*, *Buddleja saligna*, *Gloveria integrifolia*, *Grewia robusta* and *Olea europea var africana*. The tree succulent *Aloe ferox* is also abundant in this unit. Dominant dwarf shrubs include: *Lycium ferocissimum*, *Pentzia incana*, *Rosenia humilus* and *Pteronia incana*. Succulents typical of this unit are: *Euphorbia mauritannica*, *Mesembryanthemum spp*, *Ruschia spp*, *Hereroa spp*, *Leipoldtia spp* and *Drosanthemum spp*. Grasses such as *Cenchrus ciliaris*, *Erharta calycina*, *Digitaria eriantha* and *Cynodon dactylon* occur after good rain (Vlok et al. 2005). This unit is described by Skowno et al. (2010) as poorly protected and vulnerable due to a relatively high concentration of locally endemic succulents and geophytes.

iii) DEGRADED OLIFANTS RIVER AND FLOODPLAIN (1.9%)

Overutilization by domestic stock resulted in the nutrient rich alluvial valley floor soils becoming exposed (Coetzee 2002). This unit is characterized by a mosaic of bare patches and a dominance of pioneer vegetation. *Acacia karroo* is still the dominant among shrubs such as: *Grewia robusta*, *Gloveria integrifolia* and *Lycium oxycarpum*, however the majority the other previously mentioned trees have been eliminated. *Galenia africana* is the dominant among pioneering dwarf shrubs such as *Pteronia pallens*, *Rosenia humilis* and *Pteronia incana*.

iv) GROOTKOP GRAVEL APRONVELD (11.9%)

This unit occurs in the south west of the reserve on gravelly clay soils with a distinct rocky surface layer derived from calcrete and cretaceous conglomerate (Coetzee 2002). The unit is dominated by Asteraceous dwarf shrubs and succulents (Vlok *et al.* 2005). Dominant dwarf shrubs include: *Elytropappus rhinocerotis*, *Eriocephalus ericoides*, *Euryops oligoglossus*, *Euryops subcarnosus*, *Hirpicium integrifolium*, *Pteronia incana*, *Pteronia pallens*, *Limeum aethiopicum*, *Pteronia paniculata*, *Zygophyllum lichtensteinianum*, *Rosenia humilis*, *Pentzia incana* and *Osteospermum sinuatum*. Dominant succulents include: *Cotyledon orbiculata*, *Drosanthemum giffenii*, *Lampranthus haworthii*, *Glottiphyllum depressum*, *Tylecodon wallichii*, *Aloe microstigma*, *Aloe variegata*, *Adromischus triflorus* and *Conophytum truncatum*. Grasses are poorly represented and include: *Digitaria eriantha*, *Fingerhuthia africana*, *Cynodon dactylon* and *Erharta calycina* (Vlok *et al.* 2005). This unit is rich in geophytes such as: *Babiana sambucina*, *Freesia refracta*, *Gladiolus permeabilis*, *Lapeirousia pyramidalis*, *Moraea polyanthos*, *Moraea polystachya*, *Ornithogalum dubium*, *Ornithogalum juncifolium* and *Tritonia securigera* (Vlok *et al.* 2005). Shrubs are mostly restricted to bushclumps and include: *Carissa haematocarpa*, *Pappea capensis*, *Euclea undulata*, *Rhigozum obovatum*, *Nymania capensis* and *Searsia undulata* (Vlok *et al.* 2005). Several rare and localised endemic species occur in this unit, including: *Adromischus sp.nov. (cf. triflorus)*, *Ceropegia fimbriata*, *Drimia sp.nov.*, *Drimia uranthera*, *Euphorbia colliculina*, *Glottiphyllum linguiformis*, *Haworthia truncata*, *Ornithogalum sp.nov.* and *Tylecodon cacalioides* (Vlok *et al.* 2005). This

unit is listed critically endangered, completely unprotected and its protection urgency is described as critical (Skowno *et al.* 2010).

v) MONS RUBER WABOOM-THICKET (11.2%)

The vegetation in this unit is still predominantly Albany Thicket however it is distinct from the other units as it contains some Fynbos elements (Vlok *et al.* 2005). The Albany Thicket elements dominate the north facing slopes and include shrubs such as: *Carissa haematocarpa*, *Euclea undulata*, *Gymnosporia buxifolia*, *Gloveria integrifolia*, *Nymannia capensis*, *Searsia undulata* and *P. afra*. Fynbos elements are prominent on the rocky outcrops and south facing slopes and include shrubs such as: *Euryops lateriflorus*, *Passerina obtusifolia*, *Pteronia incana*, *Pteronia fasciculata*, *Dodonaea viscosa* and *Aspalathus spp.* Dwarf shrubs are well represented and include; *Agathosma recurvifolia*, *Hermannia cuneifolia*, *Rosenia humilis* as well as various *Pelargonium spp.* The restio *Rhodocoma arida* is also common. One of the distinctive features of this vegetation type is the presence of waboom (*Protea nitida*). However due to past grazing and burning practices the species is poorly represented in BPGR. Even though the unit is classified as least threatened (Skowno *et al.* 2010), several rare and localized endemic species occur here, including *Babiana sp.nov*, *Haworthia blackburniae var. derustensis*, *Lachenalia latimeriae*, *Machairophyllum brevifolium*, *Machairophyllum latifolium* and *Manulea derustiana*.

2.6 LARGE HERBIVORES

The study population consisted of approximately 30 nyala. A family group of twelve (4♂; 8♀) were introduced to BPGR during April 2004. The origin of the group, before introduction to the Southern Cape is unknown. The nyala were kept in a boma for one week and released in May 2004. Apart from the nyala population, BPGR also has sixteen other large mammal species: common duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*), kudu (*Tragelaphus strepiceros*), eland (*Taurotragus oryx*), giraffe (*Giraffa camelopardalis*), grey rhebuck (*Pelea capreolus*), springbuck (*Antidorcas marsupialis*), black wildebeest (*Connochaetes gnou*), Cape

mountain zebra (*Equus zebra zebra*), buffalo (*Syncerus caffer*), white rhino (*Ceratotherium simum*), oryx (*Oryx gazella*), red hartebeest (*Alcelaphus bucelaphus*), waterbuck (*Kobus ellipsiprymnus*), hippopotamus (*Hippopotamus amphibious*) and elephant (*Loxodonta africana*) (Table 2.1). The hippopotamus, rhino and buffalo are given lucerne as supplementary feeding during the dry seasons. The elephants are tame, used in recreational tourist activities and only use a small designated portion of the reserve.

Table 2.1: Results of road counts (mean \pm SD) conducted by BPGR staff during January 2013.

Species	Mean \pm SD (N = 3)
Kudu	23.0 \pm 3.0
Red Hartebeest	20.3 \pm 1.5
Black Wildebeest	20.3 \pm 2.3
Buffalo	7.0 \pm 0.0
Grey rhebuck	17.0 \pm 1.0
Waterbuck	12.3 \pm 0.6
Eland	9.0 \pm 0.0
Nyala	26.0 \pm 1.0
Oryx	23.3 \pm 1.5
Common duiker	8.7 \pm 3.5
Springbuck	31.3 \pm 3.1
Giraffe	15.0 \pm 0.0
Cape Mountain zebra	11.0 \pm 0.0
White rhino	1.0 \pm 0.0
Steenbok	4.0 \pm 2.0
Hippopotamus	6.0 \pm 0.0
Elephant	3.0 \pm 0.0

CHAPTER 3: DIET COMPOSITION

3.1 INTRODUCTION

Food available to large mammalian herbivores can be categorized into three different groups; plant form (e.g. grasses, succulents, forbs, dwarf shrubs and shrubs), plant parts (e.g. leaves and stems) and plant species (Grunow 1980; Everett *et al.* 1991; Watson and Owen-Smith 2000). The principal focus of diet composition is the proportional contribution of dietary components to the diet of the large mammalian herbivore (Petrides 1975; Holecheck *et al.* 2004; Venter and Watson 2007). In this study dietary components are considered to be plant forms and plant species.

Diet assessment of large mammalian herbivores is a valuable tool in the management of natural rangelands (Holecheck *et al.* 1982; McInnis *et al.* 1983). Such information allows an evaluation of the impacts that these herbivores could have on the ecosystem as well as highlight the potential competition with other herbivores (Hanley and Hanley 1982; McInnis *et al.* 1983; Duncan and Poppi 2008).

The anatomy and physiology of a large mammalian herbivores digestive tract, as well as its metabolic requirements, will ultimately determine its food choice (Hofmann and Stewart 1972; Owen-Smith 1988; Clauss *et al.* 2003a; Villalba and Provenza 2005). However, the essential link between the herbivore and its food choice is the relationship between food availability and food intake (Johnson 1980; Owen-Smith 1988; Clauss *et al.* 2007). Food intake is determined by the availability, accessibility and quality of foods (Heady 1964; Owen-Smith and Novellie 1982; Codron *et al.* 2007c). Food quality varies, since plant material varies in chemical and structural characteristics and hence in nutritive value (Owen-Smith 2004; Duncan and Poppi 2008; Mithofer and Boland 2012). Availability can be defined as accessible plant species presented to the herbivore (Johnson 1980; Owen-Smith and Cooper 1987a). Accessibility refers to plant features that constrain the rate of harvest by the herbivore, such as above ground height of edible parts or structural features such as spinescence and growth form (Cooper and Owen-Smith 1986; Hanley *et al.* 2007). These features differ between plant species, vary between seasons and the degree of their effect on selection varies between mammalian herbivores with different

ecological requirements (Heady 1964; Owen-Smith 1982; Owen-Smith 1988; Scoggings *et al.* 2004). Thus diet selection by mammalian herbivores is dependent on a range of chemical and physical plant features operating independently or together (Westoby 1974; Owen-Smith 1982; Van Soest 1994; Clauss *et al.* 2003b; Beckerman 2005).

The principal foods of a mammalian herbivore in a certain system are those plant species which it eats in the greatest quantities and preferred food species are those species that are consumed in a greater proportion than their representation in the environment (Petrides 1975). A principal food species can also be a preferred food species, but a preferred food species is not automatically a principal food species (Petrides 1975; Everett *et al.* 1991). Principal food species may be less palatable than preferred species, but they form the bulk of the ungulates nutritional intake (Grunow 1980). Evaluating the proportional contributions of principal food species to the diet of a large herbivore in a particular ecosystem provides data regarding the scale of feeding pressure exerted by the herbivore on the selected plant species (Grunow 1980; Goheen *et al.* 2004; Dharhani *et al.* 2008).

Nyala are classified as mixed-feeders preferring browse (Hofmann 1973; Jarman 1974; Hoffmann 1989; Woodall and Skinner 1993; Woodall and Skinner 1994). They feed selectively, preferring a diet of low fiber and high protein (Anderson and Pooley 1977; Anderson 1978; Van Rooyen 1992) within a fairly large home range (Jarman 1974; Skinner and Chimimba 2005). Nyala utilize a narrow range of habitats concentrating in areas that provide sufficient cover from heat and predation (Hayes 1967; Tello and Van Gelder 1975; Anderson 1978; Anderson 1980; Van Rooyen 1992; Coates and Downs 2005; Kazembe 2010). They are sexually dimorphic; males have a shoulder height of 1.1 m and a mean mass of 110 kg, while females have a mean shoulder height of 0.9 m and a mean mass of 65 kg (Vincent *et al.* 1968; Skinner and Chimimba 2005; Kirby *et al.* 2008).

Nyala have recently been introduced into a number of private reserves in the Southern Cape, including the Arid Mosaic Thicket areas of the Little Karoo (Cape Nature 2011). Abundant medium sized browsers have been shown to have a substantial impact on the woody vegetation recruitment and community dynamics of savanna ecosystems (Prins and Van Der Jeugd 1993). Nyala herbivory has not co-evolved with the vegetation of Arid Mosaic Thicket since nyala are extralimital to the

southern Cape (Skead 1987; Skead *et al.* 2007). Nyala are therefore likely to impact on the plant communities through browsing pressure and on the naturally occurring herbivores through interspecific competition (Pienaar 1974; Vlok and Coetzee 2008; Ritchie *et al.* 2009; Richard *et al.* 2012). Understanding the possible impacts of nyala on biodiversity in an Arid Mosaic Thicket environment can facilitate the more effective management of the vegetation using the herbivores as tools in conservation management (Duncan and Poppi 2008).

Recent studies found considerable differences in the feeding ecology of sexually dimorphic species (Bowyer 2004; Shannon *et al.* 2006; Kirby *et al.* 2008; Shannon *et al.* 2013). A school of thought suggests that for the efficient management of sexually dimorphic mammalian herbivores, species such as nyala may have to be considered as ecologically separate species (Bowyer 2004; Shannon *et al.* 2006; Kirby *et al.* 2008).

The evolution of sexual dimorphism in large mammalian herbivores has mainly been attributed to sexual selection and mating strategies (Ruckstuhl and Neuhaus 2000; Ruckstuhl and Neuhaus 2002; Stokke and Du Toit 2002). Males have a lower investment in reproduction relative to females and are only limited by the availability of receptive mates, while females are inhibited by the high energetic demands linked to weaning and gestation (Clutton-Brock *et al.* 1982; Clutton-Brock 1989). Consequently females actively select males on the basis of their strength and dominance (Allonzo and Warner 2000). Being larger and stronger thus gives a male a greater chance of reproductive success (McElligot *et al.* 2001).

Several hypotheses predict that sexual dimorphism may have a significant influence on habitat use and feeding behaviour of males and females due to differences in; (a) nutrient and energy demands; (b) activity budgets; (c) predator avoidance strategies; (d) intersexual competition and (e) social preferences (Ruckstuhl and Neuhaus 2000; Main 2008). These differences are driven by differing reproduction strategies and the allometric relationships linked to increasing body size (Ruckstuhl and Neuhaus 2000; Stokke and Du Toit 2002; Kirby *et al.* 2008). A larger body size means males have higher absolute food requirements than females, which obligates them to ingest lower quality forage if high quality forage is not readily available (Kirby *et al.* 2008; Shannon *et al.* 2013). Whereas females have to select for high quality forage in order to meet their high energy demand due to gestation

and lactation (Clutton-Brock *et al.* 1982; Main *et al.* 1996; Bowyer 2004). Hence there may be differences in diet composition between males and females in BPGR, which could lead to spatial segregation of the sexes at the plant and/or habitat scale.

The objectives of this chapter are: a) to investigate the seasonal variation in diet composition of nyala in Buffelsdrift Private Game Reserve and b) to investigate diet composition between the sexes brought about by a marked sexual dimorphism.

3.2 METHODS

3.2.1 STUDY SITE

Refer to Chapter 2.

3.2.2 FEEDING OBSERVATIONS

In this study diet composition was measured in terms of the proportional distribution of feeding time between plant forms and plant species. For browsers, feeding time is a more accurate measure of quantity of food ingested than bite frequency (Bjugstad *et al.* 1970; Owen-Smith 1979). This is due to variations in bite size between forage types, as well as the difficulty in counting bites taken by animals in the wild (Du Toit 1988).

Nyala spend most of the day feeding, with peaks in intensity in the early mornings and late afternoons and a decrease in intensity during the mid-day, especially in summer months (Tello and Van Gelder 1975, Skinner and Chimimba 2005). Direct observations were thus made from an open vehicle for four consecutive hours in the mornings and afternoons respectively. Summer: (06:00-10:00) mornings and (15:00-19:00) afternoons; winter: (07:00-11:00) mornings and (14:00-18:00) afternoons. The observation sessions were for five days a month from May 2012 to April 2013. All available survey routes in the study area were used, covering all the available vegetation types in order to have temporally distributed observations.

The focal animal was chosen as the first nyala observed feeding within an acceptable viewing distance (± 20 m). The distance was deemed acceptable when the individual plants being fed on could be clearly identified using a pair of 10 x 20 Bushnell binoculars. Observations on an individual continued for as long as an acceptable viewing distance could be maintained. The study population was habituated to vehicles and humans and focal animals could thus be approached, by vehicle and when necessary on foot, to within ± 20 m without disturbing the behaviour of the animals. Due to the nature of the thicket vegetation, some animals were obscured as they moved into denser areas, thus when circumstances demanded it, the focal animal was observed on foot.

Feeding duration was recorded using a handheld stopwatch. The plant species, plant form, feeding duration, location, date and sex was noted on field observation data sheets. In some cases it was unclear which species was utilized, due to terrain characteristics. When this was the case, the time spent feeding was temporarily allocated to an alphabetical value. When the animal was no longer within an acceptable viewing distance, close investigation was made for verification of plant species. A plant species was only considered utilized if green, moist, freshly severed tissue was evident. If verification of the assumed plant species was not transparently clear, the observation was disregarded. Plant species eaten by nyala were categorised into five plant forms: grasses (graminoids), succulents (dicotyledons with fleshy leaves), forbs (soft-stemmed dicotyledons), dwarf shrubs (woody-stemmed dicotyledons < 1 m in height when mature) and shrubs (woody-stemmed dicotyledons > 1 m in height when mature). No distinction was made between shrubs and trees. Forbs sprouting after rain (opslag) were grouped together as annuals. These species grew entwined making it difficult to determine a feeding duration for individual species.

3.2.3 DATA ANALYSIS

The percentage contributions of plant form *i* and plant species *i* to the nyala diet was calculated as:

$$ps_i = (t_i/t) \times 100$$

where t_i is the time spent feeding on plant form *i* or plant species *i* and t is the total observation time for all forms or species. The ps_i was calculated for each day of sampling and twenty days of sampling were used for every season. For each form and species eaten, the hypothesis of equal proportions of ps_i across seasons was tested using the Kruskal-Wallis one-way ANOVA. The multiple comparisons by mean ranks test was used to determine which pairs of means were considered different.

The ps_i for the respective sexes was calculated for each day of sampling using the formula above and twenty days of sampling were used for each season. For each season, hypothesis of equal proportions of ps_i between the sexes was tested using the Mann–Whitney U-test.

3.3 RESULTS

3.3.1 NYALA DIET COMPOSITION

Browse contributed 87.8% to the annual nyala diet, while grass contributed 12.2% (Table 3.1). In each season browse formed the bulk of the diet, but nyala consumed more browse in the spring/wet and summer/dry seasons than in the winter/wet season. Shrubs formed the highest proportion of the diet in every season; however shrub consumption by nyala varied significantly between seasons. Shrub consumption was at its lowest in the winter/wet season and at its highest in the summer/dry season. Dwarf shrubs consistently contributed > 20% to the diet throughout the year and did not differ significantly between seasons. Forbs and grasses were important during the winter/wet season, but significantly less in spring and summer. Succulents consistently contributed the lowest proportion of the diet in all seasons.

The recorded diet consisted of 42 browse species and five grass species. Species considered important are those contributing > 1% to the annual nyala diet (Table 3.2). All species eaten are included in Appendix 3.1. Of the important species only six formed > 5% of the annual diet. Of these six only three species formed > 10% of the annual nyala diet; they are the shrubs *Acacia karroo*, *Pappea capensis* and *Grewia robusta*. These were followed by the shrub *Portulacaria afra*, the dwarf shrub *Zygophyllum lichtensteinianum* and the grass *Cynodon dactylon* all contributing between 5 - 10% to the annual diet.

For the majority of plant species, composition in the nyala diet varied significantly between seasons. The evergreen shrubs *Pappea capensis* (12.1%), semi deciduous *Grewia robusta* (9.2%) and the evergreen dwarf shrub *Zygophyllum lichtensteinianum* (7.8%) contributed consistently high proportions to the diet through all seasons. Of the other seasonally important species, the contribution of the perennial grass *Cynodon dactylon* was the highest to the nyala diet (16.4%) during the winter/wet season, but it contributed significantly less in the other seasons. Similarly, the annual grass *Erharta calycina* was important in the winter/wet season (7.6%), but contributed significantly less in the other seasons. During the spring/wet season the deciduous shrub *Acacia karroo* contributed the most to the diet (21.2%), but it was eaten significantly less in the other seasons. During the summer/dry season the evergreen shrub *Portulacaria afra* contributed the most to the nyala diet (14.6%), followed by the deciduous shrubs *Rhigozum obovatum* (8%) and *Nymania capensis* (6.9%) all eaten significantly more during summer/dry season than in the other seasons. The evergreen shrub *Zygophyllum morgsana* contributed significantly less in the winter season than in the other seasons.

3.3.2 THE DIET COMPOSITION OF MALE AND FEMALE NYALA

Males and females ate similar proportions of browse and grass during the study period. However, at the plant form level dwarf shrubs were eaten significantly more by females than males throughout the year (Table 3.3), peaking during the spring/wet season. Females ate significantly more forbs than males on an annual basis and in the winter/wet and spring/wet seasons. Shrubs contributed significantly

more to the male diet during the winter/wet and spring/wet seasons. Succulents consistently contributed the lowest proportion of both diets.

On an annual basis all of the important plant species in the nyala diet featured in the diet of both sexes (Table 3.4). The shrubs *P. capensis* and *P. afra* were eaten more by males than females on an annual basis, whereas the dwarf shrubs *Z. lichtensteinianum*, *L. aethiopicum*, *R. humilis* and *A. semibaccata* were eaten more by females on an annual basis. The shrubs *P. capensis*, *R. obovatum*, *N. capensis* and *Z. morgsana* were eaten more by males during the winter/wet season, while annual forbs and the dwarf shrubs *Z. lichtensteinianum*, *L. aethiopicum*, *R. humilis* and *A. semibaccata* were eaten more by females. *Portulacaria afra* contributed significantly more to the male diet during the spring/wet season, but not in the other seasons, while *P. capensis* and *N. capensis* continued to contribute more to the male diet during the spring/wet season. In the spring/wet season the dwarf shrubs *Osteospermum sinuatum* and *R. humilis* were the only species eaten more by females. During the summer/dry season the sexes ate similar proportions of species, with the only exceptions being *Z. lichtensteinianum* and *L. aethiopicum* that were eaten more by females.

Table 3.1: Seasonal contribution of plant forms (mean \pm SD) to the annual diet of nyala as determined by direct observations. Values are percentages. Codes: n = number of days of observations.

Plant form	Annual n = 60	Winter/wet n = 20	Spring/wet n = 20	Summer/dry n = 20	Kruskal Wallis = $H_{2, 60}$.
Shrubs	53.5 \pm 19.8	33.3 \pm 11.3 ^a	57.2 \pm 12.1 ^b	70.0 \pm 10.6 ^c	37.8**
Dwarf shrubs	27.5 \pm 12.3	23.6 \pm 13.3	32.5 \pm 11.4	26.3 \pm 11.0	6.6
Forbs	6.4 \pm 9.6	16.5 \pm 10.8 ^a	2.3 \pm 3.3 ^b	0.6 \pm 0.5 ^b	37.4*
Succulents	0.4 \pm 0.9	0.1 \pm 0.2	0.2 \pm 0.3	0.8 \pm 1.5	12.4
Grasses	12.2 \pm 13.0	26.5 \pm 12.0 ^a	7.7 \pm 5.9 ^b	2.3 \pm 1.8 ^c	41.1**
Total	100	100	100	100	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 3.2: Plant species (mean \pm SD) that contributed $> 1\%$ to the annual diet of nyala as determined by direct observations. Values are percentages. Codes: n = number of days of observations, S = semi-deciduous, D = deciduous, E = evergreen, s = shrub, d = dwarf shrub, g = grass.

Species	Habit	Annual	Winter/ wet n = 20	Spring/ wet n = 20	Summer/ dry n = 20	Kruskal Wallis = $H_{2,60}$
Shrubs						
<i>Acacia karroo</i>	Ds	11.8 \pm 11.9	2.5 \pm 6.3 ^a	21.2 \pm 10.7 ^b	10.3 \pm 8.9 ^c	32.0***
<i>Pappea capensis</i>	Es	11.7 \pm 8.8	12.1 \pm 9.5	12.2 \pm 8.9	10.9 \pm 8.2	0.3
<i>Grewia robusta</i>	Ss	10.7 \pm 8.4	9.2 \pm 6.1	11.1 \pm 11.3	11.8 \pm 7.2	1.7
<i>Portulacaria afra</i>	Es	6.8 \pm 7.8	2.9 \pm 2.3 ^a	3.1 \pm 3.0 ^a	14.6 \pm 9.0 ^b	29.0**
<i>Rhigozum obovatum</i>	Ss	3.3 \pm 5.8	0.3 \pm 1.4 ^a	1.7 \pm 1.2 ^a	8.0 \pm 8.1 ^b	31.1**
<i>Nymania capensis</i>	Es	3.1 \pm 4.4	0.8 \pm 1.2 ^a	1.6 \pm 2.2 ^a	6.9 \pm 5.4 ^b	24.3**
<i>Zygophyllum morgsana</i>	Es	4.0 \pm 3.8	1.6 \pm 2.0 ^a	5.4 \pm 5.0 ^b	4.7 \pm 3.3 ^b	16.3**
Dwarf shrubs						
<i>Zygophyllum lichtensteinianum</i>	Ed	8.8 \pm 6.3	7.8 \pm 4.9	9.2 \pm 7.6	9.4 \pm 6.1	0.8
<i>Limeum aethiopicum</i>	Ed	3.5 \pm 3.7	2.3 \pm 4.2 ^a	5.1 \pm 4.0 ^b	2.4 \pm 2.3 ^{ab}	9.8*
<i>Atriplex lindleyi subsp. inflata</i>	Ed	3.0 \pm 3.6	3.8 \pm 4.7	2.9 \pm 2.5	2.4 \pm 3.2	2.1
<i>Osteospermum sinuatum</i>	Ed	2.8 \pm 3.5	3.4 \pm 3.1 ^a	3.5 \pm 3.0 ^a	2.2 \pm 4.3 ^b	12.2*
<i>Pentzia incana</i>	Ed	2.2 \pm 1.6	2.8 \pm 2.0	2.3 \pm 0.6	2.0 \pm 1.8	1.6
<i>Galenia cymosa</i>	Ed	1.6 \pm 1.8	1.2 \pm 1.7 ^a	1.3 \pm 1.7 ^a	2.7 \pm 2.0 ^b	10.3*
<i>Atriplex semibaccata</i>	Ed	1.5 \pm 2.0	2.2 \pm 1.8 ^a	0.6 \pm 1.1 ^b	1.7 \pm 2.5 ^{ab}	10.2**
<i>Rosenia humilis</i>	Ed	1.4 \pm 1.3	1.6 \pm 1.2 ^{ab}	2.0 \pm 1.7 ^a	0.9 \pm 0.7 ^b	7.6*
Forbs						
Annuals		4.2 \pm 8.0	11.0 \pm 10.1 ^a	0.7 \pm 1.7 ^b	-	47.6***
Grasses						
<i>Cynodon dactylon</i>	g	7.8 \pm 9.6	16.4 \pm 11.5 ^a	5.0 \pm 5.4 ^b	2.1 \pm 1.8 ^b	27.0***
<i>Erharta calycina</i>	g	3.1 \pm 5.0	7.6 \pm 6.3 ^a	1.4 \pm 1.9 ^b	-	40.6**
Total		91.0	90.0	90.3	93.0	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

a – means within the same row with the same letters do not differ significantly.

Table 3.3: Pant forms (mean \pm SD) in the annual diet of male and female nyala, as determined by direct observations. Values are percentages. Codes: n = number of days of observations.

Plant form	Annual n = 60		Man-Whitney U - test	Winter/wet n = 20		Man-Whitney U - test	Spring/wet n = 20		Man-Whitney U - test	Summer/dry n = 20		Man-Whitney U - test
	♂	♀	Z	♂	♀	Z	♂	♀	Z	♂	♀	Z
Shrubs	62.5 \pm 13.8	42.6 \pm 16.3***	3.5	47.1 \pm 23.7	20.5 \pm 11.4***	3.7	63.5 \pm 21.2	46.6 \pm 24.3*	2.1	77.3 \pm 17.8	65.7 \pm 20.3	1.9
Dwarf shrubs	22.3 \pm 17.5	36.4 \pm 20.0***	4.5	16.5 \pm 13.3	34.7 \pm 16.6***	3.4	27.8 \pm 20.8	41.4 \pm 23.7*	2.3	16.5 \pm 17.0	31.1 \pm 19.0*	2.0
Forbs	3.3 \pm 3.7	8.8 \pm 4.8*	2.3	11.4 \pm 22.1	18.1 \pm 19.1*	2.0	0.5 \pm 1.9	4.8 \pm 8.9*	9.0	1.5 \pm 0.9	0.9 \pm 1.2	1.2
Succulents	0.4 \pm 1.2	0.4 \pm 1.7	0.5	0.1 \pm 0.3	-	0.7	0.4 \pm 0.7	0.2 \pm 0.5	1.8	1.7 \pm 2.0	1.1 \pm 1.8	1.5
Grasses	11.5 \pm 17.6	11.8 \pm 15.9	0.02	24.9 \pm 23.8	26.7 \pm 18.6	0.7	7.8 \pm 9.4	7.0 \pm 7.8	0.04	3.0 \pm 2.8	1.2 \pm 2.9	0.8
Total	100	100		100	100		100	100		100	100	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 3.4: Pant species (mean \pm SD) contributing $> 1\%$ to the annual diet of male and female nyala, as determined by direct observations. Values are percentages. Codes: n = number of days of observations, S = semi-deciduous, D = deciduous, E = evergreen, P = perennial, A = annual, s = shrub, d = dwarf shrub, g = grass.

Species	Habit	Annual n = 60			Winter/wet n = 20			Spring/wet n = 20			Summer/dry n = 20		
		♂	♀	Man-Whitney U - test Z	♂	♀	Man-Whitney U - test Z	♂	♀	Man-Whitney U - test Z	♂	♀	Man-Whitney U - test Z
Shrubs													
<i>Acacia karroo</i>	Ds	12.8 \pm 19.8	10.7 \pm 16.0	1.1	3.9 \pm 8.6	1.0 \pm 2.0	1.7	22.6 \pm 26.4	19.8 \pm 19.9	0.8	10.8 \pm 16.0	9.8 \pm 16.6	0.1
<i>Pappaea capensis</i>	Es	14.8 \pm 17.0	8.5 \pm 12.3**	5.9	17.6 \pm 15.4	6.5 \pm 10.8*	1.7	15.4 \pm 17.7	8.9 \pm 10.4*	4.3	11.0 \pm 10.7	10.8 \pm 15.3	0.2
<i>Grewia robusta</i>	SDs	10.4 \pm 14.2	10.9 \pm 15.0	0.1	8.9 \pm 12.0	9.4 \pm 11.6	3.0	10.3 \pm 16.7	11.9 \pm 17.2	0.6	12.2 \pm 14.1	11.4 \pm 16.2	0.2
<i>Portulacaria afra</i>	Es	8.1 \pm 15.2	5.5 \pm 11.0*	3.2	3.2 \pm 7.4	2.5 \pm 6.0	1.3	4.2 \pm 5.6	1.9 \pm 1.9*	4.5	15.8 \pm 15.7	13.4 \pm 22.7	0.3
<i>Rhigozum obovatum</i>	SDs	5.1 \pm 11.4	1.5 \pm 3.8	1.6	1.7 \pm 7.5	0.1 \pm 0.5*	2.5	1.8 \pm 3.8	1.6 \pm 3.3	0.9	8.9 \pm 16.0	7.0 \pm 5.4	1.4
<i>Nymanya capensis</i>	Ds	3.3 \pm 7.3	2.9 \pm 9.0	2.7	1.4 \pm 2.8	0.2 \pm 0.7*	2.3	2.0 \pm 1.8	1.1 \pm 3.7*	3.6	7.5 \pm 11.5	6.2 \pm 13.9	0.2
<i>Zygophyllum morgsana</i>	Es	4.9 \pm 8.4	3.1 \pm 5.9	0.5	2.2 \pm 5.5	0.9 \pm 1.0*	2.9	6.7 \pm 11.5	4.0 \pm 5.0	0.5	4.9 \pm 7.0	4.6 \pm 8.4	0.0
Dwarf shrubs													
<i>Zygophyllum lichtensteinianum</i>	Ed	6.0 \pm 12.1	11.5 \pm 12.8**	4.3	4.0 \pm 6.3	11.2 \pm 12.0*	6.0	8.2 \pm 16.9	10.2 \pm 14.7	1.3	6.9 \pm 10.8	12.3 \pm 12.2*	4.2
<i>Limeum aethiopicum</i>	Ed	2.8 \pm 4.3	4.2 \pm 6.7*	3.0	0.3 \pm 2.5	4.2 \pm 7.5*	3.3	5.6 \pm 12.6	5.4 \pm 7.4	1.6	1.6 \pm 3.3	3.1 \pm 4.6*	3.1
<i>Atriplex lindleyi</i> subsp. <i>inflata</i>	Ed	2.8 \pm 6.1	3.2 \pm 6.2	0.4	3.7 \pm 8.4	3.9 \pm 4.4	1.3	2.7 \pm 4.8	3.1 \pm 8.5	0.5	2.1 \pm 4.5	2.6 \pm 5.2	0.6
<i>Osteospermum sinuatum</i>	Ed	2.5 \pm 7.7	3.1 \pm 6.3	1.0	2.8 \pm 5.7	4.0 \pm 5.5	6.0	1.4 \pm 2.1	5.6 \pm 6.9**	9.0	2.0 \pm 12.0	2.4 \pm 6.3	0.3
<i>Pentzia incana</i>	Ed	1.8 \pm 3.5	2.6 \pm 4.7	1.2	2.7 \pm 4.4	2.9 \pm 4.5	0.7	1.8 \pm 2.7	2.4 \pm 4.5	1.5	1.8 \pm 3.1	2.1 \pm 5.3	1.7
<i>Galenia cymosa</i>	Ed	1.0 \pm 2.5	2.2 \pm 3.7	1.4	0.6 \pm 0.9	1.7 \pm 2.8	3.0	0.7 \pm 0.8	1.8 \pm 2.9	0.2	2.3 \pm 4.0	3.1 \pm 5.0	0.6
<i>Atriplex semibaccata</i>	Ed	0.8 \pm 1.7	2.2 \pm 4.0**	3.7	1.0 \pm 2.2	3.4 \pm 4.3*	2.8	0.3 \pm 0.6	0.9 \pm 1.7	1.4	1.3 \pm 1.9	2.1 \pm 5.1	1.2
<i>Rosenia humilis</i>	Ed	0.6 \pm 1.2	2.1 \pm 2.9**	3.2	0.9 \pm 1.2	2.2 \pm 1.8*	2.9	0.9 \pm 1.3	3.1 \pm 4.0**	5.3	0.5 \pm 1.1	1.3 \pm 2.0	1.8
Forbs													
Annuals		2.8 \pm 13.0	5.5 \pm 11.7	0.8	6.3 \pm 21.1	15.7 \pm 18.0*	3.0	0.4 \pm 1.1	1.0 \pm 3.0	0.4	-	-	-
Grasses													
<i>Cynodon dactylon</i>	Pg	8.1 \pm 14.9	7.4 \pm 12.3	0.2	15.4 \pm 21.8	17.3 \pm 18.4	0.0	4.8 \pm 8.7	5.2 \pm 6.1	0.1	2.4 \pm 2.8	1.7 \pm 3.0	0.6
<i>Erharta calycina</i>	Ag	2.9 \pm 7.8	3.3 \pm 8.4	0.5	7.3 \pm 11.8	8.2 \pm 12.7	0.8	1.0 \pm 4.6	1.8 \pm 3.3	0.01	-	-	-
Total		91.5	90.4		83.9	95.2		90.8	89.7		89.6	96.3	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

3.4 DISCUSSION

Nyala are considered mixed-feeders mainly eating woody browse, but selecting for herbaceous vegetation during the wet seasons (Hofmann 1988; Woodall and Skinner 1993; Woodall and Skinner 1994; Skinner and Chimimba 2005). My findings in BPGR support this classification as nyala ate greater proportions of herbaceous vegetation during the winter months (June – September), when the study site received most of its rainfall. The driest part of the year was from February to May, during this time nyala focused almost exclusively on woody browse.

3.4.1 USE OF THE GRASS COMPONENT

Grasses were consumed in significantly greater proportions during the winter/wet season than the other seasons. Grasses were most likely selected for in the winter/wet season because they were still young and young forbs and grasses are considered less fibrous and having a higher nutrient content than most shrubs and dwarf shrubs during wet seasons (Owen-Smith *et al.* 1983; Codron *et al.* 2007b). Albeit low, grasses were available throughout the year, but their contribution was the highest in the early winter/wet season and declined towards the summer/dry season. During the dry season grasses store nutrients in underground storage organs as an avoidance strategy (Wolfson and Tainton 1999). During the growing season the plant redistributes the nutrients to the leaves (Skarpe and Hester 2008). This may explain why grasses were favoured during the winter/wet and spring/wet seasons and not during the summer/dry season.

Although five grass species were consumed by nyala in BPGR, *C. dactylon* and *E. calycina* were the most important. According to van Oudtshoorn (2002), *E. calycina* is one of very few grasses in South Africa that offer good grazing during winter. *C. dactylon* can sustain heavy grazing and it offers excellent grazing in rainy seasons (van Oudtshoorn 2002). Grass contribution to the nyala diet declined together with its availability down to very low proportions in the summer/dry season.

3.4.2 USE OF THE BROWSE COMPONENT

In order to maintain a high level of foraging efficiency throughout the year, mammalian herbivores need to substitute preferred food species with alternative food species, as availability declines (Owen-Smith *et al.* 1983; Scoggings *et al.* 2004). With the decline in forbs and grass, shrubs and dwarf shrubs became the most important food throughout the year. Several studies conducted on nyala diet (Tello and Van Gelder 1975; Anderson and Pooley 1977; Anderson 1978; Van Rooyen 1992; Van Eeden 2006; Kirby *et al.* 2008) concur that maintaining their diet of low fibre and high protein is made possible by a gradual change in selection for high protein, herbaceous plants during the wet seasons to high protein, woody plants during the dry seasons (Codron *et al.* 2007b).

On an annual basis shrubs formed the majority of the diet (53.5%) followed by dwarf shrubs (27.5%). The shrubs *A. karroo*, *P. capensis*, *P. afra*, *G. robusta* and the dwarf shrub *Z. lichtensteinianum* formed the bulk of the annual diet. *P. capensis*, *G. robusta* and *Z. lichtensteinianum* were important throughout the year, as they consistently contributed > 5% to the nyala diet. *A. karroo* was the most important food species in the spring/wet season. Its contribution was lower in the summer/dry season and very low during the winter/wet season. This was likely due to three characteristics of *A. karroo*: (a) it offers new foliage through fresh new browse shoots during spring; (b) its deciduous nature, as deciduous species are less available during winter due to leaf shedding (Sauer *et al.* 1977; Sauer 1983) and (c) its crude protein content is the highest during early summer and gradually decreases until winter (Kok and Opperman 1980; Teague 1988).

Z. morgsana contributed significantly less in the winter season than in the spring and summer seasons. According to Bellstedt *et al.* (2008), some species of Zygophylleaceae display a high increase in phytochemicals such as alkaloids during flowering time (June - September). This chemical defence probably prevents herbivores from removing the flowers before they can become seed bearing fruits, optimizing seed development (Bellstedt *et al.* 2008). This may be a reason for the low proportion of *Z. Morgsana* in the nyala diet during the winter/wet season.

During the driest part of the year (February to May), the contributions of *P. capensis*, *G. robusta* and *Z. lichtensteinianum* remained relatively high, however the contribution of *A. karroo* declined and *P. afra*, *R. obovatum* and *N. capensis* increased significantly. This is probably due the decline in availability of forbs and grass and the decline in crude protein content of *A. karroo*. The drought tolerant nature of *P. afra*, *R. obovatum* and *N. capensis* gives the plants the ability to consistently produce palatable forage during drought (Vlok and Schutte-Vlok 2010). During the study period BPGR received an above average rainfall (Chapter 2). However, the Oudtshoorn area has experienced extended droughts in the past (Hoare *et al.* 2006) and it may be that during the dry years drought tolerant, palatable browse such as *P. afra* will become a vital part of the nyala diet.

3.4.3 DIET COMPOSITION BETWEEN THE SEXES

Nyala in BPGR displayed differences in foraging behaviour between the sexes at the plant form level with males concentrating more on shrubs and females more on dwarf shrubs (Table 3.3). This was also the case at the plant species level with males concentrating most on the shrubs *P. capensis*, *N. capensis*, *P. afra* and *Z. morgsana* and females concentrating most on the dwarf shrubs *Z. lichtensteinianum*, *L. aethiopicum*, *Pentzia incana*, *Rosenia humilis*, *Atriplex semibaccata* and *Osteospermum sinuatum* (Table 3.4). Both sexes preferred feeding in the River and Floodplain areas, where *A. karroo* made up the bulk of feeding observations. Females were observed feeding in the Gravel Apronveld areas more than males where the aforementioned dwarf shrubs were most common. Males were observed feeding in the Kruisrivier Spekboom-Pruimveld areas more than females where *P. capensis* and *P. afra* were most common.

Results indicate that certain browse species were positively selected for by either males or females (Table 3.4). This may relate to any of the five hypotheses mentioned earlier. However, in accordance with the suggestions of Kirby *et al.* (2008), I suggest that the primary driver in sexual segregation of nyala in BPGR may be body size and consequent nutrient requirements (Main *et al.* 1996). The forage selection hypothesis states that sexes segregate because differences in body size lead to different energy requirements and thus food selection (Main *et al.* 1996). The

larger bodied males may be targeting lower quality forage, offering greater standing biomass in the form of shrubs in order to maximize their intake to satisfy their higher absolute forage requirements (Bell 1971; Jarman 1974; Woolnough and Du Toit 2001). Females on the other hand may be selecting higher quality forage because of the high energy demands of gestation and nutrient transfer through lactation (Clutton-Brock *et al.* 1982; Clutton-Brock 1989).

The results of this chapter are significant in terms of presenting additional confirmation of the considerable differences in the feeding ecology of sexual dimorphic species, suggesting that for the efficient management and conservation of priority areas they may have to be considered as ecologically separate species (Bowyer 2004; Shannon *et al.* 2006; Kirby *et al.* 2008).

3.4.4 MANAGEMENT IMPLICATIONS

Of the five browse species making up the bulk of the annual nyala diet only *A. karroo* has some defence against herbivory through its thorns (Vlok and Schutte-Vlok 2010). *P. afra*, *G. robusta*, *Z. lichtensteinianum* and *P. capensis* are all palatable unarmed species (Vlok and Schutte-Vlok 2010), that were heavily browsed by nyala. The impact that severe browsing pressure can have on unarmed species in Kuilsrivier Spekboom-Pruimveld is already evident in some areas, as over utilization by domestic stock prior to establishment of the reserve altered plant community composition and structure, leaving the southern areas of BPGR in a pseudo-savanna state (Coetzee 2002). The main difference between this pseudo-savanna state and intact Kuilsrivier Spekboom-Pruimveld is the almost complete elimination of *P. afra* in the degraded areas. According to Lechmere-Oertel *et al.* (2005) this pseudo-savanna state is not a stable alternative state to intact thicket, but rather an intermediate stage on the way to a highly degraded state. The restoration of degraded thicket is a very slow process, even when completely resting an area from herbivory (Vlok *et al.* 2003). Therefore if nyala as well as other herbivores indefinitely apply pressure on these species in a finite area, without management intervention, the intact thicket areas could degrade into a pseudo-savanna state.

The majority of feeding observations (> 50%) on dwarf shrubs that are considered palatable such as *Z. lichtensteinianum* and *L. aethiopicum* (Vlok and Schutte-Vlok

2010), were recorded in the critically endangered Grootkop Apronveld habitat, where various endangered geophytes and succulents occur (Skowno *et al.* 2010). Succulents and geophytes were not an important plant form in the nyala diet (Table 3.1). No geophytes or succulents listed as rare or endangered were eaten by nyala during the study. However, this observation does not automatically mean that nyala have no impact in Grootkop Apronveld, as geophytes and/or succulents may have been consumed that were not detected by the feeding observations. In addition nyala may still have an effect on adult plant mortality and seedling recruitment of the selected food plants through trampling or nurse plant disturbance, which could result in the alteration of composition and structure, ultimately having cascading effects on other taxa (Lechmere-Oertel *et al.* 2005; Van Wieren and Bakker 2008).

3.5 CONCLUSION

The nyala in BPGR were found to be mixed-feeders preferring browse during the study period. They fed selectively with only five browse and one grass species forming the bulk of the annual diet. Their preferred diet was one of woody browse for most of the year, supplemented by forbs and grass during the winter/wet season. This shift is suggested to be a strategy for maintaining a high protein, low fiber diet throughout the year. The selection for different plant species in different parts of the year in order to maintain their preferred diet is supported by other nyala feeding studies. However, seasonal food selection in the Arid Mosaic Thicket of the Southern Cape is of particular interest, as nyala are extralimital to the area and the information is lacking.

Male and female nyala in BPGR consumed different proportions of plant forms and plant species. I suggest that differences in body size leading to different energy requirements and therefore food selection plays an important role.

Overall, results suggests that intensive monitoring of the priority areas is essential to determine the impact of nyala feeding behaviour on the composition and structure of the vegetation through ongoing browsing pressure, as this could have cascading effects on biodiversity.

CHAPTER 4: DIET PREFERENCE

4.1 INTRODUCTION

Large mammalian herbivores are surrounded by a variety of plant species while foraging, however some species may be eaten more readily than others (Westoby 1974; Owen-Smith 1982; Owen-Smith and Novellie 1982); an occurrence described as selective feeding (Owen-Smith 1982; Augustine and McNaughton 1998; Owen-Smith and Chafota 2012). Selectivity can be defined as the relative proportion of selected forage divided by the relative availability of that forage in the feeding site (Senft *et al.* 1987; Senft 1989; Laca *et al.* 2010). Selection of food items in a given habitat takes place when a food item is examined by the herbivore and it is accepted or rejected (Leuthold 1972; Hobbs and Bowden 1982; Owen-Smith and Cooper 1987a; Watson and Owen-Smith 2002). Plant species can be considered preferred by a mammalian herbivore if they are accepted significantly more than they are rejected (Owen-Smith and Cooper 1987a; Laca *et al.* 2010).

The unique morphology (e.g. mouth size), digestive anatomy and body size of a particular mammalian herbivore may place limitations on which plant species it can consume; for example large herbivores with a small body size such as steenbok, have lower energy requirements relative to an elephant, hence it eats less food, but it is limited to higher quality food (Bell 1971; Jarman 1974). However, in general, acceptability of plant species to mammalian herbivores is determined by the following factors: (a) soil nutrient, water and light availability (Hanley 1982; Craine *et al.* 2012); (b) growth stage of the entire plant and its leaves (Owen-Smith and Novellie 1982; Turnley *et al.* 2013); (c) secondary compounds such as alkaloids and condensed tannins (the concentrations of which vary between plant parts) (Caister *et al.* 2003; Owen-Smith and Cooper 1987b; Cooper *et al.* 1988; Mithofer and Boland 2012); (d) structural features such as spinescence and growth form (Cooper and Owen-Smith 1986; Hanley *et al.* 2007) and (e) defoliation history (Owen-Smith and Novellie 1982; Caister *et al.* 2003; Turnley *et al.* 2013). These features differ between plant species and vary between seasons (Owen-Smith and Novellie 1982; Owen-Smith 1994; Scoggings *et al.* 2004; Skarpe and Hester 2008). Consequently

the food base mammalian herbivores have to select from varies greatly in availability and palatability (Owen-Smith and Novellie 1982; Owen-Smith and Cooper 1987a). Availability can be defined as accessible plant species presented to the herbivore (Johnson 1980; Owen-Smith and Cooper 1987a). Thorns and spines do not render edible plant parts inaccessible; instead it only reduces the rate of harvest by the herbivore (Hanley *et al.* 2007). All spiny plant species are thus still considered accessible to the browser. Palatability refers to plant parts high in nutrients and low in anti-feedants such as fibre, lignin and secondary compounds that are readily eaten when accessible (Owen-Smith and Novellie 1982; Owen-Smith and Cooper 1987b).

An assessment of plant species preference requires a comparison of usage and availability of each species and is best expressed as an index (Johnson 1980; Hobbs and Bowden 1982; Owen-Smith and Cooper 1987a). In this chapter the focus was mainly on browse species, as nyala in BPGR consume a much greater proportion of browse than grass (Chapter 3). Because food resources are heterogeneously distributed in space and time (Senft *et al.* 1987; Bailey *et al.* 1996; Illius and O' Connor 2000; Hobbs *et al.* 2003; Fryxell *et al.* 2005), availability measurements are most relevant when recorded in the immediate vicinity of the feeding site at the actual time of feeding (Johnson 1980; Laca *et al.* 2010). Therefore the available food component of the habitat can be defined in terms of vegetation included in the herbivores feeding path, as animals move slower and circle more repeatedly in favoured habitats than in neglected ones (Crawley 1983; Senft *et al.* 1987; Bailey *et al.* 1996; Wiens 2000; Bartumeus *et al.* 2005). Vegetation immediately available to the herbivore occurs in the feeding path because of selection for certain food plants and the association of other plants with these food plants (De Knegt *et al.* 2007; Emerson *et al.* 2011). The use of a feeding path to measure availability thus generates a register of preferred and neglected plant species in respective habitats (Johnson 1980; Owen-Smith and Cooper 1987a).

Nyala are classified as mixed-feeders (Hofmann 1973; Jarman 1974; Hoffmann 1989; Woodall and Skinner 1993; Woodall and Skinner 1994; Kirby *et al.* 2008). They are characterized by the ability to change their diet over a relatively short period and generally focus on plants that are low in fiber and high in protein (Hofmann and Stewart 1972; Anderson and Pooley 1977; Anderson 1978; Van

Rooyen 1992). Previous studies have shown considerable variation in nyala diet selection through seasonal cycles in savanna ecosystems (Tello and Van Gelder 1975; Van Rooyen 1992; Botha and Stock 2005; Codron *et al.* 2007a; Kirby *et al.* 2008). However, no studies have examined nyala plant species preference in an ecosystem where they are extralimital.

Since nyala are extralimital to the Southern Cape (Skead 1987; Skead *et al.* 2007), the vegetation of Arid Mosaic Thicket has not been subjected to their feeding preferences. Different herbivores have different feeding preferences (Owen-Smith and Novellie 1982; Owen-Smith and Cooper 1987a), thereby impacting on different plant species (Wilson and Kerley 2003). Some preferred plant species may be proportionately less available in the environment than their representation in the nyala diet and this preference could result in increased pressure on the selected species (Hester *et al.* 2006a), especially in small fenced areas where pressure on the vegetation will be greater due to increasing densities of herbivores on a limited area (Augustine and McNaughton 2004; Jacobs 2008; Rutherford *et al.* 2012). At this stage the conservation authority Cape Nature, does not know if nyala feeding preferences could result in adult plant mortality, influence the distribution and abundance of plants, retard seedling recruitment as well as disturb the competitive interactions between these plants. Information on nyala selectivity in BPGR could thus help identify areas of concern for future monitoring, in turn facilitating the more effective management of the animal in the Arid Mosaic Thicket areas of the Southern Cape (Duncan and Poppi 2008).

Some studies suggest that sexually dimorphic mammalian herbivores may be required to be managed as ecologically separate species (Kie and Bowyer 1999; Bowyer *et al.* 2001; Stewart *et al.* 2003; Bowyer 2004; Shannon *et al.* 2006). In addition nyala has shown differences in foraging behaviour between the males and females (Kirby *et al.* 2008). Consequently, information on the possible feeding effects of the animal in BPGR for conservation management purposes could not be complete if it does not consider the separate diets of males and females.

Differences in proportions of plant forms and species between the sexes in the previous chapter may be explained by differences in activity budgets (Ruckstuhl 1998; Ruckstuhl and Neuhaus 2000) and/or as hypothesised by Main *et al.* (1996) and suggested by Kirby *et al.* (2008), differences in nutrient and energy demands

driven by body size dimorphism and divergent reproduction strategies. However, because principal food species dealt with in the previous chapter may be different from preferred food species (Petrides 1975) in this chapter, the assessment of plant species preference between the sexes could strengthen or oppose the current explanations for sexual segregation in BPGR, further facilitating our understanding of the feeding ecology of the extralimital animal in the Arid Mosaic Thicket of the Southern Cape.

The objectives of this chapter are: (a) to investigate the seasonal variation in diet preference of nyala; (b) to investigate the seasonal diet preferences of male and female nyala.

4.2 METHODS

4.2.1 STUDY SITE

Refer to chapter 2.

4.2.2 FEEDING OBSERVATIONS

Diet preference observations were made concurrent with the diet composition observations of the preceding chapter. See Chapter 3 for details on locating survey sites, timing of observations, focal animal selection, acceptable viewing distance and equipment used.

The preference of nyala for different plant species was determined using the acceptability indices of Owen-Smith and Cooper (1987a). Acceptability was based on plants immediately available to the animal in feeding stations along its feeding path, since selection of a plant species only takes place when the herbivore actually chooses a food item among others available (Johnson 1980). The feeding station was defined in terms of plants available within 2 m radius around where the animal is observed feeding. This was because immediately available plants species are those located within a certain distance of the animal that will allow them to be selected for immediately after the termination of feeding on the previous plant (Du Toit 1988). This distance represents the nyala's approximate neck reach (Mkanda 1996; Kirby *et*

al. 2008) and it was easy to replicate in the field. This method of availability measurement is analogous to quadrat sampling along the foraging path (Du Toit 1988; Watson and Owen-Smith 2002).

To ensure independence of sampling, plant species occurring within the feeding station were recorded during every third feeding event. If the third feeding event was not separated by at least 2m from the previous feeding station, the observation was ignored. A plant species can only be considered available if it is accessible to the browser (Johnson 1980). Hence, all plants spinecscnt or otherwise were recorded as available within the feeding station if the plant was alive (defoliated browse was considered alive if moist, green tissue was evident in the stems and defoliated grass was considered alive if the roots were not gray and brittle) (Venter and Watson 2007) and if the plant was at a reachable height (females ≤ 1.2 m, males ≤ 2 m) (Mkanda 1996; Kirby *et al.* 2008). Forbs sprouting after rain (opslag) were grouped together as annuals. These species grew entwined making it difficult to determine a selection for individual species. All available plants within the feeding station were then identified at species level and recorded as accepted or rejected (Owen-Smith and Cooper 1987a).

4.2.3 DATA ANALYSIS

For each season, the seasonal acceptability index (a_i) was calculated as:

$$a_i = n_i / t_i$$

where n_i is the number of times the plant species was accepted and t_i is the number of times the plant species was available.

A seasonal site availability index was calculated to measure the relative availability of plant species i through the seasons. For each season, the seasonal site availability index (s_i) was calculated as:

$$s_i = t_i / tn$$

where t_i is the total number of feeding stations where plant species i was recorded as available and tn is the total number of feeding stations surveyed. For each species a

2 x 3 Chi-square contingency table was used to determine if plant species acceptability and availability was independent of season.

Plant species acceptability and availability to the respective sexes was calculated on the same basis using the formulas above. Log-linear analyses of frequency tables, using both tests of marginal and partial association, as well as *K*-factor analyses was used to indicate the importance of associations between acceptability/availability frequencies, seasons and sexes. The important associations indicated were then further analysed using 2 x 2 Yates corrected Chi-square contingency tables. Acceptability and availability indices of respective plant species were reported with 95% binomial confidence intervals in tables (Zar 1984). Indices are reported in terms of low (0.0 – 0.29), moderate (0.3 – 0.49) and high (> 0.5) acceptability/availability.

4.3 RESULTS

4.3.1 PLANT SPECIES ACCEPTABILITY AND AVAILABILITY

A total of 630 feeding stations were surveyed from May 2012 to April 2013. A total of 112 plant species were recorded as available to nyala on an annual basis, however only 47 species were accepted in total (Appendix 3.1). Most preferred plant species were also principal food species (Chapter 3); those contributing > 1% to the annual nyala diet that are considered important in terms of diet composition.

For most plant species acceptability varied significantly through the study period (Table 4.1). The acceptability of *A. karroo*, *P. capensis*, *N. capensis*, *P. afra*, *R. obovatum* and *Z. morgesana* was high in the spring/wet and summer/dry seasons, but moderate to low in the winter/wet season. The same was true for the evergreen dwarf shrub *A. lindleyi* subsp. *inflata* and the deciduous dwarf shrub *F. muricata*. The semi deciduous shrub *G. robusta* and the evergreen dwarf shrubs *Z. lichtensteinianum* and *L. aethiopicum* were the only species highly acceptable throughout the study period. The evergreen dwarf shrubs *P. incana* and *R. humilis* were moderately acceptable throughout the study period. The evergreen shrubs *L. oxycarpum*, *E. undulata* and *C. haematocarpa* were moderate to low in acceptability throughout. Annual forbs were highly acceptable during the winter/wet season,

moderately acceptable in the spring/wet season and low in the summer/dry season. The grass species *C. dactylon* and *E. calycina* were high in acceptability during the winter/wet and spring/wet seasons, but moderate to low in the summer/dry season. The creeping dwarf shrub *A. semibaccata* was the only woody species following the same trend as grasses. The dwarf shrub *O. sinuatum* was the only species highly acceptable in the spring/wet season, but moderate in the other seasons.

For most plant species, site availability to nyala varied significantly through the study period (Table 4.2). The majority of species were of moderate to high site availability throughout all seasons. The evergreen shrub *N. capensis* was of low site availability throughout the study. The evergreen dwarf shrubs *F. muricata*, *O. sinuatum* and *L. aethiopicum* were low in availability in the winter/wet season and moderate in the other seasons. Annual forbs were of high site availability in the winter/wet season, moderate in the spring/wet season and low in the summer/dry season. The grasses *C. dactylon* and *E. calycina* were of high site availability in the winter/wet and spring/wet seasons, but low in the summer/dry season.

Table 4.1: Seasonal variation in acceptability of important and commonly encountered plant species in BPGR (index \pm 95% confidence intervals). Codes: Ai = seasonal acceptability index, S = semi-deciduous, D = deciduous, E = evergreen, s = shrub, d = dwarf shrub, g = grass, Ai = seasonal acceptability index; χ^2 = Chi-square value.

Species	Habit	Winter/wet Ai	Spring/wet Ai	Summer/dry Ai	χ^2 df = 2
Shrubs					
<i>Acacia karroo</i>	Ds	0.31 (0.23 - 0.38)	0.90 (0.79 - 0.92)	0.68 (0.56 - 0.76)	25.32***
<i>Pappea capensis</i>	Es	0.43 (0.31 - 0.51)	0.76 (0.68 - 0.85)	0.70 (0.64 - 0.81)	42.97***
<i>Nymanina capensis</i>	Es	0.19 (0.10 - 0.32)	0.60 (0.49 - 0.76)	0.73 (0.62 - 0.85)	40.66***
<i>Portulacaria afra</i>	Es	0.31 (0.10 - 0.40)	0.68 (0.57 - 0.78)	0.80 (0.72 - 0.87)	87.85***
<i>Grewia robusta</i>	Ss	0.60 (0.52 - 0.72)	0.70 (0.67 - 0.82)	0.88 (0.79 - 0.93)	27.35***
<i>Rhigosum obovatum</i>	Ss	0.20 (0.14 - 0.33)	0.69 (0.56 - 0.76)	0.71 (0.60 - 0.81)	38.42***
<i>Zygophyllum morgsana</i>	Es	0.11 (0.10 - 0.27)	0.70 (0.58 - 0.78)	0.59 (0.45 - 0.66)	53.58***
<i>Lycium oxycarpum</i>	Es	0.13 (0.06 - 0.18)	0.10 (0.05 - 0.18)	0.20 (0.13 - 0.30)	7.35*
<i>Euclea undulata</i>	Es	0.10 (0.05 - 0.15)	0.10 (0.04 - 0.15)	0.12 (0.08 - 0.21)	5.70
<i>Carissa haematocarpa</i>	Es	0.24 (0.17 - 0.40)	0.24 (0.16 - 0.31)	0.30 (0.24 - 0.43)	8.56*
Dwarf shrubs					
<i>Pentzia incana</i>	Ed	0.32 (0.26 - 0.42)	0.44 (0.30 - 0.51)	0.44 (0.35 - 0.60)	3.77
<i>Rosenia humilis</i>	Ed	0.30 (0.21 - 0.36)	0.41 (0.28 - 0.51)	0.40 (0.30 - 0.52)	6.99*
<i>Felicia muricata</i>	Dd	0.14 (0.10 - 0.32)	0.80 (0.74 - 0.90)	0.69 (0.58 - 0.80)	93.90***
<i>Zygophyllum lichtensteinianum</i>	Ed	0.60 (0.51 - 0.72)	0.69 (0.75 - 0.88)	0.80 (0.68 - 0.86)	25.23***
<i>Atriplex lindleyi subsp. inflata</i>	Ed	0.44 (0.28 - 0.50)	0.58 (0.46 - 0.64)	0.58 (0.47 - 0.67)	29.26***
<i>Atriplex semibacatta</i>	Ed	0.53 (0.43 - 0.58)	0.50 (0.39 - 0.55)	0.40 (0.25 - 0.46)	9.18*
<i>Osteospermum sinuatum</i>	Ed	0.40 (0.25 - 0.56)	0.71 (0.60 - 0.82)	0.41 (0.35 - 0.56)	52.28***
<i>Limeum aethiopicum</i>	Ed	0.70 (0.54 - 0.82)	0.89 (0.77 - 0.92)	0.72 (0.60 - 0.83)	36.77***
Forbs					
Annuals		0.80 (0.67 - 0.94)	0.40 (0.32 - 0.52)	-	48.42***
Grasses					
<i>Cynodon dactylon</i>	g	0.80 (0.65 - 0.86)	0.70 (0.60 - 0.83)	0.38 (0.30 - 0.56)	32.12***
<i>Erharta calycina</i>	g	0.90 (0.74 - 0.97)	0.65 (0.77 - 0.82)	-	19.13***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 4.2: Seasonal variation in important and commonly encountered plant species availability in nyala feeding stations (index \pm 95% confidence intervals). Codes: Si = seasonal availability index, S = semi-deciduous, D = deciduous, E = evergreen, s = shrub, d = dwarf shrub, g = grass, χ^2 = Chi-square value.

Species	Habit	Winter/wet Si	Spring/wet Si	Summer/dry Si	χ^2 df = 2
Shrubs					
<i>Acacia karroo</i>	Ds	0.70 (0.67 - 0.78)	0.50 (0.44 - 0.55)	0.48 (0.39 - 0.51)	26.37***
<i>Pappea capensis</i>	Es	0.40 (0.33 - 0.46)	0.48 (0.41 - 0.52)	0.54 (0.48 - 0.61)	12.88**
<i>Nymania capensis</i>	Es	0.22 (0.19 - 0.30)	0.28 (0.21 - 0.31)	0.29 (0.24 - 0.36)	4.32
<i>Portulacaria afra</i>	Es	0.31 (0.24 - 0.36)	0.40 (0.35 - 0.47)	0.50 (0.47 - 0.60)	17.15***
<i>Grewia robusta</i>	Ss	0.42 (0.38 - 0.51)	0.61 (0.52 - 0.64)	0.51 (0.45 - 0.58)	11.23**
<i>Rhigosum obovatum</i>	Ss	0.30 (0.28 - 0.35)	0.42 (0.40 - 0.52)	0.40 (0.34 - 0.45)	5.15
<i>Zygophyllum morgsana</i>	Es	0.32 (0.27 - 0.40)	0.47 (0.40 - 0.52)	0.48 (0.38 - 0.58)	8.94*
<i>Lycium oxycarpum</i>	Es	0.50 (0.44 - 0.58)	0.50 (0.42 - 0.54)	0.40 (0.39 - 0.51)	5.75
<i>Euclea undulata</i>	Es	0.61 (0.68 - 0.57)	0.67 (0.60 - 0.71)	0.59 (0.52 - 0.64)	5.45
<i>Carissa haematocarpa</i>	Es	0.60 (0.67 - 0.61)	0.70 (0.60 - 0.72)	0.50 (0.45 - 0.57)	8.36*
Dwarf shrubs					
<i>Pentzia incana</i>	Ed	0.49 (0.43 - 0.57)	0.40 (0.33 - 0.45)	0.31 (0.27 - 0.39)	6.77*
<i>Rosenia humilis</i>	Ed	0.48 (0.42 - 0.55)	0.34 (0.30 - 0.42)	0.39 (0.34 - 0.45)	5.33
<i>Felicia muricata</i>	Dd	0.20 (0.17 - 0.29)	0.48 (0.40 - 0.52)	0.40 (0.32 - 0.46)	14.32***
<i>Zygophyllum lichtensteinianum</i>	Ed	0.44 (0.33 - 0.46)	0.59 (0.51 - 0.62)	0.57 (0.53 - 0.64)	4.31
<i>Atriplex lindeyi subsp. inflata</i>	Ed	0.30 (0.21 - 0.44)	0.51 (0.42 - 0.63)	0.52 (0.43 - 0.56)	5.23
<i>Atriplex semibacatta</i>	Ed	0.50 (0.42 - 0.55)	0.70 (0.68 - 0.72)	0.51 (0.40 - 0.52)	11.28**
<i>Osteospermum sinuatum</i>	Ed	0.25 (0.17 - 0.40)	0.40 (0.37 - 0.45)	0.38 (0.29 - 0.43)	21.02***
<i>Limeum aethiopicum</i>	Ed	0.29 (0.26 - 0.36)	0.39 (0.36 - 0.47)	0.42 (0.24 - 0.46)	5.40
Forbs					
Annuals		0.70 (0.55 - 0.76)	0.38 (0.30 - 0.42)	-	24.41***
Grasses					
<i>Cynodon dactylon</i>	g	0.84 (0.66 - 0.89)	0.61 (0.50 - 0.83)	0.32 (0.20 - 0.51)	22.22***
<i>Erharta calycina</i>	g	0.82 (0.73 - 0.91)	0.55 (0.47 - 0.62)	-	11.53***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

4.3.2 PLANT SPECIES ACCEPTABILITY/AVAILABILITY BETWEEN THE SEXES

4.3.2.1 ACCEPTABILITY

Log-linear K -factor analysis between acceptability, season and sex indicated that the two way interactions were significant (Pearson $\chi^2 = 713.01$, $df = 61$, $P < 0.0001$). Log-linear tests of marginal and partial association indicated that of two way interactions, the associations between acceptability and season (Part. ass. $\chi^2 = 390.03$, $df = 2$, $P < 0.0001$) as well as between acceptability and sex (Part. ass. $\chi^2 = 55.30$, $df = 14$, $P < 0.0001$) were the most important (Table 4.3). Variation in acceptability and availability of plant species between the seasons are reported in Tables 4.1 and 4.2. Consequently the following focuses on important associations between preference and sex as well as availability and sex.

The evergreen shrubs *P. capensis* and *P. afra* varied significantly in acceptability between the sexes, the same was true for the evergreen dwarf shrubs *Z. lichtensteinianum*, *L. aethiopicum* and *A. semibaccata*. In the winter/wet season *P. capensis* and *P. afra* were accepted significantly more by males where *Z. lichtensteinianum* was accepted significantly more by females. In the spring/wet season *P. capensis* was accepted significantly more by males, whereas *Z. lichtensteinianum*, *L. aethiopicum* and *A. semibaccata* were accepted significantly more by females. In the summer/dry season *A. semibaccata* was accepted significantly more by females.

R. obovatum, *N. capensis* and *Z. morgesana* were eaten in greater proportions by males (Chapter 3), but showed no difference in acceptability between the sexes. The same pattern was evident for the dwarf shrubs *O. sinuatum* and *R. humilis* that were eaten more by females. This may be explained by the availability of these plants to the respective sexes, as the more regularly encountered plants constituted a greater proportion to the respective diets (Table 4.4).

There were no important associations between acceptability frequencies and sex for the shrubs *A. karroo*, *G. robusta*, *R. obovatum*, *N. capensis* and *Z. morgesana*. This was also the case for the dwarf shrubs *A. subsp. inflata*, *O. sinuatum*, *P. incana*, *R. humilis* and *F. muricata* as well as for forbs and grasses.

4.3.2.2 AVAILABILITY

The two way interactions between availability, season and sex were significant (Pearson $\chi^2 = 252.52$, $df = 61$, $P < 0.0001$). Of these two way interactions, the associations between availability and season (Part. ass. $\chi^2 = 208.28$, $df = 2$, $P < 0.0001$) as well as between availability and sex (Part. ass. $\chi^2 = 62$, $df = 14$, $P < 0.0001$) were the most important (Table 4.4).

The shrubs *P. capensis*, *Z. morgsana*, *R. obovatum*, *P. afra* and *N. capensis* varied significantly in site availability between the sexes. The same was true for the dwarf shrubs *Z. lichtensteinianum*, *L. aethiopicum*, *A. semibaccata*, *F. muricata* and *R. humilis*. The shrub *P. capensis* was available more to males through all seasons while *P. afra* was significantly more available to males during the winter/wet and spring/wet seasons. *R. obovatum* was available significantly more to males during the winter/wet season and *N. capensis* was available significantly more to males through all seasons. The dwarf shrubs *Z. lichtensteinianum* and *A. semibaccata* were available more to females during the winter/wet and summer/dry seasons. *R. humilis* was available more to females during the winter/wet and spring/wet seasons. *F. muricata* was available more to females in the spring/wet season only. The shrubs *A. karroo* and *G. robusta* and the dwarf shrubs *A. subsp. inflata*, *O. sinuatum* and *P. incana* did not have important associations between availability and sex. The same was true for forbs and grasses.

4.4 DISCUSSION

Nyala are classified as mixed-feeders (Hofmann 1973; Jarman 1974; Hoffmann 1989; Woodall and Skinner 1993; Woodall and Skinner 1994). They select for fresh grass in season, but their diet comprises primarily of browse material (Vincent *et al.* 1968; Tello and Van Gelder 1975; Anderson and Pooley 1977; Anderson 1978; Van Rooyen 1992; Botha and Stock 2005; Codron *et al.* 2007a; Kirby *et al.* 2008).

Previous studies have shown them to be selective of only a small portion of plant species available to them in a given area (Tello and Van Gelder 1975; Van Rooyen 1992; Van Eeden 2006). My findings support this, as nyala fed selectively, preferring only 43.2% of the plant species available to them during the winter/wet season,

39.6% in the spring/wet season and 37.8% in the summer/dry season. A total of 91.2% of preferred plant species in the annual nyala diet were also principal food species (Petrides 1975); species considered important in terms of diet composition (species contributing > 1% to the annual nyala diet, Table 3.1). (See Appendix 3.1 for selected species not included in this chapter).

4.4.1 SELECTION OF THE HERBACEOUS COMPONENT

Annual forbs and the grasses *C. dactylon* and *E. calycina* had the highest acceptability of all plants consumed during the winter/wet season. This was probably because the grasses were still young and most forbs and young grasses have a lower fibre and higher nutrient content than most woody browse (Owen-Smith 1982; Codron *et al.* 2007b). During the winter/wet season the site availability of annual forbs and grasses were significantly higher than the spring/wet and summer/dry seasons. This pattern appears to be related to habitat use as nyala positively selected for the Olifants River and Floodplain habitat (Chapter 5) occurring along major drainage lines on alluvial soils where herbaceous growth was abundant during the rainy season.

4.4.2 SELECTION OF THE WOODY COMPONENT

The shrubs *A. karroo*, *P. capensis*, *N. capensis*, *P. afra*, *R. obovatum* and *Z. morgesana* were favoured by nyala (acceptability index ≥ 0.5) during both the spring/wet and summer/dry seasons and the shrub *G. robusta* was favoured throughout the year. All of these species are considered palatable and favoured by game and domestic stock (Aucamp and Scheltema 1984; Ganqa 2008; Sigwela *et al.* 2009; Vlok and Schutte-Vlok 2010). Furthermore, previous studies have shown these shrubs to be an important part of the diet for mixed-feeders such as Bushbuck (*Tragelaphus scriptus*), elephants (*Loxodonta Africana*) and domestic goats (*Capra hircus*) as well as for browsers such as kudu (*Tragelaphus strepiceros*). Haschick and Kerley (1997) showed *P. afra*, *Z. morgesana* and *A. karroo* to be favoured by bushbuck. McLeod (1992) and Wilson and Kerley (2003) indicated the importance of *A. karroo* in the bushbuck diet. Stuart-Hill (1992) showed a strong selection for *G. robusta*, *P. capensis* and *R. obovatum* by goats and elephants. Sigwela (1999)

showed a strong selection for *P. capensis*, *P. afra* and *Z. morgsana* by kudu and Hendricks *et al.* (2002) and Du Toit and Blom (2005) found *N. capensis* to be a preferred food species of goats in the Richtersveld National Park and in the Noorsveld of the Karoo respectively. The strong selection for these plant species by nyala and other mixed-feeders indicate they may be important in evaluating the capacity of a property in Albany Thicket to sustain nyala.

The acceptability of the deciduous species *A. karroo* increased dramatically from the winter/wet season to the spring/wet season. This increase in acceptability was probably due to the development of new shoots, as protein content of deciduous species is highest during early summer when growing new foliage (Coley *et al.* 1985; Teague 1988; Aerts and Chapin 2000).

As for the dwarf shrub component, the deciduous *F. muricata* followed the same pattern as *A. karroo*. The low acceptability of *F. muricata* in the winter/wet season may be due to the proportion of senescent leaves on the plant during this time. Watson and Owen-Smith (2002) found that even though *F. muricata* was favoured by eland throughout the year, the proportion of senescent leaves on *F. muricata* during the dry winter season caused a lower acceptability relative to other seasons in Mountain Zebra National Park. The evergreen *L. aethiopicum* and *Z. lichtensteinianum* were favoured throughout the study period. *L. aethiopicum* and *Z. lichtensteinianum* are considered highly palatable plants throughout the year and they are remarkably resilient to heavy browsing (Vlok and Schutte-Vlok 2010). The evergreen dwarf shrub *R. humilis* is considered to be of medium palatability, being browsed more in some areas than others (Vlok and Schutte-Vlok 2010). This is reflected in the nyala diet as the species was eaten throughout the year, but never favoured. The evergreen dwarf shrub *P. incana* followed a similar pattern. Watson and Owen-Smith (2002) found the acceptability of *P. incana* to be related to the proportion of young shoots on the plants during the growing seasons. It may be that the moderate acceptability of *P. incana* in BPGR was because the plant had moderate to low proportions of young shoots throughout the study period.

Even though the evergreen shrubs *Lycium oxycarpum*, *Euclea undulata* and *Carissa haematocarpa* were commonly encountered throughout the year, they were never favoured. *L. oxycarpum* has high anti-feedant content as well as thorns as a mechanical defence (Haschick and Kerley 1997), which may explain its neglect. *E.*

undulata was probably neglected because of its high fibre content and hard sclerephyllous leaves (Haschick and Kerley 1997; Vlok and Schutte-Vlok 2010), whereas *Carissa haematocarpa* is considered high in nutrients, but it has sharp, rigid thorns making the edible parts of the shrub nearly inaccessible for browsers (Stuart-Hill 1992).

The majority of plant species were of moderate to high site availability throughout all seasons. With the exceptions of the aforementioned unfavoured species and *A. karroo*, all woody browse species show an increase in site availability from the winter/wet to the spring/wet season. This pattern seems to be related to habitat use, as nyala moved out of the Olifants River and Floodplain habitat into the Apronveld and Spekboom-Pruimveld habitats as forb and grass availability declined. The site availability of the deciduous *A. karroo* was significantly higher during the winter/wet season than the other seasons, even though it was neglected by nyala. This was because the Olifants River and Floodplain habitat unit which nyala positively selected (Chapter 5), contained dense stands of *A. karroo*.

Table 4.3: Seasonal variation in important plant species acceptability between male and female nyala (index \pm 95% confidence intervals). Codes: Ai = seasonal acceptability index, χ^2 = Chi-square value, (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

Species	Winter/wet Ai			Spring/wet Ai			Summer/dry Ai			Log-linear χ^2	
	♂	♀	χ^2	♂	♀	χ^2	♂	♀	χ^2	Sex	Season
Shrubs											
<i>Acacia karroo</i>	0.35 (0.25 - 0.48)	0.22 (0.14 - 0.32)	0.85	0.88 (0.76 - 0.96)	0.87 (0.75 - 0.95)	0.01	0.62 (0.53 - 0.70)	0.70 (0.50 - 0.78)	0.36	1.34	90.04***
<i>Pappia capensis</i>	0.59 (0.41 - 0.69)	0.44 (0.20 - 0.50)	4.29*	0.90 (0.77 - 0.97)	0.71 (0.65 - 0.93)	3.49*	0.90 (0.65 - 0.96)	0.82 (0.68 - 0.95)	0.62	10.12**	44.90***
<i>Grewia robusta</i>	0.61 (0.51 - 0.75)	0.60 (0.41 - 0.73)	0.01	0.88 (0.62 - 0.93)	0.86 (0.69 - 0.96)	0.00	0.84 (0.61 - 0.89)	0.86 (0.66 - 0.92)	0.00	0.00	24.95***
<i>Portulacaria afra</i>	0.45 (0.27 - 0.53)	0.21 (0.16 - 0.30)	3.53*	0.75 (0.60 - 0.85)	0.67 (0.54 - 0.80)	1.87	0.88 (0.72 - 0.94)	0.61 (0.53 - 0.80)	0.58	6.16*	22.08***
<i>Rhigosum obovatum</i>	0.31 (0.15 - 0.44)	0.18 (0.12 - 0.27)	1.54	0.70 (0.61 - 0.84)	0.60 (0.51 - 0.74)	1.02	0.86 (0.64 - 0.95)	0.83 (0.56 - 0.89)	0.01	2.85	56.33***
<i>Nymania capensis</i>	0.17 (0.06 - 0.36)	0.13 (0.03 - 0.32)	0.01	0.73 (0.61 - 0.79)	0.62 (0.52 - 0.72)	1.94	0.81 (0.65 - 0.89)	0.73 (0.60 - 0.87)	0.18	2.96	52.33***
<i>Zygophyllum morgsana</i>	0.26 (0.13 - 0.39)	0.21 (0.12 - 0.36)	0.07	0.85 (0.69 - 0.91)	0.63 (0.57 - 0.72)	3.21	0.78 (0.62 - 0.86)	0.74 (0.59 - 0.91)	0.04	1.62	53.10***
Dwarf shrubs											
<i>Zygophyllum lichtensteinianum</i>	0.49 (0.33 - 0.65)	0.61 (0.46 - 0.76)	3.87*	0.62 (0.52 - 0.80)	0.85 (0.65 - 0.95)	4.22*	0.65 (0.47 - 0.75)	0.75 (0.55 - 0.82)	0.85	5.50*	12.63***
<i>Limeum aethiopicum</i>	0.45 (0.23 - 0.68)	0.56 (0.33 - 0.73)	0.34	0.67 (0.63 - 0.82)	0.90 (0.83 - 0.94)	5.48*	0.85 (0.51 - 0.96)	0.91 (0.62 - 1.00)	0.11	5.91*	28.06***
<i>Atriplex lindleyi</i> subsp.	0.31 (0.15 - 0.44)	0.48 (0.23 - 0.64)	2.61	0.53 (0.37 - 0.63)	0.63 (0.45 - 0.87)	1.15	0.76 (0.55 - 0.81)	0.82 (0.58 - 0.95)	0.22	2.19	34.53***
<i>Osteospermum</i> spp.	0.48 (0.28 - 0.55)	0.50 (0.22 - 0.65)	0.02	0.70 (0.57 - 0.83)	0.80 (0.67 - 0.93)	1.10	0.77 (0.60 - 0.91)	0.80 (0.51 - 0.94)	0.00	1.18	12.13***
<i>Pentzia incana</i>	0.44 (0.33 - 0.59)	0.48 (0.35 - 0.61)	0.00	0.52 (0.33 - 0.61)	0.50 (0.34 - 0.69)	0.13	0.55 (0.35 - 0.71)	0.67 (0.53 - 0.81)	0.39	3.47	4.83
<i>Atriplex semibaccata</i>	0.45 (0.25 - 0.62)	0.55 (0.38 - 0.71)	0.54	0.58 (0.54 - 0.70)	0.80 (0.62 - 0.92)	12.84*	0.50 (0.45 - 0.63)	0.81 (0.57 - 0.93)	10.40*	32.33***	4.38
<i>Rosenia humilis</i>	0.44 (0.29 - 0.60)	0.49 (0.36 - 0.63)	0.13	0.74 (0.59 - 0.88)	0.80 (0.56 - 0.91)	3.80	0.46 (0.30 - 0.67)	0.54 (0.23 - 0.74)	0.21	3.45	8.37*
<i>Felicia muricata</i>	0.27 (0.17 - 0.40)	0.25 (0.10 - 0.37)	0.46	0.81 (0.65 - 0.90)	0.84 (0.74 - 0.92)	0.01	0.85 (0.66 - 0.93)	0.93 (0.65 - 0.99)	0.26	1.40	63.94***
Forbs											
Annuals	0.60 (0.50 - 0.72)	0.70 (0.62 - 0.79)	0.21	0.41 (0.30 - 0.51)	0.35 (0.21 - 0.42)	0.08	-	-	-	-	-
Grasses											
<i>Cynodon dactylon</i>	0.73 (0.63 - 0.82)	0.77 (0.60 - 0.81)	0.16	0.65 (0.56 - 0.81)	0.69 (0.61 - 0.76)	0.11	0.55 (0.36 - 0.65)	0.58 (0.44 - 0.65)	0.19	1.64	5.02
<i>Erharta calycina</i>	0.60 (0.50 - 0.72)	0.70 (0.62 - 0.79)	0.21	0.57 (0.50 - 0.67)	0.64 (0.58 - 0.72)	0.82	-	-	-	-	-

Table 4.4: Seasonal variation in important plant species availability between male and female nyala (index, \pm 95% confidence intervals).

Codes: Si = seasonal availability index, χ^2 = Chi-square value, (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

Species	Winter/wet Si			Spring/wet Si			Summer/dry Si			Log-linear χ^2	
	♂	♀	χ^2	♂	♀	χ^2	♂	♀	χ^2	Sex	Season
Shrubs											
<i>Acacia karroo</i>	0.72 (0.61 - 0.76)	0.80 (0.69 - 0.83)	0.15	0.51 (0.39 - 0.55)	0.52 (0.43 - 0.61)	0.08	0.50 (0.40 - 0.58)	0.43 (0.33 - 0.50)	0.30	0.20	39.02***
<i>Pappia capensis</i>	0.57 (0.43 - 0.59)	0.31 (0.22 - 0.37)	4.30*	0.60 (0.47 - 0.63)	0.30 (0.24 - 0.42)	6.42*	0.71 (0.58 - 0.75)	0.42 (0.35 - 0.52)	4.97*	26.70***	11.13***
<i>Grewia robusta</i>	0.53 (0.41 - 0.57)	0.44 (0.33 - 0.48)	0.47	0.62 (0.50 - 0.66)	0.61 (0.52 - 0.67)	0.02	0.52 (0.44 - 0.62)	0.51 (0.41 - 0.59)	0.04	0.92	6.20*
<i>Portulacaria afra</i>	0.40 (0.29 - 0.45)	0.24 (0.16 - 0.30)	4.38*	0.74 (0.58 - 0.75)	0.41 (0.32 - 0.49)	3.80*	0.42 (0.33 - 0.53)	0.42 (0.32 - 0.50)	0.21	12.00***	24.16***
<i>Rhigosum obovatum</i>	0.52 (0.33 - 0.59)	0.30 (0.29 - 0.41)	3.85*	0.50 (0.44 - 0.60)	0.45 (0.31 - 0.49)	0.88	0.42 (0.36 - 0.45)	0.41 (0.34 - 0.45)	0.22	4.80*	2.65
<i>Nymania capensis</i>	0.40 (0.35 - 0.46)	0.20 (0.15 - 0.28)	4.26*	0.46 (0.32 - 0.49)	0.22 (0.15 - 0.29)	3.67*	0.43 (0.30 - 0.47)	0.20 (0.15 - 0.29)	3.75*	17.95***	0.20
<i>Zygophyllum morgsana</i>	0.51 (0.37 - 0.55)	0.36 (0.24 - 0.39)	4.50*	0.60 (0.57 - 0.62)	0.40 (0.29 - 0.45)	3.77*	0.50 (0.39 - 0.57)	0.40 (0.32 - 0.49)	0.33	9.85**	9.45**
Dwarf shrubs											
<i>Zygophyllum lichtensteinianum</i>	0.40 (0.33 - 0.49)	0.61 (0.54 - 0.62)	5.22*	0.50 (0.45 - 0.55)	0.60 (0.52 - 0.70)	0.70	0.40 (0.35 - 0.52)	0.62 (0.47 - 0.65)	3.96*	9.50**	3.61
<i>Limeum aethiopicum</i>	0.30 (0.24 - 0.39)	0.50 (0.45 - 0.63)	5.11*	0.43 (0.33 - 0.44)	0.50 (0.43 - 0.52)	0.03	0.40 (0.32 - 0.50)	0.63 (0.51 - 0.66)	3.96*	27.26***	2.51
<i>Atriplex lindleyi subsp.</i>	0.40 (0.36 - 0.45)	0.50 (0.46 - 0.52)	0.41	0.42 (0.36 - 0.46)	0.51 (0.57 - 0.63)	0.13	0.41 (0.38 - 0.45)	0.51 (0.45 - 0.56)	0.97	2.10	1.00
<i>Osteospermum spp.</i>	0.20 (0.11 - 0.35)	0.21 (0.17 - 0.25)	0.01	0.26 (0.14 - 0.40)	0.52 (0.42 - 0.60)	3.27*	0.43 (0.31 - 0.49)	0.42 (0.30 - 0.51)	0.04	1.60	20.90***
<i>Pentzia incana</i>	0.50 (0.39 - 0.56)	0.50 (0.45 - 0.61)	0.03	0.50 (0.24 - 0.39)	0.45 (0.33 - 0.51)	0.68	0.24 (0.16 - 0.31)	0.43 (0.25 - 0.46)	2.42	3.17	23.70***
<i>Atriplex semibaccata</i>	0.40 (0.33 - 0.46)	0.60 (0.52 - 0.62)	4.27*	0.43 (0.32 - 0.45)	0.51 (0.43 - 0.54)	0.44	0.45 (0.37 - 0.51)	0.54 (0.45 - 0.59)	3.14*	13.61***	13.96***
<i>Rosenia humilis</i>	0.21 (0.16 - 0.27)	0.50 (0.44 - 0.60)	5.20*	0.30 (0.26 - 0.41)	0.50 (0.31 - 0.58)	5.13*	0.33 (0.22 - 0.39)	0.43 (0.30 - 0.47)	0.01	5.03*	0.35
<i>Felicia muricata</i>	0.21 (0.16 - 0.30)	0.31 (0.27 - 0.45)	0.45	0.41 (0.37 - 0.43)	0.60 (0.57 - 0.63)	4.50*	0.33 (0.25 - 0.42)	0.40 (0.36 - 0.53)	0.81	9.90**	8.58*
Forbs											
Annuals	0.70 (0.67 - 0.73)	0.70 (0.60 - 0.72)	0.14	0.30 (0.21 - 0.38)	0.40 (0.31 - 0.48)	0.21	-	-	-	-	-
Grasses											
<i>Cynodon dactylon</i>	0.60 (0.50 - 0.72)	0.71 (0.62 - 0.79)	0.21	0.47 (0.32 - 0.61)	0.49 (0.30 - 0.56)	0.15	0.34 (0.23 - 0.53)	0.44 (0.31 - 0.52)	1.10	2.46	6.21*
<i>Erharta calycina</i>	0.64 (0.50 - 0.72)	0.72 (0.61 - 0.89)	0.19	0.41 (0.30 - 0.51)	0.35 (0.21 - 0.42)	0.80	-	-	-	-	-

4.4.3 SELECTIVITY OF MALE AND FEMALE NYALA

Although there is still discussion about which hypotheses best explains ecological segregation in dimorphic ungulates (Main 2008), five hypotheses have received the most attention in recent literature (Ruckstuhl and Neuhaus 2000; Main 2008), they are: (a) The forage selection hypothesis; (b) the reproductive strategy hypothesis; (c) the activity budget hypothesis; (d) the social preference hypothesis and (e) the scramble competition hypothesis. Sexual segregation hypotheses can be broadly grouped into social and ecological explanations, however only ecological explanations can effectively describe why ungulates use different food and habitat resources (Main 2008). To date the leading social explanations were the activity budget and social preference hypotheses (Main 2008). However, these social explanations were recently acknowledged as inadequate to explain sexual segregation in ungulates (Neuhaus and Ruckstuhl 2004). The reproductive strategy hypotheses and the forage selection hypotheses remain as the leading ecological explanations (Main *et al.* 2008).

Sexual dimorphism in mammalian herbivores is considered to have considerable influence on forage selectivity, mainly due to divergent reproduction strategies and allometric relationships linked to increasing body size (Ruckstuhl and Neuhaus 2000; Stokke and Du Toit 2002; Kirby *et al.* 2008; Shannon *et al.* 2013). Because of these differences, males and females are considered to have different nutrient and energy requirements (Clutton-Brock *et al.* 1982; Clutton-Brock *et al.* 1987; Main *et al.* 1996). The forage selection hypothesis by Main *et al.* (1996) extends the arguments of Bell (1971) and Jarman (1974) to differences between sexually dimorphic mammalian herbivores. A larger body size means males have higher absolute forage requirements and thus need higher forage intake rates and are consequently less selective compared to females (Bell 1971; Jarman 1974; Clutton-Brock *et al.* 1982; Clutton-Brock 1989; Conradt *et al.* 1999). Whereas high energy demands associated with a smaller body size, gestation and lactation obligate females to select for higher quality forage (Clutton-Brock *et al.* 1982; Main *et al.* 1996; Bowyer 2004).

Both male and female nyala concentrated on forbs and grasses when they were readily available during the winter/wet season. However, males accepted shrub

species such as *P. capensis* and *P. afra* significantly more than females during the winter/wet season. This may be because males were attempting to maximize their foraging opportunities by incorporating more quantity in the form of palatable shrubs such as *P. capensis* and *P. afra* (Haschick and Kerley 1997). During the spring/wet and summer/dry seasons females selected more for species such as *P. capensis* and *P. afra* relative to the winter/wet season, which may be to compensate for the significant decline in forbs and grasses. Females selected more for the dwarf shrubs *A. semibaccata*, *L. aethiopicum* and *Z. lichtensteinianum* than males. Even though these species are considered highly palatable (Vlok and Schutte-Vlok 2010), so are the shrubs *P. capensis* and *P. afra* selected more by males (Haschick and Kerley 1997; Vlok and Schutte-Vlok 2010), which makes segregation merely on the basis of food quality selection difficult to justify. This may indicate that the quantity of quality forage plays an important role in food selection by males. Males may be attempting to maximize their foraging opportunities by selecting for more quantity.

The differences in plant species preference between the sexes in BPGR may be due to a combination of feeding height, muzzle morphology and quantity of available forage. Male and female nyala have been shown to forage at significantly different heights of the vegetation (Kirby *et al.* 2008), which may be a contributing factor to why females select more for certain low growing species than males. Furthermore, Clutton-Brock *et al.* (1987) suggests that the larger male red deer (*Cervus elaphus*) may be less selective feeders than females because of allometric relationships of bite-size to body-size (Illius and Gordon 1987). They have a comparatively small incisor arcade width in relation to their body size relative to females and higher absolute metabolic requirements (Illius and Gordon 1987). The smaller female red deer thus selected a lower plant quantity than larger males but select plants higher in quality (Clutton-Brock *et al.* 1987; Illius and Gordon 1987; Ruckstuhl and Neuhaus 2000). Similarly, the smaller female nyala may have a larger incisor arcade width in relation to body size and lower absolute food requirements (Bell 1971; Jarman 1974; Clutton-Brock *et al.* 1987). Female nyala may be able to select a lower plant quantity than larger males in the form of *L. aethiopicum* and *Z. lichtensteinianum* and still meet their nutritional demands (Clutton-Brock *et al.* 1987; Illius and Gordon, 1987; Clutton-Brock 1989; Main *et al.* 1996; Ruckstuhl and Neuhaus 2000). In order to satisfy their higher absolute food requirements, males may be selecting more for

quantity in the form of large shrub species such as *P. capensis* and *P. afra*. Male and female nyala in BPGR may thus be segregating at the plant scale because of allometric relationships linked to increasing body size; females select for quality, but they can afford to select plants offering smaller relative quantities than males. Males appear to select for plants offering more quantity relative to females, however the quantity males select is not necessarily of inferior quality, since quality in the form of large shrub species such as *P. capensis* and *P. afra* (Haschick and Kerley 1997) was readily available in BPGR.

The forage selection hypothesis thus appears to explain nyala plant species preference in BPGR; however the forage selection hypothesis is a proximate explanation and can thus not completely explain sexual segregation in BPGR (Main 2008). The reproductive strategy hypothesis functions at an ultimate level of causation and explains sexual segregation as an evolutionary response to differences in reproductive strategies (Main 2008). It predicts that males select habitats to maximize energy gains in preparation for rut and females select habitats with combinations of resources that best contribute to offspring survival (Main 2008). The reproductive strategy hypothesis and the forage selection hypothesis both assume that females are highly selective feeders and select the best forages they find because of smaller body size and the high energy costs of reproduction (Barboza and Bowyer 2001; Main 2008). However it also states that females may avoid certain habitats due to predation and therefore feed on lower quality (Main 2008).

Differences in site availability between the sexes may be an indication that males and females altered their feeding strategies to forage in different habitats or to use different feeding paths within the same habitat. Mammalian herbivores with differences in body size should select different foraging paths while feeding through a particular habitat (Du Toit 1988). Larger browsers (e.g. giraffe) would be expected to move between trees, while smaller browsers (e.g. steenbok) would be expected to move between smaller shrubs (Owen-Smith 1982; Du Toit and Owen-Smith 1989). Mammalian herbivores may thus segregate within a habitat by using different feeding paths (Johnson 1980; Du Toit 1988; Spalinger and Hobbs 1992; Laca *et al.* 2010). The feeding path is governed by diet selection (Owen-Smith 1982; Du Toit 1988; Bailey *et al.* 1996; Laca *et al.* 2010), hence the forage selection hypothesis in

conjunction with the reproductive strategy hypotheses may be a reasonable explanation for the segregation between male and female nyala in BPGR, since the sexes appear to be segregating because males choose feeding paths that will maximise their foraging opportunities and females choose feeding paths that will offer high quality food.

It may well be that male and female nyala are choosing different feeding paths in BPGR as a result of intersexual competition, however hypotheses on intersexual competition have been widely criticized in the literature (Bowyer 2004; Main 2008). Several authors have proposed that sexual segregation in ungulates was as a result of competitive exclusion of males by females (Clutton-Brock *et al.* 1987; Main and Coblentz 1996; Conradt *et al.* 1999). This hypothesis has been rejected repeatedly since the 1980's by experimental and observational studies (Bleich *et al.* 1997; Du Toit 1995; Kie and Bowyer 1999; Miquelle *et al.* 1992; Spaeth *et al.* 2004), which includes authors who originally supported the suggestion (Conradt *et al.* 1999; Conradt *et al.* 2001). Even though intersexual competition hypotheses are still proposed as an explanation for segregation by some studies (Focardi *et al.* 2003), it is generally proposed without any critical testing of the hypothesis (Bowyer 2004). In a review of sexual segregation studies, Bowyer (2004) concludes that intersexual competition resulting in competitive exclusion of males by females is a doubtful explanation for sexual segregation and that it is not a productive area for future research. I therefore suggest that intersexual competition is not a suitable explanation for sexual segregation in BPGR.

These results provide additional confirmation of the considerable differences in feeding strategies between sexually dimorphic ungulates. In addition these results are significant in terms of the management of the habitats listed as areas of conservation concern (Chapter 2). BPGR is a small area with high densities of herbivores and a history of over utilisation by domestic stock (Coetzee 2002). The presence of an extralimital and evidently selective large herbivore may exacerbate negative effects on plants. In this case these effects could include: (a) instant death through trampling or consumption of the entire plant (Crawley 1983; Skarpe and Hester 2008); (b) decreased or retarded growth through repeated herbivory (Makhabu and Skarpe 2006); (c) reduced reproductive success by removing reproductive parts (Danell and Bergström 1989; Crawley 1997; Bergström *et al.*

2000) and (d) competitive ability, since selective utilization of plants with low resistance to herbivory favours the persistence of plants with high resistance to herbivory (Skarpe 1991; Belsky 1992; Vourc'h *et al.* 2001). These effects could ultimately alter species composition and community structure, consequently having cascading effects on biodiversity (Wilson and Kerley 2003; Kerley *et al.* 2004; Hester *et al.* 2006b; Van Wieren and Bakker 2008). Confirmation of the differences in plant species preference between the sexes suggests that future monitoring of vegetation change to determine the extent of the aforementioned effects should focus on the separate influence of males and females and not just on the species as a whole.

4.5 CONCLUSION

Nyala fed selectively, preferring only a low portion of the plants available to them in BPGR. There are definite seasonal dietary shifts in preferences between different plant species. The shift takes place between the wet seasons (winter and spring) and the dry season (summer). Herbaceous species such as *Cynodon dactylon* and *Erharta calycina* were favoured in winter. Shrubs such as *P. capensis*, *P. afra* and dwarf shrubs such as *L. aethiopicum* and *Z. lichtensteinianum* were favoured during the spring/wet and summer/dry seasons.

The forage selection hypothesis as well as the reproductive strategy hypothesis appears to apply between male and female nyala in BPGR. Male and female nyala appear to be adjusting their foraging strategies to select the plants that will best satisfy their individual forage and nutrient requirements.

CHAPTER 5: HABITAT USE

5.1 INTRODUCTION

Large mammalian herbivores are not evenly distributed across the landscape while foraging, but rather favour certain habitat types over others (Lamprey 1963; Owen-Smith *et al.* 2010), therefore a particular large mammalian herbivore population may not have a completely homogenous distribution across their range (Jarman 1974; Johnson 1980; Senft *et al.* 1987; Bailey *et al.* 1996; Henley 2001; Pérez-Barbería *et al.* 2013).

Habitat selection is the process of herbivores occupying and utilising areas which provide the essential resources for survival (Leuthold 1978; Hopcraft *et al.* 2010; Morris 2011). A preferred habitat type is one that is used more than expected from its availability (Neu *et al.* 1974; Aebischer *et al.* 1993; Manly *et al.* 2003; Mclean *et al.* 1998; Garshelis 2000; Alldredge and Griswold 2006). Knowledge of the habitat preference of large herbivores is crucial to any management program in a reserve and a pre-requisite to determining stocking densities and translocations (Ben-Shahar and Skinner 1988; Dekker 1996). In order to sustainably manage the different herbivore populations in a finite area, it is essential to know which habitat factors are influencing them (Scoggings *et al.* 1990; Van Rooyen 1990; Beest *et al.* 2013).

The factors responsible for selection of a particular habitat may be: (a) the distribution and availability of water (Leuthold 1978; McNaughton and Georgiadis 1986; Shannon *et al.* 2009); (b) the distribution and availability of quality forage (Sinclair 1979; Wilmshurst *et al.* 2000) as well as the distribution and availability of forage quantity (McNaughton and Georgiadis 1986; Winnie *et al.* 2008); (c) the extent of interspecific competition (Lamprey 1963; Ferrar and Walker 1974; Ritchie *et al.* 2009; Richard *et al.* 2012); (d) predation (Sinclair 1985; Sinclair *et al.* 2003; Valeix *et al.* 2009); (e) the distribution and availability of shelter (McNaughton and Georgiadis 1986; Dekker *et al.* 1996; Dörgeloh 1998). Among these factors, food seems to be the most important in influencing habitat selection among large mammalian herbivores (McNaughton 1987; Owen-Smith 1988; Valeix *et al.* 2011). Herbivores respond to variation in forage quality and quantity at a variety of spatial

and temporal scales (Orians and Wittenberger 1991; Bailey *et al.* 1996; Winnie *et al.* 2008; Hopcraft *et al.* 2010). This includes local or large-scale movements tracking areas of highest-quality forage (Fryxell *et al.* 1988; Bartumeus *et al.* 2005; Laca *et al.* 2010; Ahrestani *et al.* 2012), or individual selectivity at finer scales (Winnie *et al.* 2008; Beest *et al.* 2013).

Habitat heterogeneity is an important factor in the niche differentiation process, as it presents the herbivore community with more alternatives (Du Toit 1990; Dekker *et al.* 1996). Habitat partitioning reduces interspecific competition and therefore contributes to the ecological separation of ungulates (Du Toit and Owen-Smith 1989; Dekker *et al.* 1996; Makhabu 2005; Owen-Smith *et al.* 2010), however because nyala have historically not occurred in the Arid Mosaic Thicket of the Southern Cape (Skead 1987; Skead *et al.* 2007), information regarding their habitat selection in this particular system is lacking. Nyala have been shown to utilise a wide range of habitats, but consistently prefer denser areas offering cover from heat and predation (Hayes 1967; Tello and Van Gelder 1975; Anderson 1978; Anderson 1980; Van Rooyen 1992; Coates and Downs 2005; Van Eeden 2006; Kazembe 2010). Nyala are likely to compete for food and habitat resources with locally indigenous species in BPGR such as eland, kudu and common duiker (Vlok and Coetzee 2008).

Furthermore due to their marked difference in body size, nyala have been shown to display differences in habitat selection between the sexes (Kirby *et al.* 2008). Habitat partitioning between male and female nyala may reduce competition for food resources between them and therefore contribute to the ecological separation of the sexes (Kirby *et al.* 2008; Main 2008). Due to the conservation status of some of the habitats in BPGR (Chapter 2), differences in habitat selection between the sexes may prove significant in how to approach managing the species in the reserve. Male and female nyala eat different proportions of plant forms and plant species in BPGR (Chapter 3). Furthermore they appear to use different foraging paths, as the site availability of plant species differs significantly between the sexes (Chapter 4). Analysing their habitat use, will indicate whether the segregation of the sexes at the plant scale happens within the same habitat or in different habitats.

The objectives of this chapter are: a) to investigate the seasonal variation in habitat use of nyala in Buffelsdrift Private Game Reserve and b) to investigate the

seasonal variation in respective habitat use of male and female nyala in Buffelsdrift Private Game Reserve.

5.2 METHODS

5.2.1 STUDY SITE

Refer to chapter 2.

5.2.2 HABITAT USE OBSERVATIONS

Nyala were located monthly and the GPS coordinates, habitat occupied and composition of the herd recorded on field observation data sheets. Because individuals within a herd are not statistically independent (Alldredge and Ratti 1986), each sighting of a family group was considered a single random observation. Records were made at two different times of the day spread across four to five respective days a month for the duration of one year. Morning and afternoon records were staggered throughout the study period. In order to prevent auto-correlation of data, the only records used were those made 24 hours apart (Swihart *et al.* 1988). All available survey routes on BPGR were used in order to get an objective estimate of nyala distribution. Encounters on survey routes were supplemented with observations from various vantage points in the study site. In order to compare nyala habitat use with other herbivores, locations of eland and kudu were recorded in the same manner.

To get an estimate of sexual segregation at the habitat scale, nyala were recorded as female groups, male groups or mixed groups. Only observations on adult animals were considered for this purpose. If juvenile males were foraging in a female group, the group was recorded as female. This was because observations for sexual dimorphism purposes are most relevant when using a sexually mature study population (Clutton-Brock *et al.* 1982; Clutton-Brock 1989; Shannon *et al.* 2013).

5.2.3 DATA ANALYSIS

Habitat availability was measured as the proportional area of each habitat within the study area. Habitat area in BPGR was measured from habitat units delineated by Vlok *et al.* (2005) for the Little Karoo, using ArcGIS 10.1 software. Chi-squared goodness-of-fit analysis was used to test for differences between the expected use and the observed frequency of use of habitats by nyala on a seasonal basis, as well as by nyala, kudu and eland on an annual basis (Byers *et al.* 1984). The expected number of observations in each habitat was calculated by multiplying the relative area of the habitat by the total number of nyala observations. The Bonferroni confidence intervals were then used in order to determine which habitats were preferred (Byers *et al.* 1984). This test was only done if the chi-square test showed a significant difference. Confidence intervals were created for the proportion of utilisation of each habitat that showed a difference between observed and expected utilisation. If the expected proportion of use was less than the confidence interval, the habitat was used more than expected and when the expected proportion of use is greater than the interval, the habitat was used less than expected (Byers *et al.* 1984). Some habitat units were combined in order to meet the required minimum expected value of 5 per habitat per season (Roscoe and Byars 1971; Byers *et al.* 1984). In order to determine the influence of topography on habitat use, observations of nyala, kudu and eland inside and outside of mountainous terrain were compared using a 3 x 2 chi-squared contingency table.

Log-linear analyses of frequency tables, using *K*-factor analysis and tests of marginal and partial association, were used to determine whether relationships existed between sexual grouping, seasons and habitats. Subsequently the important relationships indicated were further analysed. A 2 x 3 chi-square contingency table was used to test variation in observed and expected frequencies of sexual grouping through the seasons. The same chi-square test and Bonferroni intervals were used to test which sexual grouping was most likely to prefer which habitat.

5.3 RESULTS

5.3.1 SEASONAL NYALA HABITAT USE

A total of 292 observations were recorded from May 2012 to April 2013. Chi-square goodness of fit analyses indicates that observed nyala habitat use differed significantly from the use expected from relative habitat area through all seasons; winter/wet ($\chi^2 = 184.3$, $df = 3$, $P < 0.0001$); spring/wet ($\chi^2 = 213.5$, $df = 3$, $P < 0.0001$); summer/dry ($\chi^2 = 247.7$, $df = 3$, $P < 0.0001$). However nyala did not display significantly different habitat preferences between seasons (Table 5.1). The Gravel Apronveld habitat as well as the River and Floodplain habitat was positively selected by nyala in all seasons. The Kruisrivier Spekboom Pruimveld/Degraded River and Floodplain habitats combined were used significantly less than expected from availability throughout the year. The Mons Ruber Waboomveld habitat was not recorded as used by nyala during the study period.

5.3.2 HABITAT USE BETWEEN THE SEXES

A total of 96 observations were recorded for male groups, 79 observations for female groups and 117 observations for mixed groups during the study period. Log-linear K -factor analysis indicated that the two way interactions were most significant (Pearson $\chi^2 = 200.9$, $df = 12$, $P < 0.0001$). Log-linear tests of marginal and partial association indicated that of these two way interactions, the association between season and habitat was not important (Part. ass. $\chi^2 = 7.7$, $df = 4$, $P > 0.05$), but that the associations between season and grouping (Part. ass. $\chi^2 = 44.5$, $df = 4$, $P < 0.0001$) and habitat and grouping (Part. ass. $\chi^2 = 144.7$, $df = 4$, $P < 0.0001$) were the most important.

Concerning season and grouping, the frequencies of male and female groups did not differ significantly from each other ($\chi^2 = 2.3$; $df = 1$; $P > 0.05$). Male groups and female groups were then combined for single sex versus mixed sex comparison (Table 5.2). The frequencies of single sex and mixed sex groups differed significantly between seasons ($\chi^2 = 44.9$, $df = 2$, $P < 0.0001$). The frequencies of single sex observations were significantly higher in the spring/wet and summer/dry seasons

than in the winter/wet season. The frequencies of observations of mixed sex groups were significantly higher during the winter/wet season than the spring/wet and summer/dry seasons.

Concerning habitat and grouping, Bonferroni analyses indicated that on an annual basis male groups used the Gravel Apronveld and Spekboom-Pruimveld/Degraded River and Floodplain habitats no different from expected, while they positively selected for the River and Floodplain habitat (Table 5.3). Mixed groups as well as female groups both positively selected for the Gravel Apronveld and River and Floodplain habitats. The Bonferroni confidence intervals could not be calculated for use of the Spekboom-Pruimveld/Degraded River and Floodplain habitat by female groups or mixed groups, as the expected use of the habitat by both was less than 5 (Roscoe and Byars 1971).

5.3.3 ANNUAL HABITAT USE OF NYALA, KUDU AND ELAND

A total of 104 observations were recorded for kudu, 114 for eland and 292 for nyala during the study period (Table 5.4). The Grootkop Gravel Apronveld habitat was positively selected for by nyala on an annual basis; however the use of this habitat by kudu and eland was too low to construct the Bonferroni intervals. All three species positively selected for the Olifants River and Floodplain habitat. The Kruisrivier spekboom/pruimveld habitat was used less than expected by nyala and used no different from expected by both kudu and eland. No use was recorded for nyala in the Mons Ruber Waboomveld habitat, but kudu and eland used this habitat no differently from what was expected. Nyala, kudu and eland used mountainous terrain in significantly different frequencies ($\chi^2 = 76.8$, $df = 2$, $P < 0.001$). Only 1.4% of the nyala observations were recorded in mountainous terrain, while 44.2% of the kudu observations and 30.7% of the eland observations were inside mountainous terrain (Table 5.5).

Table 5.1: Seasonal nyala habitat preference in BPGR as determined by direct observations. Codes: p_{ei} = expected proportion, p_{oi} = observed proportion, 95% intervals = Bonferroni 95% confidence intervals.

Habitat unit	Expected proportion (p_{ei}^1)	Observed proportion (p_{oi}^2)								
		Winter/wet (N = 91)			Spring/wet (N = 97)			Summer/dry (N = 104)		
		(p_{oi})	95% intervals ⁴	Pref ³	(p_{oi})	95% intervals ⁴	Pref ³	(p_{oi})	95% intervals ⁴	Pref ³
1. Gravel Apronveld	0.119	0.374	0.252 ≤ P ≤ 0.496	+	0.443	0.321 ≤ P ≤ 0.565	+	0.346	0.234 ≤ P ≤ 0.458	+
2. River and Floodplain	0.098	0.462	0.336 ≤ P ≤ 0.588	+	0.371	0.253 ≤ P ≤ 0.489	+	0.394	0.279 ≤ P ≤ 0.509	+
3. Kruisrivier Spekboom-Pruimveld/ Degraded River and Floodplain	0.671	0.165	0.071 ≤ P ≤ 0.259	-	0.186	0.091 ≤ P ≤ 0.281	-	0.260	0.156 ≤ P ≤ 0.364	-
4. Mons Ruber Waboomveld	0.112	0.000	-		0.000	-		0.000	-	

¹Taken as the relative area of the habitat. ²Calculated for habitat i as $p_{oi} = ni/N-1$ where ni is the number of times nyala were located in that habitat and N is the total number of observations across all habitats. ³Preference: + = use significantly greater than expected; - = use significantly less than expected.

⁴calculated only for p_{oi} when $N(1- p_{oi})$ and Np_{oi} where both ≥ 5 .

Table 5.2: Observation frequencies of nyala single sex groups versus mixed sex groups relative to seasons in BPGR. Codes: χ^2 = Chi-square value.

Grouping	Winter/wet	Spring/wet	Summer/dry	χ^2
Single sex groups	31 (34.1%)	62 (63.9%)	82 (78.8%)	44.9*
Mixed sex groups	60 (65.9%)	35 (36.1%)	22 (21.2%)	

* $P < 0.001$.

Table 5.3: Respective habitat preferences of males, females and combined sex groups of nyala on an annual basis in BPGR.

Codes: p_{ei} = expected proportion, p_{oi} = observed proportion, 95% intervals = Bonferroni 95% confidence intervals

Habitat unit	Expected proportion		Observed proportion								
	(p_{ei})	Male groups ($N = 96$)			Female groups ($N = 79$)			Mixed groups ($N = 117$)			
		(p_{oi})	95% intervals	Pref	(p_{oi})	95% intervals	Pref	(p_{oi})	95% intervals	Pref	
1. Gravel Apronveld	0.119	0.219	$0.117 \leq P \leq 0.321$	o	0.709	$0.586 \leq P \leq 0.832$	+	0.313	$0.210 \leq P \leq 0.416$	+	
2. Olifants River and Floodplain	0.098	0.208	$0.108 \leq P \leq 0.308$	+	0.266	$0.146 \leq P \leq 0.386$	+	0.661	$0.556 \leq P \leq 0.766$	+	
3. Kruisrivier Spekboom-Pruimveld/ Degraded Olifants River and Floodplain	0.671	0.573	$0.451 \leq P \leq 0.695$	o	0.025	-		0.026	-		
4. Mons Ruber Waboomveld	0.112	0.000	-		0.000	-		0.000	-		

¹Taken as the relative area of the habitat. ²Calculated for grouping i as $p_{oi} = n_i/N-1$ where n_i is the number of times nyala were located in that grouping and N is the total number of observations of combined groupings. ³Preference: + = use significantly greater than expected; - = use significantly less than expected; o = use no different to expected. ⁴calculated only for $p_{oi} N(1 - p_{oi})$ and Np_{oi} where both ≥ 5 .



Figure 5.1: Nyala, kudu and eland habitat use observations in BPGR from May 2012 to April 2013.

Table 5.4: Annual habitat preference of nyala, kudu and eland in BPGR as determined by direct observations. Codes: p_{ei} = expected proportion, p_{oi} = observed proportion, 95% intervals = Bonferroni 95% confidence intervals.

Habitat unit	Expected proportion (p_{ei}^1)	Observed proportion (p_{oi}^2)								
		Nyala ($N = 292$)			Kudu ($N = 104$)			Eland ($N = 114$)		
		(p_{oi})	95% intervals ⁴	Pref ³	(p_{oi})	95% intervals ⁴	Pref ³	(p_{oi})	95% intervals ⁴	Pref ³
1. Gravel Apronveld	0.119	0.387	$0.318 \leq P \leq 0.456$	+	0.039	-	0.000	-		
2. River and Floodplain	0.098	0.408	$0.339 \leq P \leq 0.477$	+	0.233	$0.133 \leq P \leq 0.486$	+	0.228	$0.133 \leq P \leq 0.323$	+
3. Kruisrivier Spekboom-Pruimveld/ Degraded River and Floodplain	0.671	0.205	$0.148 \leq P \leq 0.262$	-	0.612	$0.496 \leq P \leq 0.728$	o	0.684	$0.579 \leq P \leq 0.789$	o
4. Mons Ruber Waboomveld	0.112	0.000	-		0.117	$0.041 \leq P \leq 0.193$	o	0.088	$0.024 \leq P \leq 0.152$	o

¹Taken as the relative area of the habitat. ²Calculated for habitat i as $p_{oi} = ni/N-1$ where ni is the number of times nyala were located in that habitat and N is the total number of observations across all habitats. ³Preference: + = use significantly greater than expected; - = use significantly less than expected; o = used no different from expected. ⁴Calculated only for p_{oi} when $N(1-p_{oi})$ and Np_{oi} where both ≥ 5 .

Table 5.5: Number of habitat use observations of nyala, kudu and eland inside compared to outside of mountainous terrain. Codes: χ^2 = Chi-square value.

Species	Inside	Outside	χ^2
Nyala	4 (1.7%)	288 (98.6%)	
Kudu	46 (44.3%)	58 (55.7%)	76.8*
Eland	35 (30.7%)	79 (69.3%)	

* $P < 0.001$.

5.4 DISCUSSION

5.4.1 NYALA HABITAT USE

Seasonal variation in habitat use is common among mammalian herbivores (Dekker 1996; Watson and Owen-Smith 2000; Winnie *et al.* 2008; Gandiwa 2013) and has been observed in several other studies on nyala (Vincent *et al.* 1968; Tello and Van Gelder 1975; Anderson 1978; Anderson 1980; Van Rooyen 1992; Mkanda 1996; Kirby *et al.* 2008; Kazembe 2010). However, nyala in BPGR did not display significantly different habitat preferences between seasons (Table 5.1).

Nyala typically prefer habitats offering a high abundance of palatable browse during dry seasons (Tello and Van Gelder 1975; Van Rooyen 1992; Kazembe 2010) and a high abundance of forbs and grass species during the wet seasons (Tello and Van Gelder 1975; Van Rooyen 1992; Kirby *et al.* 2008). Similarly, nyala in BPGR positively selected the River and Floodplain habitat due to high herbaceous vegetation abundance during the winter/wet season, as herbaceous vegetation contributed most to their diet in this habitat, during this time. During the spring/wet and summer/dry seasons the availability of forbs and grasses declined significantly (Chapter 4) and did not make up the bulk of the diet, but nyala still positively selected for the Olifants River and Floodplain habitat. This selection appeared to be due to the high concentration of *A. karroo* in these areas, since *A. karroo* had the highest contribution to the diet of all species in the spring/wet season and remained

important during the summer/dry season (Chapter 3). The positive selection for this habitat type throughout the year is thus for palatable browse species such as *A. karroo* (Haschick and Kerley 1997) in the spring/wet and summer/dry seasons and high abundances of forbs and palatable grass species such as *C. dactylon* and *E. calycina* (Van Oudtshoorn 2002) in the winter/wet season.

Nyala are classified as mixed-feeders (Hofmann 1973; Jarman 1974; Hoffmann 1989; Woodall and Skinner 1993; Woodall and Skinner 1994) and the observation of preference for areas with high herbaceous vegetation during wet seasons is similar to other studies on mixed-feeders (Hoffman 1989; Du Toit 1988; Van Rooyen 1992; Owen-Smith 1994; Watson and Owen-Smith 2000; Van Eeden 2006). This seasonal shift from herbaceous yielding habitats to others, is in order to maintain a high level of foraging efficiency throughout the year (Owen-Smith *et al.* 1983; Scoggings *et al.* 2004; Beckerman 2005; Owen-Smith and Chafota 2012).

Nyala are known to prefer habitats close to water (Tello and Van Gelder, 1975; Skinner and Chimimba 2005). They generally drink water approximately once a day during the dry season, but less in the wet season as the leaves on which they browse contain more water (Tello and Van Gelder 1975). They have been found to persist for a number of months without free drinking water (Roberts 1936; Davison 1971). This observation suggests that permanent water is not an essential habitat requirement, however more recent studies (Van Eeden 2006; Canter 2008; Gandiwa 2013) suggest that where water is available they will drink readily and it would be an important factor in determining their habitat selection. It may be that water plays an important role in their selection of habitats in BPGR, since the two habitats that were not preferred (Kuilsvier Spekboom-Pruimveld and Mons Ruber Waboomveld) are the ones situated the furthest from water sources.

Another important habitat requirement for nyala is the presence of dense vegetation, as nyala never venture more than a few hundred meters away from the safety of thickets (Tello and Van Gelder 1975; Pfitzer and Kobes 2005; Kazembe 2010). The preferred Olifants River and Floodplain habitat contains dense stands of *A. karroo*, however the Gravel Apronveld habitat is not densely vegetated, but bush clumps do occur in patches throughout the habitat (Vlok *et al.* 2005; Skowno *et al.* 2010). The observations of nyala in Gravel Apronveld were never further than a few meters from the safety of bush clumps, or from the River and Floodplain ecotone.

The Kruisrivier Spekboom-Pruimveld habitat is the densest of the available habitats, with an abundance of palatable plants such as *Portulacaria afra* and *Pappea capensis* (Stuart-Hill 1992; Vlok *et al.* 2005), yet it was not positively selected for by nyala. This could be due to the fact that the habitat is not situated as close to water as the two preferred habitats and/or because of the topography related to the unit, as the habitat occurs on steep mountainous terrain. This is an aspect that nyala tended to avoid in KwaZulu-Natal (Tello and Van Gelder 1975); similarly the topography aspect appears to influence nyala's habitat selection in BPGR, since only 1.7% of nyala observations were on mountainous terrain. The negatively selected Mons Ruber Waboomveld habitat also contains steep mountainous terrain and an abundance of palatable shrubs such as *Portulacaria afra* and *Pappea capensis* (Stuart-Hill 1992; Vlok *et al.* 2005), however it is not as densely vegetated as the Kruisrivier Spekboom-Pruimveld habitat. The density factor combined with distance from water may explain the neglect of Mons Ruber Waboomveld.

The abundance of food in proximity of water and dense vegetation in lower lying areas appears to be the combination driving nyala habitat selection in BPGR. The preference for this combination has been shown in several other studies (Hayes 1967; Vincent *et al.* 1968; Davison 1971; Tello and Van Gelder 1975; Anderson 1978; Anderson 1980; Van Eeden 2006; Kirby *et al.* 2008) and nyala in BPGR appear to be no exception.

5.4.2 HABITAT USE OF MALE AND FEMALE NYALA

Following from the significant differences in plant species site availability between the sexes (Chapter 4), it became evident that males and females in BPGR select different areas to feed in. The question then is whether they segregate within the same habitat or between habitats. Results indicate that males and females as single sex groups used habitats differently to mixed sex groups (Table 5.4). The majority (57.3%) of male group habitat use was recorded in the Kruisrivier Spekboom-Pruimveld/Degraded Olifants River and Floodplain habitat (Table 5.3). Female groups used the Gravel Apronveld habitat the most (71.0%) and mixed sex groups used the Olifants River and Floodplain habitat the most (66.1%).

From the previous research chapters, I suggest that the segregation between male and female nyala in BPGR is due to different nutritional and energy demands driven by body size differences and divergent reproduction strategies (Main *et al.* 1996; Kirby *et al.* 2008; Main 2008). Males selected a higher standing biomass in the form of tall shrubs and females selected for quality forage in the form of forbs (Codron *et al.* 2007b), palatable grass such as *C. dactylon* and *E. calycina* (Van Oudtshoorn 2002;) and dwarf shrubs considered highly palatable such as *L. aethiopicum* and *Z. lichtensteinianum* (Vlok and Schutte Vlok 2010) (Chapter 3).

Even though a larger body size does not necessarily imply a greater digestive efficiency (Clauss and Hummel 2005; Clauss *et al.* 2007), I suggest that due to their larger body size and consequent larger gut size males probably have a faster throughput rate of food than females, they need to achieve a higher forage intake rate and therefore they focus on habitats offering quality biomass where they can maximize their foraging opportunities (Main 2008).

The females seem to be able to satisfy the majority of their energy requirements on dwarf shrubs in the Gravel Apronveld habitat as they spent the majority of their feeding time in this area. This may be because they have lower absolute forage requirements than males, hence less food, but more selective of the food (Clutton-Brock *et al.* 1982; Clutton-Brock *et al.* 1987). The smaller females thus select a lower plant biomass than larger males, but still meet their nutritional demands due to the quality they select (Clutton-Brock *et al.* 1987; Illius and Gordon 1987; Ruckstuhl and Neuhaus 2000; Rubin and Bleich 2005).

When males forage alongside females in Apronveld, differences in site availability suggests that they select different feeding paths offering a higher standing biomass and in the process avoid competition. The Olifants River and Floodplain habitat was the only habitat used in similar frequencies between the sexes. When males and females forage together in the Olifants River and Floodplain habitat, the resource in the form of the target species *Acacia karroo* may be partitioned through males and females probably feeding at different heights (Du Toit 1990; Kirby *et al.* 2008). Thus the reason for the positive selection may be because both sexes can satisfy their nutrient and energy requirements in the same area. Another reason for females positively selecting for the Olifants River and Floodplain habitat throughout the year may be to increase the chance of offspring survival. The reproductive strategy

hypothesis predicts that females select for habitats providing the best chance of offspring survival first and secondly select for quality forage (Main 2008). The dense stands of *A. karroo* in the Olifants River and Floodplain habitat provide both cover for young as well as quality food. This provides additional support for the forage selection hypothesis as a proximate explanation and the reproductive strategy hypothesis as an ultimate explanation for sexual segregation of nyala in BPGR.

Since the habitat segregation between male and female nyala appears to be as a result of individual nutrient and energy requirements, food resources are partitioned between the sexes (Jenks *et al.* 1994; Dekker 1996; Makhabu 2005). The school of thought suggesting that the sexes may be regarded as ecologically separate species (Kie and Bowyer 1999; Bowyer *et al.* 2001; Stewart *et al.* 2003; Bowyer 2004; Shannon *et al.* 2006) does thus apply in BPGR. Male and female nyala function spatially as two separate mixed-feeders, as they segregate at the plant form, plant species and habitat scales. Monitoring of vegetation change in BPGR for nyala management purposes should thus be planned around the individual influences of males and females and not only on the species as a whole.

5.4.3 THE INFLUENCE OF OTHER BROWSING UNGULATES

Interspecific competition is an important factor influencing the habitat selection of large mammalian herbivores (Du Toit and Owen-Smith 1989; Du Toit 1990; Dekker *et al.* 1996; Owen-Smith *et al.* 2010). Large mammalian herbivore species are able to co-exist through spatial resource partitioning (Richie and Olff 1999; Wilmshurst *et al.* 2000; Arsenault and Owen-Smith 2002; Cromsigt and Olff 2006). Spatial resource partitioning can occur at different scales; from plant species and feeding patches to larger landscape scales (Senft *et al.* 1987; Bailey *et al.* 1996). At the landscape scale body mass differences between large mammalian herbivores can affect their habitat selection (Du Toit and Owen-Smith 1989; Cromsigt *et al.* 2009). It is hypothesised that larger mammalian herbivore species have a wider food quality tolerance (Bell 1971; Jarman 1974; Gordon and Illius 1996) and can thus utilise a larger proportion of the landscape by using a higher diversity of habitats, including habitats that are of too low resource quality for the smaller more selective species (Du Toit and Owen-Smith 1989; Cromsigt *et al.* 2009).

Kudu and eland are suggested to compete with nyala for food and habitat resources (Vlok and Coetzee 2008). Kudu are mainly browsers (Hofmann 1973; Jarman 1974; Hoffmann 1989; Sigwela 1999), they tend to select for habitats offering an abundance of shrubs and select for forbs during the wet seasons (Hofmann 1973; Jarman 1974; Owen-Smith *et al.* 1983). They are also not deterred by the slope aspect, as they have been shown to select mountainous areas in the past (Du Toit 1995; Fritz *et al.* 1996; Sigwela 1999). Even though kudu observations were widespread in BPGR, the majority of the observations were in the northern parts of the Kuilsrivier Spekboom-Pruimveld habitat in steep, dense terrain (Figure 5.1). This was probably due to the abundance of palatable shrubs such as *P. afra* and *P. capensis* (Stuart-Hill 1992).

Eland are classified as mixed-feeders preferring browse (Hofmann 1973; Jarman 1974; Hoffmann 1989). However, the diet of the species has been recorded in various different vegetation types and their diet varies considerably between areas (Watson and Owen-Smith 2000). In a semi arid shrubland environment, eland were found to be mainly browsers feeding predominantly on shrubs and dwarf shrubs (Watson and Owen-Smith 2000). One would thus expect them to prefer the same habitat as nyala in the semi arid BPGR. Eland observations were also widespread in BPGR, but the majority of the observations were in the southern, more open and degraded parts of the Kuilsrivier Spekboom-Pruimveld habitat. This relatively open area, degraded by domestic stock (Chapter 2) has a reduced shrub layer and contains more dwarf shrubs relative to shrubs. Eland often forage in open areas away from cover (Watson and Owen-Smith 2000) and may thus have concentrated in this open area in order to select for dwarf shrubs. This being said, one would then also expect eland to positively select the Gravel Apronveld habitat that has an abundance of dwarf shrubs (Vlok and Schutte-Vlok 2010), however, this is a habitat positively selected by nyala throughout the year, which suggests that nyala may be forcing eland to utilise lower quality dwarf shrubland through interspecific competition (Du Toit and Owen-Smith 1989; Richie *et al.* 2009).

Nyala, kudu and eland all positively selected for the Olifants River and Floodplain habitat, but differed in preference for all the other habitats in BPGR. Even though all three large herbivores positively selected for the Olifants River and Floodplain habitat, their spatial distribution within the habitat varied considerably (Figure 5.1).

From this distribution, it is evident that nyala had a much smaller range than kudu and eland. Nyala's small range in BPGR is likely because they can satisfy all their needs during the time period of a year in that small area (Leuthold 1972). The small area they used offered them all their ecological requirements namely quality food and shelter in the proximity of water (Tello and Van Gelder 1975; Skinner and Chimimba 2005). Kudu and eland are considered less selective than nyala, because of their enhanced tolerance for lower quality foods (Bell 1971; Jarman 1974) stemming from the allometry of the metabolic rate-gut capacity relationship (Demment and Van Soest 1985). I suggest that because of this enhanced tolerance, kudu and eland used a much larger proportion of BPGR and in the process habitat resources were partitioned between these species.

The co-existence of these mammalian herbivores in BPGR through spatial resource partitioning suggests that nyala may have an effect on naturally occurring herbivores through interspecific competition in an Arid Mosaic Thicket ecosystem. However, browsers may ultimately show spatial segregation within woody habitats due to the increased spatial heterogeneity that is produced by the complex structure of the habitat itself (Woolnough and Du Toit 2001; Kirby *et al.* 2008). Thus given that a property contains a heterogeneous distribution of woody habitats that will offer browsers in the guild adequate suitable alternatives, any browsing guild that is well balanced between selective and less selective browsers may be able to co-exist in the Arid Mosaic Thicket of the Southern Cape (Du Toit and Owen-Smith 1989; Woolnough and Du Toit 2001).

From a general management perspective, the results of this chapter are significant in terms of the management of the habitats listed as priority areas. Since nyala concentrate in the priority habitats throughout the year, they exert browsing pressure in a localised area. Management should consider lowering the stocking rate of the animals to relieve browsing pressure in these habitats.

5.5. CONCLUSION

Nyala in BPGR used habitats disproportionate to their availability. However they did not display differences in selection of habitats between seasons. Abundant palatable browse in combination with proximity to water and thickets for cover appear to be the combination dictating the habitat selection of nyala in BPGR.

Male and female single sex groups and mixed sex groups showed significantly different habitat selection patterns. Females selecting significantly more for Apronveld, males for Spekboom-Pruimveld and mixed sex groups for River and Floodplain. These differences in selection indicate that males and females are partitioning the food resource base to some extent. The resource partitioning is due to selection for plants that will satisfy the individual energy and nutrient requirements of the respective sexes.

Nyala, kudu and eland appear to co-exist in BPGR as a result of spatial resource partitioning. I suggest that this is as a result of differences in body size and digestive efficiency, as mammalian herbivores with larger body sizes are less selective and have a wider food quality tolerance than smaller more selective mammalian herbivores.

CHAPTER 6: OVERVIEW

6.1 INTRODUCTION

Feeding ecology investigates the relationship between a mammalian herbivore and its available food supply (Johnson 1980; Owen-Smith *et al.* 1983). Food resources available to mammalian herbivores vary in distribution, quality and quantity (Westoby 1974; Owen-Smith 2002; Owen-Smith *et al.* 2010). Herbivores have evolved different strategies to be able to select appropriate food resources in heterogeneous environments (Owen-Smith and Novellie 1982; Senft *et al.* 1987; Owen-Smith *et al.* 2010). These strategies include foraging at different scales i.e. selecting different habitats to feed in as well as different plant species to feed on (Bailey *et al.* 1996; Owen-Smith *et al.* 2010).

In this thesis the feeding ecology of extralimital nyala in the Arid Mosaic Thicket of the Southern Cape was investigated by determining diet composition, diet preference and habitat use in Buffelsdrift Private Game Reserve. The objectives of this chapter are: (a) to provide an overview of nyala feeding ecology in BPGR; (b) to make recommendations on the management of nyala in Arid Mosaic Thicket and (c) to make suggestions on possible future research that may build on the findings of this study.

6.2. NYALA FEEDING ECOLOGY

6.2.1 NYALA AS A SPECIES

Nyala are classified as mixed-feeders (Hofmann and Stewart 1972; Jarman 1974; Hoffmann 1989; Woodall and Skinner 1993; Woodall and Skinner 1994). They select for fresh grass in season, but their diet comprises primarily of browse material (Vincent *et al.* 1968; Tello and Van Gelder 1975; Anderson and Pooley 1977; Anderson 1978; Codron *et al.* 2007a; Kirby *et al.* 2008).

My findings support this classification, as the nyala in BPGR were found to be mixed-feeders preferring browse during the study period. Browse contributed 87.8% to the annual nyala diet, while grass contributed 12.2%. Shrubs formed the highest

proportion of the diet in every season; however shrub consumption by nyala varied significantly between seasons. Shrub consumption was at its lowest in the winter/wet season and at its highest in the summer/dry season. Dwarf shrubs consistently contributed > 20% to the diet throughout the year and did not differ significantly between seasons. Forbs and grasses were important during the winter/wet season, but significantly less in spring and summer. Succulents consistently contributed the lowest proportion of the diet in all seasons. Only six species formed > 5% of the annual diet. Of these six only three species formed > 10% of the annual nyala diet; the shrubs *Acacia karroo*, *Pappea capensis* and *Grewia robusta*. These were followed by the shrub *Portulacaria afra*, the dwarf shrub *Zygophyllum lichtensteinianum* and the grass *Cynodon dactylon* all contributing between 5 -10% to the annual diet. Nyala's principal diet was one of woody browse for most of the year, supplemented by forbs and grass during the winter/wet season. This shift is suggested to be a strategy for maintaining a high protein, low fibre diet throughout the year. The selection for different plant species in different times of the year in order to maintain their preferred diet is supported by other nyala feeding studies (Tello and Van Gelder 1975; Van Rooyen 1992; Botha and Stock 2005; Kirby *et al.* 2008). However, seasonal food selection in the Arid Mosaic Thicket of the Southern Cape is of particular interest, as nyala are extralimital to the area and the information is lacking.

Nyala fed selectively, preferring only 33.4% of the plant species presented to them in BPGR (acceptability index > 0.5). There are definite seasonal dietary shifts in preferences between different plant species. The shift takes place between the wet seasons (winter and spring) and the dry season (summer). Herbaceous species such as *Cynodon dactylon* and *Erharta calycina* were favoured in winter. Shrubs such as *P. capensis*, *P. afra* and dwarf shrubs such as *L. aethiopicum* and *Z. lichtensteinianum* were favoured during the spring/wet and summer/dry seasons.

Nyala in BPGR used habitats disproportionate to their availability. However they did not display differences in selection of habitats between seasons. Abundant palatable browse in combination with proximity to water and thickets for cover appear to be the combination dictating the habitat selection of nyala in BPGR. Interspecific competition may also play a role in their habitat selection, as their co-

existence with kudu and eland may stem from competition for food resources (Dekker *et al.* 1996; Richie *et al.* 2009).

6.2.2 FEEDING ECOLOGY OF THE RESPECTIVE SEXES

Male and female nyala in BPGR consumed different proportions of plant forms and plant species. The sexes also preferred different plant species throughout the study period. Males preferred the shrubs *P. capensis*, *P. afra*, *R. obovatum*, *N. capensis* and *Z. morgsana* more than females, whereas females preferred the dwarf shrubs *Z. lichtensteinianum*, *L. aethiopicum*, *R. humilis* and *A. semibaccata* more than males.

Male and female single sex groups and mixed sex groups showed significantly different habitat selection patterns. Female groups and mixed groups positively selected for the Gravel Apronveld habitat, while male groups used this habitat no different from expected. All groupings positively selected for the Olifants River and Floodplain habitat throughout the year. The Kruisrivier Spekboom-Pruimveld habitat was used no different from expected by male groups, but female and mixed groups neglected this habitat.

Differences in plant form, plant species and habitat selection indicate that males and females are partitioning the food resource base between them in BPGR. I suggest that the forage selection hypothesis (Main *et al.* 1996) as a proximate explanation in conjunction with the reproductive strategy hypothesis (Main 2008) as an ultimate explanation applies to nyala sexual segregation in BPGR. This suggestion is in accordance with a recent study on nyala sexual segregation (Kirby *et al.* 2008). The smaller females have lower absolute forage requirements than males, but they are more selective of the food they eat (Clutton-Brock *et al.* 1982; Clutton-Brock *et al.* 1987). The smaller females thus select a lower plant biomass than larger males, but still meet their nutritional demands due to the higher quality forage they select (Clutton-Brock *et al.* 1987; Illius and Gordon 1987; Ruckstuhl and Neuhaus 2000; Rubin and Bleich 2005). Even though a larger body size does not necessarily imply a more efficient digestive system (Clauss and Hummel 2005; Clauss *et al.* 2007), I suggest that due to their larger body size and consequent larger gut size males have a faster throughput rate of food than females, they need to achieve a higher forage intake rate and therefore they focus on habitats offering

quality biomass where they can maximize their foraging opportunities (Main 2008). Males and females appear to be adjusting their foraging strategy to select the plants that will best satisfy their individual nutrient and energy requirements.

6.2.3 THE INFLUENCE OF OTHER BROWSING UNGULATES

Nyala, kudu and eland appear to co-exist in BPGR as a result of spatial resource partitioning. I suggest that this is as a result of differences in body size and digestive efficiency, as mammalian herbivores with larger body sizes are less selective and have a wider food quality tolerance than smaller more selective large herbivores (Du Toit and Owen-Smith 1989).

Kudu are classified as browsers (Hofmann 1973; Jarman 1974; Hoffmann 1989; Sigwela 1999), they tend to select for habitats offering an abundance of shrubs and select for forbs during the wet seasons (Owen-Smith *et al.* 1983). Kudu are not deterred by steep slopes, as they have been shown to select for mountainous terrain (Du Toit 1995; Sigwela 1999). Kudu observations were widespread in BPGR; however the majority of the observations were in the northern parts of the Kuilsrivier Spekboom-Pruimveld habitat, in dense mountainous terrain. I suggest that this is due to an abundance of palatable shrubs such as *P. afra* and *P. capensis* (Stuart-Hill 1992).

Eland are classified as mixed-feeders preferring browse (Hofmann 1973; Jarman 1974; Hoffmann 1989). In a semi arid shrubland environment, eland were found to be mainly browsers feeding predominantly on shrubs and dwarf shrubs (Watson and Owen-Smith 2000). One would thus expect them to prefer the same in the semi arid BPGR. Eland observations were also widespread in BPGR, but the majority of the observations were in the southern, more open and degraded parts of the Kuilsrivier Spekboom-Pruimveld habitat. This relatively open area, degraded by domestic stock (Chapter 2) has a reduced shrub layer and contains more dwarf shrubs relative to shrubs. Eland often forage in open areas away from cover (Watson and Owen-Smith 2000) and may thus have concentrated in this open area in order to select for dwarf shrubs. This being said, one would then also expect eland to select for the Gravel Apronveld habitat that has an abundance of dwarf shrubs (Vlok and Schutte-Vlok 2010), however, this is a habitat positively selected by nyala throughout the year,

which suggests that nyala may be forcing eland to utilise lower quality dwarf shrubland through interspecific competition (Du Toit and Owen-Smith 1989; Richie *et al.* 2009).

6.3 MANAGEMENT IMPLICATIONS

Since this study was conducted on a single property in Arid Mosaic Thicket, assumptions and/or generalizations regarding resource use across the vegetation type is limited to the study site. This study thus only represents a sample of the possible feeding effects of extralimital animal in the greater system. Nevertheless, the results of this study provide important basic information to build future research on.

Large mammalian herbivores are considered important regulators of change in ecosystems (Hobbs 1996; Gordon *et al.* 2004). Sudden shifts in primary production caused by disturbances such as intense herbivore pressure, has the potential to rearrange the dynamics of an ecosystem either temporarily or semi permanently into a new state (Van de Koppel *et al.* 2002; Scheffer and Carpenter 2003; Hopcraft *et al.* 2010). Plant-herbivore interactions that affect vegetation changes are confined to the area the herbivore occupies; therefore management of mammalian herbivore impacts on vegetation may demand a site-specific approach (Gordon *et al.* 2004; Van Wieren and Bakker 2008). The most appropriate management plan for a specific property will depend on its available resources and on the specific objectives of the landowner (Stuart-Hill 1999; Brink *et al.* 2011). Every game reserve is unique with a different suite of objectives and expectations (Cousins *et al.* 2010; Brink *et al.* 2011). However, monitoring and record-keeping are crucial tools for sustainability in game and nature reserves as well as intensive game farming (Bothma and Van Rooyen 2002; Lynam and Stafford Smith 2004; Carruthers 2008).

Abundant medium sized browsers have been shown to have a substantial impact on the woody vegetation recruitment and community dynamics of savanna ecosystems (Prins and Van Der Jeugd 1993). Since nyala as medium sized browsers are extralimital to the Southern Cape (Skead 1987; Skead *et al.* 2007), nyala herbivory has not co-evolved with the vegetation of Arid Mosaic Thicket and hence their feeding preferences may have an effect on the vegetation. In addition to being a selective

feeder (Tello and Van Gelder 1975; Kirby *et al.* 2008) nyala have shown differences in foraging behaviour between males and females in this study as well as others (Tello and Van Gelder 1975; Kirby *et al.* 2008). From the results of this study it is clear that nyala spent most of their feeding time in Olifants River and Floodplain and Grootkop Gravel Apronveld listed as vulnerable and critically endangered respectively. Females concentrated most in the critically endangered site, males were fairly widespread and mixed sex groups mostly concentrated in the vulnerable site. No plant species listed as rare or endangered were eaten by nyala during the study. However, this observation does not necessarily imply that nyala have no impact on listed species, as plants may have been consumed that were not detected by the feeding observations. In addition nyala may still have an effect on adult plant mortality and seedling recruitment of listed species through trampling or nurse plant disturbance. Hence it is critically important to monitor the changes in vegetation condition in these areas.

Changes in vegetation condition may give an indication of nyala browsing pressure on the system, but in order to pinpoint negative effects of one herbivore or one sex of herbivore on the vegetation, one would have to exclude all the other herbivores. Therefore methods that may allow for isolating herbivore impacts should be investigated. This may include keeping nyala in feeding enclosures with key browse species indicated in this study such as *A. karroo*, *G. robusta* and *P. afra*.

The possible effects of sustained browsing pressure on the vegetation in BPGR may include: (a) instant death through trampling or consumption of the entire plant (Crawley 1983; Skarpe and Hester 2008); (b) reducing reproductive success by removing reproductive parts (Danell and Bergström 1989; Crawley 1997; Bergström *et al.* 2000); (c) facilitating reproductive success through pollination or seed dispersal (Du Toit 2003; Bodmer and Ward 2006); (d) decreased or retarded growth through repeated herbivory (Makhabu and Skarpe 2006); (e) increased growth, as certain plants such as clonal grasses are stimulated to some extent by utilization (Briske 1996; Van Oudtshoorn 2002; Briske *et al.* 2003) and (f) competitive ability, since selective utilization of plants with low resistance to herbivory favours the persistence of plants with high resistance to herbivory (Skarpe 1991; Belsky 1992; Vourc'h *et al.* 2001).

The scale of the effects will depend on: (a) the plants resistance strategy, (b) rate and intensity of defoliation, (c) growth stage when defoliated, (d) plant parts affected and (e) external factors such as previous and subsequent disturbance, inter- and

intraspecific competition and resource availability before and after defoliation (Teague 1985; Strauss and Agrawal 1999; Hester *et al.* 2006a; Skarpe and Hester 2008). These effects could result in the alteration of composition and structure, ultimately having cascading consequences on other taxa (Lechmere-Oertel *et al.* 2005; Van Wieren and Bakker 2008).

The monitoring of these possible effects on the vegetation in BPGR could be done by examining the utilization and reproductive success of key browse species such as *A. karroo*, *P. capensis*, *P. afra*, *G. robusta*, *L. aethiopicum* and *Z. lichtensteinianum* shown in this study. This could be done through fixed point photography (Hurt and Hardy 1989; Stuart-Hill 1989b; Willis and Trollope 1987; Heard *et al.* 1986) and/or by comparing utilization and reproductive success of selected species inside and outside of monitoring exclosures (Augustine and Mcnaughton 2004; Côté *et al.* 2004; Kraaij and Milton 2006). In terms of the photography method, the sites should be photographed and examined at the end of the dry season and during the peak flowering/seeding period (Birnie *et al.* 2005). If there is a clear negative impact, such as the appearance of a browse line and a reduction in the quantity of leaves, flowers/fruit and seedlings from one year to the next, browse stocking rates could be re-evaluated (Birnie *et al.* 2005). In addition, fixed point photography sites should preferably be supplemented with quantitative monitoring techniques (Coetzee 2005). In terms of the exclosure method, effects of large herbivores on plant growth and community dynamics could be evaluated by monitoring leaf density and biomass, twig growth, sapling recruitment and whole-shrub growth rates of different species inside and outside the exclosures (Augustine and Mcnaughton 2004).

Several studies have highlighted the possible negative impacts of extralimital wildlife in terms of; competition with indigenous species for resources, competitive exclusion, loss of sensitive species and a consequent loss of biodiversity (Castley *et al.* 2001; Bond and Loffell 2001; Burkett *et al.* 2002; Kerley *et al.* 2004; Palmer *et al.* 2006; Spear 2008). However it should be kept in mind that the impacts of extralimital large herbivores can be mitigated by sound reserve management principles (Bothma 2005; Jacobs 2008; Spear 2008). For example in this study: (a) relocating the main water source from inside the critically endangered vegetation type to a more suitable site will relieve browsing pressure on the vegetation; (b) re-evaluating stocking densities of nyala as well as other herbivores in order to stock smaller populations could relieve

browsing pressure and in the process assist ecosystem resilience; (c) since the value of the nyala for game viewing and hunting stems mostly from the larger more impressive males (Bothma 2010), management may consider adjusting the sex ratio of nyala to ensure that the females who concentrate more in the critically endangered site, do not significantly outnumber males and most importantly (d) monitoring programs are currently absent in the reserve, so management should design and implement suitable monitoring programs to assess impacts and identify areas of concern.

An adaptive management approach, based on sound monitoring and feedback is suggested to ensure sustainable utilization of natural resources in BPGR (Stuart-Hill 1989b; Biggs and Rogers 2003; Brink *et al.* 2011). Adaptive management involves setting specific reserve management goals and then continuously evaluating progress towards these goals (Esler *et al.* 2006; Brink *et al.* 2011). Furthermore it requires recording of management actions and environmental fluctuations concurrently so that for example changes in vegetation condition can be related back to the management applied and/or the environmental conditions experienced (Stuart-Hill 1999).

6.4 SUGGESTIONS FOR FUTURE RESEARCH

This study was conducted on a single reserve, because it was the only known site where nyala occurred in relatively intact Arid Mosaic Thicket that could facilitate simple direct observations. Hence the focus was on an isolated population within a confined area. Comments on possible impact can realistically only be confined to the site. It is recommended that future research consider the feeding ecology of nyala in Albany Thicket across all vegetation types and landscapes in conditions where the animal occurs with different herbivore assemblages. From this suitability estimates can be obtained for different vegetation types in different conditions. This will also assist in refining stocking rate recommendations.

Monitoring the direct and indirect feeding effects of nyala as well as other herbivores on rare and endangered plants in the Little Karoo is recommended. Many game reserves in the Little Karoo are relatively small fenced areas, exacerbating herbivore pressure. Because of the sensitive nature of the vegetation in the Little Karoo, monitoring programmes to assess the possible impacts of over stocking is

essential. I propose that the most suitable method for this is comparing the utilization and reproductive success of selected plant species inside and outside of monitoring exclosures. Such information will assist conservation authorities in their decision making for permit applications to allow nyala in similar habitat types across the region.

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APPENDIX 3.1: Plant species available in nyala feeding stations from April 2012 to May 2013.

Species	Accepted	Rejected
<i>Acacia karroo</i>	x	
<i>Acrotis spp.</i>	x	
<i>Aloe microstigma</i>		x
<i>Ammocharis coranica</i>		x
<i>Andromischus filicaulis</i>		x
<i>Aptosimum depressum</i>	x	
<i>Artiplex semibaccata</i>	x	
<i>Asclepias fruticosa</i>		x
<i>Asparagus africanus</i>		x
<i>Asparagus capensis</i>		x
<i>Asparagus retrofractus</i>		x
<i>Asparagus striata</i>		x
<i>Atriplex lindeyi subsp inflata</i>	x	
<i>Augea capensis</i>		x
<i>Babiana karooica</i>		x
<i>Blepharis capensis</i>		x
<i>Bromus catharticus</i>		x
<i>Brunsvigia striata</i>		x
<i>Bulbine mesembryanthemoides</i>		x
<i>Cadapha aphylla</i>	x	
<i>Carrissa haematocarpa</i>	x	
<i>Cissampelos torulosa</i>		x
<i>Conyza scabrida</i>		x
<i>Cotula zeyheri</i>		x
<i>Cotyledon cuneata</i>		x
<i>Cotyledon orbiculata</i>		x
<i>Crassula expanza</i>		x
<i>Crassula muscosa</i>		x
<i>Crassula perforata</i>		x
<i>Crassula subaphylla</i>		x
<i>Cuspidia cernua</i>	x	
<i>Cynodon dactylon</i>	x	
<i>Cyperaceae spp.</i>	x	
<i>Cysticapnos vesicaria</i>	x	
<i>Delosperma perensis</i>		x
<i>Diascia bicolor</i>	x	
<i>Drimia anomala</i>		x
<i>Drosanthemum hispidum</i>		x
<i>Drosanthemum peltatum</i>		x
<i>Erharta calycina</i>	x	
<i>Eriocephalus ericoides</i>	x	
<i>Eriospermum capensis</i>		x
<i>Erodium mochatum</i>		x
<i>Euphorbia mauritannica</i>		125 ^x
<i>Euryops lateriflorus</i>		x
<i>Felicia muricata</i>	x	
<i>Fingerhuthia africana</i>	x	
<i>Galenia Africana</i>		x
<i>Galenia fruticosa</i>	x	
<i>Gasteria brachyphylla</i>		x

<i>Gazania krebsiana</i>	x	
<i>Gazania lichtensteinii</i>	x	
<i>Glottiphyllum depressum</i>		x
<i>Gloveria integrifolia</i>		x
<i>Grewia robusta</i>	x	
<i>Guieminea densa</i>	x	
<i>Gymnosporia buxifolia</i>	x	
<i>Helichrysum cymosum</i>		x
<i>Hemimeris racemosa</i>		x
<i>Hermannia althaefolia</i>	x	
<i>Hermannia filifolia</i>	x	
<i>Hermannia sp.novcf. Cernua</i>	x	
<i>Hibiscus trionum</i>		x
<i>Hirpicium integrifolium</i>	x	
<i>Ifloga glomerata</i>		x
<i>Lampranthus spp.</i>		x
<i>Lessertia annularis</i>	x	
<i>Leucas capensis</i>		x
<i>Limium aethiopicum</i>	x	
<i>Lolium perenne</i>	x	
<i>Lycium cinerium</i>		x
<i>Lycium oxycarpum</i>	x	
<i>Macedium spinosum</i>		x
<i>Malephora lutea</i>		x
<i>Massoinia depressa</i>		x
<i>Mesembryanthemum excavatum</i>		x
<i>Mesembryanthemum splendens</i>		x
<i>Moquinella rubra</i>		x
<i>Moraea spp.</i>		x
<i>Nemesia spp.</i>		x
<i>Nerine humilis</i>		x
<i>Nicotiana glauca</i>		x
<i>Nymanina capensis</i>	x	
<i>Osteospermum moniliferum</i>	x	
<i>Osteospermum sinuatum</i>	x	
<i>Othonna amplexicaulis</i>		x
<i>Oxalis spp.</i>	x	
<i>Pappea capensis</i>	x	
<i>Pentzia dentata</i>		x
<i>Pentzia incana</i>	x	
<i>Phragmites australis</i>		x
<i>Portulacaria afra</i>	x	
<i>Pteronia incana</i>		x
<i>Pteronia pallens</i>		x
<i>Putterlickia pyracantha</i>		x
<i>Rhigosum obovatum</i>	x	
<i>Searsia lucida</i>	x	
<i>Rosenia humilis</i>	x	
<i>Salsolla aphylla</i>		x
<i>Sarcostemma viminale</i>	x	
<i>Solanum tomentosum</i>		x

<i>Thesium lineatum</i>	x	
<i>Tylocodon paniculatum</i>		x
<i>Tylocodon wallichii</i>		x
<i>Uclea undulata</i>	x	
<i>Ursinia anthemoides</i>		x
<i>Ursinia nana</i>		x
<i>Veltheimia capensis</i>		x
<i>Viscum rotundifolium</i>	x	
<i>Zygophyllum debile</i>	x	
<i>Zygophyllum lichtensteinii</i>	x	
<i>Zygophyllum morgesana</i>	x	

