The ecology of the African buffalo in the eastern Kalahari region, South Africa

by

Marzanne Cromhout

Submitted in partial fulfillment of the requirements for the degree

MAGISTER SCIENTIAE (WILDLIFE MANAGEMENT)

in the Centre for Wildlife Management
Department of Animal and Wildlife Sciences
Faculty of Natural and Agricultural Sciences
University of Pretoria
Pretoria

Supervisor: Prof. J. du P. Bothma
Co-supervisor: Prof. M.W. van Rooyen

March 2006

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ABSTRACT

This study was conducted on Tswalu Kalahari Reserve in the eastern Kalahari region of South Africa. The long-term sustainability of the valued African or Cape buffalo *Syncerus caffer caffer* was investigated in an area that falls outside their permanent historical distribution. The habitat utilisation of the buffalo population and their range use patterns were investigated. Seasonal differences were apparent in habitat utilisation and were guided by nutritional needs and climatic variables. Range use patterns revealed an increase in range size during the cold, dry season. The buffalo density on Tswalu was the lowest recorded in the literature to date with 0.15 buffalo/km². The animals showed seasonal changes in their feeding preferences with occasional browsing. During the cold, dry season the population was under severe nutritional stress. Population growth during the study period was 11.8% but this was within the norm expected for a free-living buffalo population. Annual recruitment for the study period was 33%, with half of the female population with calves at heel. However, the population is ageing with 54.2% of the population in the adult age class. Optimising the sex ratio and age structure could improve the productivity. Together with this, the nutritional needs of the buffalo should be met by supplementation, especially during periods of poor rainfall, to assist in optimal production and survival. Population viability analysis showed that the population is vulnerable over the medium term.

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CHAPTER 1

INTRODUCTION

During the months of April and May 1995, a founder herd of 44 buffalo (*Syncerus caffer caffer*) was introduced to Tswalu Kalahari Reserve (hereafter referred to as Tswalu), an area outside their permanent historic distribution (Shortridge 1934; Sinclair 1977; Ebedes 1996; Plug & Badenhorst 2001). The intention at the time of the introduction was to produce surplus animals to restock other reserves and wildlife ranches, all in the name of species conservation. During the annual aerial count of 2002, 73 buffalo were recorded.

In view of the historical occurrence of the African buffalo (Chapter 2), it is clear that it requires a habitat with abundant water, an annual rainfall of > 250 mm, and good quality grazing especially during the dry season, in order to satisfy their energy maintenance requirements (Shortridge 1934; Sinclair 1977; Krüger 1996; Prins 1996). Parturition must preferably take place when the cow is in a peak condition in the wet season, and for optimal productivity the calf must be weaned at 9 months of age. To obtain a weaning age of 9 months for optimal population growth, the veld must be in a condition to sustain a young growing calf. If the veld is in a poor condition or has a low nutrient quality, the calf will want to suckle longer than usual, therefore extending the inter-calving period and resulting in a limited and reduced productivity for the cow and the population as a whole (Sinclair 1977; Mloszewski 1983; Prins 1996).

If free-ranging animals are kept, long-term sustainability is a prerequisite. This is questionable in view of the current productivity of the buffalo on Tswalu. The buffalo population on Tswalu occurs in a marginal habitat, it may not be genetically and numerically self-sustaining in the long term, and the buffalo could be under severe food stress during the winter, thus impeding their productivity. It was therefore necessary to study the ecology of the buffalo population on Tswalu in some detail to provide a basis for its future management, and to formulate decisions on the sustainability of the introduction of the buffalo to Tswalu.

The current study was aimed at investigating the possible reasons for the observed low productivity level of the buffalo on Tswalu. The hypothesis tested was that the buffalo on Tswalu could survive and breed successfully in this arid Kalahari region where they did not occur historically.

In order to test this hypothesis, the following key questions were examined in the current study:

- What is the ecological capacity of the reserve for the African buffalo, and what population management measures must be taken? This involved three major subquestions:

    - What are the habitat use characteristics and habitat preferences of buffalo in terms of the quality and quantity of the habitat available to and used by the buffalo?
    - What are the range use characteristics of the buffalo?
    - What are the feeding preferences of the buffalo?
- What is the current and expected population growth of the buffalo population? This involved two major subquestions:
    - What are the reasons for the current low population growth rate of the buffalo, and can it be improved?
    - What is the long-term sustainability of the buffalo population under natural conditions on Tswalu?

The dissertation is broadly formatted into three themes, bounded by a short introduction (Chapter 1) and a concluding synthesis (Chapter 8). Chapter 2 gives some information on the historical background of the African buffalo, which is essential in understanding the ecology of the species. Chapter 3 outlines the inception and setting of Tswalu and include a description of the wildlife and vegetation found on the reserve. The first theme, regarding the spatial ecology of the buffalo on Tswalu is discussed in Chapters 4 and 5, followed by the second theme in Chapter 6, which investigated the feeding ecology of the buffalo. Finally, the last theme on the population ecology of the buffalo is presented in Chapter 7.

In Chapter 4 the habitat utilisation of the buffalo is examined by exploring movements and preferences for certain vegetation units. Emphasis is given towards seasonal utilisation in relation to different activities. Possible reasons for the apparent selection of certain vegetation units are examined and discussed. Related to Chapter 4, buffalo range use patterns are explored in Chapter 5. Sighting data were used to determine the range size of the buffalo and comparisons were made with other studies.

The grazing patterns of buffalo have been well documented (Vesey-Fitzgerald 1974; Field 1976; Sinclair 1977; Beekman & Prins 1989) and the relation to population growth is obvious (Caughley & Sinclair 1994). In Chapter 6 this important aspect of buffalo ecology is examined. Selection of plant species and parts, and the constituents of preferred plant species are reviewed. The quality of food available to the buffalo on Tswalu was determined, while possible consequences are discussed. Chapter 7 investigates the population size and structure of the Tswalu buffalo. Using a population viability assessment, comments are made regarding the long-term sustainability of the population on Tswalu.

Finally, Chapter 8 provides a synthesis of the main findings of this study and management recommendations aimed at the effective and sustainable management of the buffalo population on Tswalu are made.

CHAPTER 2

THE AFRICAN BUFFALO

Historical background

From the earliest years, various hunters and explorers have endeavoured to capture the essence and nature of the African or Cape buffalo *Syncerus caffer caffer* in their journals (Mloszewski 1983; Prins 1996) with descriptions dating as far back as 1627 (Skead 1980). However, this animal was only formally described in 1779 by the Swedish naturalist Sparrman, from a specimen shot near Port Elizabeth, South Africa (Skinner & Smithers 1990; Grubb 1999). Few references to the African buffalo were made in diaries and journals in the 17^{th} and 18^{th} century, and it was only during the second half of the 19^{th} century that the first useful accounts on the buffalo appeared, most of them regarding its distribution (Mloszewski 1983). Hunters' tales, especially those about wounded buffalo, gave rise to the cliché surrounding the African buffalo as being a fierce and dangerous animal. In this way the knowledge that accumulated only involved buffalo that had faced the armed hunter, being biased towards behaviour just before or after the animal had been shot. Little was ever mentioned about herds of buffalo grazing green fields like gazelle, or herds that would flee at the mere smell of an approaching human (Sinclair 1977). A dictionary of the late 1840s described the African buffalo as a savage and dangerous animal (Goodrich 1849 In: Prins 1996) and by 1875 it was still regarded as a savage and formidable brute that would fiercely attack hunters and travellers (Goodrich 1875 In: Prins 1996).

The African buffalo was prized as one of the few adversaries that had to be vanquished by European man in his struggle to conquer the dark continent of Africa. Many such hunting stories were implausible, while others aimed to expose the brutality of the buffalo. Williams (1859 In: Prins 1996) described the extreme ferocity of buffalo when he thus recalled a hunt: " A British officer was pursued by a wounded buffalo and took refuge amidst the branches of a low, stunted tree. The infuriated animal, though unable to reach him with its horns, effectually used its tongue as a weapon of offence, with whose rough, grating surface – by licking the legs and the thighs of the unfortunate sufferer – it so completely denuded them from flesh, that although at last rescued from so dreadful a situation, the colonel only lingered on for a few days, when he died in the most excruciating agonies".

By the turn of the 19^{th} century, naturalists gradually changed the commonly held view on the buffalo when R. Lydekker initiated a new trend in buffalo systematics (1898 In: Mloszewski 1983). Another naturalist and one of Africa's first wildlife photographers, Radclyffe Dugmore, depicted buffalo in his books written in the early 1900's as being relaxed in a herd, tending to flee rather than attack, just as most animals do. M. Johnson, another famous photographer of the late 1920s, described the buffalo to be "like a man who is always being stampeded by the latest rumour. He is continually and unnecessarily on the alert, not sensibly… but in a silly, apprehensive way that must take much of the joy out of his life" (1928 In: Prins 1996).

Taxonomy

Originally named *Bos caffer* in 1758 by Linnaeus (Du Toit 2001), the generic name *Syncerus* was introduced in 1847 by B.H. Hodgson and has now displaced all the earlier generic names such as *Bos* and *Bubalus*. *Syncerus* is an African endemic genus, originating from either the Ethiopian highlands or the great plains of East Africa during the late Pleistocene. Since 1779, a staggering 92 zoological names have been given to the African buffalo, with many local variations being thought to be different species, and with as many as 43 subspecies (Mloszewski 1983; Du Toit 2001).

Showing the greatest range of morphological variation of all herbivore species in Africa, the buffalo can be divided into two definite subspecies (Skinner & Smithers 1990; Prins 1996), ranging from the lightly built, reddish, small-horned forest buffalo *Syncerus caffer nanus* to the heavily built, darker, big-horned savanna buffalo *Syncerus caffer caffer* (Ansell 1972; Mloszewski 1983; Skinner & Smithers 1990; Prins 1996; Stuart & Stuart 2000; Du Toit 2001; Furstenburg 2003). Where the ranges of these subspecies overlap, various intermediate forms between them are found, and taxonomists have debated and regarded these intermediates either to be *Syncerus caffer aequinoctialis* (Ansell 1972; Mloszewski 1983; Du Toit 2001, 2005; Furstenburg 2003) or *Syncerus caffer brachyceros* (Ansell 1972; Mloszewski 1983; Prins 1996; Du Toit 2005).

Geographical distribution

The buffalo formerly occurred over most of Africa, with isolated populations in eastern Guinea Bissau to southwest Somalia on the east coast. From north to south their distribution stretched from the Niger basin southward to Cape Hangklip in South Africa. They originally did not occur in a few places in the interior of Africa. Parts of the Kalahari Desert in Botswana and South Africa were also uninhabited (Shortridge 1934; Du Plessis 1969; Ansell 1972; Skinner & Smithers 1990; Winterbach 1999; Furstenburg 2003). However, Campbell & Child (1971) indicated buffalo to be present in the northern parts of the Central Kalahari Game Reserve in Botswana during the early 20th century. Shortridge (1934) refers to a buffalo being shot near Kuruman in 1813. Unfortunately, during 1888 rinderpest was introduced by traction oxen from either Arabia or India to Eritria during a military expedition, and rapidly spread through Africa, nearly decimating the buffalo population all over Africa (Shortridge 1934; Sinclair 1977; Meltzer 1996; Prins 1996; Winterbach 1999; Furstenburg 2003). Buffalo were said to be the most susceptible to the disease and were more affected than any other species in Africa (De Vos & Bengis 1992). Consequently an estimated 10 000 buffalo died for every one that survived during the rinderpest epizootic that lasted from 1888 to 1899 (Estes 1997).

The correct historical distribution of the buffalo in South Africa is debatable due to exaggerations by early chroniclers, giving rise to inaccurate translations, confusion in terminology and thus places names, which might have been used to indicate animal distribution. Although it is widely believed that buffalo occurred in and around Cape Town dating as far back as Van Riebeeck's time, no reliable records can be found of this (Skead 1980). The buffalo sighting recorded closest to Cape Town was in 1777 at Cape Hangklip (Du Plessis 1969; Skead 1980). Numerous references were made to buffalo in the Sundays River Valley (Shortridge 1934; Honacki, Kinman & Koeppl 1982), the Cape Peninsula (Shortridge 1934; Skinner & Smithers 1990; Derwent 2001), from George and Knysna eastwards including Tsitsikamma (Shortridge 1934; Skead 1980) and Plettenberg Bay (Du Plessis 1969; Skead 1980). Unfortunately, the last buffalo in the Tsitsikamma area was shot near Blaauwkrantz in 1883 (Skead 1980). Figure 1 gives an overview of the historical distribution of the buffalo in South Africa based on Shortridge (1934), Du Plessis (1969), Campbell & Child (1971), Skead (1980), Skinner & Smithers (1990), Rowe-Rowe (1991), Rowe-Rowe & Taylor (1996), and Plug & Badenhorst (2001).

Historically, buffalo never occurred in the arid areas of South Africa, including most of the southern Kalahari (Ansell 1972; Sinclair 1977) and the Karoo (Ansell 1972; Ebedes 1996; Plug & Badenhorst 2001). They were absent from the central part of the country including the Free State grasslands, Gauteng, western Mpumalanga and the southeastern and southwestern parts of the North West province (Shortridge 1934; Du Plessis 1969; Ebedes 1996; Furstenburg 2003). Anderson (1998b) noted that early travellers recorded seeing buffalo in the eastern parts of the southern Kalahari close to Kuruman, whilst Campbell & Child (1971) mentioned buffalo were observed along the Nossob River as far south as Twee-Rivieren and Bokspits during the late 19th century. Although buffalo have been observed in the southeastern Kalahari during the previous century, it is doubtful whether they occurred for long periods in the areas west of the Korannaberg Mountains, the area where Tswalu is situated and where the current study was done. Figure 2 illustrates the historical buffalo distribution in the Northern Cape province with regard to the location of Tswalu. It is based on reports by Shortridge (1934), Du Plessis (1969), Campbell & Child (1971), Skead (1980), and Plug & Badenhorst (2001).

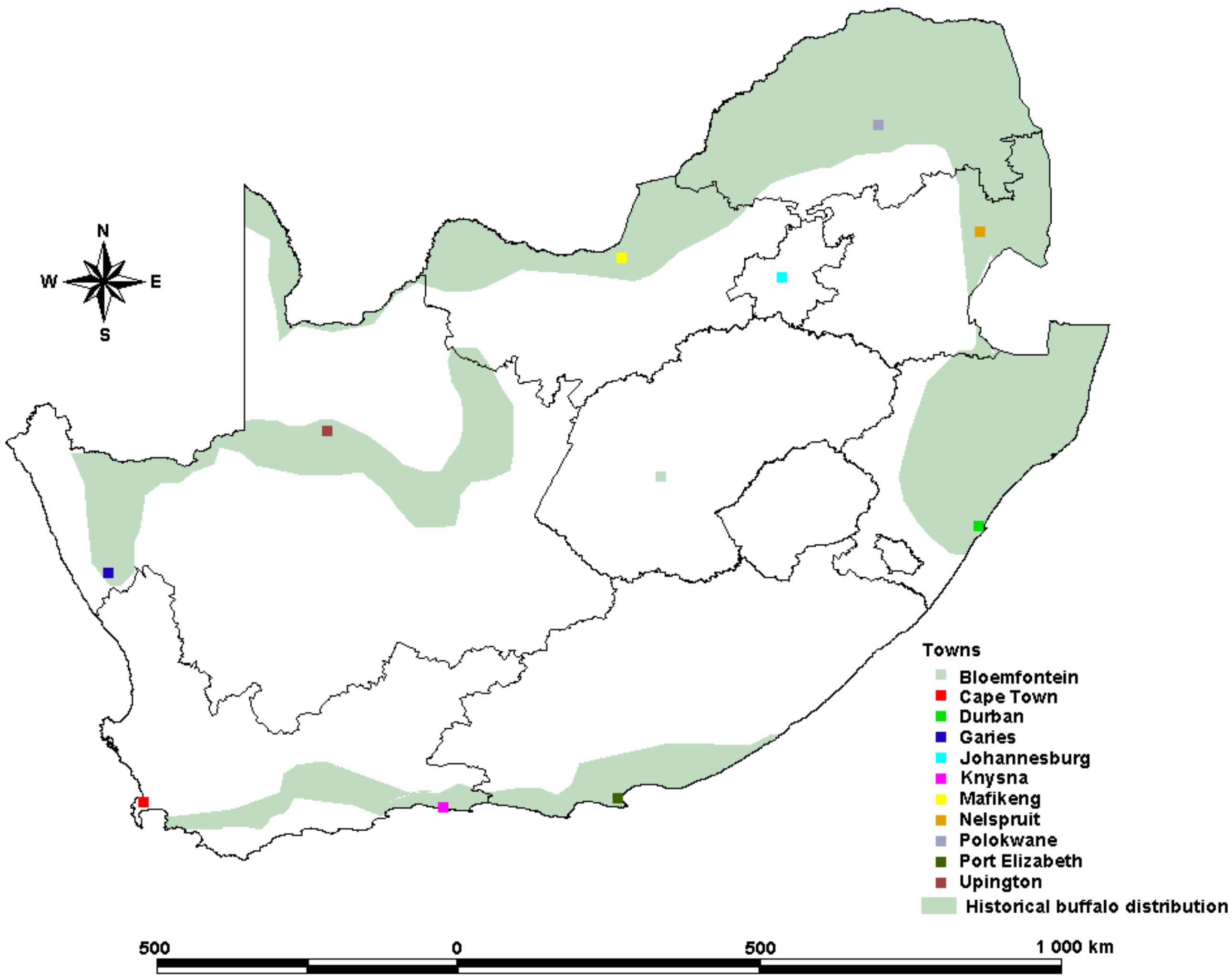


Figure 1: Historical distribution of the buffalo in South Africa as based on Shortridge (1934), Du Plessis (1969), Campbell & Child (1971), Skead (1980), Skinner & Smithers (1990), Rowe-Rowe (1991), Rowe-Rowe & Taylor (1996) and Plug & Badenhorst (2001).

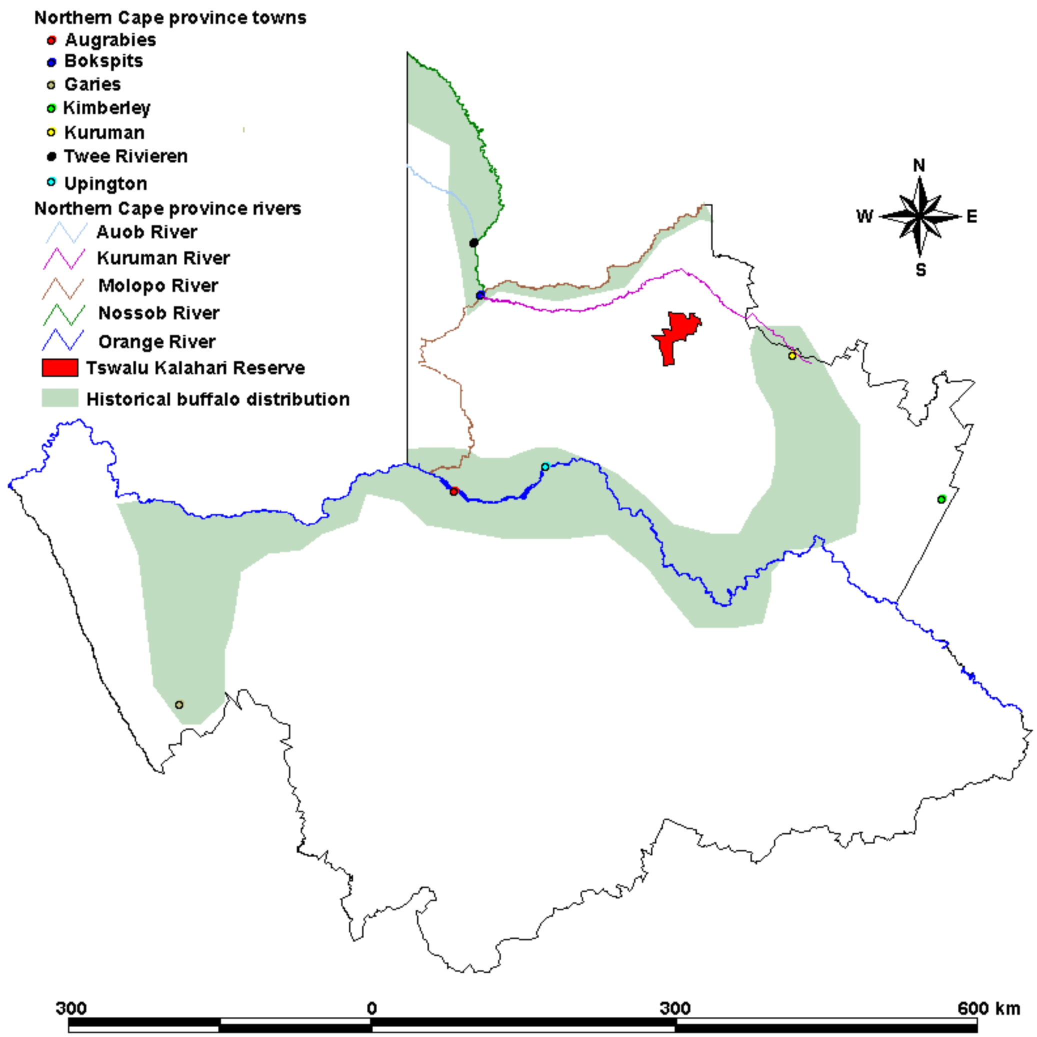


Figure 2: Historical distribution of the buffalo in the Northern Cape province of South Africa in relation to Tswalu Kalahari Reserve. Based on Shortridge (1934), Du Plessis (1969), Campbell & Child (1971), Skead (1980) and Plug & Badenhorst (2001).

Therefore, buffalo occurrence in this area might be limited to occasional visits during migrations along the Nossob, Molopo and Kuruman Rivers.

Habitat

Buffalo were once the most ubiquitous of all large herbivores in Africa (Grimsdell 1969; Furstenburg 2003), except for Burchell's zebra *Equus burchellii* and the red hartebeest *Alcelaphus buselaphus caama*. They were also the most successful species in Africa with regard to geographical range, abundance and biomass (Sinclair 1977; Prins 1996; Estes 1997; Winterbach 1999; Plug & Badenhorst 2001). Buffalo occurred in habitats ranging from dense lowland forest, montane forest, moist and dry woodlands, *Acacia* savannas, to the plains of East Africa (Sinclair 1977; Prins 1996; Estes 1997; Furstenburg 2003). Mention was made of buffalo in the arid areas of the Kalahari in Botswana up to 1895. All the latter sightings, however, can be associated with rivers or springs for water provision and reed beds for protection (Campbell & Child 1971). More generally, buffalo occurred wherever an abundant supply of water was found (Grimsdell 1969), and it is suggested that they only occur in regions with a mean annual rainfall exceeding 250 mm (Shortridge 1934; Sinclair 1977; Krüger 1996). They can tolerate altitudes of > 4000 m where frost is commonly experienced, while in other regions they tolerate high temperatures accompanied by high humidity of the air (Sinclair 1977; Estes 1997; Winterbach 1999). On Mount Kenya, a frozen buffalo carcass was found near a glacier, 4800 m above sea level (Ross 1911 In: Sinclair 1977).

Significance

While the conservation status of buffalo can be classified as satisfactory with no immediate threat of extinction (Friedmann & Daly 2004), the number of them occurring in large, free-ranging populations in southern Africa declined by more than 60% before 1999 (Winterbach 1999). Reasons for this recent decline in numbers include livestock diseases such as bovine tuberculosis, drought, overstocking of wildlife ranches, poaching, strict veterinary regulations and a decline in range because of the ever-growing human population resulting in fencing, ploughing and felling (Campbell & Child 1971; Prins 1996; Winterbach 1999). The overall result is less suitable habitat and a loss of genetic diversity (Sinclair 1977; Prins 1996; Winterbach 1999). Hunting and meat production have also played a significant role in the decline in buffalo numbers, with buffalo in Mozambique being decimated because of the need for meat for the rural communities (Prins 1996). However, with appropriate education of the local communities, wise sustainable utilisation of this natural resource could be achieved. For example, it could be domesticated and then utilised as a natural source of food and fuel like the Asian buffalo *Bubalus bubalis* in the Far East, Europe and Australia (Condy 1980). The African buffalo could also be trained to assist farmers in ploughing, carting and delivering (Condy 1980), or buffalo-based food products could be marketed such as cheese (Grasso, Napolitano, De Rosa, Quarantelli, Serpe & Bordi 1999), milk and meat. Hoffman, Muller, Schutte & Crafford (2004) found that wildlife meat generally is of better quality than beef, lamb or pork with a lower fat content and added health benefits (Ebedes & Meyer 2002).

The African buffalo is one of the Big Seven species of ecotourism and one of the Big Five species of hunting. The buffalo is sought after in trophy hunting (Gandy & Reilly 2004), and consequently its economic value is enormous. Although providing the ultimate hunt, the African buffalo is only dangerous when wounded, and it will more often flee from humans rather than attack spontaneously when not wounded (Sinclair 1977; Prins 1996). Because of its reputation as a killer animal, many tourists would rather look at buffalo from a vehicle than track it for the ultimate hunt. Therefore, the buffalo fulfils an important tourism role in the African bush, especially in southern Africa. The buffalo has also attained an enormous commercial value depending on its disease and reproductive status (De Vos & Bengis 1992). Individual buffaloes that are free of bovine tuberculosis, foot-and-mouth disease and corridor disease can easily attain prices of up to R250 000 per animal (Hume 2004, *pers. comm.*[1]). The commercial value of a buffalo has increased by 29.7% since 1994 (Van der Merwe, Saayman & Krugell 2004). Ecologically, the buffalo is equally important by opening up habitats that are preferred by short-grass grazers (De Vos & Bengis 1992; Winterbach 1999).

Past research

Various detailed studies have been done on the buffalo, and a list of such references can be found in Penzhorn (1996). Grimsdell (1969) described the ecology of the buffalo in Uganda with emphasis on reproduction, age structure and grazing patterns. From 1966 to 1972, Sinclair (1977) did the first comprehensive study on the social behaviour and nutrition of the buffalo in the Serengeti National Park, Lake Manyara Park and the Arusha Park in Tanzania. Mloszewski (1983) worked in East, Central and West Africa between 1964 and 1978 to improve our understanding of the social organization of this species under wilderness conditions, and especially concentrated on its nutrition and social behaviour. Prins (1996) did some pioneering work on the social organization and nutrition of buffalo in northern Tanzania. Vesey-Fitzgerald (1969, 1974) assessed the habitat utilisation and grazing patterns of buffalo in Tanzania. Its feeding ecology was investigated in Uganda by Field (1976), and in Zaire by Mugangu, Hunter & Gilbert (1995). Eltringham & Woodford (1973) recorded buffalo numbers and distribution in Uganda. Buffalo range use, movements and feeding behaviour were studied in Kenya by

[1] Mr. J. Hume, Buffalo breeder, Mauricedale, Malelane, 1320, South Africa.

Leuthold (1972), and in Zimbabwe by Conybeare (1980). Taolo (2003) studied the population ecology and movement patterns of buffalo in the Chobe National Park, Botswana, and Halley & Mari (2004) investigated the social affiliation of buffalo bulls in the same Park.

Buffalo in South Africa were studied by Pienaar (1969), who revised various aspects of buffalo developmental ecology in the Kruger National Park. De Graaff, Schulz & Van der Walt (1973) investigated the rumen contents of buffalo in the Addo Elephant National Park, and Landman & Kerley (2001) investigated the diet of buffalo in the same Park. In the Kruger National Park, Van Hoven (1980) looked at rumen fermentation and methane production in buffalo, while Funston (1992) studied the spatial, temporal and social organization of the buffalo in the Sabie Sand Game Reserve, South Africa for a 14-month period.

During an 11-month period, Winterbach (1999) studied a herd of buffalo in the Free State province of South Africa to determine the habitat and activity patterns of buffalo outside their historical distribution. Perrin & Brereton-Stiles (1999) studied resource partitioning among buffalo and the white rhinoceros *Ceratotherium simum* in the Hluhluwe-Umfolozi Game Reserve, while Knetchtel (Van Hoven 2003 *pers. comm.*[2]) has completed a long-term study on the ontogeny of buffalo in the Klaserie Private Nature Reserve. Macandza, Owen-Smith & Cross (2004) reported on forage selection in the Kruger National Park. One recent published work on the buffalo in South Africa is that of Cross, Lloyd-Smith & Getz (2005) who formulated a fission decision index that could assist in an improved understanding of the fission-fusion phenomenon of buffalo in the Kruger National Park.

[2] Prof. W. van Hoven, Centre for Wildlife Management, University of Pretoria, Pretoria, 0002, South Africa

CHAPTER 3

STUDY AREA

Introduction

This study was conducted in the Korannaberg section of Tswalu Kalahari Reserve (hereafter referred to as Tswalu) in the Northern Cape province of South Africa (Fig. 3). Situated in the southeastern Kalahari region, Tswalu was founded in 1995 by Mr Stephen Boler, an English entrepreneur. The name Tswalu means "new beginning" in the Tswana language. Formerly, Tswalu consisted of 34 farms that were mostly utilised as cattle farms, the majority of which Mr Boler bought between 1995 and 1997. He removed 7 000 head of cattle; game-fenced the boundary of these farms, demolished the existing farmhouses and cleared away most of the existing internal infrastructure. During this period, one of the largest wildlife translocations in South Africa took place with about 5 000 head of wildlife being released on Tswalu. Mr Boler dedicated himself to one of the largest conservation projects in the Kalahari, with the ultimate dream of returning this part of the Kalahari to its original state, but he sadly passed away in late 1998 (Begg 1997). The Oppenheimer family purchased the reserve in 1999.

Currently, Tswalu is the largest privately owned nature reserve in South Africa and covers a surface area of approximately 104 000 ha (1 040 km^2). However, only 94 200 ha is currently utilised as a wildlife area, the remainder of the property being rented out to neighbours for farming purposes. The 94 200 ha wildlife reserve is divided into four sections: Tsamma, Korannaberg, Bluesky and Lekgaba (Fig. 3).

The study area comprises the Korannaberg section in which the buffalo occur (Fig. 3). No buffalo occur in the Lekgaba section due to the presence of large predators such as the Kalahari lion *Panthera leo* there, and the potentially high economic loss if a buffalo were killed by a predator. Previously buffalo were present in the Tsamma section but these animals were moved to the Korannaberg section, currently making the latter the only one on Tswalu where buffalo roam freely. According to the annual wildlife count of 2004, the reserve now carries 9 248 head of wildlife, of which the 83 buffalo form 0.9%.

Tswalu supports ecotourism by providing a unique Kalahari experience with two luxurious, elegant African lodges overlooking the Kalahari dune veld. It also contributes to conservation by annually selling live wildlife and protecting the critically endangered desert dwelling black rhinoceros *Diceros bicornis bicornis*, the white rhinoceros and the Kalahari lion.

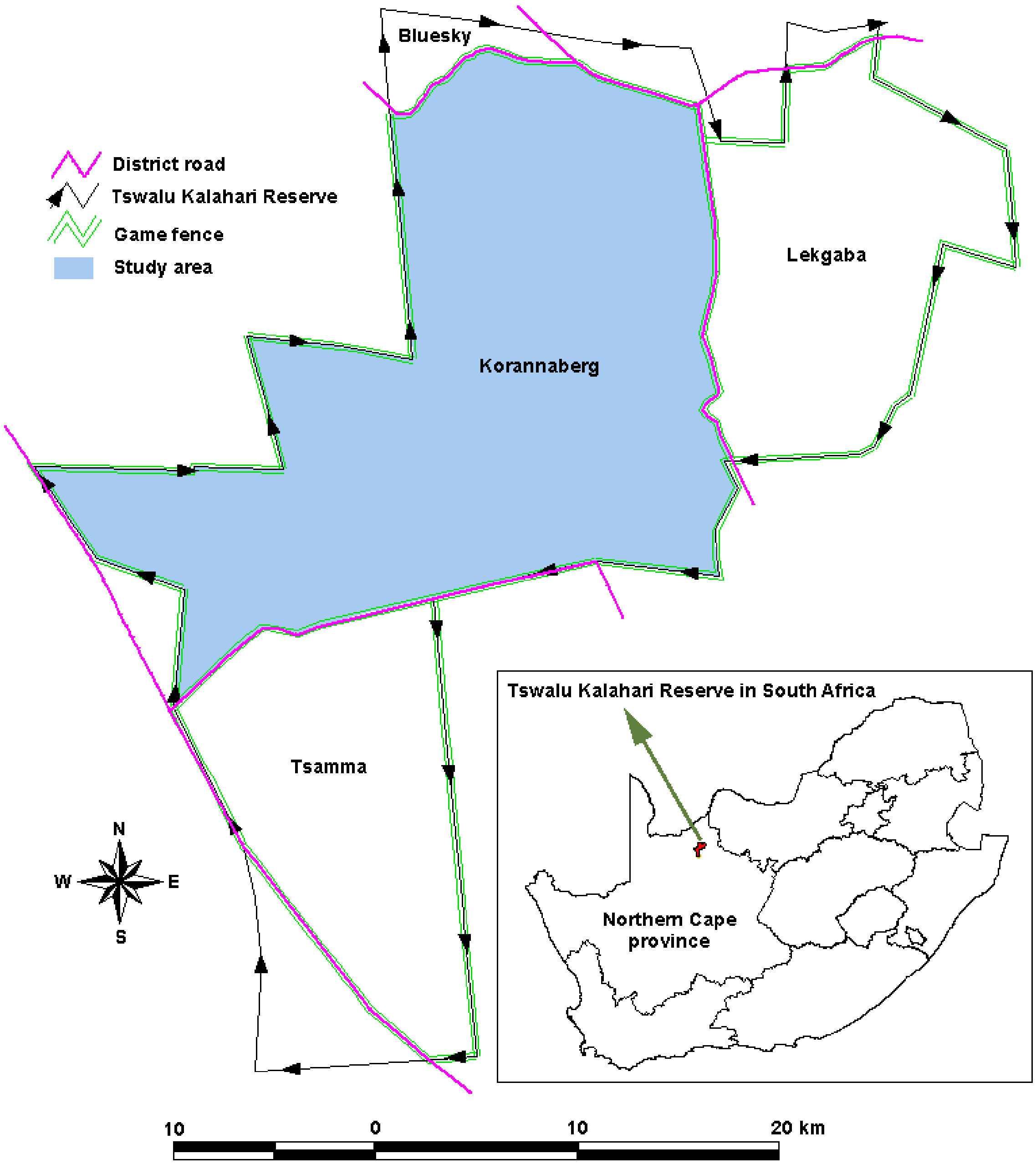


Figure 3: The study area within Tswalu Kalahari Reserve in the Northern Cape province of South Africa.

Location

The Kalahari sands stretch for some 2.5 million km² from the Orange River in South Africa northwards until it reaches the Congo (Leistner 1967; Knight, Joyce & Dennis 1997; Smit 2000), and are characterized by a flat and waterless terrain (Du Toit 1927). Tswalu lies between latitudes 27°04' and 27°44' S and longitudes 22°10' and 22°36' E in the southeastern portion of this vast, continuous surface of sand.

The nearest small settlement to Tswalu is Van Zylsrus to the north and Deben to the south, with the nearest large town being Kuruman to the east. Tswalu lies approximately 700 km west of Johannesburg, and 1 200 km northeast of Cape Town. The Korannaberg section of Tswalu is approximately 54 079 ha (541 km²) in size, and consists of parts of 21 former farms.

Physiognomy

Tswalu has an altitudinal range from 1 020 m above sea level in the west to 1 568 m in the southeastern corner. Van Rooyen (1999) described the terrain morphology of Tswalu as sandy plains, parallel dunes with dune streets interspersed with lowlands, a few pans in the west and some outcropping hills in the east. The Korannaberg Mountain Range is a dominant feature of the landscape in the eastern Lekgaba section. The dunes on Tswalu have a predominant north-south orientation, consistent with the dominant wind direction. Irregularly shaped dunes are also encountered in the far north, which is possibly the result of a wind funnel effect produced by the Korannaberg Mountain Range. The parallel dunes are steeper on the western than the eastern slopes. Individual dunes on Tswalu can vary in length from 400 m to 15 km, the latter usually forming a continuous but branched dune.

Drainage

The Kuruman River, situated 50 km east of Tswalu, has a potential water delivery of 20 million litres per day at "the eye" in Kuruman (Leistner 1967; Anderson 1998a) making it the closest major river to Tswalu, but it does not reach the reserve. Tswalu is dependent upon three sources of water. The first is the eastern Kalahari pipeline that originates at the Orange River and runs through the reserve from south to north and is accessible through drain valves. The second is underground water that is sourced through boreholes and accumulated in reservoirs. The third is natural rainwater that is the most unreliable and erratic source of water in the Kalahari. There are approximately 44 waterholes on the reserve (Loots 2002), most of which are man-made and receive water from boreholes, the pipeline or the occasional rainwater runoff. A few pans are also present, consisting of more or less rounded, shallow depressions varying in diameter from 30 to 1 000 m with a clayey bottom to prevent drainage after rain. The pans in the west of Tswalu are natural water points. One of them is filled with water from the pipeline in times of water scarcity, but the rest are filled by rainwater alone and are thus dry for the major part of the year. Local, ephemeral watercourses drain the mountains in different directions during times of high rainfall.

Geology

The Kalahari system originated some 65 million years ago during the Cenozoic era (Knight *et al.* 1997). The Olifantshoek Supergroup is represented by the mountains and hills of the Korannaberg and Langeberg Mountains and is dominated by the Matsap Formation from the Volop Group, consisting of subgreywacke, quartzite and conglomerate rocks. The Kalahari Group forms the aeolian plains and dunes and is part of the Gordonia Formation, consisting of limestone rock, silcrete, alluvium deposits and some gravel (Malherbe 1984; Van Rooyen 1999; URL: http://www.agis.agric.za/agisweb.html).

Soil

The Kalahari sands show great diversity in colour, texture, structure, depth and age (Walter 1979; Thomas & Shaw 1991; Van der Walt & Le Riche 1999). Two main soil textures are found, namely coarse and fine textured soils (Leistner 1967). The coarse textured soils are found over 90% of the surface of the Kalahari, and consist mainly of quartzite and are poor in minerals and clay (Leistner & Werger 1973; Skarpe 1986). These sands can range from white as is found in the pans, to the deep red colour found on the dune systems and undulating plains (Leistner 1967). The red colour of the sand is due to a thin ferric oxide layer (Leistner & Werger 1973). Variation in the colour of the sand is a result of the reduction of the ferric oxide by leaching or mechanical abrasion (Van der Walt & Le Riche 1999).

The fine-textured soils are found in the riverbeds and pans and are high in minerals, organic material and clay (Leistner 1967). Usually white or pink in colour, these finer grains of sand are sometimes coated with lime (Leistner 1967; Leistner & Werger 1973). These sands have poor drainage and are virtually impenetrable, with associated high water losses due to evapotranspiration (Leistner 1967; Skarpe 1986). Soil temperatures at 300 mm depth can vary between 32° and 11° C, with open sand surface temperatures reaching 70° C (Leistner 1967).

The soil of most of the Kalahari region, but especially that of the dunes and plains, represent the *Oxisol* soil order (Van der Watt & Van Rooyen 1995). The sand on Tswalu possibly falls into one of the following soil forms: Hutton, Oakleaf, Clovelly, Katspruit, Dundee, Mispah, Fernwood or Longlands (URL: http://www.agis.agric.za/agisweb.html). The four soil pattern types present on Tswalu according to Van Rooyen (1999) and URL: http://www.agis.agric.za/agisweb.html are:

- Red-yellow apedal, poorly structured, freely drained soil with a high base status and being deeper than 300 mm, consisting mainly of dunes.
- Red-yellow apedal, poorly structured, freely drained, red and yellow soil with a high base status and consisting of more than 15% clay.
- Red-yellow apedal, poorly structured, freely drained soil with a high base status and being deeper than 300 mm, but not consisting of dunes.
- Miscellaneous with rocky areas containing weakly developed, shallow soils.

Climatology

According to Leistner (1967), the Kalahari is situated within the “Horse Latitudes” (25° to 35° S) with arid conditions that are due to a high atmospheric pressure cell, resulting in low rainfall. The Hadley cell of atmospheric circulation dominates the Kalahari, resulting in anticyclonic circulation patterns with generally cloud-free skies (Tyson & Crimp 1998). Five aridity categories have been classified by the United Nations Convention to Combat Desertification. To determine in which category an area falls, the MAP:PET (mean annual precipitation: potential evapotranspiration) ratio must be calculated (Hoffman & Ashwell 2001). The five categories with their MAP:PET ratio are: hyper-arid (< 0.05), arid (0.05-0.2), semi-arid (0.2-0.5), dry sub-humid (0.5-0.65) and humid (> 0.65). According to this ratio, Tswalu (MAP:PET of 0.11) lies in the arid zone. The Kalahari receives approximately 80% of the total possible annual sunshine, the highest annual sunshine duration in South Africa, with February being the cloudiest month (Leistner 1967). Cloud cover during the winter seldom reaches 20% cover (Tyson & Crimp 1998). Annual evapotranspiration is approximately 2 000 mm (Schulze 1997; Tyson & Crimp 1998), with the maximum monthly evapotranspiration of 260 mm during January (Schulze 1997).

Three climatic phases dominate the ecology of the Kalahari: a wet phase where an exceptional amount of rain falls at intervals of 10 to 20 years; an arid phase that characterises extended periods of drought, and a transition phase when the rainfall varies around the annual mean (Van der Walt & Le Riche 1999). Wet and dry periods lasting a few years are a natural phenomenon in the Kalahari (Fourie, De Wet & Page 1987).

During the study period several unusual weather phenomena occurred. Exceptionally high winds combined with wind-blown sand resulted in poor visibility on Tswalu during August 2003; hail occurred in April 2004; and frost occurred in June 2004. The Van Zylsrus Weather Station

(Station number: 0427083A3), the closest to Tswalu and situated approximately 50 km north of northwest of Tswalu, was used for the climatic data in the present study (URL: http://www. weathersa.co.za).

The current man-induced global climate change could result in a warmer and drier Kalahari region (Tyson & Crimp 1998; Mason & Tyson 2000). Temperatures are predicted to increase by 2.0º to 2.5º C in both summer and winter, and precipitation may decrease by approximately 10% during the rainfall season (Tyson & Crimp 1998).

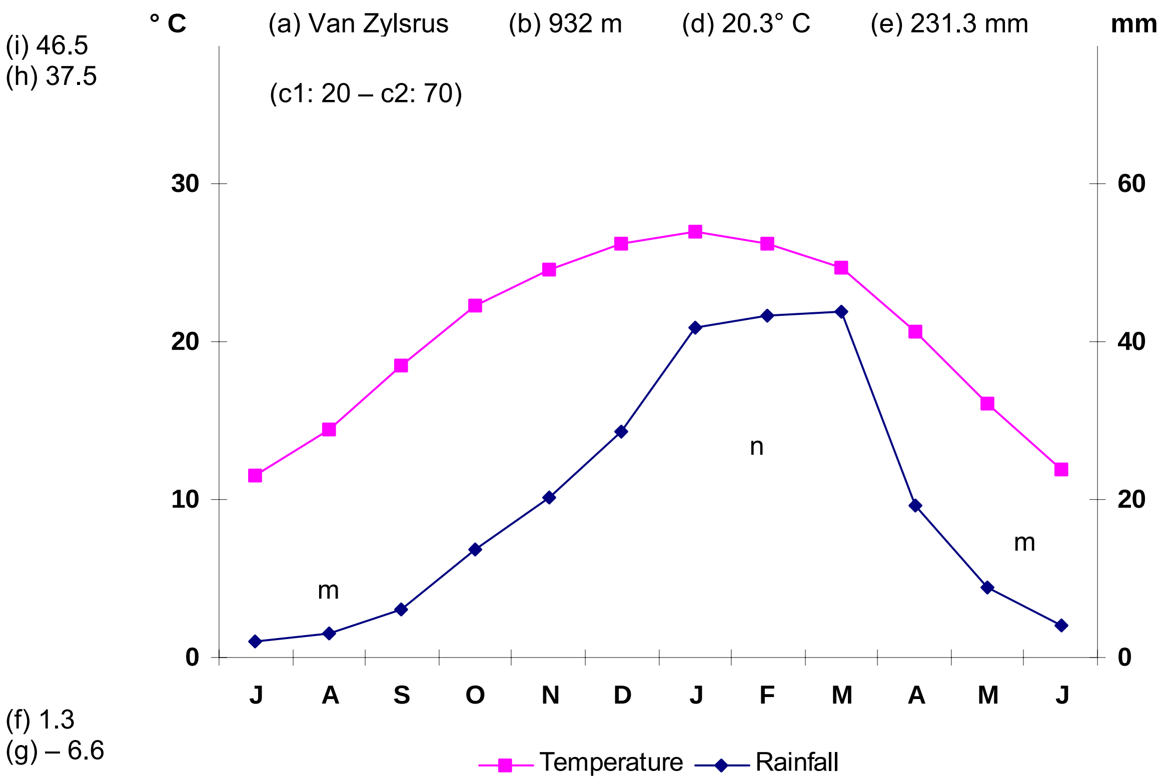
Temperature

The Kalahari is known to be the warmest area in South Africa during summer, but it has cold winters (Leistner & Werger 1973; Lubbinge 1998; Van Rooyen 2001) with considerable daily and seasonal temperature fluctuations due to continuous insulation by day followed by rapid heat radiation at night (Leistner 1967). Significant variation occurs between day and night temperatures (Debenham 1952), with differences of up to 20.1º C occurring in a 12-hour cycle. Cold snaps and heat waves occur when the temperature suddenly drops or increases by more than 5%, and usually last 3 to 4 days (Tyson & Crimp 1998). The warmest month is January with a mean maximum of 37.5º C and an absolute maximum of 46.5º C, while the coldest one is July with a mean minimum of 1.3º C and an absolute minimum of -6.6º C (Fig. 4).

For the purpose of this study two seasons were defined; a warm, wet season was defined as months where the monthly mean was higher than 20.5º C (October to April), while the cold, dry season included months with a monthly mean minimum temperature of < 10º C (May to September). The long-term annual mean is 20.3º C, with an annual mean maximum of 29.5º C and a minimum of 11.1º C. The long-term mean temperature for the warm, wet season is 26.1º C and for the cold, dry season is 12.7º C.

Rainfall

Rainfall in the Kalahari is erratic and low, occurring as localised but short, violent convectional storms (Leistner 1967), usually in the late afternoon and early evening (Tyson & Crimp 1998). The area where Tswalu is situated receives a mean of 3 lightning strikes/km^2/year (Van Zyl 2003). Rainfall in the Tswalu region is associated with tropical easterly airflow resulting in a decreasing isohyetal gradient from east to west (Tyson & Crimp 1998). Tswalu lies between the 200 and 300 mm isohyets (Fourie & Visagie 1985). Situated in the summer rainfall area, the



a = Weather station

b = Altitude

c1 = Duration of temperature data recording

c2 = Duration of rainfall data recording

d = Mean annual temperature

e = Mean annual long-term rainfall

f = Mean daily minimum temperature for coldest month

g = Absolute minimum temperature

h = Mean daily maximum temperature for warmest month

i = Absolute maximum temperature

m = Dry period

n = Wet period

Figure 4: Climate diagram for temperature (° C) and rainfall (mm) as determined from data obtained from the Van Zylsrus Weather Station, following Walter's convention (Walter 1979).

majority of the precipitation falls from November to April (Fig. 4). Rainfall on Tswalu usually comes from either the northeast or the west. Data over the past 70 years from the Van Zylsrus Weather Station show the mean annual rainfall for the area to be 231.3 mm (Fig. 5), ranging from 46.4 mm (1992) to 714.1 mm (1974). Rainfall is unpredictable, with some years receiving rain for only four of the possible 12 months. Prolonged periods of drought are quite common for this area and the worst drought recorded was a 7-year drought in the Kuruman area lasting from 1820 to 1827 (Endfield & Nash 2002). During the 20^{th} century, an 18- to 20-year oscillation dominated rainfall in South Africa, with wet and dry spells lasting approximately 9 years each (Tyson & Crimp 1998). Rainfall at Van Zylsrus reaches a maximum in March (mean: 43.8 mm) and a minimum in July (mean: 1.9 mm) (Fig. 4).

Rainfall data for Tswalu, gathered from approximately 37 regularly checked rain gauges, are available since July 1997. The mean annual rainfall on Tswalu for the 8 years since 1997 was 253.5 mm, with a range of 151 mm (2003) to 421 mm (1999) (Fig. 6). Data obtained from the Van Zylsrus Weather Station showed that Tswalu received 22.2 mm more rain annually than the Van Zylsrus area. A possible reason for this is the position of Tswalu in the Korannaberg Mountain Range, giving rise to more intense rainfall. The rainfall gradient in the Kalahari transect is from east to west (Tyson & Crimp 1998), with Van Zylsrus situated north of northwest of Tswalu.

Wildlife

Although an arid savanna with a perceived low biodiversity, various different types of wildlife are found on Tswalu, including indigenous and exotic ones. The abundant wildlife types according to the annual count of 2004 were the springbok *Antidorcas marsupialis*, followed by the gemsbok *Oryx gazella gazella*, the red hartebeest, the blue wildebeest *Connochaetes taurinus taurinus*, the greater kudu *Tragelaphus strepsiceros*, and the common eland *Taurotragus oryx oryx*.

Within the Korannaberg section of Tswalu, the buffalo occurs with all the above wildlife. Other animals of high economic value are also present in the Korannaberg section. They include the black rhinoceros, white rhinoceros, roan antelope *Hippotragus equinus equinus*, sable antelope *Hippotragus niger niger* and tsessebe *Damaliscus lunatus lunatus*. Other herbivores present include the blesbok *Damaliscus pygargus phillipsi*, black wildebeest *Connochaetes gnou*, impala *Aepyceros melampus*, steenbok *Raphicerus campestris*, grey duiker *Sylvicapra grimmia*, giraffe *Giraffa camelopardalis giraffa*, nyala *Tragelaphus angasii*, waterbuck *Kobus ellipsiprymnus*, Burchell's zebra, Cape mountain zebra *Equus zebra zebra*, mountain reedbuck *Redunca fulvorufula*, warthog *Phacochoerus africanus* and savanna baboon *Papio hamadryas ursinus*.

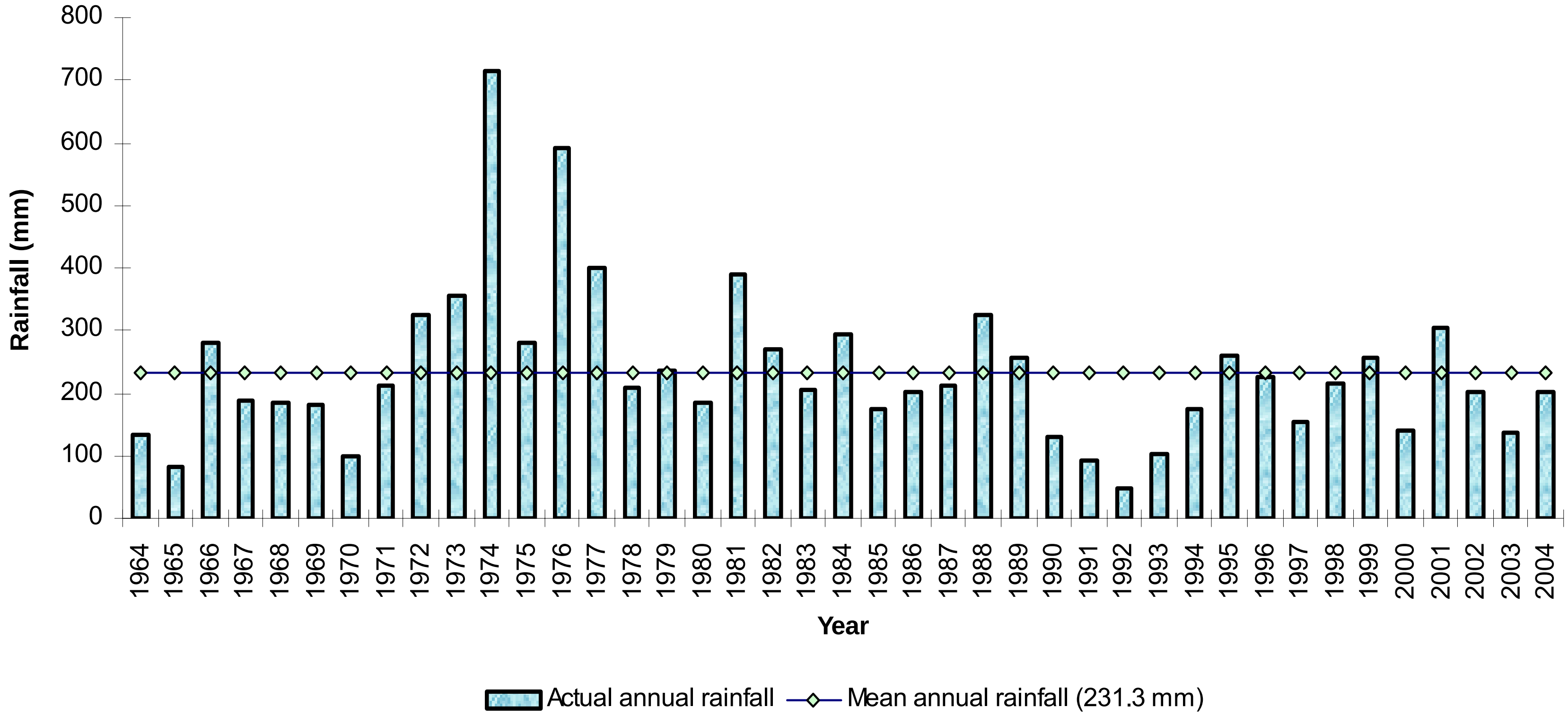


Figure 5: Actual and mean annual rainfall for the Van Zylsrus Weather Station, closest to Tswalu Kalahari Reserve in the Northern Cape province of South Africa, from 1964 to 2004.

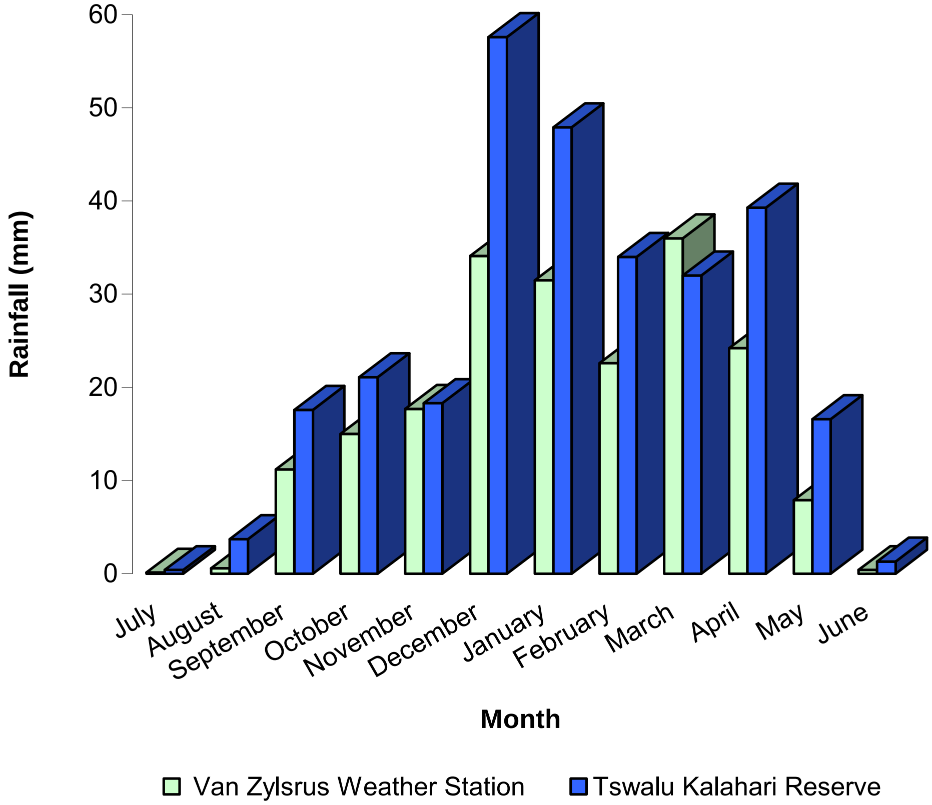


Figure 6: A comparison of the mean monthly rainfall at Tswalu Kalahari Reserve with that of the Van Zylsrus Weather Station from 1997 to 2004.

Also present on Tswalu are mammals such as the aardvark *Orycteropus afer*, scrub hare *Lepus saxatilis*, Cape hare *Lepus capensis*, springhare *Pedetes capensis*, ground squirrel *Xerus inauris* and southern African porcupine *Hystrix africaeaustralis*. Carnivores and scavengers include the Cape fox *Vulpes chama*, bat-eared fox *Otocyon megalotis*, black-backed jackal *Canis mesomelas*, genet *Genetta genetta*, African wildcat *Felis silvestris*, yellow mongoose *Cynictis penicillata*, aardwolf *Proteles cristatus*, cheetah *Acinonyx jubatus*, Kalahari lion, wild dog *Lycaon pictus*, striped polecat *Ictonyx striatus* and suricate *Suricata suricatta*. However, the Kalahari lion and wild dog are absent from the Korannaberg section.

Various rodent, bat, reptile, insect and bird species are also present on the reserve but they are beyond the scope of this study and a detailed list of them is not relevant. Scientific names to all the species were derived from Skinner & Smithers (1990), Grubb (1999) and Friedmann & Daly (2004).

Vegetation

According to Acocks's (1988) classification the vegetation of Tswalu is part of the Kalahari Thornveld. A more recent classification (Low & Rebelo 1996) distinguished several vegetation types within the boundaries of Tswalu that include the Shrubby Kalahari Dune Bushveld, Kalahari Plains Thorn Bushveld and the Kalahari Mountain Bushveld.

Van Rooyen (1999) did a comprehensive phytosociological study and classified the vegetation of Tswalu into three main vegetation types. He referred to vegetation types as plant communities that were subdivided into a further seven subcommunities, of which some were further subdivided into variants and subvariants. The three main plant communities are: The *Acacia erioloba – Eragrostis lehmanniana* open shrubveld community, the *Croton gratissimus – Digitaria polyphylla* hills and mountains community, and the *Pentzia incana – Enneapogon desvauxii* panveld community. Van Rooyen (1999) identified 267 plant species on the reserve, including amongst others 45 grass species, six tree species and 19 shrub species.

Van Rooyen (1999) also compiled a vegetation map (Fig. 7) of Tswalu based on his phytosociological study. Because some of the subvariants are closely related, it is difficult to distinguish between them in the veld, making plotting of individual subvariants difficult. As a result the vegetation map contains only 12 vegetation mapping units. Table 1 is a summary of the mapped units (hereafter referred to as vegetation units) in the Korannaberg section. It also shows their respective sizes in the Korannaberg section, as determined with the Geographic Information System (GIS) package, ArcView 3.2 (ESRI Inc. 1998).

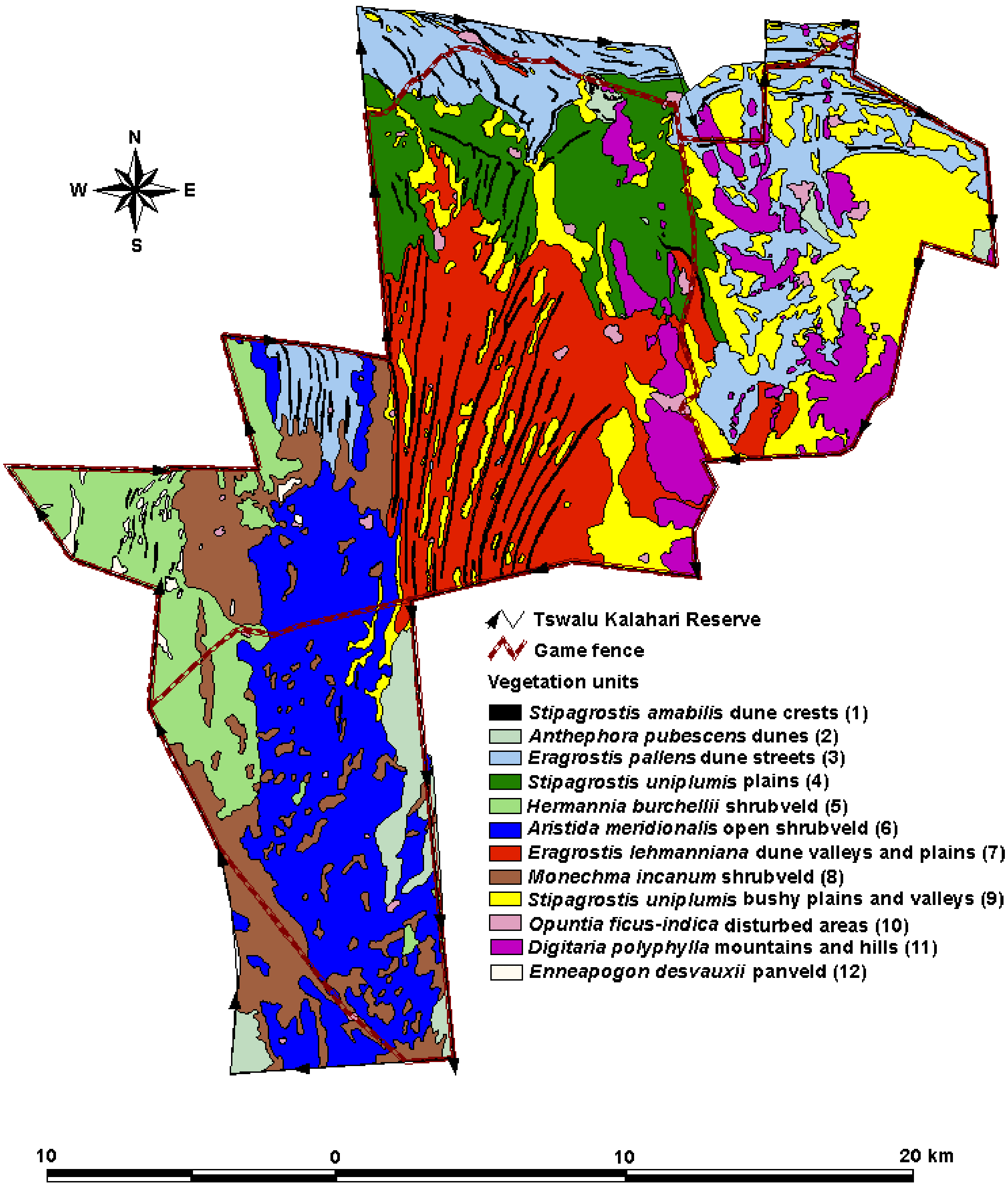


Figure 7: Vegetation map of Tswalu Kalahari Reserve in the Northern Cape province of South Africa, based on Van Rooyen (1999). Full community names are given in Table 1.

Table 1: The respective sizes in ha of the vegetation units of the Korannaberg management section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa. Unit number refers to the vegetation unit number, as mapped on Figure 7

UNIT NUMBER	NAME OF PLANT COMMUNITY AS CLASSIFIED BY VAN ROOYEN (1999)	VEGETATION UNIT NAME AS USED IN THIS STUDY (FIG. 7)	SIZE
1	*Terminalia sericea – Stipagrostis amabilis* dune crests	*Stipagrostis amabilis* dune crests	2 052.4
2	*Terminalia sericea – Acacia haematoxylon – Anthephora pubescens* dunes	*Anthephora pubescens* dunes	237.0
3	*Acacia erioloba – Acacia haematoxylon – Eragrostis pallens* dune streets	*Eragrostis pallens* dune streets	1 689.4
4	*Acacia mellifera – Stipagrostis uniplumis* plains and patches	*Stipagrostis uniplumis* plains	8 574.4
5	*Acacia haematoxylon – Centropodia glauca – Hermannia burchellii* shrubveld	*Hermannia burchellii* shrubveld	7 628.8
6	*Acacia haematoxylon – Grewia flava – Aristida meridionalis* open shrubveld	*Aristida meridionalis* open shrubveld	4 358.0
7	*Acacia haematoxylon – Grewia flava – Eragrostis lehmanniana* dune valleys and plains	*Eragrostis lehmanniana* dune valleys and plains	15 998.8
8	*Acacia mellifera – Rhigozum trichotomum – Monechma incanum* shrubveld	*Monechma incanum* shrubveld	4 351.2
9	*Acacia mellifera – Rhigozum trichotomum – Stipagrostis uniplumis* bushy plains and valleys	*Stipagrostis uniplumis* bushy plains and valleys	5 407.2
10	*Prosopis glandulosa – Opuntia ficus-indica* disturbed areas	*Opuntia ficus-indica* disturbed areas	426.0
11	*Croton gratissimus – Digitaria polyphylla* hills and mountains	*Digitaria polyphylla* mountains and hills	2 876.0
12	*Pentzia incana – Enneapogon desvauxii* panveld	*Enneapogon desvauxii* panveld	480.5

According to Van Rooyen (1999) the plant communities of Tswalu consist of:

1. Acacia erioloba – Eragrostis lehmanniana open *shrubveld*

1.1. *Acacia* haematoxylon – *Stipagrostis uniplumis* dunes and open shrubveld (not mapped, Fig. 7)

1.1.1. *Terminalia sericea – Crotalaria spartioides – Eragrostis pallens* dunes (not mapped, Fig. 7)

- *Terminalia sericea – Stipagrostis amabilis* dune crests (Vegetation Unit 1, Fig. 7)
- *Terminalia sericea – Acacia haematoxylon – Anthephora pubescens* dunes (Vegetation Unit 2, Fig. 7)

1.1.2. *Acacia erioloba – Stipagrostis uniplumis* dune streets

- *Acacia erioloba – Acacia haematoxylon – Eragrostis pallens* dune streets (Vegetation Unit 3, Fig. 7)
- *Acacia mellifera – Stipagrostis uniplumis* plains and patches (Vegetation Unit 4, Fig. 7)

1.1.3. *Acacia haematoxylon – Grewia flava – Centropodia glauca* shrubveld

- *Acacia haematoxylon – Centropodia glauca – Hermannia burchellii* shrubveld (Vegetation Unit 5, Fig. 7)
- *Acacia haematoxylon – Grewia flava – Aristida meridionalis* open shrubveld (Vegetation Unit 6, Fig. 7)
- *Acacia haematoxylon – Grewia flava – Eragrostis lehmanniana* dune valleys and plains (Vegetation Unit 7, Fig. 7)

1.2. *Acacia mellifera – Rhigozum trichotomum* plains (not mapped, Fig. 7)

1.2.1. *Acacia mellifera – Rhigozum trichotomum – Monechma incanum* shrubveld (Vegetation Unit 8, Fig. 7)

- *Rhigozum trichotomum – Monechma incanum – Antizoma angustifolia* plains (not mapped, Fig. 7)
- *Rhigozum trichotomum – Monechma incanum – Stipagrostis obtusa* plains (not mapped, Fig. 7)

1.2.2. *Acacia mellifera – Rhigozum trichotomum – Stipagrostis uniplumis* bushy plains and valleys (Vegetation Unit 9, Fig. 7)

- *Acacia mellifera – Rhigozum trichotomum – Euphorbia rectirama* plains (not mapped, Fig. 7)
- *Acacia mellifera – Rhigozum trichotomum – Eragrostis rigidior* plains (not mapped, Fig. 7)
- *Acacia mellifera – Rhigozum trichotomum – Sansevieria aethiopica* valleys (not mapped, Fig. 7)

1.3. *Prosopis glandulosa – Opuntia ficus-indica* disturbed areas (Vegetation Unit 10, Fig. 7)

2. *Croton gratissimus – Digitaria polyphylla* hills and mountains (Vegetation Unit 11, Fig. 7)

2.1. *Croton gratissimus – Euphorbia avas-montana* hills and mountains (not mapped, Fig. 7)

2.2. *Croton gratissimus – Pellaea calomelanos* hills and mountains (not mapped, Fig. 7)

3. *Pentzia incana – Enneapogon desvauxii* panveld (Vegetation Unit 12, Fig. 7)

3.1. *Ruschia griquensis – Enneapogon desvauxii* panveld (not mapped, Fig. 7)

3.2. *Salsola etoshensis – Sporobolus rangei* pans (not mapped, Fig. 7)

In Korannaberg, the *Acacia haematoxylon – Grewia flava – Eragrostis lehmanniana* dune valleys and plains (Vegetation Unit 7, Fig. 7) dominate in size, with the *Terminalia sericea – Acacia haematoxylon – Anthephora pubescens* dunes (Vegetation Unit 2, Fig. 7) being the smallest vegetation unit. *Eragrostis lehmanniana* dominates the herbaceous stratum, followed by *Stipagrostis uniplumis*. The sparsely scattered trees and shrubs of the *Acacia haematoxylon – Grewia flava – Eragrostis lehmanniana* dune valleys and plains (Vegetation Unit 7, Fig. 7) are represented by *Acacia mellifera, Acacia erioloba, Rhigozum trichotomum* and *Grewia flava* (Van Rooyen 1999).

CHAPTER 4

HABITAT UTILISATION

Introduction

For centuries it has been known that a specific relationship exists between animals and a given environment (Beardall, Joubert & Retief 1984). Knowledge about this relationship, habitat preference and the ecological requirements of large herbivores is important for any wildlife management programme (Ferrar & Walker 1974; Riney 1982; Scogings, Theron & Bothma 1990; Traill 2004) and to gain an understanding of animal ecology (Conner, Smith & Burger 2003). Caughley & Sinclair (1994) considered a habitat to be the suite of environmental conditions and resources that determine the presence, reproduction and survival of a species. According to Joubert (2002), the habitat is the area consisting of given geomorphological characteristics, including topography, soil types and vegetation, in which animals occur by choice.

Habitat selection by an animal affects the fitness of that animal (Lombardi, Fernandez, Moreno & Villafuerte 2003). Availability of food, the size of the area available for various activities, the absence of competition, escape cover from predators, surface water availability, opportunity for reproduction and escape from climatic extremes, all determine the preference of herbivores for a specific habitat type (Pettifer & Stumpf 1981; Funston 1992; Mugangu *et al.* 1995; Krüger 1996). If a species can be associated with a specific habitat, or elements of that habitat, it means that the specific habitat provides the minimum requirements for existence, but it does not necessarily mean that high numbers of that species can be sustained by the specific habitat (Riney 1982). The species composition and structure of the vegetation play a determining role in habitat preference. Plant species composition determines the feeding ecology, and vegetation structure plays a role in habitat suitability for a herbivore (Joubert 2002).

Some features of a specific habitat and the requirements of large herbivores change with time and space (Ben-Shahar 1995; Dörgeloh 1998). Seasonal changes include alteration in climatic conditions and phenological changes in forage availability and quality, resulting in seasonal herbivore movement (Munthali & Banda 1992). It is therefore important to understand the habitat requirements of a given type of herbivore in a seasonal context, because this is essential in the management of the species during critical seasons when resources are limited (Sinclair 1974a, 1977; Riney 1982; Traill 2004).

Local wildlife migrations may occur because of a change in forage quality and quantity, water availability, and landscape features such as vegetation composition and vegetation structure (Ben-Shahar & Coe 1992; Ben-Shahar 1995). Shrubs and deciduous trees may lose their leaves in the winter, causing a thicket to appear to change into an open woodland. When this occurs, it may not provide enough protection for a species against extreme environmental conditions (Krüger 1996).

According to Sinclair (1977), habitat utilisation is selective if the available habitat is used disproportionately to its relative availability. Four natural orders of selection are distinguished by Johnson (1980). They are:

- First order selection: the geographical area in which a species occurs.
- Second order selection: the range of the species within a given geographical area.
- Third order selection: the utilisation of different habitat components within the range of the species.
- Fourth order selection: the selection of certain food plants from the available habitat components.

The introduction of exotic species refers to the release of animals into a geographical area not historically occupied by them. Used as a conservation or tourism strategy, such introductions have often failed as a result of unsuitable habitat for the species in question (Du Plessis 1969; Novellie & Knight 1994). Introduction is regarded to be successful if the introduced species can develop a self-sustaining population (Griffith, Scott, Carpenter & Reed 1989), or if the species is still present on the property 22 years after its first release (Novellie & Knight 1994). The 83.3% unsuccessful introductions of ungulates by the South African National Parks into areas not historically occupied by them (Novellie & Knight 1994) illustrate the need for a thorough knowledge about the preferred habitat of a species. One example is the unsuccessful introduction of gemsbok into the Limpopo province, which resulted in the death of some animals and a low population growth rate (Strauss 2003). Gemsbok were also unsuccessfully introduced into areas in the Free State, historically unknown to this species because of unsuitable habitat (Pienaar 1974). Various other studies have also proved that introductions were successful only when they were associated with the required habitat quality (Griffith *et al.* 1989).

The African buffalo historically never occurred for long periods in the dune-covered part of the Kalahari (Sinclair 1977; Ebedes 1996; Estes 1997; Winterbach 1999; Plug & Badenhorst 2001), where the current study was done. The lack of especially natural surface water may have been one reason why buffalo did not prefer this area historically, because buffalo prefer areas with abundant grazing and water of good quality (Shortridge 1934; Sinclair 1977; Krüger 1996; Prins 1996).

Sinclair (1974a) defined the best available habitat for the African buffalo to be that specific habitat most often selected by the buffalo during the dry season. According to Winterbach (1999), there are four main factors that affect habitat selection by buffalo: seasonal changes in the food supply; patchy distribution of the food supply; the availability of cover for daytime resting sites; and protection against low night temperatures and frost. Because buffalo are dependent on surface water, they have to drink water at least once every 38 hours (Du Toit & Ebedes 2002). Therefore the distance from water also appears to influence habitat selection. Furthermore, buffalo also utilise water for thermoregulation during hot days (Sinclair 1977). Mugangu *et al.* (1995) found that buffalo in Zaire selected habitats with a high food quality, close to water and a low predation risk. Ben-Shahar (1995) stated that daily grazing sites of herbivores would be selected if water and shade requirements were satisfied. Sinclair (1977) found that buffalo in the Serengeti selected habitat according to the presence of green grass, and water quantity and quality.

For effective management of the buffalo on Tswalu it is necessary to know what the critical factors regarding their habitat requirements are. The Korannaberg section, where the buffalo are kept, does not have any large predators and therefore predation risk does not play a role. Because Tswalu is outside the natural area of long-term occurrence of the buffalo (Sinclair 1977; Ebedes 1996; Estes 1997; Winterbach 1999; Plug & Badenhorst 2001) it is expected to be a sub-optimal habitat and buffalo would be expected to be selective of food (Winterbach 1999). The vegetation types as defined in Chapter 3 combined with the vegetation map of Van Rooyen (1999) (Fig. 7) were used in the habitat utilisation study.

The hypothesis that was tested here was that the buffalo on Tswalu would use all the habitat components in proportion to their availability. In order to investigate this hypothesis, it was necessary to quantify the habitat use characteristics and habitat preferences of the buffalo in terms of the quality and quantity of the habitat available to and used by them.

Methods

Field study

Today, a multitude of methods exist to study habitat preferences, one of which is a transect method with repeated observations (Scogings *et al.* 1990; Mugangu *et al.* 1995; Von Holdt 1999). This method is dependent upon the terrain morphology and road network that is available in a given study area. Sinclair (1977) encountered three problems during a study of the habitat selection by buffalo in the Serengeti. The first was the large area that he had to cover because of the aggregation of the buffalo into large herds. Therefore, transects across vegetation types would have resulted in too great a variance for significant results. The second was social facilitation where juveniles followed their mothers and did not make an independent choice of habitat. Because of this, observations on individual animals could not be taken as independent data points and a herd had to be recorded as a single unit. The third problem was the edge effect where the buffalo used one vegetation type for feeding only and another for cover. It was quite difficult to delineate edge effect because of the diffuse ecotones between vegetation types.

Similar problems to those of Sinclair (1977) were encountered in the present study. Data collection lasted from April 2003 to July 2004 and represented two seasons. The cold, dry season was from May to September 2003 and again from May 2004 to July 2004, the latter date being when the study ended. The warm, wet season was April 2003, and from October 2003 to April 2004. Rainfall in the study area was often erratic and rainfall records on Tswalu might not reflect the true rainfall due to a change in management staff and questionable record keeping at times. Therefore, seasons were selected based on the long-term rainfall records of the Van Zylsrus Weather Station (Chapter 3).

Areas with known buffalo activity were patrolled on a quad bike for the first hours after sunrise and the last hours before sunset, until fresh tracks were found. If the buffalo were not in sight, tracking commenced until the herd was located. However, if a herd was clearly visible, observations were made with the aid of a set of 8 X 42 binoculars and a 0.5 m spotting scope. If the natural behaviour of the herd appeared disturbed, tracking and observations would cease and another herd was located for observational purposes.

Observation locations were marked with a global positioning system receiver (GPS), and these points were later imported into the detailed vegetation map of Van Rooyen (1999) with ArcView 3.2 (ESRI Inc. 1998). Individual buffalo were not used as recordings in this part of the study and If two or more animals were observed in close proximity to each other, they were considered as one data point. Pertinent environmental characteristics were recorded at each buffalo occurrence and they were considered to be part of the habitat preference of the buffalo. The environmental characteristics recorded on the field form were subjected to the SAS® statistical computer program with the help of Statomet[3], the data were divided into the two seasons to detect any possible seasonal preferences. During the months of November and December 2003, observations were made by the field guides. Although there were 83 buffalo on Tswalu during the

[3] Ms. R. Owen, Research Support, Department of Statistics, University of Pretoria, Pretoria, 0002, South Africa.

study, they tended to split up into smaller herds containing between three and 78 animals, with the structure and number of the herds varying on a daily basis. Therefore, observations were only based on herds with more than 20 individuals. Thomas & Taylor (1990 In: Dörgeloh 1998) suggested at least 50 observations on herds of at least 20 animals each are required for adequate hypothesis testing.

Data analysis

The interaction between herbivores and their habitat can be analysed by numerous methods (Beardall *et al.* 1984; Alldredge & Ratti 1992), either qualitatively or quantitatively (Von Holdt 1999; Strauss 2003). The simplest form of such a method is the proportion of animals seen in each habitat type (Scogings *et al* 1990; Pienaar, Bothma & Theron 1992; Watson, Odendaal, Barry & Pietersen 2005).

Multivariate analysis techniques are often used for studies on the relationship between habitat and herbivores and the approach used includes detrended correspondence analysis (Beardall *et al.* 1984, Scogings *et al.* 1990) and discriminant function analysis (Ferrar & Walker 1974). Traditional multivariate analysis is often difficult to apply to ecological data for two reasons. Firstly, it is often not possible to obtain quantitative data because this process is expensive, time-consuming and the data is difficult to gather. Secondly, normally distributed data is a postulation seldom justified in ecological data (Beardall *et al.* 1984). The best-suited computerized method is the Johnson method (Johnson 1980), which compares ranks of habitat availability to ranks of usage, while other methods include the Quade and Friedman methods (Alldredge & Ratti 1992). A more complex method is the categorical modelling procedure (CATMOD) that was used successfully by Von Holdt (1999) and Strauss (2003). In the final analysis, the hypothesis to be tested will ultimately determine which statistical method is best suited to answer the biological question of interest (Alldredge & Ratti 1992).

A preference index (PI_x) of use for each vegetation unit was calculated with an adaptation of Ivlev's Electivity Index (Jacobs 1974), the equation used was adopted from Viljoen (1989), Pienaar *et al.* (1992) and Admasu, Thirgood, Bekele & Laurenson (2004). A value of PI_x = -0.5 to 0.5 indicated that a vegetation unit was being used proportional to its relative occurrence. Values of PI_x > 0.5 (maximum +1) indicated usage that was greater than the proportional occurrence of the vegetation unit, while values of PI_x < -0.5 (minimum -1) indicated usage of a vegetation unit that was less than its proportional occurrence. The equations used to determine the preference index (PI_x) are:

If $U_x < A_x$ then $PI_x = (1/ A_x) \times (U_x - A_x)$

If $U_x > A_x$ then $PI_x = (-1/ U_x) \times (A_x - U_x)$

where:

PI_x	=	preference for vegetation unit x
A_x	=	proportional availability of vegetation unit x, as determined by a_x/At
U_x	=	proportional usage of vegetation unit x, as determined by n_x / N_t
A_t	=	the total area (km²) of the Korannaberg section of Tswalu
a_x	=	the total surface area (km^2) covered by vegetation unit x
N_t	=	the total number of buffalo observed in the Korannaberg section of Tswalu
n_x	=	the number of buffalo present in vegetation unit x

The preference index is not based on a statistical test but only gives a ratio of habitat use to habitat availability. To overcome the criticism of the above method, a chi-square test (Neu, Byers & Peek 1974; Alldredge & Ratti 1992) was used to test for the goodness-of-fit of utilised versus available vegetation unit (Marcum & Loftsgaarden 1980; Byers, Steinhorst & Krausman 1984). With the chi-square (χ^2) goodness-of-fit test, it is determined whether an observed distribution (observed frequency of utilisation) differs significantly from a predetermined distribution (expected frequency of utilisation), at a significance level of $\alpha \leq 0.05$. This method is also referred to as the Neu method (Downie & Heath 1974; Alldredge & Ratti 1992).

When significant differences were detected between the frequencies of utilisation and availability, Bonferroni Z-statistics were used to construct 95% simultaneous confidence intervals (Byers *et al.* 1984; Samuels 1989; Alldredge & Ratti 1992; Alvarez-Cárdenas, Guerrero-Cárdenas, Diaz, Gallina-Tessaro & Gallina 2001). These intervals were calculated with the following equation (Miller 1980; Byers *et al.* 1984; Alldredge & Ratti 1992):

$$U \pm Z_{1-\alpha/2k} [U(1-U)/n]^{1/2}$$

where:

U	=	the proportion of use of a habitat
$Z_{1-\alpha/2k}$	=	the upper standard normal table value corresponding to a tail area of α/2k
n	=	the total number of observations
k	=	the number of vegetation types

To determine possible preference of a vegetation unit, the Bonferroni simultaneous confidence interval was compared for overlap with the available proportion of the corresponding vegetation units. A vegetation unit was considered to be preferred for use if the lower level of the confidence interval exceeded the available proportion. If the vegetation unit proportion fell within the confidence intervals, then it was used in proportion to its availability. A vegetation unit was considered not to be preferred for use if the available proportion exceeded the upper level of the confidence interval (Byers *et al.* 1984; Alldredge & Ratti 1992; Pienaar *et al.* 1992).

The data were divided into 3 categories of activity levels and were subsequently analysed according to the two seasons identified in this study viz. the warm, wet and the cold, dry season. The three activity levels were:

1. All activities, where any possible activity of the buffalo was pooled and recorded as a data entry in 20 minute intervals
2. Grazing activity, where data were recorded only if buffalo were actively grazing, usually walking with the head close to the ground while collecting graze or occasionally browse
3. Resting activity, where recordings were made if buffalo were lying down with head held low or reposes on a neighbour's body, or lying stretched on one side, often with eyes closed (Mloszewski 1983).

Results

Habitat analysis commenced with the determination of preference indices at plant community level by using the three main plant communities of Van Rooyen (1999). In total, 1043 observations were made on Tswalu: 476 of them being for the cold, dry season and 567 for the warm, wet season. From these indices it became clear that for the duration of the study period from April 2003 to July 2004, the buffalo on Tswalu was most often observed in the *Eragrostis lehmanniana* open shrubveld community there (U_x = 0.981) but utilised this plant community in proportion to its occurrence in Korannaberg (PI_x = 0.0437; A_x = 0.938; U_x = 0.981).

Analysis on a finer scale, by using the 12 vegetation units according to the vegetation map of Van Rooyen (1999), refined the habitat preferences of the buffalo in the Korannaberg section of Tswalu. The respective size of each vegetation unit is summarised in Table 1 (Chapter 3). From a total of 1043 observations, the buffalo were most often observed in the *Stipagrostis uniplumis* plains (38.3% of all the observations), followed by the *Stipagrostis uniplumis* bushy plains and valleys (15.3%). No buffalo were ever observed in the *Anthephora pubescens* dunes or the *Digitaria polyphylla* mountains and hills.

Seasonal preference indices that were determined for the individual vegetation units are presented in Table 2. Seasonally the *Eragrostis pallens* dune streets (Vegetation Unit 3) for the

Table 2: Vegetation unit utilisation data for buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa, based on an adaptation of Ivlev's Electivity Index (PI_x) of use during two seasons from April 2003 to July 2004 for all the activities studied. Vegetation unit numbers correspond with those of Table 1 in Chapter 3

VEGETATION UNIT	COLD, DRY SEASON				WARM, WET SEASON			
	Proportion of habitat (A_x)	Proportion of observed use (U_x)	Preference index (PI_x)	Conclusion*	Proportion of habitat (A_x)	Proportion of observed use (U_x)	Preference index (PI_x)	Conclusion*
1	0.038	0.032	-0.156	Not preferred	0.038	0.036	-0.051	Not preferred
2	0.004	0.000	-1.000	Not used	0.004	0.000	-1.000	Not used
3	0.031	0.106	0.704	Preferred	0.031	0.029	-0.071	Not preferred
4	0.159	0.437	0.637	Preferred	0.159	0.317	0.501	Preferred
5	0.141	0.136	-0.035	Not preferred	0.141	0.097	-0.312	Not preferred
6	0.081	0.041	-0.491	Not preferred	0.081	0.124	0.350	Not preferred
7	0.296	0.041	-0.861	Not used	0.296	0.078	-0.736	Not used
8	0.080	0.071	-0.123	Not preferred	0.080	0.092	0.125	Not preferred
9	0.100	0.113	0.115	Not preferred	0.100	0.202	0.505	Preferred
10	0.008	0.000	-1.000	Not used	0.008	0.013	0.394	Not preferred
11	0.053	0.000	-1.000	Not used	0.053	0.000	-1.000	Not used
12	0.009	0.025	0.644	Preferred	0.009	0.013	0.316	Not preferred

∗ The PI_x values represent the following categories: not preferred $-0.5 < PI_x < 0.5$; not used $-0.5 < PI_x < -1.00$; preferred $0.5 < PI_x < 1.0$

all activities level, the *Enneapogon desvauxii* panveld (Vegetation Unit 12) and *Stipagrostis uniplumis* plains (Vegetation Unit 4) were preferred during the cold, dry season. During the warm, wet season the most preferred unit was the *Stipagrostis uniplumis* bushy plains and valleys (Vegetation Unit 9) followed by the *Stipagrostis uniplumis* plains (Vegetation Unit 4). When analysis was done for grazing activity (Table 3), the buffalo showed preference for the *Eragrostis pallens* dune streets (Vegetation Unit 3) and the *Stipagrostis uniplumis* plains (Vegetation Unit 4) during the cold, dry season. The preferred vegetation unit for the warm, wet season while grazing was the *Stipagrostis uniplumis* plains (Vegetation Unit 4). During the warm, wet season the *Stipagrostis uniplumis* bushy plains and valleys (Vegetation Unit 9) and the *Aristida meridionalis* open shrubveld (Vegetation Unit 6) were preferred, but the *Stipagrostis uniplumis* plains (Vegetation Unit 4) was the only unit to be preferred during the cold, dry season when resting was regarded as the only activity (Table 4). A summary of the outcome of the preference indices appears in Figures 8 and 9. For the 15-month study period, the buffalo preferred the *Stipagrostis uniplumis* plains (Vegetation Unit 4) and did not use the *Anthephora pubescens* dunes (Vegetation Unit 2) and the *Digitaria polyphylla* mountains and hills (Vegetation Unit 11). The chi-square goodness-of-fit test showed a significant ($p < 0.001$) difference in use versus availability for all the different vegetation units on Tswalu (Table 5).

Table 6 summarises the Bonferroni simultaneous confidence intervals for the all activity level of the buffalo. The *Stipagrostis uniplumis* plains (Vegetation Unit 4) was used in greater proportion than its occurrence during both seasons, and the *Anthephora pubescens* dunes (Vegetation Unit 2), the *Eragrostis lehmanniana* dune valleys and plains (Vegetation Unit 7) and the *Digitaria polyphylla* mountains and hills (Vegetation Unit 11) were used in lesser proportion than their occurrence in both seasons. When the grazing activity was analysed, the *Eragrostis pallens* dune streets (Vegetation Unit 3) and *Stipagrostis uniplumis* plains (Vegetation Unit 4) were used in greater proportion than their occurrences during the cold, dry season and the *Stipagrostis uniplumis* plains (Vegetation Unit 4) and the *Monechma incanum* shrubveld (Vegetation Unit 8) during the warm, wet season (Table 7). The Bonferroni simultaneous confidence intervals showed that for the resting activity, the *Stipagrostis uniplumis* plains (Vegetation Unit 4) was used in greater proportion than its occurrence in Korannaberg during both seasons (Table 8). The *Stipagrostis amabilis* dune crests (Vegetation Unit 1) was used in proportion to its occurrence in the Korannaberg section, during both seasons and for all three levels of activities (Table 9). For the duration of the study period, the *Stipagrostis uniplumis* plains (Vegetation Unit 4) was the only preferred vegetation unit during all activity levels, while three vegetation units were not used (Table 9). The unused vegetation units were the *Anthephora pubescens* dunes (Vegetation Unit 2), the *Eragrostis lehmanniana* dune valleys and plains (Vegetation Unit 7) and the *Digitaria polyphylla* mountains and hills (Vegetation Unit 11).

Table 3: Vegetation unit utilisation for grazing by buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa, based on an adaptation of Ivlev's Electivity Index (PI_x) of use during two seasons from April 2003 to July 2004. Vegetation unit numbers correspond with those of Table 1 in Chapter 3

VEGETATION UNIT	**COLD, DRY SEASON**				**WARM, WET SEASON**			
	Proportion of habitat (A_x)	Proportion of observed use (U_x)	Preference index (PI_x)	Conclusion*	Proportion of habitat (A_x)	Proportion of observed use (U_x)	Preference index (PI_x)	Conclusion*
1	0.038	0.035	-0.069	Not preferred	0.038	0.035	-0.080	Not preferred
2	0.004	0.000	-1.000	Not used	0.004	0.000	-1.000	Not used
3	0.031	0.104	0.698	Preferred	0.031	0.041	0.243	Not preferred
4	0.159	0.501	0.683	Preferred	0.159	0.330	0.519	Preferred
5	0.141	0.087	-0.382	Not preferred	0.141	0.098	-0.302	Not preferred
6	0.081	0.035	-0.562	Not used	0.081	0.121	0.496	Not preferred
7	0.296	0.040	-0.864	Not used	0.296	0.083	-0.721	Not used
8	0.080	0.075	-0.064	Not preferred	0.080	0.095	0.154	Not preferred
9	0.100	0.120	0.166	Not preferred	0.100	0.181	0.447	Not preferred
10	0.008	0.000	-1.000	Not used	0.008	0.013	0.379	Not preferred
11	0.053	0.000	-1.000	Not used	0.053	0.000	-1.000	Not used
12	0.009	0.019	-1.000	Not used	0.009	0.013	-1.000	Not used

∗ The PI_x values represent the following categories: not preferred $-0.5 < PI_x < 0.5$; not used $-0.5 < PI_x < -1.00$; preferred $0.5 < PI_x < 1.0$

Table 4: Vegetation unit utilisation for resting by buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa, based on an adaptation of Ivlev's Electivity Index (PI_x) of use during two seasons from April 2003 to July 2004. Vegetation unit numbers correspond with those of Table 1 in Chapter 3

VEGETATION UNIT	COLD, DRY SEASON				WARM, WET SEASON			
	Proportion of habitat (A_x)	Proportion of observed use (U_x)	Preference index (PI_x)	Conclusion*	Proportion of habitat (A_x)	Proportion of observed use (U_x)	Preference index (PI_x)	Conclusion*
1	0.038	0.028	-0.256	Not preferred	0.038	0.073	0.476	Not preferred
2	0.004	0.000	-1.000	Not used	0.004	0.000	-1.000	Not used
3	0.031	0.042	0.261	Not preferred	0.031	0.015	-0.535	Not preferred
4	0.159	0.507	0.687	Preferred	0.159	0.275	0.424	Not preferred
5	0.141	0.194	0.284	Not preferred	0.141	0.087	-0.383	Not preferred
6	0.081	0.014	-0.825	Not used	0.081	0.203	0.602	Preferred
7	0.296	0.056	-0.809	Not used	0.296	0.044	-0.853	Not used
8	0.080	0.099	0.184	Not preferred	0.080	0.044	-0.459	Not preferred
9	0.100	0.054	-0.463	Not preferred	0.100	0.232	0.568	Preferred
10	0.008	0.000	-1.000	Not used	0.008	0.015	0.456	Not preferred
11	0.053	0.000	-1.000	Not used	0.053	0.000	-1.000	Not used
12	0.009	0.000	-1.000	Not used	0.009	0.015	0.387	Not preferred

∗ The PI_x values represent the following categories: not preferred $-0.5 < PI_x < 0.5$; not used $-0.5 < PI_x < -1.00$; preferred $0.5 < PI_x < 1.0$

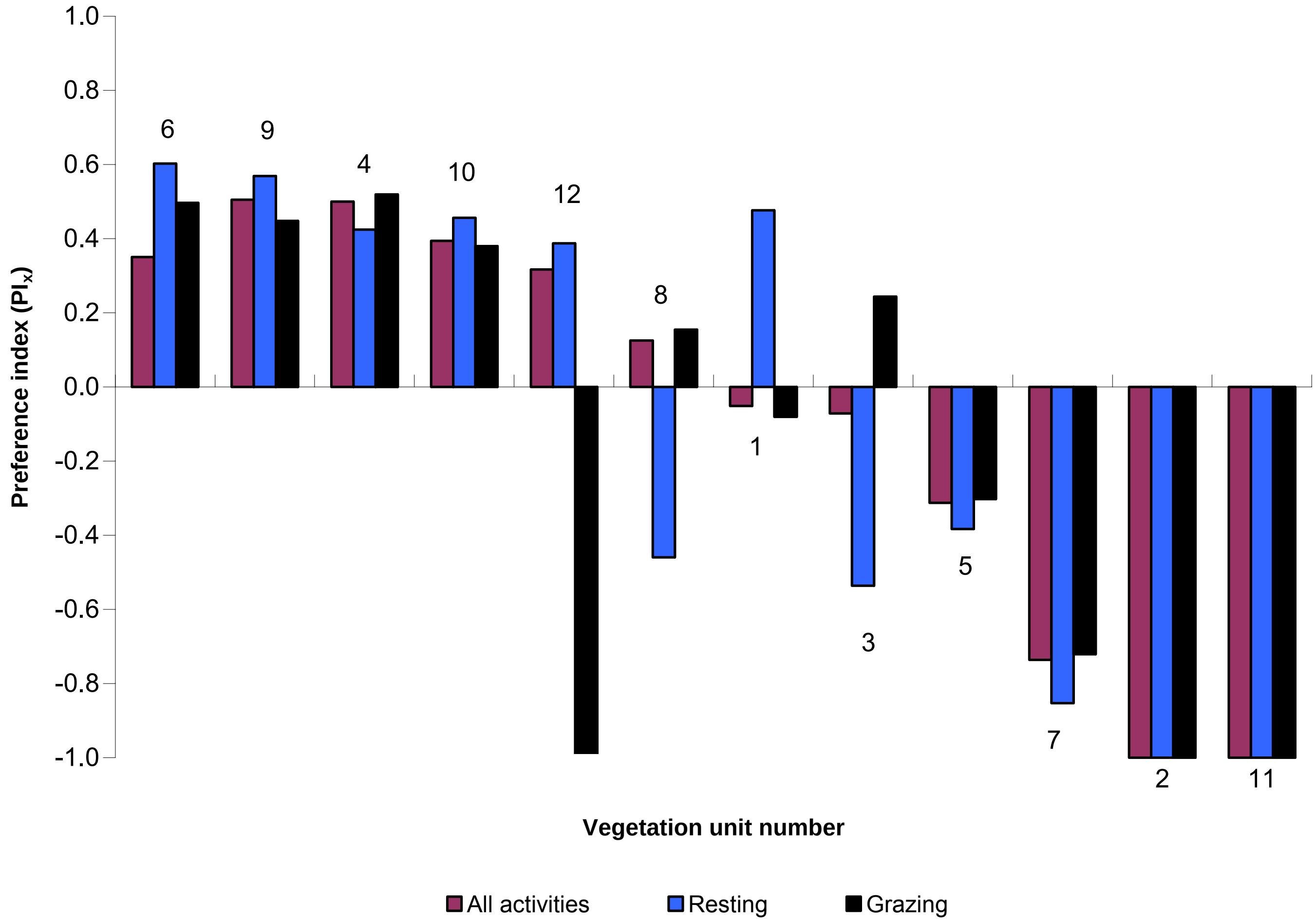


Figure 8: Graphical summary of the preference index (PI_x) results for the buffalo activities on Tswalu Kalahari Reserve in the Northern Cape province of South Africa during the warm, wet season of 2003/2004. The PI_x values represent the following categories: not preferred $-0.5 < PI_x < 0.5$; not used $-0.5 < PI_x < -1.00$; preferred $0.5 < PI_x < 1.0$

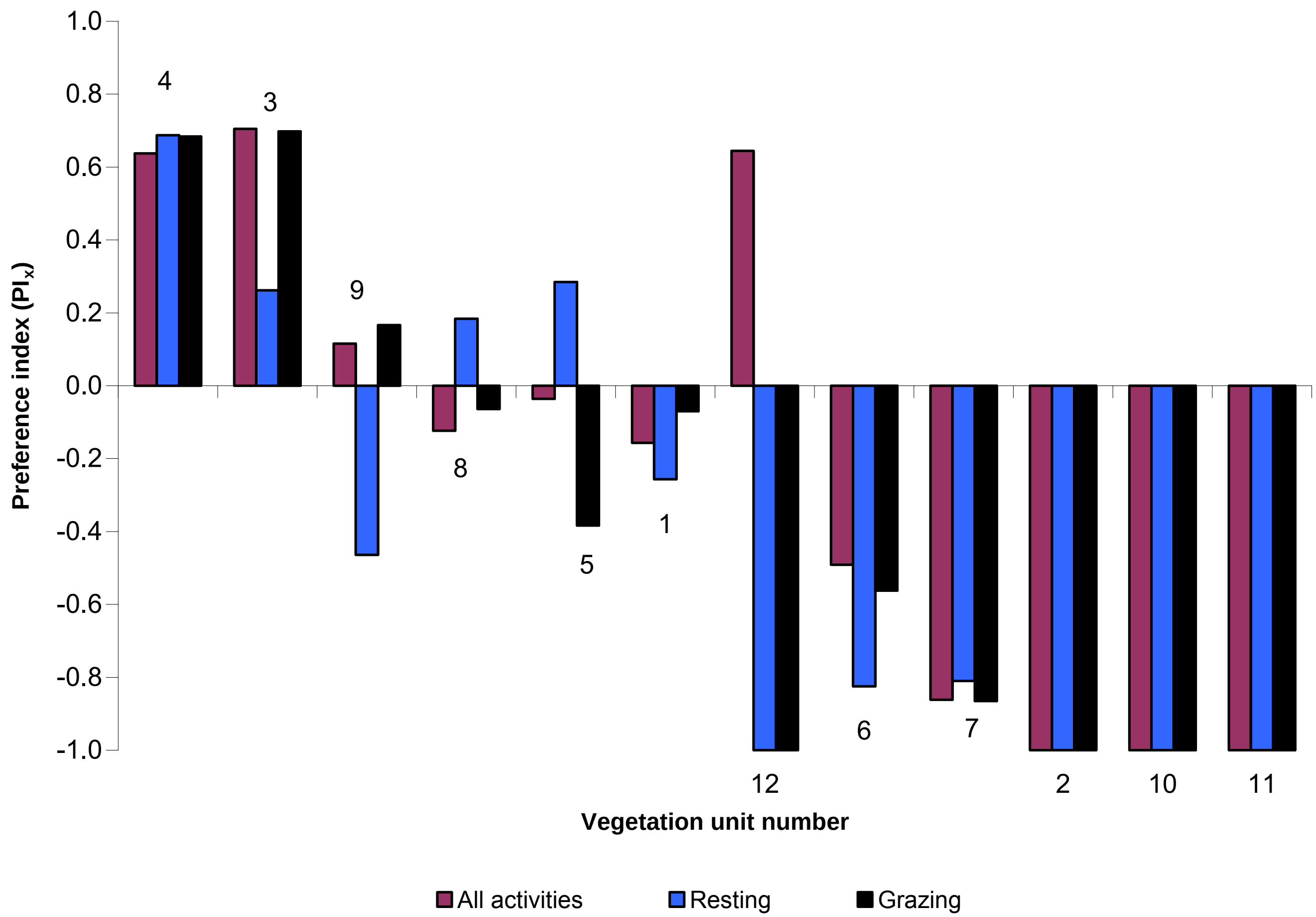


Figure 9: Graphical summary of the preference index (PI_x) results for the buffalo activities on Tswalu Kalahari Reserve in the Northern Cape province of South Africa during the cold, dry season of 2003/2004. The PI_x values represent the following categories: not preferred -0.5 < PI_x < 0.5; not used -0.5 < PI_x < -1.00; preferred 0.5 < PI_x < 1.0

Table 5: Summary of chi-square goodness-of-fit tests to evaluate the habitat utilisation of buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa, from April 2003 to July 2004

ACTIVITY LEVEL	COMPARISON LEVEL	COLD, DRY SEASON			WARM, WET SEASON		
		χ^2	d*f*	*p*	χ^2	d*f*	*p*
All	Community	46.94	2	0.001	27.29	2	0.001
All	Vegetation unit	570.54	11	0.001	249.59	11	0.001
Grazing	Vegetation unit	537.25	11	0.001	162.15	11	0.001
Resting	Vegetation unit	81.01	11	0.001	55.60	11	0.001

Table 6: Simultaneous Bonferroni confidence intervals for the all activities level during two seasons from April 2003 to July 2004 (α = 0.05; k = 12; $Z_{1-\alpha/2k}$ = 2.86), for the utilisation of vegetation units by buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa. Vegetation unit numbers correspond with those of Table 1 in Chapter 3

VEGETATION UNIT	COLD, DRY SEASON			WARM, WET SEASON		
	Proportion of habitat (A_x)	Bonferroni confidence interval	Conclusion	Proportion of habitat (A_x)	Bonferroni confidence interval	Conclusion
1	0.038	$0.010 \leq A_1 \geq 0.053$	No pattern	0.038	$0.011 \leq A_1 \geq 0.060$	No pattern
2	0.004	$0.000 \leq A_2 \geq 0.000$	Not used	0.004	$0.000 \leq A_2 \geq 0.000$	Not used
3	0.031	$0.070 \leq A_3 \geq 0.142$	Preferred	0.031	$0.007 \leq A_3 \geq 0.051$	No pattern
4	0.159	$0.377 \leq A_4 \geq 0.497$	Preferred	0.159	$0.256 \leq A_4 \geq 0.378$	Preferred
5	0.141	$0.094 \leq A_5 \geq 0.177$	No pattern	0.141	$0.058 \leq A_5 \geq 0.135$	Not used
6	0.081	$0.017 \leq A_6 \geq 0.064$	Not used	0.081	$0.080 \leq A_6 \geq 0.167$	No pattern
7	0.296	$0.017 \leq A_7 \geq 0.064$	Not used	0.296	$0.042 \leq A_7 \geq 0.113$	Not used
8	0.080	$0.039 \leq A_8 \geq 0.101$	No pattern	0.080	$0.054 \leq A_8 \geq 0.129$	No pattern
9	0.100	$0.075 \leq A_9 \geq 0.151$	No pattern	0.100	$0.149 \leq A_9 \geq 0.254$	Preferred
10	0.008	$0.000 \leq A_{10} \geq 0.000$	Not used	0.008	$-0.001 \leq A_{10} \geq 0.027$	No pattern
11	0.053	$0.000 \leq A_{11} \geq 0.000$	Not used	0.053	$0.000 \leq A_{11} \geq 0.000$	Not used
12	0.009	$0.006 \leq A_{12} \geq 0.043$	No pattern	0.009	$-0.001 \leq A_{12} \geq 0.027$	No pattern

Table 7: Simultaneous Bonferroni confidence intervals for grazing during two seasons from April 2003 to July 2004 (α = 0.05; k = 12; $Z_{1-\alpha/2k}$ = 2.86) for the utilisation of vegetation units by the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa. Vegetation unit numbers correspond with those of Table 1 in Chapter 3

VEGETATION UNIT	**COLD, DRY SEASON**			**WARM, WET SEASON**		
	Proportion of habitat (A_x)	Bonferroni confidence interval	Conclusion	Proportion of habitat (A_x)	Bonferroni confidence interval	Conclusion
1	0.038	$0.009 \leq A_1 \geq 0.060$	No pattern	0.038	$0.005 \leq A_1 \geq 0.064$	No pattern
2	0.004	$0.000 \leq A_2 \geq 0.000$	Not used	0.004	$0.000 \leq A_2 \geq 0.000$	Not used
3	0.031	$0.061 \leq A_3 \geq 0.145$	Preferred	0.031	$0.009 \leq A_3 \geq 0.073$	No pattern
4	0.159	$0.431 \leq A_4 \geq 0.570$	Preferred	0.159	$0.254 \leq A_4 \geq 0.405$	Preferred
5	0.141	$0.048 \leq A_5 \geq 0.126$	Not used	0.141	$0.050 \leq A_5 \geq 0.146$	No pattern
6	0.081	$0.009 \leq A_6 \geq 0.060$	Not used	0.081	$0.068 \leq A_6 \geq 0.173$	No pattern
7	0.296	$0.012 \leq A_7 \geq 0.067$	Not used	0.296	$0.038 \leq A_7 \geq 0.126$	Not used
8	0.080	$0.038 \leq A_8 \geq 0.111$	No pattern	0.080	$0.047 \leq A_8 \geq 0.142$	Preferred
9	0.100	$0.074 \leq A_9 \geq 0.165$	No pattern	0.100	$0.119 \leq A_9 \geq 0.243$	No pattern
10	0.008	$0.000 \leq A_{10} \geq 0.000$	Not used	0.008	$-0.005 \leq A_{10} \geq 0.030$	No pattern
11	0.053	$0.000 \leq A_{11} \geq 0.000$	Not used	0.053	$0.000 \leq A_{11} \geq 0.000$	Not used
12	0.009	$0.000 \leq A_{12} \geq 0.000$	Not used	0.009	$0.000 \leq A_{12} \geq 0.000$	Not used

Table 8: Simultaneous Bonferroni confidence intervals for resting during two seasons from April 2003 to July 2004 (α = 0.05; k = 12; $Z_{1-\alpha/2k}$ = 2.86) for the utilisation of vegetation units by the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa. Vegetation unit numbers correspond with those of Table 1 in Chapter 3

VEGETATION UNIT	**COLD, DRY SEASON**			**WARM, WET SEASON**		
	Proportion of habitat (A_x)	Bonferroni confidence interval	Conclusion	Proportion of habitat (A_x)	Bonferroni confidence interval	Conclusion
1	0.038	$-0.028 \leq A_1 \geq 0.084$	No pattern	0.038	$-0.016 \leq A_1 \geq 0.161$	No pattern
2	0.004	$0.000 \leq A_2 \geq 0.000$	Not used	0.004	$0.000 \leq A_2 \geq 0.000$	Not used
3	0.031	$-0.026 \leq A_3 \geq 0.110$	No pattern	0.031	$-0.026 \leq A_3 \geq 0.055$	No pattern
4	0.159	$0.337 \leq A_4 \geq 0.676$	Preferred	0.159	$0.121 \leq A_4 \geq 0.429$	Preferred
5	0.141	$0.062 \leq A_5 \geq 0.332$	No pattern	0.141	$-0.010 \leq A_5 \geq 0.184$	No pattern
6	0.081	$-0.025 \leq A_6 \geq 0.054$	Not used	0.081	$0.064 \leq A_6 \geq 0.341$	No pattern
7	0.296	$-0.021 \leq A_7 \geq 0.134$	Not used	0.296	$-0.026 \leq A_7 \geq 0.113$	Not used
8	0.080	$-0.002 \leq A_8 \geq 0.199$	No pattern	0.080	$-0.026 \leq A_8 \geq 0.113$	No pattern
9	0.100	$-0.022 \leq A_9 \geq 0.130$	No pattern	0.100	$0.086 \leq A_9 \geq 0.377$	No pattern
10	0.008	$0.000 \leq A_{10} \geq 0.000$	Not used	0.008	$-0.026 \leq A_{10} \geq 0.055$	No pattern
11	0.053	$0.000 \leq A_{11} \geq 0.000$	Not used	0.053	$0.000 \leq A_{11} \geq 0.000$	Not used
12	0.009	$0.000 \leq A_{12} \geq 0.000$	Not used	0.009	$-0.026 \leq A_{12} \geq 0.055$	No pattern

Table 9: Summary of the simultaneous Bonferroni confidence intervals for all activities studied from April 2003 to July 2004 (α = 0.05; k = 12; $Z_{1-\alpha/2k}$ = 2.86), for the utilisation of vegetation units by buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa. Vegetation unit numbers correspond with those of Table 1 in Chapter 3

VEGETATION UNIT	**CONCLUSION**					
	Cold, dry season			Warm, wet season		
	All activities	Grazing	Resting	All activities	Grazing	Resting
1	No pattern	No pattern	No pattern	No pattern	No pattern	No pattern
2	Not used	Not used	Not used	Not used	Not used	Not used
3	Preferred	Preferred	No pattern	No pattern	No pattern	No pattern
4	Preferred	Preferred	Preferred	Preferred	Preferred	Preferred
5	No pattern	Not used	No pattern	Not used	No pattern	No pattern
6	Not used	Not used	Not used	No pattern	No pattern	No pattern
7	Not used	Not used	Not used	Not used	Not used	Not used
8	No pattern	No pattern	No pattern	No pattern	Preferred	No pattern
9	No pattern	No pattern	No pattern	Preferred	No pattern	No pattern
10	Not used	Not used	Not used	No pattern	No pattern	No pattern
11	Not used	Not used	Not used	Not used	Not used	Not used
12	No pattern	Not used	Not used	No pattern	Not used	No pattern

Discussion

The buffalo on Tswalu showed specific habitat use patterns over a 15-month study period. The *Stipagrostis uniplumis* plains (Vegetation Unit 4) were the only preferred vegetation unit for all levels of activities during both seasons (Figs. 8 and 9; Table 9). Although representing only 15.9% of the total surface area of the Korannaberg section, the buffalo were observed most in this unit (38.3% of all observations). The *Stipagrostis uniplumis* plains include the dune streets and plains in the northwestern area of Korannaberg (Van Rooyen 1999). Shade is sparse throughout the Kalahari, but field observations showed that shade was available in this vegetation unit in the form of scattered clumps of *Acacia mellifera* shrubs. All six grass species preferred by the buffalo for feeding were present in the poorly developed herbaceous layer of this vegetation unit namely: *Centropodia glauca*, *Schmidtia pappophoroides*, *Stipagrostis uniplumis*, *Eragrostis lehmanniana*, *Digitaria eriantha* and *Eragrostis pallens*. Two shrub species that were occasionally browsed by the buffalo, *Rhus tenuinervis* and *Grewia flava*, also occurred in this vegetation unit. The grazing capacity and veld condition score of this vegetation unit were the second highest of all the vegetation units present in the Korannaberg section (Fouché & Avenant 2003, 2004). Three water points were present in this vegetation unit, and consequently the buffalo were never more than 4 km away from a source of water. One of the water points was a large earth impoundment that was used by the buffalo for wallowing during the warm summer months. It therefore seemed that the *Stipagrostis uniplumis* plains fulfilled most of the buffalo's needs in terms of preferred grazing, water and protection from climatic extremes. Another factor that might have played a role in the high degree of occurrence of buffalo in this vegetation unit may have been that supplementary feeding was done in this unit during the study period.

The buffalo were never observed in the *Anthephora pubescens* dunes (Vegetation Unit 2) or the *Digitaria polyphylla* mountains and hills (Vegetation Unit 11) during any of the seasons (Figs. 8 and 9). The *Anthephora pubescens* dunes occurred in patches on broad and flat dune crests and deep sandy areas (Van Rooyen 1999) and only covered 0.4% of the surface area of the Korannaberg section. The *Digitaria polyphylla* mountains and hills covered the rocky and often quite steep mountains and hills (Van Rooyen 1999) and were relatively inaccessible to the buffalo. The buffalo probably did not to use these areas because of the deep, sandy soil and steep rocky nature of these two vegetation units.

The preference index (PI_7) showed that the *Eragrostis lehmanniana* dune valleys and plains (Vegetation Unit 7) were not used during any of the seasons for any of the activity levels (Figs. 8 and 9). The Bonferroni simultaneous confidence intervals confirmed that the buffalo did not use this vegetation unit in proportion to its occurrence in Korannaberg (Table 9). However, buffalo have been recorded to move through this unit. The degree of occurrence of the buffalo within the *Eragrostis lehmanniana* dune valleys and plains was lower than expected (5.8% of all observations). Covering the dune streets in the central and western areas of Korannaberg (Van Rooyen 1999), and with a total surface area of 15 998 ha (29.6% of Korannaberg), this was the largest vegetation unit in the study area. Buffalo were predominantly recorded in the northern parts of this vegetation unit. According to Fouché & Avenant (2004), the *Eragrostis lehmanniana* dune valleys and plains on Tswalu have a low veld condition score. Despite the size of this vegetation unit, the low veld condition score might explain the reason why the buffalo used this vegetation unit less frequently than expected based on its occurrence in the Korannaberg section.

The *Stipagrostis amabilis* dune crests (Vegetation Unit 1) occurred on deep, sandy dune crests (Van Rooyen 1999) and formed 3.8% of the total area of the Korannaberg section. In this vegetation unit, a few scattered trees occurred in the poorly developed herbaceous layer. *Stipagrostis amabilis* was the dominant grass species and was not used by the buffalo. Although the buffalo often occurred in this vegetation unit, field observations showed that it was predominantly used for resting in the shade of *Terminalia sericea* trees during the warm season, and for protection against cold winds during the cold season. This was confirmed by the positive preference index for this vegetation unit in the warm, wet season for the resting activity (Fig.8). The buffalo did not prefer this vegetation unit for grazing (Table 3), and they usually moved out to the plains to graze. Movement in this unit was limited and the buffalo never walked great distances over the dune crests, probably because the energy cost was too high when walking in such deep, sandy areas. Because of the small surface area of this vegetation unit and the limited number of observations of buffalo (3.4% of all observations) there, it was concluded that this unit was used in the same ratio as its proportional occurrence in Korannaberg (Table 9).

Comprising 3.1% of the surface area of the Korannaberg section, the *Eragrostis pallens* dune streets (Vegetation Unit 3) covered large areas consisting of dune streets and plains (Van Rooyen 1999). Trees and shrubs were sparse but the grass layer was moderately developed, with species like *Stipagrostis uniplumis* and *Eragrostis lehmanniana*. Observations of buffalo in this unit were limited to the northeastern part of the Korannaberg section. During the warm, wet season 2.9% of all the buffalo observations were in this unit, but during the cold, dry season it rose to 10.6%. The preference indices (PI_3) calculated for this vegetation unit revealed a preference for the unit during the cold, dry season for the all activity and grazing activity levels (Fig. 9). When submitted to statistical analysis, the Bonferonni simultaneous confidence intervals confirmed that the buffalo only showed a preference for this unit during the cold, dry season for the all activity level and when grazing (Table 9). The high incidence of *Stipagrostis uniplumis* and *Eragrostis lehmanniana*, together with the presence of three water points and the limited shade present in this unit might explain the preference for this unit in the cold, dry season. The high buffalo preference during the cold, dry season was likely influenced by supplementary feeding during the winter months of 2005 in the Sunbeam area that lies within this unit. This vegetation unit was utilised in proportion to its occurrence by the buffalo when resting in the Korannaberg section during the cold, dry season and for all activities during the warm, wet season (Table 9).

The *Hermannia burchellii* shrubveld (Vegetation Unit 5) contributed to 14.1% of the surface area of the Korannaberg section and was found on the dunes and deep, sandy plains around the pans in the west (Van Rooyen 1999). Trees were sparse but the shrub layer was better developed with *Acacia mellifera* being abundant. *Eragrostis lehmanniana* was the dominant grass species, followed by *Centropodia glauca* and *Schmidtia pappophoroides*. A few pans in the west provided the buffalo with water. During the warm, wet season this vegetation unit was not preferred by the buffalo for any activity level (Table 9). Buffalo did not select this vegetation unit for grazing during the cold, dry season possibly because some of the pans dried up during the winter months. Moreover, it had a low grazing capacity (Fouché & Avenant 2004). However, when subjected to the Bonferonni simultaneous confidence intervals, it became clear that the buffalo did prefer to rest in this vegetation unit during the cold, dry season (Table 9).

Contributing only 8.1% to the surface area of the Korannaberg section, buffalo were not often recorded (7.9% of all observations) in the *Aristida meridionalis* open shrubveld (Vegetation Unit 6). This vegetation unit covered the low dunes and deep sandy plains, with a low tree cover although it had a dense shrub layer of especially *Acacia mellifera* and *Rhigozum trichotomum* (Van Rooyen 1999). The herbaceous layer was moderately developed, with grass species like *Eragrostis lehmanniana*, *Schmidtia pappophoroides* and *Centropodia glauca* being present. Although the buffalo did show a preference for this unit when resting and grazing during the warm, wet season (Fig. 8), if analysed statistically this unit was used by the buffalo in proportion to its degree of occurrence (Table 9). This vegetation unit was not preferred during the cold, dry season for any activity level (Table 9).

Sinclair (1977) found that buffalo in the Serengeti utilised open fields with limited cover to ruminate, even on warm days. However, buffalo in this study did not utilise the open plains while grazing, neither did they do so in the Free State province of South Africa (Winterbach 1999). Funston (1992), found that the buffalo in the Sabie Sand Game Reserve did not utilise the grass communities present in proportion to their occurrence. On Tswalu, buffalo were often observed to rest and ruminate in an open area with no cover during the cold, dry season. However, during the warm, wet season cover always played a role when the buffalo chose areas with a well-developed shrub or tree layer to rest in, or to ruminate. Buffalo have a poor tolerance of extreme heat and thus need protection during the hot hours of the day (Krüger 1996).

Found in patches on the plains, in the dune streets and in the depressions around the pans in the west (Van Rooyen 1999), the *Monechma incanum* shrubveld (Vegetation Unit 8) formed 8.0% of the surface area of the Korannaberg section. Its dense shrub layer, consisting of *Rhigozum trichotomum* and *Acacia mellifera* provided abundant shade during the warm, wet summer months. *Schmidtia pappophoroides* was the dominant grass species in this moderately developed herbaceous layer, followed by *Eragrostis lehmanniana* and *Centropodia glauca*. The latter two grass species flowered in the summer and provided good summer grazing to the buffalo. The dwarf shrub *Monechma incanum* was abundant and the buffalo occasionally browsed it. According to the Bonferonni simultaneous confidence intervals (Table 9), this vegetation unit was utilised in greater proportion than its degree of occurrence only during the warm, wet season for grazing. For all other activities during the two seasons, it was used in proportion to its occurrence in Korannaberg.

Although spread all over Korannaberg (10.0% of the total surface area), the *Stipagrostis uniplumis* bushy plains and valleys (Vegetation Unit 9) was used selectively by the buffalo. Use of this vegetation unit was concentrated in the northeastern areas of Korannaberg. Related to the *Monechma incanum* shrubveld (Vegetation Unit 8), the *Stipagrostis uniplumis* bushy plains and valleys occurred in patches on the plains, dune streets and valleys (Van Rooyen 1999). The tree layer was poorly developed, but shrubs were abundant, with *Acacia mellifera* being dominant, while *Rhigozum trichotomum*, *Grewia flava* and *Monechma incanum* were also present. The herbaceous layer was moderately developed with grass species like *Stipagrostis uniplumis*, *Schmidtia pappophoroides*, *Eragrostis lehmanniana* and *Panicum maximum* being present. With the second highest buffalo density (15.3% of all observations) this vegetation unit was used in a greater proportion than its occurrence during the warm, wet months than in the cold, dry months (Table 9) for the all activity level. The reason for the summer selection could have been the high incidence of grass species that were green during the summer months, the abundant shade, and the large water point at Merec's Dune, which was also used for wallowing during the warm months. The preference indices (PI_9) indicated a preference of the buffalo for this vegetation unit during the warm, wet season for the all activity and resting activity levels (Fig. 8). However, the Bonferonni simultaneous confidence intervals confirmed that this unit was used in proportion to its relative occurrence in Korannaberg, except for the all activity level during the warm, wet season (Table 9).

The *Opuntia ficus-indica* disturbed areas (Vegetation Unit 10) only covered 0.8% of the total surface area of the Korannaberg section and were scattered over locally disturbed sites like old homesteads, kraals and watering points. Trees and shrubs were sparsely present, and there was no herbaceous layer. During the cold, dry season, this unit was not used at all (no observations) and during the warm, wet season it was not preferred by the buffalo (Fig. 8), but it was used in proportion to its occurrence in the Korannaberg section (Table 9). This could have been due to the relatively small area covered by this unit and the limited observations (0.58% of all observations).

Covering the pans and depressions in the west, the *Enneapogon desvauxii* panveld (Vegetation Unit 12) only covered 0.9% of the Korannaberg section. The shrub layer was well developed, with a sparse tree layer and a poorly developed herbaceous layer. Due to the scattered nature of this vegetation unit, there was only localised utilisation of it by the buffalo. With limited observations (1.9% of all observations) of buffalo use in this unit, the vegetation unit was preferred by the buffalo for the all activity level in the cold, dry season (Fig. 9). During the warm, wet season the buffalo did not use this unit for grazing (Fig. 8). The Bonferonni simultaneous confidence intervals did not confirm any preference for this vegetation unit for the all activity level (Table 9). This unit was not used for grazing at all, which is not surprising because of the units' poor grass layer (Van Rooyen 1999; Fouché & Avenant 2003, 2004).

Conclusions

The buffalo on Tswalu showed clear differences in the proportional occurrence of the vegetation units in the Korannaberg section. The *Stipagrostis uniplumis* plains (Vegetation Unit 4) were used most intensively throughout the study period and were a key habitat type for the buffalo on Tswalu. They did not use the *Anthephora pubescens* dunes (Vegetation Unit 2) and the *Digitaria polyphylla* mountains and hills (Vegetation Unit 11). These vegetation units clearly did not suite the ecological needs of the buffalo on Tswalu. The buffalo did not utilise steep areas extensively like the *Digitaria polyphylla* mountains and hills (Vegetation Unit 11), nor did they prefer to utilise areas with deep sand like the *Anthephora pubescens* dunes (Vegetation Unit 2) (Table 9), probably because of the energy cost required to sustain themselves when searching for the limited supply of good quality food.

Sinclair (1977) and Winterbach (1999) concluded that the optimum habitat for buffalo was determined predominantly by the presence of good quality grazing and water, followed by protection from climatic extremes and predators. During the present study, the buffalo on Tswalu were supplementary fed on occasion, and this could have influenced their general habitat utilisation pattern. However, the main factor determining their habitat utilisation seemed to be good quality grazing and the presence of water points that were large enough for wallowing, especially during the warmer months. Buffalo did not utilise an entire vegetation unit, but stayed as close as possible to the nearest water point because of their dependence on water. This dependency upon nearness to water was also the major driving force behind habitat selection of buffalo in Zaire (Mugangu *et al.* 1995). After their nutritional needs have been satisfied, the availability of water and protection from climatic extremes seemed to play an important role in the habitat selection of the buffalo on Tswalu.

CHAPTER 5

RANGE USE

Introduction

Animal range, also known as the radius of mobility (Riney 1982), has been researched by biologists from as early as 1909 (Sanderson 1966) and various meanings and methods to estimate animal range have evolved over time. The concept of a specific range for an animal or group of animals referred to that area occupied while conducting the normal activities of food gathering, mating and caring for young by the individual or group (Burt 1943; Harris, Cresswell, Forde, Trewhella, Woollard & Wray 1990). Alternatively, the range of an animal can be described as the smallest area that accounts for a specific percentage (usually 95%) of the animal or herd's space utilisation (Anderson 1982).

The size and shape of a range can be related to social structure (Krüger 1996), population density, resource abundance and resource distribution (Sanderson 1966; Sinclair 1977; Cooper 1978; Ortega 1990). Sinclair (1977) stated that a buffalo herd consists of a number of subgroups with preferred overlapping areas, where the combined areas of these subgroups make up the herd's range. As early as 1927, the importance of fluctuations in animal numbers was recognised in applied ecology of wildlife management (Lamprey 1964). The African buffalo is a member of the tribe Bovini that has a well-developed fusion-fission behavioural pattern (Estes 1997). This pattern is used as a means of staying in contact with the information gathered by successful members of the herd (Prins 1996). An animal's physiological requirements are influenced by its body size (Swihart, Slade & Bergstorm 1988) and it was suggested that there exists a relationship between an animal's range size and its body size (Harestad & Bunnell 1979; Lindstedt, Miller & Buskirk 1986; Swihart *et al.* 1988).

Lindstedt *et al.* (1986) concluded that animals select a range as a function of energy availability, which meets the animal's metabolic demands during biologically critical periods. Morphological and physiological restrictions, limit animals to a sector of their total environment, and these restrictions can be diagnostic of an animal's response to its environment (Ford & Krumme 1979). It is perceived that the essential requirements of a species fall within the boundaries of its range (Riney 1982; Lindstedt *et al.* 1986), but not all usable areas within this range boundary are utilised by the species (Riney 1982). Sinclair (1977) stated that the limits of an animal's range are not the maximum area an animal can cover or learn. In the Serengeti, blue wildebeest were smaller than buffalo but their range was larger than that of buffalo, possibly due to the nature and distribution of the two species' preferred food resources. Buffalo utilise a known area more efficiently because the energy expended while searching for food is lower in a known, than an unknown area (Sinclair 1977). Funston (1992) concluded buffalo selected the most suitable and not necessarily the perceived best habitat in terms of food, water and shelter resources, with a seasonal alteration between ranges.

Animals use their available space within the boundary of their range disproportionately (Dixon & Chapman 1980; Samuel, Pierce & Garton 1985). The area where space use exceeds the expected level of use in a uniform use distribution is termed the core area of use (Samuel *et al.* 1985) or the centre of activity (Dixon & Chapman 1980). Core areas of use can contain resting sites, and preferred food and water sources, and they contribute to understanding the selection parameters of a specific range (Burt 1943).

From past research it was concluded that buffalo range characteristics were likely to be influenced primarily by food and water availability (Krüger 1996; Winterbach 1999; Furstenburg 2003), and secondarily by resource abundance (Sinclair 1977; Mloszewski 1983; Funston 1992). Range use studies on buffalo in East Africa include the work done by Leuthold (1972), Sinclair (1977), Conybeare (1980) and Mloszewski (1983). Studies on buffalo range in South Africa are limited to the studies by Brooks (1982) in the Hluhluwe-Umfolozi Corridor in KwaZulu-Natal, Funston (1992) in the Sabi Sand Game Reserve and Winterbach (1999) in the Free State province.

This part of the present study investigated whether suitable buffalo habitat was spread uniformly across the Korannaberg section of Tswalu. The range use characteristics of the buffalo, including range size and core area of use, were also examined.

Methods

Field data

Range use data can be collected from indirect or direct observations (Sanderson 1966). Direct observations are time consuming and may alter the behaviour of animals. However, doing so the animals do not have to be handled, which saves time, labour and limits stress to the animal (Sanderson 1966). The earlier indirect methods used to study range of animals, analysed natural signs like tracks, beds and droppings (Sanderson 1966). The most widely used technique during the previous century for movement studies was the live trapping method where animals were captured and marked for future identification (Sanderson 1966; Ford & Krumme 1979). Radio-active materials, dyes for urine and faeces and photographic material were also used, but were expensive and not accurate in providing reliable range use data (Sanderson 1966).

Radio-telemetry was introduced as a technique for the evaluation of range use in the early 1960s (Harris *et al.* 1990). Numerous mammal species have since been radio-tracked successfully, ranging from small rodents to dolphins (Sanderson 1966) to caracal (Van Heezik & Seddon 1998) and leopards (Bothma, Knight, Le Riche & Van Hensbergen 1997). Sinclair (1977) and Conybeare (1980) radio-collared buffalo and Sinclair (1977) found that such radio-collars last for approximately 6 to 9 months on female buffalo, while the bulls lost the collars within one or two days. Taolo (2003) also found that buffalo bulls tended to lose their collars quickly, which limits data collection. Recently, radio-telemetry has included the use of satellites and Global Positioning System receivers (GPS) for more detailed animal movement studies (URL: http://www.televilt.se).

Radio-tracking can be done in a continuous way from radio fixes taken at short intervals of 5 to 15 minutes over a set period of time. Discontinuous radio-tracking involves locating the animals at random, or at discrete time intervals throughout the study period. Predictive radio-tracking is used when an animal is only located and then studied with direct observations without further use of radio tracking (Harris *et al.* 1990). The problems associated with radio-tracking of animals are four-fold: it is an expensive method, it is time consuming and labour intensive, and the effect of the transmitter on the animal's movements is unknown (Sanderson 1966; Harris *et al.* 1990). The animal must also be captured and radio-collared, and all the equipment has to be in a proper working condition (Harris *et al.* 1990; Nams & Boutin 1991). Although radio-collars are helpful in research, field managers and tourists often regard a collar as being unsightly and unnatural. Tswalu is a tourism destination that focuses on portraying the natural aspects of conservation. Therefore, the use of radio-collars on the buffalo was not considered an option at the onset of the current project.

Tracking of buffalo in sandy regions has been done successfully by Conybeare (1980) in Zimbabwe. The buffalo on Tswalu were located for 10 days each month from April 2003 until July 2004. Herds were located by driving areas of known buffalo activity. If fresh tracks were found, position co-ordinates were taken and the spoor was followed until the buffalo were visible. These co-ordinates were later imported into the detailed vegetation map of Van Rooyen (1999) through a Geographic Information System (GIS) package, and ArcView 3.2 (ESRI Inc. 1998).

Data analysis

The significance of the differences of mean seasonal herd size of the buffalo was tested with the student *t*-distribution (Sachs 1982; Samuels 1989), at a significance level of $\alpha \leq 0.05$.

In any study, it is important to state the period when range use was measured because an individual's range use pattern can change over time. The exact size and shape of the range may be meaningless as they are dependent on the method used to determine them (Funston 1992). To analyse range use data, various techniques of data analysis are available (e.g.: Van Winkle 1975; Harris *et al.* 1990; Seaman & Powell 1996). Such methods include the minimum convex polygon (Mohr & Stumpf 1966; Ford & Krumme 1979; Schoener 1981; Anderson 1982; Worton 1987; Harris *et al.* 1990), non-statistical grid cells (Anderson 1982; Worton 1987; Harris *et al.* 1990) and probabilistic methods (Anderson 1982; Harris *et al.* 1990). The harmonic means method (Worton 1987, 1989; Harris *et al.* 1990; Seaman & Powell 1996), cluster analysis (Harris *et al.* 1990), and kernel estimators (Worton 1989; Seaman & Powell 1996) are also frequently used.

For the purpose of the current study, two methods were used for range analysis. The first was a non-parametric method (kernel analysis) and the second was a parametric method (minimum convex polygon method). There are various different computer based programmes available to determine range size (Gallerani Lawson & Rodgers 1997). In this study two extensions of the ArcView 3.2 Geographical Information System package (ESRI Inc. 1998) were used. The first was the Animal Movement Extension to ArcView (Hooge & Eichenlaub 2000; URL: http://www.absc.usgs.gov/glba/gistools/animal_mvmt.htm) and the second was the Home Range Extension to ArcView (Carr & Rodgers 1998; URL: http://www.blueskytelemtry.com/hre.asp). It was decided to determine range size for the two seasons: the warm, wet season (October to April) and the cold, dry season (May to September).

The kernel density method

Kernel methods are non-parametric and form an ideal basis for quantitative analysis of the amount of time that an animal spends at a specific location (Worton 1989; Seaman & Powell 1996). The term kernel refers to a scaled-down probability function that is placed over the data points or observations of an individual or a herd of animals (Worton 1989; Seaman & Powell 1996). A fix, or sample point, can be overlaid over each location point of the animal. By combining the distributions of all the individual fixes, a distribution is obtained that is used to determine the probability density function. Areas of regular use will be displayed as high-density areas because of a concentration of fixes, in comparison with areas where the animal was found less often. A few options are possible when using the kernel analysis. Fixed kernel estimates will give the least biased results, but if accuracy is a prerequisite the adaptive kernel method should be used in conjunction with a least square cross validation (Worton 1989; Seaman & Powell 1996).

The kernel method allows for smoothing of location data to make more efficient use of data than when a histogram is used (Worton 1989). The only deficiency of this method is that a large number of independent location fixes (minimum of 100 fixes) is needed for maximum effectiveness (Worton 1987; Seaman & Powell 1996). The kernel method has proved successful in range analysis (Seaman & Powell 1996; Bothma *et al.* 1997; Lent & Fike 2003), and it has been suggested that a 95% isopleth reliably represents the range for many species.

The minimum convex polygon method

In polygon methods, the peripheral locations of an animal are joined to determine the range (Schoener 1981; Worton 1987). The minimum convex polygon method is one of the earliest and simplest techniques used for range analysis (Schoener 1981; Worton 1987; Harris *et al* 1990). The outermost points of an animal's range are connected to circumscribe the area, and no internal angles of the polygon exceed 180° (Schoener 1981). The polygon is called minimum because it is the smallest area polygon containing all the location points (Anderson 1982). A process of peeling has been suggested where 5% of the location points lying furthest away from the arithmetic mean centre of the range are disregarded, resulting in the minimum convex polygon being determined on 95% of the locations (Mizutani & Jewell 1998).

This method is appealing because it is easy to evaluate by hand and has been used successfully by various authors (Mizutani & Jewell 1998; Van Heezik & Seddon 1998; Admasu *et al.* 2004). The advantage of this method is the highly comparable nature between studies. Moreover, this method is the only one that allows such comparisons (Harris *et al* 1990). Disadvantages include a possible overestimation of range size because space not actually utilised by the animal is included (Worton 1987; Gallerani Lawson & Rogers 1997). A second problem is that areas of high or low intensity of use within the range cannot be measured (Anderson 1982; Harris *et al.* 1990). Lastly, this method is highly correlated with sample size, and more than 25 observations are needed per animal or group of animals (Schoener 1981; Worton 1987; Harris *et al.* 1990).

In the present study, the total range size was determined with the 100% and a peeled 95% minimum convex polygon method using the Home Range Extension (Carr & Rodgers 1998) to

ArcView 3.2. Core areas of use were determined with the adaptive kernel method at 50% isopleths with the Animal Movement Extension (Hooge & Eichenlaub 2000) to ArcView 3.2.

Results

Buffalo group size fluctuated within and between seasons, but the total population on Tswalu was determined to be 83 animals in July 2004. The largest aggregation of 78 buffalo was observed once during April 2004. The mean herd size for the study period was 28 individuals (minimum 4; maximum 78). The mean seasonal herd size of the buffalo was significantly smaller (t = 6.49; df = 938; $p \leq 0.05$) during the warm, wet season (mean = 26 buffalo; SD = 15 buffalo; n = 491) than during the cold, dry season (mean = 33 buffalo; SD = 18 buffalo; n = 449). Range use was based on 1 056 locations, 822 from visual location sightings with 234 being based on tracks. Location recordings were made on any group size of buffalo, but recordings of individual buffalo were not considered in range size estimates. The density of buffalo in the Korannaberg section (540.8 km^2) of Tswalu was determined as 0.15 buffalo/km^2.

The total range size of the buffalo population in the Korannaberg section of Tswalu calculated from April 2003 until July 2004 with the 100% minimum convex polygon method was 231.4 km^2. The peeled 95% minimum convex polygon method revealed the total range size for the 16-month study period was 205.7 km^2 (38.0% of the total surface area of Korannaberg). The results of the seasonal range size of the Tswalu buffalo are summarised in Table 10. The total seasonal buffalo range size was determined with the 100% minimum convex polygon method and was the largest during the warm, wet season (195.7 km^2) (Fig. 10). The seasonal range use of the buffalo in Korannaberg determined with the 100% minimum convex polygon method and the relation to the selection of vegetation units, are demonstrated in Figure 11. In contrast, total range size according to the peeled 95% minimum convex polygon differed with 1.7 km^2, and could be considered alike, although the range area differs between the seasons (Fig. 12). The results obtained when using the adaptive kernel method to determine the range use of the Tswalu buffalo, is demonstrated in Figure 13 for the cold, dry season and in Figure 14 for the warm, wet season. If the 95% adaptive kernel method was considered in total range determination, the cold, dry season showed the larger range use by the buffalo on Tswalu of 33.1% of the total surface area of Korannaberg.

The mean core area of use was determined with the 50% adaptive kernel method and increased from 13.1 km^2 in the warm, wet season to 45.2 km^2 in the cold, dry season. The same result was

Table 10: Estimates of the seasonal range size of buffalo in the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa for the period April 2003 to July 2004 based on various methods

METHOD	**TYPE OF RANGE SIZE DETERMINED**	**SEASONAL RANGE SIZE (km²)**	
		Warm, wet	Cold, dry
100% Minimum convex polygon	Total range	195.7	175.5
95% Minimum convex polygon	Total range	170.0	171.7
75% Minimum convex polygon	Core area	116.4	161.5
50% Minimum convex polygon	Core area	74.6	123.3
95% Adaptive kernel	Total range	136.8	179.4
75% Adaptive kernel	Core area	25.8	84.6
50% Adaptive kernel	Core area	13.1	45.2

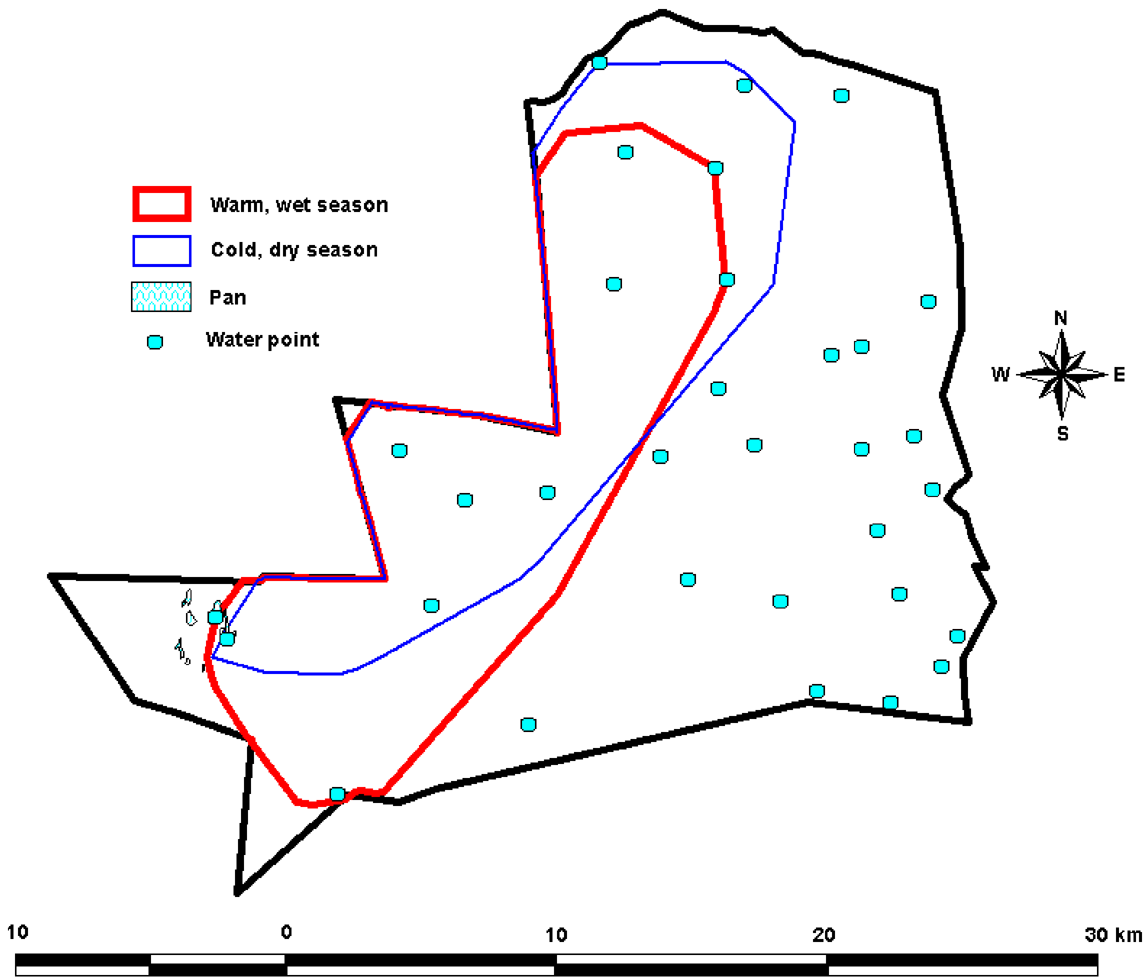


Figure 10: Seasonal range use by the buffalo in the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa, based on the 100% minimum convex polygon method.

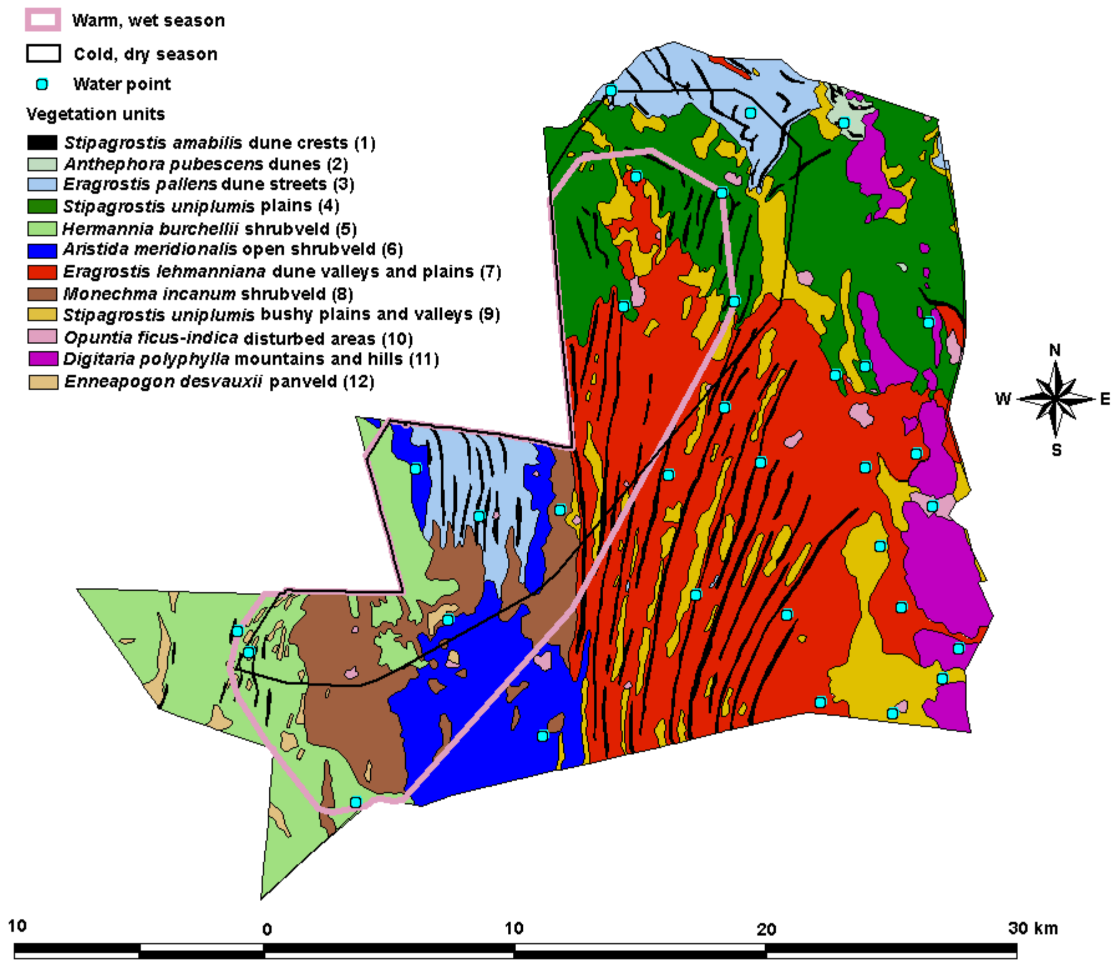


Figure 11: Seasonal range use of the buffalo in the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa, relative to the vegetation units present, based on the 100% minimum convex polygon method.

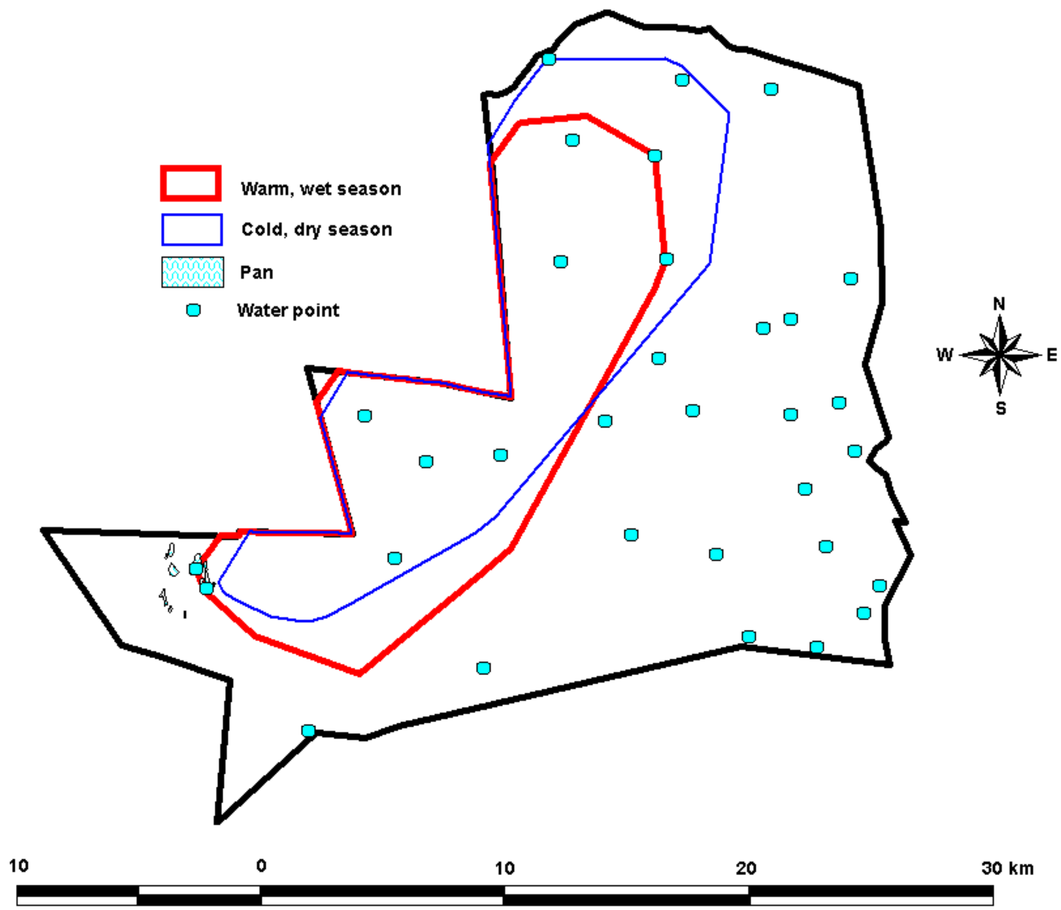


Figure 12: Seasonal range use of the buffalo in the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa, based on the 95% minimum convex polygon method.

Figure 13: Range use of the buffalo in the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa for the cold, dry season from May 2003 to September 2003, and May 2004 to July 2004, based on the adaptive kernel method with least square cross-validation.

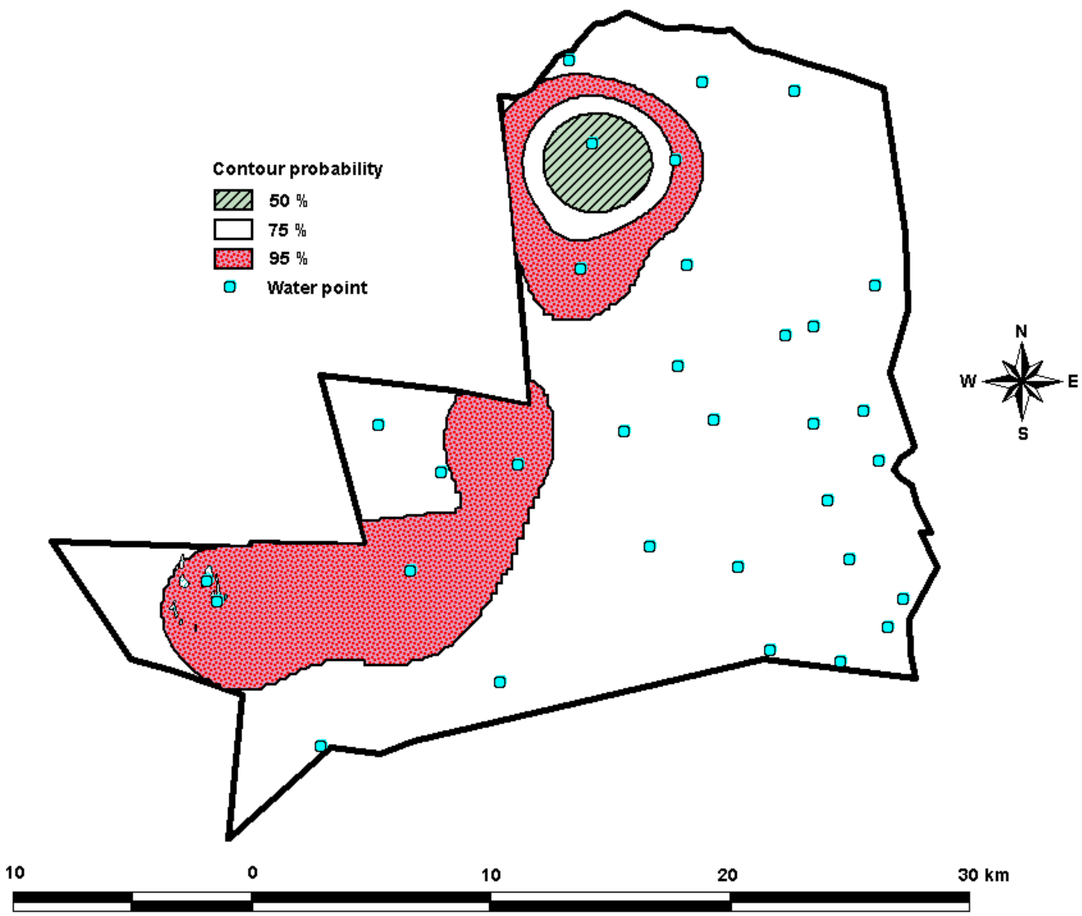


Figure 14: Range use of the buffalo in the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa for the warm, wet season from October 2003 to April 2004, based on the adaptive kernel method with least square cross-validation.

obtained when the 50% minimum convex polygon method was used, with the mean core area of use being 3.5% larger in the cold, dry season compared to the warm, wet season.

Discussion

Herd fragmentation has been observed by various researchers including Leuthold (1972), who found that buffalo in Kenya tended to split up into smaller units. Prins (1996) suggested that a relationship existed between herd size and its propensity to break up, and stated that fragmentation of herds was not seasonal, but that severe drought may induce herd fragmentation. Taolo (2003) found that the buffalo in the Chobe National Park fragmented during the dry season, as did Funston (1992) who demonstrated that the buffalo in the Eastern Lowveld of South Africa maintained a stable herd structure, with fragmentation during periods of drought. In contrast, Mloszewski (1983) stated that buffalo herds in Kenya did not split up on a seasonal basis. Sinclair (1977) stated that buffalo herds in the Serengeti fragmented seasonally and aggregated in the wet season, as did Conybeare (1980) in Zimbabwe. Vesey-Fitzgerald (1974) observed that buffalo group sizes in Tanzania fluctuated seasonally with fragmentation mainly in the wet season.

The buffalo on Tswalu only once aggregated into a herd of 78 animals during the warm, wet season, but group sizes fluctuated both within and between the seasons, and sometimes even did so on a daily basis. This agreed with the results of Winterbach (1999) on buffalo in the Free State province of South Africa, but is in contrast to the above findings where herds aggregated in the wet season. Reasons for herd fragmentation as proposed by Sinclair (1977) include degradation of the habitat into patches too small to sustain large herds, and the beginning of the rutting season. On Tswalu, a herd of 53 animals (64% of the population) was regularly observed in the same area towards the end of the cold, dry season. This could have been due to the area previously being an enclosed camp of which the fences were lifted during August/September 2003, thus providing verdant graze.

A summary of the crude buffalo densities by various researchers all over Africa appears in Table 11. Sinclair (1977) demonstrated that buffalo density was dependent on food supply, and as food supply was dependent on rainfall, the crude buffalo density will be related to the mean annual rainfall (Fig. 15). The functional relationship between mean annual rainfall (mm) and buffalo density (buffalo/km²) is presented in Figure 15. This relationship appears strong ($R = 0.650$; regression equation: $y = 0.0188x - 8.396$, with y = buffalo density in buffalo/km² and x = mean

Table 11: Summary of the known crude buffalo densities (buffalo/km²) found in various studies in Africa

STUDY AREA	SOURCE	SIZE OF STUDY AREA IN km²	NUMBER OF BUFFALO PRESENT	CRUDE DENSITY	MEAN ANNUAL RAINFALL IN mm
Uganda (Acholi District)	Grimsdell (1969)	4 091.9	5487	1.3	1 029
South Africa (Kruger National Park)	Funston (1992)	20 000.0	26 400	1.3	577
South Africa (Willem Pretorius Game Reserve)	Winterbach (1999)	86.0	160	1.8	576
Botswana (Chobe National Park)	Taolo (2003)	5 494.0	2 747	2.0	600
South Africa (Sabi Sand Game Reserve)	Funston (1992)	570.0	1 230	2.2	577
South Africa (Hluhluwe-Umfolozi Corridor)	Brooks (1982)	900.0	2 430	2.7	850
Zimbabwe (Sengwa Wildlife Research Area)	Conybeare (1980)	373.0	1 040	2.8	600
Tanzania (Serengeti National Park - Moru)	Sinclair (1977)	271.4	900	3.3	700
Kenya (Tsavo National Park)	Leuthold (1972)	85.0	350	4.1	510
Tanzania (Serengeti National Park - Banagi)	Sinclair (1977)	143.8	800	5.5	787
Uganda (Queen Elizabeth National Park)	Grimsdell (1969)	1 568.6	16 036	10.2	952
Uganda (Ruwenzori National Park)	Eltringham & Woodford (1973)	1 559.0	18 708	12.0	1 200
Tanzania (Northern Serengeti National Park)	Sinclair (1977)	83.5	1 100	13.2	1 000
Uganda (Queen Elizabeth National Park)	Field & Laws (1970)	155.6	2 430	15.6	952

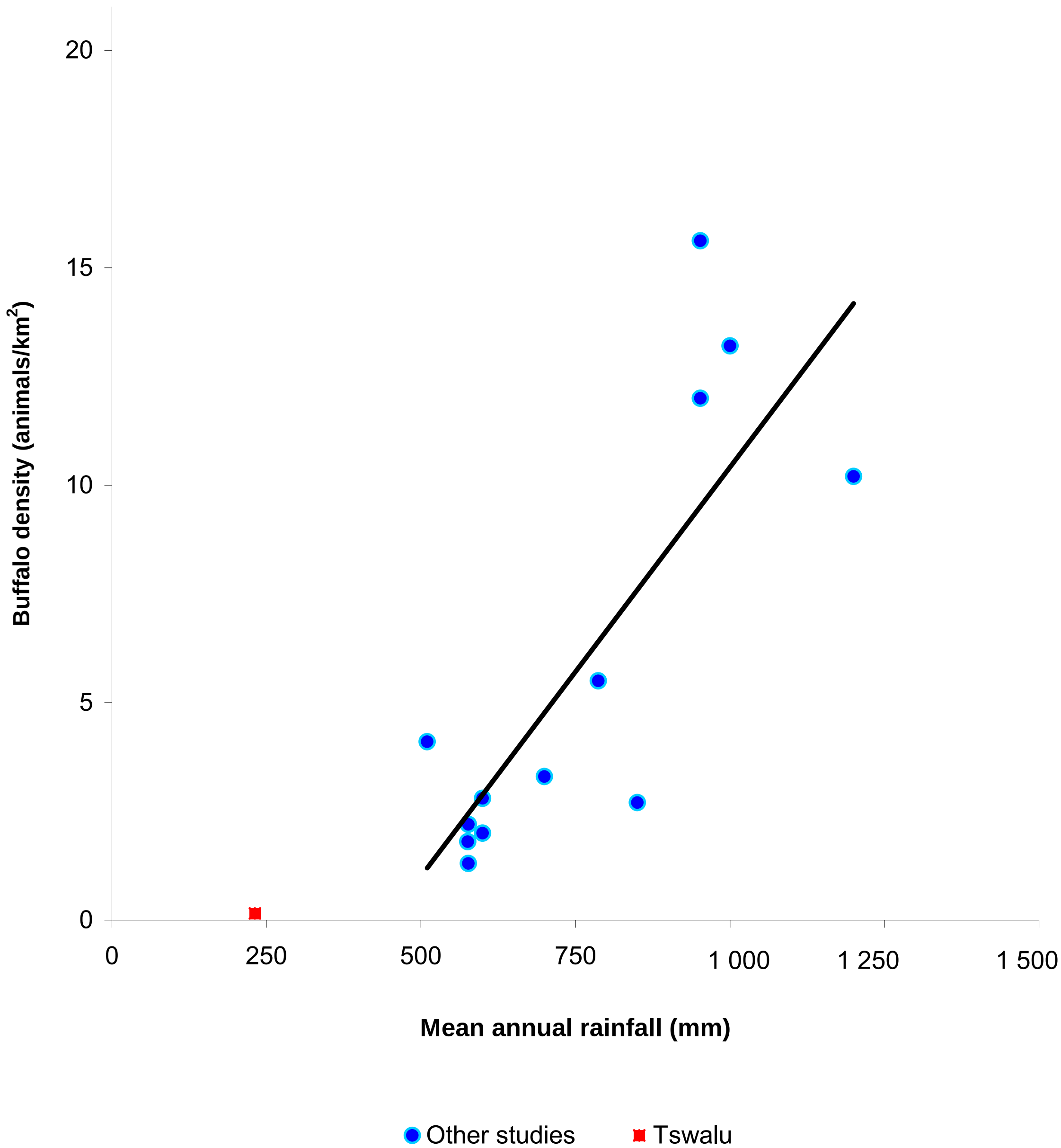


Figure 15: Buffalo densities according to various studies in Africa in relation to rainfall, compared to the buffalo density that was found on Tswalu Kalahari Reserve in the Northern Cape province of South Africa from April 2003 to July 2004.

annual rainfall in mm), where 49% of the variance of the buffalo density can be accounted for by the mean annual rainfall. This relationship was confirmed by Brooks (1982) for buffalo in KwaZulu-Natal, South Africa. In the studies of Funston (1992) and Winterbach (1999), the determined crude buffalo densities conformed to Sinclair's regression equation, but this equation could not be used for Tswalu because of its low rainfall. This may indicate that the low rainfall (annual mean: 229 mm) on Tswalu would be insufficient to sustain buffalo.

Range size of herbivores is related to habitat, with small ranges in wet regions and forested areas and larger ranges in drier open areas (Sinclair 1977). African buffalo ranges vary from 9.4 km² recorded in the Ruwenzori National Park (Eltringham & Woodford 1973) to 1 000 km² (Mloszewski 1983) in comparison with the water buffalo with a mean range of 10 km² (Mloszewski 1983).

Recorded buffalo range sizes in South Africa vary from 27.0 km² in the Free State (Winterbach 1999), 127 to 138 km² in northwestern Mpumalanga (Funston 1992) and 21.6 to 135.7 km² in KwaZulu-Natal (Brooks 1982). The total range size of the buffalo on Tswalu for the study period (205.7 km²) is therefore the largest recorded buffalo range in South Africa and is consistent with the theory of Sinclair (1977), who stated that herbivores in dry areas will have a larger range size than herbivores in wet or forested regions.

During the warm, wet season of October 2003 to April 2004, the range size (100% minimum convex polygon) of the buffalo on Tswalu was the largest recorded seasonal range (195.7 km²) during the study period (Fig. 10). Western (1975) found that buffalo range in the semi-arid Amboseli ecosystem decreased during the dry season when the herds concentrated around water. In Zimbabwe (Conybeare 1980), range size increased during the wet season, consistent with the results of Winterbach (1999) for buffalo in the Free State province of South Africa. However, total range size of the buffalo was also recorded to increase during the dry season in the Sabi Sand Game Reserve in South Africa (Funston 1992). From Figure 11 it can be seen that the buffalo utilised a larger area in the *Monechma incanum* shrubveld (Vegetation Unit 8) and the *Aristida meridionalis* open shrubveld (Vegetation Unit 6) during the warm, wet season than in the cold, dry season. Reasons for this could be the abundant shade and good summer grazing presented to the buffalo in the latter two vegetation units, and the presence of the pans in the west, which were utilised by the whole herd for wallowing during the warm months. During the warm, wet season, but especially after good rains, water puddles occasionally formed in the veld, which might also explain why the buffalo on Tswalu then utilised a large range.

During the cold, dry season the range of the buffalo included larger areas of the *Stipagrostis uniplumis* plains (Vegetation Unit 4), possibly because it fulfilled most of the buffalo's needs for grazing and water (Chapter 6). Another factor that might have played a role in the high degree of occurrence of buffalo in this vegetation unit may have been that supplementary feeding was done in this unit.

Nevertheless, the 100% minimum convex polygon tends to give an overestimate of range because areas not frequently visited by the buffalo were included. The peeled range (95% minimum convex polygon) for the warm, wet season was 170.0 km² compared to 171.7 km² in the cold, dry season, which is 31.8% of the total surface area of Korannaberg. This suggests a similar range size during both seasons but the range area still differs with a shift in utilisation towards the northern part of Korannaberg during both seasons. This confirmed that the *Hermannia burchellii* shrubveld (Vegetation Unit 5) around the pan areas was not preferred during the cold, dry season and was only visited occasionally as determined with the 100% minimum convex polygon method (Chapter 4). The reasons for this could be the limited amount of available water to the water dependent buffalo, present in the pans during this time together with a low grazing capacity (Fouché & Avenant 2004).

During the cold, dry season the buffalo also moved north into the *Eragrostis pallens* dune streets (Vegetation Unit 3), and this could be because of abundant good quality grazing, three water points and the limited shade present in this unit (Chapter 4). However, the high buffalo preference during the cold, dry season there was likely influenced by supplementary feeding during the winter months of 2004. During the warm, wet season the buffalo utilised the area around the pans although they only occasionally visited the area to the south of the pans (Fig. 12 compared to Fig. 10) and were never observed in the area west of the pans. Two possible reasons for this could be the deep, sandy nature of this area and the low grazing capacity (Fouché & Avenant 2004) that does not make it rewarding in nutritional terms, for the buffalo to explore this area more, most probably they have learnt this on past explorations. The buffalo only utilised the western part of the *Stipagrostis uniplumis* plains (Vegetation Unit 4), and this vegetation unit fulfilled most of the buffalo's needs in terms of preferred grazing, water and protection from climatic extremes (Chapter 4). The absence of water in the eastern part of this vegetation unit might explain why this area is not part of the buffalo range. The reason for the absence of buffalo range in the eastern part of Korannaberg could be due to the presence of the Korannaberg Mountain Range that is covered by rocky and often quite steep hills (Van Rooyen 1999), which were relatively inaccessible to the buffalo. The reason for the large part of the *Eragrostis lehmanniana* dune valleys and plains (Vegetation Unit 7) that were not within the buffalo range could not be explained.

In the current study, core area of range use (50% adaptive kernel) was the largest during the cold, dry season adding up to a surface area of 45.2 km² (22.1% of the total range in Korannaberg of 205.7 km²) distributed over two different clusters (Fig. 13). During the warm, wet season the core area of range use was only 13.1 km² (Fig. 14) or 6.4% of the total range size (205.7 km²) in Korannaberg. The buffalo core area of range in the northern part of Korannaberg included one water point within this cluster in the warm, wet season (Fig. 14) compared to three water points during the cold, dry season (Fig 13). This seasonal difference in the size and locality of the core area of use could be due to the water dependant nature of buffalo (Prins 1996), combined with their attempts to seek out the most suitable habitat in terms of food, and shelter resources (Funston 1992).

The core area of buffalo range use was larger during the cold, dry season because they had to search more for adequate quality food, however their movements were always guided by proximity to water. The smaller warm, dry season range coincided with the peak calving season on Tswalu and the smaller range size could be explained by the reduced ability of the herd to move large distances with young calves. The eastern edge of this cluster during the warm, wet season (Fig. 12) was in the *Stipagrostis amabilis* dune crests (Vegetation Unit 1) and field observations showed that it was predominantly used for resting in the shade of *Terminalia sericea* trees during the warm season. From the results obtained, it was clear that the buffalo on Tswalu preferred the northwestern part of the Korannaberg section. However, the population received supplementary feeding there during the latter part of the cold, dry season in 2004, and this could have influenced their movement patterns.

Funston (1992) determined the buffalo density on the total terrestrial surface of his study area, (termed crude buffalo density), to be 2.16 buffalo/km² compared to the buffalo density within their range size, (termed range density), to be 2.07 buffalo/km². The similarity between crude and range densities implied that the suitable buffalo habitat was distributed uniformly through the area. Winterbach (1999) found a difference in the crude and range densities of the buffalo in the Willem Pretorius Game Reserve of 3.9 buffalo/km² (crude density: 1.8 buffalo/km² and range density: 5.7 buffalo/km²). This was an indication of the localised occurrence of suitable buffalo habitat in the Willem Pretorius Game Reserve (Winterbach 1999). On Tswalu, the crude buffalo density was 0.15 buffalo/km² (83 buffalo on the total surface area of Korannaberg), compared with the range density of 0.40 buffalo/km² (83 buffalo on the year round range of 205.7 km²). The three-fold difference between these estimates suggests localised suitable habitat rather than uniform habitat for the buffalo on Tswalu.

Working in East, Central and West Africa, Mloszewski (1983) concluded that buffalo walked a mean distance of 5.4 km/day, along a fixed route by using landmarks rather than wind as an indication of direction. Funston (1992) found buffalo in the South African Lowveld to walk up to 10 km on a winter night in search of better grazing, while buffalo in the Free State province of South Africa travelled a mean distance of 6.9 km/day (Winterbach 1999). Daily distances walked by buffalo were not studied intensively in the current study, but the furthest recorded distance moved by buffalo during 24 hours was 16.03 km, that is much further than the other recorded daily movements of buffalo in South Africa.

Conclusions

Tswalu has a low buffalo density when compared with that found in other studies. The suitable available buffalo habitat occurs in localised patches in the Korannaberg section, and the northwest of the Korannaberg section is clearly being preferred during both seasons by the buffalo. It appears that the main driving force behind their range selection was the protection from climatic extremes (Chapters 4), the quality and quantity of food (Chapters 4 and 6), and proximity to water points. These were regardless of the fact that supplementary feeding could have altered the movement patterns, and thus range size of the buffalo in the Korannaberg section of Tswalu Kalahari Reserve.

CHAPTER 6

FEEDING ECOLOGY

Introduction

The dietary requirements of an animal are central to animal ecology (Sinclair 1977; Johnson 1980) and the management of any species depends on a thorough knowledge of its nutritional requirements (Robbins 1993; Von Holdt 1999; Theobald 2002). Animals are dependent upon energy and nutrients obtained from ingested food (Pellew 1983; Prins 1996), and their survival and fertility are directly affected by nutrition (Field 1972, 1976; Wrench, Meissner & Grant 1997; Gordon 2003). Sinclair (1977) found by that the need for food and water by buffalo were more important than protection from environmental extremes during the dry season.

The quality and quantity of forage for herbivores in African savannas fluctuates seasonally and spatially (Field 1972; Macandza *et al.* 2004). In arid systems, water is the most important limiting factor and influences the nutrient uptake by plants (Noy-Meir 1973). In the arid Northern Cape province, a critical minimum of 20.6 mm rainfall/year is needed before any production would occur, and then the forage production is estimated at approximately 5 kg/ha/mm of rain (Lloyd & Fairall 1992). Seely & Louw (1980) found that the vegetation in the Namibian dune system responds dramatically after rains; with the energy contained in the plant biomass increasing nine-fold. Eland and blue wildebeest died in the southern Kalahari region during the droughts of 1982 and 1985 due to the limited moisture content of the plants (Van Hoven 2002).

Numerous studies have been completed on aspects of buffalo feeding ecology and include the work of Leuthold (1972), De Graaff *et al.* (1973), Vesey-Fitzgerald (1974), Field (1976), Sinclair (1977), Prins (1996), Taolo (2003) and Halley & Minanawa (2005). The buffalo is one of the most important ecological agents of a wild herbivore community in Africa. Because its total biomass exceeds that of any other ungulate, its grazing and trampling can have a detrimental effect on the vegetation (Funston 1992). Buffalo are believed to be bulk grazers (Sinclair & Gwynne 1972; Landman & Kerley 2001), however, it has been demonstrated that there is a dietary shift in buffalo during periods of severe drought and food shortage, when they temporarily become browsers (De Graaff *et al.* 1973).

Buffalo require a combination of high-quality grass with high fibre content, and will select nutritious grass species (Sinclair 1974c; Perrin & Brereton-Stiles 1999). At the end of the dry season on Tswalu, the availability of food and the nutrient concentration of the available food are expected to be low, while the intake of quality food by the buffalo is expected to be impaired. The purpose of this part of the dissertation was therefore to determine the feeding preferences of the buffalo on Tswalu. Following this, it might be possible to determine whether there was a specific period when the buffalo population was under severe nutritional stress.

Methods

Field data

Four basic older methods can be used to asses the diet of a herbivore: examination of the stomach contents, examination of faecal material, microscopic examination of plant residue recovered from oesophageal fistulae, and direct visual observation of feeding behaviour (Lamprey 1963; Mcinnis, Vavra & Krueger 1983; Caughley & Sinclair 1994; Wrench *et al.* 1997). A more modern approach is the use of stable isotope analysis, but this is a costly exercise (Sponheimer, Grant, De Ruiter, Lee-Thorp, Codron & Codron 2003; Arceo, Mandujano, Gallina & Perez-Jimenez 2005; Codron, Codron, Lee-Thorp, Sponheimer & De Ruiter 2005; Halley & Minagawa 2005). The examination of faecal samples is simple and unobtrusive (Wrench *et al.* 1997), although the determination of the chemical composition of the faeces is expensive. With the study of rumen ingesta the animal has to be sacrificed or surgically fistulated (Mcinnis *et al.* 1983). Fistulation is an expensive method that includes surgery but has been used with success in feeding trials of domestic animals (McDonald, Edwards, Greenhalgh & Morgan 1998).

In the current study, direct observations were used to determine preferences of the buffalo for specific food species. To determine the quality of these preferred species, plant material was collected and chemically analysed. Faeces were collected for chemical analysis to determine the current nutritional state of the buffalo on Tswalu.

Direct observations

Direct observation of feeding behaviour in wildlife is widely used in research (Strauss 2003). This method is unobtrusive, simple and does not require expensive laboratory work (Cornelis, Casaer & Hermy 1999). The technique has one problem in that it can be difficult to identify plants from a distance, but this can be overcome by investigating the feeding site after the animals have moved away (Jarman 1971; Ben-Shahar 1991; Strauss 2003).

The feeding ecology of the buffalo on Tswalu was studied with direct observations using a set of 8 X 42 binoculars and a 0.5 m spotting scope. Species fed upon that could not be identified from a distance were inspected after the buffalo had left the feeding site. Direct observations of the feeding buffalo started in April 2003 and continued until July 2004, for 10 days of each month with the exception of November and December 2003. Recordings were made randomly by identifying an individual buffalo and recording the species of each new plant selected by that individual. If the identified buffalo moved out of sight, another one would be selected and the observations were continued. The plant parts being utilised were recorded if possible, when the identified buffalo lifted its head and a part of the plant became exposed to observation, or the grazing patch was investigated after the buffalo had left and comparisons were made with the available plant parts from the same species not utilised in that area. Observations were made in 20-minute intervals, spread over 2 hours of feeding, during both the morning grazing and the evening grazing sessions. Only grass species fed upon were recorded during these observation times. A total of 960 feeding records were made in the cold, dry season and 718 in the warm, wet season.

Plant material collections

The preferred grass species were identified and samples were collected to determine the quality of the grazing available to the buffalo population. The areas of buffalo preference on Tswalu were identified as (Chapter 4), and grass samples were collected in ten randomly placed plots of 5.0 m x 5.0 m each, in these different areas, giving 30 sample plots. Four grass species were collected in August 2003 to represent utilisation of the buffalo during the cold, dry season of 2003, and included *Eragrostis lehmanniana*, *Centropodia glauca*, *Schmidtia pappophoroides* and *Stipagrostis uniplumis*. During February and April 2004, six grass species were collected for representation of grass species utilisation by the buffalo during the warm, wet season and included the above-mentioned species, together with *Digitaria eriantha* and *Eragrostis pallens*.

Each grass plant was cut to a height of approximately 0.05 m above ground, weighed and stored in Ziploc bags for transportation to the laboratory. Approximately 2.5 kg fresh mass of each species was collected in each plot, and the same grass species from the different plots and areas were pooled for chemical analysis. *Stipagrostis uniplumis* was cut at a height of 0.05 m from the top of the plant and only the top 0.15 m of the inflorescence of *Eragrostis pallens* was cut because the buffalo did not utilise these plants lower than the mentioned heights. *Digitaria eriantha* was sampled with its roots, because these were included in the buffalo utilisation.

The samples were analysed with the assistance and facilities of the UP Nutrilab[4] at the University of Pretoria. The dry matter (DM) content of all samples was analysed to express results on a dry matter basis as described in the publication of the Association of Analytical Chemists (A.O.A.C.

[4] Department of Animal and Wildlife Sciences, University of Pretoria, Pretoria, 0002, South Africa.

1984). Faecal and plant samples were oven-dried at 40° C for 48 hours. Samples were then milled to uniform consistency in an IKA 10 analytical mill (Kika Werke, Germany). Dry matter content was determined by placing 0.01 kg of the sample in a porcelain crucible in an oven for 12 hours at 100° C. The crucibles were then placed in a desiccator to cool down and then weighed. Ash content was determined by placing the crucibles from the dry matter study in an oven at 600° C for 4 hours. After a cooling period of 2 hours, the samples were weighed.

Nitrogen content was determined with the Makro-Kjeldahl method (AOAC 1984), and the amount of nitrogen obtained was multiplied by a factor of 6.25 to yield the approximate protein value (McDonald *et al.* 1998). The gross energy value of the faecal samples was determined with a bomb calorimeter (Robbins 1993). *In vitro* digestibility was determined with the centrifuge method, using rumen liquid from a rumen fistulated sheep fed on lucerne (Czerkawski 1986; McDonald *et al.* 1998). The neutral detergent fibre (NDF) was determined with the extraction method using the Dosi Fibre System (Robertson & Van Soest 1981), and the acid-detergent fibre (ADF) fraction was determined after refluxing with 0.5 M sulphuric acid and cetyltrimethyl-ammonium bromide (Goering & Van Soest 1970). The minerals were analysed with a Perkin-Elmer Atomic Absorption Spectrophotometer after wet digestion in a temperature-contolled digestion block (McDonald *et al.* 1998). Bovine liver and lucerne (National institute of Standards and Technology, standard reference material 1577a) served as laboratory controls.

Neutral-detergent fibre (NDF) was determined in the present study to give an indication of lignin, cellulose and hemicellulose present in the plants eaten and gives an indication of the rate of digestion. The acid-detergent fibre (ADF) represents crude lignin and cellulose fractions, together with silica. Acid-detergent fibre was also determined in the present study to give an indication of digestibility (McDonald *et al.* 1997).

The studies of Sinclair (1977) and Prins (1996) were used to evaluate the current nutrient status of the buffalo on Korannaberg. The maintenance requirements of the buffalo on Tswalu were derived from the nutrient requirements of cattle as outlined in the publications of the National Research Council (NRC). An animal is considered to be in a state of maintenance when its body composition is constant, no product such as milk is produced and no work is being performed (McDonald *et al.* 1998). Adult buffalo requirements were derived from the requirements of beef cattle (National Research Council 1996), and those of lactating buffalo from dairy cattle (National Research Council 2000).

Faecal collections

Faeces were collected twice weekly during September 2003, from animals in different stages of production. Collections were made in the early morning when the herd grazed, and during late afternoon after the herd got up from their morning resting period. A total of 10 faecal samples were collected during each of the collection periods, thus representing 10 different animals per sample time. With each collection, at least 200 g wet mass faeces were collected in Ziploc bags. Care was taken not to collect samples that were contaminated with soil, dung beetles or insects, and samples older than one day were considered too old for analysis and collection (Wrench, Meissner, Grant & Casey 1996). For analytical and financial purposes, the samples were pooled according to sex and production status into adult bulls, lactating females and adult non-lactating females. After weighing the samples, brown paper bags were used to air-dry the samples.

Physical condition scoring

The physical condition of animals influences mortality and reproduction (Sinclair & Duncan 1972), and it could give an indication of the response of a given population to their ecosystem (Riney 1956). Once a condition assessment method has been standardised, it is possible to evaluate the effects of current and past management practices and ecological conditions (Smith 1970), while the physical condition of the animals can also be compared between areas. Several methods have been described and used with success in determining physical condition of animals. These include kidney and bone marrow fat (Smith 1970; Sinclair & Duncan 1972), liver analysis (Berry & Louw 1982), other fat deposits (Smith 1970), live mass ratio (Smith 1970), blood analysis (Berry & Louw 1982), and physical condition scores (Riney 1960; Berry & Louw 1982). According to Prins (1996), physical condition, or changes in condition rather than changes in mass, are more reliable for evaluating the nutritional status of cattle. Condition scores also provide a reliable measure of the animal's nutritional reserves (Ferguson, Galligan & Thomsen 1994).

The physical condition of the buffalo in the current study was determined with the non-invasive physical condition scoring system. Observations were made during June 2003, October 2003, February 2004 and June 2004. The system used here, was compiled with guidelines from Riney (1960), Berry & Louw (1982), and Wildman, Jones, Wagner, Boman, Troutt & Lesch (1982). The following classes were used (Appendix A):

- **Emaciated** (Condition score 1 to 1.9): Spinous processes are conspicuous, giving a saw-tooth appearance, with an overhanging shelf effect in the loin region. The area between the spinous and transverse processes shows a deep depression. False ribs are clearly visible with the tuber coxae (hook bones) and tuber ischii (pin bones) appearing extremely sharp and without any fat cover. The pelvic area between the hook bones is severely depressed with no fat cover on the sacro-sciatic ligament (tailhead ligament), resulting in a cavity under the tail giving the tail an angular appearance.

- **Poor** (Condition score 2 to 2.9): Individual spinous processes are evident with a sharp, prominent ridge. There is an obvious depression in the area between the spinous and transverse processes. Less than a quarter of the false ribs is clearly visible, the tuber coxae (hook bones) are visible and the tuber ischii (pin bones) have an angular appearance. The pelvic area shows signs of limited flesh covering and the area between the tailhead and pin bones shows evidence of fat deposition.
- **Moderate** (Condition score 3 to 3.9): Individual spinous processes are not distinguishable and appear smooth. The area between the spinous and transverse processes appears as a smooth slope. The transverse processes are just discernable and the tuber coxae (hook bones) are tuber ischii (pin bones) appear covered and rounded. The area between the hook and pin bones appears as a slight depression as do the area between the pin bones. No bones are visible in the pelvic area and the sacral and tailhead ligaments are visible.
- **Good** (Condition score 4 to 4.9): Spinous processes not visible and appear smooth and filled. The area between the spinous and transverse processes appears nearly flat in the loin region. The edge of the transverse processes is just visible and the tuber coxae (hook bones) are barely visible and the tuber ischii (pin bones) are buried in flesh. The area between the hook and the pin bones is flat. No bones are visible in the pelvic area and a slight fat-filled depression is visible under the tail.
- **Excellent** (Condition score 5): Spinous processes, tuber coxae (hook bones) and the tuber ischii (pin bones) are not visible and buried in fat. The overall appearance of the animal is rounded and bulging. The tail head is not clearly visible and appears buried.

Grazing capacity and stocking density

A key concept in the management of wildlife populations is correct habitat management (Bothma, Van Rooyen & Van Rooyen 2004). Plant communities, especially the grass component, are not static but show marked temporal variation. Consequently the ability of a plant community to sustain animals also shows temporal variation. The main reason for the temporal variation is rainfall (Van Rooyen 2002a), especially in arid environments (Fourie, Van Niekerk & Fouché 1985). Other reasons for temporal variation in the ability of a plant community to sustain animals include soil type, topography and veld condition (Fourie *et al.* 1985). Rainfall cannot be controlled, but veld condition can be monitored and managed through the control of animal numbers. One method to monitor the grazeable proportion on a property is to determine the so-called carrying capacity. The carrying capacity concept was based on the area of land required to maintain a steer of 450 kg with a mass increase of 500 g per day, on feed with a mean digestible energy of 55%, also termed Large Stock Unit (LSU), and is expressed as ha/LSU (Meissner 1982). The carrying capacity concept based on domesticated grazers, was later implemented in the wildlife industry where comparisons were made between wildlife and the metabolic energy requirements of an adult steer (Meissner 1982), from here grazing capacity was determined. Trollope (1990) later defined grazing capacity as '' *the productivity of the grazeable portion of a homogeneous unit of vegetation expressed as the area of land required to maintain a single large stock unit over an extended number of years without deterioration of vegetation or soil*''. However, wildlife usually graze and browse proportionally depending on their digestive physiology (Landman & Kerley 2001), and the characteristics of the specific vegetation type where the animal occurs (De Graaff *et al.* 1973; Gordon 2003).

Bothma *et al.* (2004) developed a model where stocking densities for wildlife can be determined as grazing and browsing capacity after evaluating the condition of the available plant resources. Grazing capacity is then the area of land needed to sustain a blue wildebeest with a mass of 180 kg, also termed grazer unit (GU), over a number of years without deterioration of the vegetation and is expressed as GU/100 ha (Bothma *et al.* 2004). A greater kudu with a mass of 140 kg is taken as one browse unit (BU), and the area needed to maintain one browse unit is termed the browsing capacity, expressed as BU/100 ha (Van Rooyen 2002b; Bothma *et al.* 2004). The ecological grazing and browsing capacity of an area is the maximum number of grazers and browsers that the area can maintain (Van Rooyen 2002b). The economic grazing and browsing capacity is aimed at optimal wildlife production and is 70 to 80% of the ecological capacities (Van Rooyen 2002b; Bothma *et al.* 2004). The amount of standing browse in each vegetation type can be used to determine the browsing capacity, with data analysis being done with the Biomass Estimates from Canopy Volume (BECVOL) computer program (Smit 1989). Only 9% of the determined standing browse is available to herbivores (Von Holdt 1999).

The management of Tswalu implemented continuous vegetation monitoring on Tswalu in 2003 under the supervision of Fouché[5] and Avenant[6]. Data from their surveys done in March/April of 2003 and 2004 were used to determine the ecological capacity for Korannaberg. From these results, the potential stocking density of the buffalo on Korannaberg was determined for the 2004 season, within each vegetation unit of Korannaberg.

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[5] Dr H Fouché, Agricultural Research Council: Range & Forage Institute, PO Box 339, University of the Free State, Bloemfontein, 9300, South Africa.
[6] Mr P Avenant, Agricultural Research Council: Range & Forage Institute, PO Box 339, University of the Free State, Bloemfontein, 9300, South Africa.

African herbivores can be divided into various feeding classes based on their diet composition (Gordon 2003), stomach-structure (Hoffmann & Stewart 1972) and body mass (Clauss & Hummel 2005). Gagnon & Chew (2000) classified herbivores into six feeding classes based on the proportion of dicotyledons (leaves, buds, shoots, twigs, flowers, blossoms, shrubs, forbs, non-grassy herbs) and monocotyledons (grasses, reeds and sedges) in the diet. A simplified classification of four feeding classes was developed by Bothma *et al.* (2004), based on the proportion of dicotyledons and monocotyledons in the diet as well as mouth anatomy. These classes include the low selective grazers (wide mouths with > 80% grass in their diet), high-selective grazers (narrow mouths with >70% grass in their diet), mixed feeders (> 30 to 70% grass or browse in their diet) and the browsers (> 80% browse and wild fruits).

Data analysis

Direct observations

The plant species selection and plant part selection were recorded on a field form and subsequently captured in Microsoft Excel. The data were then subjected to the PROC FREQ procedure in the SAS® statistical computer program to detect any seasonal differences in selection and utilisation.

Plant and faecal samples

Dry matter intake can be determined with the equation used by Sinclair (1974a) on buffalo in East Africa:

$$DMI = 0.09 \times W^{0.75}$$

where:

DMI = dry matter intake (kg/day)

W = the mean mass of the animal (kg)

Metabolizable energy values (digestable energy taking into account energy losses in urine and during gas production) can be calculated with the relationship between protein and energy content in the food, which is related to the digestible organic matter as (Prins 1996):

$$ME = [1657 + (50.9208 \times CP)] / 1000 \times 4.184.$$

where:

ME = metabolizable energy (MJ/kg DM)

CP = crude protein (%)

If the metabolizable energy (MJ/kg DM) content of each grass species is multiplied by the daily intake of a buffalo bull or cow, the approximate daily metabolizable energy intake per sex can be determined.

The chemical analyses were done in duplicate, and the percentage error between the two duplicates analysed for each fraction of each sample, was ascertained by using the following equation:

$$\% \text{ error} = A - B / A * 100$$

where:

A = maximum value obtained during the analysis

B = minimum value obtained during the analysis

If the percentage error between the duplicate samples of the crude protein was higher than 5%, the analysis was repeated. The critical values for all other fractions were 10% because of less accurate analytical methods, and because the smaller a specific fractions is, the larger the influence of a relatively small experimental error on the percentage error.

Differences between the nutritive values of the different grass species were tested with the student *t*-distribution (Sachs 1982; Samuels 1989), at a significance level of $\alpha \leq 0.05$. Significance of the differences found in the mineral content between different sexes and the productivity level of the sexes in the faecal samples, were also tested with the student *t*-distribution at a similar significance level.

Grazing capacity and stocking density

To determine the grazing capacity of the buffalo on Tswalu, the *Opuntia ficus-indica* disturbed areas and the *Enneapogon desvauxii* panveld were not included in calculations because both vegetation units do not contribute to the grazing capacity of Tswalu (Van Rooyen 1999; Fouché & Avenant 2003). The model of Bothma *et al.* (2004) was used to determine the grazing capacity of Korannaberg. The range-condition index was determined by classifying the grasses and forbs into five ecological classes, and then calculating the contribution of each class to the range-condition score, multiplied by a weighted constant that reflects the grazing value, palatability and productivity in phytomass. The classes were as follow (Bothma *et al.* 2004):

Class 1: Valuable and palatable tufted or stoloniferous grass species with a high productivity and grazing value (weighted constant of 10).
Class 2: Tufted, perennial grass species with an intermediate productivity and moderate grazing value (weighted constant of 7).
Class 3: Tufted, tall, perennial grass species with a high productivity but low grazing value (weighted constant of 5).
Class 4: Unpalatable annual and perennial tufted or stoloniferous grass species with an intermediate productivity and a low grazing value (weighted constant of 4).
Class 5: Unpalatable annual grass and forb species with an intermediate productivity and low grazing value (weighted constant of 1).

The long-term grazing capacity was calculated with the equation of Coe, Cumming & Phillipson (1976) that was developed for areas receiving from 156 to 650 mm rainfall annually. The equation is:

$$LHB = (8.684 \times AP) - 1205.9$$

where:
LHB = large herbivore biomass (kg/km^2)
AP = annual precipitation (mm)

The optimum grazing capacity can be estimated annually with the regression equation of Fourie *et al.* (1985), developed for the arid area of the Northern Cape, based on rainfall. The equation is:

$$GC = 41.71 - (0.080 \times R)$$

where:
GC = grazing capacity (ha/LSU)
R = rainfall (mm)

Calculation of the recommended buffalo grazing capacity was based on the overall grazing capacity of Korannaberg for 2004. The *Opuntia ficus-indica* disturbed areas and the *Enneapogon desvauxii* panveld were not included as discussed above, and the *Anthephora pubescens* dunes and *Digitaria polyphylla* mountains and hills were also not included in calculations, because the buffalo were never observed in these two vegetation units during the study period (Chapter 4). This reduced the available habitat of the buffalo to 50 060.2 ha. The preliminary grazing capacity was calculated as 25% of the total grazing capacity allocated to low selective grazers, and the recommended buffalo grazing capacity was calculated assuming that buffalo will utilise 40% of the graze available to low selective grazers.

Browsing capacity was determined with the results obtained from the survey data of Fouché & Avenant (2004), and the method described in Bothma *et al.* (2004). The available browse was determined as 9% of the mean standing browse, which was then divided by the amount of browse (kg) needed to maintain one BU/year. One greater kudu that weighs 140 kg is the equivalent of one BU and needs 3% of its body weight on a daily basis (Von Holdt 1999). Therefore, one BU will need 4.2 kg browse per day, or 1 533 kg browse/year.

The current stocking density of Korannaberg was determined with the method described in Bothma *et al.* (2004), where a conversion factor was used for each type of wildlife to convert animal numbers into GU/animal and BU/animal. The conversion factors were based on the relative metabolic mass of each type of animal (Meissner 1982). The total number of GU and BU present on the reserve, as determined by the amount of animals of each type present on Korannaberg in 2004, would indicate whether Korannaberg has reached ecological grazing and browsing capacity.

Results

Direct observations

During this study the buffalo on Tswalu utilised 19 plant species of which 13 were grass species (Table 12). The buffalo favoured *Schmidtia pappophoroides*, *Eragrostis lehmanniana* and *Centropodia glauca* during the study period. During the cold, dry season *Stipagrostis uniplumis* was also selected and *Digitaria eriantha* was preferred during the warm, wet season (Table 12). The grass component dominated during the cold, dry season in the diet of the buffalo on Tswalu with 7.9% of the diet consisting of shrubs (Fig. 16). During the warm, wet season grasses still dominated, but utilisation of forbs was 22.2%, with *Merremia verecunda* being utilised 12.5% (Fig. 17). Roots, leaves and inflorescences were predominately utilised during the warm, wet season, with culms being preferred during the cold, dry season (Fig. 18).

Table 12: Percentage of the different plant species utilised by the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa, during the two ecological seasons, determined by direct observations on the feeding buffalo

SPECIES	**PERCENTAGE**	
	Cold, dry season	Warm, wet season
Grasses		
Anthephora pubescens	5.7	4.2
Cenchrus ciliaris	2.2	0.0
Centropodia glauca	11.9	8.9
Digitaria eriantha	2.2	10.7
Digitaria polyphylla	0.0	0.9
Eragrostis lehmanniana	20.0	8.9
Eragrostis pallens	0.0	4.5
Panicum coloratum	0.0	4.5
Panicum maximum	2.2	0.9
Schmidtia pappophoroides	27.7	21.4
Stipagrostis ciliata	4.2	2.1
Stipagrostis obtusa	4.2	1.8
Stipagrostis uniplumis	10.6	5.4
Shrubs		
Grewia flava	4.7	1.8
Rhus tenuinervis	3.2	0.0
Dwarf shrubs		
Monechma incanum	0.0	1.8
Forbs		
Indigofera alternans	0.0	4.5
Merremia verecunda	1.2	12.5
Tribulus zeyheri	0.0	5.2

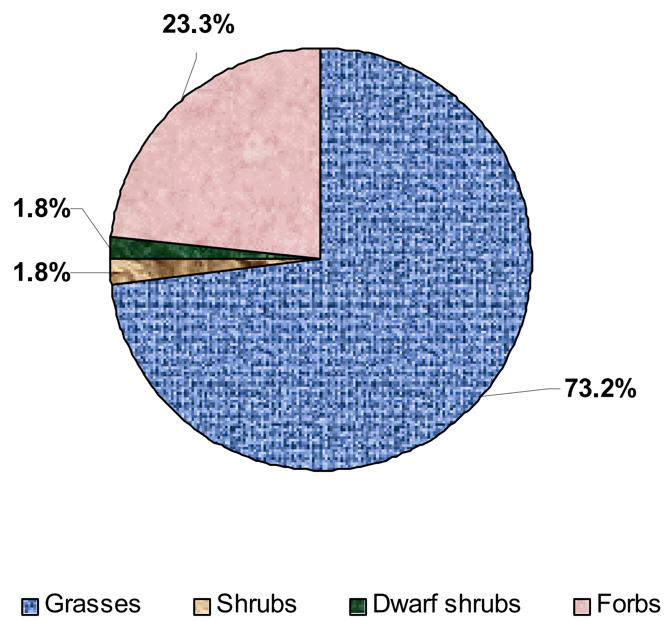

Figure 16: The utilisation of different vegetation growth forms by the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa during the cold, dry season. Utilisation was determined by direct observations on the feeding buffalo.

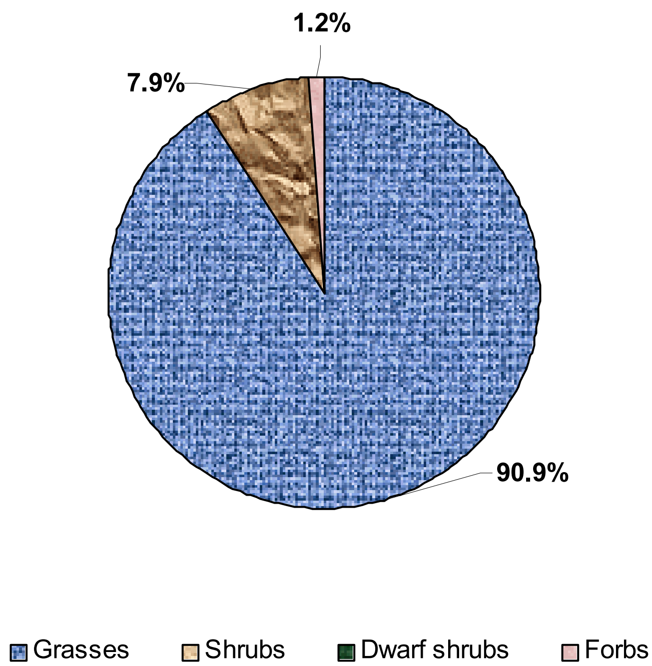

Figure 17: The utilisation of different vegetation growth forms by the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa during the warm, wet season. Utilisation was determined by direct observations on the feeding buffalo.

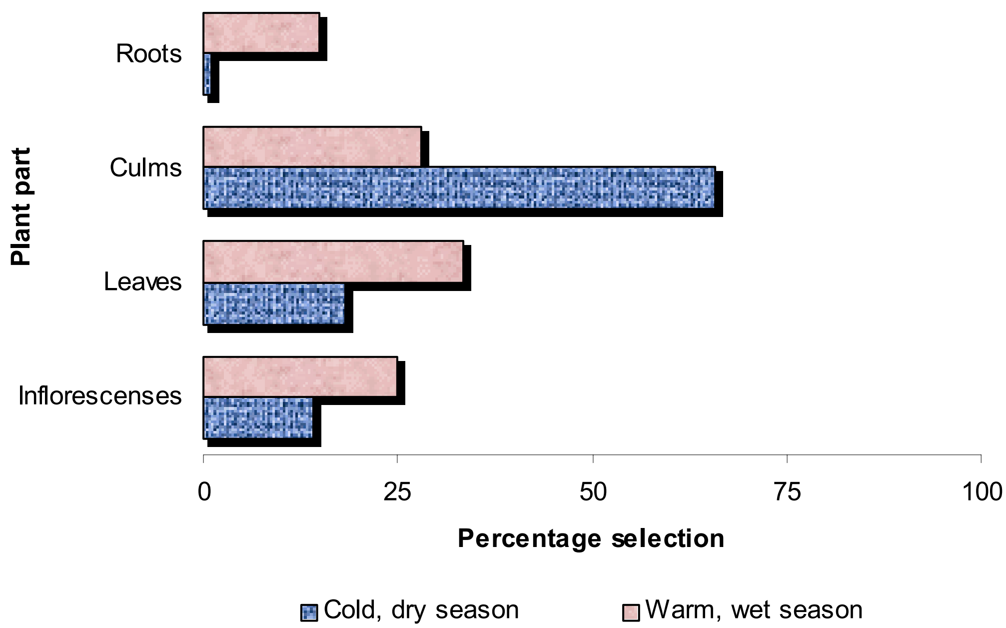

Figure 18: The selection of plant parts of the utilised vegetation by the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa during the two ecological seasons.

Plant material analysis

The mean mass for animals in this study was estimated to be 450 kg for an adult female buffalo and 600 kg for an adult bull (Sinclair 1974c, 1977; Van Hoven 1980; Prins 1996; Du Toit 2002, 2005). This resulted in a dry matter intake for adult females (450 kg) of 8.8 kg/day, and that for adult bulls (600 kg) to be 10.9 kg/day. The estimated annual consumption of grass by the subadult and adult buffalo on Tswalu is 203 000 kg, based on a mean mass of 400 kg for the subadult and adult proportion of the population, numbering 69 animals, that consumed a mean of 8.0 kg/buffalo/day.

Grasses generally have a mean gross energy value of 18.5 MJ/kg DM (McDonald *et al.* 1998). The *in vitro* digestibility of the grasses gives an estimate of the digestibility of the foods eaten. For example, for an energy value of 18.5 MJ/kg, and for *Centropodia glauca* with an *in vitro* digestibility of 38.8%, only 7.0 MJ/kg DM is available to the buffalo. The metabolizable energy provided by the grasses on Tswalu is represented in Table 13. Prins (1996) described the requirements of buffalo for protein in terms of metabolic mass, as indicated in Table 14.

Eragrostis lehmanniana and *Centropodia glauca* had the highest crude protein content (5.49%) of the four preferred grass species during the cold, dry season, with *Centropodia glauca* having the highest crude protein content (9.24%) during the warm, wet season (Table 15). There was also a significant increase in apparent *in vitro* digestibility of *Centropodia glauca* from the cold, dry season to the warm, wet one (t = 24.61; df= 4; $p \leq 0.05$).

Eragrostis lehmanniana seemed to be the most constant in cell wall content and apparent digestibility during the two seasons. *Schmidtia pappophoroides* showed a significant decrease in cell wall content (NDF) from the cold, dry season to the warm, wet one (t = 9.34; df = 3; p ≤ 0.05). Significant decrease in acid detergent fibre was observed in *Centropodia glauca* (t = 8.47; df = 3; $p \leq 0.05$) and *Schmidtia pappophoroides* (t = 8.18; df= 3; $p \leq 0.05$) from the cold, dry season towards the warm, wet season.

The micro-mineral contents of the preferred grass species are given in Table 16. The iron content of *Schmidtia pappophoroides* showed a significant increase towards the warm, wet season (t = 13.90; df = 3; $p \leq 0.05$), while the iron content in the remainder of the species decreased significantly. Manganese content did not change significantly in *Eragrostis lehmanniana*, but did decreased significantly in the remaining species towards the warm, wet season. All the analysed species demonstrated a significant increase in copper and zinc content towards the warm, wet season. *Centropodia glauca* showed significant increases for copper and zinc content towards

Table 13: Metabolizable energy (ME), provided by the preferred grass species eaten in relation to intake for buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa

SPECIES	COLD, DRY SEASON			WARM, WET SEASON		
	ME (MJ/kg DM)	ME intake (MJ/day) bull [a]	ME intake (MJ/day) cow [b]	ME (MJ/kg DM)	ME intake (MJ/day) bull [a]	ME intake (MJ/day) cow [b]
Centropodia glauca	7.9	86.2	69.5	8.9	97.0	78.3
Schmidtia pappophoroides	7.9	86.2	69.5	8.7	97.1	76.6
Eragrostis lehmanniana	8.1	88.3	71.3	8.6	93.7	75.7
Stipagrostis uniplumis	7.6	82.8	69.9	8.7	94.8	76.6
Digitaria eriantha	-	-	-	8.8	95.9	77.4
Eragrostis pallens	-	-	-	8.6	92.7	75.7

a = Intake is based on a daily dry matter intake of 10.9 kg/adult bull

b = Intake is based on a daily dry matter intake of 8.8 kg/adult cow

Table 14: Protein requirements of the African buffalo (Prins 1996)

EQUATION	ADULT COW (450 kg)	ADULT BULL (600 kg)
CP_r * (g/day) = 5.83 x $W^{0.75}$	569.6	706.8
DMI** (kg/day) = 0.0635 x $W^{0.75}$	6.2	7.7
CP_{feed}*** (%) = CPr (g/day) / DMI (kg/day) x 0.1	9.2	9.2

*CP_r = crude protein requirement (g/day)

**DMI = dry matter intake to maintain energy needs for maintenance (kg/day)

*** CP_{feed} = crude protein in feed needed for maintenance (%)

Table 15: Summary of the nutritional content (%) of the preferred grass species eaten by the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa. Cold refers to the cold, dry season and warm to the warm, wet season

GRASS SPECIES	ASH		CRUDE PROTEIN		NITROGEN		NEUTRAL DETERGENT FIBRE		ACID DETERGENT FIBRE		APPARENT *IN VITRO* DIGESTIBILITY	
	Cold 2003	Warm 2004	Cold 2003	Warm 2004	Cold 2003	Warm 2004	Cold 2003	Warm 2004	Cold 2003	Warm 2004	Cold 2003	Warm 2004
Centropodia glauca	7.45*	8.22*	4.97*	9.19*	0.79*	1.47*	71.13	71.20	45.29*	41.00*	38.84*	59.94*
Schmidtia pappophoroides	4.56*	13.22*	4.82*	8.50*	0.77*	1.36*	78.08*	71.40*	49.26*	43.44*	54.63	59.02
Eragrostis lehmanniana	3.42	3.47	5.44*	7.75*	0.87*	1.24*	77.80	82.00	47.74	49.73	47.08	50.81
Stipagrostis uniplumis	2.75*	5.76*	4.81*	8.38*	0.77*	1.34*	74.17	76.49	45.59	46.96	64.63*	61.86*
Digitaria eriantha	-	3.12	-	8.88	-	1.42	-	60.56	-	32.68	-	67.79
Eragrostis pallens	-	3.73	-	8.00	-	1.28	-	80.51	-	43.12	-	42.76

∗ Means within the same species that differ significantly between two seasons ($p \leq 0.05$)

Table 16: Summary of the micro-mineral content (mg/kg) of the preferred grass species eaten by the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa. Cold refers to the cold, dry season and warm to the warm, wet season

GRASS SPECIES	COPPER		IRON		ZINC		MANGANESE	
	Cold 2003	Warm 2004	Cold 2003	Warm 2004	Cold 2003	Warm 2004	Cold 2003	Warm 2004
Centropodia glauca	3.68*	5.93*	155.72*	102.35*	5.78*	16.14*	40.20*	22.79*
Schmidtia pappophoroides	3.39*	5.57*	216.00*	393.69*	5.22*	21.94*	54.50*	34.39*
Eragrostis lehmanniana	4.46*	5.46*	163.05*	95.11*	8.13*	32.77*	42.51	43.45
Stipagrostis uniplumis	3.93*	7.77*	218.45*	167.71*	7.33*	20.57*	68.11*	49.17*
Digitaria eriantha	-	7.26	-	475.92	-	35.34	-	68.18
Eragrostis pallens	-	8.45	-	83.09	-	25.17	-	63.25

∗ Means within the same species that differ significantly between the seasons ($p \leq 0.05$)

The warm, wet season (Cu: $t = 15.47$; Zn: $t = 15.53$; $df = 3$; $p \leq 0.05$), but manganese decreased significantly (Mn: $t = 14.92$; $df = 3$; $p \leq 0.05$) from the cold, dry season to the warm, wet one.

The macro-mineral contents of the preferred grass species are given in Table 17. Significant increases were observed towards the warm, wet season in the calcium content of both *Schmidtia pappophoroides* ($t = 10.49$; $df = 3$; $p \leq 0.05$), and *Stipagrostis uniplumis* ($t = 11.76$; $df = 3$; $p \leq 0.05$). The phosphorus content of all the species except for *Eragrostis lehmanniana* increased significantly during the warm, wet season. The magnesium content of *Centropodia glauca* decreased significantly from the cold, dry season to the warm, wet one ($t = 24.61$; $df = 4$; $p \leq 0.05$), while it increased significantly in the remaining species.

No information could be found on the mineral requirements of buffalo, and therefore the requirements of beef cattle provided by the National Research Council (1996) were used for requirements of bulls and non-lactating females. For the lactating females, requirement values for dairy cows were used (National Research Council 2000) (Table 18).

Faecal analysis

The results for the crude protein, gross energy and phosphorus content of the faeces are summarised in Table 19. There was a significant difference in the crude protein concentration between lactating and non-lactating females ($t = 3.99$; $df = 4$; $p \leq 0.05$), with non-lactating females having a greater crude protein content in their faeces. Another significant difference was detected between the gross energy values in the faeces of lactating females and adult bulls ($t = 2.88$; $df = 4$; $p \leq 0.05$), and non-lactating and lactating females ($t = 1.67$; $df = 4$; $p \leq 0.05$), with lactating females having the highest gross energy value (17.6 MJ/kg). The phosphorus content also showed significant differences between the three production levels, with non-lactating females having the highest content of 2.10 g/kg.

Physical condition scoring

There was an improvement in the physical condition of the buffalo from June 2003 to June 2004 (Table 20). During the assessment made in June 2003, the majority of the buffalo population (65%) was in condition class 2, while the majority of the population (85%) was in condition class 3 during the June 2004 assessment.

Table 17: Summary of the macro-mineral content (%) of the preferred grass species eaten by the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa. Cold refers to the cold, dry season and warm to the warm, wet season

GRASS SPECIES	CALCIUM		PHOSPHORUS		MAGNESIUM	
	Cold 2003	Warm 2004	Cold 2003	Warm 2004	Cold 2003	Warm 2004
Centropodia glauca	0.76	0.75	0.03*	0.08*	1.12*	0.20*
Schmidtia pappophoroides	0.24*	0.36*	0.03*	0.08*	0.07*	0.16*
Eragrostis lehmanniana	0.21	0.20	0.04	0.05	0.05*	0.08*
Stipagrostis uniplumis	0.28*	0.42*	0.04*	0.08*	0.06*	0.09*
Digitaria eriantha	-	0.38	-	0.06	-	0.45
Eragrostis pallens	-	0.25	-	0.10	-	0.09

∗ Means within the same species that differ significantly between the seasons ($p \leq 0.05$)

Table 18: Mineral requirements of beef (National Research Council 1996) and dairy cattle (National Research Council 2000). Toxic levels are for both beef and dairy cattle (Puls 1994)

ANIMAL	**MINERAL REQUIREMENT**						
	P (%)	Ca (%)	Mg (%)	Cu (mg/kg)	Fe (mg/kg)	Zn (mg/kg)	Mn (mg/kg)
Adult bull	0.19	0.20	0.10	8.0	50.0	30.0	40.0
Lactating females	0.32	0.62	0.18	11.0	12.3	43.0	14.0
Non-producing females	0.22	0.44	0.11	12.0	13.0	21.0	16.0
Toxic level	> 1.00	> 1.40	> 1.00	> 95.0	> 4 000.0	> 5 000.0	> 2 000.0

Table 19: Summary of the chemical faecal composition of the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa during September 2003

AGE AND PRODUCTION CLASS	**CHEMICAL COMPOSITION**				
	Ash (%)	Crude protein (%)	Faecal nitrogen (g/kg)	Gross energy (MJ/kg)	Phosphorus (g/kg)
Adult bulls	18.26 [a]	6.78 [a]	10.84 [a]	16.96 [a]	1.63 [a]
Lactating cow	17.16 [a]	6.71 [a]	10.74 [a]	17.65 [b]	1.74 [b]
Non-lactating cow	21.79 [b]	6.85 [b]	10.96 [b]	16.85 [a]	2.10 [c]

a, b, c Means within the same column with different superscripts differ significantly ($p \leq 0.05$)

Table 20: Summary of the physical condition scores of the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa. The proportion of buffalo with a specific condition score class is given as a percentage of the entire population

TIME	PHYSICAL CONDITION SCORE (%)				
	1	2	3	4	5
June 2003	5	65	22	8	0
October 2003	0	8	74	15	3
February 2004	4	7	71	12	6
June 2004	4	8	85	3	0

The condition of the buffalo during the months of October 2003 and February 2004 was moderate to good, with more than 80% of the population within condition classes 3 and 4. The adult female class demonstrated the largest shift in condition classes, with 68% in condition class 2 during June 2003, but during June 2004, only 19% of the female buffalo were in this class (Fig. 19).

Grazing capacity and stocking density

The overall ecological grazing capacity for Korannaberg during 2004 was 6.1 GU/100 ha (32.7 ha/LSU), and the economical grazing capacity was 4.2 GU/100 ha (47.6 ha/LSU) (Table 21). The recommended stocking rate for buffalo on Korannaberg, based on the ecological grazing capacity was 292.2 GU or 149 buffalo (Table 22), with a conversion factor of 2.2 GU per buffalo (Bothma *et al.* 2004), when buffalo consume 89% graze. The long-term grazing capacity of Korannaberg determined with the equation of Coe *et al.* (1976) was 965 LSU (802.71 kg/km²).

According to the equation of Fourie *et al.* (1985) the grazing capacity of Tswalu over the long-term was 23 ha/LSU or 2 351.3 LSU. For the growing season of September 2003 to March 2004 with a rainfall of 140.4 mm it was 30 ha/LSU (1 802.7 LSU). The mean standing browse of Korannaberg was 201.5 kg/ha (Fouché & Avenant 2004), and the available browse was 972 790.4 kg/ha giving an ecological browsing capacity for Korannaberg of 1.2 BU/100 ha. Korannaberg could thus maintain 634.6 BU.

The ratio of feeding categories in terms of GU present on Korannaberg in 2004 was 21.9% low selective grazers: 57.1 high selective grazers: 20.0 mixed feeders: 1.0 browsers (Table 23). Actual stocking densities for the grazing herbivores present on Korannaberg was 2 976 GU, 7.7% lower than the ecological stocking density of 3 224 but 31.9% higher than the economical stocking density (2 257 GU). At the calculated ecological browsing capacity, Korannaberg could only sustain 635 BU, but the current ecological stocking density is 1 784 BU. Therefore Korannaberg was overstocked with 280.9% in terms of BU (Table 24).

Discussion

Direct observations

Buffalo in the Kruger National Park of South Africa adjusted their selection of grass species in relation to seasonal changes in forage quality and quantity, where unpalatable grass species were accepted for bridging the critical transition period between the late dry season to the start of the rains (Macandza *et al.* 2004). Sinclair (1974c) provided convincing evidence that buffalo have the ability to select different grass species and that species selection is influenced by the nutrient

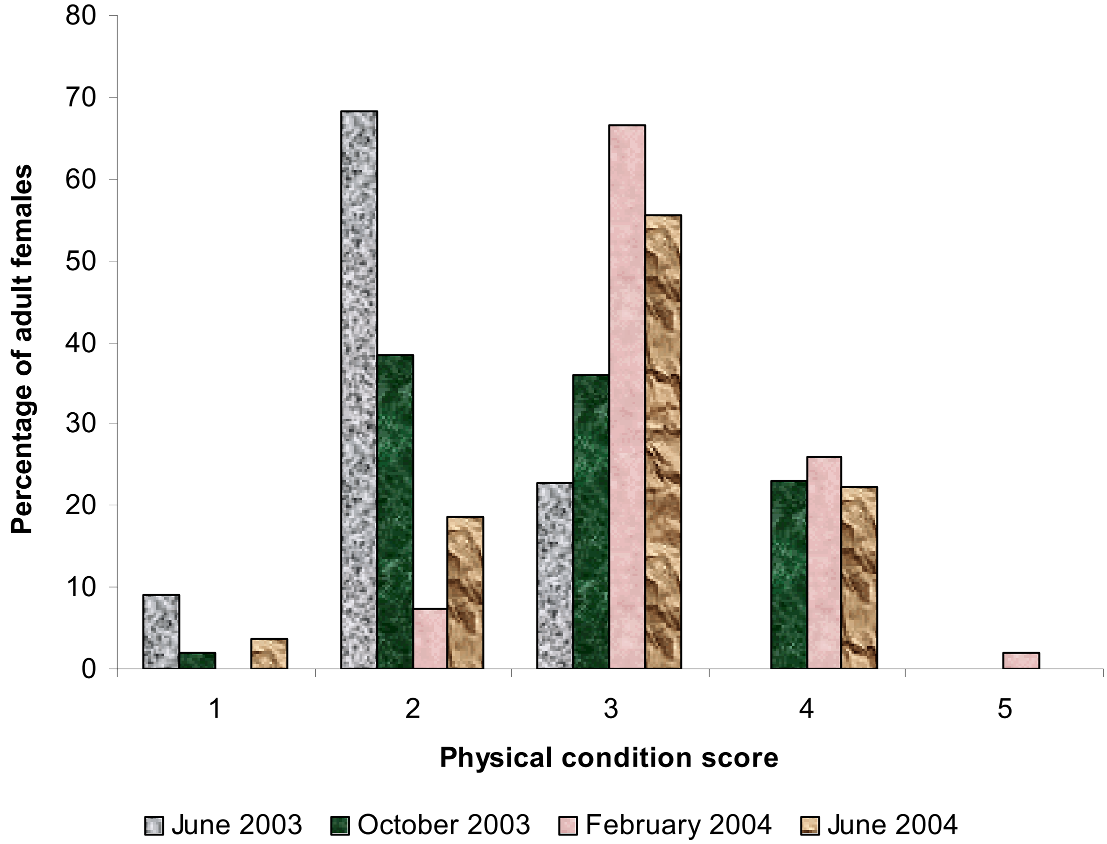

Figure 19: The physical condition scores of the adult female buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa during the study period.

Table 21: Ecological and economical grazing capacity of the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa in April 2004

VEGETATION TYPE*	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**11**
Size (ha)	2 052.4	237.0	1 689.4	8 574.4	7 628.8	4 358.0	15 998.8	4 351.2	5 407.2	2 876.0
Tree cover (%)	40	12	10	5	15	2	5	3	5	1
Shrub cover (%)	8	6	5	12	20	14	16	35	33	25
Contribution of ecological classes (%)										
Class 1	20	42	24	24	83	47	17	55	32	65
Class 2	26	36	32	43	2	11	36	1	27	14
Class 3	0	0	3	3	0	0	0	0	0	0
Class 4	0	0	0	0	0	0	0	0	0	0
Class 5	54	22	38	28	4	36	43	11	25	19
Bare soil	0	0	3	2	11	6	4	33	16	2
Range condition index (%)	43.6	69.4	51.7	58.4	84.8	58.3	46.5	56.8	53.4	76.7
Grass cover (%)	28	41	41	28	37	33	31	31	25	22
Topography index of accessibility**	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.8
Fire factor***	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Ecological grazing capacity:										
GU/100 ha	0.2	13.5	4.5	7.2	19.8	7.7	1.6	6.2	4.3	11.1
Total GU in each vegetation type	3	28	65	518	1386	277	219	244	209	275
Total ecological GU for Korannaberg										**3 224.4**
Mean ecological grazing capacity (GU/100 ha)										**6.1**
Economical grazing capacity:										
GU/100 ha	0.1	9.5	3.1	5.0	13.9	5.4	1.1	4.4	3.0	7.8
Total GU in each vegetation type	2	20	45	362	970	194	153	171	146	192
Total economical GU for Korannaberg										**2 257**
Mean economical grazing capacity (GU/100 ha)										**4.2**

∗ Vegetation type: numbers correspond with Table 1 in Chapter 3

∗∗Topography index of accessibility: 0.1 = Inaccessible to plains wildlife; 1.0 = Fully accessible to plains wildlife

∗∗∗Fire factor: 0.8 = Recent fires; 1.0 = No recent fires

Table 22: The recommended ecological grazing capacity of the preferred buffalo habitat in the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa in 2004. The grazing capacity allocated to the low selective grazers was determined as 25% of the grazing capacity of Korannaberg, of which 40% was allocated to the buffalo, to determine the recommended grazing capacity for buffalo

PREFERRED VEGETATION TYPE	AREA (ha)	GRAZING CAPACITY 2004 (GU)	GRAZING CAPACITY ALLOCATED TO LOW SELECTIVE GRAZERS (GU)	RECOMMENDED GRAZING CAPACITY FOR BUFFALO (GU)
Stipagrostis amabilis dune crests	2 052.4	3.5	0.9	0.4
Eragrostis pallens dune streets	1 689.4	64.8	16.2	6.5
Stipagrostis uniplumis plains	8 574.4	517.7	129.4	51.8
Hermannia burchellii shrubveld	7 628.8	1 385.6	346.4	138.6
Aristida meridionalis open shrubveld	4 358.0	277.3	69.3	27.7
Eragrostis lehmanniana dune valleys and plains	15 998.8	219.3	54.8	21.9
Monechma incanum shrubveld	4 351.2	244.1	61.0	24.4
Stipagrostis uniplumis bushy plains and valleys	5 407.2	209.3	52.3	20.9
Total	**50 060.2**	**2 921.6**	**730.4**	**292.2**

Table 23: The Grazer Units (GU) for the wildlife present on the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa for 2004, based on the model of Bothma *et al.* (2004)

TYPE OF WILDLIFE	NUMBER	PERCENTAGE GRAZE IN DIET	GRAZER UNITS PER ANIMAL	GRAZER UNITS EQUIVALENT	PERCENTAGE OF ECOLOGICAL GRAZING CAPACITY
Low-selective grazers					
African buffalo	83	89	2.20	162.5	5.5
Burchell's zebra	219	98	1.32	283.3	9.5
Cape mountain zebra	32	95	0.80	24.3	0.9
White rhinoceros	33	100	5.50	181.5	6.1
Subtotal				**651.6**	**21.9**
High-selective grazers					
Blesbok	48	90	0.50	21.6	0.7
Gemsbok	801	80	1.10	704.9	23.7
Hartebeest: red	445	80	0.70	249.2	8.4
Mountain reedbuck	7	90	0.20	1.3	0.0
Roan antelope	20	90	1.20	21.6	0.7
Sable antelope	13	85	1.20	13.3	0.5
Tsessebe	63	95	0.70	41.9	1.4
Waterbuck	117	90	1.10	115.8	3.9
Wildebeest: black	13	95	0.90	11.1	0.4
Wildebeest: blue	547	95	1.00	519.7	17.5
Subtotal				**1 700.3**	**57.1**
Mixed feeders					
Eland	210	70	2.00	249.0	9.8
Impala	255	50	0.30	38.3	1.3
Ostrich	227	70	0.50	79.5	2.7
Springbok	1 649	32	0.30	158.3	5.3
Warthog	122	70	0.30	25.6	0.9
Subtotal				**595.6**	**20.0**
Browsers					
Black rhinoceros	16	4	3.10	1.9	0.1
Giraffe	59	0	3.20	0.0	0.0
Grey duiker	143	12	0.20	3.4	0.1
Kudu	415	5	0.80	16.6	0.6
Steenbok	113	30	0.20	6.8	0.2
Subtotal				**28.8**	**1.0**
Total	**5 650**			**2 976.3**	**100.0**

Table 24: The Browser Units (BU) for the wildlife present on the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa for 2004, based on the model of Bothma *et al.* (2004)

TYPE OF WILDLIFE	NUMBER	PERCENTAGE BROWSE IN DIET	BROWSE UNITS PER ANIMALS	BROWSE UNIT EQUIVALENT	PERCENTAGE OF ECOLOGICAL BROWSING CAPACITY
Low-selective grazers					
African buffalo	83	11	2.68	24.5	1.4
Burchell's zebra	219	2	1.59	7.00	0.4
Cape mountain zebra	32	5	1.50	2.4	0.1
White rhinoceros	33	0	6.58	0.0	0.0
Subtotal				**33.9**	**1.9**
High-selective grazers					
Blesbok	48	10	0.56	2.7	0.2
Gemsbok	801	20	1.36	217.1	12.2
Hartebeest: red	445	20	0.89	79.2	4.4
Mountain reedbuck	7	10	0.26	0.2	0.0
Roan antelope	20	10	1.50	3.0	0.2
Sable antelope	13	15	1.40	2.7	0.2
Tsessebe	63	5	0.92	2.9	0.2
Waterbuck	117	10	1.33	15.6	0.9
Wildebeest: black	13	5	1.11	0.7	0.0
Wildebeest: blue	547	5	1.21	33.0	1.9
Subtotal				**357.1**	**20.0**
Mixed feeders					
Eland	210	30	2.44	153.7	8.6
Impala	255	50	0.40	50.8	2.8
Ostrich	227	30	0.59	40.2	2.3
Springbok	1 649	68	0.37	414.9	23.3
Warthog	122	30	0.51	18.6	1.0
Subtotal				**678.2**	**38.0**
Browsers					
Black rhinoceros	16	96	3.76	57.8	3.2
Giraffe	59	100	3.80	224.1	12.6
Grey duiker	143	88	0.22	27.7	1.6
Kudu	415	95	1.00	394.3	22.1
Steenbok	113	70	0.14	10.3	0.6
Subtotal				**714.8**	**40.1**
Total	**5 650**			**1 783.8**	**100.0**

content, tensile strength and silica content of a plant. This was confirmed in the current study, where the Tswalu buffalo altered their species utilisation between seasons.

Short-term grass species variation is visible in the Kalahari in reaction to rainfall (Van Rooyen, Theron & Bredenkamp 1991), and the buffalo on Tswalu became more selective of grass species during the dry season, as was found by Sinclair (1977) and Beekman & Prins (1989). *Eragrostis lehmanniana* reacts favourably to the first seasonal rains in the Kalahari region (Van Rooyen *et al.* 1991), but its protein quality will increase gradually, and Knight (1991) found that it peaked in February which was later than other grass species in the Kgalagadi Transfrontier Park. Despite this proposed peak in February, this species only made up 7.1% of the diet of the buffalo on Tswalu in the warm, wet season compared to a 20.0% utilisation in the cold, dry season. *Eragrostis lehmanniana* has a known low digestibility (Fourie & Roberts 1976), and this was confirmed in the current study where this species had an *in vitro* digestability of 47.08 to 50.81% (Table 15). This, together with the availability of a larger variety of good quality species, could be a possible reason why the buffalo did not utilise this species as much during the warm, wet season as during the cold, dry season. Buffalo in Botswana, however, preferred *Eragrostis lehmanniana* (Taolo 2003).

Schmidtia pappophoroides, a perennial tufted grass, was favoured during both seasons of the current study period. *Digitaria eriantha* became favoured on Tswalu during the peak of the rainy season. This is in contrast to Macandza *et al.* (2004), who found buffalo in the Kruger National Park to favour this species during the late dry season. Kruger (1998) classified *Schmidtia pappophoroides* and *Stipagrostis uniplumis* as desirable grasses by cattle in Namibia. Stipagrostis species are prominent during drought periods and are an extremely important component of the Kalahari duneveld, although these species would increase during a wet phase, they can eventually die off after a prolonged wet period (Fourie *et al.* 1987).

There exists a relationship between body mass and dietary preferences in bovids, however, this relation is weak (R = 0.32) (Gagnon & Chew 2000), and suggests that body mass is not the only factor influencing dietary preferences in bovids. The current study confirmed that buffalo are predominantly grazers, as was demonstrated by others (Lamprey 1963; Mloszewski 1983; Prins 1996; Taolo 2003). Gagnon & Chew (2000) classified buffalo as variable grazers consuming 22.5% dicotyledons and 77.5% monocotyledons. The buffalo occasionally browsed on Tswalu, especially during the cold, dry season with preferences for *Grewia flava* and *Rhus tenuinervis* (Table 12). In East and West Africa, Mloszewski (1983) found that buffalo would start to browse when pasture conditions deteriorate, but 5.0% browse in the diet is normal, even in the best conditions. The crude protein content of browse species could be as high as four times that of grass during the dry season, resulting in buffalo browsing during the dry period (Beekman & Prins 1989; Field 1976). Codron *et al.* (2005) found that browse in the Waterberg region of the Limpopo province in South Africa had significantly higher nitrogen content than grasses ($p \leq 0.01$). Browse was utilised but not preferred by the buffalo in South Africa (Pienaar 1969; Perrin & Brereton-Stiles 1999; Landman & Kerley 2001; Codron *et al.* 2005), in East Africa (Field 1976; Sinclair 1977; Beekman & Prins 1989), and in Botswana (Taolo 2003). This limited browse utilisation could be ascribed to the assembly of the gut microbes or rumen morphology (Landman & Kerley 2001). Buffalo utilise limited proportions of browse because large quantities are undesirable and do not provide the necessary energy. Higher water intake is also needed for the excretion of the excess nitrogen (Field 1976).

During the warm, wet season, plant part selection was for more leaf and less stem in the present study; the same result was obtained in other studies (Field 1976; Sinclair 1974c; Beekman & Prins 1989; Perrin & Brereton-Stiles 1999). *Eragrostis lehmanniana* and *Digitaria eriantha* had limited leaf production during both seasons, while the *Stipagrostis* spp. yielded a relative good leaf: stem ratio during the warm, wet season. Although roots were not a preferred plant part to utilise, the Tswalu buffalo utilised the roots of *Digitaria eriantha* during the warm, wet season. A possible reason why the roots of other grass species were not utilised is the presence of a sand covered sheath surrounding the root that assists the roots in moisture retention. The buffalo on Tswalu only utilised *Eragrostis pallens* during the warm, wet season, and then only the inflorescences were utilised. Upon closer investigation, it became apparent that this species is tough and fibrous. According to Sinclair & Gwynne (1972) low nutrient content, high tensile strength and a high silica content are detrimental in the selection of grass species by buffalo.

It was thus concluded that the high tensile strength and low digestibility (Table 15) of *Eragrostis pallens* contributed to the low utilisation of this species by the buffalo on Tswalu. *Eragrostis pallens* is known to have a low acceptability to cattle, and a low digestibility (Fourie & Roberts 1976). *Centropodia glauca* contributed only 8.9% to the buffalo diet on Tswalu during the warm, wet season and although the digestibility was moderate (54.6%), this species had an aromatic quality when green and lush and this could have contributed to the buffalo not utilising this species as much as what would be expected on Tswalu. This was in accordance with findings in East Africa, where buffalo demonstrated reduced preferences for grass species with an aromatic smell or that were bitter in taste (Field 1976; Leuthold 1972; Sinclair 1974c, 1977; Prins 1996).

Plant material analysis

Intake

The daily intake of dry matter by buffalo is governed by the crude protein content of the food and energy requirements of the animal (Prins 1996; Smallegange & Brunsting 2002). Although the silica content was never chemically analysed, after wet digestion for the determination of mineral content there was a high visible content of silica present in the grass species that were analysed. High silica content reduces palatability and intake (Field 1976), and grass silification has been described as a defence mechanism in the Serengeti ecosystem, with the possibility of causing fatal silica urolithiasis (McNaughton, Tarrants, McNaughton & Davis 1985), and an increase in tooth degradation (McDonald *et al.* 1998). Old animals do not increase their rate of chewing to compensate for the poor grinding surfaces of their teeth, and are more severely affected by food shortages (Sinclair 1974b).

Energy

According to Meissner (1982), the energy requirements for buffalo are as follows:

- Adult bull: 87.7 MJ ME/day
- Adult lactating cow: 99.3 MJ ME/day
- Adult dry cow: 79.1 MJ ME/day

From the results obtained (Table 13), adult bulls on Tswalu would obtain enough energy from *Eragrostis lehmanniana* during the cold, dry season, and from all the analysed grass species during the warm, wet season. None of the analysed grasses would provide in the energy requirements of lactating females or non-production females during any of the seasons.

Protein

Forage quality can be evaluated in terms of protein and expressed as nitrogen, because nitrogen is usually the most important limiting nutrient for grazers (Field 1976; Sinclair 1977; Grant, Biggs, Meissner & Basson 1996; Grant, Peel, Zambatis & Van Ryssen 2000; Smallegange & Brunsting 2002). Nitrogen is used by the animal for protein synthesis (McDonald *et al.* 1998). At low levels of protein in the feed, the rumen micro-organisms are limited in producing volatile fatty acids that are responsible for the majority of the energy requirements of the host animal (McDonald *et al.* 1998). To produce volatile fatty acids, microbial protein must be synthesised from the breakdown of the nitrogen fraction of the food (McDonald *et al.* 1998).

There is a minimum level of protein where it becomes uneconomical for an animal to digest the food because the nitrogen excretion is greater than the nitrogen intake (Sinclair 1974c; Dehority 2003). The rumen micro-organisms are then inhibited, slowing the rate of food passage through the rumen and the nitrogen deficit cannot be compensated for by increasing food intake (Sinclair 1974c; McDonald *et al.* 1998). This was observed in the Lake Manyara buffalo, where the selected grass species during the dry season were low in crude protein content, and total intake was impaired because of this low concentration of nutrients in the diet (Beekman & Prins 1989). Six herbivore species were studied in East Africa for rumen activity, and buffalo had the slowest rate of fermentation because of an inverse relationship between body mass and the fermentation rate (Maloiy, Clemens & Kamau 1982). This can be explained by the metabolisable energy requirements per unit of body mass that is smaller in larger herbivores (Sinclair & Duncan 1972). Consequently, large animals can retain food in their alimentary canal for longer periods and can digest fibrous food (Gagnon & Chew 2000). The minimum protein level in plant quality needed for the maintenance requirements of buffalo is 9.2% (Table 14). If the nitrogen quality of the food ingested by buffalo falls below 6.0%, the buffalo will lose mass and start to metabolise body reserves (Sinclair & Duncan 1972; Sinclair 1974c; Knight 1991; McDonald *et al.* 1998).

The protein content of the grasses on Tswalu did differ significantly seasonally (Table 15), which could be due to nitrogen being meagre during dry periods, or the nutrients being conveyed to the storage organs of the grasses, thus being unavailable to the buffalo (Field 1976; Fourie, Dry & Hamman 1981). This mobilisation of the nutrients to the storage organs is evident in perennial grasses (Mloszewski 1983). The protein levels of all the analysed grasses on Tswalu, with the exception of *Centropodia glauca* during the warm, wet season (CP = 9.24%), was below the minimum required 9.1% needed by an adult buffalo for maintenance (Table 14). During the cold, dry season, all the grasses on Tswalu had a crude protein level below the minimum 6.0% necessary to avoid a loss in mass (Sinclair & Duncan 1972; Sinclair 1974c; Knight 1991; McDonald *et al.* 1998). Although *Centropodia glauca* had the highest protein content during the warm, wet season on Tswalu, it only made up 9.0% of the grass component of the buffalo diet, which confirms the findings of Beekman & Prins (1989) who demonstrated that buffalo do not always select the best quality diet, but rather attempts to obtain a balanced intake.

Minerals

On Tswalu there was a deficiency of copper in all the analysed grass species during both seasons (Table 16). Grobler (1996) indicated copper values of grasses in the Phalaborwa district of the Limpopo province to range from 14.1 to 58.9 mg/kg, although the latter value could be considered as abnormal and was exceptionally high because of the presence of a copper mine in the Palaborwa area. Osteochondrosis has been observed in copper deficient animals eventually resulting in arthritis (Puls 1994; Grace & Wilson 2002). Copper deficiency can also result in reduced fertility (McDonald *et al.* 1998; Underwood & Suttle 1999), a reduced growth rate, delayed puberty, low conception and ovulation rates in cows, and a rough hair coat (Puls 1994). Iron and manganese are in excess during both seasons on Tswalu for the three production levels. If iron content exceeds 400 mg/kg DM, feed intake can be reduced and copper absorption impaired (Puls 1994). Zinc on Tswalu is deficient during the cold, dry season in all the analysed grasses for all the production levels and during the warm, wet season zinc is also deficient for lactating females in all the grass species. Deficiencies in zinc can cause stiffness in bones, reduced conception, impaired spermatozoan maturation and reduced feed intake (Puls 1994). Manganese required by lactating females is adequate in all grass species except *Schmidtia papphoroides* and *Eragrostis lehmanniana*. Manganese deficiency can result in silent heat, reduced conception and abortions (Puls 1994; Underwood & Suttle 1999).

All the grass species on Tswalu are deficient in calcium and could not satisfy the requirements of lactating females. The only exception is *Centropodia glauca* with calcium content high enough to provide in the requirements of the lactating females. A deficiency in calcium can lead to weak bones, subclinical hypocalcaemia resulting in stillborn calves (Puls 1994). Phosphorus and selenium are the most frequently prescribed mineral supplement for cattle in South Africa (Van Ryssen 2001). The tolerable calcium: phosphorus ratio for cattle is 7:1 (Sutton, Maskall & Thornton 2002), but on Tswalu this relationship reached ratios as high as 24:1, and can result in reduced weight gain in cattle (Puls 1994). This accentuates the phosphorus deficiency present on Tswalu, with a maximum phosphorus concentration of 0.16% in *Centropodia glauca* during the warm, wet season, which is still half of the requirement of lactating females (Table 18). Phosphorus deficiency may cause reduced milk yield (McDonald *et al.* 1998), reduced reproduction, and pica (Puls 1994). Tswalu buffalo have been seen to be cripple, which could be the result of a deficiency in phosphorus, calcium and even copper (McDonald *et al.* 1998; Puls 1994; Kriek *pers. comm*. 2003[7]). With the exception of an excess in *Centropodia glauca* and adequate levels in *Digitaria eriantha* during the warm, wet season, all the remainder of the analysed grass species were deficient in magnesium.

Geophagia was observed by Field (1976) and Mahaney & Hancock (1990), and was also observed on Tswalu when the buffalo utilised salt licks, especially during the end of the warm, wet season. The mineral content of plants that comprise the diets of herbivores is influenced by the soil (Sutton *et al.* 2002). These observed mineral deficiencies of the buffalo on Tswalu are

[7] Dr. J.C. Kriek, Wildlife Veterinarian, 3 Boschendal Avenue, Royldene, Kimberley, 8301, South Africa.

only a rough guideline, because the risk of mineral deficiencies will also be influenced by the supply of nutrients from surface water (Sutton *et al.* 2002).

Fibre

Neutral-detergent fibre (NDF) gives an indication of the plant cell wall material present in the plants eaten, and the acid-detergent fibre (ADF) represents crude lignin and cellulose fractions, together with silica and gives an indication of digestibility (McDonald *et al.* 1998). With increased fibre content in the food (NDF), the rate of food passage is slower and the dry matter digestibility improves at the cost of intake, resulting in larger losses of endogenous bacterial material in the faeces (Grimsdell & Field 1976; Sinclair 1974c; McDonald *et al.* 1998; Clauss & Hummel 2005). In the present study, *Eragrostis pallens* and *Eragrostis lehmanniana* are both very fibrous with high NDF values. *Digitaria eriantha* has a low cell wall content (NDF) and a low ADF value, indicating good digestibility and could explain the selection of this grass species by the buffalo during the warm, wet season.

Faecal analysis

Faecal nutrient levels have been used to predict dietary levels in elk *Cervis elaphus* (Mould & Robbins 1981), white tailed deer *Odocoileus virginianus* (Jenks, Leslie, Lochmiller, Melchiors & Warde 1989), cattle *Bos* spp. (Grant *et al.* 1996), duiker, eland, blue wildebeest, impala, zebra (Wrench *et al.* 1997) and sable antelope (Dörgeloh 1998). Faecal nitrogen and phosphorus can be used as indicators of the nutritional status and ecology of animals (Erasmus, Penzhorn & Fairall 1978; Caughley & Sinclair 1994), and the nutritive content of the veld (Wrench *et al.* 1997; Grant *et al.* 2000). It is important to consider faecal phosphorus and nitrogen concentrations together because their excretion is linked. When faecal phosphorus concentrations are below 2.0 g/kg organic matter (OM), faecal nitrogen concentrations will increase and cause a decrease in faecal phosphorus (Grant, Meissner & Schultheiss 1995).

Faecal nitrogen is positively correlated with dietary protein, dry matter intake and digestibility, and mass changes in mature animals (Grant *et al.* 1995; Wrench *et al.* 1997). A faecal nitrogen concentration of less than 14 g N/kg DM indicates a nitrogen deficiency in grazers (Wrench *et al.* 1997). Grant *et al.* (1996) found a significant relationship between physical condition and faecal nitrogen for buffalo. Physical condition will decrease if faecal nitrogen falls below 11.5 g/kg DM. The minimum nitrogen concentration that is necessary in grass to maintain rumen fermentation is between 11.0 and 12.0 g N/kg DM (Grant *et al.* 1995, 2000). During the drought of 1992-1993 in the Kruger National Park, the mean faecal nitrogen concentration of buffalo was 11.5 g/kg DM and some of the animals were in a poor physical condition, and the population declined in numbers with calving percentages as low as 4.2% (Grant *et al.* 1995). According to Grant *et al.* (2000) September falls within the critical season for buffalo and a faecal nitrogen level of 9.0 g N/kg DM was recorded in the Kruger National Park during this critical period. It is clear that the faecal nitrogen concentration of 10.7 g N/kg on Tswalu was below the required minimum of 14.0 g N/kg, and that the buffalo should theoretically lose physical condition. Furthermore, the faecal nitrogen concentration of 10.7 g N/kg of the buffalo on Tswalu was below the required minimum of 11.0 g N/kg DM necessary in grass to maintain rumen fermentation.

Phosphorus is the most common cause of poor fertility in Africa (Puls 1994; Wrench *et al.* 1997; Grant *et al.* 2000), and a faecal phosphorus concentration of less than 2.0 g/kg organic matter (OM) indicates a deficiency in most species (Wrench *et al.* 1997). Grant *et al.* (2000) recorded high faecal phosphorus concentrations in buffalo of 4.5 g P/kg OM during the wet season with the lowest (2.1g P/kg OM) during the dry season. On Tswalu, the phosphorus in the faeces of the adult males (1.63 g P/kg) and lactating females (1.74 g/kg) for September 2003 was below the required 2.0 g P/kg. This could lead to reproductive problems (Wrench *et al.* 1997).

Physical condition scoring

The improvement in the physical condition score of the buffalo on Tswalu from June 2003 to September 2003 could be attributed to the supplementary feeding that the buffalo received during this period. However, supplementary feeding ceased in September 2003 and during December 2003 an adult female died. Upon closer examination, the colour and consistency of the bone marrow of this female implied death due to starvation (Sinclair & Duncan 1972), rumen stasis was also observed. Supplementary feeding commenced again in late November 2003 and resulted in the majority of the population being in a moderate condition class in February 2004. The condition of the veld also contributed to the improved condition of the buffalo with November to March being the peak-growing season for vegetation in the Kalahari. Supplementary feeding was again ceased in March 2004. This together with the fact that the buffalo were in the rutting and lactation period, resulted in a slight reduction in overall body condition, although it was better than during June 2003. It became clear that the supplementary feeding had a positive effect on the physical condition of the buffalo on Tswalu.

Buffalo conceive during periods of high nutritional status, and conception takes place during times of high rainfall (Grimsdell 1969). With a 5-kg/day milk yield, a lactating female needs quadruple the minimum requirements for protein for lactation, resulting in physiological stress during the last two months of pregnancy and the first few months of lactation (Sinclair 1977). The situation on

Tswalu indicated that the buffalo conceived from January to May and that the calving season stretched from December to April, leaving the females to lactate during the end of the warm, wet season and continuing into the cold, dry season. Lactating females on Tswalu would thus enter periods of high nutritional demands during periods of low food quality. The buffalo on Tswalu should lose physical condition during the cold, dry season because the grass species present have a crude protein content that is below the minimum of 6%, which is needed for buffalo to avoid a loss of physical condition. Therefore, it is extremely important to supplement the adult female buffalo age class during these periods. The positive effect of supplementary feeding was demonstrated with the poor physical condition of the adult female class during June 2003 (Fig. 17) compared to the majority of the adult female class being in condition class 3 and some in condition class 4 during June 2004, after moderate supplementary feeding.

Grazing capacity and stocking density

Animal populations reach equilibrium in their growth at a point where natural deaths and births are more or less in balance, and no growth is observed. This equilibrium is also known as the ecological capacity of an area (Odum 1983; Bothma 2002a). Eventually, the natural resources will become depleted and cause deficiencies, which will ultimately cause a fluctuating equilibrium. The importance of maintaining a conservative ecological capacity on a reserve was highlighted by the population crash in the Willem Pretorius Game Reserve where 33% of the buffalo population died during 1991 due to disregarding recommended stocking densities (Winterbach 1999).

Veld condition and thus grazing capacity has a positive correlation with rainfall if based on basal cover of the vegetation. However, the botanical composition in the Kalahari has a negative correlation with rainfall, and will improve during a dry cycle, because the valuable, high productive grass species with a high grazing value are more drought resistant than the low productive grass species with a low grazing value (Fourie *et al.* 1987). The range-condition index of Korannaberg (Table 21) varied from 43.6 to 84.8% indicating the range was in poor to excellent condition. The current grazing capacity of Korannaberg is 32.7 ha/LSU and seems to be low, but considering the low rainfall of the area (annual mean: 231.3 mm) it can be seen as a reliable representation of the ecological ability of the veld to maintain grazing herbivores. This grazing capacity also conforms well to the equation of Fourie *et al.* (1985), which determined the grazing capacity to be 30 ha/LSU (1 802.7 LSU) for the period of September 2003 to March 2004 with a rainfall of 140.4 mm. Reported grazing capacities for the Northern Cape are 18 ha/LSU (Fourie *et al.* 1987) and 16 to 18 ha/LSU (Fourie *et al.* 1985).

The recommended stocking density of Korannaberg of 3 224 GU was only an approximation and changes in rainfall, range condition and physical condition of the animals could cause an alteration in this stocking density. Rainfall is very important in this arid landscape and plants react rapidly to changes in rainfall. A slight change in the mean annual rainfall of 10% can have a dramatic effect. For example, if the mean annual rainfall would fall to 208.2 mm, the ecological grazing capacity would decrease to 4.3 GU/100 ha or 46.5 ha/LSU. Consequently, if the mean annual rainfall rises 10% to 254.2 mm, the ecological grazing capacity would increase to 8.2 GU/100 ha (24.4 ha/LSU). Compare the above ecological grazing capacities with the current ecological capacity on Korannaberg (6.1 GU/100 ha or 32.7 ha/LSU), and the importance of active adaptive management regarding the grazing capacity becomes clear if veld deterioration and animal mortalities were to be avoided. Tswalu was overstocked with 15% at a mean annual rainfall of 250.0 mm during a previous veld condition assessment done by Van Rooyen (1999), when grazing capacity was calculated as 36.5 ha/LSU. A portion of the current Korannaberg section (then called Estate), was overstocked by 148.4% with a grazing capacity of 38 ha/LSU (Van Rooyen 1999).

If buffalo were the only low-selective grazers kept on Korannaberg, and 25% of the total grazing capacity of Korannaberg was devoted to this class, a total of 730.4 GU or 373 buffalo could roam the dunes of Korannaberg. However, this is not the case according to the annual aerial count of Tswalu during 2004 (Table 23). Korannaberg also had 31 white rhinoceroses, 219 Burchell's zebras and 32 mountain zebras that shared the low-selective class on the plains and dunes of Korannaberg with the buffalo. Assuming that the buffalo will use 40% of the available 25% ecological grazing capacity utilised by low-selective grazers, the recommended stocking rate for buffalo on Korannaberg was 292.2 GU or 149 buffalo. However, due to the fact that buffalo did not historically occur in this part of the Kalahari (Chapter 2), combined with the proved nutritional struggle of the buffalo on Tswalu, it is recommended that the economical grazing capacity for buffalo on Korannaberg (204.5 GU or 104 buffalo) is used as a maximum stocking density for buffalo in this section of Tswalu. The recommended economical grazing capacity for the buffalo of 204.5 GU can be seen as a reliable conservative recommendation of buffalo grazing capacity on Korannaberg, and could prevent animal losses, even in years of poor rainfall.

It is recommended that the ratio of different feeding classes in savanna regions should be 25% low selectivity grazers, 35% high selective grazers, 20% mixed feeders and 20% browsers for the composition of the GU, although this is just a general guideline (Van Rooyen 2002b). However, this ratio must be adjusted depending on the available vegetation resources present, together with the management objectives of the specific reserve (Bothma *et al.* 2004). The ratio of feeding classes on Korannaberg during 2004 was 25.3:56.7:16.8:1.1. If the stocking density was to be reapportioned based on reaching the ecological grazing capacity and disregarding the ecological browsing capacity, a maximum of 149 buffalo could be sustained on Korannaberg (Table 25). However, the limited amount of browse (634.6 BU) that is available to herbivores do not allow for this stocking density, and therefore the current ratio of feeding classes is satisfactory in terms of the current condition of the vegetation. However, because Korannaberg is currently overstocked in terms of the ecological browsing capacity, the stocking density has to be reapportioned. Table 26 summarises the recommended stocking ratio based on the ecological browsing capacity of 1.2 BU/100 ha for the wildlife currently present on Korannaberg, with a maximum of 104 buffalo.

The final choice of wildlife types and amounts can be varied according to the management objectives of Tswalu. Wildlife production takes on two forms that are not compatible: the one is aimed at animal production where exotic animals could be produced intensively, and the second one is aimed at conservation where wildlife production is extensive with indigenous species (Bothma 2005). Animals could be indigenous to South Africa, while being exotic to localized parts within it, like the eastern Kalahari region of the Northern Cape province. The word indigenous is derived from indigena that is a Latin word meaning to be born in a specific area (Bothma 2005), and therefore indigenous species occur naturally in a specific area (Anon. 2004). Species like the African buffalo, blesbok, the vulnerable Cape mountain zebra, mountain reedbuck, nyala, the vulnerable roan antelope, the vulnerable sable antelope, the endangered tsessebe and the waterbuck are exotic to the Kalahari region and their presence and purpose on Korannaberg should be reconsidered (Skinner & Smithers 1990; Friedmann & Daly 2004). The National Environmental Biodiversity Act of South Africa – Act 10 of 2004 (Anon. 2004), regulates the translocation of indigenous species to areas where they are locally exotic in South Africa. Based on the exotic nature of some of the species currently present on Korannaberg and the revised Biodiversity Act, another recommended stocking density is proposed in Table 27 based on indigenous wildlife to the Kalahari with the browsing capacity as limiting factor.

The recommended stocking density should be re-evaluated annually alongside the annual rainfall and adjustments should be made through active adaptive management to ensure sustained optimal animal and vegetation condition on Korannaberg.

Conclusions

Although it is generally regarded as unselective, the buffalo on Tswalu did show clear dietary preferences with limited browsing, as was also found by Macandza *et al.* (2004) in the Kruger National Park of South Africa. Buffalo will suffer severely during periods of drought, because of a

Table 25: The stocking density of the wildlife present on the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa during 2004, based on the model of Bothma *et al.* 2004

TYPE OF WILDLIFE	NUMBER OF ANIMALS	TOTAL GRAZE UNITS	TOTAL BROWSE UNITS	PERCENTAGE OF ECOLOGICAL GRAZING CAPACITY	PERCENTAGE OF ECOLOGICAL BROWSING CAPACITY
Low-selective grazers					
African buffalo	83	162.5	24.5	5.5	1.4
Burchell's zebra	219	283.3	7.0	9.5	0.4
Cape mountain zebra	32	24.3	2.4	0.8	0.1
White rhinoceros	33	181.5	0.0	6.1	0.0
Subtotal		**651.6**	**33.8**	**21.9**	**1.9**
High-selective grazers					
Blesbok	48	21.6	2.7	0.7	0.2
Gemsbok	801	704.9	217.1	23.7	12.2
Hartebeest: red	445	249.2	79.2	8.3	4.4
Mountain reedbuck	7	1.3	0.2	0.0	0.0
Roan antelope	20	21.6	3.0	0.7	0.2
Sable antelope	13	13.3	2.7	0.5	0.2
Tsessebe	63	41.9	2.9	1.4	0.2
Waterbuck	117	115.8	15.6	3.9	0.9
Wildebeest: black	13	11.1	0.7	0.3	0.0
Wildebeest: blue	547	519.7	33.0	17.5	1.9
Subtotal		**1 700.3**	**357.1**	**57.0**	**20.1**
Mixed feeders					
Eland	210	294.0	153.7	9.9	8.6
Impala	255	38.3	50.7	1.3	2.8
Ostrich	227	79.5	40.2	2.7	2.3
Springbok	1 649	158.3	414.9	5.3	23.3
Warthog	122	25.6	18.6	0.9	1.0
Subtotal		**595.6**	**678.2**	**20.1**	**38.0**
Browsers					
Black rhinoceros	16	2.0	57.8	0.1	3.1
Giraffe	59	0.0	224.1	0.0	12.6
Grey duiker	143	3.4	27.7	0.1	1.6
Kudu	415	16.6	394.3	0.6	22.1
Steenbok	113	6.8	10.9	0.2	0.6
Subtotal		**28.8**	**714.7**	**1.0**	**40.0**
Total	**5 650**	**2 976.3**	**1 783.8**	**100.00**	**100.00**

Table 26: The recommended stocking density for the wildlife of the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa, based on the condition of the vegetation in 2004 and the model of Bothma *et al.* 2004

TYPE OF WILDLIFE	RECOMMENDED NUMBER OF ANIMALS	TOTAL GRAZE UNITS	TOTAL BROWSE UNITS	PERCENTAGE OF ECOLOGICAL GRAZING CAPACITY	PERCENTAGE OF ECOLOGICAL BROWSING CAPACITY
Low-selective grazers					
African buffalo	104	203.6	30.7	15.7	4.8
Burchell's zebra	41	53.0	1.3	4.1	0.2
Cape mountain zebra	20	15.2	1.5	1.2	0.2
White rhinoceros	18	99.0	0.0	7.6	0.0
Subtotal		**370.9**	**33.5**	**28.6**	**5.3**
High-selective grazers					
Gemsbok	183	161.0	49.6	12.4	7.8
Hartebeest: red	169	94.6	30.1	7.3	4.7
Mountain reedbuck	18	3.2	0.5	0.3	0.1
Roan antelope	47	50.8	7.1	3.9	1.1
Sable antelope	22	22.4	4.6	1.7	0.7
Tsessebe	82	54.5	3.8	4.2	0.6
Waterbuck	64	63.4	8.5	4.9	1.3
Wildebeest: blue	279	265.1	16.8	20.5	2.7
Subtotal		**715.1**	**120.9**	**55.2**	**19.1**
Mixed feeders					
Eland	68	95.2	49.8	7.3	7.8
Impala	45	6.8	9.0	0.5	1.4
Ostrich	101	35.4	17.9	2.7	2.8
Springbok	461	44.3	116.0	3.4	18.3
Warthog	63	13.2	9.6	1.0	1.5
Subtotal		**194.8**	**202.2**	**15.0**	**31.9**
Browsers					
Black rhinoceros	18	2.2	65.0	0.2	10.2
Giraffe	20	0.0	76.0	0.0	12.0
Grey duiker	86	2.1	16.6	0.2	2.6
Kudu	117	4.7	111.2	0.4	17.5
Steenbok	98	5.9	9.5	0.5	1.5
Subtotal		**14.9**	**278.2**	**1.1**	**43.8**
Total	**2 124**	**1 295.5**	**634.8**	**100.0**	**100.0**

Table 27: The recommended stocking density for the wildlife that are indigenous to the area of the Korannaberg section of Tswalu Kalahari Reserve in the Northern Cape province of South Africa, based on the condition of the vegetation in 2004 with browsing capacity as limiting factor. The model is based on the model of Bothma *et al.* 2004

TYPE OF WILDLIFE	RECOMMENDED NUMBER OF ANIMALS	TOTAL GRAZE UNITS	TOTAL BROWSE UNITS	PERCENTAGE OF ECOLOGICAL GRAZING CAPACITY	PERCENTAGE OF ECOLOGICAL BROWSING CAPACITY
Low-selective grazers					
Burchell's zebra	143	185.0	4.5	16.0	0.7
White rhinoceros	28	154.0	0.0	13.3	0.0
Subtotal		**339.0**	**4.5**	**29.3**	**0.7**
High-selective grazers					
Gemsbok	237	208.6	64.2	18.1	10.1
Hartebeest: red	191	107.0	34.0	9.3	5.4
Wildebeest: blue	279	265.1	16.8	22.9	2.7
Subtotal		**580.6**	**115.1**	**50.3**	**18.1**
Mixed feeders					
Eland	72	100.8	52.7	8.7	8.3
Impala	45	6.8	9.0	0.6	1.4
Ostrich	146	51.1	25.8	4.4	4.1
Springbok	461	44.3	116.0	3.8	18.3
Warthog	77	16.0	11.6	1.4	1.8
Subtotal		**218.9**	**215.1**	**18.9**	**33.9**
Browsers					
Black rhinoceros	22	2.7	79.4	0.2	12.5
Giraffe	20	0.0	76.0	0.0	12.0
Grey duiker	93	2.2	18.0	0.2	2.8
Klipspringer	22	0.4	3.0	0.0	0.5
Kudu	119	4.8	113.1	0.4	17.8
Steenbok	108	6.5	10.4	0.6	1.6
Subtotal		**16.5**	**299.9**	**1.4**	**47.3**
Total	**2 062**	**1 155.1**	**634.6**	**100.0**	**100.0**

decline in food quality before food quantity becomes critical (Grant *et al.* 1995). Perennial grasses tend to translocate all their nutrients to the root system before the dry period (Mloszewski 1983), especially in arid environments with localised rainfall like the Kalahari, resulting in animals having to work harder in order to find suitable food in dry months (Knight 1991). This will result in a higher fibre content, slower rate of food passage and lower nutrient contents of available grass species.

The buffalo on Tswalu entered a period of nutritional stress during the winter months. The observed deficiencies of the buffalo on Tswalu in crude protein, copper, manganese, zinc, calcium and phosphorus could all result in reproductive problems. Although crude protein values increased during the warm, wet season they were still not sufficient for maintenance requirements, and during the cold, dry season all the analysed grasses had a crude protein content below the minimum 6.0% needed to avoid a loss in mass.

Buffalo in East Africa were resource limited, demonstrating two forage strategies: one with emphasis on bulk feeding and one with extensive selection (Sinclair 1977; Beekman & Prins 1989). The buffalo on Tswalu were also resource limited and even with extensive selection, they were unable to ingest an adequate quantity of food, needed for maintenance requirements. The importance of supplementary feeding was emphasised by the difference in condition scores obtained after a period of feeding in the winter period.

It is, therefore, recommended that no more than 104 buffalo be kept on Korannaberg at a mean annual rainfall of 231.3 mm to avoid mortalities, and that these animals are nutritionally supplemented throughout the entire year. If these management recommendations cannot be met, it is recommended that the presence of the buffalo on Korannaberg be reconsidered.

CHAPTER 7

POPULATION DYNAMICS

Introduction

The second strongest impulse of nature is the perpetuation of a species (Bearden & Fuquay 1997). As early as the 1800s the importance of reproductive success in the long-term was acknowledged by scientists (Caughley & Sinclair 1994). The successful production of young is the determining factor for success in population ecology (Bothma 2002a).

Population dynamics reflects the physiological and reproductive reaction of members of a population to intrinsic and extrinsic factors (Strauss 2003). Density independent or extrinsic control is where occasional regulation takes place, but independent environmental factors disguise it (Sinclair 1977). Extrinsic factors include disease, famine, hunting (Bothma 2002a), habitat changes, stress (Bronson 1985), natural catastrophes (Bronson 1985; Bothma 2002a), and also food quality and quantity (Grimsdell 1969). All the above factors have a negative feedback mechanism that ultimately controls population size (Sinclair 1977). Bronson (1985) determined that cellular maintenance, thermoregulation and locomotor costs had to be satisfied first from food ingested, while the energy that remains will be used for individual growth, and thereafter for reproduction. The importance of a sufficient nutrient intake that is reflected in population growth was emphasized by Knight (1991) in studies on the gemsbok and blue wildebeest in the southern Kalahari. Intrinsic factors, also known as self-regulation, are where social behaviour or genetic polymorphism plays a role in fertility or mortality (Sinclair 1977). Pienaar (1969) noted calving in buffalo in alternate years only, with a calf being produced twice in 3 years only in good rainfall years.

Population viability analysis is a data modelling process whereby the likelihood that a population will persist for a chosen time in the future can be determined (Miller & Lacy 2005). The fate of small populations of animals that become isolated from other populations and that might serve as migration sources to stabilise genetics, can become questionable (Shaffer 1981). Population viability is also influenced by either deterministic or stochastic factors. Deterministic factors include over-harvest, habitat destruction and disease. Four main stochastic factors exist, namely demographic stochasticity, genetic stochasticity, environmental stochasticity and catastrophes (Shaffer 1981). Population viability has been a popular modelling tool in conservation although there is disagreement in the literature on the usefulness of population viability analysis based on the quality of the input data (Ludwig 1999). It has been suggested that the outcomes among model alternatives should be compared, rather than to interpret the results as being exact (Beissinger & Westphal 1998).

Buffalo are believed to be highly productive to such a degree, that culling is necessary in protected areas to avoid habitat degradation due to overpopulation (Estes 1997). Spinage (1972) demonstrated that buffalo population sizes could stabilize in size in 9 years after establishment, but only when a favourable habitat is present. The small buffalo population that was introduced to Tswalu in 1995, has initially been utilised for hunting and tourism. The management of Tswalu has stopped all hunting activity and it became important to optimise production for tourism and live sales.

The key management questions that therefore had to be answered concerning the population of buffalo in the present study were:

- What is the current and expected population growth rate of the buffalo population?
- What are the reasons for the apparent current low population growth rate of the buffalo and can it be improved?
- What is the long-term sustainability of the buffalo population under natural conditions on Tswalu?

Methods

Field study

Population structure

In a buffalo population, a ratio of five to 15 sexually mature females per sexually active male is recommended for maximum productivity (Bothma 2002a). However, most recorded natural populations have a 1:1 sex ratio (Pienaar 1969; Sinclair 1977). Sexing of immature animals in the field is difficult, and animals less than 24 months of age can only be sexed correctly on their external genitalia (Prins 1996). Adult males have a heavy horn shield, known as a boss, that covers the top of the head above the eyes. Females have horns that are narrower than males, and the head seems flat in profile due to the absence of the forehead ridge (Sinclair 1977; Du Toit 2005).

A balanced age structure must be maintained in any animal population for optimal productivity, because deviation from such an age structure could affect the population growth rate. Yet, the ratio of the age classes in a population can be an indication of its current and expected reproductive state (Odum 1983). Bothma (2002a) recommended that 30 to 40% of a large herbivore population must consist of young, reproductive animals.

There are various methods to age mammals, including the following:

- A change in body size (Pienaar 1969; Grimsdell 1973; Hornsveld 1996) and body mass (Pienaar 1969; Morris 1972)
- An increase in the eye lens mass which indicates increased age (Morris 1972)
- Degradation of teeth (Grimsdell 1969; Morris 1972) and changes in incremental growth lines in bone (Morris 1972)
- Changes in bone marrow with red bone marrow being replaced by fat in older animals (Morris 1972)
- Fusion of the epiphyses (Morris 1972), changes in external features (Grimsdell 1969) and horn or claw development (Pienaar 1969; Morris 1972; Sinclair 1977).

Prins (1996) concluded that it is impossible for a human observer to accurately estimate an adult buffalo bull's age based on horn morphology or size alone. Although it is impossible to age animals accurately in the field unless the date of birth is known, broad age classes can be determined (Funston 1992). Pienaar (1969) developed the most useful field criteria for age classification of buffalo, by providing a description and a series of photographs of different age classes. Grimsdell (1973) produced sketches of buffalo of various ages, with a scale based on the attainment of asymptotic shoulder height. Sinclair (1977) also sketched the age and sex classes based on horn shape and size. For the purpose of this study, age class determination was done in the field based on horn shape and development, body measurements, and changes in the colour and texture of the coat. The age classes identified were as follows:

- **Infants**

  This age group, also referred to as the neonatal or the young calf group, included all the calves from the latest calving season up to the age of 12 months. This group was distinguished by active suckling of the young up to approximately 6 months of age (Pienaar 1969), and a strong observable parent/offspring bond (Estes 1997). At birth, the animal's coat is a dark olive brown to black, and appears smooth and silky (Pienaar 1969). At 2 weeks of age, the coat becomes lighter, turning a chocolate brown, and horn buds are visible (Funston 1992). Short, clearly visible horns are present at 3 months of age, and the coat is a dirty yellow-brown (Funston 1992). At 6 months of age, the horns project upwards in a V-shape, and at 9 months of age the horns are straight, growing outwards and backwards (Pienaar 1969). Heifer calves have a straight nasal profile, whereas bull calves have a convex one (Pienaar 1969).

- **Juveniles**

  For the purpose of this study, buffalo from 12 to 24 months of age were classified as juveniles. The coat of juveniles becomes darker and rough and is chocolate brown at 24-months (Pienaar 1969). Horn length is about twice that of the ears at 12 months of age (Funston 1992), and the horns curve slightly outwards but are still widely separated at the tips (Pienaar 1969). Juvenile females are slightly taller and longer in the body than males of the same age (Grimsdell 1973).

- **Subadults**

  This group included buffalo from 25 to 48 months of age. The coat is uniformly smooth and a dark chocolate brown in colour. In females, the coat colour starts to change into the typical black of the adult hair coat at around 36 months of age (Pienaar 1969). The horn tips start their inward sweep after 24 months of age (Pienaar 1969), and by 4 years of age the horns begin their backward sweep and attain the adult horn shape (Funston 1992). Hair loss in the skin between the horn bases becomes apparent in subadult males (Prins 1969), the crown of females is well covered with hair (Funston 1992). Male buffalo have a heavy shield of horn, commonly known as the boss, that covers the whole top of the skull above the eyes. The boss is present from 30 months of age, starting as a thickening of the base of the horn (Sinclair 1977).

- **Adults**

  Buffalo older than 48 months were classed as adults. The coat colour changes to a black (Pienaar 1969). The tips of the horns of females begin the backward sweep and are wide, dipping lower than those of subadult females (Pienaar 1969). The crown of the head shows signs of abrasion and hair loss, and old females have shrunken and bony faces that are associated with a deteriorating physical condition (Pienaar 1969; Sinclair 1977). The boss of adult males is a complete shield when the two horn bases have met in the centre of the skull, usually after 7 years of age (Sinclair 1977). Bulls older than 11 years are classed as old and are seldom seen in a herd. These animals are massive, with numerous scars on their bodies (Funston 1992). The areas above the eyes and on the cheeks are usually speckled with patches of grey-white hair (Sinclair 1977). Areas on the neck, belly and hindquarters become hairless (Pienaar 1969). Dewlap and testicle size can also be used in ageing old males and could even be an indication of social dominance (Grimsdell 1973; Sinclair 1977).

In the present study, field observations were made with the aid of binoculars as often as possible. The first total count of the buffalo was done in May 2003 and compared with that of the annual aerial census that was done in the same month. Total counts of the buffalo population on Tswalu were made whenever the opportunity arose. The results of the annual aerial census done in May 2004 were also compared with the total counts of the buffalo that were done in June 2004. Estimates of the population totals based on the annual aerial counts before 2003 were also obtained from the Tswalu database and will be analysed later in this chapter.

Age and sex classification were done at the same time as the ground-based herd counts. To do accurate total counts on buffalo in a Kalahari system sometimes proved more difficult than initially thought. The first reason for this difficulty was due to the vegetation composition of Tswalu, and the second was the vast habitat in which various subgroups of buffalo roamed. When the buffalo were observed in open plains, accurate counting was possible, but whenever they were present in dense thickets or shrubveld, accurate counting, age and sex classification could not be done. However, it was still attempted then to obtain precise counts to provide an estimate of trends because they are repeatable (Bothma 2002c). For accurate counting and classification into age and sex classes, the buffalo had to move at a constant slow speed in a long, single file while crossing a relatively open area. The best counts and classification were done when the buffalo grazed while moving towards waterholes. Under such circumstances, they tended to walk in a long, single file and arrived in this fashion at the waterhole. This made counting and classification easy and accurate.

Data analysis

Population structure

A crude population growth rate can be determined by the ratio of births to deaths in a given year. The finite growth rate (λ) can be determined as the ratio of the population size in two consecutive years, thus giving the mean growth rate over the whole period of observation (Caughley 1977; Bothma 2002a).

The exponential growth rate (r) can be determined from consecutive count data with the following equation (Odum 1983; Bothma 2002a):

$$\text{Log}_e (N_t) = \text{Log}_e (N_0) + rt$$

where:

N_t = population size after time t

N_0 = population size at beginning of time t

r = exponential growth rate
e = a constant with a value of 2.71828

The exponential growth rate (r) only gives an indication of the growth at a particular time for the population, and not whether the population will continue to grow or if the grazing and browsing capacity have been reached (Bothma 2002b). The exponential growth rate is more useful than the finite growth rate in describing population growth for three reasons: firstly, it is centred at zero with positive values indicating increases and negative values indicating decreases (Caughley 1977; Bothma 2002a). Secondly, r can easily be converted from one unit of time to another (Odum 1983; Bothma 2002a). Thirdly, the time that a population will take to double can also be determine with the value 0.6931/r (Odum 1983; Caughley & Sinclair 1994; Bothma 2002b).

The mean population growth rate can be determined from successive count data and gives an indication if the population is growing and assist in harvesting quotas (Bothma 2002b). The relevant equation (Caughley 1977; Bothma 2002b) is:

$$\check{r} = \Sigma(\text{Log}_e P)(t) – [(\Sigma \text{Log}_e P)(\Sigma t)/n]/ \Sigma t^2 – [(\Sigma t)^2/n]$$

where:
ř = mean exponential rate of increase
P = game count data
n = number of counts
t = time interval in years
Σ = sum off
e = a constant with a value of 2.71828

All species have a maximum rate of increase called their intrinsic rate of increase r_m, and can be determined with the formula (Caughley & Sinclair 1994):

$$r_m = 1.5W^{-0.36}$$

where:

r_m = intrinsic rate of increase
W = the mean adult live mass (kg)

The deviation of the buffalo sex ratio for each age class from parity was determined with the χ^2 method (Sachs 1982; Samuels 1989), at a significance level of $\alpha \leq 0.05$.

Population viability analysis

The VORTEX computer-based program version 9.57 of Lacey, Borbat & Pollak (2005) was used to assess the long-term sustainability of the buffalo population on Tswalu. It has been used with success to assess population viability of a number of wildlife types including the Cape mountain zebra (Novellie, Milller & Lloyd 1996), warthog (Somers 1997), Burchell's zebra (Bowland, Bishop, Taylor, Lamb, Van der Bank, Van Wyk & York 2001), and the Arabian oryx *Oryx leucoryx* (Strauss 2003). VORTEX analysis simulates stochastic extinction processes of a population under a given set of conditions. The model is based on a Monte Carlo simulation of the effects of demographic and environmental stochastic events on wildlife populations, as well as catastrophic events. VORTEX analysis simulates a population by stepping through the series of events describing the life cycle of a population. These events include mate selection, mortality, increment of age, migration, removals, supplementation and the truncation to the ecological capacity (Miller & Lacey 2005). Simulations can be iterated by a user specified amount, and the results mimic situations that the population might experience under similar conditions. Four VORTEX models were run for the buffalo on Tswalu and include an introductory, proposed, catastrophes and harvesting model, each with their own assumptions and subsequent models.

Introductory model

An introductory model was run over a short-term period of 10 years with 1 000 iterations as well as over a long-term period of 100 years with 1 000 iterations. The assumptions made to develop these models were as follow:

- Inbreeding depression was incorporated and the default value in VORTEX was used for the number of lethal alleles (3.14) and as the percentage of the genetic load (50% due to the lethal alleles)
- Catastrophes were not included in the introductory model
- Mating was polygynous and males older than 8 years were considered part of the breeding pool
- Sexual maturity was taken as the age when the animal reached full reproductive capacity (Bertschinger 1996), thus when females conceived for the first time (Sinclair 1977), usually around 58 months in buffalo (Grimsdell 1969). Males achieve sexual maturity when a combined testicular-epididymal mass of 300 g is attained (Grimsdell 1969), usually around 54 months of age (Berry 1996). Young adult bulls will not get the opportunity to breed until they reach 7 or 8 years of age (Pienaar 1969). For the purpose of this model, the age of first breeding for females was taken as 5 years and the maximum age of reproduction was estimated to be 15 years. First age of reproduction for

the males was 8 years. The sex ratio at birth was 50% with a 90% calf survival rate, for calves younger than three months of age

- It was assumed that the overall pregnancy rate was 60%, with an intercalving period of 24 months (Sinclair 1977; Bothma 2002b), and a production of 0.5 calves per adult female per year (Sinclair 1977)
- Mortality rates were estimated at 10% in the first year (Prins 1996), 2% between ages three and four and 10% for animals older that 5 years
- The initial population size was 44 buffalo that were introduced on Tswalu during 1995
- The ecological capacity of the buffalo on Korannaberg was determined to be 149 buffalo, but it was recommended that the maximum number of buffalo on Korannaberg never exceed the ecological capacity of 104 buffalo (Chapter 6). The estimated standard deviation was 20% (21 animals)
- No supplementation or harvesting took place in the introductory model.

Proposed model

Few management plans work out according to plan. The limited records on Tswalu showed that the buffalo population had been harvested since 1996. It was decided to simulate the population based on the data obtained during the study period. The buffalo population was already close to its proposed economical capacity for the Korannaberg section in 2004, and therefore projections were only made for 10 years based on the observed sex ratio during the study period as well as a stable sex ratio for comparative purposes. The actual observed sex ratio of the buffalo was altered in an attempt to determine which sex ratio would yield maximum population growth.

Catastrophes

Catastrophes related to environmental conditions were incorporated into the proposed model and run over a 100-year period to produce a second set of scenarios. Wet and dry periods lasting a few years are a natural phenomenon in the Kalahari (Fourie *et al.* 1987). Three climatic phases dominate the ecology of the Kalahari: a wet phase at intervals of 10 to 20 years where an exceptional amount of rain falls; an arid phase that characterises extended periods of drought, and a transition phase when the rainfall varies around the annual mean (Van der Walt & Le Riche 1999). The great variability in annual rainfall in the Kalahari region affects the vegetation and consequently reproduction in animals (Sinclair 1977; Knight 1991). A variation in annual rainfall of as little as 10% around the mean could have dramatic effects on the primary production of the Kalahari (Chapter 6). Three different drought scenarios were modelled, each with a different effect on reproduction and survival. One fire catastrophe was modelled because fire is a real threat to the veld of the Korannaberg section of Tswalu due to the intensity of lightning storms and the high iron content of both the Kalahari sands (Leistner & Werger 1973), and the Korannaberg Mountain Range. A severity factor with respect to reproduction and survival was chosen for each catastrophe. This severity factor ranges from 0.0 to 1.0, with 0.0 indicating a total loss of reproduction and no survival of the population. A severity factor of 1.0 indicates that the catastrophe will have no effect on the reproduction or the survival of the population (Miller & Lacy 2005). For example, if the severity factor was chosen as 0.67 with respect to reproduction, it means that if 60% adult females normally bred in a given year, only 40.2% (60% x 0.67 = 40.2%) would breed in a year of a given catastrophe. Therefore, fecundity and survival rate for catastrophe years were obtained by multiplying the normal values during years of no catastrophe by the specified severity factor. The four catastrophes modelled were:

- Fire catastrophe: extreme fire situation with limited control and severe damage to the veld. The severity factor for reproduction was set at 0.50, while survival over all the buffalo age classes was set at 0.50. The probability that such a catastrophe would occur was estimated at 10%.
- Extended drought catastrophe: rainfall was taken as 2 years of rainfall representing 60% of the annual mean, followed by normal rainfall for 2 years. Normal rainfall was perceived as years where the annual rainfall oscillated from 80% to 120% of the long-term annual mean, therefore from 185.0 to 277.6 mm. The severity factor for reproduction was set at 0.60, while survival over all the buffalo age classes was set at 0.70. The probability that such a catastrophe would occur was estimated at 8.5% based on the long-term rainfall pattern measured at the Van Zylsrus weather station.
- Low impact catastrophe: rainfall was taken as normal for 2 years, followed by a year of rainfall representing only 50% of the long-term annual mean. The severity factor for reproduction was set at 0.70, while survival over all the buffalo age classes was set at 0.90. The probability that such a catastrophe would occur was estimated at 7.0%, based on the long-term rainfall pattern measured at the Van Zylsrus weather station.
- Long-term drought catastrophe: extreme periods of drought were modelled for once every 71 years. This period was characterised by a 3-year period when rainfall represented 20 to 45% of the long-term annual mean, followed by normal rainfall. The severity factor for reproduction was set at 0.20, while survival over all the buffalo age classes was set at 0.45. The probability that such a catastrophe would occur was estimated at 1.4%, based on the data obtained from the Van Zylsrus weather station that demonstrated this phenomenon to have only occurred once since 1933.

Harvesting

Harvesting of buffalo can be financially viable due to the high prices obtained for live buffalo sales (Bothma 2005), and would keep the population in a constant growing state by reducing the population size below ecological capacity (Bothma 2002b). The effect of different harvesting quotas was therefore also investigated with the assumptions of the proposed model.

Results

Population structure

A total of 217 sightings of buffalo groups were made which ranged in size from lone animals to a herd of 78 animals. The annual aerial count of 2003 revealed 85 buffalo, and 74 buffalo were counted in the one of 2004. In contrast, ground counts of the total buffalo population of Tswalu during 2003 indicated the presence of 74 buffalo, but in 2004 the numbers increased to 83. This resulted in a finite growth rate of $\lambda = 1.12$, and an exponential growth rate of $r = 0.11$ from 2003 to 2004. The expected doubling time for the population of 83 to 166 animals based on this growth rate is 6.3 years. The mean growth rate of the buffalo population on Tswalu for the 9 years from 1996 to 2004 was $\check{r} = 0.07$ (7.8%), determined from annual aerial count data obtained from the Tswalu database (Table 28). The intrinsic rate of increase r_m for the Tswalu buffalo was determined as 0.16 or 16% annual growth. The growth curve of the Tswalu buffalo is presented in Figure 20.

The age and sex composition of the initial buffalo population introduced on Tswalu in 1995 were obtained from the Tswalu database and are summarised in Table 29. From the 44 buffalo that were introduced to Tswalu in 1995, the majority (57% of the total population) was in the subadult class, with an adult sex ratio of one male to six females. The age and sex ratio determined during the study period of 2004 are summarised in Table 30. The sex ratio of the buffalo in 2004 in the infant class was dominated by females, with a ratio of two females per male, compared with the sex ratio of the male-dominated juvenile class of two males per one female. The subadult age class had a sex ratio that did not deviate significantly from parity ($\chi^2 = 0.67$, df = 1, $p \leq 0.1$), but the adult age class had a sex ratio that did deviate significantly from parity ($\chi^2 = 1.80$, df = 1, $p \geq 0.1$). The age structure of the buffalo population on Tswalu was biased towards adults, with only 10.8% infants and 6% juveniles, as opposed to 54.2% adults (Fig. 21).

Table 28: The growth rate of the buffalo population on Tswalu Kalahari Reserve in the Northern Cape province of South Africa, based on annual aerial game counts

YEAR	BUFFALO COUNTED	FINITE GROWTH RATE (λ)	INSTANTANEOUS GROWTH RATE (r)
1996	39	1.00	0.00
1997	49	1.26	0.23
1998	57	1.16	0.15
1999	58	1.02	0.02
2000	55	0.95	- 0.05
2001	70	1.27	0.24
2002	76	1.09	0.08
2003	85	1.12	0.11
2004	74	0.87	- 0.14

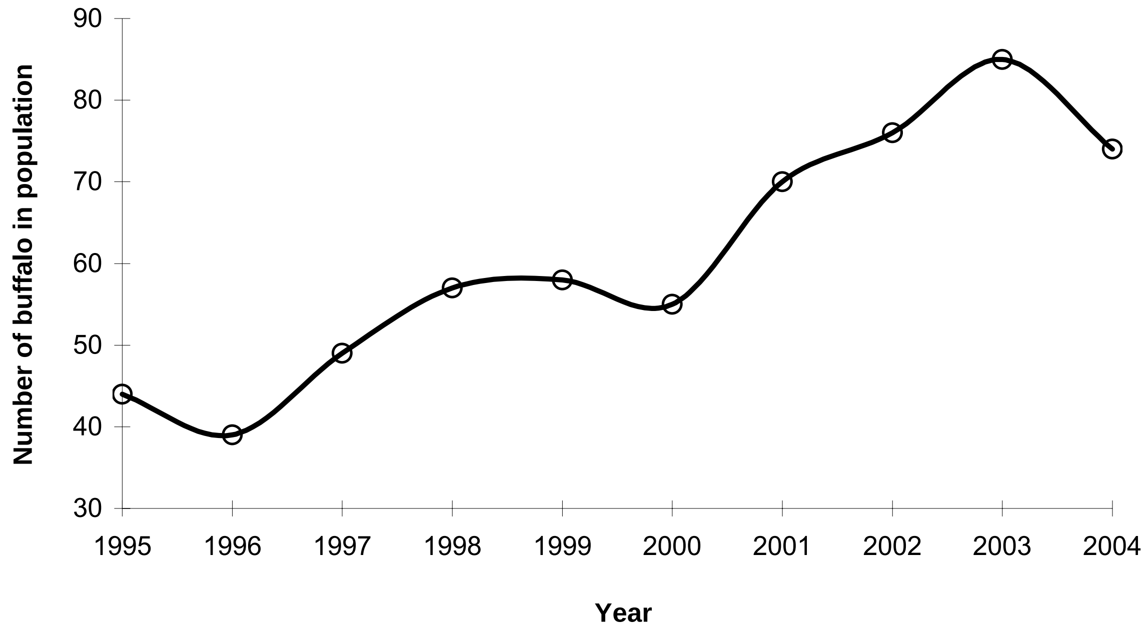

Figure 20: The actual growth of the buffalo population on Tswalu Kalahari Reserve in the Northern Cape province of South Africa from 1995 to 2004, based on the annual aerial count data.

Table 29: The sex and age classification of the initial introduced group of buffalo to the Tswalu Kalahari Reserve in the Northern Cape province of South Africa during 1995. The data was obtained from the Tswalu database

AGE CLASSIFICATION	**SEX CLASSIFICATION**	
	Female	Male
Infants (0 to 12 months)	2	0
Juveniles (13 to 24 months)	8	2
Subadults (25 to 48 months)	12	13
Adults (> 48 months)	6	1
Total	**28**	**16**

Table 30: The sex and age classification of the buffalo population on Tswalu Kalahari Reserve in the Northern Cape province of South Africa in 2004

AGE CLASSIFICATION	**SEX CLASSIFICATION**		**AGE CLASS AS PERCENTAGE OF THE POPULATION**
	Female	Male	
Infants (0 to 12 months)	6	3	**10.8**
Juveniles (13 to 24 months)	2	4	**6.0**
Subadults (25 to 48 months)	10	14	**29.0**
Adults (> 48 months)	27	18	**54.2**
Sex classification as percentage of the population	**53.6**	**46.4**	

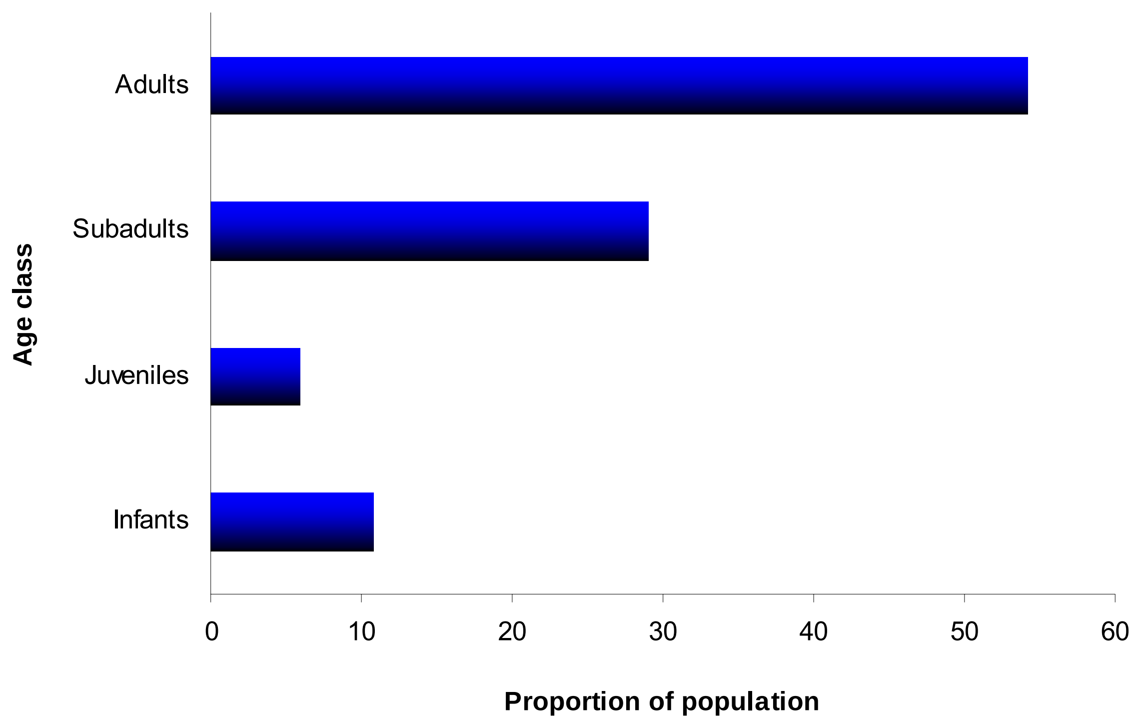

Figure 21: The distribution of the age classes of the buffalo population on Tswalu Kalahari Reserve in the Northern Cape province of South Africa in 2004.

Population viability analysis

Introductory model

VORTEX modelling predicted a mean projected buffalo population of 114.89 (SD ± 11.81) after 10 years, based on the previously specified assumptions. The probability of persistence over the modelling period was 1.00, which means that the model predicts certain survival over the 10-year modelling period. The projected population growth rate before proposed ecological capacity (104 buffalo) truncation was r = 0.098 (SD ± 0.076) and was higher that the determined mean growth rate of ř = 0.07, but was close to the actual observed growth rate of 2004 (r = 0.11). Over the long-term period (100 years) the buffalo population had a mean projected growth rate of r = 0.093 (SD ± 0.056) with a mean projected population size of 123.06 buffalo (SD ± 3.68), with a persistence of 1.0. The difference between the predicted growth rate and the determined mean growth rate can be attributed to the stochastic nature of the modelling processes and differences in calculation methods (Strauss 2003).

Proposed model

When the observed data was included in the model, the mean projected growth rate of the population over a 10-year period was r = 0.044 (SD ± 0.068) with an equilibrium population size of 115.3 (SD ± 11.18) and with ecological capacity being reached after 4 years. If a stable age structure was included into the model assumptions, the projected growth rate over a 10-year period was r = 0.025 (SD ± 0.065) and the final population size was 104.5 (SD ± 16.72). The projected growth rate at the age of first breeding was the lowest for a population with a stable age and sex composition (Table 31). A maximum growth rate was achieved for a sex ratio of 15 females per male.

Catastrophes

The probability of the long-term (100 years) survival of the buffalo on Tswalu under current conditions with no catastrophes occurring is 99% with a projected growth rate of r = 0.021. The results of the effects that the different modelled catastrophes would have on the buffalo are presented in Table 32. The predicted time to extinction varied from 40 years for the fire catastrophe to 76 years for the low impact catastrophe. However, the survival probability of the buffalo for the low impact catastrophe was 98.3%, compared to the 3.4% survival probability of the fire catastrophe. The extended drought yielded a negative growth rate (r = - 0.013, SD ± 0.135), with a mean final population size of 21.7 buffalo (SD ± 28.6).

Table 31: The projected population sizes and growth rate of the buffalo population on Tswalu Kalahari Reserve in the Northern Cape province of South Africa, with different ratios of adult productive females per adult male, and with a normal age distribution in the initial founder population, as modelled over a 10-year period

FEMALES PER MALE	MEAN POPULATION SIZE AT YEAR					POPULATION GROWTH RATE	
	2	4	6	8	10	r	SD
1	104.8	112.6	101.9	111.6	115.4	0.032	0.083
2	93.9	104.2	105.8	113.4	116.3	0.048	0.070
5	85.5	96.8	105.8	113.1	116.1	0.060	0.069
10	85.5	94.6	106.6	113.1	115.6	0.061	0.071
15	83.5	94.3	105.6	112.8	115.9	0.063	0.070
Current	97.7	107.3	112.2	114.8	115.3	0.044	0.069
Stable	87.3	92.2	97.2	101.6	104.6	0.025	0.065

Table 32: The projected effect of different catastrophes as simulated for the buffalo population on Tswalu Kalahari Reserve in the Northern Cape province of South Africa, simulated over a 100-year period with 1 000 iterations

CATASTROPHE	SEVERITY FACTOR		FREQUENCY PERCENTAGE	MEAN FINAL POPULATION		POPULATION GROWTH RATE		PERCENTAGE SURVIVAL PROBABILITY	YEARS TO FIRST EXTINCTION
	Breeding	Survival		Size	SD	r	SD		
None	No effect	No effect	-	109.5	18.2	0.021	0.068	99.9	85
Low impact	0.70	0.90	7.0	89.4	31.8	0.011	0.079	98.3	76
Long-term drought	0.20	0.45	1.4	70.1	43.2	0.008	0.124	88.4	68
Extended drought	0.60	0.70	8.5	21.7	28.6	- 0.013	0.135	47.5	65
Fire	0.50	0.50	10.0	1.3	7.3	- 0.033	0.216	3.4	40

Harvesting

When animals were modelled to be harvested over a 10-year period, a positive growth rate was predicted for all scenarios (Table 33). The highest growth rate for harvesting was predicted for 15 males to be removed, 5 years into the model (r = 0.036; SD ± 0.083). However, when no animals were harvested, the predicted growth rate was higher (r = 0.044; SD ± 0.068) than for the above mentioned scenario where buffalo were harvested. Although there is no apparent benefit between harvesting and not harvesting over the short-term, there is a definite financial benefit when harvesting buffalo.

Discussion

Population structure

During April 2003, a total ground count of the buffalo on Tswalu revealed the presence of 74 animals. Later during that year, five adult bulls were removed and one adult female died in December 2003. Nine calves were born during the 2003 to 2004 calving season, and one adult bull, one subadult bull, two adult females and one subadult female were removed during February 2004. A total ground count that was done in May 2004 revealed 83 buffalo, giving a growth rate of r = 0.11 for the period 2003 to 2004.

When the annual recruitment for the same period was determined according to the ratio given by Sinclair (1974b), as the number of yearlings, thus the amount of calves that survived their first year of life, per total number of adult females (from Table 30), it gave a recruitment rate of 33% (9 calves were born) for 2004. The recruitment rate for 2002 to 2003 was 25% (6 calves born). Sinclair (1974b) found recruitment rates of 32 to 44% for the buffalo in the Serengeti, with predation being present together with observed calf mortalities. Prins (1996) found a recruitment rate of 12% for buffalo in East Africa, with 70% calf mortality if based on the calculation of Sinclair (1977). Taolo (2003) determined recruitment rate to be to be from 23% to 77% for buffalo in Botswana. Buffalo that were relocated to the Bontebok National Park in the Cape province showed low production after 12 years, and they were removed. Possible reasons for this low recruitment rate (19%) could have been a population dominated by males, and a high calf mortality that was attributed to adult aggression (Van der Walt, Van Zyl & De Graaff 1976). Although it seems that the buffalo on Tswalu had a recruitment rate that lies within the expected norms for free-living buffalo, the rates of Sinclair (1977) and Prins (1996) can be compared to the 33% found on Tswalu during 2004 because the method used to determine these rates were the same. The recruitment rate on Tswalu seems to be within the recorded boundaries of buffalo

Table 33: The projected effect of the different harvesting quotas as simulated for the buffalo population on Tswalu Kalahari Reserve in the Northern Cape province of South Africa

HARVESTING YEARS			FEMALES HARVESTED			MALES HARVESTED			GROWTH RATE		MEAN FINAL POPULATION	
First	Last	Interval in years	Juveniles	Subadults	Adults	Juveniles	Subadults	Adults	r	SD	Size	SD
0	0	0	0	0	0	0	0	0	0.044	0.069	115.3	11.180
5	5	0	0	1	5	0	1	9	0.028	0.088	107.7	16.271
2	8	2	0	0	2	0	2	1	0.015	0.074	98.1	19.042
5	5	0	2	5	5	2	1	7	0.023	0.094	104.3	17.090
5	5	0	0	0	0	5	5	5	0.036	0.083	112.1	14.017

elsewhere, however, it must be remembered that recruitment rates of both Sinclair (1977) and Prins (1996) included known predation and calf mortalities, therefore the rate on Tswalu should theoretically be much higher than these observed rates in East Africa because there was no predation or calf mortalities observed on Tswalu.

Sinclair (1974b) investigated the effect that rainfall could have on annual recruitment, especially during the year preceding conception, but his results suggested no such relationship. However, there was a relationship between rainfall during the last part of pregnancy and lactation, which effected yearling survival (Sinclair 1977). The primary production of areas in Africa receiving less than 700 mm annual rainfall are more affected by variation in annual rainfall than areas receiving more than 700 mm annual rainfall (Coe *et al.* 1976; Novellie 1986), which ultimately influence buffalo production through food resources. Knight (1991) also concluded that the amount of gemsbok calves that was born in the Kgalagadi Transfrontier Park was related to the rainfall in the previous summer. This does not hold true for Tswalu because the actual annual summer rainfall preceding the calving season of 2002 to 2003 was 141.1 mm and for the 2003 to 2004 season, it was 128.8 mm. The amount of calves born during the 2002 to 2003 season was 6, while it was 9 for the 2003 to 2004 season. One possible reason for the low recruitment rate of the buffalo on Tswalu buffalo could well have been unobserved calf mortalities or abortions because of the difficulty of finding such evidence.

The Tswalu population has an age distribution containing 54.2% adult reproductive animals, 29% subadults, 6.0% juveniles and 10.8% infants (Fig. 21). This is characteristic of a declining population (Odum 1983). Female buffalo older than 10 years of age produce fewer offspring than younger ones (Grimsdell 1969; Sinclair 1974b; Carmichael, Patterson, Gräger & Breton 1977) because of an increased calving interval (up to 29.6 months) caused by the older buffalo taking longer to reach an optimal body condition for conception (Grimsdell 1969; Carmichael *et al.* 1977). Because of the older age structure of the buffalo population on Tswalu, together with the age of the introduced animals in 1995, 17 of the 28 introduced females would be older than 10 years in 2004, giving rise to the possibility of an increased calving interval due to the reasons discussed above. All of this could also lead to a low recruitment rate on Tswalu.

Studies on herbivores have confirmed that puberty is only reached once a certain body mass, rather than an age is reached (Joubert 1963; Bertschinger 1996). Puberty in a herbivore is therefore influenced by the availability and quality of the food, especially protein intake (Grimsdell 1969; Bothma 2002a). Nutritional conditions in the first 2 years of life could therefore have an effect on the fertility of an animal, with fertility being delayed under conditions of nutrient stress (Sinclair 1977). Therefore, rainfall, which influences the nutritional state of the forage, would be the primary factor affecting herbivore ovulation and conception rates (Grimsdell 1969; Knight 1991). Another reason for the low conception and reproduction rate of the buffalo on Tswalu could therefore be that the female buffalo do not reach a target mass and hence delay puberty. This would delay conception, causing the females to start reproducing later in life than elsewhere.

The gestation period of buffalo is approximately 340 days (11.5 months) (Grimsdell 1969; Sinclair 1977), with the first calving occurring between their 5th (Carmichael *et al.* 1977; Du Toit 2002) and 6th year of age (Grimsdell 1969). Buffalo are seasonal breeders with a calving peak that is correlated with ingested food quality and the amount of rainfall received (Sinclair 1974b). Births peak during summer or in times of high rainfall, as have been confirmed by Sinclair (1974b) and Grimsdell (1969) in East Africa, and by Carmichael *et al.* (1977) in Southern Africa. Fairall (1968), Pienaar (1969), Bertschinger (1996) and Visscher, Van Aarde & Whyte (2004) observed the same phenomenon in the Kruger National Park of South Africa, as was done on Tswalu during the 2003 to 2004 calving season, with births occurring from December 2003 and continuing until early April 2004.

Lactation in buffalo can last up to the 7th month of the next pregnancy (Grimsdell 1969) as was observed in the present study (n = 4). This extended lactation period and a low quality diet in the dry season could result in undernutrition of the foetus, resulting in underweight calves with impaired survival being produced. In the Serengeti, such underweight calves were known to be abandoned and they eventually died (Sinclair 1974b). Undernourished calves lose mass soon after birth and it could take up to 1 month to recover their original birth mass (Grimsdell 1969). Ideally, calves are weaned at 5 months of age (Bertschinger 1996), but suckling can be tolerated for as long as 9 months (Sinclair 1977). Optimal conception rates result from optimal feeding conditions for pregnant cows between parturition and oestrus, this is because of a higher food requirement during late pregnancy and lactation (Sinclair 1974b). This higher food requirement during the last two months of pregnancy is accentuated because rumen fill decreases to compensate for space for the growing foetus (Grimsdell 1969). A post-partum anoestrus was observed in Botswana (Carmichael *et al.* 1977), and in South Africa Pienaar (1969) recorded a lactation anoestrus without follicular growth or sexual activity. The Tswalu buffalo had a recruitment rate of 33% during 2004. If it is assumed that 22% of the females that had calves 12 months earlier were still in lactational anoestrus or in their intercalving period, together with the 33% of females that had suckling calves, it means that 45% of the productive females showed no sign of reproduction. One possible reason for this could be the high physiological stress on the females, with extended lactation periods and impaired target condition for conception.

The sex ratio in buffalo foetuses is usually at parity (Grimsdell 1969), with the majority of implants in the right uterine horn (Sinclair 1977). The infant and juvenile buffalo of Tswalu in 2004 had a sex ratio of 0.5 and 2 males per female respectively. The data as presented here on the sex ratio of the infant and juvenile buffalo on Tswalu revealed the possibility of an interesting phenomenon known as the Trivers and Willard hypothesis. According to this hypothesis, paternal condition could be central in influencing the sex ratio of the offspring, with more male offspring being produced when females are in a good physical condition (Trivers & Willard 1973). Resource availability often relates to variations that are found in sex ratios at birth (Hewison & Gaillard 1999; Mysterud, Yoccoz, Stenseth & Langvatn 2000). Due to the pronounced sexual dimorphism of size in buffalo, optimum production will favour the production of male offspring as opposed to female offspring (Côté & Festa-Bianchet 2001; Grant 2003). This happens because a bull can produce a potentially higher number of offspring than a cow in a lifetime (Funston 1992). According to Lee & Moss (1986), male elephant calves have a greater nutritional demand than female ones. This could play a significant role in times of food stress, when producing female calves will be the better option, as was found by Mysterud *et al.* (2000) in red deer *Cervus elaphus*. Cameron & Linklater (2000) also confirmed that female feral horses *Equus caballus* that were in a good physical condition favoured male foals. Wauters, De Crombrugghe, Nour & Matthysen (1995) found that roe deer *Capreolus capreolus* adjusted their foetal sex ratio according to their physical condition, moreover as was confirmed by Sheldon & West (2004) for various ungulate species.

As the amount of rainfall received on Tswalu oscillates, it affects the annual rainfall received at the time of conception in the buffalo. The cows then tend to give birth to male offspring in years with a lower annual rainfall. Due to a lack in recruitment data for the period before 2003, this assumption was based on only 2 years of observations, and is therefore only a tentative hypothesis, although Funston (1992) formulated the possibility of such a hypothesis in the Sabi Sand Game Reserve where more female calves were produced during the drought years in the 1980's. On Tswalu, the rainfall during the 2002 to 2003 conception period was 184 mm with four male calves being produced, compared with the rainfall during the 2003 to 2004 parturition period (191 mm) with six female calves being produced. More research is clearly needed to test this validity. Pienaar (1969) found that male suckling buffalo calves were heavier than female ones, which suggested higher maternal cost for males. Visscher *et al.* (2004) found no evidence that buffalo could adjust foetal sex ratio relative to their physical condition with females in good condition tending to produce female progeny, and seem to be consistent with the results found on Tswalu, but are contradictory to the Trivers and Willard hypothesis. They also found that the production of male foetuses decline with increasing age of the mother. Long-term studies are needed in order to determine conclusively whether the buffalo, or any other wildlife species, can modify its sex ratio at conception according to the rainfall received (Carranza 2002). Although different sex ratio trends have been reported in the same species (Hewison & Gaillard 1999; Côté & Festa-Bianchet 2001), specific physiologically-based studies of more species are required to test if females can adjust their foetal sex ratios relative to their physical condition (Côté & Festa-Bianchet 2001).

The adult age class had a sex ratio (1.67 females per male) that did deviate significantly from parity (χ^2 = 1.80, df = 1, $p \geq 0.1$). Funston (1992) found the adult sex ratio of buffalo in the Sabie Sand Game Reserve, South Africa deviates from parity with females outnumbering males significantly (χ^2 = 37.33, df = 1, $p \leq 0.001$). Mloszewski (1983) obtained the same results in East Africa, as did Winterbach (1999) in the Free State, and Taolo (2003) in Botswana. In most of the above studies, hunting, predation and bachelor males all played a role in the female favoured sex ratio. Reasons for the near parity sex ratio of buffalo on Tswalu could be attributed to the lack of natural predators that will favour the survival of the males (Sinclair 1977; Prins 1996), and the harvesting of males during 2003 and 2004. Bachelor male groups were only observed on a few occasions (n = 11) on Tswalu during the dry season and there were never more than six bulls together at any given time. This meant that almost all the adult males were part of the breeding herd, which is in contrast to other studies where bachelor bull groups were always present (Sinclair 1977; Mloszewski 1983; Funston 1992).

Funston (1992) and Prins (1996) observed re-entrant consecutive polygyny where adult bulls move in and out of mixed breeding herds depending on breeding opportunities, body condition and dominance hierarchies between bulls. Taolo (2003) determined that buffalo bulls in Botswana were associated with the herd only during the rutting season and moved out thereafter, as was also suggested by Sinclair (1977) for buffalo in the Serengeti. Bulls older than 11 years leave the herd due to a decline in androgen production and thus decreased libido which is caused by a testicular interstitial tissue increase and thus a loss in interstitial cell function (Grimsdell 1969). On Tswalu, flehmen was observed when cows urinated, whereafter subordinate bulls attempted to mount cows but were often displaced by the dominant bull present. Dominant breeding bulls were observed to move in and out of the breeding herd, but they kept a close distance to the herd during the breeding season. When they were not associated with the breeding herd they were observed as lone bulls, except for two old bulls that remained together. On a few occasions (n = 18), dominant bulls drove subordinate ones out of the breeding herd, but no aggressive fighting was ever observed between the bulls during the study period.

According to Tswalu archives a total of 44 buffalo were introduced to Tswalu during April and May 1995, of which 11% were reproductively active females, with 46% heifer calves. If these data were indeed accurate, and it is assumed that all the females would have survived, then Tswalu should have had an active breeding female population of 57%, or 27 reproductively active females by 1999. From the data obtained during the study period, 27 reproductively active females were present in 2004 on Tswalu. The growth rate could first be determined in 1997 (Table 28) and was 0.23, equating to a doubling time of 3 years. Therefore, there should have been 98 buffalo on Tswalu in 1999 if none died or were removed between 1997 and 2002. This is more than the total observed buffalo on Tswalu during the study period (83 buffalo in 2004).

Most mammals have a clearly defined sigmoid growth pattern over time (Fig. 22) (Odum 1983; Bothma 2002a). Growth is initially slow in the establishment phase when births and deaths are equal, but the growth rate will accelerate into a logarithmic phase. The latter will vary between species and according to the availability of natural resources (Odum 1983; Bothma 2002a), such as food and shelter (Sinclair 1977). Eventually, the natural resources become depleted and cause deficiencies, which will ultimately cause a fluctuating equilibrium. This equilibrium, also known as the ecological capacity of an area for a given population, is that point where natural deaths and births are more or less in balance and no further growth is observed. This capacity is strongly influenced by the availability of suitable habitat for the population (Bothma 2002a). Sustainable yield or optimal sustainable yield is only possible when a population is reduced below its ecological capacity (Bothma 2002b). When a population has reached its ecological capacity under given habitat conditions, and no further growth is observed, growth can be initiated again by reducing the population first, or by increasing the available environmental resources (Bothma 2002b).

Data on the buffalo population size on Tswalu were obtained from the Tswalu database, except for that of 2003 and 2004 where ground count totals were used. From these records, it was noted that two buffalo had died during the establishment phase in 1995, and that two infants were born then. This is what would be expected from the establishment phase when births roughly equal deaths (Bothma 2002a). The exponential growth rate increased to r = 0.23 in 1997, which could be due to the amount of rainfall received in 1996 (225.6 mm), resulting in females achieving a good body condition which is ideal for conception. The sudden drop in population size from 1999 to 2000 was due to the combined hunt and capture of seven animals during that period. The same sudden drop in population size (Fig. 20) happened in 2002 to 2003 when five animals were removed.

All species have a maximum rate of increase that can be attained, called their intrinsic rate of increase rm (Caughley & Sinclair 1994). This rate would, however, rarely be reached in natural populations due to resource limitations. For the Tswalu buffalo population, this rate was r_m = 0.16

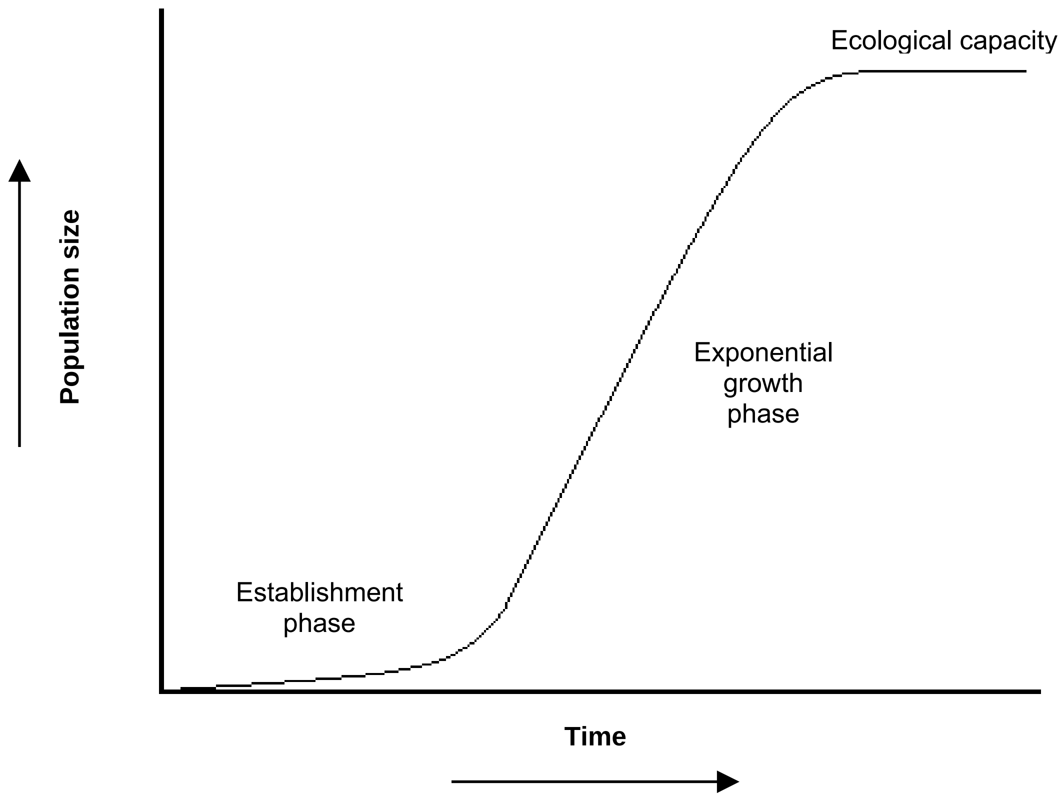

Figure 22: Graphical presentation of the sigmoid growth curve of mammal species (Bothma 2002a).

or 16% annual growth. The mean annual population growth expected in wild populations of buffalo is 6.0 to 12.0% (Du Toit 2005). For larger species, the inherent growth rate is seldom more than 40% (Bothma 2002a). For the buffalo an inherent growth rate of 8% has been suggested in area with large predators, and 12% in years of good rainfall (Bothma 2002a). Winterbach (1999) found a long-term population growth rate of 16% in the Free-State and Funston (1992) observed a 12% growth rate in the Sabi Sand Private Game Reserve. The buffalo on Tswalu had a mean growth rate of $\check{r}$ = 0.07 and is also well below their intrinsic rate of increase of 16% annual growth from 1995 to 2004. However, the growth rate for 2003 to 2004 was r = 0.11 or 11% growth, which is within the documented norms for buffalo (Funston 1992; Winterbach 1999; Du Toit 2005).

Population viability analysis

When it is decided to introduce animals into an area, it is important to choose the founder group carefully in an attempt to maximise natality and minimise mortality during the establishment phase. The rate of increase of any species is dependent upon the age at first breeding and the interbreeding period. Buffalo only start to produce offspring at five years of age with a mean calving interval of 24 months (Sinclair 1977; Prins 1996; Du Toit 2005), resulting in slow breeding. Maximum production on Tswalu (r = 0.063; SD ± 0.070) was obtained with a sex ratio of 15 females per male (Table 31). Sinclair (1977) found the pregnancy rate of adult buffalo cows in the Serengeti to be 75% resulting in 0.80 calves per female (pregnancy rate x 365/gestation time). Prins (1996) found a pregnancy rate of 52% resulting in 0.56 calves per female per year, in the Lake Manyara buffalo. The observed pregnancy rate of the buffalo on Tswalu for the 2003/2004 calving season was 33%. If the mean interbreeding period on Tswalu was taken as 24 months, a female would produce 0.40 calves per year. This is extremely low when compared with the studies of Sinclair (1977) and Prins (1996) in East Africa. The stable sex distribution yielded a lower population growth resulting in proposed economical capacity being reached later, after 9 years, compared with it being reached after 3 years with the current sex ratio of the adult buffalo on Tswalu. The reason for this is that the VORTEX analysis automatically assigns a proportion of the population to most of the recognised age and sex classes. As a result, some members of the modelled population would be considered to be below breeding age, and there is a reproductive delay.

Populations with a probability of survival lower than 90% should be considered vulnerable (Mace & Lande 1991). Under current conditions, the buffalo on Tswalu will not survive any form of catastrophe, except for the low-impact catastrophe, with survival probabilities of between 88% and 3% over 100 years. Buffalo are dependent on good quality grazing and abundant water

(Sinclair 1977) and a possible reason for their projected extinction on Tswalu could be a decreased or lack of acceptable quality and quantity of nutrition and adequate water. From these results, it is questionable if it is viable to keep buffalo under the current conditions on Tswalu. However, the buffalo could be harvested over a short-term period to generate income and to keep them below economical capacity and in a productive state. The harvest should, however, be conservative and quotas should always be kept above 50% of the economical capacity and less than the observed intrinsic growth rate (r = 0.16).

Conclusions

During 1995, buffalo were established on Tswalu through three releases that took place during the months of April and March of that year. The growth rate of the Tswalu buffalo (r = 0.11) determined during the study period lies within the expected growth rates (6 to 12%) for a buffalo population (Bothma 2002a; Du Toit 2005). From the results obtained from this part of the study, it is suggested that the buffalo on Tswalu was regulated by extrinsic factors such as food quality and quantity and removals through capture. Intrinsic factors were secondary population control measures. Attention should be given to the fact that the current Tswalu buffalo population is an ageing population and the introduction of younger females should contribute to a more productive population. The recruitment rate could also increase if the females were in top condition during conception and lactation to ensure good conception rates and calf survival. This would require a population well below the long-term ecological capacity for buffalo on Tswalu, and the economical capacity for buffalo on Korannaberg should be used as a guideline for buffalo stocking densities (Chapter 6).

During the surveys conducted in 2004, only 33% of identifiable breeding age females had calves at heel. This is low if compared to the 44% observed by Sinclair (1977) where predation and calf mortalities were observed, or to Prins (1996) with a observed 70% calf mortality, remembering that none of the above factors were present on Tswalu. The data presented in this chapter focussed on the possible reasons for the observed low pregnancy rate of the buffalo. These reasons seem to be linked to poor environmental conditions that led to poor female physical condition at the time of conception, and poor fecundity. In addition, the ageing population in combination with the poor environmental conditions that were experienced resulted in the females taking longer to reach a target mass for conception. One suggestion is to remove some of the breeding age males in order to obtain a sex ratio of 15 females per male for better production. Focus should also be placed on the females' physical condition, especially during periods of poor rainfall when the females could be supplemented with food to improve their physical condition. It is imperative that the buffalo population be monitored continually in terms of fecundity and physical condition.

Under the specified assumptions and environmental conditions, the population viability analysis predictions that the buffalo population on Tswalu was secure in the short term and could reach ecological capacity in 2008. However, the population could become vulnerable over the medium term. Supplementation of male buffalo to the current population would be expensive but could contribute to the genetic stability and fitness of the population. To compensate for the cost of bull supplementation, buffalo could be harvested conservatively.

CHAPTER 8

MANAGEMENT RECOMMENDATIONS

Introduction

According to Bailey (1984), wildlife management is the art of making land produce populations of wildlife for the primary purpose of harvesting. Wildlife management is a science which has boundaries prescribed by legislation and official policy. Attitudes like ''game can look after itself'' resulted in severe overutilisation and land degradation in several wildlife production areas of the world. Population numbers of wildlife can rise to levels where undesirable changes in the vegetation composition and cover occur. Because of such poor management practices, soil erosion and degradation take place with a reduction in grazing available for grazer species. Wildlife-proof fences, the elimination of predators and the introduction of permanent artificial water points, prevent migration of animals or the natural reduction of population numbers. It is clear that modern extensive wildlife production is far from natural and management is essential in order to obtain optimal production and prevent land degradation.

Conservation and preservation are two concepts pertaining to the management of wildlife (Thomson 1992). Conservation includes the sustainable use of animals for the benefit of man, but these animals must not be listed as endangered or vulnerable by the International Union for the Conservation of Nature and Natural Resources. Preservation includes the protection of endangered species, for later placement under conservation management and subsequent sustainable utilisation of the species. The consumptive sustainable utilisation of animals on Tswalu includes the live selling of wildlife, while eco-tourism is a non-consumptive method of sustainable use.

Conservation should be the primary objective of the management of the buffalo on Tswalu. According to Whyte (1996) the reason for managing a large buffalo population is to promote the sustainable utilisation of natural resources. Water is the most limiting factor for ungulates in arid ecosystems receiving less that 500 mm annual rainfall (Seely & Louw 1980). This was confirmed by Coe *et al.* (1976) in the relationship between rainfall, primary productivity and large herbivore biomass. Therefore, if water is provided artificially, the next limiting factor is food quality and quantity. Buffalo are water-dependent bulk grazers (Du Toit 2005), and both of these characteristics are limited in the arid Kalahari region. Because Tswalu Kalahari Reserve is not within the natural historical area of occurrence of buffalo, special attention should be given to the active management of this population.

General discussion

Protection from climatic extremes, the quality and quantity of available food, and proximity to water points big enough to aid in thermoregulation through wallowing, seemed to be the main requirements of the buffalo on Tswalu Kalahari Reserve in terms of resources. All of the above-mentioned factors could pose a problem to the population under discussion.

The first and last factor, the protection from climatic extremes and thermoregulation, could be satisfied to a degree during the warm summer months of the Kalahari where temperatures can reach 40° C. The buffalo did try to escape the scorching sun by resting in the limited shade available, preferably in the shade of *Terminalia sericea* trees in the *Stipagrostis amabilis* dune crests (Vegetation Unit 1). Movement in this unit was however limited, and the buffalo never walked great distances over the dune crests, probably because the energy cost was too high when walking in such deep, sandy areas. The water points present in the buffalo habitat was an observed problem, with only 3 of them, of which one is Rogellapan in the west of Korannaberg, being large enough to allow wallowing. The other smaller water points tended to run empty before the whole herd have satisfied their water needs, especially if the herd is bigger than 25 animals.

The second resource factor, quality and quantity of available food, is a problem and the maintenance requirements of the buffalo were not always satisfied and even with extensive selection, enough food of adequate quantity could not be ingested. The buffalo on Tswalu entered a period of nutritional stress during the winter months with the deficiency in protein severe enough to result in a loss of physical condition. The observed deficiencies on Tswalu in the preferred grass species by buffalo included deficiencies in crude protein, copper, manganese, zinc, calcium and phosphorus that could all lead to reproductive problems. The importance of supplementary feeding was emphasised by the difference in condition scores obtained after a period of supplementary feeding in the winter period. The substandard quality of the available vegetation to the buffalo could lead to a delayed puberty leaving heifers to start breeding later in life thus, shortening their productive lifecycle. It could also lead to females reaching the needed target mass for conception slower or later, and a reproductive cycle could be skipped. Calf survival could also be impaired and abortions or stillbirths could occur.

The final choice of wildlife types on a property can differ depending on the management objectives. Wildlife production takes on two forms that are not compatible: the one is aimed at animal production where exotic animals could be produced intensively, and the second one is aimed at conservation where wildlife production is extensive with indigenous species. The National Environmental Biodiversity Act of South Africa – Act 10 of 2004 (Anon. 2004), regulates the translocation of indigenous species to areas where they are locally exotic in South Africa (Anon. 2004). Species like the African buffalo is exotic to the Kalahari region. In view of the current management objective of Tswalu to restore the Kalahari ecosystem to a natural state, and the revised Biodiversity Act, the presence and purpose of the buffalo on Korannaberg should be reconsidered.

Under specified assumptions and environmental conditions, the population viability analysis predictions that the buffalo population on Tswalu was secure in the short term and could reach the recommended economical capacity in 2008. However, the population could become vulnerable over the medium term. Supplementation of the current population with male buffalo would be expensive, but could contribute to the genetic stability and fitness of the population. To compensate for the cost of bull supplementation, buffalo could be harvested conservatively.

It is recommended that the no more than 104 buffalo be kept on Korannaberg at a mean annual rainfall of 231.3 mm to avoid mortalities, and that these animals are nutritionally supplemented throughout the entire year. If these management recommendations cannot be met, it is recommended that the presence of the buffalo on Korannaberg is reconsidered. The intensive or extensive production of exotic wildlife for reasons other than relocation into areas of origin where they became rare or extinct does not contribute to conservation, and there is no legal or ecological justification for the extensive production of free-ranging exotic wildlife on native habitats (Bothma 2005).

Management recommendations

Due to the fact that ecotourism and the restoration of the Kalahari ecosystem are part of the management objectives of Tswalu, the presence of buffalo on the reserve is questionable. Buffalo also pose a problem when it comes to ecotourism. During the study period it was observed that the physical condition of the buffalo was poor when they did not receive any food supplementation. This became so bad, that the field guides avoided possible sightings of this species. It is clear that these animals should not be in the reserve because they historically were never permanently present in this area, and cannot be kept on the reserve if the management of Tswalu wants to restore the Kalahari ecosystem to a natural state. It was clear from the results of this study that the buffalo population could not survive under natural conditions in the medium-term (Chapter 6), and that the current population is under constant nutritional stress (Chapter 5), hampering productivity.

In view of the above-mentioned facts, there are three possible management strategies that could be followed for the current buffalo population on Tswalu:

- The complete removal of the animals from Tswalu Kalahari Reserve in an attempt to restore the Kalahari ecosystem there.
- Keep the buffalo on the reserve for ecotourism purposes, with food supplementation.
- Implement an intensive breeding project for the buffalo at Sonstraal or Tsamma, in view of the disease-free status of the current population.

If the animals are to be kept in the Korannaberg section, additional supplementation of food should be given to the animals. This can be achieved with the addition of 2 kg of lucerne per adult animal twice weekly. Animals would also have to be monitored closely for the effects of mineral deficiencies, such as lameness and a loss of hair. Special attention should be given to the females during conception and lactation. Improved monitoring of the population should also be implemented for other parameters including calf mortalities and fecundity.

If a decision is made to implement an intensive breeding project on Sonstraal or Tsamma two approaches could be followed:

- All animals can be removed from the Korannaberg section, and the productive females identified and put into the breeding system together with all the heifers currently present on the reserve. The remainder of the population can be sold, and new bulls are acquired to add new genetic material. All progeny produced here can also be sold, except if heifer calves are kept for later placement into the breeding system.
- The productive females and heifers can be removed and put into the breeding system with new bulls that should be introduced. The remainder of the population can be kept on the veld in the Korannaberg section, but should be supplemented with food as described above. Male progeny produced in the system, can be put back into the Korannaberg section and kept on the veld while being supplemented with food, for ecotourism purposes, or to be sold to other reserves.

Future research perspectives

Possible future work associated with and following from the current study on Tswalu Kalahari Reserve include:

- An in-depth study of the ecological separation of the buffalo, eland and white rhinoceros because these animals compete for the same food resources, especially in terms of quantity during the dry season (Lamprey 1963; Perrin & Brereton-Stiles 1999). Among other things, this could indicate whether the eland and white rhinoceros numbers are potentially limiting the buffalo population growth.

- There is an interesting hypothesis that silica acts as a defence mechanism in plants and can cause diseases in herbivores (Field 1976; Sinclair 1974b; McNaughton *et al.* 1985). During the chemical analysis of the grass species during the present study there was a large amount of silica present in all the grass species and the dung samples. An intensive study could be done to determine to what extent silica plays a role in plant defence in the Kalahari and what the effect of it is on tooth degradation in all the herbivores present.

The ecology of the African buffalo in the eastern Kalahari region, South Africa

by

Marzanne Cromhout

Supervisor: Prof. J. du P. Bothma
Co-supervisor: Prof. M.W. van Rooyen

in the Centre for Wildlife Management
Department of Animal and Wildlife Sciences
Faculty of Natural and Agricultural Sciences
University of Pretoria
Pretoria

MAGISTER SCIENTIAE (WILDLIFE MANAGEMENT)

SUMMARY

This study was conducted on Tswalu Kalahari Reserve in the Northern Cape province, South Africa. The study area was the Korannaberg section of the reserve and covered a surface area of approximately 541 km². The area forms part of the southeastern Kalahari and was classified as arid, receiving a mean of 231.3 mm rainfall annually.

The dynamics of the herbivore-habitat relationship were investigated, with the emphasis on seasonal differences in habitat selection. The buffalo on Tswalu Kalahari Reserve showed clear differences in the proportional use of the various vegetation units in the Korannaberg section. The *Stipagrostis uniplumis* plains (Vegetation Unit 4) were used most intensively throughout the study period and were a key habitat for the buffalo on Tswalu Kalahari Reserve. They did not use the *Anthephora pubescens* dunes (Vegetation Unit 2) or the *Digitaria polyphylla* mountains and hills (Vegetation Unit 11). Possible reasons for this could be the deep sandy nature of the soil of the *Anthephora pubescens* dunes (Vegetation Unit 2) and the rocky, often steep hills present in the *Digitaria polyphylla* mountains and hills (Vegetation Unit 11). The main factor determining their habitat utilisation seemed to be good quality of grazing and the presence of water points that were large enough for wallowing, especially during the warm months. The buffalo used the different vegetation units locally, based on their proximity to water.

The lowest recorded buffalo density compared with that in other studies, was found on Tswalu Kalahari Reserve at 0.15 buffalo/km². The range use patterns of the buffalo on Tswalu Kalahari Reserve were investigated with the kernel analysis technique using the Geographic Information System (GIS) package, ArcView 3.2. The total range size of the buffalo on Tswalu for the study period (205.7 km²) is therefore the largest recorded buffalo range in South Africa. The peeled range (95% minimum convex polygon) for the warm, wet season was 170.0 km² compared to 171.7 km² in the cold, dry season which is 31.8% of the total surface area of Korannaberg. This suggests a similar range size during both seasons but the range area still differs with a shift in utilisation towards the northern part of Korannaberg during both seasons. The core area of range use (50% adaptive kernel) increased from 13.1 km² in the warm, wet season to 45.2 km² during the cold, dry season and was distributed over two different clusters. This increase was after the peak calving season and can be explained by the reduced ability of the herd to move large distances with young calves, as well as possible preferred grazing in localised areas. The suitable available buffalo habitat occurs in localised patches in the Korannaberg section, and the northwest of the Korannaberg section was clearly being preferred during both seasons. Regardless of the fact that supplementary feeding could have altered the movement patterns and thus range size of the buffalo on Tswalu Kalahari Reserve, it appeared that the main driving force behind their range selection was the quality and quantity of food available, and the distribution and size of the water points, the latter being important when wallowing.

The feeding activities of the buffalo were investigated, to determine whether the nutritional requirements of the buffalo on Tswalu Kalahari Reserve were sattisfied. From nutrient analyses done on the preferred grass species of the buffalo, it became apparent that these animals were under nutritional stress during the dry season, with deficiencies in protein, copper, calcium and phosphorus. This was also confirmed with the monitoring of the physical condition of the buffalo. During the cold, dry season of 2003 the buffalo was in a poor physical condition, but this improved during the cold, dry season of 2004 after they received supplementary feeding. It was concluded that the buffalo on Tswalu Kalahari Reserve were resource limited with the producing females in exceptional nutritional stress during lactation. The recommended ecological grazing capacity for the buffalo is 292.2 GU or 149 buffalo. However, due to the fact that buffalo did not historically occur in this part of the Kalahari (Chapter 2), combined with the proved nutritional struggle of the buffalo on Tswalu, it is recommended that the economical grazing capacity for buffalo on Korannaberg (204.5 GU or 104 buffalo) is used as a maximum stocking density for buffalo in this section of Tswalu. This is a reliable and conservative recommendation for the maximum amount of buffalo on Korannaberg, even during times of poor rainfall.

During the study period only 33% of identifiable breeding age females had calves at heel, with 9 calves being born and one old female that died. It is suggested that the buffalo on Tswalu Kalahari Reserve was regulated by extrinsic factors such as food quality and quantity and removals through live capture. Intrinsic factors were regarded as secondary population control measures. Attention should be given to the fact that the Tswalu Kalahari Reserve buffalo population is an ageing population and that the introduction of younger females should contribute to a more productive population.

The viability of the buffalo population on Tswalu Kalahari Reserve was assessed by using a stochastic simulation of the extinction process with the VORTEX 9.50 program. Under the current management conditions, the buffalo would reach their ecological capacity of 104 animals in 2008. Maximum production could be reached with 15 reproductive adult females per reproductive adult bull. However, the population should be regarded as being vulnerable over the medium-term (100 years). The buffalo would not survive any form of catastrophe over the medium-term, especially not severe fire situations.

Because Tswalu Kalahari Reserve is not within the natural historical area of occurrence of buffalo, special attention would have to be given to the active management of this population. Management recommendations regarding the buffalo population on Tswalu Kalahari Reserve are therefore made.

Die ekologie van die Afrika buffel in die oostelike Kalahari streek, Suid Afrika

deur

Marzanne Cromhout

Leier: Prof. J. du P. Bothma
Mede-leier: Prof. M.W. van Rooyen

in die Sentrum vir Natuurlewebestuur
Departement Vee- en Wildkunde
Fakulteit Natuur- en Landbouwetenskappe
Universiteit van Pretoria
Pretoria

MAGISTER SCIENTIAE (NATUURLEWEBESTUUR)

OPSOMMING

Hierdie studie is uitgevoer in die Korannabergafdeling van Tswalu Kalahari Reservaat in die Noordkaap provinsie van Suid-Afrika. Die studiegebied van ongeveer 541 km², is geleë in die ariede suidoostelike Kalahari en ontvang 'n gemiddelde jaarlikse reënval van 231.3 mm.

Die dinamika van die verhouding tussen die buffels en hul habitat is ondersoek, met klem op die seisoenale verskille in habitatbenutting. Duidelike seisoenale verskille is gevind in die manier waarop die buffels hul beskikbare habitat benut, met definitiewe voorkeure en afkeure vir die verskeie plantegroeitipes in die Korannabergafdeling. Die *Stipagrostis uniplumis* vlaktes (Plantegroeitipe 4) was die intensiefste benut regdeur die studieperiode, en word beskou as die sleutelhabitat van die buffels op Tswalu Kalahari Reservaat. Hulle is nooit opgemerk in die *Anthephora pubescens* duine (Plantegroeitipe 2) of die *Digitaria polyphylla* berge en koppies (Plantegroeitipe 11) nie. Moontlike redes waarom die buffels nie in bogenoemde plantegroeitipes opgemerk is nie, kan die diep sanderige, klipagtige en steil hellings wees wat onderskeidelik kenmerkend is van hierdie twee plantegroeitipes. Die bepalende faktor in die habitatseleksie van die buffels was goeie kwaliteit en genoegsame kwantiteit weiding, en die beskikbaarheid van geskikte waterpunte wat gedurende die somermaande benut word vir termoregulering. Die buffels het die onderskeie plantegroeitipes baie gelokaliseerd benut, met die afstand na 'n geskikte waterbron as beperkende faktor.

Die laagste aangetekende buffeldigtheid in die literatuur is op Tswalu Kalahari Reservaat gevind, en was 0.15 buffels/km². Die loopgebied van die buffels is ook ontleed met behulp van ‘n Geografiese Inligtingsisteempakket, in die ArcView program. Die totale loopgebied van die buffels gedurende die studieperiode was 205.7 km² en is die grootste buffel-loopgebied opgeteken in Suid-Afrika. Die grootte van die loopgebied het afgeneem gedurende die warm, nat seisoen. Die sentrale gebied van benutting soos bepaal deur die nie-parametriese kernel-analise (50% aanpassings kernel) het toegeneem van 13.1 km² in die warm, nat seisoen tot 45.2 km² tydens die koue, droë seisoen. Hierdie toename kan verduidelik word deur die teenwoordigheid van kalwers tussen 4 weke en 6 weke oud wat lei tot die verminderde vermoë van die trop om groot afstande af te lê, asook die gelokaliseerde voorkoms van voorkeurweiding in areas wat gesentreer is om waterpunte. Die noordwestelike deel van die Korannabergafdeling was duidelik tydens beide seisoene verkies. Addisionele voeding wat aan die buffels voorsien is, kon die bewegingspatrone en die loopgebied van die buffels affekteer, maar steeds was weiding kwaliteit en kwantiteit die bepalende faktor wat loopgebied beïnvloed het.

Die voedingsvoorkeure van die buffels is ook bestudeer in ‘n poging om te bepaal of die voedingsbehoeftes van die buffels op Tswalu Kalahari Reservaat bevredig word. Voedingstofanalises is uitgevoer op die voorkeurgras-spesies van die buffels en dit was duidelik dat die diere onder voedingsdruk is tydens die droë seisoen, met tekorte in onder andere proteïne, koper, kalsium en fosfor. Die fisiese kondisie van die buffels was swak gedurende die koue, droë seisoen van 2003, maar het verbeter na gemiddeld in die koue, droë seisoen van 2004 nadat die buffels addisionele voeding ontvang het. Die gevolgtrekking is dat die buffels op Tswalu Kalahari Reservaat beperk word deur beperkte hulpbronne, met die reproduserende diere wat onder geweldige voedingsdruk verkeer tydens veral laktasie. Die aanbevole ekologiese weikapasitiet vir die buffels is 292.2 wei-eenhede of 149 buffels. Weens die feit dat Tswalu Kalahari Reservaat buite die historiese loopgebied van buffels lê, tesame met die voedingsdruk wat die buffels verduur, word dit aanbeveel dat die ekonomiese kapasiteit van buffels op Korannaberg eerder gebruik word as norm vir buffel drakrag. Hierdie ekonomiese kapasitiet beloop 204.5 wei-eenhede of 104 buffels en kan beskou word as ‘n betroubare, konserwatiewe aanbeveling vir die getal buffels wat Korannaberg kan dra, ook ten tye van swak reënval.

Slegs 33% van die reproduktiewe vroulike diere het kalwers gehad tydens die studieperiode met 9 geboortes, en een mortalitiet van ‘n volwasse vrouilike dier in die 2003 tot 2004 seisoen. Die buffels op Tswalu Kalahari Reservaat is gereguleer deur ekstrinsieke faktore soos weiding kwalitiet en kwantitieit en wildoes. Intrinsieke faktore was sekondêr in bevolkingsregulering. Aandag moet geskenk word aan die feit dat die buffels op Tswalu Kalahari Reservaat ‘n verouderde populasie is, en die byvoeging van jonger vroulike diere sal bydrae tot ‘n meer produktiewe populasie.

Die lewensvatbaarheid van die buffelbevolking op Tswalu Kalahari Reservaat is getoets met behulp van die VORTEX 9.50 program waarmee bevolkingsmodellering gedoen is. Onder die huidige bestuurstoestande sal die buffels die aanbevole ekonomiese kapasitiet (104 buffels) bereik in 2008. Maksimum produksie kan bereik word met 15 volwasse koeie per bul. Die populasie is egter kwesbaar oor die mediumtermyn (100 jaar), en sal nie omgewingskatastrofes oorleef nie, veral nie droogte of veldbrande in ‘n erge graad nie.

Omdat Tswalu Kalahari Reservaat nie binne die historiese loopgebied van buffels lê nie, moet spesiale aandag geskenk word aan die aktiewe bestuur van die populasie. Bestuursriglyne rakende die buffelbevolking op Tswalu Kalahari Reservaat word gemaak.

ACKNOWLEDGEMENTS

Any study on a free-living population of wildlife is difficult and expensive and logistics are sometimes difficult. Therefore I would like to acknowledge the following people and institutions for their contributions during my term of study:

Special thanks to my supervisor, Prof. J. du P. Bothma of the Centre for Wildlife Management at the University of Pretoria. He was the reason why I pursued a career in this industry and it was indeed an enormous privilege to work under him. I am indebted towards him for his constant encouragement, valuable assistance and advice whenever needed. Also for his uncompromising and critical examination of my dissertation, it is much appreciated.

Prof. M.W. van Rooyen from the Department of Botany at the University of Pretoria who was my co-supervisor, needs an exceptional thanks for her continuous guidance, support, and countless advice and encouragement throughout my study. Her critical examination of my work is appreciated.

Sincere and humble thanks are due to the Oppenheimer family who allowed this study on their property. Also, the Board of Directors and the management of Tswalu Kalahari Reserve who allowed the study and assisted me with the financial support to do the laboratory work for the feeding ecology part.

Special thanks goes towards Nicolene Kotze for her patience, friendship and logistical organisation on Tswalu, as well as Seun and Ina Dennis for their technical support, motivation and friendship during my time on Tswalu. The team of scouts, Andries, Johannes, John and Doctor whose endless enthusiasm and continuous support will remain with me forever.

Dr H. Neil and Mrs. M. Barwise who gave valuable advice on language skills. Rina Owen and Dr F. Kamfer from the Department of Statistics at the University of Pretoria for their valuable advice and assistance regarding the statistical analyses of habitat utilisation. Dr N. Van Rooyen who spent hours with me on the stocking densities of the buffalo on Tswalu. Prof J.B.J. van Ryssen and Prof W.A. van Niekerk from the Department of Animal and Wildlife Sciences at the University of Pretoria, for their insight regarding feeding ecology. The personnel of the UP Nutrilab at the Department of Animal and Wildlife Sciences of the University of Pretoria for allowing me to use their laboratory to analyse the grass and faecal samples. Mr T. Lourens who gave valuable advice and guidance on the feeding ecology chapter. Dr J. C. Kriek, wildlife veterinarian in

Kimberley who commented on the initial physical condition score of the buffalo done in June 2003, as well as giving general advice regarding animal nutrition in the Kalahari.

The Centre for Wildlife Management who provided me with vehicles for my field work, as well as financial support. The University of Pretoria who provided financial support.

Liset Swanepoel for her organisational skills, support and endless encouragement during my time at the Centre for Wildlife Management.

My parents, siblings and friends deserve thanks and praise for their endless encouragement and support on various aspects during my period of study. Also Koos and Martie Uys, who initiated a financial support system for me, and Fred Rabie who modified the quad bike to make it more practical for field work.

The following institutions who gave financial support or donated equipment:

- AG Sprayers (Pty) Ltd
- Delkor Makelaars
- Eloptro – Denel
- Fournel (Pty) Ltd
- Kodak South Africa (Pty) Ltd
- Lynx Optics (Pty) Ltd
- Motrek Oos
- National Tents and Sails S.A. c.c
- Outdoor Deli
- Ramrod (Pty) Ltd
- Rossouw Boerdery

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APPENDIX A

Photographs assisting in the description of the physical condition classes used in assessing the physical condition of the buffalo on Tswalu Kalahari Reserve in the Northern Cape province of South Africa, during 2003 and 2004

Emaciated - Physical condition score: 1 to 1.9

Poor - Physical condition score: 2 to 2.9

Moderate - Physical condition score: 3 to 3.9

Good - Physical condition score: 4 to 4.9

Excellent - Physical condition score: 5