HABITAT UTILISATION, ACTIVITY PATTERNS AND MANAGEMENT OF CAPE BUFFALO IN THE WILLEM PRETORIUS GAME RESERVE

by

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Submitted in partial fulfillment of the requirements for the degree

MAGISTER SCIENTIAE (WILDLIFE MANAGEMENT)

in the Center for Wildlife Research
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Abstract

The range use behaviour and activity patterns of a single herd of disease-free Cape buffalo *Syncerus caffer* in the Willem Pretorius Game Reserve, Free State, was investigated. This reserve falls outside the historical distribution of these buffalo. It has sub-optimal habitat for buffalo, a long history of severe overgrazing and no large predators. The veld condition and grazing capacity of six management units identified in the reserve were investigated, and a long-term grazing capacity of 750 L.S.U. calculated. A maximum long-term buffalo stocking rate of 82,2 L.S.U. was determined from their range use. The main factors, which appear to regulate habitat selection by the buffalo, are seasonal changes in the food supply, the availability of cover for daytime resting, and protection against low night temperatures. Effective management of the buffalo depends on protecting the woody riverbank and vlei grasslands, which are the most crucial vegetation types for the buffalo.

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Contents

CHAPTER 1

Introduction

As one of the most widespread bovids in southern Africa before the influence of European settlers, the Cape buffalo *Syncerus caffer caffer* (Sparrman, 1779) ranged over most of southern Africa and Angola, through central and East Africa, to the southern borders of Sudan and Ethiopia (Sinclair 1977; Mloszewski 1983). In South Africa its range extended over the northern grass savanna regions along the east coast and southwards to the southern coast. They did not occur in the more arid areas such as the Kalahari, Karoo, and the treeless plains of the Free State and the southwestern and southeastern parts of the Mpumalanga and Northwest Provinces, respectively (Du Plessis 1969).

During the last century the Cape buffalo continental population was decimated, first by rinderpest and then by large-scale extermination done mainly because of the perceived threat of buffalo-associated diseases to humans and the cattle industry (Sidney 1965; Condy 1979; Pringle 1982; Main 1990; Thomson 1994). The status and distribution of Cape buffalo in southern Africa are discussed in Chapter 4. Present localised declines in buffalo numbers are attributed to various factors including drought, diseases such as bovine tuberculosis, poaching, the steady shrinking of range, strict veterinary regulations and the ever-present shortage of conservation management funds.

As one of eco-tourism's 'Big Seven' and one of hunting's 'Big Five', the Cape buffalo has a high economic value, making it a highly sought after species in the game ranching industry. Ecologically, the buffalo plays an important role as a bulk feeder, which grazes on tall grass and opens up habitats for short-grass grazers. The market value of live buffalo varies depending on their disease status, with disease-free buffalo having a much higher value than those infected with foot-and-mouth disease or corridor disease. In southern Africa 97,6% of the buffalo are infected with either foot-and-mouth disease or corridor disease, or both. A mere 2,3% of the buffalo are disease-free, of which the majority are found in South Africa (Winterbach 1998).

In 1990 one of the largest herds of disease-free Cape buffalo in southern Africa was found in the Willem Pretorius Game Reserve in the Free State of South Africa. One of the aims for this reserve is the preservation of a viable population of disease-free buffalo to act as a core breeding herd for restocking elsewhere. However, the Willem Pretorius Game Reserve falls outside the historical distribution of the buffalo (Du Plessis 1969) in the Moist Cool Highveld Grassland (39) (Bredenkamp & Van Rooyen 1996). The latter is one of only five principal conservation areas for this grassland type and consists of mixed sourveld, which is sub-optimal habitat for buffalo.

To successfully maintain a large herbivore such as the buffalo in a confined and relatively small conservation area without damaging the habitat requires an intensive management plan, with close monitoring of the grazing capacity (Novellie, Hall-Martin & Joubert 1991; Bothma 1996). The effective management of wildlife depends on a thorough knowledge of the way in which a given species interacts with its specific environment (Leuthold 1977).

The aim of this study was to determine the interaction of the Cape buffalo with the sub-optimal habitat available to them in an area outside their historical distribution with a long history of severe over-grazing (Borquin 1973; Vorster 1989; Vrahimis, Vorster & Terblanche 1989) where there are no large predators. Specifically the study focused on the seasonal changes in the activity pattern of the buffalo which are governed primarily by the quality and quantity of food available (Leuthold 1972; Sinclair 1974; Field 1976; Beekman & Prins 1989), and the seasonal variation in their range use, movements and habitat selection to determine the main factors which appear to regulate their habitat selection in the study area. To be able to formulate an effective management strategy for the buffalo in the reserve, the veld condition, grazing capacity and current stocking rates of the different management units with grazers were also investigated. The proposed management strategy focuses on protecting the limited suitable habitat available to the buffalo in the reserve.

The results obtained during this study either have been published as scientific papers or have been submitted for publication. The layout and presentation of each chapter therefore follows the guidelines laid down by the respective journals. A summary of the methods used during this study is given in Chapter 3. All tables and figures are numbered consecutively within each chapter, and the literature cited in each chapter is referenced at the end of that chapter. A full literature list is referenced at the end of this work.

CHAPTER 2

Description of the study area

Introduction

Field work for this study was done in the Willem Pretorius Game Reserve which is situated approximately 140 km northeast of Bloemfontein between 28°16' to 28°21'S and 27°07' to 27°23'E in the Free State of South Africa (Figure 2.1). The reserve surrounds the Allemanskraal Dam and its altitude varies between 1 375 and 1 510 m above sea level. The reserve covers a surface area of 12 082 ha, of which 2 771 ha is water surface when the dam is full. The holiday resort covers another 975 ha. The effective game habitat area of the reserve therefore is approximately 8 682 ha. This habitat is elongated, being 23 km long with a varying width of 2 to 8 km.

The Willem Pretorius Game Reserve does not owe its existence to any significant ecological feature, but to the building of the Allemanskraal Dam which was completed in 1960. The original farmland surrounding the dam was then bought by the State and made available to the Provincial Administration to develop as a nature reserve. Although this development began in 1956 the area was only proclaimed as a nature reserve in 1971 (Borquin 1973).

Prior to the building of the Allemanskraal Dam extensive farming occurred in the area, with cattle, sheep and maize as the main products. It was during this period that the foundation for soil erosion as it occurs today was laid, and most of the current large eroded areas have originally been caused by water runoff from the ploughed lands. Exotic plants, such as blue-gum (*Eucalyptus* sp.), poplar (*Populus* sp.) and willow trees (*Salix babylonica*) were also introduced during this time.

With subsequent habitat changes and hunting all the larger game animals were eradicated,

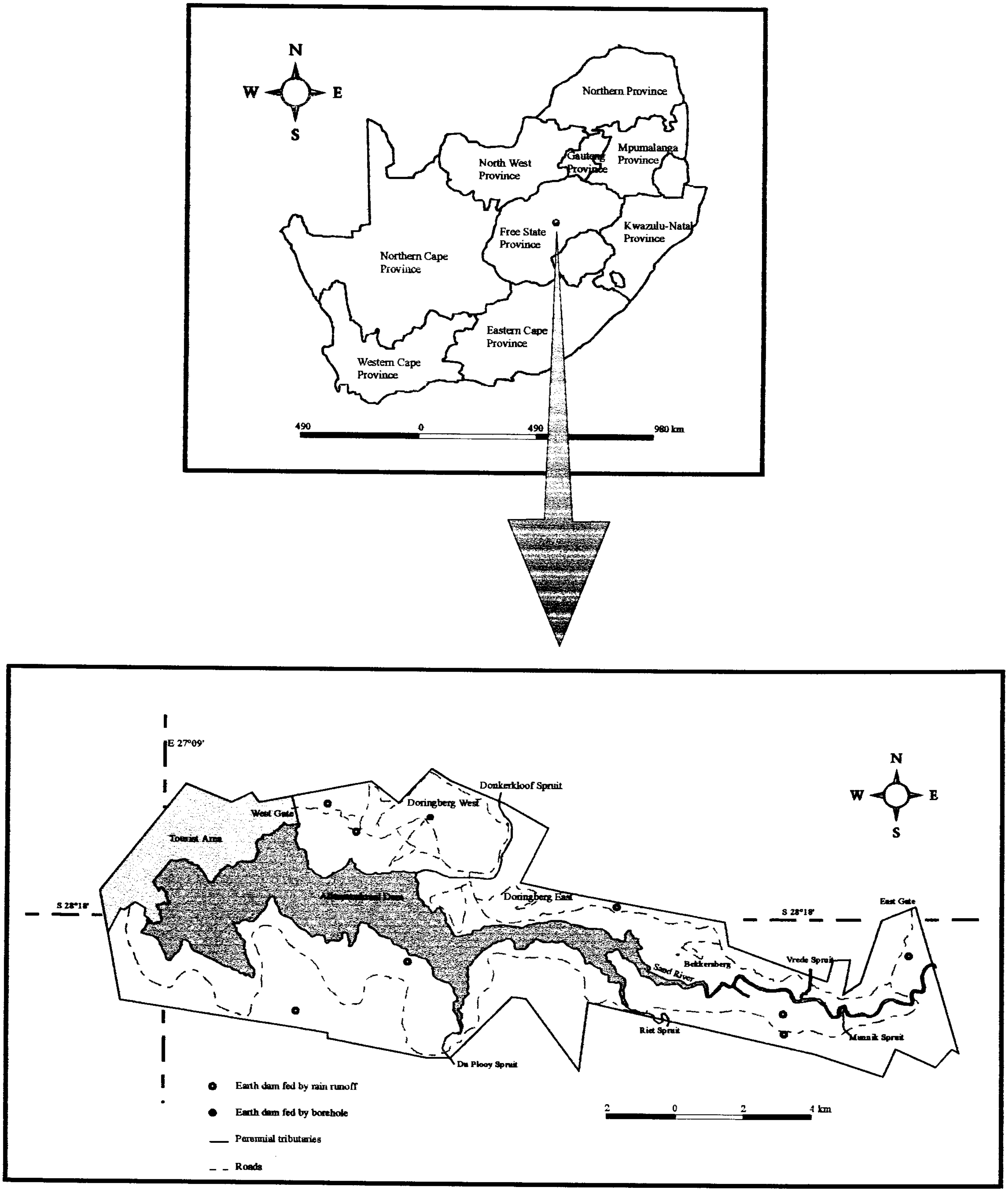

Figure 2.1: Location of the Willem Pretorius Game Reserve in the central Free State of South Africa

leaving only a few mountain reedbuck *Redunca fulvorufula*, steenbok *Raphicerus campestris* and common duiker *Sylvicapra grimmia* at the time of proclamation (Borquin 1973).

Through the years the Willem Pretorius Game Reserve has played a major role as a source of the relocation of game to other provincial nature reserves in the Free State, and in supplying game to private nature reserves and game ranches throughout South Africa.

Topography and water

The landscape in the Willem Pretorius Game Reserve slopes from the north and from the south to the central valley of the Sand River, which flows from east to west through the reserve and in which the Allemanskraal Dam was built. Some topographic features of the reserve are shown in Figure 2.2. In topography the area south of the Sand River and the Allemanskraal Dam is mainly a flat grass plain, with slopes of not more than 5°. In a small area adjacent to the Du Plooy Spruit, however, a series of low dolerite ridges occurs with slopes of 10 to 20°. The altitude south of the Sand River and the Allemanskraal Dam varies from 1 375 to 1 435 m above sea level (Müller 1986).

In the area north of the Sand River and the Allemanskraal Dam a series of dolerite and sandstone ridges stretch from east to west along the river and dam. The altitude there varies between 1 375 and 1 510 m above sea level. Although slopes of more than 40° occur, the slopes generally are from 11 to 20°. Virtually flat plains interrupt the ridges and such flat areas also occur on the plateaux of the ridges (Müller 1986).

The Allemanskraal Dam and Sand River form the main perennial water resources in the reserve (Figure 2.1). Two perennial tributaries of the Sand River, the Du Plooy and Riet Spruits, flow from the south through the reserve into the Allemanskraal Dam. A spring feeds a third perennial tributary, the Vrede Spruit that traverses the northeastern part of the reserve. Other tributaries such as the Donkerkloof and Munnik Spruits are seasonal with a few pools

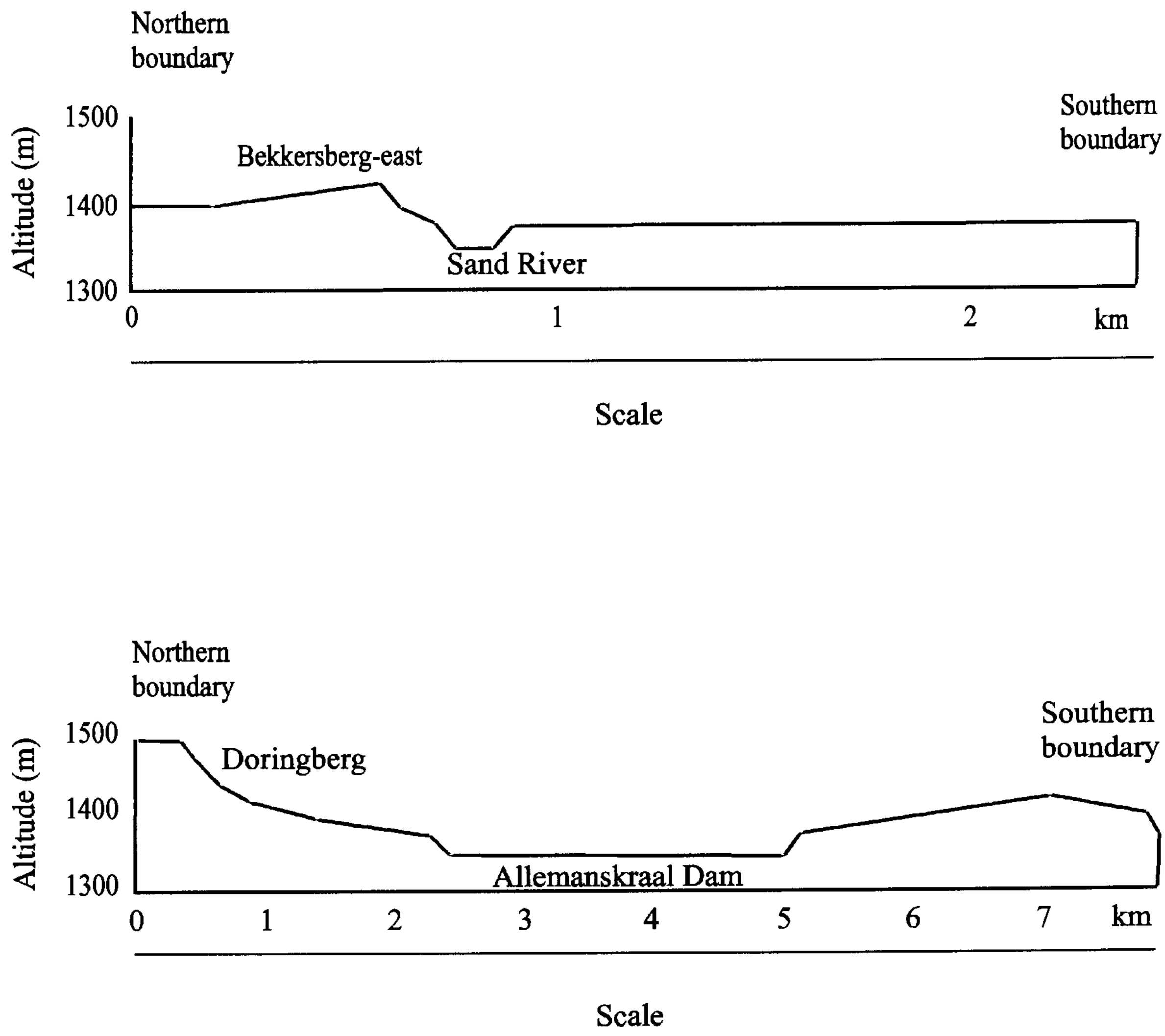

Figure 2.2: Topographic profile of two sections of the Willem Pretorius Game Reserve in the Free State of South Africa.

persisting well into the dry season. One earth dam equipped with a borehole supplies an additional permanent water source north of the Allemanskraal Dam. An additional eight earth dams which are only fed by rain runoff and which dry up at some time during the dry season, also occur over the reserve (Figure 2.1).

Geology and soils

Müller (1986) has described the geology and soils of the reserve in detail. Its geology consists mainly of the Beaufort Serie of the System Karoo. Soils found in the reserve are mainly heavy clay from a dolerite origin, but lighter sandy soils from a sandstone origin also occur. According to Müller (1986) three basic land types can be found in the reserve. They are:

1. The Ea-land type which is found mainly on the elevated areas such as Bekkersberg in the east and Doringberg in the north. The dominant soils here are dark and have more than 35% clay, a shallow solum and lie on top of the dolerite. South of the Allemanskraal Dam the Ea-land type occurs on the low dolerite ridges in the vicinity of the Du Plooy Spruit and on the low sandstone ridge east of the Riet Spruit.
2. The Dc-land type is found on the low-lying areas north of the Allemanskraal Dam and the Sand River and in large areas to their south. Karoo encroachment is more evident in the grasslands of this land type under heavy grazing as soil with a high clay content restricts root growth and ramification, especially when long periods elapse between precipitation (Müller 1986).
3. The Ca-land type is found mainly south of the Allemanskraal Dam and the Sand River. Most areas on the Ca-land type have been ploughed previously, resulting in seriously disturbed vegetation.

Climate

The reserve has a subtropical climate with summer rains, a definite temperature cycle and a dry, cold season (Figure 2.3). The absolute and mean daily maximum temperatures for

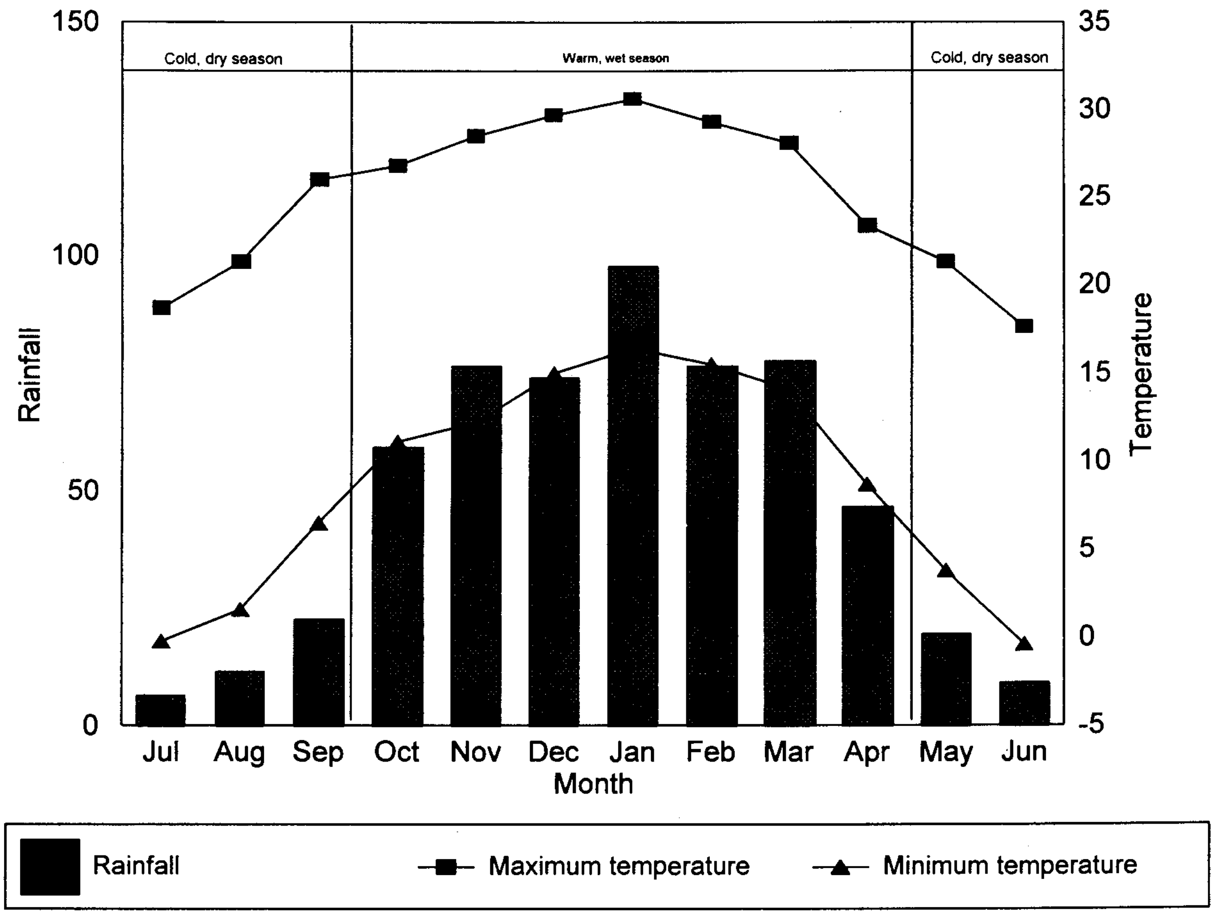

Figure 2.3: Mean monthly rainfall (mm) for the Willem Pretorius Game Reserve in the Free State for the period 1960 to 1992, and mean maximum and minimum temperatures (°C) for the period 1962 to 1971 to illustrate the cold, dry season and the warm, wet season experienced there.

January are 37,8 and 30,6 °C respectively, with a mean daily minimum temperature of 16,4 °C. Winters are cold with absolute and mean daily minimum temperatures for June of –6,7 and –0,4 °C respectively, and a mean daily maximum temperature of 17,6 °C. A long thermic summer with mean daily temperatures of more than 16,4 °C occurs for 7 months of the year from October to April. Frost may occur from May to September (Müller 1986).

The mean annual rainfall from 1961to 1992 was 576,0 mm, with the highest mean monthly rainfall of 97,7 mm in January and the lowest of 6,3 mm in July (Department of Water Affairs, Allemanskraal Dam *in litt.*). The highest rainfall occurs from January to March, followed by November and December. The lowest rainfall occurs during winter (June, July and August). Precipitation occurs mostly as local thunderstorms, causing variations in the amount of precipitation over short distances. According to Schulze (1965, *In* Müller 1986) the Willem Pretorius Game Reserve lies in an area where the rainfall for a given year may vary from 50 to 200% of the mean annual rainfall.

Game

The following types of game were reintroduced over time into the reserve: black wildebeest *Connochaetes gnou*, red hartebeest *Alcelaphus buselaphus*, blesbok *Damaliscus pygargus phillipsi*, springbok *Antidorcas marsupialis*, eland *Taurotragus oryx*, Burchell's zebra *Equus burchellii*, square-lipped or white rhinoceros *Ceratotherium simum*, kudu *Tragelaphus strepsiceros*, bushbuck *Tragelaphus scriptus*, grey rhebok *Pelea capreolus* and Cape buffalo *Syncerus caffer caffer*. Types of game that did not occur historically in the area, but which were introduced there are the gemsbok *Oryx gazella*, impala *Aepyceros melampus*, reedbuck *Redunca arundinum* and giraffe *Giraffa camelopardalis*. The common duiker *Sylvicapra grimmia*, steenbok *Raphicerus campestris* and mountain reedbuck *Redunca fulvorufula* were still present in the reserve when its development began in 1956 (Bourquin 1973).

In 1960 five Hartmann's mountain zebras *Equus zebra hartmannae* were introduced into the reserve. However, all 15 were again removed between 1984 and 1985 because of the threat of potential inbreeding with the Burchell's zebra. Eight klipspringer *Oreotragus oreotragus* were also introduced in 1965. As only one of these was a female the population steadily declined and consequently became extinct during the 1970s. From 1967 to 1968, seven disease-free Cape buffalo were successfully translocated to the Willem Pretorius Game Reserve from the Addo Elephant National Park. By 1991 this population had grown to an estimated 266 (r=0,16 per year) of which 63 buffalo have been relocated from the reserve to elsewhere or were sold, approximately 26 have died of natural causes and 17 were hunted. At the time of the study 160 buffalo were present in a single herd. The population structure in April 1991 consisted of 102 adults with a sex ratio of 1 male to 3 females, 28 sub-adults of 1 to 2 years old, 27 calves and three unknowns.

Vegetation

The Willem Pretorius Game Reserve lies in the mixed grasslands of the central Free State. According to Bredenkamp & Van Rooyen (1996) the main vegetation of the reserve can be described as Moist Cool Highveld Grassland (Veld Type 39). The reserve is one of only five principal conservation areas for this grassland type. The dominant vegetation in the reserve is grassland, which covers approximately 78,0% (6 778 ha) of the terrestrial surface area of the reserve. An estimated 5 800 ha (66,8%) of the grasslands are found on the plains in the south, and between the ridges in the north. The woody vegetation on the reserve is restricted to the ridges and banks of the Sand River, and the dry watercourses (Müller 1986).

Müller (1986) did a comprehensive phytosociological classification of the vegetation of the Willem Pretorius Game Reserve. Five main vegetation types were identified, which were subdivided into 24 homogeneous vegetation units (Figure 2.4, Table 2.1). In all 424 plant species were identified for the reserve.

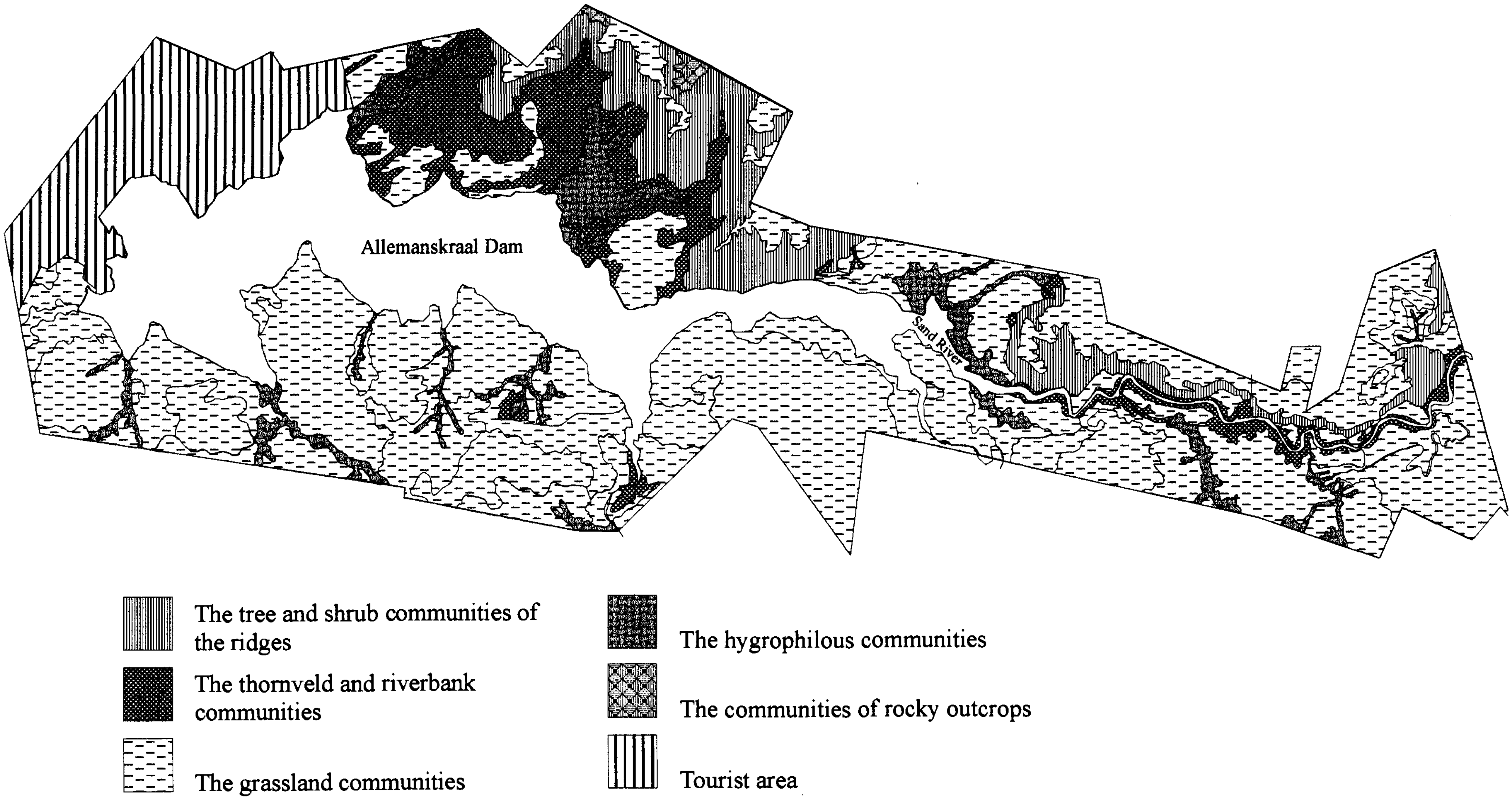

Figure 2.4: The five main vegetation types identified by Müller (1986) in the Willem Pretorius Game Reserve in the Free State of South Africa.

Table 2.1: The five main vegetation types according to Müller (1986) of the Willem Pretorius Game Reserve in the Free State and their respective homogeneous units with accompanying habitat descriptions and size in hectares (ha).

VEGETATION UNIT		HABITAT DESCRIPTION	SIZE (ha)
The tree and shrub communities of the ridges:			
A	Rhoo-Celtidetum	Sheltered ravines	79
B	Rhoo-Celtidetum rhoosum burchellii	Cooler, moist south-facing slopes	38
C	Rhoo-Celtidetum rhoosum lanceae	On plateaux amongst ruins of stone buildings	32
D	Rhoo-Panicetum	Shallow sandy soil on steep, warm and dry sandstone slopes	67
E	Rhoo-Aristidetum	Shallow soil on warm, dry dolerite slopes	91
F	Rhoo-Aristidetum oleosum	Deeper soil on dry, warm slopes	211
G	Rhoo-Aristidetum aloetosum	Steep dry, warm slopes	136
H	Rhoo-Schismetum	Shallow soil on dolerite and steep, cool slopes	177
I	Rhoo-Koelerietum	Steep, south-facing slopes on dolerite	33
The thornveld and riverbank communities:			
K	Rhoo-Diospyretum acasietosum karroo	Woody riverbanks and dry watercourses	189
L	*Acacia karroo* variant of the Rhoo-Diospyretum celtidetosum	Shores of dry rivulets near ridges	63
M	Setario-Protasparagetum	Clay soil on moist, low-lying areas and low shrubs	97
N	Setario-Protasparagetum acacietosum	High shrubs, low trees on transition from clay soil	77
O	Enneapogon-Acacietum	Higher, drier areas on plains with trees and shrubs near foothills	575
The grassland communities:			
Q	Brachiario-Elionurodetum vernonietosum	At foot of ridges on south-facing slopes	36
R	Brachiario-Elionurodetum aristidetosum	Grasslands on shallow, rocky soil on slopes and plateaux of ridges	942
S	Digitario argyrograptae-Elionurodetum	Grasslands on shallow soil on plains	724
T	Euryopo empetrifoliodis-Themedetum	Shallow, rocky soils on ridges	119
U	Eragrostio gummifluae-Cynodetum dactyloni	Grasslands on light, sandy soil mostly cultivated in past	2449
V	Eragrostio gummifluae-Cynodetum dactyloni Pogonarthrietosum	Grasslands on sandy soil on plains	267
W	Aristidetum bipartitae	Grasslands on heavy, clay soil	1480
X	Saisolo glabrescentis-Felicietum	Pioneer vegetation on brackish soil	113
The hygrophilous communities:			
Y	Setarietum incrassatae	Vlei grasslands on clay soil	648
The communities of rocky outcrops:			
Z		In fissures and hollows in solid dolerite rocks	39

Tree and shrub communities of the ridges

These communities are found on the slopes of the ridges north of the Sand River and the Allemanskraal Dam (Figure 2.4). They cover approximately 864 ha or 10,0% of the land surface area of the reserve. The ridges are mainly dolerite, although sandstone does occur. Müller (1986) identified nine vegetation units within this community (Table 2.1).

Two or more vegetation strata occur in these communities and the height of the crown stratum varies between 1,8 and 6,7 m. The dominant plant species is *Rhus burchellii* which has a 78% frequency of occurrence (Müller 1986). The ground layer is characteristically represented by *Cheilanthes hirta* (47% frequency of occurrence), *Cheilanthes eckloniana* (47%), *Clutia pulchella* (31%) and *Crassula schimperi* var. *lanceolata* (30%). Shade-loving grasses such as *Panicum deustum* and *Stipagrostis uniplumis* occur frequently but not dominantly.

Other characteristic plants restricted to this vegetation type according to Müller (1986) are: *Scolopia zeyheri*, *Euclea crispa* var. *crispa*, *Rhus erosa*, *Maytenus heterophylla*, *Grewia occidentalis*, *Ehretia rigida*, *Clematis brachiata*, *Olea europaea* subsp. *africana*, *Enneapogon scoparius*, *Digitaria monodactyla*, *Eragrostis remotiflora*, *Pellaea viridis*, *Ceterach cordatum*, *Isoglossa grantii*, *Pavonia patens*, *Commelina erecta*, *Sutera argentea*, *Lantana rugosa*, *Sutera pinnatifida* and *Achyranthes aspera*.

The thornveld and riverbank communities

The thornveld and riverbank communities have a restricted range in the reserve, covering an estimated 1 001 ha or 11,5% of the terrestrial surface area. According to Müller (1986) these communities are found mainly in the northern and eastern parts of the reserve on the banks of the Sand River, along dry watercourses, on the footslopes of some of the ridges and next to vlei areas (Figure 2.4). The drier thornveld communities which are found in some parts of the plains and on the footslopes of some of the ridges occur on various types of soil and are secondary communities according to Müller (1986), who also states that some stands of the thornveld and riverbank communities were established through long-term overgrazing of these areas. Five vegetation units occur in this community (Table 2.1).

Two or more vegetation strata occur in these communities, with the crown stratum height varying from 2 to 6,5 m. The only characteristic woody plant is *Acacia karroo* which may occur either as a tree or as a shrub. Characteristic plant species more or less restricted but not exclusive to these communities are *Protasparagus laricinus*, *Cynodon hirsutus*, *Panicum maximum*, *Atriplex semibaccata* and *Urochloa panicoides*. Differential species include *Rhus pyroides*, *Ziziphus mucronata*, *Setaria verticillata* and *Protasparagus cooperi* (Müller 1986).

The grassland communities

The grassland communities cover an estimated 6 130 ha or 70,6% of the terrestrial surface area of the Willem Pretorius Game Reserve. These communities occur in a variety of habitats, such as the slopes and plateaux of the ridges and the plains on sandy, heavy clay and brackish soils (Figure 2.4). Approximately 52,0% (978 ha) of the total surface area of the ridges are covered by grassland communities and 85,0% that of the plains.

The grassland communities on the sandy soil cover approximately 3 559 ha, those on the heavier clay soils 1 593 ha and those in moist vlei areas 648 ha. Both sourveld and sweetveld individually and a mixture of both occur in the reserve together with Karoo elements. Müller (1986) identified eight homogeneous vegetation units in the grassland communities (Table 2.1). Characteristic plants include *Themeda triandra*, *Eragrostis curvula*, *E. chloromelas*, *E. obtusa*, *Aristida congesta* subsp. *congesta*, *Setaria sphacelata* var. *sphacelata*, *Heteropogon contortus*, *Cymbopogon plurinodis*, *Gazania krebsiana* subsp. *krebsiana*, *Sporobolus discosporus* and *Hermannia coccocarpa* (Müller 1986).

The hygrophilous communities

These communities are found in the vlei and natural drainage areas through which excess water drains into the Allemanskraal Dam and the Sand River (Figure 2.4). The soils in these areas are mostly heavy clay. The hygrophilous communities cover approximately 648 ha or 7,5% of the terrestrial surface area of the reserve They are a single homogeneous vegetation unit (Table 2.1).

The dominant plants in these communities are *Setaria incrassata* with a 96% frequency of occurrence and *Pennisetum sphacelatum* with a 52% frequency of occurrence (Müller 1986). Other characteristic plants include *Ciclospermum leptophyllum*, *Conyza podocephala*, *Cynodon dactylon*, *Sporobolus fimbriatus*, *Eragrostis curvula*, *E. plana*, *E. planiculmis*, *Hyparrhenia dregeana*, *Cyperus marginatus*, *C. fastigiatus*, *Hemarthria altissima*, *Alternanthera sessilis*, *Phragmites australis*, *Typha capensis*, *Agrostis lachnantha* var. *lachnantha* and *Paspalum dilatatum*.

The communities of the exposed rocky outcrops

These communities are mainly found in fissures and hollows in the solid, dolerite rock of the exposed rocky outcrops where little topsoil is present (Figure 2.4). The erstwhile shallow layers of soil were probably lost through erosion over time. The habitat on these rocks is characteristically warm with excessive fluctuations in daily temperatures. The vegetation communities of the exposed rocky outcrops form only 39 ha or 0,4% of the terrestrial surface area of the reserve, and are one homogeneous vegetation unit (Table 2.1).

Characteristic plants found here are *Oropetium capense*, *Euryops empetrifolius*, *Cyperus usitatus*, *Digitaria eriantha*, *Ruschia putterilli*, *Cheilanthes eckloniana*, *Anacampseros ustulata*, *A. filamentosa*, *A. telephiastrum*, *Tragus racemosus*, *Cotyledon orbiculata*, *Sarcostemma viminale*, *Crassula corallina* and *Enneapogon desvauxii* (Müller 1986).

CHAPTER 3

Methods

Introduction

As each chapter either was published in a scientific journal or has been submitted for publication, a comprehensive description of the methods used is given in each chapter. The following is merely a summary of the methods used during this study.

Procedure to determine the status and distribution of Cape buffalo in southern Africa

Data on the status and distribution of buffalo in Botswana, Zimbabwe, Namibia and South Africa between 1992 and 1996 were obtained from the respective government departments concerned with wildlife conservation and veterinary services (Chapter 4). In Zimbabwe additional information was obtained from WWF Zimbabwe and the Wildlife Producers' Association of Zimbabwe. Extensive information was also obtained through personal communication with persons in southern Africa.

In South Africa the information obtained from the Veterinary Registration Report of Game Ranches for 1992 and 1994 (Anon 1992, 1994) were updated, as far as possible, for 1995/1996 through personal communication. The only information obtained on buffalo numbers and distribution in Mozambique was restricted to the Marromeu Complex and was again obtained through personal communication.

Determining the activity patterns of the buffalo

Activity patterns of the buffalo were investigated from October 1990 to September 1991. Direct field observations were done by using the scan sampling method of Altmann (1973) (Chapter 5). The subsequent data sets were taken at 5-minute intervals

(Grimsdell & Field 1976; Sinclair 1977). The total sample was 161 observation hours during daylight and 85 observation hours at night. The activities of the buffalo were divided into the following categories: grazing, resting/ruminating (lying down), standing, walking, drinking and other activities. The latter included all activities, such as running, which did not feature strongly in the general activity pattern.

Seasonal divisions used in the analyses of the activity data were based on the actual rainfall during the observation period, obtained from the weather station (Order: Rainfall Station) at the Willem Pretorius Game Reserve (Chapter 5, Figure 1). Day and night divisions for the data analyses were based on the mean timing of sunrise and sunset for that particular season. Such data were obtained from the Bloemfontein Airport Weather Station located at 26° 18'S and 29° 06'E.

Because the number of buffaloes per observation even varied between consecutive observations, all the observations were standardised to a percentage basis before analysis to remove the effect of group size. The 24-hour activity patterns were obtained by using standardised data grouped per hour to calculate the proportion of time devoted to each type of activity in any given hour (Chapter 5, Figures 2 to 5).

The Mann-Whitney test (Zar 1984) was used to test the null hypothesis that there was no difference between the time spent by the buffalo for a given type of activity in the day versus the night (Chapter 5, Table 1). An Analysis of Variance (Statistica for Windows 4.3. 1993. Statsoft Inc.) was performed to test the null hypothesis that there were no differences in the level of each type of activity in the three seasons (Chapter 5, Table 2). It was followed by the Tukey test if the null hypothesis was rejected (Zar 1984). With the large number of observations available per cell it was assumed that deviation from normality did not matter. This assumption was based on the central limit theorem of Frank & Althoen (1994). To allow for Bonferonni Inequality by testing for day/night and seasonal differences, all p-values were multiplied by the number of comparisons, which were two (Stevens 1990).

Ascertaining the seasonal variation in range use, movements and habitat selection of the buffalo in the study area

Range use and movement patterns

Buffalo were located weekly by vehicle or on foot. Herd movements were recorded at 30-minute intervals as part of the study on activity patterns of the same buffalo. All buffalo herd localities were plotted on 1:50 000 aerial photographs of the study area. The vegetation map of Müller (1986) and a 250 m x 250 m grid were then superimposed over the aerial photographs. The grid allowed plotting of the exact position of any buffalo herd with an accuracy of 10 m or less.

Range use estimates were based on 1 211 locations. The national coordinate reference system on 1:10 000 ortophotos were used to divide the study area in 500 m x 500 m grid cells. An Analysis of Variance test followed by a Tukey test measured the statistical significance of seasonal differences in mean group size (Statistica for Windows 4.3. 1993. Statsoft Inc.), and a chi-square test was used to compare the significance of differences in the mean 24-hour distances moved in the three seasons (Chapter 6).

Habitat selection

A chi-square test was used to test the hypotheses that the buffalo used the available habitat types in proportion to their relative occurrence. Bonferroni simultaneous confidence intervals (Byers, Steinhorst & Krausman 1984) were calculated for each season to determine preference for habitats in relation to their availability at the 0,05 level of significance (Statistica for Windows 4.3. 1993. Statsoft Inc.) (Chapter 6, Tables 2 to 6). The following habitat characteristics were used in the analysis: veld condition, physiographic unit and plant unit. At the plant unit level habitat preference was also tested for resting/ruminating (lying down), recorded as one activity, and grazing (Chapter 6, Tables 2 to 6).

The relative areas of available habitat characteristics were calculated for the whole reserve from area sizes (ha) as provided in Müller (1986). The distribution function of the IDRISI programme was used to determine a 1-km zone around all points where buffalo have been observed (Idrisis 4.1. 1987-1993. Clark University). This data were used to demarcate the seasonal range use of the buffalo on the vegetation map (Chapter 6, Figure 1). The relative sizes of the different plant units in the buffalo range use were then calculated with the IDRISI area function.

Ascertaining the grazing capacity and veld condition of the study area to formulate a management strategy for the buffalo in a sub-optimal habitat

Veld condition assessment

Vegetation data were collected from February to May 1991 in 47 stratified random sample sites per plant unit. Line transects and quadrants were placed following Scoggings (1988). The dry-weight-rank method of t'Mannetje & Haydock (1963) as modified by Jones & Hargreaves (1979) was combined with the comparative yield method of Haydock & Shaw (1975) to estimate the above-ground plant biomass composition simultaneously with the herbaceous yield. Twenty-four of the original 47 sample sites were re-surveyed from April to May 1992 to determine the above-ground plant biomass.

During the 1991 survey the step-point method was used at 35 of the 47 sample sites to obtain a veld condition assessment by estimating the percentage species composition (Mentis 1981). Veld condition for each of the management units identified was determined by using the Ecological Index Method of Tainton, Edwards & Mentis (1980) as applied by Bredenkamp ([1]1986 pers. comm.) (Chapter 7, Table 2). To do so the grass species were categorised as increasers or decreasers for the different management units based on grazing degradation models for the Winburg District ([2]Van der Westhuizen 1996 pers. comm.), using the Integrated System for Plant Dynamics (ISPD) software.

[1] Bredenkamp, G. 1986. Ecotrust CC. P.O. Box 2553, Monument Park, Pretoria, South Africa, 0105.
[2] Van der Westhuizen, M.E. 1996. Department of Agriculture, Private Bag X01, Glen, South Africa, 9360.

The ecological index values for individual sample sites, and the percentage occurrence, the percentage contribution to the standing plant biomass and the percentage utilisation of the grass species, excluding the encroachers, in the six management units in 1991 are given in Appendix A.

The grazing capacity of each management unit was calculated according to the guidelines of Meissner, Hofmeyer, Van Rensburg & Pienaar (1983) (Chapter 7, Table 1). The long and short-term grazing capacities of the reserve were calculated according to the method of Coe, Cumming & Phillipson (1976) (Chapter 7).

The estimated game numbers present on the study area in December 1991 after the calving season were used here to determine the actual stocking rate of the reserve (Chapter 7, Table 3). Bredenkamp's (1986 pers. comm.) classification of game was used to reflect their relative potential for defoliation and any possible selective grazing of the vegetation.

Determination of a buffalo stocking rate

The size (ha) of the plant units in the potential buffalo habitat, based on those parts of the plant units in the year-round range of the buffalo that have not yet degraded to Karoo encroachment, was determined with a planometer from 1:10 000 aerial photographs. A preliminary buffalo stocking rate for the reserve was then calculated according to the guidelines of Meissner *et al.* (1983), considering the above-ground plant biomass of grass species present as determined during the 1991 veld condition assessment (Chapter 7, Table 4). Calculation of the recommended buffalo stocking rate was based on the 1991 grazing capacity of the critical dry season buffalo habitat, excluding areas with Karoo encroachment (Chapter 7, Table 4).

CHAPTER 4

Research review

The status and distribution of Cape buffalo *Syncerus caffer caffer* in southern Africa

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The present status and distribution of Cape buffalo *Syncerus caffer caffer* in southern Africa is reviewed. The present estimate of southern Africa's buffalo populations are Botswana 29 300 (± 9 000), Zimbabwe 48 200 (± 21 000), Namibia 2 800 (± 1 000) and South Africa 31 500 (± 10 000). Buffalo numbers for Mozambique are incomplete, but a decline is estimated at 79% in the buffalo population in the Marromeu Complex. The total number of buffalo in the six largest free-ranging populations in southern Africa, excluding Mozambique, has decreased by more than 50% between 1991 and 1996. The main factor influencing buffalo numbers and distribution in the sub-region is the development of the cattle industry, followed by drought and disease. Only South Africa and Zimbabwe actively produce surplus buffalo for translocation or sale. However, the cumulative loss of genetic diversity in these small, isolated populations may have potentially serious consequences.

Keywords: Cape buffalo, distribution, southern Africa, status, *Syncerus caffer caffer*

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As one of the most widespread bovids in southern Africa, Cape buffalo *Syncerus caffer caffer* (Sparrman 1779) could formerly be found "roaming in large numbers" in most of the major vegetation types, including lowland and montane forest, moist and dry woodlands, savanna and steppe (Sidney 1965; Du Plessis 1969; Sinclair 1977). Its former range, before the influence of European settlers, extended over most of southern Africa and Angola, through central and East Africa, to the southern borders of Sudan and Ethiopia (Sinclair 1977; Mloszewski 1983).

The most recent authoritative map of buffalo distribution in southern Africa is in Smithers (1983) as illustrated in Skinner and Smithers (1990). However, subsequent large-scale loss of available habitat, and the translocation of buffalo to new areas calls for a review of the present status and distribution of buffalo in southern Africa.

The current status and distribution of buffalo in Botswana were obtained from the Botswana Departments of Wildlife and National Parks (Research Division) and Animal Health and Production, and the Aerial Census of Animals in Botswana Reports to the Botswana Department of Wildlife and National Parks for the period 1992 to 1995.

The Zimbabwe Department of National Parks and Wildlife Management supplied data from their 1995 aerial counts. Additional information was obtained from the Zimbabwe Department of Veterinary Services, the WWF Zimbabwe and the Wildlife Producers' Association of Zimbabwe. Buffalo numbers and distribution in Namibia were obtained from the Namibian Ministry of Environment and Tourism, Directorate of Resource Management and the Directorate of Veterinary Services.

The Veterinary Registration Report of Game Ranches for 1992 (Anon. 1992) and 1994 (Anon. 1994) were used as an indication of the status and distribution of buffalo in South Africa. These records were updated, as far as possible, for 1995/1996. Extensive information was also obtained through personal communication with persons in southern Africa.

The only information obtained on buffalo numbers and distribution in Mozambique was restricted to the Marromeu Complex.

Historical overview of buffalo

The first major decline in buffalo numbers in southern Africa occurred between 1890 and 1900 when rinderpest and pleuro-pneumonia swept through Africa, causing mortalities as high as 95% among livestock and wild ungulates. It is estimated that more than 5,5 million cattle died south of the Zambezi, and among wild ungulates kudu, eland and buffalo suffered most (Pringle 1982; Main 1990).

Recovery of the buffalo population in southern Africa has been slow, due mainly to the threat of buffalo-associated diseases to human settlement and accompanying development. In the early to mid 1900s the control of tsetse flies (*Glossina* spp.), which transmit trypanosomiasis (nagana) to cattle, and sleeping sickness to humans, led to the large-scale extermination of wild ungulates, including buffalo, in Botswana, Zimbabwe and South Africa in an effort to eradicate the tsetse fly through extermination of its host (Sidney 1965; Pringle 1982; Main 1990). As buffalo are the only free-living species known to maintain host for all three types of the foot-and-mouth disease[1] virus (FMD SAT-1, 2 and 3) for indefinite periods, concerted efforts have been made since the 1930s to eliminate buffalo from areas outside designated wildlife management zones (Condy 1979; Pringle 1982; Thomson 1994) to protect the growing cattle industry. As an added control measure, a proliferation of game and cattle fences have been erected since 1960 (East 1989; Main 1990). As there is now strong evidence that carrier buffalo could be a source of foot-and-mouth disease infection in cattle (Taylor 1984; Thomson 1994, 1996), strict veterinary regulations will continue to control the distribution of buffalo in southern Africa.

Corridor disease[2], which is highly pathogenic and usually fatal to cattle, is also associated with buffalo. After foot-and-mouth disease, corridor disease is the most important disease transmitted from buffalo to cattle, and has contributed significantly to the confinement of buffalo to well-fenced protected areas, and stringent veterinary control measures in corridor disease endemic areas in southern Africa (Stoltsz 1988, 1996).

The status and distribution of buffalo in southern Africa between 1994 and 1996

The distribution of buffalo in southern Africa between 1994 and 1996 is illustrated in Figure 1. Buffalo numbers in southern Africa are derived from different survey techniques, ranging from total counts of buffalo in small protected areas, without confidence intervals, to aerial

[1] Published in journal as FMD
[2] Published in journal as CD

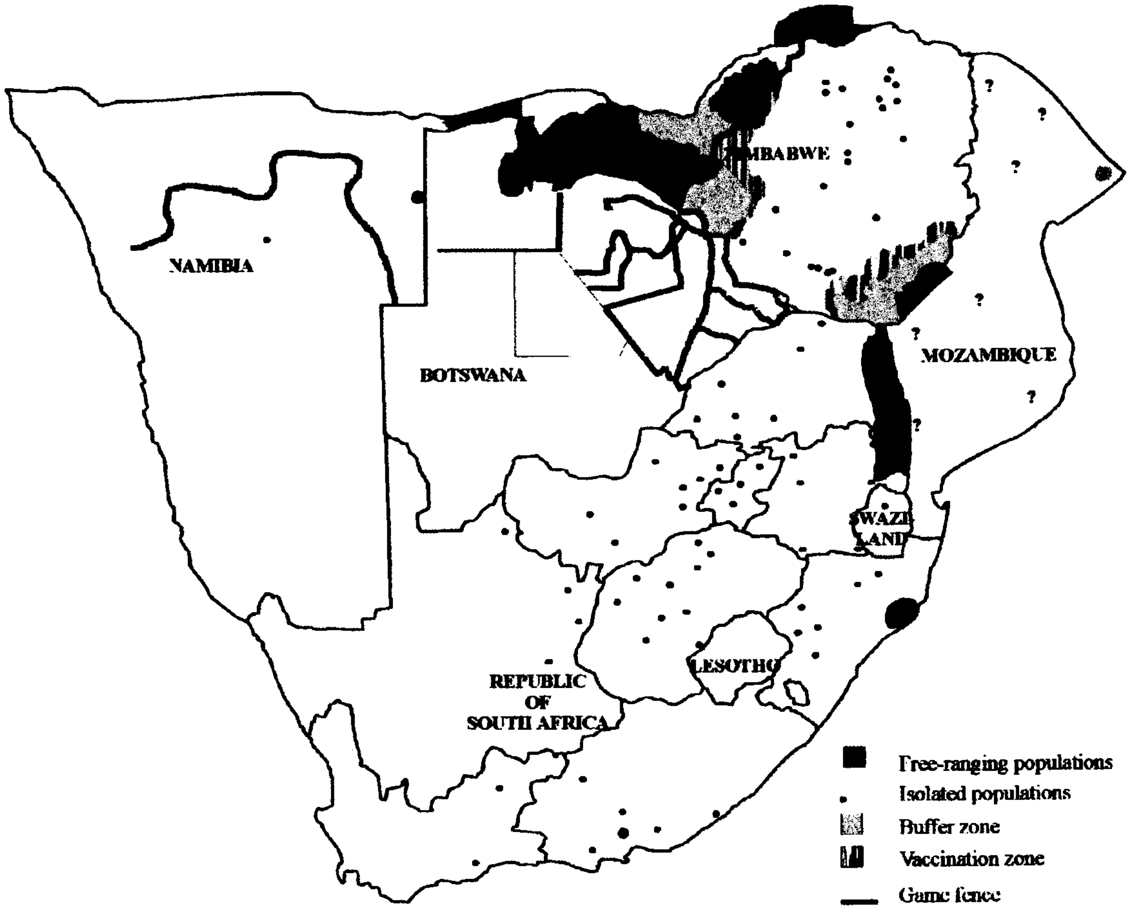

Figure 1 Distribution of Cape buffalo *Syncerus caffer caffer* in southern Africa between 1994 and 1996.

surveys of the larger areas. These aerial surveys are conducted at varying percentage coverage of the areas ranging from 100% coverage in the Kruger National Park to as low as only 4% in parts of Botswana. The fact that buffalo are often aggregated in large herds affects the accuracy of estimated buffalo numbers from aerial surveys.

Botswana

The mean estimate for the Botswana buffalo population in 1994 was 29 000 ± 9 000 (Anon. 1995; ULG 1995). A summary of the estimated numbers and localities of buffalo in Botswana appears in Table 1. Buffalo are found only north of 20°S in the Okavango-Chobe region, east of the veterinary Okavango Buffalo Fence (Figure 1). Approximately 36% of the buffalo are inside Moremi Game Reserve and Chobe National Park, although this may vary seasonally (Table 1) (ULG 1994a, 1994b). All buffalo in Botswana are both foot-and-mouth disease and corridor disease-infected (D. Gibson 1995 pers. comm.; S. Modise 1996 pers. comm.).

In 1987 the estimated buffalo population in Botswana was 72 290 (Anon. 1995). Between 1989 and 1991 buffalo numbers decreased to an estimated 41 380 animals, of which 21% were in national parks (Bonfica 1992). According to ULG (1995) buffalo numbers in Botswana are declining by an estimated 14,9% per annum. The reasons are not yet known and are being investigated by the Botswana Department of Wildlife and National Parks.

All buffalo in Botswana are state-owned, and occur in wildlife management areas (protected state land) and national parks. Although they can be termed free-ranging (that is, not confined to a single national park, game reserve or farm), they remain within the confines of the veterinary cordon fences which all but surround the Okavango Delta and Chobe area, cutting off any movement to the south and west. The buffalo are, however, known to move across the borders into Namibia and Zimbabwe (Anon. 1995).

Botswana has no legislation prohibiting the keeping of buffalo on private land, but, with the restriction of foot-and-mouth disease and corridor disease-infected buffalo to within the Okavango buffalo fence and north-eastern veterinary cordon fences, there are no buffalo in private ownership.

Table 1 Status of Cape buffalo in Botswana, Zimbabwe and Namibia in 1995/1996, with reference to their health status.

Locality	Total	Disease-free	Foot-and-mouth disease and corridor disease-infected	Corridor disease-infected
Botswana				
Chobe National Park	2370	0	2370	0
Moremi Game Reserve	7327	0	7327	0
Okavango Delta area	14923	0	14923	0
Other	4747	0	4747	0
Total	29367	0	29367	0
Zimbabwe				
North-west Matabeleland	5900	0	5900	0
Zambezi Valley	19500	0	19500	0
Sebungwe	21000	0	21000	0
South-east Lowveld	1290	0	1290	0
Central Plateau	511	0	0	511
Total	48201	0	47690	511
Namibia				
Mamili National Park	1100	0	1100	0
Kwando	1100	0	1100	0
West-Caprivi and Mahango	450	0	450	0
Bushmanland	40	0	40	0
Waterberg Plateau Park	150	150	0	0
Total	2840	150	2690	0
Total	80408	150	79747	511
Percentage (%)		(0,2%)	(99,2%)	(0,6%)

Zimbabwe

The aerial counts for 1995 resulted in estimates for total buffalo numbers in Zimbabwe to be approximately 48 200 (Table 1), the bulk (97%) of which can be considered free-ranging (Foggin & Taylor 1996). Most buffalo (72%) in Zimbabwe are inside designated wildlife zones (national parks, safari areas and forest land), and 25% occur on communal land. These buffalo are carriers of both foot-and-mouth disease and corridor disease. Only approximately 3% of the buffalo in Zimbabwe are privately owned. All buffalo in Zimbabwe carry corridor disease (Foggin & Taylor 1996; Department of Veterinary Services *in litt.*).

In 1984 the number of buffalo in Zimbabwe was estimated at 66 590 (Taylor 1984) and in 1989 at approximately 80 000 (Department of Veterinary Services *in litt.*). In the Hwange National Park buffalo numbers decreased from 17 000 animals in 1989 to 5 080 in 1995. The buffalo population in the Gona-re-zhou National Park has decreased from approximately 4 500 in 1989 to only an estimated 40 in 1995.

The wildlife zones, which are foot-and-mouth disease endemic areas and mostly free of cattle, are situated in north-western Matabeleland, in the Sebungwe area south of Lake Kariba (including Matusadona National Park), in the Zambezi Valley and the south-eastern Lowveld. These zones are separated from the central part of the country by game-proof fencing, and two buffer zones (green zones) and associated vaccination zones (red zones) fenced with cattle fences (Figure 1). During the demarcation of the buffer and vaccination zones (mainly between 1977 and 1982) the Destruction of Buffalo Order was promulgated and an estimated 5 500 buffalo were shot, or driven across the fence-lines into the wildlife zones (S.K. Hargreaves 1996 pers. comm.). The number of buffalo killed by farmers with open licenses to kill buffalo is unknown. This destruction of buffalo was carried out in support of the beef export industry to the European Economic Community[3], but with the understanding that foot-and-mouth disease-free buffalo populations would be established. Four hundred and seventy eight foot-and-mouth disease-free buffalo now occur on private land, mainly on the Central Plateau of the country, as well as a small number (33) on government land (Department of Veterinary Services *in litt.*). Foot-and-mouth disease-free buffalo were initially obtained by removing calves less than three-months-old from their

[3] Published in journal as EEC

foot-and-mouth disease-infected mothers, and rearing them in a quarantine area (Condy & Hedger 1978; Department of Veterinary Services *in litt.*). Conditions for keeping foot-and-mouth disease-free buffalo are under very strict veterinary control, including specified fencing regulations (Statutory Instrument No. 278 of 1986). Up to 1 000 foot-and-mouth disease-infected buffalo occur on private land adjacent to, but outside the buffalo-proof game fence, but strict fencing regulations are enforced (Foggin & Taylor 1996).

It is not clear whether the buffalo population in Zimbabwe is recovering from the 1991/1992 drought (P. Mundy 1995 pers. comm.), but an increase of approximately 8% per annum is suggested by available data (S.K. Hargreaves 1996 pers. comm.).

Namibia

An estimated 2 840 buffalo occur in Namibia, of which 2 650 are in the eastern and western Caprivi and north-eastern Kavango (now Okavango) (Figure 1). There are 40 buffalo in the former Bushmanland, and an estimated 150 in the Waterberg Plateau Park (Table 1).

In the past the buffalo population in the Caprivi and Kavango fluctuated considerably as buffalo migrated out of the flooded Caprivi area during the rainy season, to the drier Chobe in Botswana. However, since 1988 the Caprivi area has been so dry that the buffalo have remained largely resident. This population has increased from less than 600 animals in 1985 to an estimated 2 650 in 1994. The buffalo in Bushmanland are a relic population from a herd of approximately 200 animals that were cut off from a migrating herd by the erection of the Namibia/Botswana border fence (B. Beytell 1995 pers. comm.). The only disease-free buffalo population in Namibia is found in the Waterberg Plateau Park (Table 1).

Although Namibian veterinary regulations do not prohibit the keeping of buffalo on private land, the government does not allow the distribution of buffalo to private game farmers at the request of the Meat Producers' Association (Directorate of Veterinary Services 1996 *in litt.*).

South Africa

South Africa has an estimated 31 500 buffalo (Table 2). Only 7,7% are disease-free, while 67,0% are foot-and-mouth disease and corridor disease-infected and 25,1% are infected with

Table 2 Status of Cape buffalo in South Africa in 1995/1996, with reference to their health status and ownership (Anon 1994, personal communications).

		Government ownership (80.3%)			Private ownership (19.6%)		
Province	Total	Disease-free	Foot-and-mouth disease-infected	Corridor disease-infected	Disease-free	Foot-and-mouth disease-infected	Corridor disease-infected
Northern	5840	128	966	0	763	3983	0
North-West	266	300	0	0	166	0	0
Gauteng	63	8	0	0	55	0	0
Mpumalanga	16210	4	15348	0	47	846	0
Free State	268	160	0	0	84	0	0
Kwazulu/Natal	8244	241	0	7878	69	0	56
Eastern Cape	316	280	0	0	36	0	0
Western Cape	20	0	0	0	20	0	0
Northern Cape	85	15	0	0	70	0	0
Total	31523	1136	16314	7878	1310	4829	56
Percentage (%)		(3.6%)	(51.8%)	(25.0%)	(4.1%)	(15.3%)	(0.2%)

corridor disease only. The largest buffalo populations in South Africa are in the Kruger National Park in the Mpumalanga and Northern Provinces (approximately 15 000 animals), and the Hluhluwe-Umfolozi Park in Kwazulu/Natal (7 878 animals) (Figure 1). Both of these populations are infected with foot-and-mouth disease and corridor disease and are the only buffalo populations in South Africa also infected with bovine TB.

In 1992 buffalo numbers in the Kruger National Park were estimated at 28 000 (Anon. 1992). Between 1992 and 1993 approximately 1 000 buffalo in the northern section of the Kruger National Park died of anthrax (R. Bengis 1995 pers. comm.). The drastic decrease in buffalo numbers in the Kruger National Park during 1994 and 1995 is ascribed to drought (I. Whyte 1995 pers. comm.) and resultant increases in predation by lions (R. Bengis 1995 pers. comm.).

Bovine TB was first diagnosed in buffalo in the Kruger National Park in 1990, presumably being transmitted from cattle (Bengis, Kriek, Keet, Raath, De Vos & Huchzermeyer 1996). At present, the prevalence of TB among infected buffalo herds in the Kruger National Park varies from 3 to 80%, and it is confined to the southern part of the Park. However, TB among buffalo is steadily spreading northwards, to other species and to areas outside the Kruger National Park (R. Bengis 1995 pers. comm.).

Table 2 summarises the estimated number and percentages of foot-and-mouth disease and corridor disease-infected buffalo, as well as disease-free buffalo, in private and government (national and provincial) ownership. South African veterinary regulations allow the translocation of buffalo, but only to land which has been registered with the Directorate of Animal Health, Department of Agriculture, and which complies with the fencing regulations for buffalo (Animal Disease Act 1984, Act No. 35 of 1984). Buffalo from TB-positive herds must be held in quarantine, tested and are only allowed to move once proven free from infection. Foot-and-mouth disease and corridor disease-infected buffalo may be moved only within the veterinary controlled areas.

Mozambique

In Mozambique buffalo numbers have decreased drastically. What was probably the largest single buffalo herd in Africa, in the Marromeu area in Mozambique, numbered an estimated 56 000 animals in 1978. Between 1979 and 1993 this population declined by 79% (Dutton

1993). Today, only approximately 2 500 animals are left (P. Nel 1996 pers. comm.). Uncontrolled poaching for meat abounds (East 1989; Dutton 1993; P. Nel 1996 pers. comm.). Poaching in the Marromeu area has been facilitated by the impoundment of floodwater in the Cahora Bassa and Kariba Dams, causing easier access into the floodplains even during the wet season (Dutton 1993).

The buffalo in Mozambique are presumed to be carriers of foot-and-mouth disease, and there are no known disease-free buffalo (P. Nel 1996 pers. comm.). The incidence of nagana is still a serious problem.

Economic value

The majority of buffalo (97,6%) in southern Africa are infected with foot-and-mouth disease, corridor disease or both. Only 2,3% of the buffalo are disease-free.

The buffalo is one of eco-tourism's 'Big Seven' and one of hunting's 'Big Five'. As a highly sought after hunting trophy, buffalo have a high economic value. Trophy fees and accommodation rates combined for a buffalo hunt in southern Africa for 1997/1998 ranged between R44 750 and R70 000. Between 1995 and 1998 buffalo trophy fees have increased by 69% in South Africa, from R25 000 to R36 000. In Zimbabwe, buffalo are the second most valuable species, after elephant, in the safari hunting industry that raised US$ 12 826 360 gross revenue in 1993 (Foggin & Taylor 1996).

The market value of live buffalo varies depending on whether they are disease-infected or disease-free, with the former having a much lower economic value. In 1996 the market value of live disease-infected buffalo in South Africa varied between R3 000 for foot-and-mouth disease-infected buffalo and R7 500 for corridor disease-infected buffalo. However, the average price for a corridor disease-infected buffalo increased in 1998 to R55 000 for a cow and R30 000 for a bull. This drastic increase in value of these buffalo resulted from an expansion in the breeding of disease-free buffalo from corridor disease-infected buffalo, with at least three such breeding programmes currently operating in South Africa (R. Saayman 1998 pers. comm.). In Zimbabwe corridor disease-infected buffalo were sold for R12 800 in 1996.

Average auction prices of disease-free buffalo in South Africa have increased from approximately R16 000 in 1992 to R130 000 in 1998 for an adult buffalo. Disease-free buffalo are used mostly as breeding stock. On auction, breeding herds of four cows and one bull fetched prices of up to R115 000 per animal, and immature buffaloes (ranging from one to three years old) were auctioned for up to R120 000 for two animals.

Discussion

The Cape buffalo have been exterminated from large areas in southern Africa and its range is now fragmented and mostly confined to protected areas. The largest free-ranging buffalo population constitutes those in the Caprivi area in Namibia, the Okavango-Chobe area in Botswana, and the Matetsi-Hwange area in Zimbabwe, which forms a single, inter-mixing and interbreeding population. This is an important conservation feature, which requires close co-operation between conservation and disease control agencies in all three countries. Other large, free-ranging buffalo populations include those in the Zambezi drainage systems in Zimbabwe, and in the Kruger National Park and Hluhluwe-Umfolozi Park in South Africa.

Since there are an estimated 111 900 ± 10 000 buffalo in southern Africa, their present conservation status can still be classified as satisfactory (East 1989); it is not listed as endangered, rare or vulnerable in the IUCN or South African Red Data Books (Thornback, Allan & Almada-Villela 1990; Smithers 1986), and it does not appear on Appendix I to III of CITES. However, the total number of buffalo in the large, free-ranging populations mentioned, has decreased by more than 50% during the past three years.

The key factor influencing the continued existence of buffalo is the range of diseases associated with buffalo and which are detrimental to cattle production. Campaigns to eradicate buffalo in commercial farming areas, mainly because of foot-and-mouth disease and corridor disease, are still in effect in Namibia, Botswana and Zimbabwe. Foot-and-mouth disease is probably the most economically important disease of livestock in southern Africa. The strict veterinary control measures in southern Africa are aimed at preventing the unrestrained movement of buffalo, through a proliferation of cattle and game fences, and veterinary controlled areas. The motivations behind these control measures are, to a large extent, international agreements on beef exports to the European Export Community (Taylor 1984). In Europe, the effects of foot-and-mouth disease outbreaks have historically been great and vast sums of money have been spent to control the disease. Today, the European Export Community is wary of re-importing the disease, especially exotic strains, and has instituted strict requirements on the import of beef. The value of the beef export industry in Namibia, Botswana and Zimbabwe is such that these countries are obliged to comply with the European Export Community requirements (Taylor 1984). Foot-and-mouth disease outbreaks in Zimbabwe in 1989 resulted in the loss of approximately ZW$ 100 million (*c.* R50 million) through suspended beef imports by the European Export Community for at least two years (Thomson 1994).

The erection of hundreds of kilometres of game-proof fencing in southern Africa has cut off migration routes and progressively isolated areas necessary to the maintenance of most wildlife species. In Botswana the most probable cause for the decline in buffalo numbers is nutritional deficiencies caused by the proliferation of fences almost surrounding the Okavango Delta. This forces the buffalo to remain in the delta, known for its low quality grazing (Main 1990), all year round, preventing their movement to better grazing during the rainy season. During 1996 additional fences have been erected in the delta area as a control measure against bovine pleuro-pneumonia. The detrimental effects of drought on wildlife are enhanced when fences cut off possible escape routes to better grazing. The severe drought in Zimbabwe during 1991/1992 and in the Kruger National Park during 1994 and 1995 is the main cause for the drastic decrease in buffalo numbers in the two respective areas (Foggin & Taylor 1996; Department of Veterinary Services *in litt.*; I. Whyte 1996 pers. comm.). The prevalence of TB among buffalo in the Kruger National Park certainly contributed to their drastic decline. TB results in emaciation and early death (Keet, Kriek, Huchzermeyer & Bengis 1994), making infected buffalo more vulnerable to the stress of drought conditions and to predation by lions.

Disease, poaching, a steady shrinkage of range and the ever-present shortage of conservation management funds within government agencies further aids the decline in buffalo numbers in the larger, free-ranging populations. Unfortunately, it seems that there is little or no co-operation between disease control and conservation agencies, and control measures are implemented with no consideration of their effects on the wildlife (Taylor 1984).

Although foot-and-mouth disease-infected buffalo is, on the one hand, being eradicated, on the other, the monetary value of foot-and-mouth disease-free buffalo is being vastly inflated by its inherent scarcity. Only two countries, South Africa and Zimbabwe, actively produce surplus buffalo which can be made available for translocation or sale, and allow buffalo in private ownership. In South Africa the distribution of buffalo is markedly more extensive now (Figure 1) than 30 years ago, mainly because of the estimated 1 300 disease-free buffalo in private ownership (Table 2). However, most of these are in small, isolated herds of 5 - 20 animals each, due to the excessively high purchase price. Economic returns from these small herds take a number of years to attain and, therefore, only a small number of excess disease-free buffalo are available on the open market each year. The cumulative loss of genetic diversity as small, isolated herds are sold to form other small, nucleus herds might have potentially serious consequences. Some buffalo populations in South Africa already show excessive loss of genetic diversity, whether due to relatively recent fragmentation of the populations or from more ancient geographical differentiation is not yet clear (C. O'Ryan pers. comm. 1996).

The number of disease-free and foot-and-mouth disease-free buffalo in private ownership is too small to contribute significantly to the conservation status of buffalo in the sub-region, and with their slow increase rate and loss of genetic diversity, this will remain the case for a long time still. However, with the declining viability of cattle production in large areas of southern Africa, the economic importance of wildlife production as a form of land use is gaining momentum. Veterinary authorities in South Africa and Zimbabwe have recognised the importance to accommodate the wildlife sector. Considerable effort has been directed towards the development of effective screening tests, which allow the successful breeding of foot-and-mouth disease-free buffalo without compromising the high standards of disease control required for beef exports. The economic value of buffalo in the tourism and hunting industry might yet play a key role in their conservation.

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CHAPTER 5

Activity patterns of the Cape buffalo *Syncerus caffer caffer* in the Willem Pretorius Game Reserve, Free State

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The daily activity of buffalo *Syncerus caffer caffer* was investigated over a 12 month period in the Willem Pretorius Game Reserve, Free State, South Africa, using the scan sampling method (Altmann 1973). Buffalo in the Willem Pretorius Game Reserve showed the same general circadian rhythm as other ruminants: a few long feeding periods, followed by a few long ruminating and resting periods. Grazing and resting/ruminating were the predominant activities (74% of the 24-hour cycle), with the percentage time spent grazing (48,2%) the highest during the warm, dry season (October to November). Nighttime grazing was favoured during the warmer months ($p<0,1$), with resting/ruminating occurring predominantly at night during the winter months ($p<0,05$). All drinking occurred during the day. There was a significant decrease in grazing ($p<0,05$) and an increase in resting/ruminating ($p<0,05$) from the warm, dry season to the cold, dry season (May to September). The time spent grazing did not differ significantly between the warm, wet and the cold, dry season, but resting/ruminating was significantly higher ($p<0,05$) during the cold, dry season. Although the study was conducted in a confined area consisting of sub-optimal habitat for buffalo (mostly Sourveld) with a long history of severe over-grazing and no large predators present, the seasonal activity patterns of the buffalo in the Willem Pretorius Game Reserve do not differ markedly from that observed in other studies.

Key words: Activity pattern, Cape buffalo, *Syncerus caffer*

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Introduction

As a single species may show different behavioural patterns in different environmental conditions (Delany & Happold 1979), effective management of a species depends on a thorough knowledge of the way in which it interacts with its specific environment (Leuthold 1977). One of the most useful methods of describing this interaction is to quantify the basic activity patterns, which exist for any species at a given time and place during the different seasons (Jarman & Jarman 1973; Leuthold & Leuthold 1978; Walther 1973; Norton 1981; Vrahimis & Kok 1993).

Ruminants have a general circadian rhythm consisting of a few long feeding periods, followed by a few long ruminating and resting periods (Jarman & Jarman 1973; Wyatt & Eltringham 1974; Waser 1975; Ben-Shahar & Fairall 1987; Vrahimis & Kok 1993; Van Aswegen 1994). Annual cycles in ungulate activity are influenced by forage quality and quantity, digestive system constraints and energy conservation needs (Jarman & Jarman 1973; Walther 1973; Mitchell 1977; Leuthold 1977; Owen-Smith 1982; Green & Bear 1990). Other environmental constraints include weather conditions, human activity and predation risk (Walther 1973; Mloszewski 1983; Funston 1992).

Detailed studies on the behaviour and activity patterns of Cape buffalo *Syncerus caffer caffer* were all conducted in areas within their historical distribution and, therefore, in habitats suitable for buffalo and which included large predators. These studies were mainly in East Africa (Grimsdell & Field 1976, Sinclair 1977, Mloszewski 1983, Prins 1987), with the exception of Taylor (1989) who studied the buffalo on the Kariba Lakeshore, Zimbabwe, and Funston (1992) who studied the buffalo in the Sabi Sand Wildtuin, South Africa. Seasonal changes in the activity pattern of buffalo were found to be governed primarily by the quality and quantity of food available (Leuthold 1972; Sinclair 1974; Field 1976; Beekman & Prins 1989). Based on the data available in the literature expected grazing and ruminating times for buffalo are short during the warm, wet season, when high quality food are abundant, but as food quality and quantity decrease during the dry season, the expected grazing and ruminating times increase (Sinclair 1974; Grimsdell & Field 1976; Taylor 1989; Funston 1992). The primary factor controlling the temporal distribution of buffalo activity patterns is ambient temperature (Sinclair 1974; Grimsdell & Field 1976; Lewis 1977; Mloszewski 1983; Taylor 1989). High ambient temperatures during the day result in nighttime grazing being favoured during the warmer seasons (Vesey-Fitzgerald 1969; Leuthold 1972; Grimsdell & Field 1976; Sinclair 1977; Taylor 1989), and low ambient temperatures during the night cause nighttime resting/ruminating being favoured during the cold season (Funston 1992).

The objective of this paper is to determine the behavioural adjustments made by the buffalo in the Willem Pretorius Game Reserve[1], which comprises an area outside their historical distribution with sub-optimal habitat for buffalo with a long history of severe over-grazing and no large predators present.

Study area

The Willem Pretorius Game Reserve (28° 16-21'S; 27° 07-23'E) is situated around the Allemanskraal Dam in the Sand River, approximately 140 km north-east of Bloemfontein in the Free State. The total surface area of the reserve is 12 082 ha, of which the dam comprises 2 771 ha when full. The effective game habitat area is approximately 8 336 ha and this area has a length of 23 km and a width varying from 2 to 8 km.

Summers are warm with a few hot days (absolute and mean daily maximum temperatures for January are 37,8°C and 30,6°C, respectively), while winters are cold (absolute and mean daily minimum temperatures for June are -6,7°C and -0,4°C, respectively). A long thermic summer with mean daily temperatures of more than 16,4°C occurs for seven months of the year from October to April (Müller 1986). Severe frost occurs during the winter. The area is semi-arid with a 31-year mean annual rainfall of 576 mm, with the highest mean rainfall in January (97,7 mm) and the lowest in July (6,3 mm). Precipitation occurs mostly as thunderstorms.

The topography comprises mainly of flat grass plains (Müller 1986). A series of

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1 Published in journal as WPGR

dolerite and sandstone ridges occur north of the Allemanskraal Dam and Sand River, stretching from east to west along the river, and are interspersed by virtually flat plains. Flat areas also occur on the plateaux of the ridges. The reserve lies on the Beaufort Series of the Karroo System, on the boundary between the Dry *Cymbopogon-Themeda* Veld (Veld type 50) and the Transitional *Cymbopogon-Themeda* Veld (Veld type 49) mainly on heavy soil (Acocks 1988). Five main vegetation types are found in the reserve namely: the tree and shrub community of the ridges, the thornveld and riverbank community, the grassland community, the hygrophilous community and the community of exposed rocky outcrops (Müller 1986).

Sixteen large herbivore species occurred in the Willem Pretorius Game Reserve and approximately 160 disease-free buffalo were present in the reserve during the study period. Between 1973 and 1989 the reserve was overstocked by between 47% and 50% (Borquin 1973; Vrahimis, Vorster & Terblanche 1989). In 1991 herbivore biomass comprised 1 416 large stock units (L.S.U.), which was 24% above the grazing capacity determined for the reserve by Winterbach (1992a). The stocking-rate of the buffalo population in the reserve during 1991 was estimated to be 100 animals (Winterbach 1992b). Caracal *Felis caracal* is the largest predator present in the reserve.

Methods

Activity patterns of the buffaloes were investigated from October 1990 to September 1991. Direct field observations were conducted on a monthly basis from a parked vehicle or other vantagepoint, using a pair of 11 x 80 binoculars during daylight hours. A 4,7 x Image Intensifier Binocular was used on moonlit nights and a 300 000 candlepower spotlight on dark moon nights. Both instruments were only switched on at those intervals when a scan sample of the activities was taken. Daylight observation sessions were continuous from sunrise to approximately 17:00, totalling 161 observation hours. Night observations were shared between two people from 16:00 to 07:00, or for as long as possible, totalling 85 observation hours. Observations at night proved difficult due to varying nighttime accessibility and visibility in different parts of the study area, and were, therefore, not as inclusive as during daylight hours. A small percentage of additional data were obtained by driving the established routes in the Willem Pretorius Game Reserve on a regular basis to record the activities of the buffalo herds encountered at that specific time. Only mixed herds were selected for observation. Bachelors, male herds and mixed herds of less than five animals were not included in the study, since they were not viewed as representative of the overall activity of the buffaloes in the reserve.

Observations on activities were recorded on data sheets, using the scan sampling method as described by Altmann (1973) with 5-minute intervals (Grimsdell & Field 1976; Sinclair 1977). Activities observed were divided into the following categories: grazing, resting/ruminating (lying down), standing, walking, drinking and other activities. The latter included all activities that did not feature strongly in the general activity pattern, such as running. If the presence of the observer caused the herd at any time to appear uneasy for more than 15 minutes, or ran off for more than 100 m, observations on that herd were discontinued on the assumption that normal activities were interfered with.

Seasonal divisions used in the analyses of the activity data were based on the rainfall during the observation period (Figure 1). Rainfall figures were obtained from the weather station at the Willem Pretorius Game Reserve. Three seasons were distinguished. The warm, dry season from October to November 1990 was characterised by low quality and largely depleted forage after the winter months. The warm, wet season from December 1990 to April 1991 was characterised by high temperatures and above-average precipitation in December 1990 and February 1991 resulting in an abundance of forage. The cold, dry season from May to September 1991 was characterised by low temperatures, often with frost, and very little rain. Day and night divisions in the data analyses were based on mean times of sunrise and sunset for that particular season, obtained from the Bloemfontein Airport Weather Station (26° 18'S; 29° 06'E).

As the number of buffalo per observation varied, even between consecutive observations, all observations were standardised to percentages before analysis to remove the effect of group size. The 24-hour activity patterns were determined using standardised data grouped per hour, to calculate the proportions of each activity per hour. The Mann- Whitney test (Zar 1984) was used to test the null hypothesis that there was no difference between the time spent per activity between day and night. An ANOVA was performed to test the null

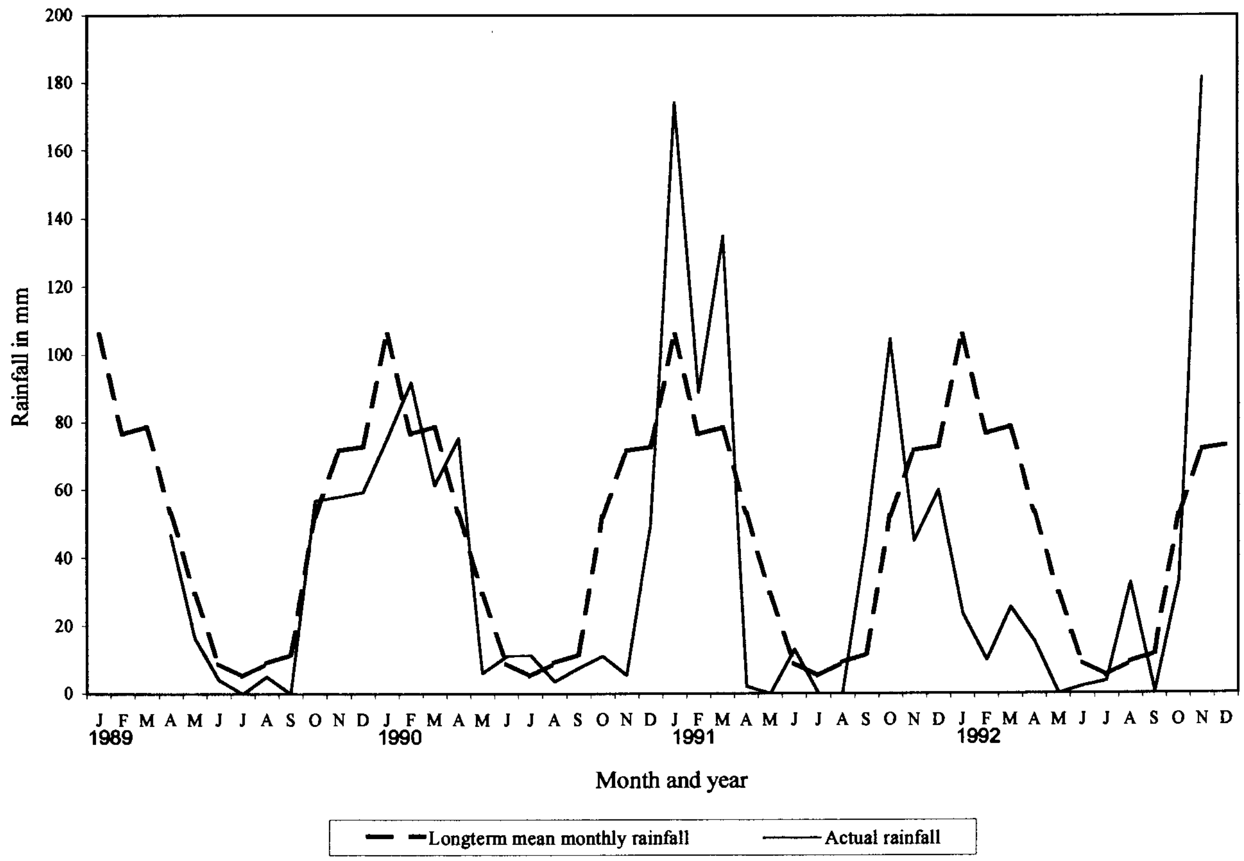

Figure 1 Actual rainfall recorded at Willem Pretorius Game Reserve: 1989-1992, in comparison with the long-term mean monthly rainfall: 1961-1992. The rainfall reflects conditions in grazing prevailing during the study period from October 1990 to September 1991.

hypothesis that no differences occurred among the three seasons for each activity, followed by the Tukey test if the null hypothesis was rejected (Zar 1984). With the large number of observations per cell, it was assumed that deviation from normality did not matter, based on the central limit theorem (Frank & Althoen 1994). To allow for Bonferonni Inequality by testing for day/night and seasonal differences, all p-values were multiplied by two, which is the number of comparisons (Stevens 1990). This may result in meaningless p-values larger than one.

Results

Basic activity patterns (24-hour totals)

The 24-hour activity pattern was characterised mainly by alternating bouts of grazing and resting/ruminating (Figure 2). Grazing was the dominant activity. The buffaloes fed an estimated 40% of the time, and allocated 34% of their time to resting/ruminating, 14% to walking and 11% to standing. Drinking and "other activities" occupied only 2% of the overall 24-hour cycle.

The main grazing period, with more than 40% of herd found grazing, was from mid-afternoon until after sunset (15:00-20:00) (Figure 2). A peak in resting/ruminating until about midnight usually followed this grazing period. During the early morning hours (01:00-05:00) short alternating bouts of grazing and resting/ruminating occurred, with another peak in grazing after sunrise between 06:00 and 07:00. The lowest incidence of grazing occurred between 10:00-12:00 when the main day resting/ruminating period was prevailing. During the early morning (05:00-08:00) there was a general movement to the daytime resting-place and during the late afternoon (15:00-18:00) a general movement to the nighttime pasture (Figure 2). Walking was either combined with grazing or done purposefully in single file, the latter more often in the mornings on the way to the daytime resting-place (pers. obs.). Walking activity during the night hours was relatively low (Figure 2). Rhythmic trends in the standing activity were less obvious as standing was both associated with grazing and resting/ruminating. The highest incidence of standing was, however, associated with the period just before the day's resting/ruminating period (08:00-09:00) (Figure 2).

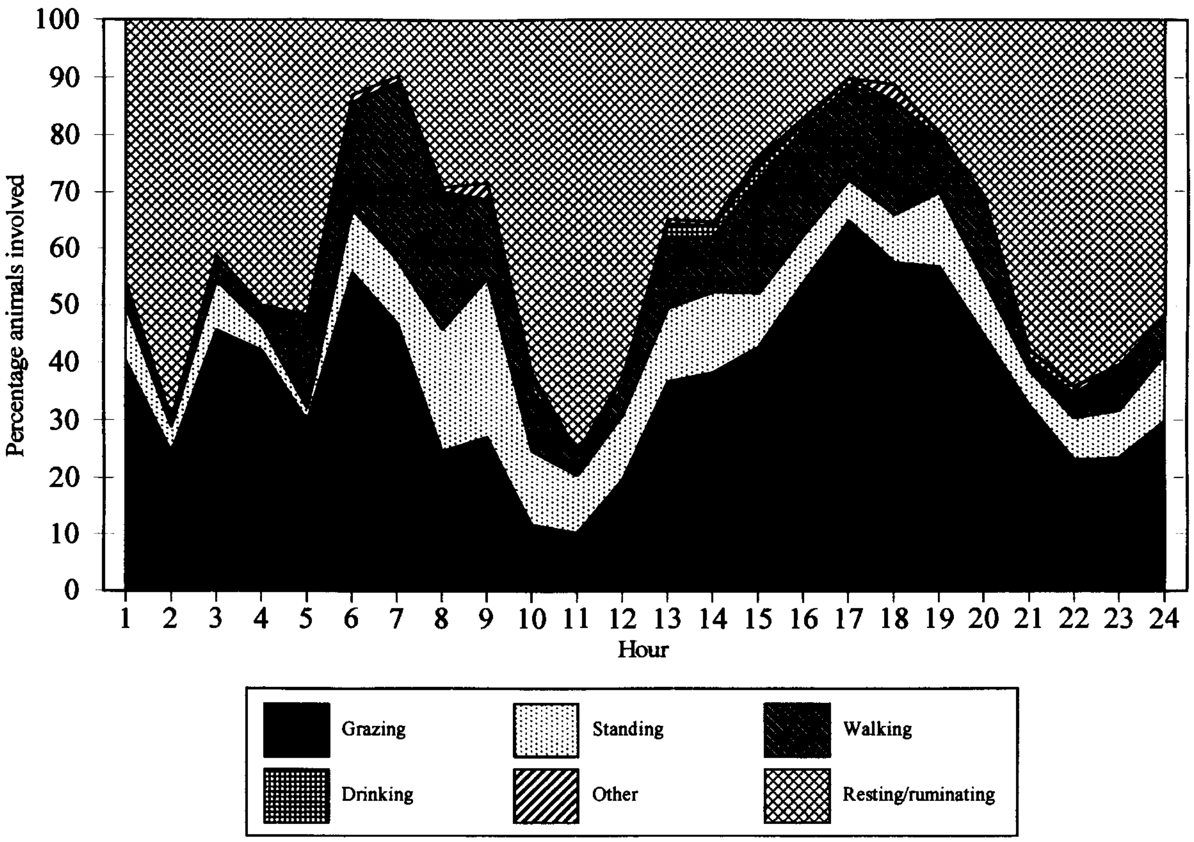

Figure 2 Overall 24-hour activity pattern of Cape buffalo in the Willem Pretorius Game Reserve during the period October 1990 to September 1991.

The buffaloes drank predominantly in the early afternoon between 13:00 and 15:00, but some drinking may take place at any time during the day. No drinking took place during the night hours.

The basic activity pattern does not reflect seasonal differences in the temporal or spatial distribution of the different activities.

Seasonal activity patterns

The overall 24-hour grazing and resting/ruminating activity pattern recorded for buffalo in the Willem Pretorius Game Reserve during the three seasons studied are illustrated in Figures 3 to 5. During the warm, dry season (Figure 3) four main grazing peaks, when more than 40% of the herd was found grazing, occurred during the 24-hour cycle. Two short, but intensive grazing bouts occurred during the night, one during the late evening (between 21:00 and 22:00) and one early morning (around 01:00). This differed from the three main grazing peaks found during the other two seasons (Figure 4 and 5), where only one short grazing bout occurred during the early morning (between 24:00 and 03:00). The three main grazing peaks found during the cold, dry season (Figure 5) were markedly shorter and less intense compared to the other two seasons.

Three main resting/ruminating periods occurred in all three seasons. The day resting/ruminating period began earlier in the morning (around 08:00) during the warm, dry season (Figure 3), but lasted longer into the early afternoon (until 15:00) during the cold, dry season (Figure 5). During the warm, dry (Figure 3) and warm, wet seasons (Figure 4) two short resting/ruminating periods occurred during the night, both being interrupted by short, but intensive, feeding bouts. This contrasted with the cold, dry season (Figure 5) where resting/ruminating during the night lasted six hours (20:00-02:00) largely uninterrupted by any other activities. After a short feeding bout around 03:00, resting/ruminating was resumed until 05:00.

Walking during the warm, wet season (Figure 4) was fairly evenly distributed between the morning and afternoon period when the herd was also actively grazing. Another peak in the walking activity occurred during late evening (around 23:00) after which grazing

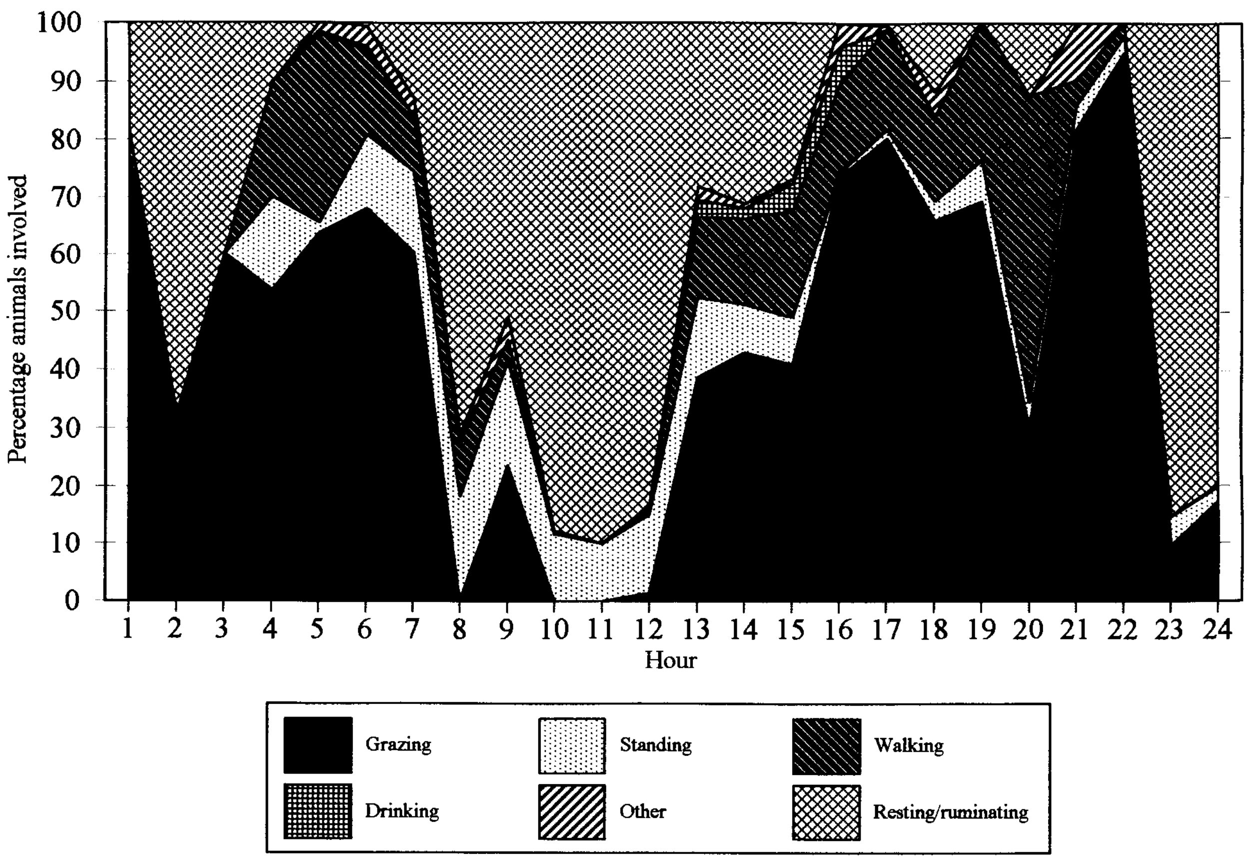

Figure 3 The 24-hour activity pattern of Cape buffalo in the Willem Pretorius Game Reserve during the warm, dry season (October to November 1990).

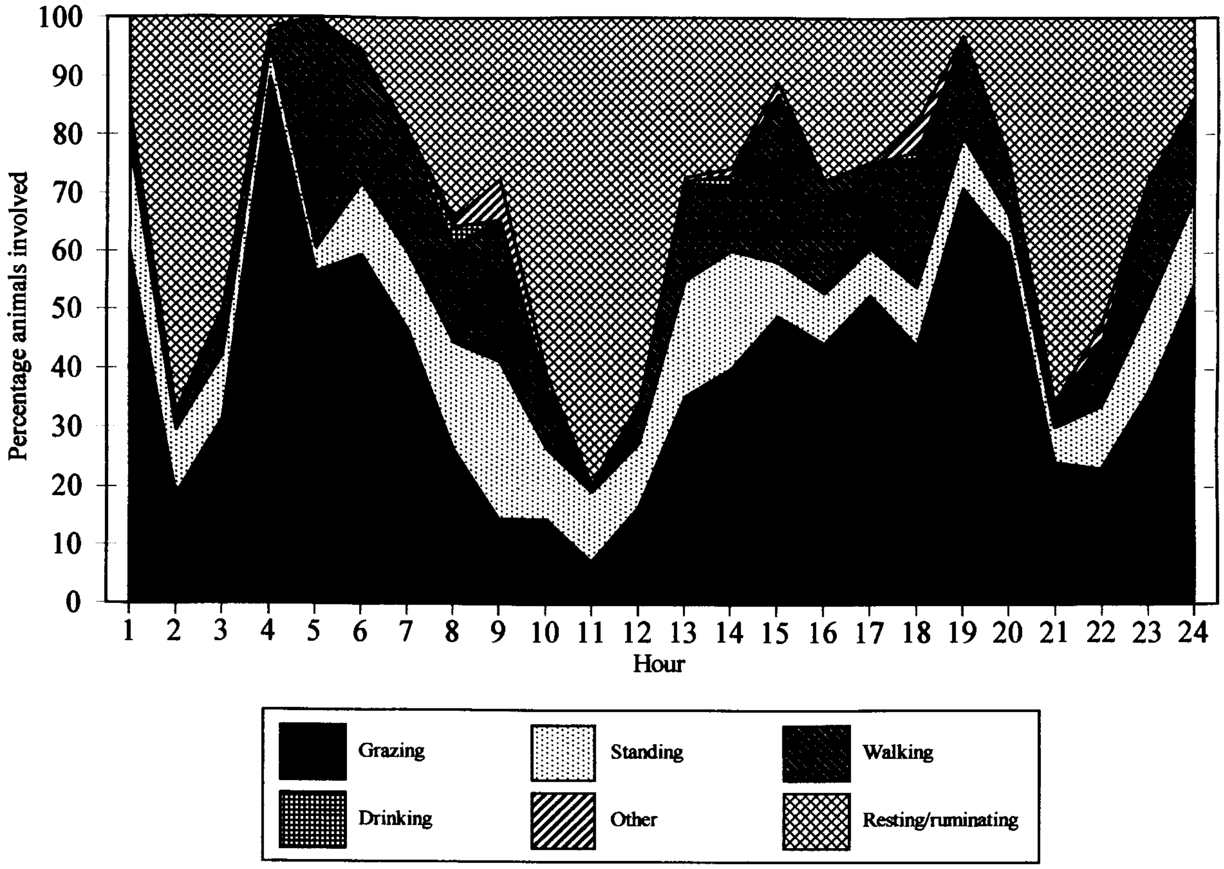

Figure 4 The 24-hour activity pattern of Cape buffalo in the Willem Pretorius Game Reserve during the warm, wet season (December 1990 to April 1991).

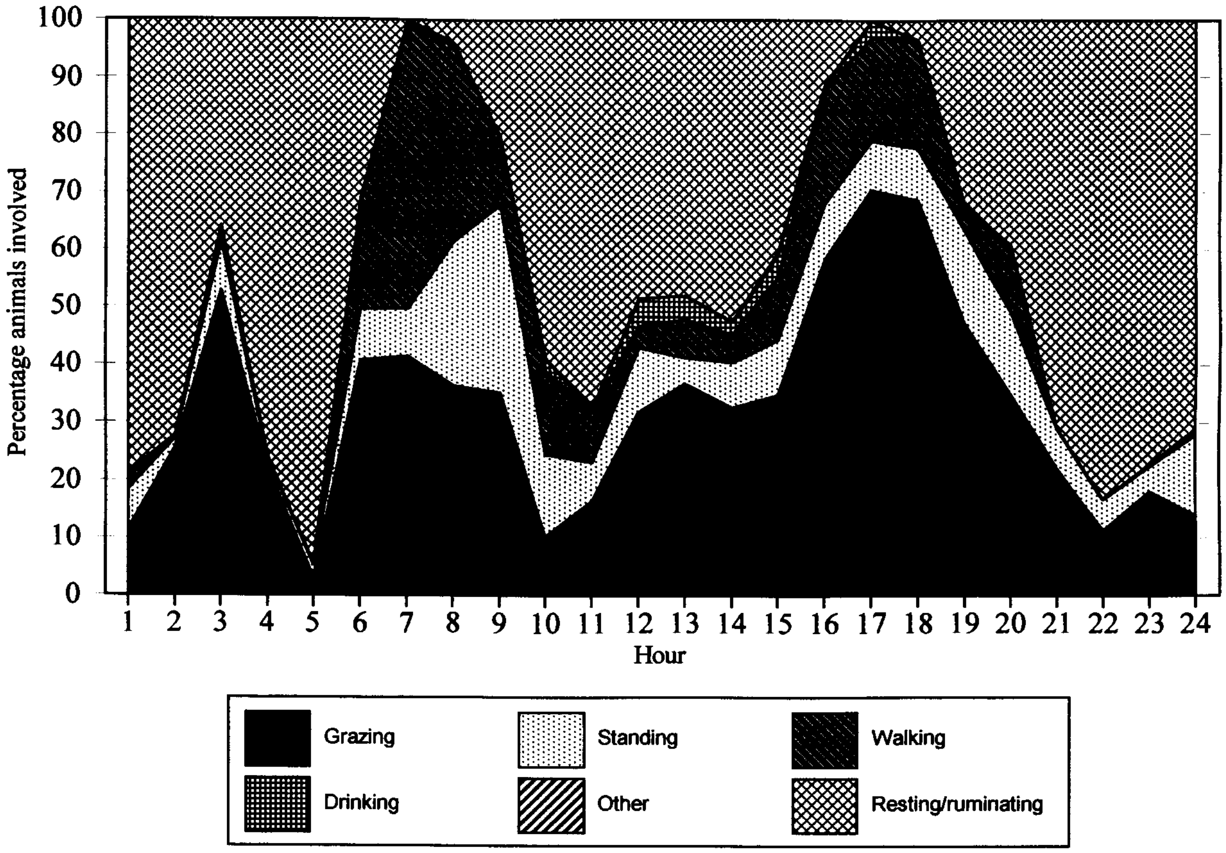

Figure 5 The 24-hour activity pattern of Cape buffalo in the Willem Pretorius Game Reserve during the cold, dry season (May to September 1991)

was actively resumed. During the warm, dry months (Figure 3) walking occurred mainly during late afternoon and continued until well after sunset, accompanied by grazing. Around 20:00 an intense walking bout occurred, after which very little walking was done during the rest of the night until just before sunrise when a peak in walking activity coincided with the morning grazing period. The highest intensity of walking during the cold, dry season (Figure 5) took place around sunrise (06:00-08:00), and again a few hours before sunset (16:00-18:00), although less intense. Very little walking took place during the night hours in the cold, dry season.

Drinking occurred only during daylight hours in all three seasons. During the cold, dry season (Figure 5) drinking occurred mainly between 10:00 and 17:00, with a peak between 12:00 and 13:00 and again around 15:00. A short peak in the drinking activity occurred around 08:00 in the warm, wet season (Figure 4). During the warm, dry season (Figure 3) drinking took place mainly between 13:00 and 16:00, with very little drinking activity taking place in the early morning hours between 05:00 and 06:00.

The temporal distribution of the various activities between day and night is summarised in Table 1. During the warm, dry and warm, wet seasons the incidence of nighttime grazing was significantly higher than daytime grazing, the reverse being true during the cold, dry season where resting/ruminating occurred predominantly at night. Walking occurred mostly during the day.

The percentage time spent grazing was the highest during the warm, dry months (Table 2). The grazing activity seemed also to be more synchronised during these months with more than 60% of the herd engaged in grazing at the same time. There was a significant decrease in grazing and an increase in resting/ruminating from the warm, dry season to the cold, dry season ($p<0,05$). The decrease in grazing from the warm, dry to the warm, wet season was significant, but not the increase in resting/ruminating, while the increase in resting/ruminating between the warm, wet and the cold, dry season was significant, but not the decrease in grazing. Walking did not differ significantly among the three seasons.

Table 1 Temporal distribution of the various activities observed for buffalo in the Willem Pretorius Game Reserve between day and night (October 1990 - September 1991).

Activity	% Time Day	% Time Night	n Day	n Night	p-value
Warm, dry season					
Grazing	46,31	52,94	290	116	0,057341*
Resting/ruminating	27,28	30,13	290	116	0,393464
Standing	10,14	3,97	290	116	0,006486**
Walking	12,86	11,55	290	116	0,042381**
Warm, wet season					
Grazing	37,15	46,04	750	249	0,000112**
Resting/ruminating	31,47	33,09	750	249	0,283946
Standing	12,77	10,66	750	249	0,002749**
Walking	16,42	9,52	750	249	0,002104**
Cold, dry season					
Grazing	40,81	32,45	601	529	0,000034**
Resting/ruminating	24,84	53,50	601	529	0,000000**
Standing	13,32	8,06	601	529	0,000020**
Walking	18,93	5,89	601	529	0,000000**

* p<0,1

** p<0,05

Table 2 Comparison of the different activities of buffalo in the Willem Pretorius Game Reserve between three seasons (October 1990 - September 1991).

Season	% Time	p-value Warm, dry	Warm, wet
Grazing			
Warm, dry	48,2		
Warm, wet	39,36	0,001444**	
Cold, dry	36,89	0,000058**	0,485556
Resting/ruminating			
Warm, dry	28,09		
Warm, wet	31,87	0,701574	
Cold, dry	38,25	0,001216**	0,001492**
Standing			
Warm, dry	8,37		
Warm, wet	12,24	0,004052**	
Cold, dry	10,85	0,151636	0,272050
Walking			
Warm, dry	12,48		
Warm, wet	14,69	0,768762	
Cold, dry	12,82	1,955568	0,371592
Drinking			
Warm, dry	0,84		
Warm, wet	0,61	1,704704	
Cold, dry	0,99	1,861650	0,671000

* p<0,1
** p<0,05

Discussion

The observed seasonal changes in feeding behaviour of the buffalo in the Willem Pretorius Game Reserve are similar to those found in other studies (Sinclair 1974; Grimsdell & Field 1976; Mloszewski 1983; Taylor 1989), with differences due to the effect of the different local environmental conditions.

During the warm, wet season food in the Willem Pretorius Game Reserve is abundant, but of mixed quality between the different habitat types (Wiltshire 1978). The long grazing time during this season is due to the buffalo being more selective in order to obtain a balanced diet between the different habitat types, which is also indicated by the extended home range used during this time (unpublished data). The abundant, good-quality food allows the buffalo to maximise their nutrient intake through longer grazing times as less rumination time is needed to digest high-quality food (Beekman & Prins 1989). During the cold, dry season the quality of the food in the Willem Pretorius Game Reserve decreases (Wiltshire 1978). There was a general move of the buffalo in the Willem Pretorius Game Reserve towards the riverine habitat during this season, resulting in a reduced home range (unpublished data). According to Sinclair (1977) and Beekman & Prins (1989) the degree of selection in the diet declines during times of abundant low quality food when the buffalo switch to a bulk feeding option. This could explain the similar grazing times observed compared to the warm, wet season, as the lower quality food available in the reserve during the cold, dry season forced the buffalo to ruminate more (Sinclair 1977; Beekman & Prins 1989; Taylor 1989). By the onset of the warm, dry season food scarcity is at its most severe, with the highest quality food available in the vlei grassveld (Wiltshire 1978). The observed grazing time increased as the buffalo become very selective (Beekman & Prins 1989), their home range being restricted to the vlei grassland habitats along the Sand River (unpublished data). However, the substantial decrease in rumination time (28%), contrary to the expected increase, indicates that the buffalo were able to gather a higher quality food from the new growth emerging in the vlei grassland at the time.

The distribution of daytime activity for the buffalo in the Willem Pretorius Game Reserve with increased activities of grazing and walking concentrated in the early morning and late afternoon and a major resting/ruminating period during the middle of the day, is similar to that observed elsewhere (Leuthold 1972; Sinclair 1974; Grimsdell & Field 1976; Conybeare 1980; Mloszewski 1983; Stark 1986; Taylor 1989; Funston 1992).

During the warm, dry and the warm, wet season, buffalo in the Willem Pretorius Game Reserve favoured grazing at night. Both in the Willem Pretorius Game Reserve and in areas where other studies found night grazing to be more common than day grazing (Vesey-Fitzgerald 1969; Leuthold 1972; Grimsdell & Field 1976; Sinclair 1977; Taylor 1989) the highest quality food available to the buffalo were in open grassland habitat with very little shade available. This inhibits grazing for long periods during the day as high ambient temperatures are the main cause in reducing, or even terminating, grazing activity and initiating resting during the middle of the day in buffalo (Sinclair 1974; Grimsdell & Field 1976; Mloszewski 1983; Taylor 1989). Lewis (1977) found that ambient temperature accounted for more than 80% of the variation in the daily activity of buffalo as they were highly susceptible to heat stress due to their coat characteristics. Funston (1992) found daylight hours to be the main feeding period for buffalo in the Sabi Sand Wildtuin. This could be explained by the fact that the buffalo in Sabi Sand selected sand savanna and mixed tree savanna, which provides both good quality food, and shade and thus limits the effects of heat stress on the grazing activity pattern.

The effects of low temperatures on the activity pattern of buffalo have only been documented by Funston (1992), who found that the low night temperatures during winter resulted in the buffalo extending their resting/ruminating period for most of the night. This was also observed at Willem Pretorius Game Reserve where the buffalo spend significantly more time resting/ruminating during the night in the cold, dry season, seeking refuge from the extreme cold underneath tree cover. This is in contrast to nighttime resting/ruminating, which occurred predominantly in open grassland during the warmer seasons.

Since buffalo generally need to drink at least once a day, depending on local conditions (Mloszewski 1983), limited water supplies play an important role in adjustments of their behaviour pattern. However, the buffalo in the Willem Pretorius Game Reserve meet their water requirements with little difficulty due to the proximity of a permanent water supply in the Allemanskraal Dam and Sand River.

Conclusions

This study presents the activity patterns of a single Cape buffalo herd in a confined area without large predators. The area consists of sub-optimal habitat for buffalo (mostly Sourveld) with a long history of severe over-grazing. The vulnerability of the buffalo in the Willem Pretorius Game Reserve to climatic changes was shown when 53 buffalo died of starvation in September 1992 after one year of below-average rainfall (332 mm). The seasonal activity patterns of the buffalo in the Willem Pretorius Game Reserve, however, did not differ markedly from that observed in other studies. Thus, although the buffalo in Willem Pretorius Game Reserve was already under nutritional stress at the time of the study, the observed activity pattern gave no conclusive indication of the severity of the problem. Activity patterns of buffalo alone are therefore not an effective management tool to determine their interaction with their environment.

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CHAPTER 6

Seasonal variation in range use, movements and habitat selection of the Cape buffalo *Syncerus caffer caffer* in the Willem Pretorius Game Reserve, Free State

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The seasonal range use, movements and habitat selection of a herd of disease-free Cape buffalo *Syncerus caffer caffer* were studied in the Willem Pretorius Game Reserve, in a sub-optimal habitat for buffalo with a long history of severe overgrazing, and no large predators. The year-round range size of 2 700 ha included a warm, wet season range of 1 775 ha, a cold, dry season range of 1 650 ha, and a warm, dry season range of only 1 175 ha. The mean distance travelled by the buffalo in 24 hours was 6,91 km. During the warm, wet season the mean 24-hour distance travelled was 4,81 km, which was significantly less than the 9,71 km travelled in the cold, dry season. Fragmentation of the herd occurred in all three seasons. The woody riverbanks, grasslands along drainage lines and vlei grasslands were selected for in all three seasons, and form the most important habitat types for the buffalo in the reserve. Use of the plains was significantly less than expected, and grazing in veld in bad condition was avoided. The main factors which appear to regulate habitat selection by the buffalo in the reserve are: seasonal changes in the food supply, the patchy distribution of the food supply, the availability of cover for daytime resting, and protection against low night temperatures and frost.

Key words: Cape buffalo, habitat selection, range use, movement, *Syncerus caffer*

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Introduction

From 1967 to 1968 seven disease-free Cape buffalo *Syncerus caffer caffer* were successfully translocated from the Addo Elephant National Park to the Willem Pretorius Game Reserve in the Free State, South Africa, to act as a core breeding herd for redistribution elsewhere. This population had increased to approximately 266 animals by 1991, of which 63 buffalo by then had been either sold or translocated to other protected areas.

The effective management of wildlife depends on a thorough knowledge of the way in which a given species interacts with its specific environment (Leuthold 1977). Studies on the range use, movements and habitat utilization of Cape buffalo elsewhere include those of Vesey-Fitzgerald (1969, 1974), Sinclair (1977), Conybeare (1980), Mloszewski (1983), Taylor (1989), Funston (1992, 1994) and Mugangu, Hunter & Gilbert (1995). Range use behaviour and social organisation would be expected to be influenced by food distribution, food abundance, the availability of water, intra-specific and inter-specific competition for food and the risk of predation (Vesey-Fitzgerald 1974; Sinclair 1977), of which the most important for buffalo appear to be seasonal change in the availability of food and water.

However, all the above studies were done in habitats suitable for buffalo within their historical distribution range where large predators also occur. The Willem Pretorius Game Reserve, in contrast, lies outside the historical distribution of the buffalo (Du Plessis 1969) and represents sub-optimal habitat for the buffalo (mixed sourveld) with a long history of severe overgrazing (Borquin 1973; Vrahimis, Vorster & Terblanche 1989; Winterbach 1992a), and no large predators. Veld deterioration is already widespread and severe in many areas (Winterbach & Winterbach, In prep.), and this aggravates the effect of rainfall-induced fluctuations in the food supply. The normal response of wild buffalo to such food shortages would be to move away in search of better grazing. However, this is not possible for the buffalo in the study area. The vulnerability of the buffalo population in the study area was sadly demonstrated when 53 died of starvation in 1992 at a time when the grazing capacity of the reserve plummeted after only one year of low rainfall (Winterbach 1992a).

To manage the buffalo population in the Willem Pretorius Game Reserve successfully, it is crucial to understand what the critical factors are regarding their specific habitat requirements in the reserve. Most of the reserve is within 2 km of water and it was expected that food availability would be the main factor influencing the seasonal range use and habitat selection of the buffalo. From other studies it was expected that the buffalo would be highly selective of food in this sub-optimal habitat, and therefore that they would not use the different habitat components in proportion to their occurrence. Habitat selection was here tested on two spatial scales; at reserve level and within the known area of buffalo range use.

Study area

The Willem Pretorius Game Reserve (28° 16-21'S; 27° 07-23'E) is situated around the Allemanskraal Dam in the Sand River, approximately 140 km northeast of Bloemfontein in the Free State province of South Africa. The total surface area of the reserve is 12 082 ha, of which the dam comprises 2 771 ha when full. The effective game habitat area is approximately 8 682 ha. This habitat is elongated, being 23 km long with a varying width of 2 to 8 km.

Summers are warm with a few hot days (absolute and mean daily maximum temperatures for January are 37,8°C and 30,6°C, respectively), while winters are cold (absolute and mean daily minimum temperatures for June are -6,7°C and -0,4°C, respectively). A long thermic summer with mean daily temperatures of more than 16,4°C occurs for seven months of the year from October to April (Müller 1986). Severe frost occurs during the winter. The area is semi-arid with a 31-year mean annual rainfall of 576 mm, with the highest mean rainfall in January (97,7 mm) and the lowest in July (6,3 mm). Precipitation occurs mostly as thunderstorms.

The topography is mainly flat grass plains (Müller 1986). A series of dolerite and sandstone ridges north of the Allemanskraal Dam and Sand River stretch from east to west along the river, and are interspersed by virtually flat plains. Flat areas also occur on the plateaux of the ridges. The reserve lies on the Beaufort Series of the Karoo System, in the Moist Cool Highveld Grassland (39) (Bredenkamp & Van Rooyen 1996). Six management units were identified in the reserve, using the five main vegetation types and the vegetation units of Müller (1986) as a guideline: the tree and shrub veld of the ridges, the thornveld of the plains, the grasslands of the ridges, the grasslands of the plains on sandy soil, the grasslands of the plains on clay soil and the vlei grasslands (Table 1). The communities of rocky outcrops were excluded as a management unit.

Sixteen large herbivore species occurred in the Willem Pretorius Game Reserve. At the time of the study a single herd of 160 buffalo were present. The population structure in April 1991 consisted of 102 adults with a 1:3 male to female sex ratio, 28 sub-adults (1 to 2 years old) and 27 calves (≤ 1 year old). Caracals *Felis caracal* were the largest predator present in the reserve, representing no threat to the buffalo.

TABLE 1

The six management units identified in the Willem Pretorius Game Reserve in the Free State, South Africa, and the habitat descriptions and size in hectares (ha) of the respective homogeneous plant units according to Müller (1986)

	Vegetation unit	Habitat description	Size (ha)
The tree and shrub veld of the ridges			
A	Rhoo-Celtidetum	Sheltered ravines	79
B	Rhoo-Celtidetum rhoosum burchellii	Cooler, moist south-facing slopes	38
C	Rhoo-Celtidetum rhoosum lanceae	On plateaux amongst ruins of stone buildings	32
D	Rhoo-Panicetum	Shallow sandy soil on steep, warm and dry sandstone slopes	67
E	Rhoo-Aristidetum	Shallow soil on warm, dry dolerite slopes	91
F	Rhoo-Aristidetum oleosum	Deeper soil on dry, warm slopes	211
G	Rhoo-Aristidetum aloetosum	Steep dry, warm slopes	136
H	Rhoo-Schismetum	Shallow soil on dolerite and steep, cool slopes	177
I	Rhoo-Koelerietum	Steep, south-facing slopes on dolerite	33
The thornveld of the plains			
K	Rhoo-Diospyretum acasietosum karroo	Woody riverbank and dry watercourses	189
L	*Acacia karroo* variant of the Rhoo-Diospyretum celtidetosum	Shores of dry rivulets near ridges	63
M	Setario-Protasparagetum	Clay soil on moist, low-lying areas and low shrubs	97
N	Setario-Protasparagetum acacietosum	High shrubs, low trees on transition from clay soil	77
O	Enneapogon-Acacietum	Higher, drier areas on plains with trees and shrubs near foothills	575
The grasslands of the ridges			
Q	Brachiario-Elionurodetum vernonietosum	At foot of ridges on south-facing slopes	36
R	Brachiario-Elionurodetum aristidetosum	Grasslands on shallow, rocky soil on slopes and plateaux of ridges	942
T	Euryopo empetrifoliodis-Themedetum	Shallow, rocky soils on ridges	119
The grasslands of the plains on sandy soil			
U	Eragrostio gummifluae-Cynodetum dactyloni	Grasslands on light, sandy soil mostly cultivated in the past	2449
V	Eragrostio gummifluae-Cynodetum dactyloni Pogonarthrietosum	Grasslands on sandy soil on plains	267
The grasslands of the plains on clay soil			
S	Digitario argyrograptae-Elionurodetum	Grasslands on shallow soil on plains	724
W	Aristidetum bipartitae	Grasslands on heavy, clay soil	1480
X	Saisolo glabrescentis-Felicietum	Pioneer vegetation on brackish soil	113
The vlei grasslands			
Y	Setarietum incrassatae	Vlei grasslands on clay soil	648

Methods

Range use and movement patterns

Buffalo were located weekly from October 1990 to September 1991 by vehicle or on foot. Herd movements were recorded at 30-minute intervals for 161 hours of daylight and 85 hours after dark as part of a study on activity patterns of the same buffalo (Winterbach & Bothma 1998). All buffalo herd localities were plotted on 1:50 000 aerial photographs of the study area. The vegetation map of Müller (1986) and a 250 m x 250 m grid were then superimposed over the aerial photographs. The grid allowed the plotting of the exact position of any buffalo herd with an accuracy of 10 m or less.

Range use estimates were based on 1 211 locations. The national coordinate reference system on 1:10 000 ortophotos were used to divide the study area in 500 m x 500 m grid cells. This method was used because it provided the most useful biological data considering the elongated and jagged outline of the reserve and the almost linear distribution of the buffalo along the lakeshore and river. By using these grid cells in relating range use with habitat utilisation on plant unit level increased the reliability of the data. An Analysis of Variance test followed by a Tukey test measured the statistical significance of seasonal differences in mean group size (Statistica for Windows 4.3. 1993. Statsoft Inc.). A chi-square test was used to compare the significance of differences in the mean 24-hour distances moved in the three seasons.

Seasonal divisions used in the data analyses were based on the actual rainfall recorded at the weather station (Order: Rainfall Station) at Willem Pretorius Game Reserve. The three seasons distinguished were: the warm, dry season from October to November 1990, the warm, wet season from December 1990 to April 1991, and the cold, dry season from May to September 1991.

Habitat selection

A chi-square test was used to test the hypotheses that the buffalo used the available habitat types in proportion to their relative occurrence. Bonferroni simultaneous confidence intervals (Byers, Steinhorst & Krausman 1984) were calculated for each season to determine preference for habitats in relation to their availability at the 0,05 level of significance (Statistica for Windows 4.3. 1993. Statsoft Inc.). The following habitat characteristics were used in the analysis: veld condition, physiographic unit and plant unit. At the plant unit level habitat preference was also tested for resting/ruminating (lying down), recorded as one activity, and grazing.

The relative areas of available habitat characteristics were calculated for the whole reserve from area sizes (ha) as provided in Müller (1986). Some plant units that were used infrequently were combined to ensure expected values of at least two observations for each cell (Steyn, Smit, Du Toit & Strasheim 1994). The two classes of veld condition were good and bad. Bad veld was visually identified as severely trampled and overgrazed, with low basal cover or elements of Karoo encroachment. All other areas were considered as good veld. Field observations were used to validate the recognition of areas of veld in bad condition from 1:10 000 aerial photographs.

The distribution function of the IDRISI programme was used to determine a 1-km zone around all points where buffalo have been observed (Idrisis 4.1. 1987-1993. Clark University). This data were used to demarcate the seasonal range use of the buffalo on the vegetation map. The relative sizes of the different plant units in the buffalo range use were then calculated with the IDRISI area function.

Results

Range use and movement patterns

The density of buffalo in the Willem Pretorius Game Reserve in the total terrestrial surface area was 1,9 buffalo/km^2. The density within the year-round buffalo range size of 2 700 ha (Fig. 1) was 5,7 buffalo/km^2. During the warm, wet season the buffalo used an area of 1 775 ha which is only 31% of the total terrestrial surface area of the reserve. The range decreased to 1 650 ha during the cold, dry season and to only 1 175 ha during the warm, dry season, increasing density to 13,2 buffalo/km^2.

The mean distance travelled by the buffalo in 24 hours was 6,91 km for the whole year. However, the warm, wet season mean distance travelled in 24 hours was 4,81 km, which was significantly less than the mean distance of 9,71 km travelled in the same period during the cold, dry season (χ^2 =-10,74; df=5; p<0,001). Sample size for the warm, dry season was too small for statistical analysis.

Group size varies considerable within and among the different seasons. The largest concentration of buffalo found was a group of 140 animals that was seen once during the warm, wet season. These buffalo tend to split into smaller groups mostly at night, with the sub-groups forming again in the early mornings on their way to the daily resting sites. The mean group size during the warm, wet season was 42,1 ± 38,3 animals, which was significantly larger than that of 23,4 ± 21,6 in the cold, dry and that of 23,0 ± 23,3 in the warm, dry seasons (p<0,001).

Habitat selection

A summary of the results of the chi-square tests appears in Table 2. The hypotheses that the buffalo of the study area use the physiographic units, the plant units and veld in bad condition in proportion to their occurrence were all rejected at the level of p<0,005 level.

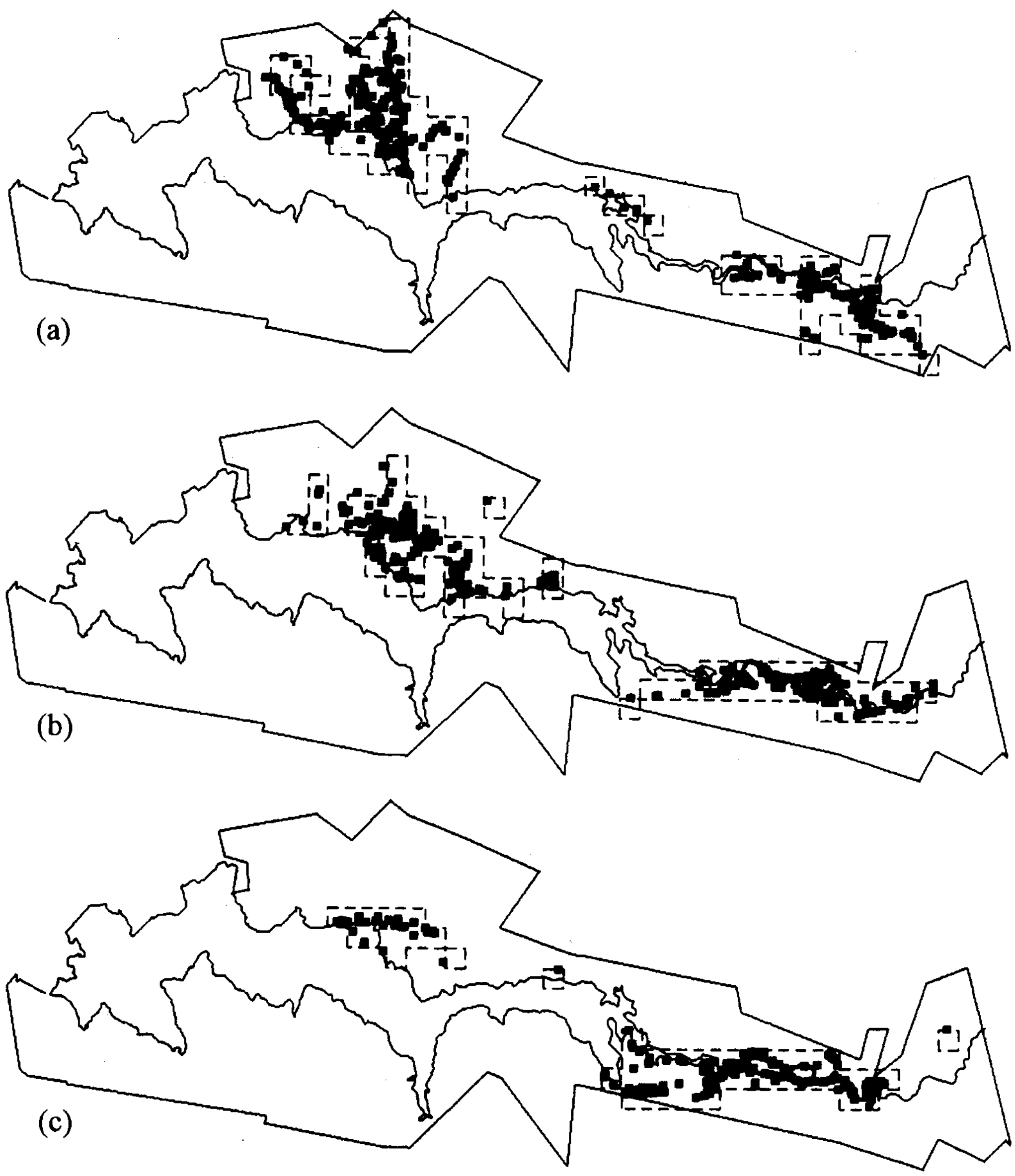

Fig. 1. The three seasonal ranges used by the buffalo in the Willem Pretorius Game Reserve in the Free State, South Africa, during 1991. Range use is based on 500 m x 500 m grid cells. The three seasons were: the warm, wet season (a), the cold, dry season (b) and the warm, dry season (c).

TABLE 2

Summary of the chi-square tests done to evaluate the hypotheses that in 1991 the buffalo in the Willem Pretorius Game Reserve of the Free State, South Africa, used the available habitat characteristics in proportion to their occurrence for different activities, analysed on reserve level (total terrestrial surface area) and buffalo range use level (P<0,005).

Hypotheses tested for:			Warm, dry season		Warm, wet season		Cold, dry season	
Buffalo activity	Habitat characteristic	Scale	χ^2–value	df	χ^2–value	df	χ^2-value	df
All activities[a]	Veld condition	Reserve	29,26	1	57,95	1	33,06	1
All activities[a]	Physiographic unit	Reserve	4309,08	5	3687,95	5	1993,57	5
All activities[a]	Plant unit	Reserve	1851,28	16	1971,44	16	1739,60	16
Grazing	Plant unit	Reserve	768,78	16	796,74	16	722,28	16
Resting/ruminating	Plant unit	Reserve	1262,70	16	917,95	16	1134,80	16
Grazing	Plant unit	Buffalo range use	498,58	15	667,67	15	499,88	15
Resting/ruminating	Plant unit	Buffalo range use	738,86	15	568,63	15	666,84	15

[a] All activities include grazing, resting/ruminating, walking, standing and drinking.

When grazing and resting/ruminating activities were included in the analysis on reserve and buffalo range level, the buffalo did not use the available habitat types in proportion to their availability ($p<0,005$). Therefore, there was clear habitat selection.

Only the riverfront and the grasslands along drainage lines physiographic units were selected for during all three seasons, while the buffalo avoided the slopes (>5°) and plateaux during all three seasons (Table 3). The lakeshore was used in proportion to availability during the warm, dry and warm, wet seasons (Table 3). Use of the plains was significantly less than expected. Within each physiographic unit the buffalo were highly selective of their use of components depending on veld condition and plant unit. Observations that buffalo avoided grazing veld in bad condition by purposefully walking through a bad patch to resume grazing when they reached the next good area, also reflect their selection against bad veld ($p<0,05$).

At reserve level the buffalo avoided all plant units of the tree and shrub veld of the ridges management unit in the warm, wet season. During the cold, dry season they used plant units ABC, DE and HI in proportion to availability, and during the warm, dry season they used plant unit HI in proportion to availability (Table 4). The use of these plant units was site specific to areas with a low incline, and did not include the whole area of each unit. Interpretation of selection of these plant units should bear in mind this site selective use. Plant units K (woody riverbanks and dry water courses) and Y (vlei grasslands) were the only plant units selected for in all three seasons (Table 4). These two plant units combined represented only 837 ha of the terrestrial surface area of the reserve (Table 1). The rest of the thornveld of the plains management unit (plant units L, MN and O) were either used more selectively or used in proportion to availability.

Habitat selection changed depending on whether analyses were done on reserve level or total buffalo range use level. For example, analysed on reserve level it was found that plant unit S was used for grazing in proportion to its occurrence during the warm, wet

TABLE 3

Simultaneous confidence intervals ($\alpha = 0{,}05$) using the Bonferroni approach for utilisation of physiographic units by the buffalo in the Willem Pretorius Game Reserve in the Free State during 1991.

Physiographic unit	*Pio*	*Pi*	Bonferroni confidence intervals for *Pi*	Use index	Selection value
Warm, dry season (z = 2,638; k = 6)					
Lakeshore	0,018	0,010	0,000 ≤P≥ 0,025	0,6	0
Plains	0,725	0,329	0,257 ≤P≥ 0,401*	0,5	-
Slopes (>5°)	0,105	0,057	0,022 ≤P≥ 0,092*	0,5	-
Plateaux	0,128	0,003	0,000 ≤P≥ 0,012*	0,0	-
Riverfront	0,021	0,530	0,454 ≤P≥ 0,606*	24,7	+
Grasslands along drainage lines	0,002	0,070	0,031 ≤P≥ 0,110*	31,1	+
Warm, wet season (z = 2,575; k = 5)					
Lakeshore	0,060	0,038	0,016 ≤P≥ 0,061	0,6	0
Plains	0,694	0,664	0,609 ≤P≥ 0,719	1,0	0
Slopes (>5°)	0,101	0,000		0,0	-
Plateaux	0,123	0,008	0,000 ≤P≥ 0,018*	0,1	-
Riverfront	0,021	0,172	0,128 ≤P≥ 0,216*	8,4	+
Grasslands along drainage lines	0,002	0,117	0,080 ≤P≥ 0,155*	54,2	+
Cold, dry season (z = 2,638; k = 6)					
Lakeshore	0,084	0,036	0,012 ≤P≥ 0,060*	0,4	-
Plains	0,676	0,563	0,499 ≤P≥ 0,627*	0,8	-
Slopes (>5°)	0,098	0,053	0,024 ≤P≥ 0,081*	0,5	-
Plateaux	0,119	0,010	0,000 ≤P≥ 0,022*	0,1	-
Riverfront	0,020	0,296	0,237 ≤P≥ 0,355	14,8	+
Grasslands along drainage lines	0,002	0,043	0,017 ≤P≥ 0,069	20,4	+

Pio = expected proportion of usage; *Pi* = actual proportion of usage * significant
Selection value: no preference (0), avoidance (-), preference (+)

TABLE 4

Simultaneous confidence intervals (α = 0,05) using the Bonferroni approach for utilisation of the different plant units by the buffalo on reserve level in the six management units identified in the Willem Pretorius Game Reserve in the Free State, South Africa, during 1991.

Plant unit	Warm, dry season (z = 2,807; k = 10)					Warm, wet season (z = 2,772; k = 9)					Cold, dry season (z = 2,913; k = 14)				
	Pio	*Pi*	Bonferroni confidence intervals for *Pi*	Use index	Selection value	*Pio*	*Pi*	Bonferroni confidence intervals for *Pi*	Use index	Selection value	*Pio*	*Pi*	Bonferroni confidence intervals for *Pi*	Use index	Selection value
The tree and shrub veld of the ridges															
ABC				0,0	-				0,0	-	0,017	0,012	-0,004 ≤P≥ 0,027	0,7	0
DE				0,0	-				0,0	-	0,018	0,031	0,006 ≤P≥ 0,056	1,7	0
F				0,0	-				0,0	-	0,024	0,000		0,0	-
G				0,0	-				0,0	-	0,016	0,000		0,0	-
HI	0,024	0,057	0,019 ≤P≥ 0,095	2,4	0	0,024	0,002	-0,004 ≤P≥ 0,008*	0,1	-	0,024	0,012	-0,004 ≤P≥ 0,027	0,5	0
The thornveld of the plains															
K	0,022	0,362	0,284 ≤P≥ 0,441*	16,6	+	0,022	0,142	0,098 ≤P≥ 0,185*	6,5	+	0,022	0,241	0,180 ≤P≥ 0,302*	11,1	+
L				0,0	-				0,0	-	0,007	0,005	-0,005 ≤P≥ 0,015	0,7	0
MN	0,020	0,037	0,006 ≤P≥ 0,068	1,8	0	0,020	0,188	0,139 ≤P≥ 0,237*	9,4	+	0,020	0,143	0,093 ≤P≥ 0,193*	7,1	+
O				0,0	-	0,066	0,115	0,076 ≤P≥ 0,155*	1,7	+	0,066	0,045	0,016 ≤P≥ 0,075	0,7	0
The grasslands of the ridges															
QR	0,113	0,020	-0,003 ≤P≥ 0,043*	0,2	-	0,113	0,008	-0,003 ≤P≥ 0,019*	0,1	-	0,113	0,005	-0,005 ≤P≥ 0,015*	0,0	-
T	0,014	0,003	-0,006 ≤P≥ 0,013*	0,2	-				0,0	-	0,014	0,007	-0,005 ≤P≥ ,019	0,5	0
The grasslands of the plains on sandy soil															
U	0,282	0,232	0,163 ≤P≥ 0,300	0,8	0	0,282	0,014	-0,001 ≤P≥ 0,029*	0,1	-	0,282	0,081	0,042 ≤P≥ 0,120*	0,3	-
V				0,0	-				0,0	-	0,031	0,000		0,0	-
The grasslands of the plains on clay soil															
S	0,083	0,003	-0,006 ≤P≥ 0,013*	0,0	-	0,083	0,077	0,044 ≤P≥ 0,110	0,9	0	0,083	0,031	0,006 ≤P≥ 0,056*	0,4	-
W	0,170	0,030	0,002 ≤P≥ 0,058*	0,2	-	0,170	0,067	0,036 ≤P≥ 0,098*	0,4	-	0,170	0,069	0,033 ≤P≥ 0,105*	0,4	-
X	0,018	0,017	-0,004 ≤P≥ 0,038	1,0	0				0,0	-	0,018	0,007	-0,005 ≤P≥ 0,019	0,4	0
The vlei grasslands															
Y	0,075	0,238	0,169 ≤P≥ 0,308*	3,2	+	0,075	0,387	0,326 ≤P≥ 0,447*	5,2	+	0,075	0,310	0,244 ≤P≥ 0,376*	4,2	+

Pio = expected proportion of usage; *Pi* = actual proportion of usage   * significant   Selection value: no preference (0), avoidance (-), preference (+)

season (selection value = 0), and was avoided by the buffalo during the warm, dry and the cold, dry season (selection value = -) (Table 4). However, analysed on range level plant unit S was positively selected for grazing during the warm, wet season and was used proportionally to its occurrence during the cold, dry season, while still avoided during the warm, dry season (Table 5). On range use level, plant unit V did not occur as a potential resource used by the buffalo. Since habitat selection by the buffalo in the study area on range use level was deemed more meaningful, only the analyses on range level were included in the results as shown in Tables 5 and 6.

Habitat selection for the two activities, grazing and resting/ruminating as determined on total buffalo range use level, were closely linked for most of the plant units as is shown by the corresponding selection values in Tables 5 and 6. However, plant units K and Y were positively selected for grazing and resting/ruminating in all three seasons, except that the buffalo did not show any preference or avoidance (selection value = 0 in Table 6) to rest/ruminate in the vlei grasslands (plant unit Y) during the warm, dry season. They did, however, clearly select to rest/ruminate in plant unit MN (selection value = +) during the warm, wet and the cold, dry season (Table 6). During the latter season the buffalo used plant units ABC and O for grazing in proportion to their occurrence (selection value = 0 in Table 5), but avoided these plant units for resting/ruminating during the same season (selection value = - in Table 6). In the grasslands of the plains on clay soil plant unit S was selected for grazing (selection value = + in Table 5) during the warm, wet season. However, the rest of the grasslands of the plains on clay soil (plant units W and X) were mostly avoided by the buffalo for grazing and resting/ruminating (selection values = - in Tables 5 and 6), except for plant unit X which was used for grazing in proportion to its occurrence (selection value = 0 in Table 5) during the warm, dry season. In the grasslands of plains on sandy soil plant unit V was not used by the buffalo for grazing or resting/ruminating, and plant unit U was used for grazing and resting/ruminating only in proportion to its occurrence (selection value = 0 in Tables 5 and 6). The grasslands of the ridges (plant units QR and T) were avoided for grazing and

TABLE 5

Simultaneous confidence intervals (α = 0,05) using the Bonferroni approach for utilisation of the different plant units for grazing by the buffalo analysed on buffalo range use level in the six management units identified in the Willem Pretorius Game Reserve in the Free State, South Africa, during 1991.

Plant unit	Warm, dry season (z = 2,807; k = 10)					Warm, wet season (z = 2,772; k = 9)					Cold, dry season (z = 2,913; k = 14)				
	Pio	*Pi*	Bonferroni confidence intervals for *Pi*	Use index	Selection value	*Pio*	*Pi*	Bonferroni confidence intervals for *Pi*	Use index	Selection value	*Pio*	*Pi*	Bonferroni confidence intervals for *Pi*	Use index	Selection value
The tree and shrub veld of the ridges															
ABC	0,028	0,000		0,00	-	0,028	0,000		0,00	-	0,028	0,013	-0,013 ≤P≥ 0,039	0,46	0
DE	0,030	0,000		0,00	-	0,030	0,000		0,00	-	0,030	0,013	-0,013 ≤P≥ 0,039	0,43	0
F	0,040	0,000		0,00	-	0,040	0,000		0,00	-	0,040	0,000		0,00	-
G	0,026	0,000		0,00	-	0,026	0,000		0,00	-	0,026	0,000		0,00	-
HI	0,040	0,035	-0,004 ≤P≥ 0,074	0,86	0	0,040	0,005	-0,008 ≤P≥ 0,018*	0,12	-	0,040	0,006	-0,012 ≤P≥ 0,025*	0,16	-
The thornveld of the plains															
K	0,036	0,289	0,192 ≤P≥ 0,386*	8,00	+	0,036	0,108	0,050 ≤P≥ 0,166*	2,99	+	0,036	0,234	0,138 ≤P≥ 0,329*	6,47	+
L	0,012	0,000		0,00	-	0,012	0,000		0,00	-	0,012	0,000		0,00	-
MN	0,033	0,023	-0,009 ≤P≥ 0,055	0,70	0	0,033	0,160	0,091 ≤P≥ 0,228*	4,80	+	0,033	0,078	0,017 ≤P≥ 0,139	2,34	0
O	0,110	0,000		0,00	-	0,110	0,085	0,032 ≤P≥ 0,137	0,77	0	0,110	0,058	0,005 ≤P≥ 0,112	0,53	0
The grasslands of the ridges															
QR	0,109	0,017	-0,011 ≤P≥ 0,045*	0,16	-	0,109	0,000		0,00	-	0,109	0,000		0,00	-
T	0,055	0,006	-0,010 ≤P≥ 0,022*	0,10	-	0,055	0,000		0,00	-	0,055	0,000		0,00	-
The grasslands of the plains on sandy soil															
U	0,162	0,254	0,161 ≤P≥ 0,347	1,57	0	0,162	0,019	-0,007 ≤P≥ 0,044*	0,12	-	0,162	0,052	0,002 ≤P≥ 0,102*	0,32	-
V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
The grasslands of the plains on clay soil															
S	0,023	0,006	-0,010 ≤P≥ 0,022*	0,25	-	0,023	0,122	0,061 ≤P≥ 0,183*	5,37	+	0,023	0,026	-0,010 ≤P≥ 0,062	1,14	0
W	0,182	0,040	-0,002 ≤P≥ 0,083*	0,22	-	0,182	0,056	0,013 ≤P≥ 0,100*	0,31	-	0,182	0,065	0,009 ≤P≥ 0,121*	0,36	-
X	0,022	0,017	-0,011 ≤P≥ 0,045	0,80	0	0,022	0,000		0,00	-	0,022	0,000		0,00	-
The vlei grasslands															
Y	0,084	0,312	0,213 ≤P≥ 0,411*	3,72	+	0,084	0,446	0,353 ≤P≥ 0,539*	5,32	+	0,084	0,455	0,342 ≤P≥ 0,567*	5,42	+

Pio = expected proportion of usage; *Pi* = actual proportion of usage   * significant   Selection value: no preference (0), avoidance (-), preference (+)

TABLE 6

Simultaneous confidence intervals (α = 0,05) using the Bonferroni approach for utilisation of the different plant units for resting/ruminating by the buffalo analysed on buffalo range use level in the six management units identified in the Willem Pretorius Game Reserve in the Free State, South Africa, during 1991.

Plant nodum	Warm, dry season (z = 2,807; k = 10)					Warm, wet season (z = 2,772; k = 9)					Cold, dry season (z = 2,913; k = 14)				
	Pio	*Pi*	Bonferroni confidence intervals for *Pi*	Use index	Selection value	*Pio*	*Pi*	Bonferroni confidence intervals for *Pi*	Use index	Selection value	*Pio*	*Pi*	Bonferroni confidence intervals for *Pi*	Use index	Selection value
The tree and shrub veld of the ridges															
ABC	0,028	0,000		0,00	-	0,028	0,000		0,00	-	0,028	0,000		0,00	-
DE	0,030	0,000		0,00	-	0,030	0,000		0,00	-	0,030	0,019	-0,016 ≤P≥ 0,054	0,62	0
F	0,040	0,000		0,00	-	0,040	0,000		0,00	-	0,040	0,000		0,00	-
G	0,026	0,000		0,00	-	0,026	0,000		0,00	-	0,026	0,000		0,00	-
HI	0,040	0,120	0,026 ≤P≥ 0,215	3,00	0	0,040	0,000		0,00	-	0,040	0,000		0,00	-
The thornveld of the plains															
K	0,036	0,578	0,435 ≤P≥ 0,721*	16,01	+	0,036	0,239	0,135 ≤P≥ 0,343*	6,63	+	0,036	0,358	0,236 ≤P≥ 0,481*	9,93	+
L	0,012	0,000		0,00	-	0,012	0,000		0,00	-	0,012	0,000		0,00	-
MN	0,033	0,048	-0,014 ≤P≥ 0,110	1,45	0	0,033	0,291	0,180 ≤P≥ 0,401*	8,74	+	0,033	0,321	0,201 ≤P≥ 0,440*	9,65	+
O	0,110	0,000		0,00	-	0,110	0,060	0,002 ≤P≥ 0,118	0,54	0	0,110	0,000		0,00	-
The grasslands of the ridges															
QR	0,109	0,012	-0,020 ≤P≥ 0,044*	0,11	-	0,109	0,000		0,00	-	0,109	0,000		0,00	-
T	0,055	0,000		0,00	-	0,055	0,000		0,00	-	0,055	0,000		0,00	-
The grasslands of the plains on sandy soil															
U	0,162	0,205	0,088 ≤P≥ 0,322	1,27	0	0,162	0,000		0,00	-	0,162	0,000		0,00	-
V	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
The grasslands of the plains on clay soil															
S	0,023	0,000		0,00	-	0,023	0,009	-0,014 ≤P≥ 0,031	0,38	0	0,023	0,047	-0,007 ≤P≥ 0,101	2,07	0
W	0,182	0,000		0,00	-	0,182	0,017	-0,015 ≤P≥ 0,049*	0,09	-	0,182	0,038	-0,011 ≤P≥ 0,087*	0,21	-
X	0,022	0,000		0,00	-	0,022	0,000		0,00	-	0,022	0,000		0,00	-
The vlei grasslands															
Y	0,084	0,036	-0,018 ≤P≥ 0,090	0,43	0	0,084	0,385	0,266 ≤P≥ 0,503*	4,58	+	0,084	0,217	0,111 ≤P≥0,323*	2,59	+

Pio = expected proportion of usage; *Pi* = actual proportion of usage   * significant   Selection value: no preference (0), avoidance (-), preference (+)

resting/ruminating (selection value = - in Tables 5 and 6) during all three seasons.

Discussion

Sinclair (1977) showed that buffalo densities depend on rainfall, which acts through the available food supply. Based on the long-term mean annual rainfall of 576 mm for the Willem Pretorius Game Reserve the crude density of 1,8 buffalo/km^2 in the reserve is approximately what would be expected from Sinclair's (1977) regression equation of mean crude buffalo density/km^2 to mean annual rainfall (mm).

In the study by Funston (1994) a small difference was found between the buffalo range density of 2,07 buffalo/km^2 and the crude density of 2,16 buffalo/km^2 for the Sabi Sand Wildtuin, suggesting that suitable buffalo habitat was relatively uniformly distributed throughout the area. In the present study, the localised occurrence of suitable buffalo habitat in the reserve is emphasized by the high range density of 5,7 buffalo/km^2 compared to the low crude density, and the total buffalo range size which covers only 31% of the total terrestrial surface area of the reserve.

The buffalo range use behaviour and density in the Willem Pretorius Game Reserve should be interpreted in the light of the reserve's long history of severe overgrazing (Winterbach & Winterbach, In prep.). At the time of the present study the veld condition in all the management units ranged from intermediate to poor, with Increaser IIc grass species mostly dominant (Appendix A). The reserve was overstocked with grazers by approximately 24% of the maximum stocking rate of herbivore grazers calculated in 1991 during a good rainfall cycle, and the buffalo population exceeded the recommended buffalo stocking rate by approximately 47 L.S.U.

Reduction of the buffalo population in the Willem Pretorius Game Reserve to the recommended buffalo stocking rate of 82,2 L.S.U., as based on the standing plant biomass available to the buffalo in their two key habitat areas (plant units K and Y) (Winterbach & Winterbach, In prep.), will however yield a density of approximately 3,0 buffalo/km^2 in their area of range use. This buffalo range density is more in line with that found by Funston (1994) for buffalo in a similar rainfall area (between 700 and 550 isohyte) which falls within their historic distribution. The recommended stocking rate for buffalo in the Willem Pretorius Game Reserve indicates that even with widespread veld deterioration there are still pockets of good quality grazing available which are able to sustain a fairly high density of buffalo.

Two main behavioural adjustments made by the buffalo in the present study can explain their ability to sustain themselves in their particular degraded environment. These are changes in the range use size and the fusion-fission activity patterns of the herd. Expansion or contraction of the range size during the different seasons depends on the habitat types and available food and water supply in the area (Conybeare 1980; Sinclair 1977; Taylor 1989; Funston 1992). Most of the game animals in the Willem Pretorius Game Reserve are within 2 to 3 km of permanent water throughout the year, suggesting that the buffalo range use adaptations were influenced mainly by the food supply. The most crucial habitat for any herbivore is that used during the most unfavourable season (Sinclair 1977). In the present study this is the warm, dry season when plant unit K in the thornveld of the plains and plant unit Y in the vlei grasslands were the only areas which were specifically selected for grazing by the buffalo. The importance of plant units K and Y to the buffalo were further emphasised with the contraction of the buffalo range during the cold, dry season which caused the concentration of the buffalo along the woody riverbanks and vlei grasslands along the Sand River (Fig. 1). However, plant units K and Y were also selected for grazing and resting/ruminating during the warm, wet season. This meant that the critical dry season habitat represented by plant units K and Y in the study area were in effect grazed by buffalo all year round.

Wiltshire (1978) showed that the vlei grasslands in the Willem Pretorius Game Reserve has the highest total herbage yield throughout the year, with production of a persistent green fraction with crude protein fluctuating between 6,25% and 11,25%. The occurrence of a high leaf:stem ratio and shade-loving, palatable grass species such as *Panicum maximum*, which has a higher herbage production when growing underneath *Acacia* species (Smit & Rethman 1989), may have influenced the buffalo's selection of plant unit K for grazing during all three seasons. However, *P. maximum* reacts negatively to heavy grazing and its production decreases under long, continuous grazing pressure (Smit & Rethman 1989).

The second behavioural adjustment of buffalo to environmental degradation in the study area occurred through changes in group size. The fusion-fission activity pattern in a buffalo herd can be related either to herd size where the larger herds divide more frequently than smaller ones (Prins 1987), or to season where splitting of the herd depends on food distribution and abundance (Sinclair 1977; Taylor 1989). The limited and patchy distribution of the food supply in the woody vegetation types of the study area impelled the splitting of the herd into smaller groups when grazing. The function of smaller buffalo group sizes would mainly be to allow better grazing opportunities for specific individuals (Mloszewski 1983) and to minimise trampling of the relatively small grazing areas. The wide range of group sizes observed in the present study during all three seasons was caused by the fact that different groups of buffalo congregated in the early mornings on their way to the daytime resting sites.

A few main established rotational routes exist between different feeding and resting sites within the buffalo range. With the buffalo always close to water the distances moved are related to the distribution of the food supply and the availability of daytime resting sites. The percentage of time spent walking during the warm, wet season was the same as during the cold, dry season (Winterbach & Bothma 1998), but the mean 24-hour distance travelled was longer during the cold, dry season even though the buffalo range contracted owing to the concentration of the buffalo on the vlei grasslands and riverbanks. This is so because walking was interspersed with grazing during the warm, wet season, resulting in shorter distances travelled. The buffalo spent significantly more time resting/ruminating during the night in the cold, dry season, when they seek refuge underneath tree cover from the extreme cold (Winterbach & Bothma 1998). This could force them to travel longer distances in search of the most favourable food during the remainder of the 24 hours available for grazing. The same reason can also explain the longer distances travelled during the day compared to the night.

Conclusions

In the Willem Pretorius Game Reserve the buffalo adjusted its range use, movements and habitat selection to the critical environmental changes experienced in the reserve. Four main factors appear to influence habitat selection. These are: 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. Plant units K (woody riverbanks and dry watercourses) and Y (vlei grasslands) were used most intensively all year round and are thus key habitat types for the buffalo. They are also the keys to the successful long-term management of the buffalo population in this sub-optimal habitat.

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CHAPTER 7

Management of a population of disease-free Cape buffalo *Syncerus caffer caffer* in a sub-optimal habitat

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The successful breeding of disease-free Cape buffalo *Syncerus caffer caffer* in the Willem Pretorius Game Reserve of the Free State, South Africa, requires an intensive management plan, because the mixed-sourveld habitat of the reserve is sub-optimal for buffalo. The veld condition, grazing capacity and stocking rate of game in the reserve were investigated, and compared between a good rainfall year (1991) and a drought year (1992). Veld condition in six management units ranged from medium to poor, with grass species composition changing towards Increaser IIc species. In the thornveld of the plains and vlei grasslands, both areas strongly selected for by the buffalo, the veld condition was extremely poor with encroachers contributing to the low ecological index. The grazing capacity in these two areas decreased by 40% during the drought year. The low grazing capacity of the reserve during 1992 resulted from only one year of poor rainfall when 58% of the long-term mean annual rainfall was recorded. This condition was aggravated by the long history of medium to severe overgrazing. A maximum stocking rate of 82,2 L.S.U. for the buffalo was determined from their range use. Failure to implement management recommendations in 1991 and 1992 led to the death of 53 buffalo from starvation and hypothermia by September 1992. The proposed management strategy focuses on protecting the limited suitable buffalo habitat available in the reserve by reducing competition with other grazers and the continuation of the veld monitoring programme initiated during this study.

Key words: Cape buffalo, grazing capacity, management, *Syncerus caffer*, veld condition

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Introduction

The official conservation objectives for the Willem Pretorius Game Reserve are the preservation of biodiversity, and the maintenance of the natural ecosystems present and an optimum number of indigenous plant and animal species and their habitats (Oberholzer 1966; Borquin 1973). One of the aims for the reserve is to maintain viable populations of black wildebeest *Connochaetes gnou*, square-lipped rhinoceros *Ceratotherium simum* and disease-free Cape buffalo *Syncerus caffer caffer* as core breeding herds for redistribution.

To successfully maintain large herbivores in a confined and relatively small conservation area without damaging the habitat requires an intensive management plan, with close monitoring of the grazing capacity (Novellie, Hall-Martin & Joubert 1991; Bothma 1996). When herbivores are forced to forage continuously in a limited array of vegetation communities, the risk of veld deterioration is high. In addition, marked environmental fluctuations, especially rainfall-induced fluctuations in the food supply for herbivores, increase the difficulty of managing such a system, and require close monitoring of the grazing capacity and setting of realistic stocking rates of game (Novellie, Hall-Martin & Joubert 1991; Van Rooyen, Bredenkamp & Theron 1996).

Veld management is usually extremely complex, but it is especially so in conservation areas where the maintenance of species diversity is generally a management goal. Each plant community possesses a unique plant species composition that is mainly a result of the specific environmental composition of its habitat. The specific potential of each plant community to act as a habitat for herbivores, its grazing capacity and its resilience to utilisation and drought depends on the combined influence of all environmental factors present and the effect of past management practices. Therefore, each plant community will react differently to given vegetation management practices and some will show signs of deterioration sooner under a certain management regime than others (Brown & Bredenkamp 1994). The basic approach to effective veld management therefore relies on adapting game stocking rates to provide for short-term fluctuations in the grazing capacity. Moreover, the smaller the area, the more intensively it must be managed (Van Rooyen, Bredenkamp & Theron 1996), and this applies to the vegetation too.

Roberts (1963) and Müller (1972) have expressed concern over the retrogression in the veld condition of the Willem Pretorius Game Reserve prior to 1973. Although Borquin (1973), Vorster (1989) and Vrahimis, Vorster & Terblanche (1989) all provided preliminary grazing capacity guidelines and recommended stocking rates of game for the reserve, few of their management recommendations were ever implemented. The result was that when the present study was done the reserve had been overstocked with game for at least 18 years. Unfortunately the probable damage to the vegetation cannot be determined, as no detailed veld monitoring was done in the reserve prior to the present study.

The buffalo population in the reserve was highly selective for certain habitat types, influenced by the patchy distribution and seasonal changes in the food supply, the availability of cover for daytime resting areas and protection against low night temperatures and frost. This resulted in the buffalo using a year-round range size of 2 700 ha, which covers only 31% of the total terrestrial surface area of the reserve (Winterbach, Winterbach & Theron, In prep.). During the warm, dry season the buffalo range shrank to a mere 1 175 ha, which is only 13,5% of the total terrestrial surface area of the reserve. The critical environmental factors required by the buffalo in the study area, and their selective use of certain habitat types requires very specific management practices.

The aim of this paper was to determine a buffalo stocking rate for the Willem Pretorius Game Reserve based on the grazing capacity, veld condition and stocking rate of the game present in the reserve during a good rainfall year in 1991 compared to a poor rainfall year in 1992. A management strategy for these buffalo is also formulated.

Study area

The Willem Pretorius Game Reserve (28° 16-21'S; 27° 07-23'E) is situated around the Allemanskraal Dam in the Sand River, approximately 140 km northeast of Bloemfontein in the Free State province of South Africa. The total surface area of the reserve is 12 082 ha, of which the dam comprises 2 771 ha when full. The effective game habitat area is approximately 8 682 ha. This habitat is elongated, being 23 km long with a varying width of 2 to 8 km.

Summers are warm with a few hot days (absolute and mean daily maximum temperatures for January are 37,8°C and 30,6°C, respectively), while winters are cold (absolute and mean daily minimum temperatures for June are -6,7°C and -0,4°C, respectively). A long thermic summer with mean daily temperatures of more than 16,4°C occurs for seven months of the year from October to April (Müller 1986). Severe frost occurs during the winter. The area is semi-arid with a 31-year mean annual rainfall of 576 mm, with the highest mean rainfall in January (97,7 mm) and the lowest in July (6,3 mm). Precipitation occurs mostly as thunderstorms.

The topography is mainly flat grass plains (Müller 1986). A series of dolerite and sandstone ridges north of the Allemanskraal Dam and Sand River stretch from east to west along the river, and are interspersed by virtually flat plains. Flat areas also occur on the plateaux of the ridges. The reserve lies on the Beaufort Series of the Karoo System, in the Moist Cool Highveld Grassland (39), being one of only five principal conservation areas for this grassland type (Bredenkamp & Van Rooyen 1996). Six management units were identified in the reserve, using the main vegetation types and the vegetation units of Müller (1986) as a guideline: the tree and shrub veld of the ridges, the thornveld of the plains, the grasslands of the ridges, the grasslands of the plains on sandy soil, the grasslands of the plains on clay soil and the vlei grasslands (Figure 1). The communities of rocky outcrops were excluded as a management unit.

Sixteen large herbivore species occurred in the Willem Pretorius Game Reserve. At the time of the study a single herd of 160 buffalo were present. The population structure in April 1991 consisted of 102 adults with a 1:3 male to female sex ratio, 28 sub-adults (1 to 2 years old) and 27 calves (≤ 1 year old). Caracals *Felis caracal* were the largest predator present in the reserve.

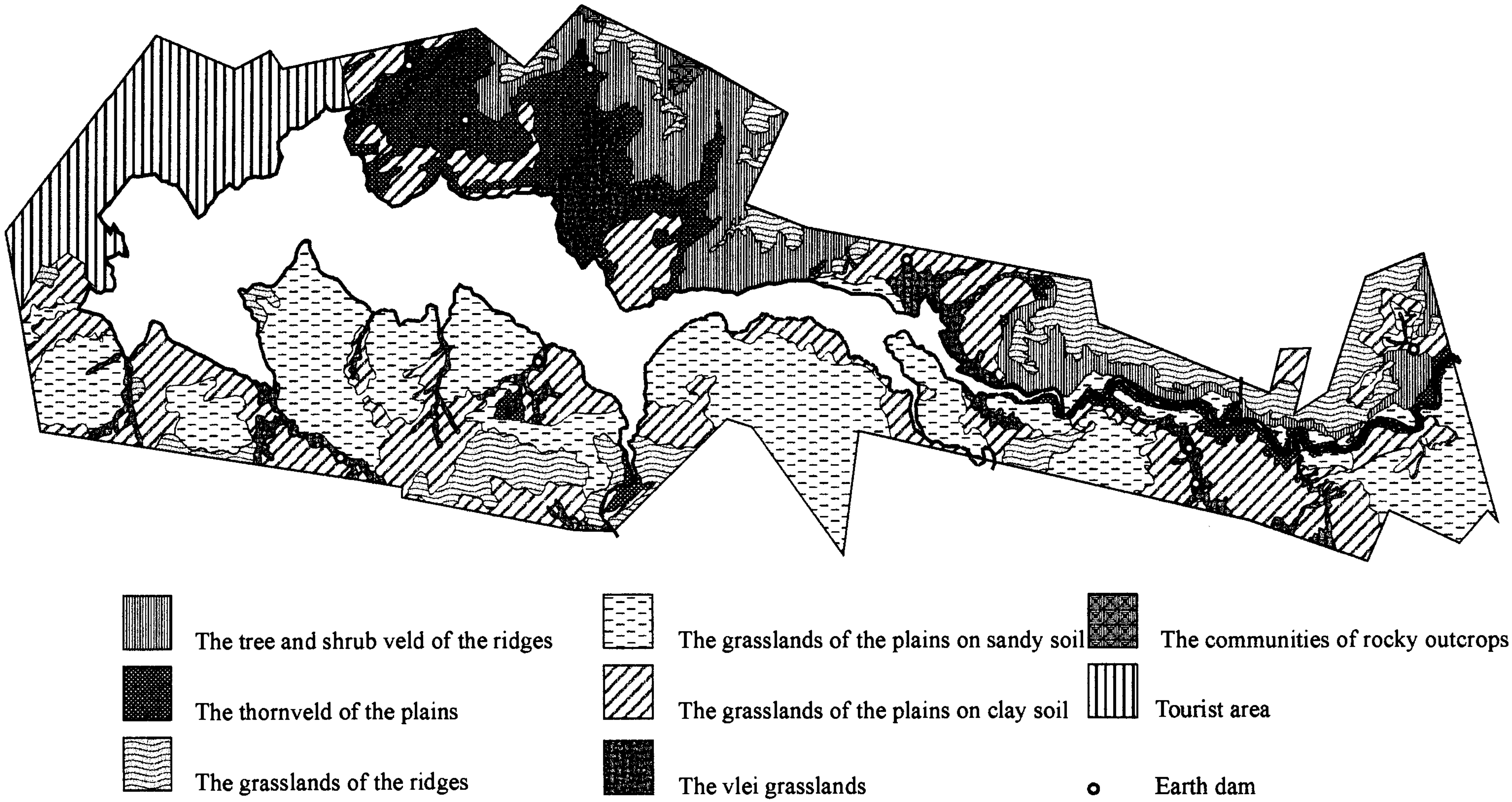

Figure 1 The six management units identified in the Willem Pretorius Game Reserve, Free State, using the main vegetation types and the vegetation units of Müller (1986) as a guideline.

Methods

Veld condition assessment

The intensive vegetation survey that was done from February to May 1991 was used as the basis of future veld monitoring in the reserve. Vegetation data were collected in 47 stratified random sample sites per plant unit. The centres of these sites were permanently marked with a metal rod driven into the ground. Line transects and quadrants were placed following Scoggings (1988). The dry-weight-rank method of t'Mannetje & Haydock (1963) as modified by Jones & Hargreaves (1979) was combined with the comparative yield method of Haydock & Shaw (1975) to estimate the above-ground standing plant biomass composition simultaneously with the herbaceous yield. The latter is defined here as the dry mass of total above-ground herbaceous vegetation per unit area. Twenty-four of the original 47 sample sites were re-surveyed from April to May 1992 to determine the standing plant biomass.

During the 1991 survey the step-point method was used at 35 of the 47 sample sites to obtain a veld condition assessment by estimating the percentage species composition (Mentis 1981). Veld condition for each of the management units identified was determined by the Ecological Index Method of Tainton, Edwards & Mentis (1980) as applied by Bredenkamp ([1]1986 pers. comm.). To do so the grass species were categorised as increasers or decreasers for the different management units, based on grazing degradation models for the Winburg District ([2]Van der Westhuizen 1996 pers. comm.), using the Integrated System for Plant Dynamics (ISPD) software.

The grazing capacity of each management unit was calculated according to Meissner, Hofmeyer, Van Rensburg & Pienaar (1983), considering the standing biomass of grass species present as determined during the 1991 veld condition assessment (Table 4). The following values were used in the calculation:

The proportion of the standing plant biomass used:	30%[3]
The digestible energy:	52%[2]
Gross energy of the grass:	18,40 MJ/kg

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[1] Bredenkamp, G. 1986. Ecotrust CC. P.O. Box 2553, Monument Park, Pretoria, South Africa, 0105.
[2] Van der Westhuizen, M.E. 1996. Department of Agriculture, Private Bag X01, Glen, South Africa, 9360.
[3] Agricultural norms for the Winburg region (De Waal, H.O. 1991. Department of Agriculture, Private Bag X01, Glen, South Africa, 9360).

Metabolizable energy of the grass:	82%
Energy requirements of the game:	75 MJ/L.S.U./day
The number of grazing days needed until the new growth:	180

The long and short-term grazing capacities of the reserve were calculated according to the method of Coe, Cumming & Phillipson (1976) using the rainfall for the period July 1991 to June 1992 (332 mm) to determine the short-term grazing capacity.

The estimated game numbers present on the study area in December 1991, after the calving season, were used here to determine the actual stocking rate for grazers (Winterbach 1992a). Bredenkamp's (1986 pers. comm.) classification of game was used to reflect their relative potential for defoliation and any possible selective grazing of the vegetation.

Determination of a buffalo stocking rate

The size (ha) of the plant units in the potential buffalo habitat, based on those parts of the plant units in the year-round range of the buffalo (Winterbach, Winterbach & Theron, In prep.) that have not yet degraded to Karoo encroachment, was determined with a planometer from 1:10 000 aerial photographs. A preliminary buffalo stocking rate for the reserve was then calculated from the grazing capacity of the various potential buffalo habitats. It was assumed that the buffalo used 40% of the grazing capacity of their range. Calculation of the recommended buffalo stocking rate (Table 4) was based on the 1991 grazing capacity of the critical dry season buffalo habitat, represented by plant units K (woody riverbanks and dry water courses) and Y (vlei grasslands) (Winterbach, Winterbach & Theron, In prep.), excluding areas within these two plant units with Karoo encroachment. For this calculation the proportion of standing plant biomass utilised by other game was assumed to be 25% in the two plant units.

Results

Veld condition assessment

In Table 1 the mean standing plant biomass (kg/ha) and grazing capacity (ha/L.S.U.) of each vegetation unit in the different management units at the end of the growing season

Table 1 The grazing capacity (ha/L.S.U.) of the Willem Pretorius Game Reserve in the Free State as calculated from the mean standing plant biomass (kg/ha) in each of the vegetation units identified by Müller (1986) in the different management units during April 1991 and April 1992

Management unit and vegetation units	Surface area in hectares	Standing plant biomass (kg/ha) 1991	Standing plant biomass (kg/ha) 1992	Grazing capacity 1991		Grazing capacity 1992	
				L.S.U.	ha/L.S.U.	L.S.U.	ha/L.S.U.
Tree and shrub veld of the ridges					**6,3**		**10,5**
A	149	240	120	6	23,9	4	39,8
D	67	995	497	12	5,8	7	9,6
E	91	868	434	14	6,6	8	11,0
F	211	415	208	15	13,8	9	23,0
G	136	1161	580	28	4,9	17	8,2
H	210	1696	848	62	3,4	37	5,6
Total	864	-	-	137	-	82	-
Thornveld of the plains					**7,6**		**19,6**
K	252	794	397	35	7,2	21	12,0
M	97	983	492	17	5,8	10	9,7
N	77	459	229	6	12,5	4	20,8
O	575	742	137	74	7,7	16	34,9
Total	1001	-	-	132	-	51	-
Grasslands of the ridges					**6,6**		**12,1**
R	978	930	441	159	6,2	90	10,8
T	119	280	56	6	20,5	1	85,4
Total	1097	-	-	165	-	91	-
Grasslands of the plains on sandy soil					**6,9**		**8,8**
U	2449	829	511	354	6,9	262	9,4
V	267	896	828	42	6,4	46	5,8
Total	2716	-	-	396	-	308	-
Grasslands of the plains on clay soil					**10,2**		**13,5**
S	724	683	611	86	8,4	93	7,8
W	1480	542	255	140	10,6	79	18,7
X	113	34	7	1	168,7	0	682,8
Total	2317	-	-	227	-	172	-
Vlei grasslands					**8,4**		**14,0**
Y	648	1369	685	77	8,4	46	14,0
Total	648	-	-	77	-	46	-
TOTAL	8643	-	-	1134	7,6	750	11,5

for 1991 and 1992 are compared. The overall grazing capacity of the reserve decreased from 1 134 L.S.U. in 1991 to only 750 L.S.U. in 1992. In the thornveld of the plains and the vlei grasslands, the grazing capacity in 1992 decreased by approximately 40% (Table 1). Both these management units were strongly selected for by the buffalo throughout the year (Winterbach, Winterbach & Theron, In prep.). In addition, these two units also obtained the lowest ecological index values for any of the management units in the reserve in 1991 (Table 2).

The decrease in grazing capacity can be attributed to poor rainfall. The total rainfall of 509 mm for July 1990 to June 1991 was 12% lower than the long-term annual mean rainfall of 576 mm for the area. However, in the 4 months from December 1990 to March 1991 some 459 mm rain fell, resulting in relatively high standing plant biomass during the 1991 veld condition assessment. In comparison, the following annual rainfall cycle (July 1991 to June 1992) yielded only 332 mm, which was only 58% of the long-term annual mean rainfall (Figure 2).

The 1991 ecological index values for each management unit (Table 2) provides an indication of the veld condition at the time of the study. By 1991 overutilised and patch-selected areas in the reserve, which consist of pioneer communities, formed an estimated 1 467 ha. Karoo element invasion with *Felicia muricata* and *Pentzia globosa* occurred in 1 051 ha of the grassveld communities on sandy and clay soils (vegetation units U, V and W). The grass species composition (percentage frequency) and percentage contribution to standing plant biomass (Table 2) showed the following veld condition assessments in the different management units:

The tree and shrub veld of the ridges

The veld in this management unit was in an intermediate condition, but overutilisation was already changing the balance in favour of Increaser IIc species. *Elionurus muticus* and *Aristida congesta* are both unpalatable grasses which were dominant in terms of plant biomass (11,5% and 11,3% of the plant biomass, respectively) (Appendix A).

The thornveld of the plains

The high incidence of Increaser IIc species (62,7% frequency) indicates that the area was being severely overutilised. This unit having the second lowest ecological index in the reserve also reflected this trend.

Table 2 The percentage frequency and the percentage contribution to the standing plant biomass of key grass species from the different ecological groups (Decreasers and Increasers), excluding encroachers and bare soil, and the ecological index values for the six management units identified in the Willem Pretorius Game Reserve in the Free State for April 1991

Management unit	Decreasers		Increasers I		Increasers IIb		Increasers IIc		Ecological Index
	Frequency	Plant biomass	Frequency	Plant biomass	Frequency	Plant biomass	Frequency	Plant biomass	
The tree and shrub veld of the ridges	36,26	34,81	13,54	6,61	12,94	21,67	37,25	36,91	496
The thronveld of the plains	23,74	33,90	4,20	6,00	9,35	18,86	62,71	41,24	344
The grasslands of the ridges	23,58	22,51	4,67	12,49	16,97	24,86	54,78	40,14	358
The grasslands of the plains on sandy soil	31,43	24,06	2,90	9,15	31,87	41,93	33,80	24,86	454
The grasslands of the plains on clay soil	22,54	18,45	5,65	15,89	32,51	44,81	39,29	20,85	375
The vlei grasslands	4,97	8,76	0,00	2,42	9,32	26,25	85,71	62,57	173

Ecological Index: 0-399, poor condition; 400-600, intermediate condition; 601-1000, good condition (Van Rooyen, Bredenkamp & Theron 1996)

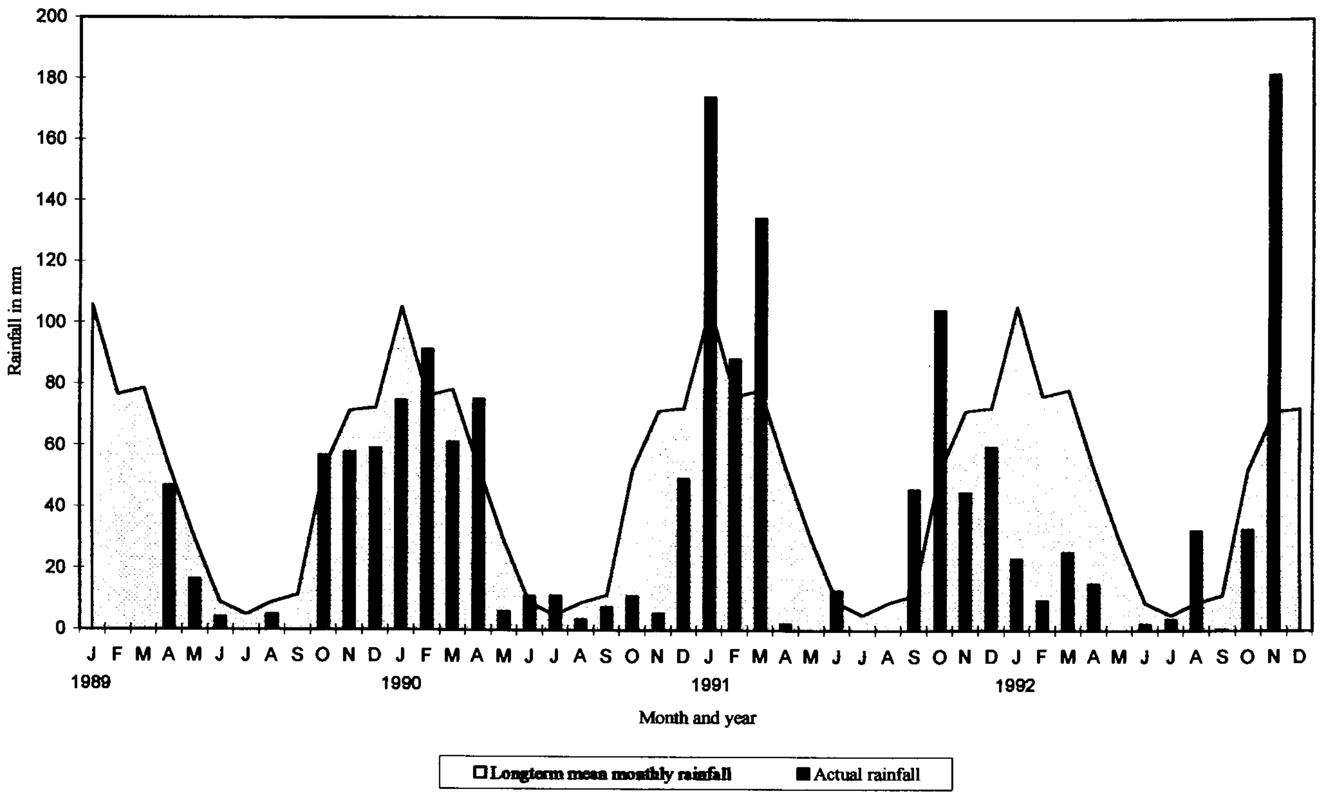

Figure 2 Actual rainfall recorded at Willem Pretorius Game Reserve in the Free State between 1989 and 1992, and a comparison with the long-term mean monthly rainfall recorded between 1961 and 1992. The rainfall reflects grazing conditions prevailing during the study period from October 1990 to September 1991

The grasslands of the ridges

The high incidence of Increaser IIc species (54,7% frequency) indicates severe overutilisation. *Aristida congesta* and *A. junciformis* were the dominant grasses in terms of plant biomass (19,3% and 14,5% of the plant biomass, respectively) (Appendix A).

The grasslands of the plains on sandy soil

The ecological index values of sample sites in this management unit varied from a high of 718 to a low of 182, with the lowest veld condition on areas ploughed in the past, before the development of the reserve. The high incidence of Increaser IIb (31,8% frequency) and Increaser IIc (33,8% frequency) species, and the presence of encroachers such as *Chrysocoma tenuifolia*, *Felicia muricata* and *Pentzia globosa* contributed to low veld condition indices. *Setaria sphacelata* was most abundant here (19,0% frequency), with *Elionurus muticus* and *Eragrostis chloromelas* the dominant grasses in terms of plant biomass (16,2% and 13,3% of the plant biomass, respectively) (Appendix A).

The grasslands of the plains on clay soil

The high incidence of Increaser IIb (32,5% frequency) and Increaser IIc (39,3% frequency) species indicate severe overutilisation, with encroachers such as *Felicia muricata*, *Lycium horridum*, *Pentzia globosa* and *Salsola glabrescens* contributing to the low ecological index. *Eragrostis chloromelas*, which has an intermediate palatability, was the dominant grass in this management unit in terms of both frequency (14,2% frequency of all plant species recorded in the unit) and plant biomass (21,7%) (Appendix A).

The vlei grasslands

The grasslands in vlei areas and along natural drainage areas, through which run-off water flows to larger streams and eventually to the Allemanskraal Dam and the Sand River, represent this management unit. The vlei grasslands have the lowest ecological index recorded in the reserve, with a high incidence of Increaser IIc species (85,7% frequency). This indicates that these areas are being severely overgrazed. *Eragrostis plana* is highly unpalatable. Yet it was the dominant grass in both frequency recorded (47,2%) and in plant biomass (38,6%) in this management unit (Appendix A).

Figure 3 gives an indication of the long history of severe overgrazing that has occurred in the reserve between 1976 and 1995. The long and short-term grazing capacity were calculated by the method of Coe *et al.* (1976) as 764 L.S.U. (3 961 kg/km^2) and 324 L.S.U. (1 677 kg/km^2) respectively. The bulk grazer:selective short-grass grazer ratio present in the reserve in December 1991 after the calving season was 1:2.5 (Table 3).

Buffalo stocking rate

A grazing capacity of 250,6 L.S.U. in the potential buffalo habitat present in the study area was determined (Table 4), assuming that the buffalo did not graze in veld which was degraded to the stage where Karoo encroachment occurred. Excluding areas with Karoo encroachment reduced the effective available grazing area in 1991 to only 1 714 ha of the year-round buffalo range of 1 775 ha (Winterbach, Winterbach & Theron, In prep.).

Discussion

The main reason for monitoring veld condition in any natural area is to provide wildlife managers with an objective means of formulating management strategies that will achieve the stated objectives for the area (Trollope, Potgieter & Zambatis 1989).

In 1989 Vrahimis, Vorster & Terblanche (1989) strongly recommended the introduction of a veld monitoring programme for the Willem Pretorius Game Reserve, especially since the reserve had one of the largest herds of disease-free buffalo in South Africa at the time. Although veld monitoring in the reserve only began in 1991, prior guidelines for stocking rates of game did exist (Borquin 1973; Vrahimis *et al.* 1989) but they were never implemented. Over the years, the reserve thus had a long history of medium to severe overgrazing (Figure 3). The result was overall deterioration of the veld condition, with the grass species composition changing in favour of Increaser IIc species (Table 2; Appendix A). There also was a general decrease in the grazing capacity of the reserve.

The management units available to plains game including the buffalo are the thornveld of the plains, the grasslands of the plains on sandy and on clay soil and the vlei grasslands. These areas total approximately 6 682 ha and form 77% of the terrestrial surface area of the reserve. The ecological indices in these habitat types varied (Table 2)

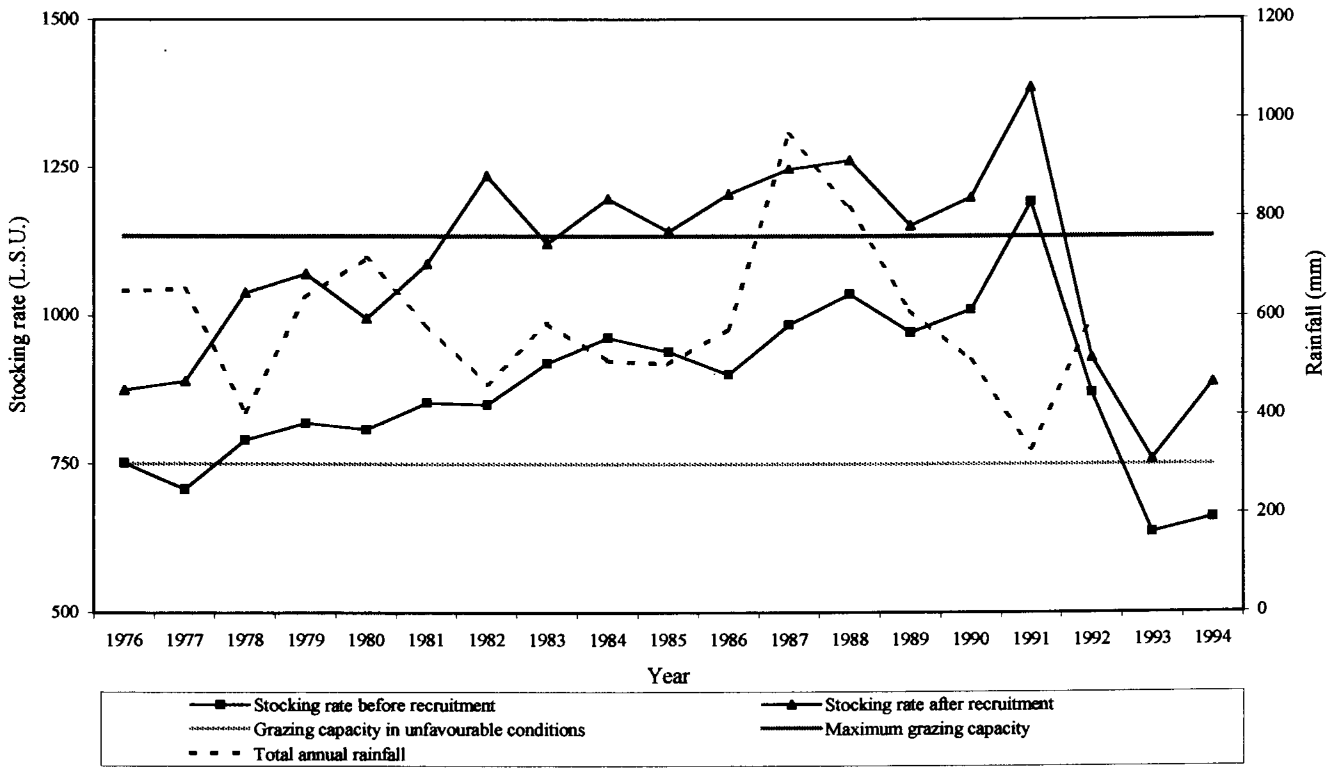

Figure 3 Comparison between the stocking rate of game (L.S.U.) before and after the annual recruitment in relation to the maximum grazing capacity and grazing capacities for unfavourable climatic conditions as calculated for the Willem Pretorius Game Reserve in the Free State and the total annual rainfall (mm) for the period 1976 to 1994

Table 3 Estimated numbers in December 1991 of herbivore grazers after the calving season, and stocking rates (L.S.U.) calculated for the herbivore grazers present in the Willem Pretorius Game Reserve in the Free State. Steenbok, duiker and other small mammals were not included. Source: Winterbach (1992a).

Herbivore	Number counted	L.S.U. Conversion	L.S.U. equivalent	Percentage of actual grazing capacity in 1991
Non-selective grazers				
Buffalo	154	1,0	154,0	13,6
Square-lipped rhinoceros	17	0,4	42,5	3,7
Burchell's zebra	84	1,8	46,7	4,1
Ostrich	438	4,2	104,3	9,2
Total	693	-	347,5	30,6
Selective grazers				
Black wildebeest	1034	2,9	356,6	31,4
Blesbok	796	4,9	162,4	14,3
Gemsbok	187	2,5	74,8	6,6
Grey rhebuck	0	7,0	0,0	0,0
Red hartebeest	186	2,0	93,0	8,2
Reedbuck	12	4,9	2,4	0,2
Springbok	1337	8,1	165,1	14,6
Total	3552	-	854,3	75,3
Mixed grazers				
Eland	156	1,1	141,8	12,5
Impala	340	6,1	55,7	4,9
Mountain reedbuck	132	8,1	16,3	1,4
Total	628	-	213,8	18,9
Total	4873	-	1415,6	124,3

Table 4 The preliminary and recommended stocking rate (L.S.U.) for buffalo in the Willem Pretorius Game Reserve, Free State, calculated according to the standing plant biomass (kg/ha) present in those parts of the plant units in the buffalo range that did not have Karoo encroachment during 1991

Plant unit in buffalo range	Size (ha) excluding areas with Karoo encroachment	Standing plant biomass (kg/ha)	Grazing capacity (L.S.U.)	Preliminary buffalo stocking rate (L.S.U.)	Recommended buffalo stocking rate (L.S.U.)
A	50	240	2,1	0,84	-
E	15	868	2,3	0,91	-
H	15	1696	4,4	1,77	-
K	252	794	34,9	13,96	26,2
M	66	983	11,3	4,53	-
N	53	459	4,2	1,70	-
O	116	742	15,0	6,00	-
R	31	930	5,0	2,01	-
S	131	683	15,6	6,24	-
U	350	829	50,6	20,22	-
W	322	542	30,4	12,17	-
Y	313	1369	74,7	29,89	56,0
Total	1714	-	250,6	100,23	82,2

with the lowest index found in the vlei grasslands management unit, which is one of the critical dry season habitats of the buffalo (Winterbach, Winterbach & Theron, In prep.). Almost 25% of the grassland communities on sandy and clay soil in the reserve already showed Karoo encroachment in 1991.

The results from the first intensive veld condition assessment done in 1991 is here regarded as the maximum grazing capacity for the reserve during exceptionally high rainfall years. The almost 34% decrease in the grazing capacity in 1992 was the result of only one season rainfall below the mean (Figure 2). The prevailing overstocking of the area aggravated this effect. In game reserves where a continuous grazing regime exists, it is advisable to set stocking rates at conservative levels (Trollope 1990; Van Rooyen, Bredenkamp & Theron 1996), mainly to cope with years of low rainfall. In view of the historical overgrazing in the Willem Pretorius Game Reserve, conservative stocking rates are even more desirable and the estimated grazing capacity of 1992 can be seen as a more realistic long-term stocking rate guideline. This stocking rate compares closely with that recommended by Vrahimis *et al.* (1989) and the long-term grazing capacity calculated with the method of Coe *et al.* (1976). Maintaining such a conservative stocking rate in the study area, even in years of above annual mean rainfall, is necessary to prevent further deterioration of the veld.

The two buffalo population crashes experienced to date in the Addo Elephant National Park (Novellie, Hall-Martin & Joubert 1991) illustrated the difficulty of managing large herbivores in confined areas that are subjected to marked environmental fluctuations. The importance of setting realistic stocking rates was highlighted by a similar population crash when 33% of the buffalo population died in the Willem Pretorius Game Reserve in 1992. During December 1991 the large herbivore stocking rate for grazers in the study area was 1 415,6 L.S.U. (Table 3), compared to the grazing capacity of 1 134 L.S.U. determined for the reserve in April 1991 (Table 1), and approximately 45% of the buffalo population were in poor condition and showed patches of hair loss. This was most notable among the older cows and young calves of between 3 and 4 months old. As the first step to adaptive management it was recommended that the stocking rate of game be reduced to 1 134 L.S.U. by removing 1 827 head of game, including 74 buffalo, instead of the 894 head of game which were officially approved for removal during 1992 (Winterbach 1992a, b). This was proposed, however, only as an intermediate step before adjusting the stocking rate to an appropriate lower long-term level. These recommendations were never implemented. By July 1992 the prevailing drought and the low grazing capacity calculated for 1992 (Table 1) prompted another recommendation to reduce the stocking rate of game to 750 L.S.U. before the warm, dry season from September to October 1992, to prevent possible wildlife mortalities (Winterbach 1992c). Again the recommendation was not implemented and in consequence 53 buffalo had died by September 1992.

Post-mortem studies on these buffalo carcasses indicated energy and protein deficiencies that led to a decrease in most of the rumen microbial population, with resultant poor fermentation rates. Analyses of the grass species utilised by the buffalo at that time showed protein and energy levels far below those needed by buffalo (Nel 1992). A combination of dehydration, malnutrition and hypothermia led to the mortalities during adverse weather conditions. Because of a general lack of disease-free buffalo in southern Africa (Winterbach 1998) and their high demand for relocation to game ranches elsewhere, the buffalo that died have had a market value of R1,5 million (1992 value). When the possible production of young in future generations is also considered, the potential loss is even greater.

To prevent similar losses in the future the buffalo population in the Willem Pretorius Game Reserve will have to be managed by setting a realistic buffalo stocking rate which takes the reigning grazing capacity and veld condition of the different vegetation types in the areas used by the buffalo, their key habitat requirements, and competition with other species into consideration.

The buffalo used only 2 700 ha (31%) of the total 8 682 ha of the terrestrial surface area of the reserve. The woodland vegetation associated with the riverbanks and dry water courses (plant unit K in the thornveld of the plains management unit) and the vlei grasslands (plant unit Y) were identified as the key habitat areas which provide the buffalo with their main habitat requirements during all three seasons (Winterbach, Winterbach & Theron, In prep.). The recommended stocking rate for buffalo in the reserve was 82,2 L.S.U. which is proposed here as a conservative maximum stocking rate taking the current poor veld condition of these management units into consideration (Table 2). By reducing the buffalo population to 70 animals during the cold, dry season each year should produce a population which fluctuates between 70 and approximately

82 animals based on a long-term population growth rate of 16% (Winterbach unpublished data). During a severe drought, however, the number of buffalo may have to be reduced to fever than 70 animals.

The long-term buffalo stocking rate in the reserve may be affected negatively by an increase in size of the grazing lawns established in the buffalo range by selective short-grass grazers. The 17% of the reserve already converted to such grazing lawns in combination with the trampled areas will increase with the current bulk grazer:selective short-grass grazer ratio of 1:2,5 (Table 3) (Winterbach 1992d). By adjusting this ratio towards the recommended 1 L.S.U. bulk grazers:1 L.S.U. selective short-grass grazers a wide range of plant communities differing in height, structure and species composition will be maintained (Mentis 1988; Novellie 1990; Van Rooyen, Bredenkamp & Theron 1996).

Proposed management strategy

The following management strategy is proposed for the study area:

- The maximum large herbivore stocking rate after the main breeding season should not exceed the long-term conservative level of 750 L.S.U. even during favourable rainfall cycles to allow an improvement of veld condition.
- Buffalo numbers should be maintained between 70 and 82 animals, but the stocking rate should never exceed 82,2 L.S.U.
- The bulk grazer:selective short-grass grazer ratio should be adjusted closer to 1:1 by reducing the black wildebeest, springbok and blesbok numbers to the stocking rates shown in Table 5.
- Black wildebeest should remain the dominant short-grass grazer in the reserve to maintain a large viable breeding population.
- Impala, which was introduced to the area, should be removed or at least limited to a maximum of 50 animals to reduce trampling of the grasslands of the thornveld of the plains management unit.
- The number of black wildebeest, blesbok and springbok present north of the Allemanskraal Dam should be limited to 30 animals of each species to reduce competition for grasslands within the buffalo range there.

Table 5 Proposed stocking rates for herbivore grazers for the Willem Pretorius Game Reserve, Free State.

Herbivore	L.S.U. Conversion	Number recommended	L.S.U. Equivalent
Non-selective grazers			
Buffalo	1	82	82,0
Square-lipped rhinoceros	0,4	20	50,0
Burchell's zebra	1,8	90	50,0
Ostrich	4,2	150	35,7
Total		342	217,7
Selective grazers			
Black wildebeest	2,9	450	155,2
Blesbok	4,9	250	51,0
Gemsbok	2,5	50	20,0
Red hartebeest	2	120	60,0
Reedbuck	4,9	25	5,1
Springbok	8,1	600	74,1
Total		1495	365,4
Mixed grazers			
Eland	1,1	100	90,9
Impala	6,1	50	8,2
Mountain reedbuck	8,1	120	14,8
Total		270	113,9
Total		2107	697,0

- The competition between other grazers and the buffalo should be monitored closely, especially so in the vlei grasslands during the dry months.
- The annual veld monitoring programme must be continued and the results implemented in adapting all stocking rates of the game.

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HABITAT UTILISATION, ACTIVITY PATTERNS AND MANAGEMENT OF CAPE BUFFALO IN THE WILLEM PRETORIUS GAME RESERVE

by
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Summary

The range use, seasonal movement, habitat selection and activity patterns of a single herd of approximately 160 disease-free Cape buffalo *Syncerus caffer caffer* in the Willem Pretorius Game Reserve in the Free State was investigated with the aim of compiling an effective management strategy for these buffalo.

The Willem Pretorius Game Reserve is a confined area with approximately 8 682 ha of effective game habitat. It occurs outside the historical distribution of the buffalo, and has sub-optimal habitat for buffalo and a long history of severe overgrazing. No large predators are present in the reserve. The veld condition and grazing capacity of six management units identified in the reserve were determined. In all the management units the veld condition ranged from intermediate to poor, with Increaser IIc grass species dominant. The maximum grazing capacity of the reserve was 1 134 L.S.U., calculated

during a favourable rainfall year in 1991. However, the lower grazing capacity of 750 L.S.U. determined during the 1992 below-average rainfall year, should be viewed as the long-term grazing capacity guideline. The long-term stocking rate of 82,2 L.S.U. for buffalo was determined relative to the above-ground plant biomass available in the critical dry season buffalo range. The vulnerability of the buffalo population in the Willem Pretorius Game Reserve to climatic cycles was shown when 53 buffalo died by September 1992 due to starvation and hypothermia when the suggested management recommendations to bring the buffalo population into balance with the grazing present were not implemented.

The seasonal activity patterns of the buffalo in the reserve did not differ markedly from that observed in other studies. Although the buffalo were already under nutritional stress by the time of the study, their activity patterns gave no conclusive evidence of the severity of the situation. The activity pattern alone was therefore not an effective management tool to determine the buffalo's interaction with their environment.

The critical habitat requirements for the buffalo in the reserve were the food supply, the availability of cover for daytime resting, and protection against low night temperatures and frost. The buffalo clearly select the woody riverbanks and vlei grasslands during all three seasons for grazing and resting. The grasslands of the plains on sandy and clay soils were mostly not used for both above activities.

The proposed management strategy includes a continuation of the veld monitoring programme and a reduction of the stocking rate of the reserve to the long-term conservative level, even during favourable rainfall years to allow improvement of the veld condition. The maximum number of buffalo maintained should be between 70 and 82 animals. Adjusting the bulk grazer:selective short-grass grazer ratio closer towards 1:1 by reducing the number of black wildebeest, blesbok and springbok should also prevent the further development of grazing lawns and trampled areas. Effective management of the buffalo herd ultimately depends on protecting the woody riverbanks and vlei grasslands as they are the most crucial vegetation types for the buffalo in the reserve.

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HABITATSBENUTTING, AKTIWITEITSRITMES EN BESTUUR VAN BUFFELS IN DIE WILLEM PRETORIUS WILDTUIN

deur

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Opsomming

'n Studie is onderneem in die Willem Pretorius Wildtuin in die Vrystaat om die loopgebied, habitatsbenutting, bewegings- en aktiwiteitsritmes te bepaal van 'n enkele trop van ongeveer 160 siekte-vrye buffels *Syncerus caffer caffer* vir die doel om 'n effektiewe bestuurstrategie vir hierdie buffels te formuleer.

Die Willem Pretorius Wildtuin beslaan ongeveer 8 682 hektaar effektiewe wildsgebied en is geleë buite die historiese verspreidingsgebied van buffels. Die reservaat bestaan uit sub-optimale habitat vir buffels en het 'n lang geskiedenis van strawwe oorbeweiding. Geen groot roofdiere kom in die wildtuin voor nie. Die veldtoestand en weidingskapasiteit is bepaal binne ses bestuurseenhede wat in die wildtuin geïdentifiseer is. Die veldtoestand binne al die bestuurseenhede het gewissel van middelmatig tot swak, met Toenemer IIc grasspesies meestal dominant. Die maksimum weidingskapasiteit van 1 134 G.V.E. vir die wildtuin is bepaal tydens 'n gunstige reënvaljaar in 1991. Die laer weidingskapasiteit van 750 G.V.E. is bepaal in 1992 tydens 'n ondergemiddelde

rëenvaljaar en behoort beskou te word as die langtermyn weidingskapasiteit-riglyn vir die wildtuin. Die langtermyn drakrag vir buffels in die wildtuin is 82,2 G.V.E. en is bepaal relatief tot die beskikbare bo-grondse plantbiomassa in die kritiese droë-seisoen loopgebied van die buffels. Die uiterste kwesbaarheid van die buffels vir klimaatveranderings is bewys nadat 53 buffels in September 1992 gevrek het as gevolg van verhongering en hipotermie omdat geen van die aanbevole bestuursaanbevelings geïmplementeer is nie wat die buffel bevolking in balans moes bring met die beskikbare weiding.

Die seisoenale aktiwiteitsritmes van die buffels in die reservaat het nie beduidend verskil van dit wat waargeneem is in ander studies nie. Alhoewel die buffels in die reservaat reeds onder voedingdruk verkeer het, het hulle aktiwiteitsritmes geen aanduiding gegee van hoe erg die situasie was nie. Die aktiwiteitsritmes van die buffels alleen was dus nie 'n effektiewe bestuursmaatstaf om die interaksie tussen die buffels en hul omgewing te evalueer nie.

Die buffels se loopgebied en habitatseleksie is beïnvloed deur seisoenale veranderings in die beskikbare wieidng, en die beskikbaarheid van skuiling vir rus gedurende die dag en vir beskerming teen die lae nagtemperature en ryp wat voorkom. Die buffels het die boomagtige rivieroewers en die grasveld in die vleiagtige gebiede geselekteer tydens al drie die seisoene vir vreet en rus. Die vlakte grasveld op sand- en kleigrond is in die algemeen nie gebruik vir beide bogendoemde aktiwiteite.

Die voorgestelde bestuurstrategie sluit in die volhouding van die veldmoniteringsprogram, en die vermindering van die wildlading na 750 G.V.E., selfs gedurende goeie rëenvaljare, om verbetering van die veldtoestand te bewerkstellig. Die buffels se getalle behoort tussen 70 en 82 diere gehandhaaf te word. Indien die aantal ruvoer en selektiewe kortgras-vreters aangepas word tot 'n verhouding van 1:1 sal dit die verdere verspreiding van vertrapte areas voorkom. Die effektiewe bestuur van die buffeltrop hang hoofsaaklik af van die beskerming van die boomagtige rivieroewers en die grasveld in die vleiagtige gebiede, aangesien hierdie plantegroeitipes die kritiese habitat vir die buffels is gedurende die droë seisoen.

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APPENDIX A

Table A.1: Ecological index values for individual sample sites in the tree and shrub veld of the ridges management unit in the Willem Pretorius Game Reserve in the Free State in 1991. The results were obtained by using the method of Bredenkamp (1986).

	PERCENTAGE OCCURRENCE							
SAMPLE SITE	1	2	3	4	5	6	7	Mean
Decreasers	34	28	25	33	39	38	36	33
Increasers I	8	3	10	14	3	33	17	12
Increasers IIa	0	0	0	0	0	0	0	0
Increasers IIb	9	7	6	19	7	18	17	12
Increasers IIc	33	58	43	26	41	8	28	35
Encroachers	6	4	0	0	1	0	0	1
Bare soil	11	1	16	9	9	2	1	7
Ecological index	462	388	388	524	481	698	580	496

Table A.2: Percentage occurrence, percentage contribution to the standing plant biomass and percentage utilisation of the grass species (excluding the encroachers) in the tree and shrub veld of the ridges management unit in the Willem Pretorius Game Reserve in the Free State during 1991. The data were calculated from the combined data of the seven sample sites surveyed in this management unit.

PLANT	PERCENTAGE OCCURRENCE	STANDING PLANT BIOMASS	PERCENTAGE UTILISATION
Decreasers:	**36,26**	**34,81**	-
Andropogon schirensis	0,20	0,39	0
Brachiaria serrata	0,49	1,42	0
Digitaria argyrograpta	1,58	0,30	13
Digitaria eriantha	5,53	8,29	16
Diheteropogon amplectans	0,10	0	0
Eustachys paspaloides	2,27	0,32	22
Heteropogon contortus	4,94	8,32	6
Panicum coloratum	0	0,29	0
Panicum deustum	0,20	0	0
Panicum maximum	1,38	0,80	36
Paspalum distichum	0,20	0,08	0
Setaria nigrirostris	2,47	0,83	4
Setaria sphacelata	11,07	3,80	4
Sporobolus fimbriatus	3,66	8,00	5
Themeda triandra	2,17	1,97	32
Increasers I:	**13,54**	**6,61**	-
Cymbopogon excavatus	1,78	1,23	0
Cymbopogon plurinodis	7,91	3,79	5
Triraphis andropogonoides	3,85	1,59	10
Increasers Iib:	**12,94**	**21,67**	-
Elionurus muticus	7,51	11,57	1
Eragrostis chloromelas	0,10	0,72	0
Eragrostis curvula	1,38	5,20	7
Eragrostis lehmanniana	1,48	1,94	7
Eragrostis racemosa	0,59	0,39	0
Eragrostis superba	0,89	0,73	0
Melica decumbens	0,99	0,93	0
Melica racemosa	0	0,19	0
Increasers IIc:	**37,25**	**36,91**	-
Aristida bipartita	0,59	0,10	0
Aristida congesta	12,85	11,36	0
Aristida diffusa	0	0,13	0
Aristida junciformis	1,68	7,92	0
Brachiaria eruciformis	0,69	0,27	0
Chloris virgata	0,10	0,16	100
Cynodon dactylon	0,69	0,10	0

Table A.2: Continued

Cynodon hirsutus	6,42	4,79	26
Digitaria ternata	0	0,21	0
Enneapogon desvauxii	0,30	0,05	0
Enneapogon scoparius	9,49	8,48	8
Eragrostis gummiflua	0	0,35	0
Eragrostis obtusa	0,20	0,28	0
Eragrostis plana	0	0,05	0
Eragrostis trichophora	0	0,47	0
Microchloa caffra	0,40	0,08	0
Oropetium capense	0,59	0,02	0
Melinis repens	0,20	0	0
Melinis nerviglume	0,30	0	0
Melinis setifolium	0	1,64	0
Setaria verticillata	0,59	0,16	0
Tragus berteronianus	0,10	0,08	0
Tragus koeleroides	1,58	0,08	0
Tragus racemosus	0,20	0,03	0
Trichoneura grandiglumis	0,30	0,10	0
Total	100,00	100,00	-

Table A.3: Ecological index values for individual sample sites in the thornveld of the plains management unit in the Willem Pretorius Game Reserve in the Free State in 1991. The results were obtained by using the method of Bredenkamp (1986).

	PERCENTAGE OCCURRENCE					
SAMPLE SITE	1	2	3	4	5	Mean
Decreasers	47	23	10	1	29	22
Increasers I	1	8	0	0	11	4
Increasers Iia	0	0	0	0	0	0
Increasers IIb	6	21	7	3	9	9
Increasers IIc	43	46	78	79	44	58
Encroachers	3	2	4	13	3	5
Bare soil	0	0	1	4	4	2
Ecological index	546	417	208	108	449	344

Table A.4: Percentage occurrence, percentage contribution to the standing plant biomass and percentage utilisation of the grass species (excluding the encroachers) in the thornveld of the plains management unit in the Willem Pretorius Game Reserve in the Free State during 1991. The data were calculated from the combined data of five sample sites surveyed in this management unit.

PLANT	PERCENTAGE OCCURRENCE	STANDING PLANT BIOMASS	PERCENTAGE UTILISATION
Decreasers:	**23,74**	**33,90**	-
Digitaria argyrograpta	0,96	0,61	50
Digitaria eriantha	0,60	0,17	40
Eustachys paspaloides	0	0,05	0
Heteropogon contortus	1,44	0,37	8
Panicum maximum	0,60	0	80
Paspalum distichum	0,72	1,13	0
Setaria nigrirostris	2,88	9,36	8
Setaria sphacelata	1,44	1,30	17
Sporobolus fimbriatus	3,72	9,71	26
Themeda triandra	11,39	11,20	46
Increasers I:	**4,20**	**6,00**	-
Cymbopogon plurinodis	4,20	6,00	37
Increasers Iib:	**9,35**	**18,86**	-
Elionurus muticus	0,24	1,18	0
Eragrostis chloromelas	1,44	1,59	8
Eragrostis curvula	3,24	6,90	100
Eragrostis lehmanniana	2,04	5,98	0
Eragrostis superba	0	0,19	0
Melica decumbens	2,16	2,92	0
Melica racemosa	0,24	0,10	0
Increasers IIc:	**62,71**	**41,24**	-
Aristida bipartita	11,03	4,74	0
Aristida congesta	8,63	0,98	0
Aristida diffusa	0	3,54	0
Aristida junciformis	1,80	0,01	0
Brachiaria eruciformis	0,36	0,05	0
Chloris virgata	0,72	1,41	0
Cynodon dactylon	5,40	9,13	13
Cynodon hirsutus	13,19	8,46	33
Digitaria ternata	0,36	0	0
Panicum coloratum	4,44	6,36	49
Enneapogon desvauxii	0,60	0,47	60
Enneapogon scoparius	13,43	4,18	24
Eragrostis obtusa	0,72	0,31	0
Eragrostis plana	0	0,11	0

Table A.4: Continued

Setaria verticillata	0,48	1,26	0
Tragus berteronianus	0,12	0,18	100
Tragus koeleroides	1,32	0,03	9
Tragus racemosus	0,12	0,02	0
Total	100,00	100,00	-

Table A.5: Ecological index values for individual sample sites in the grasslands of the ridges management unit in the Willem Pretorius Game Reserve in the Free State in 1991. The results were obtained by using the method of Bredenkamp (1986).

	PERCENTAGE OCCURRENCE						
SAMPLE SITE	1	2	3	4	5	6	Mean
Decreasers	15	40	30	14	26	4	22
Increasers I	3	7	7	4	1	2	4
Increasers Iia	0	0	0	0	0	0	0
Increasers Iib	14	20	19	10	13	17	16
Increasers IIc	67	32	41	72	59	45	52
Encroachers	0	1	0	0	1	0	0
Bare soil	1	0	3	0	0	32	6
Ecological Index	294	562	466	280	379	167	358

Table A.6: Percentage occurrence, percentage contribution to the standing plant biomass and percentage utilisation of the grass species (excluding the encroachers) in the grasslands of the ridges management unit in the Willem Pretorius Game Reserve in the Free State during 1991. The data were calculated from the combined data of six sample sites surveyed in this management unit.

PLANT	PERCENTAGE OCCURRENCE	STANDING PLANT BIOMASS	PERCENTAGE UTILISATION
Decreasers:	**23,58**	**22,51**	-
Brachiaria serrata	0,20	0,19	0
Digitaria argyrograpta	3,35	1,16	3
Digitaria eriantha	2,95	4,43	10
Diheteropogon amplectans	0	0,05	0
Eustachys paspaloides	0,20	0,78	0
Heteropogon contortus	8,43	8,42	14
Panicum coloratum	0,10	0	0
Setaria sphacelata	5,28	3,06	4
Sporobolus discosporus	0,30	0	0
Sporobolus fimbriatus	0,10	0	0
Themeda triandra	2,64	4,42	8
Increasers I:	**4,67**	**12,49**	-
Cymbopogon excavatus	0,10	2,78	0
Cymbopogon plurinodis	2,54	8,28	0
Triraphis andropogonoides	2,03	1,43	0
Increasers IIb:	**16,97**	**24,86**	-
Elionurus muticus	5,79	10,95	0
Eragrostis chloromelas	1,32	3,50	0
Eragrostis curvula	2,03	4,54	5
Eragrostis lehmanniana	2,34	3,82	0
Eragrostis racemosa	4,88	1,28	2
Eragrostis superba	0,61	0,77	17
Increasers IIc:	**54,78**	**40,14**	-
Aristida congesta	24,09	19,32	0
Aristida diffusa	0,41	1,13	0
Aristida junciformis	7,52	14,55	0
Brachiaria eruciformis	0,41	0,27	0
Chloris virgata	0,10	0,82	0
Cynodon dactylon	0	0,25	0
Cynodon hirsutus	0,10	0,02	0
Digitaria ternata	0,71	0,09	0
Enneapogon desvauxii	0,10	0	0
Enneapogon scoparius	1,22	1,62	0
Eragrostis obtusa	0,20	0,13	0
Microchloa caffra	2,95	0,93	0
Oropetium capense	6,40	0,28	0

Table A.6: Continued

Melinis setifolium	0,10	0	0
Tragus berteronianus	0,91	0,08	0
Tragus koeleroides	9,04	0,53	0
Tragus racemosus	0,20	0,06	0
Trichoneura grandiglumis	0,30	0,06	33
Total	100,00	100,00	

Table A.7: Ecological index values for individual sample sites in the grasslands of the plains on sandy soil management unit in the Willem Pretorius Game Reserve in the Free State in 1991. The results were obtained by using the method of Bredenkamp (1986).

	PERCENTAGE OCCURRENCE							
SAMPLE SITE	1	2	3	4	5	6	7	Mean
Decreasers	40	23	57	21	53	2	3	28
Increasers I	4	9	5	1	0	0	0	3
Increasers IIa	0	0	0	0	0	0	0	0
Increasers IIb	12	55	26	21	38	31	20	29
Increasers IIc	34	10	6	25	8	65	66	31
Encroachers	10	3	6	29	1	2	11	8
Bare soil	1	0	0	3	0	0	0	1
Ecological index	513	525	718	341	691	210	182	454

Table A.8: Percentage occurrence, percentage contribution to the standing plant biomass and percentage utilisation of the grass species (excluding the encroachers) in the grasslands of the plains on sandy soil management unit in the Willem Pretorius Game Reserve in the Free State during 1991. The data were calculated from the combined data of seven sample sites surveyed in this management unit.

PLANT	PERCENTAGE OCCURRENCE	STANDING PLANT BIOMASS	PERCENTAGE UTILISATION
Decreasers	**31,43**	**24,06**	-
Andropogon schirensis	1,76	3,34	10
Digitaria argyrograpta	0,09	0,35	0
Digitaria eriantha	2,63	1,76	7
Eustachys paspaloides	0,09	0	0
Heteropogon contortus	4,13	1,61	36
Panicum coloratum	1,14	0,41	23
Setaria sphacelata	19,05	12,96	2
Setaria nigrirostris	0	0,22	0
Sporobolus fimbriatus	0,09	0,02	0
Themeda triandra	2,46	3,39	46
Increasers I	**2,90**	**9,15**	-
Cymbopogon excavatus	0,61	1,07	0
Cymbopogon plurinodis	2,02	8,03	9
Triraphis andropogonoides	0,26	0,05	33
Increasers Iib	**31,87**	**41,93**	-
Elionurus muticus	10,62	16,24	0
Eragrostis chloromelas	11,24	13,34	2
Eragrostis curvula	3,25	6,21	5
Eragrostis lehmanniana	6,76	6,07	16
Eragrostis superba	0	0,07	0
Increasers IIc	**33,80**	**24,86**	-
Aristida congesta	6,32	3,65	0
Aristida diffusa	0,26	0,13	0
Aristida junciformis	0,79	0,50	11
Chloris virgata	0	0,01	0
Cynodon dactylon	9,92	5,83	6
Cynodon hirsutus	0,97	0,09	36
Eragrostis gummiflua	5,00	11,09	0
Eragrostis obtusa	0	0,04	0
Eragrostis plana	0	0,41	0
Microchloa caffra	1,05	0,01	8
Pogonarthria squarrosa	0,61	0,37	14
Trichoneura grandiglumis	8,87	2,73	2
Total	100,00	100,00	

Table A.9: Ecological index values for individual sample sites in the grasslands of the plains on clay soil management unit in the Willem Pretorius Game Reserve in the Free State in 1991. The results were obtained by using the method of Bredenkamp (1986).

	PERCENTAGE OCCURRENCE									
SAMPLE SITE	1	2	3	4	5	6	7	8	9	Mean
Decreasers	39	19	30	1	15	38	22	5	5	19
Increasers I	5	15	6	0	7	5	6	0	0	5
Increasers Iia	0	0	0	0	0	0	0	0	0	0
Increasers Iib	7	18	40	48	62	11	19	30	11	28
Increasers IIc	43	40	22	25	14	30	51	24	50	33
Encroachers	6	8	1	20	2	15	2	41	29	14
Bare soil	0	0	1	6	0	1	0	0	5	1
Ecological Index	499	411	525	237	462	497	390	215	159	375

Table A.10: Percentage occurrence, percentage contribution to the standing plant biomass and percentage utilisation of the grass species (excluding the encroachers) in the grasslands of the plains on clay soil management unit in the Willem Pretorius Game Reserve in the Free State during 1991. The data were calculated from the combined data of nine sample sites surveyed in this management unit.

PLANT	PERCENTAGE OCCURRENCE	STANDING PLANT BIOMASS	PERCENTAGE UTILISATION
Decreasers	**22,54**	**18,45**	-
Brachiaria serrata	0,07	0	0
Digitaria argyrograpta	2,68	0,63	22
Digitaria eriantha	2,83	1,56	24
Eustachys paspaloides	0	0,30	0
Heteropogon contortus	1,12	0,63	13
Panicum maximum	0,07	0	0
Paspalum distichum	0,07	0	0
Setaria nigrirostris	1,34	2,98	0
Setaria sphacelata	3,42	2,14	4
Sporobolus discosporus	0,60	0	0
Sporobolus fimbriatus	0,15	0,73	50
Themeda triandra	10,19	9,48	28
Increasers I	**5,65**	**15,89**	-
Cymbopogon excavatus	0,45	2,67	0
Cymbopogon plurinodis	5,21	13,22	7
Increasers IIb	**32,51**	**44,81**	-
Elionurus muticus	4,91	13,53	3
Eragrostis chloromelas	14,21	21,71	8
Eragrostis curvula	2,01	5,12	7
Eragrostis lehmanniana	10,49	3,87	25
Eragrostis plana	0,37	0	0
Eragrostis remotiflora	0,37	0,13	0
Eragrostis superba	0,15	0,45	50
Increasers IIc	**39,29**	**20,85**	-
Aristida bipartita	4,99	3,81	0
Aristida congesta	3,50	1,52	2
Aristida junciformis	2,16	2,98	0
Brachiaria eruciformis	1,34	0,09	0
Chloris virgata	0,67	0,18	33
Cynodon dactylon	4,02	1,50	4
Cynodon hirsutus	7,89	0,21	20
Digitaria ternata	0,07	0	0
Eragrostis gummiflua	0,22	0,49	33
Eragrostis obtusa	1,79	0,45	21
Eragrostis plana	0	0,55	0
Eragrostis trichophora	0,15	0,02	0

Table A.10: Continued

Microchloa caffra	0,52	0,02	0
Oropetium capense	0,03	0	0
Panicum coloratum	11,09	8,97	0
Tragus berteronianus	0,52	0,03	0
Trichoneura grandiglumis	0,07	0,03	0
Total	100,00	100,00	

Table A.11: Ecological index values for individual sample sites in the grasslands of the vlei grasslands management unit in the Willem Pretorius Game Reserve in the Free State in 1991. The results were obtained by using the method of Bredenkamp (1986).

	PERCENTAGE OCCURRENCE
SAMPLE SITE	1
Decreasers	5
Increasers I	0
Increasers IIa	0
Increasers IIb	9
Increasers IIc	86
Encroachers	0
Bare soil	0
Ecological Index	173

Table A.12: Percentage occurrence, percentage contribution to the standing plant biomass and percentage utilisation of the grass species (excluding the encroachers) in the vlei grasslands management unit in the Willem Pretorius Game Reserve in the Free State during 1991. The data were calculated from the data of one sample site surveyed in this management unit.

PLANT	PERCENTAGE OCCURRENCE	STANDING PLANT BIOMASS	PERCENTAGE UTILISATION
Decreasers	**4,97**	**8,76**	-
Digitaria argyrograpta	0,62	0	0
Digitaria eriantha	3,11	0,58	0
Setaria nigrirostris	0	6,63	0
Setaria sphacelata	1,24	0	0
Themeda triandra	0	1,55	0
Increasers I	**0,00**	**2,42**	-
Cymbopogon sp.	0	2,42	0
Increasers IIb	**9,32**	**26,25**	-
Elionurus muticus	0	1,40	0
Eragrostis chloromelas	6,83	9,23	0
Eragrostis curvula	1,86	15,62	0
Eragrostis lehmanniana	0,62	0	0
Increasers IIc	**85,71**	**62,57**	-
Aristida bipartita	0	8,40	0
Aristida congesta	0	0,11	0
Cynodon dactylon	26,09	6,80	5
Cynodon hirsutus	0	0,02	**0**
Eragrostis obtusa	0	0,26	0
Eragrostis plana	47,20	38,69	4
Panicum coloratum	12,42	8,29	10
Total	100	100	